Measurement of physiological parameters with respect to yield

P. Hadley and J.H.H. Yapp
Department of Horticulture, University of Reading, U.K.

A simple conceptual framework for analysing yield development in cocoa is presented based on light capture, the efficiency of conversion of light into dry matter (i.e., photosynthetic efficiency) and the partitioning of dry matter between vegetative, reproductive and storage components of the tree. This approach is contrasted with traditional methods for assessing yield potential of cocoa genotypes. Experimental data are presented in an attempt to establish the physiological determinants of growth in juvenile cocoa and yield development in immature and mature cocoa stands. Large variation was detected in net photosynthetic activity of non-bearing cocoa genotypes measured under field conditions. Maximum photosynthetic rates (P_m) of clones were positively related to vegetative shoot growth such that fast growing clones tended to express higher P_m. For young, bearing cocoa (48 months after transplanting at conventional spacing) precocity and yield were linearly related to fractional light interception. However, precocity and yield efficiency (ratio of yield:intercepted radiation) were independent of inherent tree vigour expressed as trunk girth. For cocoa planted at high density in which canopy closure had occurred, yield was not related to fractional light interception but to light distribution through the canopy quantified as light extinction coefficient(k). Canopies with lower k values (characterized by greater axillary branching) permitted greater light penetration; allowing the lower shade leaves to make a greater photosynthetic contribution to dry matter production. These results are discussed in relation to developing a more rational approach to parental selection for yield potential.

Introduction

Crop production involves the capture and utilization of light, water and minerals for the fixation of atmospheric CO_2 into dry matter and its efficient partitioning among vegetative and reproductive components of the crop. During the last two decades, great strides have been made both in our understanding of and also the instrumentation needed to measure the physiological parameters which determine yield (Woodward and Sheehy, 1983; Coombs *et al.*, 1985; Field *et al.*, 1989; Hay and Walker, 1989; Squire, 1990). There is now an increasing body of literature which shows, for a diverse range of plant species, that a simple relationship exists between crop yield (both in terms of total dry matter and the harvestable fraction) and total solar radiation intercepted by the crop canopy thus:

$$W = Qi\epsilon \qquad (1)$$

where W is the total dry matter produced ($g.m^{-2}$), ϵ is the coefficient for conversion of radiation into total dry matter ($g.MJ^{-1}$), i is the fraction of radiation intercepted by the crop and Q is the amount of solar radiation incident on the surface of the canopy. Where yield is concerned, the above relationship can be expanded thus:

$$Y = Qi\epsilon H \qquad (2)$$

where Y is total dry matter yield produced ($g.m^{-2}$) and H is the proportion of dry matter partitioned into yield (Harvest Index).

For most canopies, fractional interception (i) may be related to leaf area index (L) of a canopy by Beer's Law (Monsi and Saeki, 1953) thus:

$$i = 1 - e^{(-k.L)} \qquad (3)$$

where k is the radiation extinction coefficient which is, in turn, a function of foliage density, solar elevation, leaf angle and other factors such as leaf folding and rolling (Ross, 1981).

The above concepts of light capture have proved invaluable in ascribing yield variation in crops to particular yield determining processes. For example, Cannell *et al.*, (1988) were able to attribute a two fold difference in wood biomass yield between *Salix* and *Populus* to differences in i and H, with *Populus* partitioning more dry matter to the root system. However, radiation extinction coefficients (k) were similar giving the same relationship between i and L.

Although harvest index (H) is a straightforward measurement in annual crops where whole plants can be easily harvested, this parameter is more problematic in perennial crops where destructive harvesting is more difficult. However, basing yield efficiency on radiation interception *i.e.*, yield per unit of intercepted radiation, indirectly estimates fruit dry matter partitioning. Yield/light relationships have been recently used for comparing planting densities and tree form in apple (Palmer, 1989; Robinson and Lakso, 1991). Palmer (1989) showed that differences in apple yields due to variation in density were attributable to differences in light interception rather than to conversion efficiency of intercepted radiation into fruit dry matter. However, Robinson and Lakso (1991) compared two apple cultivars in four growing systems and showed that differences in yield were associated with variation in the efficiency of the conversion of intercepted solar radiation into fruit, in addition to differences in light interception.

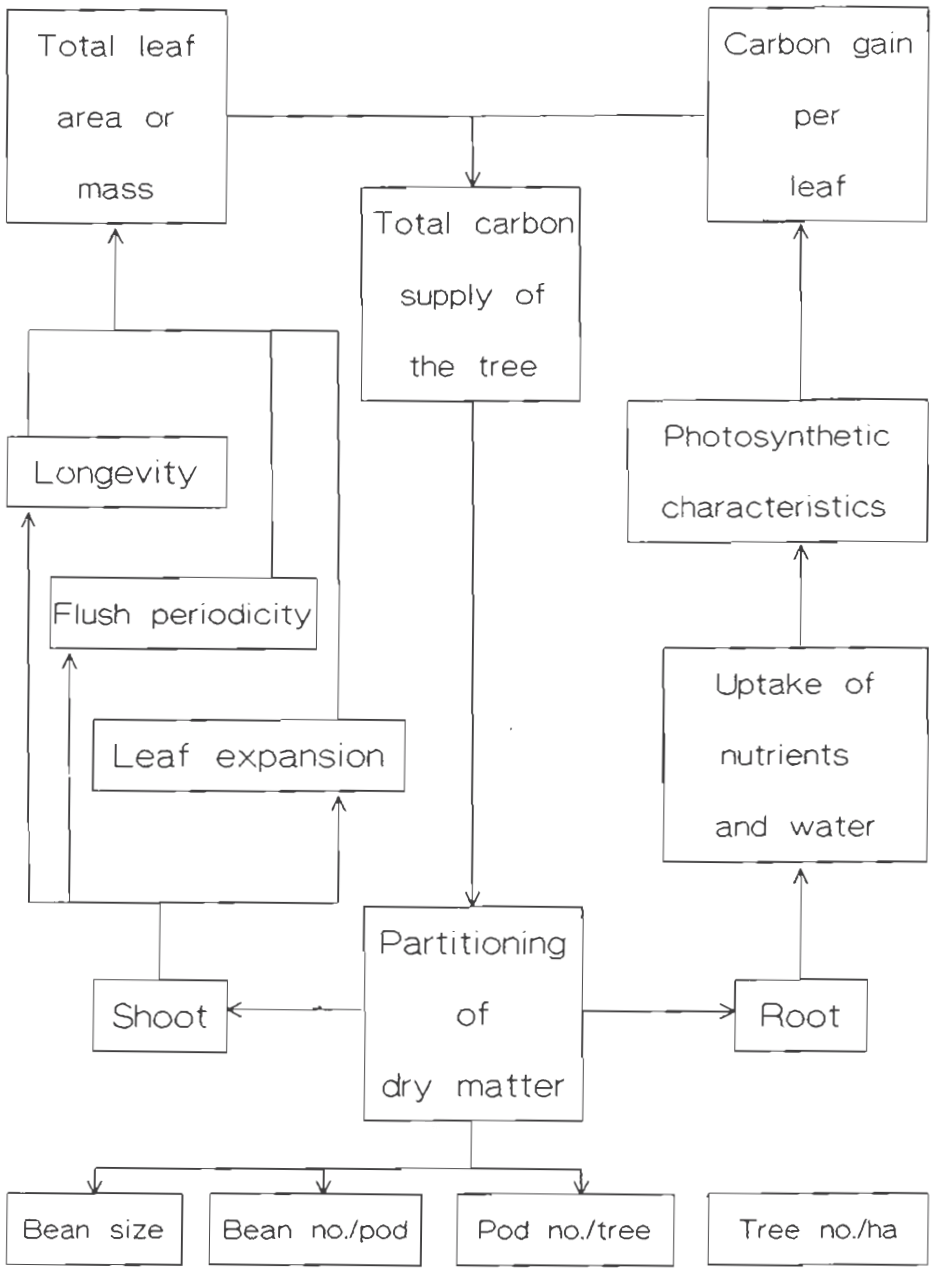
In cocoa, the approaches described above have not been adopted. Therefore, it is generally not possible to ascribe yield variation between genotypes and/or planting systems to differences in radiation interception, canopy architecture or the partitioning of dry matter between vegetative and reproductive components. Little is known concerning the factors controlling yield determination in cocoa such that even a basic understanding is lacking as to whether yield is limited by assimilate availability or by the growth potential of the reproductive components of the tree.

