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SEASONAL VARIATION IN YIELD AND DEVELOPMENTAL PROCESSES IN AN OIL PALM DENSITY TRIAL ON A PEAT SOIL:
1. YIELD AND BUNCH NUMBER COMPONENTS

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ABSTRACT

Bunch production in an oil palm density trial on a peat soil in Perak, West Malaysia, displayed a regular annual cycle that was highly synchronized across densities. The phase of the cycle differed from that displayed for West Malaysia as a whole but resembled those at some other sites. Annual cycles were found in both bunch number and mean bunch weight and in the proportion of palms that yielded bunches in any one month. While the long-term trends in bunch numbers and single bunch weights were negatively correlated, in the short-term there was a highly significant positive correlation between the two.

The variation in mean bunch weight was also reflected in the variation in the main bunch components. There were also seasonal variations in the ratios of bunch components.

In addition to yield, regular annual cycles were also apparent in the rates of frond emission, male and female inflorescence production and sex ratio, and in inflorescence abortion. While the phases of bunch and female inflorescence cycles could be matched using physiologically meaningful lag periods, the cycles of frond emission and total inflorescence production, and of frond emission and female inflorescence production could not, giving rise to non-significant or negative correlations.

Abortion rates were low throughout the trial and while a regular sex ratio cycle became apparent from the eighth year, this was not the main determinant of bunch number cycling. Rather, variation in the rates of inflorescence development may be the crucial factor in causing the yield cycles.

Other external and internal factors that might contribute to the yield cycles are discussed.

Keywords: oil palm, yield cycles, frond production, flowering, planting density.

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INTRODUCTION

Seasonal (*i.e.* annual) cycles are a characteristic feature of yield behaviour in oil palm (Corley, 1977). In climates with extreme and regular dry seasons, such as those of West Africa, such cycles can be accounted for by large seasonal differences in rainfall, soil water supply, radiation and related climatic conditions. In the more uniform climates of Southeast Asia, the causes of yield cycles are less obvious although rainfall and other climatic factors do exhibit seasonality and could still play a role. However, even in the absence of obviously varying external factors there may be internal, *i.e.* endogenous, processes regulating development which give rise to cyclic behaviour. These may operate such that the cycles persist even when the external factors appear uniform or non-limiting.

Several developmental processes may contribute to cycles in fruit bunch production in oil palm. These include variation in the rate of frond emission, timing of inflorescence development stages, inflorescence

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sex determination, rate of inflorescence development both before and after frond emission, inflorescence abortion, pollination efficiency and other factors affecting the bunch weight and rate of bunch development and ripening. While the general nature of each of these factors has been described, the extent to which they contribute individually to the final yield pattern has not been determined. Also, the relative contribution and nature of the interaction between external and internal factors contributing to yield variation is likewise unclear.

Many records of seasonal yield variation exist for individual trials but they often cover limited periods and lack detailed records of the flowering pattern. In the large density trial at Teluk Intan in Perak described by Henson and Mohd Tayeb (2003), individual fresh fruit bunch harvest records were available from the start of harvest up to the 17th year after planting. In addition, counts were made quarterly of new frond and inflorescence production, inflorescence abortion and the number of rotten and harvested bunches, providing a large database for examination of cyclic behaviour. Bunch analyses were carried out allowing an examination of seasonal changes in bunch composition. This paper examines the yield and bunch number components and compares the seasonal yield patterns with national trends and with those for other sites. Possible external factors leading to the annual cycles are reviewed. The bunch weight components are examined in a subsequent paper (Henson and Mohd Tayeb, 2004).

MATERIALS AND METHODS

Density Trial: Measurements

Full details of the site, experimental design and the measurements made are given in Henson and Mohd Tayeb (2003). Briefly, the trial compared three planting densities - 120, 160 and 200 palms ha^{-1} - on a deep peat soil in Perak. There were two replicate blocks with the density treatments split into 18 sub-plots with factorial fertilizer treatments. However, as the nutritional treatments had little effect on the yields (which were mainly a function of the planting density), they are not further considered. There were initially eight recording palms per plot giving a total of 288 palms per density. However, attack by *Ganoderma* progressively reduced the palm numbers so that, as previously reported, the actual densities decreased.

