CAMBRIDGE
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RESEARCH ARTICLE

Factors influencing the variation in canopy light extinction coefficient (*k*) among *pisifera* parents of two oil palm origins

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Summary

The canopy light extinction coefficient (*k*) is defined as the exponential decline in the amount of light passing through the leaf layers as a function of leaf area index (LAI). This definition is standard in oil palm breeding trials and models of canopy photosynthesis, where *k* is sometimes assumed to have a fixed value. The present experiment aims to validate the alleged constancy of *k*. Therefore, *k* was inferred from the fractional transmission of photosynthetically active radiation (PAR) and LAI, as obtained from *dura* x *pisifera* test crosses of Nigeria and Ghana *pisifera* origins. The palms were planted at two densities (135 and 160 palms ha^{-1}) in North Sumatra in 2010. At the age of 7.5 years after planting, the area of newly opened leaves approached a maximum. Transmission of PAR remained very low and was only weakly related to *k*. By contrast, LAI exerted a strong negative effect on *k*, which generated, under both densities, considerable differences in *k* between both origins and among *pisifera* within an origin. The assumption of applying a fixed *k* value for a certain genotype or palm density, as obtained during leaf expansion at closed canopy, may therefore not be realistic. The present study suggests that the relationship of *k* with LAI over time merits further investigation, starting just before canopy closure.

Keywords: canopy extinction coefficient; *pisifera* parents; oil palm progenies; leaf area expansion; leaf area index; leaf angle; PAR transmission

Introduction

In oil palm, as in other plants, the rate of canopy photosynthesis is a function of the amount of photosynthetically active radiation (PAR) intercepted by the canopy (*cf.* Monteith and Unsworth, 1990). Moreover, since individual leaves are already light-saturated at about 30% of full sunlight (Gerritsma, 1988), the capacity of converting PAR into photosynthates improves when light is more evenly distributed over the various layers of the canopy (*cf.* Breure, 1988).

The amount of light that is extinguished when passing through the canopy is expressed by the extinction coefficient (*k*). In the commonly used formula of Monsi and Saeki (1953), *k* is inferred from the fraction of incident solar radiation transmitted through the canopy and leaf area index (LAI), that is the total leaf surface per unit ground area (for details, reference is made to the Materials and Methods section). It is well documented that light penetration into a canopy enhances under a more erect (*erectophile*) leaf arrangement, which results in a lower *k* value (*cf.* Saeki, 1960; Verhagen *et al.*, 1963; Duncan, 1971).

In oil palm, *k* values ranged between 0.29 and 0.48, as obtained in several studies (*cf.* Henson and Chang, 2000). These outcomes were based on leaf area, and hence LAI, which was estimated by using the formula of Hardon *et al.* (1969). Levels of *k* within this range were also reported by

Lamade and Setiyo (1996), who measured leaf area following the method of Tailliez and Koffi (1992). These k values are lower than in other plants with a spherical leaf angle distribution, that is when the leaves have no preferential direction, like in oil palm.

The low k values of previous studies are usually considered to be a specific characteristic of oil palm, assumed to be due to the clumping of the foliage at distinct centres of growth (Dufrene et al., 1990; Gerritsma, 1988; Squire, 1984). From a recent assessment of the formula for estimating leaf area (cf. Breure and Siregar, 2021) it appears, however, that the main cause was an overestimation of leaf area.

Moreover, k is usually considered to be a genetically determined or species-specific constant (cf. Monteith and Unsworth, 1990). Therefore, a constant (default) value of k has been applied in some simulation models of yield and growth (cf. Dufrene, 1989; Henson, 2007). Constancy of k is also commonly assumed for determining progeny values of radiation use efficiency (RUE), that is, the weight of dry matter produced per unit PAR captured by the canopy (cf. Rajanaidu and Zakri, 1988; Rosenquist et al., 1990). The latter assumption is not supported by the study of Lamade and Setiyo (1996), who found a clear difference in k between two distinct dura x pisifera families.

