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Modeling heliotropic tree growth in hardwood tree species—A case study on *Maesopsis eminii*

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ABSTRACT

There are many impacts during a tree's life that affect bole development. In *Maesopsis eminii*, a high-potential timber species in Uganda, studies have shown that the occurrence of strongly bent boles is the overwhelming reason that boles fail quality criteria. This observation is incongruous with the tree architecture model of Roux, which describes *M. eminii* as a tree with a strong apical dominance, meaning that it has a strong genetically based preference for vertical growth of the terminal sprout relative to side branches. As external causes for bent boles could be excluded, we demonstrate in this study the proof of heliotropic growth, i.e. an active bending towards light, for *M. eminii* beyond the sapling stage. We develop a model used to describe the effects of competition on bole quality using bole form parameters and basic information about the neighbouring trees, and without having to incorporate crown parameters. By means of calculated bole parameters and a mathematical equation to calculate the intensity and direction of competition, we prove the existence of a heliotropic growth reaction. However, we are not able to predict the intensity of this reaction. Finally, general silvicultural recommendations are discussed for tree species with strong heliotropic growth.

1. Introduction

Heliotropism in tree boles can be defined as the active growth reaction of the bole towards the light. The heliotropic reaction of trees whenever competition for light is intense can seriously affect bole quality, especially in case of irregular side competition. However, research on heliotropism in trees is rare. There are publications on heliotropism including Engler (1924), Büsgen et al. (1927), Hartmann (1932), Kubler (1988), Zobel and van Buijtenen (1989), and Lyr (1992), which explain heliotropism generally, focusing on wood variation or physiological properties. However, none of these publications discusses the broader influence of heliotropism on bent boles or present silvicultural tools to prevent heliotropism. More recent studies on directionally asymmetric competition concentrate on crown development, often with modelling focused on stand growth in uneven-aged stands, such as the Forest Growth Simulator Silva (Pretzsch, 2010) or the Forest Vegetation Simulator (United States Forest Service, 2010). Some also focus on heliotropism to analyze general tree growth mechanisms (e.g. Chiba et al., 1994). In general, these studies and models include few implications on bole development and subsequent timber quality. The application oriented approach to prove the effects of heliotropic growth introduced in the following text is unique as it uses bole data only, with tree crown parameters playing a subordinate role. In other words, the following approach is very efficient as it depends only on measuring bole parameters to prove heliotropic growth and its effects on bole quality and development.

The tree species *M. eminii* – referred to as Maesopsis in this article – first attracted attention during a study of the silvicultural potentials of Ugandan native tree species. This fast growing light-demanding pioneer species is known to produce high quality timber. Its timber is a light but mechanically loadable hardwood, similar in weight and strength to *Pinus sylvestris* (Anonymous, 1953). It is easy to handle and well suited for construction. It is able to produce good veneer and, therefore, plywood because of its straight, branchless bole with a medium, even texture and density, a cylindrical shape and the absence of buttresses (Tack, 1956).

Maesopsis is classified in the tree architecture model of Roux. This model is defined by a monopodial orthotropic trunk with continuous growth and plagiotrophic branches (Hallé et al., 1978, p. 205). A monopodial trunk development is defined as indefinitely growing from an apical or terminal bud. Orthogeotropism, the special case of orthotropism required by the Roux model, is defined as a geotropic reaction determining a vertical position, or with the growth direction opposing gravity. Plagiotropic branches are char-

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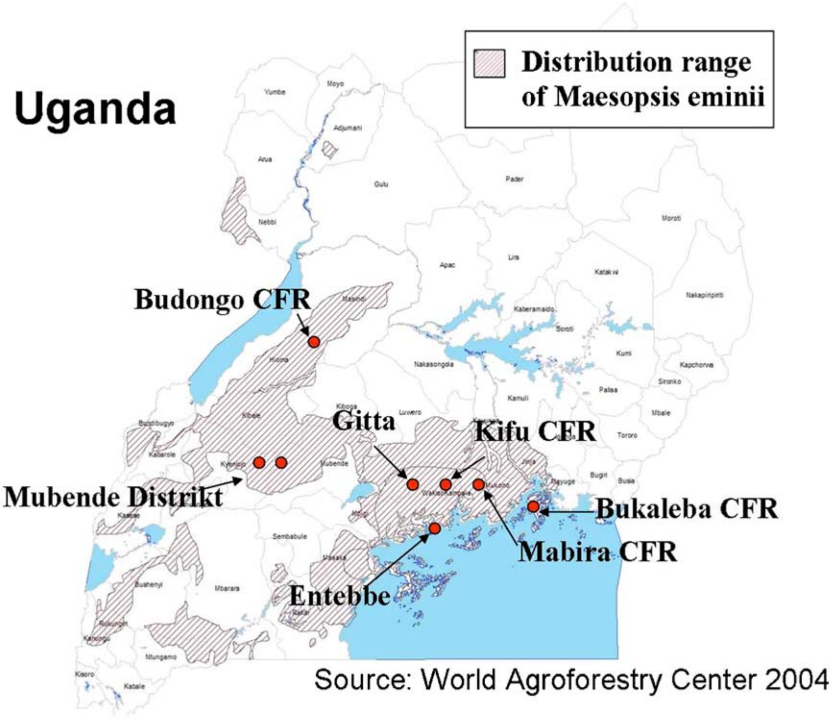

Source: World Agroforestry Center 2004

Fig. 1. Location of Maesopsis stands recorded for this study. Hatched areas indicate the natural distribution range of Maesopsis in Uganda.

acterized by a direction of growth approaching horizontal (Borriss and Bernhard, 1985). This model describes trees with a very strict symmetry in stem development and a strong apical dominance, meaning a strong genetically based preference in vertical growth of the terminal sprout relative to side branches.