The purpose of this paper is to review the concepts currently being used to investigate yield potential in crops and to show how these can and have been applied to study the variation in yield potential amongst cocoa germplasm. As examples, the physiological determinants of growth in juvenile cocoa and bearing cocoa grown at low and high density are examined to evaluate the implications and opportunities for both cultural and genetic improvement of the cocoa crop.

Yield development in cocoa: a theoretical framework

The processes that govern the growth and productivity of the cocoa tree interact in a complex way and are best illustrated by way of a schematic diagram (Fig. 1). The quantity of assimilates produced by a canopy will be dictated by its photosynthetic rate, its size (L), its structure (the arrangement of the leaf area) and the radiation to which the canopy is exposed. The assimilates produced by the tree (*i.e.*, after respiratory losses) are partitioned either between vegetative and reproductive components of the tree or stored as carbohydrate reserves. Although canopy characteristics and solar radiation incident on the canopy determine the rate of dry matter accumulation, it is the partitioning of this dry matter amongst the different components of the tree that will determine the long-term productivity of the tree. The partitioning of assimilates between reproductive and vegetative components determines what quantity of assimilates which are available, for instance, for pod growth. Of course, if more assimilates are available for the trees' vegetative components, less will be available for reproductive growth. However, the greater the availability of assimilates to leaves is, the faster the rate of leaf production and expansion will be. [Experimental evidence indicates that flushing in cocoa is determined to a large extent by the availability of carbohydrates to the

Figure 1 A physiological framework for analysing growth and yield development in cocoa.



vegetative components of the tree (Machado and Hardwick, 1988; Taylor and Hadley, 1988)]. In time, this will lead to more radiation being intercepted and a greater rate of canopy photosynthesis, at least where the canopies are not closed, and thus more assimilates will be available for reproductive growth. In dense canopies, increases in leaf area may not lead to increases in canopy photosynthesis; increases in L under these circumstances may lead to a decline in canopy photosynthesis as a greater part of the canopy will be deeply shaded and may become a sink for assimilates. Under these circumstances, it is likely that high rates of partitioning to the trees reproductive components will lead to higher yields since the only assimilates needed by the vegetative components are those to maintain their integrity. Excessive vegetative growth under these circumstances is likely to be wasteful.

Clearly, variation in any one of the components indicated in Figure 1 might affect crop yield. Traditionally, the study of physiological processes in crops has tended to concentrate on their responses to environmental variables, however, there is increasing interest in how these processes vary amongst genotypes and whether there is potential for exploiting such variation in breeding programmes (Mahon, 1983; Graham, 1984; Blum,1988; Duncan and Baligar, 1991).

Traditional approaches to studying yield potential in cocoa

Historically, breeding strategies in cocoa improvement programmes have sought to increase the realized yield through maximizing pest and disease resistance (Toxopeus, 1969; Bartley, 1971). However, recently attention has shifted to place more emphasis on the maximization of potential yield (Kennedy *et al.*, 1987). Complementary work has sought to increase yield through improvements in agronomic management practices to minimize yield constraints, however, these constraints are still poorly understood.

Breeding for increased yield potential in cocoa has mainly centred on components such as pod numbers per tree, bean numbers per pod and bean size (Toxopeus and Wessel, 1970; Toxopeus and Jacob, 1970; Ang and Shepard, 1978; Yapp and Phua, 1987). Yield manipulation through altering tree number per unit area has only recently received attention (Lim and Pang, 1989; Lim *et al.*, 1991; Lam and Lim,1991). Recently, Mooleedhar and Lauckner (1990) have reported significant genotype x density interactions amongst three Trinidad Selected Hybrids (TSH) planted at three densities. However, an understanding of the underlying physiological basis for such interactions is needed before plant forms suitable for high density planting can be defined.

Because trunk girth can be easily and rapidly measured, it has been traditionally used to measure yield efficiency in cocoa *i.e.* yield per unit trunk size (Thong and Ng, 1978) or trunk cross sectional area (Tan, 1991). However, girth data are usually linked with dry mass rather than to mass distribution. Thus it is unlikely that such measurements can be used to indicate yield improvement amongst genotypes or growing systems which are the result of more efficient partitioning of assimilates to the reproductive sinks within the plant.

Genotypic variation in photosynthetic traits amongst non-bearing cocoa clones and its relation to vigour.

Genotypic variability in instantaneous net photosynthetic rate per unit leaf area (P_n) has been identified within several annual crop species (Elmore, 1980) as well as perennial tree crops *e.g.* oil palm (Corley *et al.*,1973; Corley, 1983) and rubber (Samsuddin *et al.*, 1987). However, differences in P_n are more often related to yield which involves a vegetative component, with only scant evidence of a positive relationship with reproductive yield components. Tree crop breeding tends to have a long selection cycle, which may be shortened by the use of a rigorous physiological approach to plant selection, assuming that these characteristics are

linked to yield. With the advent of inexpensive portable instruments, which can be used to measure photosynthesis in the field, greater interest has been generated in studying photosynthetic variation amongst genotypes, with the aim of selecting potentially high yielding clones for incorporation into hybridization programmes.

We have recently carried out a study to assess genotypic variation in photosynthetic characteristics amongst a range of contrasting cocoa clones grown in the field at ICG,T in Trinidad. A portable infra-red gas analyser (Analytical Development Company Model LCA 2) with an artificial light source was used to enable the production of photosynthesis light response curves under field conditions. Vegetative growth for the various clones was measured in conjunction with gas exchange parameters to examine the inter-relationship between morphological and physiological attributes. The photosynthetic data produced were summarized using a non-rectangular hyperbola fitted to the raw data (Marshall and Biscoe, 1980).