Furthermore, Breure (1988) inferred from measurements in commercial oil palm plantings of several ages that, due to low light transmission, k reached a clear peak at the final years of leaf area expansion. However, enhanced light interception per unit leaf area (LAI) may be caused by a (temporary) strong support between leaves of neighbouring palms at the uppermost leaf layers, as generated by high LAI and elongation of the leaves due to etiolation (cf. Breure, 2010). Thereafter, support between leaves gradually diminished, because of increased variation in height with palm age, whereupon k attained the level of young palms again.

Powel (unpublished data, 1981) found in a 10-year-old oil palm density experiment that the leaf angle becomes steeper with higher LAI. Under these conditions, k would, therefore, decrease with increasing LAI values.

The present investigation is directed to the influence of LAI on k in 7.5-year-old dura x pisifera test crosses, where leaf area varied considerably among pisifera parents (cf. Breure and Siregar, 2020). The progenies were studied at two densities (135 and 160 palms ha^{-1}). We could therefore also trace a possible effect of LAI on k due to planting density. Moreover, k was obtained for individual pisifera of two origins (Ghana and Nigeria), which offers the opportunity to verify the genetic variation in k, as found by Lamade and Setiyo (1996), and also to test the current idea of applying a constant k value when calculating RUE in progeny trials.

Based on the outcome of Lamade and Setiyo (1996), Corley (2017) suggested selecting for low k, which, as mentioned before, would ameliorate light penetration into the canopy. Besides a positive effect on canopy photosynthesis, improved light distribution over the leaf layers would enhance the optimal LAI for attaining maximum yield per ha and, hence, allow the planting at a higher density (cf. Breure and Siregar, 2020).

The value of k is, therefore, one of the crucial traits that determine yield per ha. Here, the k values were inferred from LAI and fractional PAR transmission, determined for individual plots of dura x pisifera progenies derived from two pisifera origins (Nigeria and Ghana), which were planted at two densities (135 and 160 palms ha^{-1}).

The aim of the present study is, first of all, to infer the k values of individual pisifera parents of the two origins (Ghana and Nigeria). The focus is also directed to the effect of parental LAI values and palm density on k. The ultimate goal is to search for improving the accuracy of k determination for breeding and modelling.

Materials and methods

The dura x pisifera progenies of our study were derived from pisifera parents of six distinct origins; only data of 15 pisifera of each Ghana and Nigeria origin are used for the present investigation.

The experiment was planted at an oil palm breeding station in North Sumatra in 2010. The progenies were arranged in rectangle (rhomboidal) 16-palm plots, with two replicates planted at a density of 135 and two at 160 palms ha^{-1}.

The crossing scheme for generating the progenies was according to an alpha design (Patterson *et al.*, 1978). Each *dura* was pollinated by two *pisifera* palms and each *pisifera* pollinated eight *dura* palms; not all crosses were realised, while some crosses produced insufficient seedlings for field planting. Only parameters of progeny plots where *dura* palms were crossed with two *pisifera* are used for calculating the *k* values.

The database consisted of records from 424 plots for Ghana and 472 plots for Nigeria per replicate.

Data collection

Canopy light extinction coefficient (*k*) of PAR was determined per plot by applying the commonly used equation of Monsi and Saeki (1953):

$$k = -\ln(I/Io)/LAI$$

where I and Io are the amount of PAR under and above the canopy, respectively, and LAI is the leaf area index, that is, the total leaf surface per unit ground area.

The measurements were taken when palms were 7.5 years old.

Fractional PAR transmission (I/Io) was obtained from simultaneous measurements of the amount of PAR under the canopy (I), at 25 equally spaced points per palm following the method of Squire (1984) and, nearby, above the canopy (Io). PAR was measured, after the removal of dry and damaged fronds, during overcast or partly clear skies between 10.00 and 14.00 hours, using a Spectrum Light Scout Quantum meter. Measurements were taken under four individual core palms and averaged per plot or, in case some neighbours were missing, under only one core palm that still had all six neighbours.