Nevertheless, despite its genetic tendency to monopodial branching and a low abundance of destructive external impacts causing bent boles (Buchholz, 2003), many boles of Maesopsis fail quality criteria due to an exceptional bending. For instance, Maesopsis trees planted along a line often develop strongly bend boles alternating towards opposite directions (see supplementary online material to this article for a figure depicting a line planting of *M. eminii* with trees bending in opposite directions in an alternating pattern). This bole development is incongruous with the Roux model. Excluding external damage and genetic influences preventing a straight bole, the only hypothesis left was the presumption of an intense active change of the bole caused by light competition. In other words, the bent bole was hypothesized to be caused by a heliotropic growth contradicting its genetically determined straight growth.

Based on this assumption a new model approach was developed to detect heliotropism in trees solely using externally measured bole parameter for a stand. We hypothesized that only those trees with bends pointing in a single direction were subject to heliotropic growth. Therefore, the finding of frequent unidirectional bends among the surveyed Maesopsis boles would support the assumption of a heliotropic growth reaction. Secondly, we hypothesized that the bends occurring due to active and present heliotropic growth would necessarily be sideways in one direction (hereafter referred to as "downwards"). For a final proof of heliotropic growth, we show how the bole parameters used to describe directions and intensities of crooks as well as downward or upward bends can be used to determine the light competition for each tree. Based on the measured stand-level parameters, we attempted to predict the direction (azimuth) and intensity of the heliotropic growth reaction of any given tree within the stand.

2. Materials and methods

2.1. Stands investigated

Both natural stands and plantations of Maesopsis were measured between September and December 2003. This covers the whole natural range of Maesopsis in Southern Uganda (Fig. 1). Table 1 gives an overview of the type and dimension of the stands investigated in this study.

2.2. Data collection and processing

The tree parameters recorded to detect heliotropism were (i) the coordinates of each tree base in the stand, (ii) tree height and bole height by means of tapes and a Vertex clinometer, (iii) the DBH, and (iv) the spatial position of bole at 2.5 m, 5 m, 7.5 m, 10 m and bole end by projecting their position on the ground and measuring the azimuth (in° to true north) and displacement (in m) to the bole position at base (Fig. 2). Bole height in this sense was defined by the point where the crown started and the branch-free lower section of the tree's total height ended. The distinct self-pruning tendency of Maesopsis shedding the lower dead trees of the crown resulted in an easy determination of this point in all cases.

Next, a spatial analysis of the bole form was performed in order to calculate bole form variables. In the first step, the tree base coordinates as well as the position of bole in 2.5 m, 5.0 m, 7.5 m, 10.0 m height and bole end, and the total tree height were converted to UTM coordinates (UTM Zone 36). In the second step, this dataset was processed with the geographic information system software program MapInfo Professional 6.5 in order to visualize the stands (for an example, see Fig. 3).

In Fig. 3, a group of Maesopsis trees is presented in a GIS visualization. The tree boles are seen from a bird's eye view. Each of the coloured circles represents the horizontal position of the bole at a certain reference height with larger circles representing lower sections of the bole. Based on this visual representation, errors and

Table 1
Description of the Ugandan *Maesopsis eminii* stands investigated in this study. Plot design: 1 = evenaged plantation with fairly regular spacing and regular side competition; 2 = group of trees with more or less irregular side competition due to open surroundings, irregular age; 3 = evenaged line; 4 = single standing tree.

Location	UTM Zone 36 East	UTM Zone 36 North	Age	No. of trees	Mean DBH	Mean height	Plot design	Origin
	m	m	years		cm	m		
Entebbe	458,830	65,490	6	32	13.13	11.5	1	Planted
Entebbe	442,599	9,487	Unknown	7	24.1	14.5	2	Planted
Entebbe	442,631	25,668	Unknown	9	26.82	18.5	3	Planted
Entebbe	458,920	22,474	Unknown	8	25.8	17.9	2	Planted
Entebbe	459,044	23,457	12–15[a]	30	23.89	17.4	1	Planted
Matiri	269,686	70,662	37	30	40.6	30.4	1	Planted
Matiri	269,536	70,662	37	1	74	33.8	4	Planted
Mubende	328,468	56,759	Unknown	27	44	29.3	1	Planted
Budongo	327,573	63,823	8	30	29.64	17.9	1	Planted
Budongo	336,421	192,724	4	14	21.84	12.1	2	Planted
Budongo	336,421	192,624	4	1	22.8	11.3	4	Planted
Budongo	336,421	193,224	Unknown	2	120.5	37.6	4	Natural
Budongo	336,414	1,887,174	Unknown	7	39.53	26.9	2	Natural
Budongo	336,421	193,093	Unknown	5	82.1	41.6	2	Natural
Budongo	336,545	193,092	Unknown	5	60.32	38.9	2	Natural
Budongo	336,854	193,092	Unknown	6	67.25	43.4	2	Natural
Budongo	337,163	193,092	Unknown	5	63.86	39.7	2	Natural
Mabira	336,359	82,157	38	29	49.26	33.9	1	Planted
Kifu	485,627	54,374	7	6	24.25	16.1	3	Planted
Kifu	485,627	54,324	7	5	29.76	19.1	3	Planted
Kifu	485,627	54,274	7	10	25.82	15.7	3	Planted
Kifu	485,627	54,224	7	5	25.44	17.4	3	Planted
Kifu	485,627	54,574	1.5	24	8.38	5.5	1	Planted
Kifu	485,627	54,674	9	6	35.55	16.7	2	Planted
Kifu	485,627	54,694	9	1	35.6	18.8	4	Planted
Kifu	485,627	54,624	9	1	44	21.3	4	Planted
Bukaleba	473,573	57,598	5	29	21.44	12.3	1	Planted
Bukaleba	473,473	57,598	4	32	16.91	11.7	1	Planted
Gitta	458,830	65,490	18	29	22.67	17.3	1	Planted
Total/mean				396	30.01	19.8		

[a] Mean age 14 years.