Large variation (53.5%) in maximum photosynthetic rate (P_m) was observed amonst cocoa clones ranging from 3.43 to 7.38 μmol CO_2 m^{-2} s^{-1} (Fig. 2). The clones IMC 67 and UF 668 expressed significantly higher P_m values than VEN A58, SCA 19, EET 397, EQX 3339 and these were more than two-fold higher than that of Stahel. Destructive growth measurements carried out over the experimental period indicated a large variation in vegetative growth and also a close relationship between shoot girth and shoot dry weight amongst the cocoa clones (Fig. 3). IMC 67 consistently showed the greatest growth increment in terms of flush size (5-6 leaves per flush) and periodicity (3 flushes). In contrast, the slow growing Stahel had only produced a single flush of 3-4 leaves during the same experimental period. Maximum photosynthetic rate was closely related to vegetative shoot growth expressed as cumulative dry matter, girth and leaf area. IMC 67 had a two-fold higher mean P_m and a four fold greater mean rate of dry matter accumulation in the shoot than the least vigorous Stahel (Fig. 4). These data suggest that variation in P_m may be a major factor determining variation in vigour amongst non-bearing cocoa and that such measurements may provide a relatively simple screen for early vigour in cocoa germplasm. Of course, this study is not comprehensive and more work would be needed to confirm such a relationship between P_m and early vigour.

Genotypic variation in canopy characteristics in relation to yield and vigour in young, bearing cocoa planted at conventional density

Similar photosynthetic measurements were performed on young, but bearing cocoa (at 48 months after transplanting) consisting of 12 progenies out of a potential 27 progenies planted in a North Carolina Model II design (Comstock and Robinson, 1952) at BAL Plantations Sdn Bhd in Sabah (Table 1). These were compared with two hybrid clones used extensively in Sabah (PA 7 x NA 32 and UIT 1 x NA 33).

Table 1 Mating design for the Inter-Upper Amazon hybrids. The number for individual progenies refers to the legends in Figure 5.

	Paternal			
Maternal	AMAZ 15-15	MO 81	PA 127	PA 300
IMC 67	(1)	(2)	(3)	(4)
SCA 9	(5)	(6)	(7)	(8)
NA 33	(9)	(10)	(11)	(12)

Figure 2 Clonal variations in the response of P_n to photon flux density (PFD), predicted using parameter constants derived from fitting a non-rectangular hyperbola to raw data.

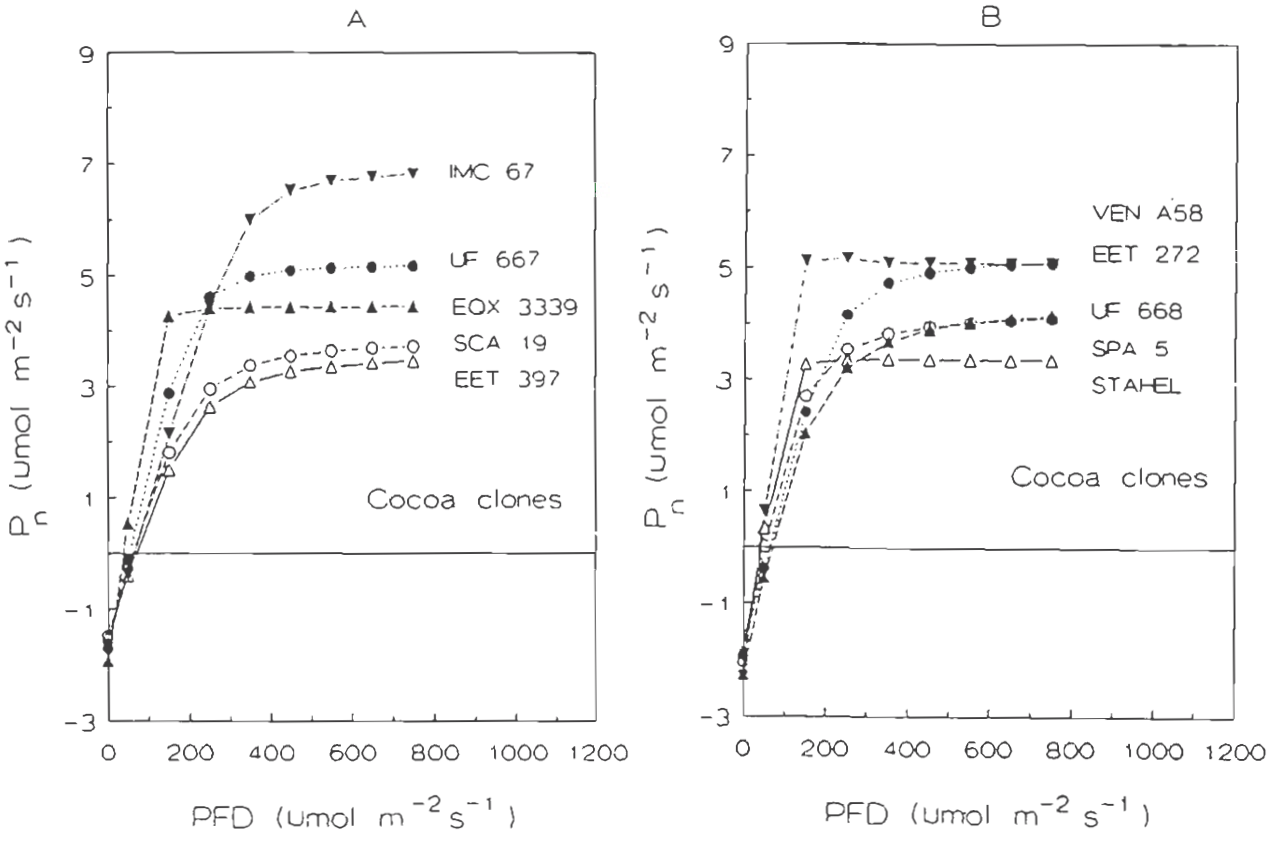


Figure 3 Relationships between different vegetative shoot growth components measured among the cocoa clones grown at the International Cocoa Genebank, Trinidad. Significant differences between clones are denoted by LSD bars at 5% probability. Each symbol represents a mean of five plants: (1) EET 272; (2) EET 397; (3) EQX 3339; (4) IMC 67; (5) SCA 19; (6) SPA 5; (7) STAHEL; (8) UF 667; (9) UF 668; (10) VEN A58.