LAI was calculated from planting density and the product of the (measured) number of green leaves per palm with the mean area of leaves that were marked (with a paint dot) just after being fully opened when palms were 7, 6, and 5.5 years old. These three (marked) leaves, or if damaged the closest leaf, were at the moment of light measurements at about the top, middle, and lower part of the canopy, respectively; they are considered to represent the mean area of all leaves at that time.

The area of individual leaves was determined according to the formula ($-0.245 + 0.455$ nlw) of Breure and Siregar (2021), where *n* is the number of leaflets and *lw* is the mean length times width of a sample of six of the longest leaflets.

Plot values of LAI were calculated from the mean of the individual four core palms and their 10 neighbours (total 14 palms) or, in case PAR was measured under one palm, from the mean of that palm and its six neighbours (total 7 palms).

Results

Extinction coefficients (*k*) of pisifera *origins at two densities*

As shown in Table 1, the mean *k* of Ghana over the two densities was higher than Nigeria (0.635 versus 0.591 for Nigeria), while *k* decreased with planting density (0.650 versus 0.576 for the means of the 135 and 160 palms ha^{-1} densities, respectively).

Extinction coefficients (*k*) of individual pisifera parents at two densities

Tables 2 and 3 present the separate plot averages of fractional PAR transmission (I/I$_0$), the respective LAI and the inferred *k* values of the individual *pisifera* at two densities. The data patterns in both tables reveal that *k* as well as LAI of the individual *pisifera* parents varied

Table 1. Mean extinction coefficients (k) of *pisifera* of Nigeria and Ghana origins at 135 and 160 palms ha^{-1} (in brackets LAI values)

	Extinction coefficient (k) at		
Origin	135 palms ha^{-1}	160 palms ha^{-1}	**Mean**
Ghana	0.673 (4.11)	0.597 (4.95)	0.635 (4.53)
Nigeria	0.627 (4.50)	0.556 (5.45)	0.591 (4.98)
Mean	0.650 (4.31)	0.576 (5.20)	

Table 2. Fractional PAR transmission (f = I/Io), leaf area index (LAI), and canopy light extinction coefficient (k) of 15 Ghana *pisifera* at 135 and 160 palms ha^{-1} densities

Pisifera	Fractional transmission of PAR (f)		LAI		Extinction coefficient (k)	
Codes	135	160	135	160	135	160
2	0.068	0.050	4.26	5.27	0.648	0.581
6	0.069	0.058	4.03	4.85	0.694	0.610
7	0.069	0.074	4.30	5.15	0.634	0.521
11	0.064	0.060	4.71	5.51	0.596	0.527
12	0.069	0.050	4.29	5.19	0.632	0.595
23	0.061	0.051	3.96	4.67	0.718	0.653
27	0.076	0.067	4.18	5.24	0.636	0.531
28	0.087	0.056	3.73	4.67	0.682	0.643
29	0.055	0.054	4.07	4.71	0.708	0.638
30	0.054	0.064	4.29	5.06	0.696	0.562
31	0.068	0.054	3.98	4.86	0.683	0.614
32	0.061	0.046	4.12	5.14	0.690	0.624
34	0.063	0.053	3.85	4.50	0.742	0.570
35	0.074	0.058	4.00	4.72	0.663	0.621
47	0.080	0.051	3.94	4.63	0.674	0.659
Mean	0.068	0.056	4.114	4.945	0.673	0.597
Min	0.054	0.046	3.730	4.500	0.596	0.521
Max	0.087	0.074	4.710	5.510	0.742	0.659

The number of fronds on the palms ranged between 39 and 41, with little, non-significant, differences among *pisifera* or between densities.

considerably. Fractional PAR transmission (f) was very low, with little difference among *pisifera* and between (135 and 160 palms ha^{-1}) densities.