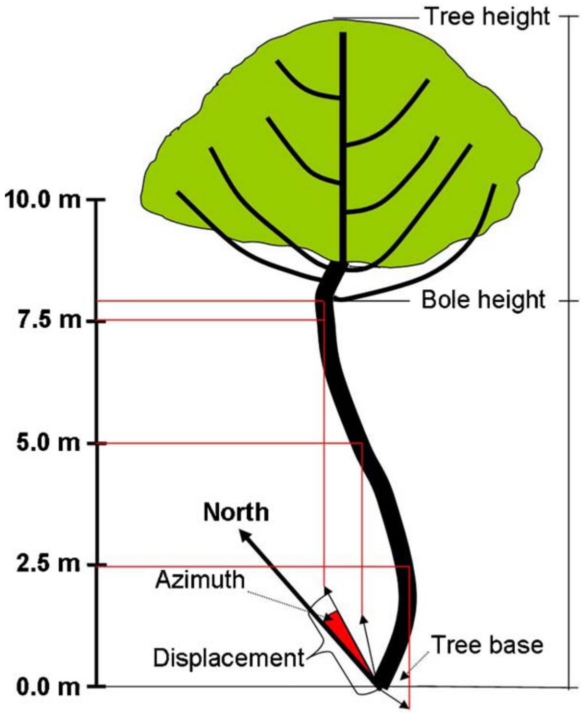

Fig. 2. Visualization of the investigated tree parameter.

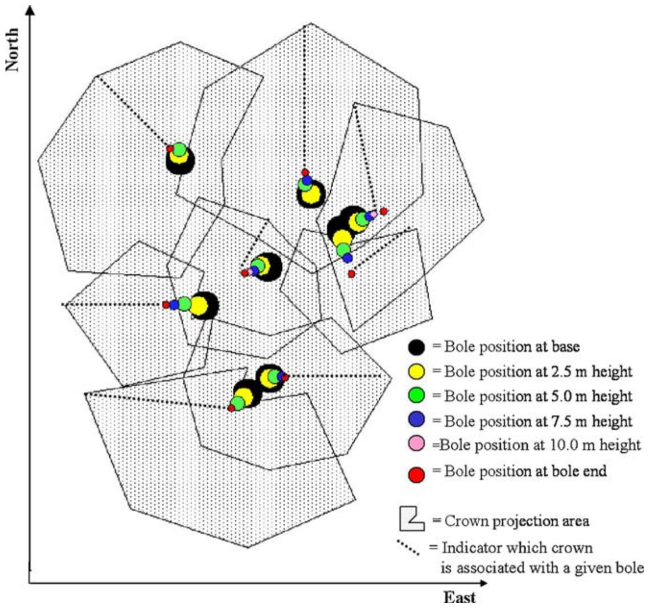

Fig. 3. Processed tree data of a *Maesopsis eminii* group planting in Entebbe, Uganda, surrounded by open space. Data on the crowns projection areas was collected for another study and is only visualized here to give a greater understanding of the trees' positioning. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article).

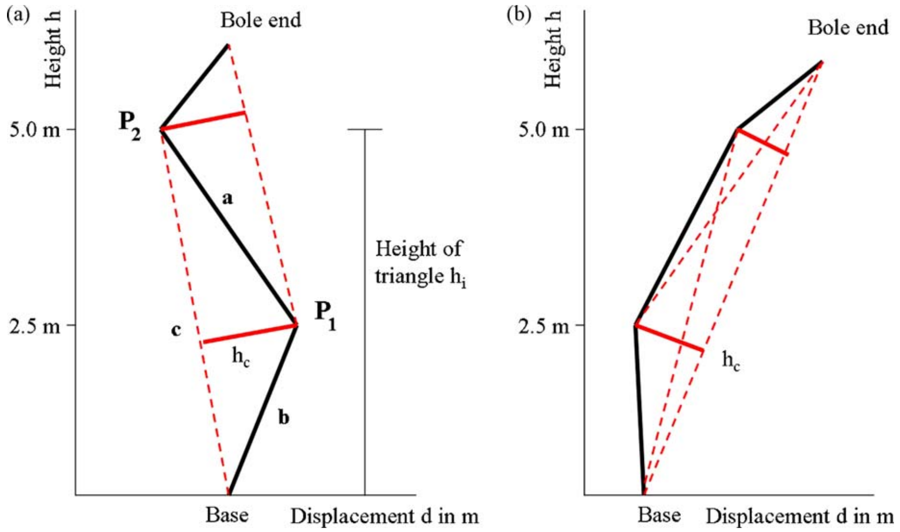

Fig. 4. Visualization of crookedness (a) and sweep (b).

irregularities were apparent, and the bole form variables could be calculated for each bole according to the bole form models developed by Weinreich (2000) and presented in the following.