Beginning in July 1988, the youngest fully-opened frond (Frond 1) was marked and the number of newly-opened fronds, male, female, hermaphrodite and aborted inflorescences, and newly harvested bunches, were subsequently recorded at three-monthly intervals using conventional techniques (Corley and Breure, 1981).

Bunch harvests were carried out twice monthly with single bunch fresh weight and bunch number being recorded for each palm. The results for individual harvests were combined to give monthly, quarterly and annual totals.

Density Trial: Data Analysis

Although there were differences due to density in the absolute yields and numbers of fronds and inflorescence produced (Henson and Mohd Tayeb, 2003), there were no substantial effects of density on cyclic patterns. Hence, the data for all densities were pooled.

For monthly values, running means (n=3) were calculated to *smooth* the data but for quarterly values, because of fewer data points, this procedure tended to dampen the cycles excessively and was omitted. To aid comparisons of different variables, the data were *de-trended, i.e.* the long-term trend, derived by fitting linear or polynomial curves to the initial data, was removed. To further facilitate comparisons the de-trended data were then expressed as a percentage of their means. Cross-correlations were performed between different cyclic variables with and without appropriate lag periods.

Bunch dry matter production (BDMP) was calculated from the bunch dry weight at harvest using a modification of the method described by Henson (1997). The method calculates the total dry matter incorporated into bunches during each month of their development based on a standard bunch dry matter accumulation curve and a 160-day period from anthesis to harvest. The BDMP calculated this way is a similar measure to the *fruiting activity* of Corley and Breure (1992).

Other Data Sources

For comparative purposes, yield data for commercial field sites and from countrywide records were also examined. Updated commercial data were obtained for the two sites described by Henson (1997). For Malaysia, monthly fresh fruit bunch (FFB) records dating from 1985, obtained from the MPOB Industry Development Unit, were used.

To supplement the study, some data collected in earlier trials that involved detailed recording of frond emission and inflorescence development rates (Chang *et al*., 1993; 1995) were reanalysed.

Meteorological data were obtained from published records of the Malaysian Meteorological Service (MMS) or directly from MMS.

RESULTS AND DISCUSSION

Cycling of FFB Yield

In many locations, FFB and palm oil yields display a major peak and a trough each year. However, the timing of the peak and trough may vary somewhat from year to year and may differ with both location and planting material (*e.g.* Nouy *et al.*, 1996).

The national Malaysian palm oil and FFB production generally exhibits a single major peak in September or October (Chow, 1988; 1992). The peak for East Malaysia tends to fall one month later than in the Peninsula (Chow, 1992). A minor yield peak can sometimes be discerned in May, especially in Sabah (*Figure 1*).

In the density trial, the FFB yield, averaged over all years, peaked in July with a trough in January (*Figure 1*). The corresponding peaks and troughs for BDMP occurred in May/June and in November, respectively. Thus, the peak in BDMP preceded that in FFB by one to two months. The yield cycles at Teluk Intan were quite regular over the years, being consistently offset from the national cycles and highly synchronized across the densities (*Figure 2*).

Comparisons of the density trial yield cycles with those at two other Peninsular sites over similar periods, also revealed differences in the timing of yield peaks (*Figure 3*). To test whether the timing of yield peaks depended on the prevailing climatic conditions (real time), or was triggered by the time of planting or of maturing of the first bunches, cross-correlations were performed between the sites. Comparisons were made using both the original running means, or after removal of the long-term trends. The latter method tended to give higher correlations. The results following trend removal (*Table 1*) suggested that the date of planting may have had the most effect in determining the timing of the yield peaks. However, there were also significant positive correlations between the sites when matched in real time and, in one out of the three cases, for harvest time. As the range in planting time was rather restricted, further comparisons with materials planted in different months are desirable.