Figures 1a and 1b show that k was only weakly related to f ($r = + 0.10$ and $+0.32$ for the combined results of the two densities of Ghana and Nigeria, respectively).

On the other hand, the highly significant negative correlation ($p = 0.001$) between LAI and k of the *pisifera* parents ($r = -0.85$ and -0.93 for Ghana and Nigeria, respectively) show that k of the *pisifera* parents was strongly influenced by LAI (Figures 1c and 1d).

A multiple regression analysis is employed on the combined *pisifera* results of the two origins, in which f and LAI are used as predictors of k. The result showed that k is only significantly affected by LAI ($r = 0.91$ and $p = 0.01$).

This outcome is supported by palm density, since, as shown in Table 1, the mean k of the 135 palms ha^{-1} density (with the lower LAI values) was higher than that of the 160 palms ha^{-1} density (0.65 and 0.58 for the 135 palms ha^{-1} versus 160 palms ha^{-1} densities, respectively).

Moreover, the last column of Table 1 shows that the influence of LAI correlates with the k values of *pisifera* origins (mean LAI of 4.53 versus 4.98 with k values of 0.635 versus 0.591 for Ghana and Nigeria, respectively).

Table 3. Fractional PAR transmission ($f = I/Io$), leaf area index (LAI), and canopy light extinction coefficient (k) of 15 Nigeria *pisifera* at 135 and 160 palms ha^{-1} densities

Pisifera	Fractional transmission of PAR (f)		LAI		Extinction coefficient (k)	
Codes	135	160	135	160	135	160
8	0.067	0.054	4.96	5.83	0.558	0.512
10	0.071	0.056	4.75	5.83	0.577	0.507
14	0.062	0.047	4.79	5.87	0.596	0.531
15	0.073	0.050	4.26	5.36	0.644	0.589
18	0.058	0.049	4.61	5.64	0.625	0.546
19	0.069	0.051	4.15	5.11	0.661	0.594
21	0.067	0.058	4.54	5.41	0.620	0.535
22	0.069	0.059	4.05	4.93	0.682	0.606
24	0.068	0.050	4.23	5.12	0.660	0.603
26	0.069	0.058	5.02	6.15	0.543	0.474
33	0.070	0.056	4.98	5.83	0.558	0.509
36	0.060	0.052	4.18	5.06	0.686	0.610
48	0.060	0.051	4.27	5.15	0.675	0.592
51	0.063	0.061	4.33	5.37	0.654	0.547
52	0.059	0.046	4.41	5.47	0.667	0.582
Mean	0.066	0.053	4.502	5.475	0.627	0.556
Min	0.058	0.046	4.050	4.930	0.543	0.474
Max	0.073	0.061	5.020	6.150	0.686	0.610