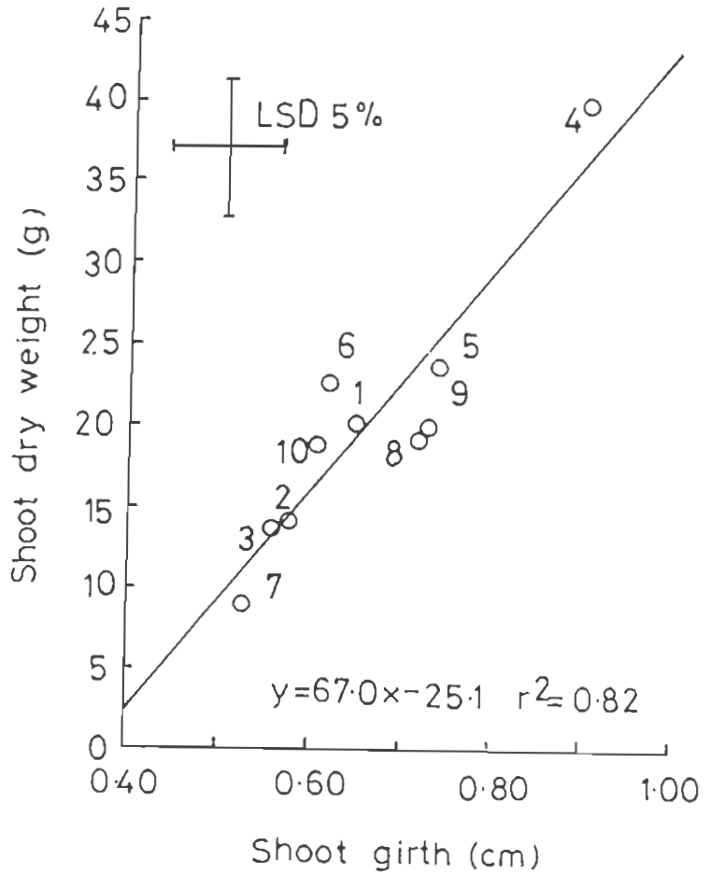
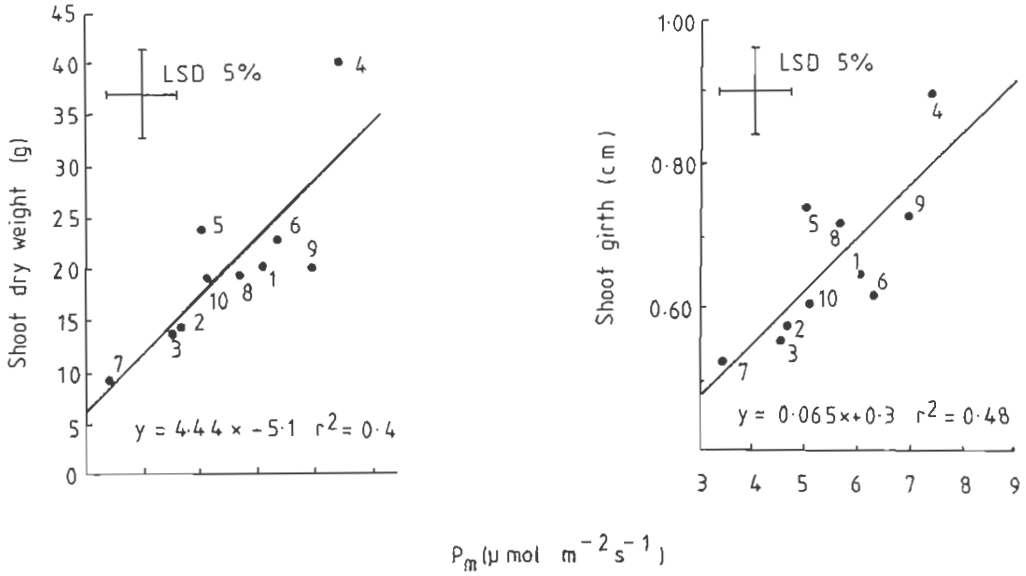


Figure 4 Relationships between vegetative shoot growth and predicted maximum photosynthetic rate (P_m). Significant differences between clones are denoted by LSD bars at 5% probability. The number refers to individual clones as shown in legend to figure 3. Each symbol represents a mean of five plants.



Although large variation was evident both in terms of their photosynthetic activity (Fig. 5) and cumulative yield (Fig. 6), there was no significant relationship between the two. However, estimated seasonal (Dec.-Apr. 90) and annual dry bean yield (Jun.-Apr. 90) were closely correlated with fractional radiation interception for the corresponding periods (Fig. 7). Based on mean radiation interception values, three groups of canopy structure were distinguished: 1. small dwarf genotypes of AMAZ 15-15 progenies with shallow canopies which intercepted less than 60% of the incident radiation; 2. intermediate genotypes which intercepted between 65 to 70%; dominated by NA 33 [x MO 81, PA 127, PA 300], IMC 67 [x MO 81, PA 127, PA 300] and the controls PA 7 x NA 32 and UIT 1 x NA 33; 3. vigorous canopies of the SCA 9 progenies [x MO 81, PA 127, PA 300] which had almost closed and intercepted over 74-82% of the incident radiation. Although no significant differences were detected among the hybrids in the slope of the yield-radiation relationship, large differences (36%) were apparent for the ratio of yield/intercepted radiation. NA 33 x PA 300 (0.133 g MJ^{-1}), NA 33 x MO 81 (0.118 g MJ^{-1}), SCA 9 x AMAZ 15-15 (0.133 g MJ^{-1}) and SCA 9 x PA 300 (0.122 g MJ^{-1}) had significantly higher yield efficiencies than the derivatives of IMC 67 (0.085-0.108 g MJ^{-1}) and UIT 1 x NA 33 (0.106 g MJ^{-1}).

These results indicate that under non-steady state situations, where the canopies are still expanding, differences in intercepted solar radiation accounted for most of the differences in yield between the progenies, whilst differences in instantaneous photosynthetic rates of mature exposed leaves were not correlated with yield. Although there were large differences in intercepted solar radiation between "dwarf" genotypes (*e.g.* SCA 9 x AMAZ 15-15) and the more vigorous genotypes (*e.g.* SCA 9 x PA 300), yield efficiency quantified as yield per unit intercepted solar radiation was similar. This indicates that yield of the dwarf genotype could be increased by planting at higher densities so that more solar radiation can be intercepted. Interestingly, although trunk girth was correlated with annual dry bean yield it was not correlated with yield efficiency indicating that it is not a suitable parameter for the determination of yield efficiency.

Inter-relationships between canopy architecture and productivity amongst mature upper-Amazon clones planted at high density.

In the previous example, where canopies were still expanding, total canopy radiation interception appeared to be the main determinant of productivity. Here parental Upper Amazon clones (AMAZ 15-15, PA 127, PA 300, MO 81, NA 33, SCA 9 AND PA 76) planted at three times conventional density (3333 trees ha^{-1}), also at BAL Plantations Sdn Bhd in Sabah, were studied. Forty-eight months after transplanting, all the clones had formed a continuous canopy with leaf area indices [estimated using a stratified method similar to that described by Alvim (1977)] of between 2.3 and 3.4, intercepting between 72% and 95% of incoming solar radiation (Table 2). Estimated annual bean yields for the period from June to April 1990 ranged from less than 1 t ha^{-1} for PA 127, even though it intercepted over 93% of the incident solar radiation, to 6.2 t ha^{-1} for the less vigorous "semi-dwarf" NA 33, even though it intercepted only 80% of incident radiation. Here yield was not associated with total solar radiation interception or leaf area index; however, radiation attenuation through the canopy appeared to be an important character in determining productivity. The lower extinction coefficients (k values) for NA 33 (0.70) and PA 300 (0.61) appear to be attributable to the clustering of leaves around the axillary side branches, possibly induced by a loss of apical dominance. Such a "clumped" branching habit would allow greater penetration of radiation through the canopy and allow the illumination of a greater volume of the canopy with minimal mutual shading. In contrast, the canopy architecture of the relatively more vigorous PA127, MO 81 and PA 76 (k values 0.86, 0.95 and 0.89 respectively) were characterized by strong apical dominance. These strong fan branches had the tendency to grow upright causing "congestion" of leaves at the top of the canopy and therefore a greater degree of mutual shading.