2.3. *Bole models to detect heliotropism*

2.3.1. *Inclination*

The inclination of the bole was calculated in order to express the intensity of a potential reaction of the tree to light competition. It was defined as the deviation of bole end compared to a vertical bole in degrees divided by bole height in meters (resulting in v_{bole} measured in°/m). The relative expression of inclination in°/m allowed a comparison of bole inclination intensities between boles of different length.

2.3.2. *Crookedness*

Crookedness expressed the intensity of directional changes in a bole. In a first step, we constructed virtual triangles with three recorded points of a bole in vertical order (see Fig. 4a). In a second step, we calculated the height h_{c} of each triangle as seen in Fig. 4a; using formulae (1) and (2) and then dividing h_{c} by the height of the triangle h_{i} as seen in formula (3); resulting in a value k_{i} for crookedness of a specific stem section measured in cm/m,

$$h_{\mathrm{c}} = \sin \frac{\arccos((b^2 + c^2 - a^2)/2bc)}{b} \tag{1}$$

where a, b, and c are the side lengths of the triangle, with a and b referring to stem segments and c being the dotted red line completing the triangle (see Fig. 4a),

$$d = \sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2 + (h_1 - h_2)^2} \tag{2}$$

where d is the side length of the triangle between the vertices $P_1(X_1/Y_1)$ and $P_2(X_2/Y_2)$.

$$k_{\mathrm{i}} = \frac{h_{\mathrm{c}}}{h_{\mathrm{i}}} \tag{3}$$

In a third step, we summed up the results for all triangles in proportion to each triangle's share of the total bole height, e.g. if triangle one represented 30% of bole height then its height h_{c} influenced the result by 30% (see formula (4)), resulting in a value k_{bole} for crookedness of the whole bole measured in cm/m.

$$k_{\mathrm{bole}} = \frac{\sum_{i=1}^{N} k_i h_i}{\sum_{i=1}^{N} h_i} \tag{4}$$

Lastly, the boles were separated in three groups based on their respective crookedness. Boles with no crooks (zero crookedness) represented one group, boles with crooks pointing in one direction represented the second group and boles with crooks pointing in several directions represented the third group. The reasoning behind this grouping was the following: when all crooks point in one direction, it can be presumed that such a phenomenon results not just from losses of terminal sprouts. This would more likely lead – in the absence of other stimuli – to replacement growth in a randomly chosen direction. Therefore, it is presumed that there is an additional influence of a stimulus that encourages growth in only one direction, which may be possibly predictable. Crooks that point in several directions are more likely a result of losses of terminal sprout. Trees in group two were more closely analyzed on potential heliotropic growth.

2.3.3. *Sweep*

Sweep represents gradual curvature, expressing the maximum deviation of any point of the bole from a direct line linking the starting point with bole end (resulting in c_{bole} measured in cm/m). Virtual triangles were constructed using the method described for the calculation process of crookedness, but this time the starting point and the bole end formed two points of each triangle. The value h_{c} of the highest triangle represented the sweep (see Fig. 4b).

The bole in Fig. 4a has two recorded bends. These bends are expressed by h_{c} for each of the bends. All recorded h_{c} of the bole are added in proportion to their respective triangle height and form the crookedness value of the bole. The h_{c} of the lower triangle influences the result by a higher percentage than the h_{c} of the upper triangle, as its length is greater. The bole in Fig. 4b has also two recorded bends. In contrast to the bole in Fig. 4a, each of the virtual triangles includes the starting point and the bole end of the tree. The highest value of all calculated h_{c} is the sweep value of the bole when divided by the bole height.

Table 2
Minimum, maximum and mean values for all bole form variables.

	Representative values for		
	Crookedness in cm/m	Inclination in°/m	Sweep in cm/m
Mean	1.47	0.31	1.86
Minimum	0.00	0.00	0.00
Maximum	11.91	3.56	18.09

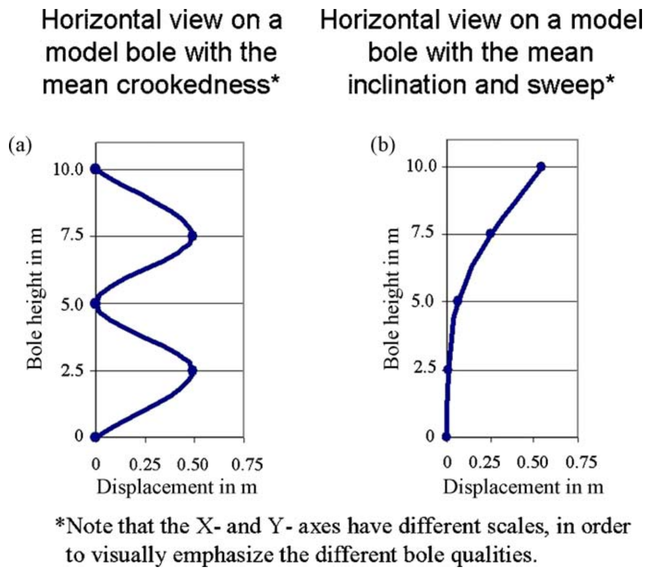

Fig. 5. Mean values visualized for crookedness (a), and inclination and sweep (b), for specific values see Table 2. The two sketches have been distorted using different scales for the *X* and *Y*-axis, respectively, in order to visually emphasize the different bole qualities.

Table 2 and Fig. 5 show the ranges and mean of the values for the bole form variables crookedness, inclination and sweep. Each of the two artificially constructed example trees (Fig. 5) represents the mean values for one or more of the indicators. The two sketches have been distorted using different scales for the *X* and *Y*-axis, respectively, in order to visually emphasize the different bole qualities.