The number of fronds on the palms ranged between 39 and 41, with little, non-significant, differences among *pisifera* or between densities.
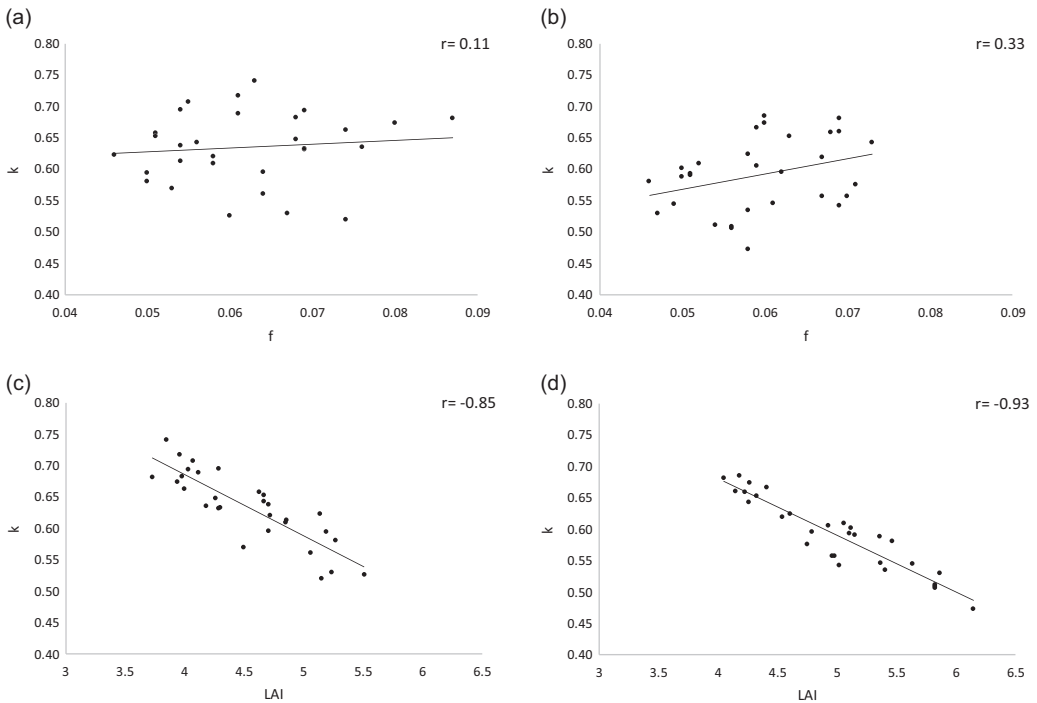
Figure 1. Relationship between fractional PAR transmission (f) and extinction coefficient (k) and between leaf area index (*LAI*) and k for *pisifera* parents of two oil palm origins: Ghana (a, c) and Nigeria (b, d). Plots consider two planting densities (135 and 160 palms ha^{-1}).

Since k is mainly determined by the leaf angle (with a more *erectophile* canopy k becomes smaller), the data patterns consistently prove that, at the stage of leaf development of this study, the canopy becomes steeper with increasing LAI.

Discussion

Levels of k

In comparing the present investigation with other reports, it is noted again that previous studies appeared to have overestimated the leaf area. For a given light penetration value, a smaller leaf area and, hence a lower LAI, as obtained by applying the formula of Breure & Siregar (2021) results in a larger k value (*cf.* Monsi and Saeki, 1953).

Note, for example, the k values of 0.67 and 0.63 for *dura* x *pisifera* progenies of Ghana and Nigeria origins at 135 palms ha^{-1} (*cf.* Table 1) of the present study, inferred from leaf areas of 7.62 and 8.34 m^{-2} (*cf.* Tables 2 and 3). In contrast, the study of Lamade and Setiyo (1996) on two distinct *dura* x *pisifera* families reported k values of 0.46 and 0.39, based on leaf areas of 10.60 and 11.48 m^{2}, respectively. Their density (143 palms ha^{-1}) was nearly identical to ours at 135 palms ha^{-1}. Furthermore, the palms were about the same age and were planted under similar environmental conditions in North Sumatra as in our study. Although the much higher leaf areas of Lamade and Setiyo (1996) could be genetic, it is more probable that leaf area was overestimated because the simplified version of the method of Tailliez and Koffi (1992) was applied. In this version, leaf area is determined from rectangles of a sample of leaflets instead of trapezes, which is standard. The authors stated that their direct measurement of LAI agrees well with area values as obtained from the Plant Canopy analyser (LAI-2000 of Li-Cor). But, the latter method also overestimates LAI. The reason is that it gives too much weight to points close to the palm where light interception is highest, as Corley and Tinker (2017) argued.

It should be kept in mind that since our results were obtained from measurements at a palm age of 7.5 years when k attains peak values (*cf.* Breure, 1988), k values are expected to be lower for younger and older palms as well. Dufrene (1989) reported a k value of 0.40 for 13-year-old palms. This outcome is in line with the 0.41 value, which Breure (1988) obtained before and after peak values of k when adapting the original leaf area measurements of his (1988) study to the formula of Breure and Siregar (2021).