Figure 5 Genotypic variation in light-saturated net photosynthetic rates measured among the immature Inter-Upper Amazon hybrids planted in June 1986 in Sabah, Malaysia. Photosynthesis was measured at 1000 µmol photon m^{-2} s^{-1} and leaf-to-air vapour pressure deficit was maintained at below 1.0 kPa(RH 75% and temperature 33°C). The numbers relating to individual progenies are given in Table 1; 13 and 14 represent hybrid controls PA 7 x NA 32 and UIT 1 x NA 33 respectively.

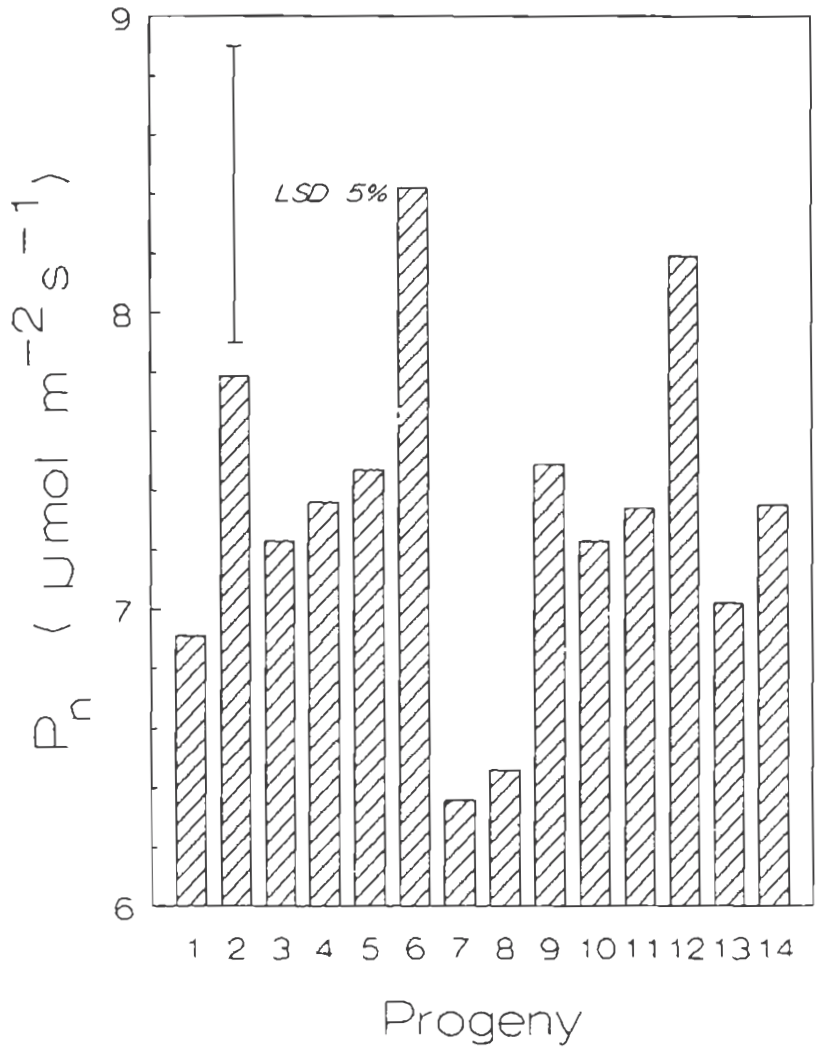


Figure 6 Cumulative yield for the periods from Dec 87 to Apr 90 (29 months) recorded among the immature Inter-Upper Amazon hybrids planted in July 86 in Sabah, Malaysia. LSD bar denotes significant difference between hybrids at 5% probability. The numbers relating to individual progenies are given in Table 1; 13 and 14 represent hybrid controls PA 7 x NA 32 and UIT 1 x NA 33 respectively.

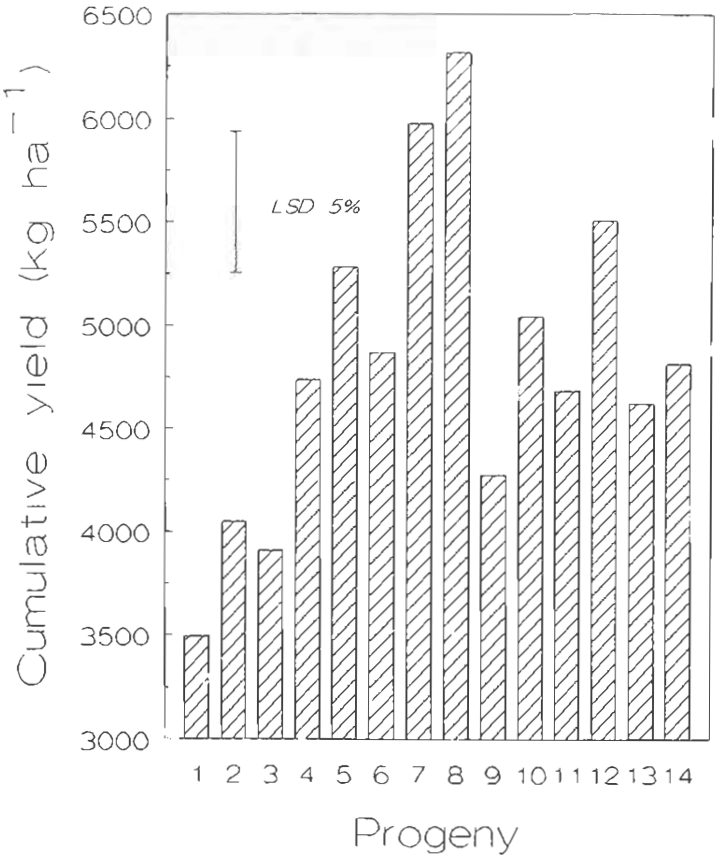


Figure 7 Linear relationships between intercepted PAR (taken as 50% total radiation) and estimated dry bean yield measured for the periods between a) Dec-Apr 90 and b) Jun-Apr 90 among the immature Inter-Upper Amazon hybrids planted in July 86 in Sabah, Malaysia. Fitted lines for a) y=2143x + 42, r^2=0.43 and b) y= 3087x + 269, r^2=0.52. LSD bars denote significant difference between hybrids at 5% probability. The numbers relating to individual progenies are given in Table 1; 13 and 14 represent hybrid controls PA 7 x NA 32 and UIT 1 x NA 33 respectively.