2.3.4. *Type of bend*

All trees with bent boles (nonzero values for one or more indicators) and a bole height exceeding 2.5 m were classified as one of the two types displayed in Fig. 6. The inclination of upper parts of the bole was compared with the inclination at a height of 2.5 m. In case the upper bole part had a higher inclination than the lower, the tree was classified as bent downwards (bole type “d”). When the upper part showed a lower inclination, the tree was classified as bent upwards (bole type “u”). Bole forms of type “u” could possibly be the result of early light competition that is no longer present. However, this form could also be a result of traumatic degenerations in an earlier stage. Bole type “u” cannot represent a bole under actual light competition. In contrast, bole type “d”, although not necessarily a result of heliotropism, is the only type in which heliotropism can manifest itself.

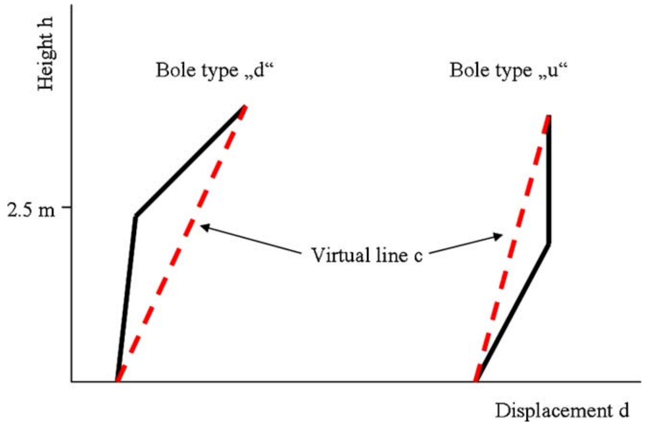

Fig. 6. Visualization of bole type “d” and bole type “u”.

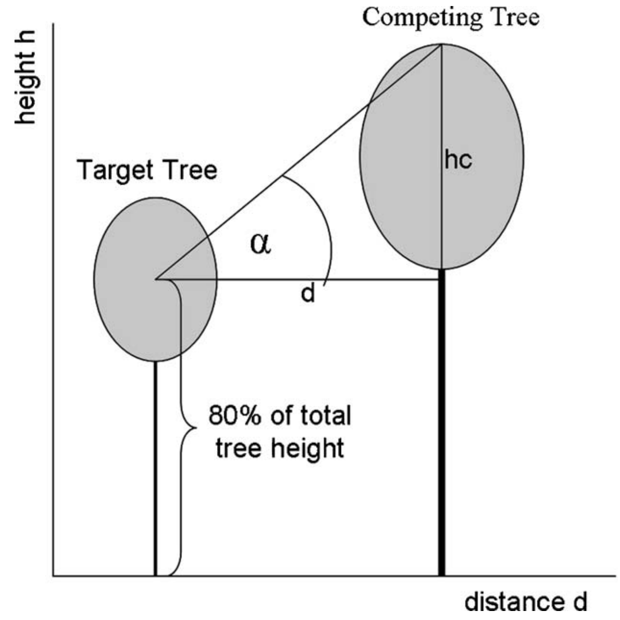

Fig. 7. Visualization of variables used in the calculation process of the competition factor.

2.3.5. *Competition factor and bole azimuth*

The selected trees for which the azimuth (see Fig. 2) of the bole was calculated had to fulfil each of the following criteria:

- The tree has a bent bole; inclination between starting point of the tree and its bole end is >0° compared to a vertical bole.
- The tree is subject to light competition; crowns of neighbouring trees overlap with its crown or touch it.
- The competition situation is completely recorded; all interfering neighbouring trees are recorded, and in case of an edge tree, the surrounding competition situation is clear (e.g. open field means no competition from that side).

The methods used for the calculations of the existence of heliotropism are based on methods developed by Pretzsch (1995) and Pukkala (1989).

A competition factor (CF) was calculated for each competing tree (CT) influencing the target tree (TT). The competition factor expresses the intensity of light competition on the target tree caused by the competing trees.

As shown in Fig. 7, the angle α was calculated by use of the following formulas:

$$h_c = h(\mathrm{CT}) - 0.8h(\mathrm{TT}) \tag{5}$$

$$\tan\alpha = \frac{h_c}{d} \tag{6}$$

$$\mathrm{CF} = \frac{\alpha^2}{d} \times \frac{\mathrm{DBH_{CT}}}{\mathrm{DBH_{TT}}} \tag{7}$$

For the use of formula (5), parameters were established that defined a competing tree with a height more than 80% of the target tree’s total height as a light competitor. Neighbouring trees with less than 80% of the target tree’s height were not recorded. This definition of a competing tree is based on a definition of the Ministerium Ländlicher Raum Baden-Württemberg (1997) whereas: “a competing tree has at least 80% of the target tree’s total height or DBH”.

Squaring the angle α in formula (7) resulted in a decreasing CF for a competing tree with increasing distance all other things being equal.

The relation between the DBH of competing tree and target tree in formula (7) increased the competition factor of an extraordinarily well-performing competing tree. Originally, Pretzsch (1995) took the crown surface areas for that relation. As the crown surface and DBH are closely related in a linear fashion in hardwoods in general (e.g. Spiecker, 2009) and has been proven particularly for Maesopsis (Buchholz et al., 2010; Dawkins, 1963), we were able to use this DBH ratio. Therefore, the competition factor is influenced by the height and DBH of both competing and target trees and the distance of the competing tree to the target tree.