A k value of about 0.40 is, therefore, typical for oil palm, which is less than usually found in other plants (Monsi and Saeki, 1953; Ross, 1981). Low k could be due, as pointed out in previous studies, to the few widely spaced growing points that result in clustering of the foliage. Moreover, oil palm, unlike dicotyledons, is unable to fill gaps in the canopy with branches of newly formed leaves, which causes partly self-shading of the leaves and, hence, decreases light interception per unit LAI.

Consequences of underestimating k values for estimating PAR transmission

As this study followed the standard method of measuring fractional light transmission, the (higher) k values inferred by using leaf area measured by the equation of Breure and Siregar (2021) would estimate the same fractional light transmission as obtained from the lower k and higher LAI of previous studies. Therefore, the calculated value of PAR interception remains the same for any method used for determining both k and LAI.

The need of accuracy in calculating k levels

The value of k is directly linked to fruit bunch yield, as Henson (2007) concluded from a model of testing the effect of varying k levels on PAR absorption, the main parameter determining biomass production.

Our study proved that k is dependent on the influence of LAI on leaf angle, towards the end of leaf expansion. When calculating RUE of progenies, it is, therefore, desirable to measure PAR transmission directly in breeding trials. Especially in young palms with low LAI, where the effect of incorrectly estimating k has the largest impact (*cf.* Henson, 2007).

Direct measurements are of course no option for modelling yield and growth over the entire lifespan, for which the relationship between LAI and k values has been used to estimate PAR interception in some simulation models.

Values of k *in relation to LAI*

Interestingly, in contrast to the negative correlations between LAI and k in our study, Breure's (1988) data from commercial estates show a clear *positive* relationship between LAI and k. This result came from three distinct age groups after the closure of the canopy. The ages were 6–7, 9–11, and 13–14 years after planting. This relationship was due to a pronounced peak of k at years 9 to 11.

Breeding for (low) k

It should be noted that the leaf area and k values of Lamade and Setiyo (1996), as mentioned before, are also negatively correlated as our data patterns of the Ghana and Nigeria *pisifera* (*cf.* Figures 1c and 1d).

The suggestion is, therefore, strong that the difference in k values they found during leaf expansion at a closed canopy is most likely due to the influence of LAI on leaf angle.

A valid genetic k value can apparently only be obtained when k is independent of LAI. In other words, when k remains the same for light transmission obtained at any LAI value. This conclusion is supported by the findings of Gerritsma (1988). In his investigation, the k values of 16-year-old palms were similar for LAI values of densities of 110, 148, and 186 palms ha^{-1}. Furthermore, there was no relationship of LAI with k for the combined 32 subplot values of the 110 and 148 palms ha^{-1} densities, with a range of individual LAI values from 4.00 to 6.44.

The appropriate developmental stage for determining genetic k values may be just at the beginning of canopy closure. Then, the leaf angle is not yet affected by the crown of neighbouring palms. Furthermore, wide gaps in the canopy that might hinder accurate light measurement under the palms are absent.

Conclusion

The value of the canopy extinction coefficient (k) is commonly inferred from fractional PAR transmission and LAI.

When transmitted PAR is very low, as during the final years of leaf area increment, the k value becomes strongly influenced by the effect of varying LAI values on leaf angle. Adopting k values found at the latter phase usually results in an overestimation. When determining RUE in breeding trials, it is recommended to measure PAR transmission directly.

The standard k value of oil palm appears to be about 0.40. Lowering this outcome by improving light penetration into the canopy can probably at best be investigated during the early stage of canopy closure.

To confirm the period at which a valid genetically determined k may be obtained, one needs to explore changes of k over time by frequent measurements of LAI, along with fractional PAR transmission. Data patterns should be assembled for various progenies, which should be obtained under, at least, two distinct densities.

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