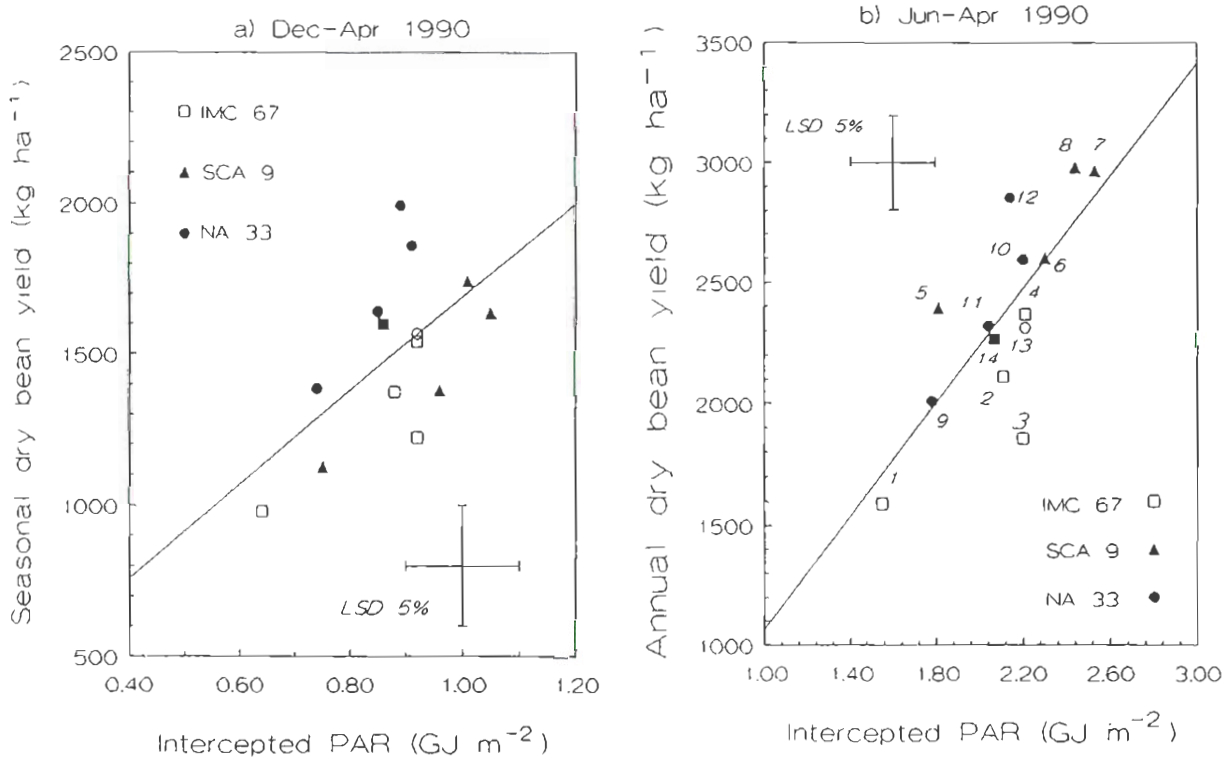


Table 2 Comparison of estimated annual bean yield (Jun-Apr 90) with canopy architecture expressed as fractional light interception (i), leaf area index (L, m^2 m^{-2}) and light extinction coefficient (k) among the Upper Amazon clones planted at high density (3333 trees ha^{-1}) in August 1986. r^2 (coefficient of determination) refers to the linear regression of ln(1-i) with L.

Clones	i	L	k	r^2	Yield (kg ha^{-1})
AMAZ 15-15	0.72	-	-	-	3000
SCA 9	0.79	-	-	-	2100
NA 33	0.80	2.3	0.70	0.87	6200
MO 81	0.93	2.8	0.95	0.86	9000
PA 127	0.94	3.3	0.86	0.89	800
PA 300	0.85	3.1	0.61	0.96	2500
PA 76	0.95	3.4	0.89	0.91	1200

The effect of variation in radiation extinction through the canopy can be clearly seen in Fig. 8 which shows the light saturated photosynthesis sampled at the top, middle and bottom of the canopies of each of the clones. NA 33 with a lower radiation extinction coefficient exhibited a smaller drop (25%) in P_m between sun and shade leaves combined with the much steeper drop in P_m with increasing canopy depth observed for the relatively more vigorous PA 127. More detailed data showing photosynthetic light response curves of even aged leaves of four clones (AMAZ 15-15, SCA 9, PA 127 and PA 300) at three canopy levels can be seen in Fig. 9. Generally, the upper sun leaves, which had a significantly higher nitrogen content per unit leaf area and specific leaf weight, had higher light-saturated rates of photosynthesis and higher light compensation points than lower shade leaves.

Discussion

A physiological analysis of yield determinants in cocoa established that variation in photosynthetic activity amongst the germplasm appeared to be responsible for the variation in vigour of juvenile cocoa. However, although variation in photosynthetic activity was evident in bearing cocoa, this was not correlated to yield. In young, bearing cocoa in which canopies were still expanding, yield appeared to be related to differences in radiation interception amongst cocoa genotypes. Where canopies had closed, fractional radiation interception showed no positive relationship with yield (in fact, in many cases, yields appeared to show a negative correlation with fractional radiation interception). In this case, radiation extinction coefficients were most highly correlated with yield variation, indicating that for mature clones, the pattern of radiation attenuation through the canopy was the most important determinant of productivity.

The lack of a positive relationship between instantaneous net photosynthetic rate and precocity and yield of bearing cocoa demonstrates that the size and duration of the effective photosynthesising surface is of greater importance in determining yield than the rate of photosynthesis *per se*.

Figure 8 Clonal variations in maximum photosynthetic rate of evenly-aged leaves samples from three canopy positions (Top, Middle and Bottom) of mature clonal cocoa planted at high density (3333 trees ha^{-1}) in Sabah, Malaysia. Significant differences between clonal means for each canopy height are denoted by LSD histograms at 5% probability. Each histogram represents a mean of nine trees.