Fig. 7 demonstrates that the difference in tree heights and the distance between target tree (TT) and competing tree (CT) influences α. The longer the distance d between the two trees and the smaller the height difference, the smaller α and the competition factor (CF) of the competing tree. The third variable influencing the competing tree is the relation of the DBH of the target tree and competing tree visualized by the different thick lines symbolizing the boles. In case the DBH of a competing tree is much bigger that of the target tree, the competition factor of this competing tree increases.

In a next step, a centre of competition (CC) was calculated:

Step 1: The coordinates of each tree were translated to a Cartesian coordinate system with X representing the eastward displacement and Y representing the northward displacement. According to the competition factor of each competing tree, the coordinates of the centre of competition were calculated as seen in formulae (8) and (9). Therefore, a high competition factor CF1 of the competing tree CT1 pulled the centre of competition more towards the respective competing tree CT1 than the low competition factor CF3 towards competing tree CT3. The formulas used to calculate the centre of competition were the following:

$$X_{\mathrm{CC}} = \frac{\sum_{i=1}^{N} X_i \mathrm{CF}_i}{\sum_{i=1}^{N} \mathrm{CF}_i} \qquad (8)$$

$$Y_{\mathrm{CC}} = \frac{\sum_{i=1}^{N} Y_i \mathrm{CF}_i}{\sum_{i=1}^{N} \mathrm{CF}_i} \qquad (9)$$

Step 2: In the second step, the distance d_{c} between the centre of competition and the base of the target tree was calculated as seen in formula (10). This distance expresses the intensity of the competition pressure on the target tree. The longer this virtual distance, the higher is the competition pressure.

$$d_{\mathrm{c}} = \sqrt{(X_{\mathrm{TT}} - X_{\mathrm{CC}})^2 + (Y_{\mathrm{TT}} - Y_{\mathrm{CC}})^2} \qquad (10)$$

Step 3: The presumed direction (red arrow in Fig. 8) of the bole displacement of the target tree was calculated and expressed by the angle β towards north (see Fig. 8). In order to measure the angle β, the angle between the arrow pointing towards the centre of competition and the direction to north was calculated. This result plus 180° gave β (see formula (11)). Finally, the difference γ between the recorded angle β_{r} and β was determined (see formula (12)).

$$\tan\beta = \frac{X_{\mathrm{CC}} - X_{\mathrm{TT}}}{Y_{\mathrm{CC}} - Y_{\mathrm{TT}}} + 180^\circ \qquad (11)$$

$$\gamma = \beta_{\mathrm{r}} - \beta \qquad (12)$$

Fig. 8 describes the calculation of a competition factor. The competing tree CT1 has a bigger dimension (in DBH and/or height; represented by a larger crown) and is closer to the target tree then the other competing trees and therefore establishes a high competition for light on the target tree. As a consequence, the centre of competition (CC) is situated near the competing tree CT1. That means that the resulting pressure caused by all competing trees on the target tree emanates from the centre of competition and points towards the base of the target tree. The bole of the target tree will theoretically be displaced in the opposite direction in the case of heliotropism (red arrow), its direction is expressed by β, its intensity by the length of the red arrow. The green arrow represents the recorded direction of the bole displacement in the field. The difference between calculated and recorded direction is expressed by γ. This difference between the red and green arrows γ should approach 0° if heliotropism in fact occurs.

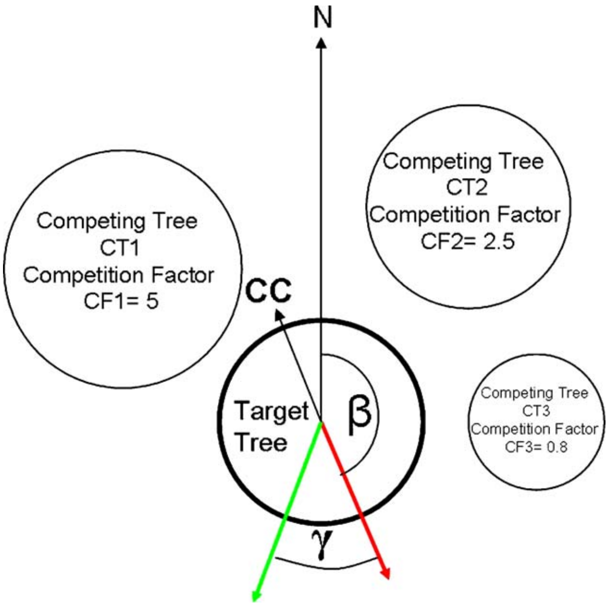

Fig. 8. Visualization of the calculation process of the centre of competition (CC) and the presumed horizontal bending direction (azimuth) of the target tree (TT).

3. Results

3.1. Inclination, crookedness, and sweep

Of all trees recorded, 49.1%, or a total of 194 trees, showed bends in one direction and 27.6% had bends in several directions (Table 3). Trees with bends pointing in several directions had generally a higher standard deviation and a higher range of values for all bole form variables (crookedness, inclination and sweep) and therefore lower bole quality than trees with crooks pointing in one direction.

3.2. Bole types and bole inclination in relation to centre of competition

Of the 194 Maesopsis trees bending in only one direction (Table 3), 71% (138 trees) were classified as type “d” (bending downwards).