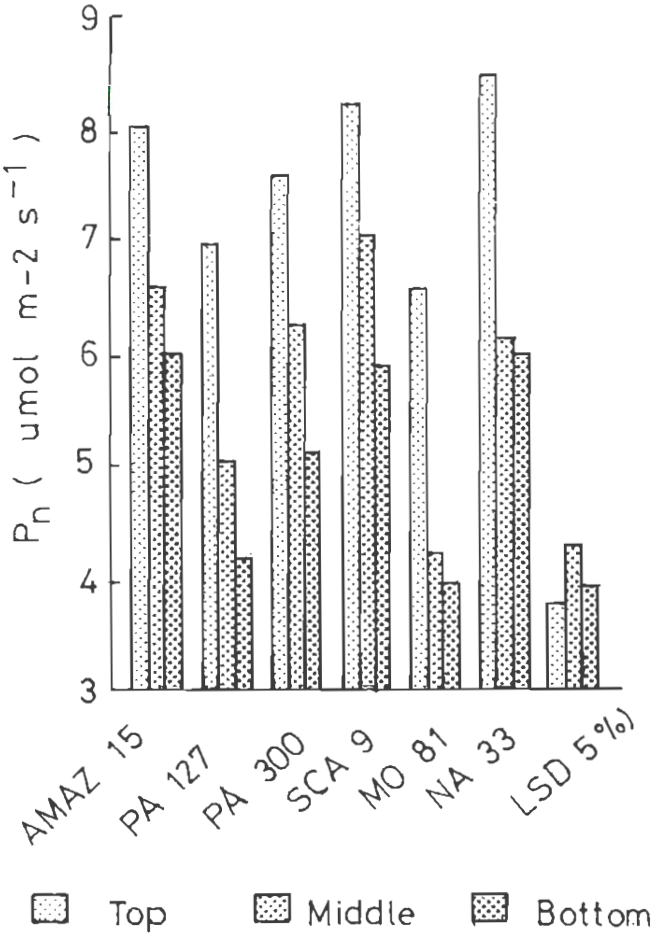
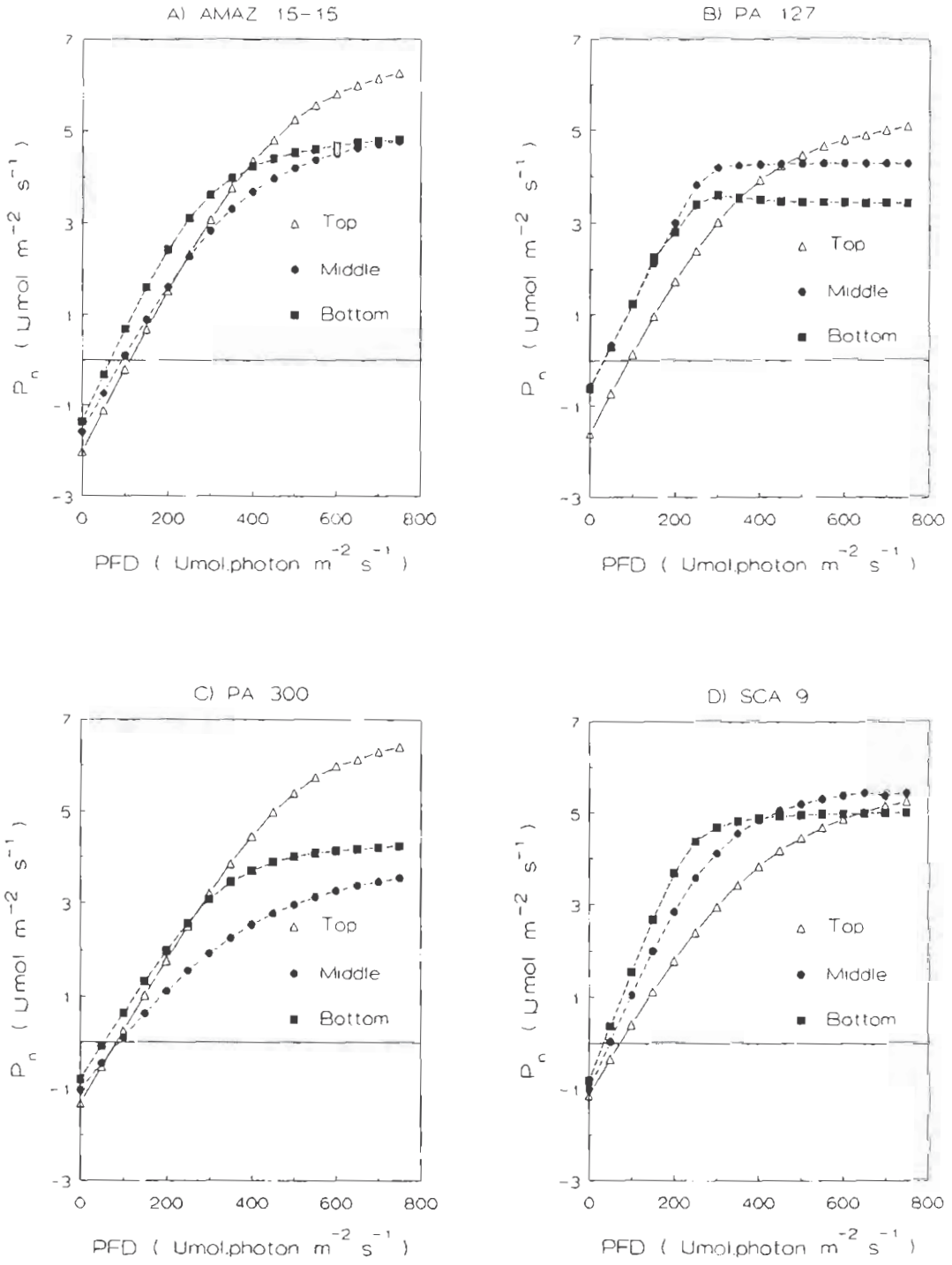


Figure 9 Clonal variations in the predicted response of P_n of evenly-aged leaves to PFD measured at three canopy levels (Top, Middle and Bottom) for a) AMAZ 15-15,b) PA 127, c) PA 300 and d) SCA 9 planted at high density (3333 trees ha^{-1}) in Sabah, Malaysia. The lines were fitted with parameter constants derived from non-rectangular hyperbola. Each symbol represents a mean of nine trees.



Precocity and yield efficiency (yield/intercepted radiation) are independent of inherent tree vigour, measured as trunk diameter; some of the less vigorous genotypes examined had similar, or higher efficiencies than more vigorous genotypes in conversion of intercepted solar radiation into dry bean yield. Trunk girth does not provide an adequate measure of yield efficiency because genotypes show differences in the partitioning of dry matter between canopy and trunk.

Although not presented here, the physiological studies were combined with a rigorous analysis of heritability, which showed that radiation interception and yield efficiency are highly heritable. Effects are largely additive with little evidence of specific combining ability. This suggests that each clone intended for hybridization needs to be evaluated in terms of canopy structure, as vigorous clones tend to give rise to hybrids with greater vigour and *vice versa*.

Traditionally cocoa trees have been widely spaced and so crop stands take a considerable time to reach full canopy closure. Our analysis indicates that since radiation interception is the main factor limiting crop yields until full canopy development, vigorous clones which expand rapidly are favoured and this indicates why, in the past, vigour and precocity have been major selection criteria.

Inherently vigorous clones are less suitable for high density planting, because excessive canopy development leads to lower canopy productivity and will take place at the expense of cropping. Chemical regulation of vegetative growth (e.g., use of paclobutrazol, Ho *et al.*, 1991) in some vigorous clones has been successfully applied with indications of positive effects on yield. However, it is clear that there are genotypes which have characteristics suited to intensive, high density planting systems without the need for chemical regulation. Dwarf stature with an open canopy allowing good radiation penetration combined with an early, precocious habit, appears to be the appropriate theoretically suitable plant form for such cropping systems.

Acknowledgements

We are indebted to the Biscuit, Cake, Chocolate and Confectionary Alliance for funding this work and to the Cocoa Research Unit, Trinidad and Bal Plantations Sdn Bhd, Sabah for providing the facilities to enable this study to be conducted. We are also gratefull to Dr. G. Lockwood for his helpful comments and criticisms during the preparation of this paper.