The relationship between the recorded and predicted bole azimuths (see Section 2.3.5), as well as the number of trees corresponding to each value, is presented in Fig. 9. A Kolmogorov–Smirnov Test confirmed a normal distribution (Kolmogorov–Smirnov Z 0.838, N = 138). There was a mean difference of 13.54° between the predicted and recorded direction of a given bole's bend. The distribution appears to follow a normal pattern but has an outlier at an azimuth difference of 42°. More than 60% of the boles had a difference between the calculated and recorded azimuth of less than 90°. Subsequently, a t-test was applied and a significant relation between the measured and the predicted value was found with a standard error of alpha 0.011 (N = 138).

Table 3
Bole form variables of different quality groups.

Bole form variables		Trees with a straight bole	Boles with crooks pointing to one direction	Boles with crooks pointing in several directions	All trees investigated
	Sample size	92	194	109	395
	In % of total	23.3	49.1	27.6	100
Crookedness in cm/m	Mean	–	1.60	2.47	1.47
	St.-deviation	–	1.22	1.51	1.47
	Minimum	–	0.07	0.55	0.00
	Maximum	–	10.52	11.91	11.91
Inclination in°/m	Mean	0.04	0.32	0.51	0.31
	St.-deviation	0.37	0.29	0.40	0.38
	Minimum	0.00	0.00	0.06	0.00
	Maximum	3.56	2.57	2.60	3.56
Sweep in cm/m	Mean	–	2.20	2.84	1.86
	St.-deviation	–	1.66	1.98	1.88
	Minimum	–	0.07	0.32	0.00
	Maximum	–	8.09	14.61	18.09

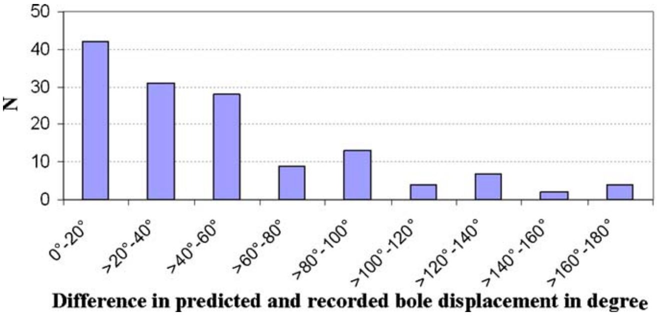

Fig. 9. Distribution of the directional difference of calculated and observed bole displacement for all boles with crooks pointing in the same direction ($N = 138$).

In a second analysis, we used a Pearson test to examine if there is a relationship between the intensity of the heliotropic reaction as expressed in terms of bole inclination and the competition intensity. The test result did not show a significant correlation between the two parameters. The standard error of alpha was 0.451 at an $N = 138$, so the value of d_c was not found to correlate with the CF value.

4. Discussion

4.1. Critical review of applied methods

The classification for bole bending used in this study included only two types of bending: upwards and downwards. The ongoing competition for light was presumed to lead to downwards bending. When light competition decreases, the stem again approaches vertical in the upper parts of the bole. Consequently, the bole form can be described as *s*-shaped. This growth pattern has already been noted by Büsgen et al. (1927). Therefore, *s*-shaped boles may reveal former heliotropic growth and should be added as type “s” to the boles bending according to type “d” or “u”. This would explain the surprisingly low mean sweep and inclination of trees where heliotropism was expected (boles with crooks pointing in one direction, see Section 3.1). It is possible that these trees had a high sweep and inclination at an earlier stage but recently developed an *s*-shape bole form.

Our model was able to predict the direction of bole bending but not its intensity. However, this model might prove to be even stronger if the three influencing variables – DBH, distance between target tree and competing tree and tree height – were weighted differently in the equation used. It is possible that this modification could produce a significant correlation between the intensity of competition and the heliotropic reaction.

4.2. Comparative discussion of heliotropism characteristics

As Weinreich (2000) noted, there is very little published research on heliotropism in tropical or even temperate tree species. The only study on heliotropic growth available was conducted by Engler (1924), who investigated heliotropic growth on the early-successional temperate tree species Ash (*Fraxinus excelsior*), Oak (*Quercus* ssp.) and Maple (*Acer pseudoplatanus* and *Acer platanoides*). Although a comparison between tropical and temperate tree species is difficult, it nevertheless seemed worthwhile to compare Maesopsis with temperate broadleaved species that occupy a similar ecological niche with regard to colonizing features and light sensitivity. In fact, Bingelli (1999) proposed that Maesopsis and ash could be considered ecologically similar. Therefore, it seems valid to compare Maesopsis to ash and other light-demanding species such as oak and maple. Engler (1924) did not quantify competition in terms of intensity and direction. In addition, only trees in an early adult stage were investigated, and the inclination of the entire tree was recorded, whereas our study on Maesopsis considers only bole inclination. The heliotropic reactions of the selected tree species in terms of their stem inclinations are presented in Table 4. With regards to the intensity of heliotropism, Maesopsis was within the range of the temperate species. However, due to the lack of information on the competition situation and the small sample size in

Table 4
Comparison of Maesopsis heliotropic growth with temperate tree species. Data on ash, oak, and maple were taken from Engler (1924).

Species	Inclination in°/m	Tree height range in m	Sample size *N* (stands)
Maesopsis eminii	0.56	12–17	36
Ash (*Fraxinus excelsior*)	0.29	15–17	4
Oak (*Quercus* ssp.)	0.68	13–13.5	2
Maple (*Acer pseudoplatanus*, *Acer platanoides*)	0.57	12.5–15	2

the study conducted by Engler (1924), it is difficult to interpret the results.

Apparently, heliotropism seems to be less relevant for other tree species or has simply attracted little research interest. In addition, the phenomenon has thus far only been investigated in trees in the early adult stage, possibly indicating that heliotropism may only be relevant at this stage for temperate tree species. This would be in contrast to Maesopsis, where heliotropism was also recorded in later stages. In summary, there is very little information available on heliotropism in trees in general and comparisons are difficult to make.

4.3. Silvicultural conclusions

For trees with a strong heliotropic growth like Maesopsis, homogenous light conditions are crucial. Therefore, a wide square spacing with high quality seedlings seems to be the only appropriate planting system, even at an early stand age, when the main goal is to produce straight boles. Disregarding the development of a branch-free bole, which might rely on a dense stocking in the beginning, planting heliotropic trees like Maesopsis in a close to final stocking density seems to be favourable from a silvicultural perspective (as described in Buchholz, 2003, Maesopsis is also characterized by an exceptional tendency to self-pruning). Establishing a stand in a wide spacing pattern obviously reduces later selective options if some trees were to develop poor bole forms or die off. However, as a strict regular spacing would need to be maintained (if straight boles are desired), the options available during Maesopsis thinnings would be already limited in order to prevent irregular light competition. In other words, thinnings are a very limited tool to improve the bole quality of stands for species with an intense heliotropic growth. If shading of the lower sections of a bole is desired to grow branch-free sections of the tree, a shrub vegetation or tree species growing in the lower canopy sections (two-storey design) might be useful as well.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.08.001

References

Anonymous, 1953. Silviculture of Species—*Maesopsis eminii*. Uganda Forest Department, pp. 3.

Bingelli, P. 1999. Maesopsis eminii Engler (Rhamnaceae). http://members.multimania.co.uk/WoodyPlantEcology/docs/web-sp8.htm (Last accessed July 1 2010).

Borriss, H., Bernhard, D., 1985. Pflanzenphysiologie. In: Wörterbücher der Biologie. Gustav Fischer, UTB.

Buchholz, T. 2003. Silvicultural potential of Maesopsis eminii—a study on tree quality. http://www.waldbau.uni-freiburg.de/ITOO/I-TOO-files/WP/I-TOO%20WP12.pdf (Last accessed July 1 2010).

Buchholz, T., Tennigkeit, T., Weinreich, A., 2010. Single tree management models: *Maesopsis eminii*. In: Bongers, Frans, Tennigkeit, Timm (Eds.), Degraded Forests in Eastern Africa: Management and Restoration (Challenges). Earthscan, London.

Büsgen, M., Münch, E., 1927. Bau und Leben unserer Waldbäume. Verlag von Gustav Fischer, Jena.

Chiba, N., Ohshida, K., Muraoka, K., Miura, M., Saito, N., 1994. A growth model having the abilities of growth-regulations for simulating visual nature of botanical trees. Comput. Graph. 18 (4), 469–479.

Dawkins, H.C., 1963. Crown diameters: their relation to bole diameter in tropical forest trees. Commonw. Forest. Rev. 42 (2), 318–333.

Engler, A., 1924. Heliotropismus und Geotropismus der Bäume und deren waldbauliche Bedeutung. Mitteilungen des Schweizerischen Amtes für Versuchswesen 13 (1), 226–333.

Hallé, F., Oldeman, R.A.A., Tomlinson, P.B., 1978. Tropical Trees and Forests: An Architectural Analysis. Springer, Berlin, Heidelberg.

Hartmann, F., 1932. Untersuchungen über Ursachen und Gesetzmäßigkeiten des exzentrischen Dickenwachstums bei Nadel- und Laubbäumen. Forstwiss. Centralbl. 54, 497–517.

Kubler, H., 1988. Silvicultural control of mechanical stresses in trees. Can. J. Forest Res. 18, 1215–1225.

Lyr, H., 1992. Physiologie und Ökologie der Gehölze. Fischer Jena, Stuttgart.

Ministerium Ländlicher Raum Baden-Württemberg, 1997. Richtlinien zur Jungbestandspflege. Ministerium ländlicher Raum Baden-Württemberg, Stuttgart.

Pretzsch, H., 1995. Zum Einfluß des Baumverteilungsmusters auf den Bestandeszuwachs. Allg. Forst Jagdztg. 166 (9–10), 190–201.

Pretzsch, H. 2010. Forest Growth Simulator Silva. http://www.wwk.forst.wzw.tum.de/research/methods/modelling/silva/ (Last accessed July 1 2010).

Pukkala, T., 1989. Methods to describe the competition process in a tree stand. Scand. J. Forest Res. 4, 187–202.

Spiecker, H. 2009. Controlling the diameter growth and the natural pruning of Sessile and Pedunculate Oaks (Quercus petraea (Matt.) Liebl. and Quercus robur L.). Freiburg. http://www.freidok.uni-freiburg.de/volltexte/6533/ (Last accessed July 1 2010).

Tack, C.H., 1956. Uganda Timbers. Forest Department Uganda, Ministry of Agriculture and Forestry, 56–57.

United States Forest Service 2010. Forest Vegetation Simulator (FVS). http://www.fs.fed.us/fmsc/fvs/ (Last accessed July 1 2010).

Weinreich, A., 2000. Qualitätsentwicklung junger Eichen in Bestandeslücken. Ph.D dissertation, Fakultät fγr Forst- und Umweltwissenschaften, Albert-Ludwigs Universität, Freiburg.

Zobel, B.J., van Buijtenen, J.P., 1989. Wood Variation. Springer Verlag, Berlin, Heidelberg, New York.