References

Alvim, P. de T. (1977) Cacao, In *Ecophysiology of tropical crops* (eds. P.de T. Alvim & T.T. Kowlowski), Academic Press, New York, 279-313

Ang, B.B. and Shepard, R. (1978) Cocoa breeding and selection investigations at Prang Besar Research Station, In *Proc. Intl. Conf. on Cocoa and Coconut*, Incorporated Society of Planters, Kuala Lumpur, Malaysia, pp. 3-17

Bartley, B.G.D. (1971) Procedures for the selection of varieties for commercial planting In *Proc. 3rd Intl. Cocoa Res. Conf*, Tafo, Ghana, pp. 584-589

Blum, A. (1988) *Plant breeding for stress environments* CRC Press, Boca Raton, Florida

Cannell, M.G.R., Sheppard, L.J. and Milne, R. (1988) Light use efficiency and woody biomass production of Poplar and Willow, *Forestry* **61**(2) 125-136

Comstock, R.E. and Robinson, H. (1952) Estimation of the average degree of dominance of genes In *Heterosis* (ed. J.W. Gowan), Iowa State College Press, Ames, pp 495-516

Coombs, J., Long, S.P., Scurlock, J.M.O. and Hall, D.O. (1985) *Techniques in Bioproductivity and Photosynthesis* Pergamon Press, Oxford

Corley, R.H.V., Hardon, J.J. and Ooi, S.C. (1973) Some evidence for genetically controlled variation in photosynthetic rate of oil palm seedlings *Euphytica* **22 22** 48-55

Corley, R.H.V. (1983) Potential productivity of tropical perennial crops *Experimental Agric.* **19** 217-237

Duncan, R.R. and Baligar, V.C. (1991) Genetics, Breeding, and Physiological mechanisms of nutrient uptake and use efficiency: an overview In *Crops as Enhancer of Nutrient use* Academic Press, London, pp.3-35

Elmore, C.D. (1980) The paradox of no correlation between leaf photosynthetic rate and crop yields In *Predicting Photosynthesis for Ecosystem Models* (eds J.D. Hesketh, & J.W. Jones), Vol. **II**, CRC Press, Florida

Field, C.B. Ball., J.T. and Berry, J.A. (1989) Photosynthesis: Principles and Field Techniques In *Plant Physiological Ecology* (eds. R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel), Chapman and Hall, London, pp 209-248

Graham, R.D. (1984). Breeding for nutritional characteristics in cereals *Advance in Plant Nutrition* **1** 57-102

Hay, K.M. and Walker, A.J. (1989) *An Introduction to the Physiology of Crop Yield*, Longman, London

Ho, S.H., Mohan, A., Lim, J.K., Pang, T.Y. and Lim, D.H.K. (1991) Effects of paclobutrazol on cocoa In *Proc. Intl. Cocoa Conf.: Challenges in the 90s*, The Incorporated Society of Planters, Kuala Lumpur (in press)

Kennedy, A.J, Lockwood, G., Mossu, D., Simmonds, N.N. and Tan, G.Y. (1987) Cocoa breeding: past, future, present *Cocoa Grower's Bull.* **38** 5-22

Lam, K.Lam, K.S. and Lim, K.H. (1991) Trials on spacing of clonal cocoa on an inland soil in Peninsular Malaysia In *Proc. Intl. Cocoa Conf.: Challenges in the 90s* The Incorporated Society of Planters, Kuala Lumpur (in press)

Lim, D.H.K. and Pang, T.Y. (1989) Advances in cocoa planting densities/patterns with special reference to high density systems - BAL experience In *Proc. Workshop on Cocoa Agric. Res.* Malaysian Cocoa Growers' Council/Malaysian Cocoa Board, Malaysia

Lim, D.H.K., Pang, T.Y. and Yow, S. (1991) Selection of cocoa genotypes for high density cocoa planting and guidelines to its management In *Proc. Intl. Cocoa Conf.: Challenges in the 90s*, The Incorporated Society of Planters, Kuala Lumpur (in press)

Machado, R.C.R. and Hardwick, K. (1988) Does carbohydrate availability control flush growth in cocoa? In *Proc. 10th Intl. Cocoa Res. Conf.* Santa Domingo, Dominican Republic, pp. 151-157

Mahon, J.D. (1983) Limitation to the use of physiological limitation in plant breeding *Can. J. of Pl. Sci.* **63** 11-21

Mahon, J.D. (1990) Photosynthetic carbon dioxide exchange, leaf area, and growth of field-grown pea genotypes *Crop Sci.* **30** 1093-1098

Marshall, B. and Biscoe, P.V. (1980) A model for C_3 leaves describing the dependence of net photosynthesis on irradiance I. Derivation *J. of Experimental Botany* **31** 29-39

Monsi, M and Saeki, T. (1953) Über den lichtfaktor in den pflanzengesell-schaften und seine bedentung, für die stoffproduktion *Japanese J. of Botany* **14** 22-52

Mooleedhar, V. and Lauckner, F.B. (1990) Effects of spacing on yield in improved clones of *Theobroma cacao* L. *Trop.Agric.* **67**(4) 376-378

Palmer, J.W. (1989) Canopy manipulation for optimum utilization of light In *Manipulation of fruiting* (ed. C.J. Wright), University of Nottingham, Cambridge University Press pp. 245-261

Robinson, T.L. and Lakso, A.N. (1991) Bases of yield and production efficiency in apple orchard systems *J. of the Amer. Soc. of Hort. Sci.* **116** (2) 188-194

Ross, J. (1981) *The Radiation Regime and Architecture of Plant Stands*, Dr. W. Junk Publishers, The Hague, Netherlands

Samsuddin, Z., Tan, H. and Yoon, P.K. (1987) Studies on photosynthetic rates, girth, and yield in *Hevea brasiliensis J. of Natural Rubber Res.* **2** 46-54

Squire, G.R. (1990) *The Physiology of Tropical Crop Production* CAB International, U.K.

Tan, G.Y. (1991) Prospects of breeding cocoa cultivars for low-input management In *Proc. Intl. Cocoa Conf.: Challenges in the 90s*, The Incorporated Society of Planters, Kuala Lumpur (in press)

Taylor, S.J. and Hadley, P. (1988) Relationships between root and shoot growth in cocoa (*Theobroma cacao* L.) grown under different shade regimes In *Proc. 10th Intl. Cocoa Res. Conf.*, Santa Domingo, Dominican Republic, pp. 177-183.

Thong, K.C. and Ng, W.L. 1978 Growth and nutrients composition of monocrop cocoa plants on inland Malaysian soils In *Proc. Intl. Conf. on Cocoa and Coconut*, Incorporated Society of Planters, Kuala Lumpur, Malaysia

Toxopeus, H. (1969) Commercial assessment of WACRI Series I and II varieties in Nigeria Cocoa Research Institute, *Ann. Rep. 1967-68*, Ibadan, Nigeria

Toxopeus, H. and Wessel, M. (1970) Studies on pod and bean values of *Theobroma cacao* L. in Nigeria I Environmental effects on West African Amelonado with particular attention to rainfall distribution *Netherlands J. of Agric. Sci.* **18** 132-139

Toxopeus, H. and Jacob, V.J. (1970) Studies on pod and bean values of *Theobroma cacao* L. in Nigeria II Number of beans per pod, with special reference to the natural pollination process *Netherlands J. of Agric. Sci.* **18** 188-194

Woodward, F.I. and Sheehy, J. (1983) *Principles and Measurements in Environmental Biology* Butterworth, London

Yapp, J.H.H. and Phua, P.K. (1987) Inter-Upper Amazon cocoa hybrids of Sabah - Series III Progeny Trial In *Seminar on current Palm Kernel Utilisation and Recent Advances in Cocoa Cultivation*, Society of Agricultural Scientist, Sabah