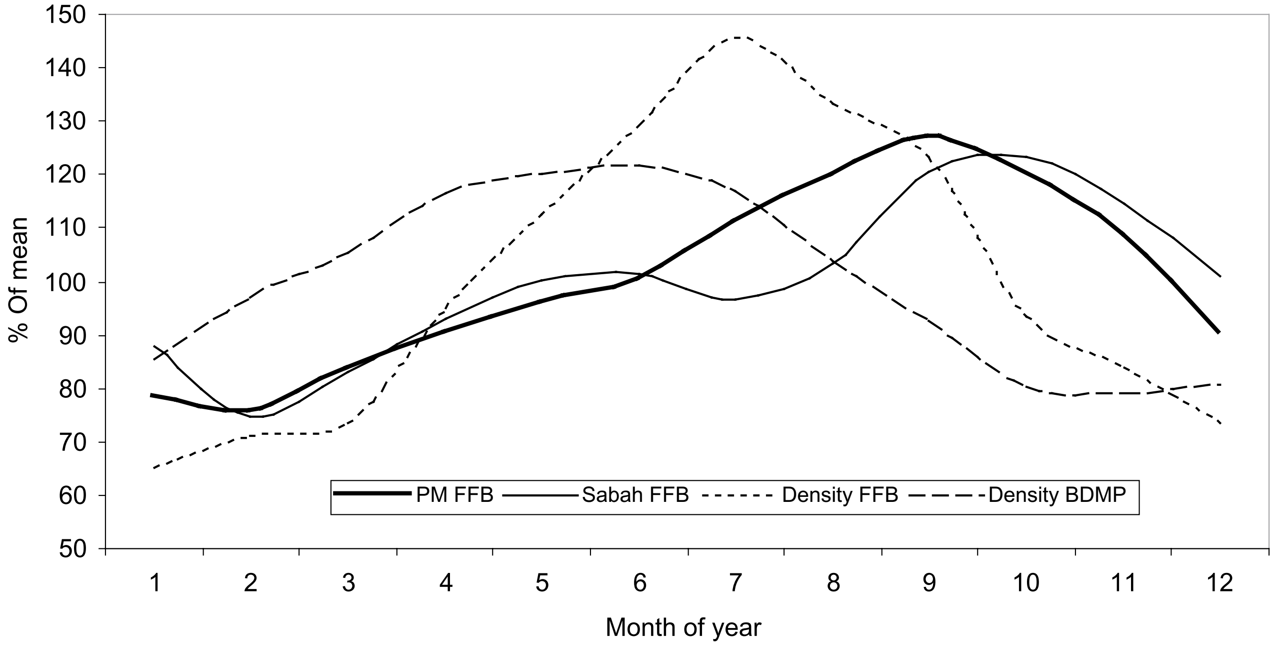
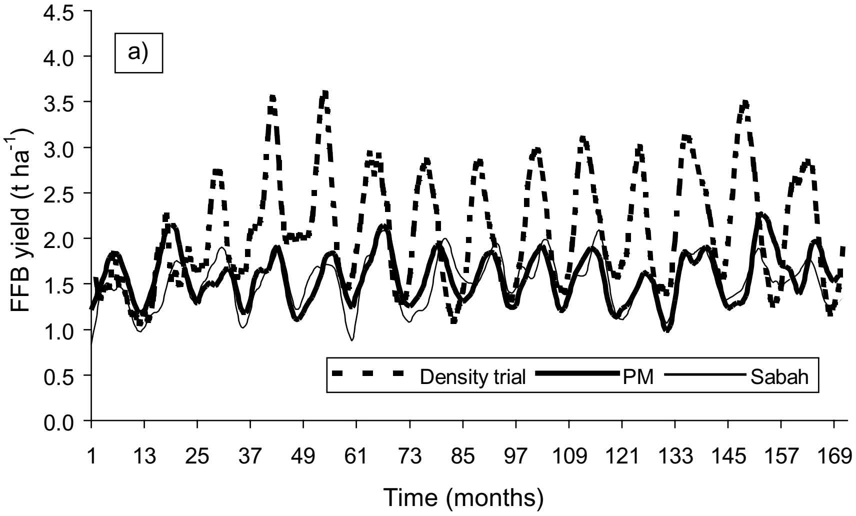


Figure 1. Mean seasonal variation in fresh fruit bunch (FFB) production and bunch dry matter production (BDMP) for the density trial in comparison with that of Peninsular Malaysia (PM) and Sabah FFB production from 1989 to 2001.



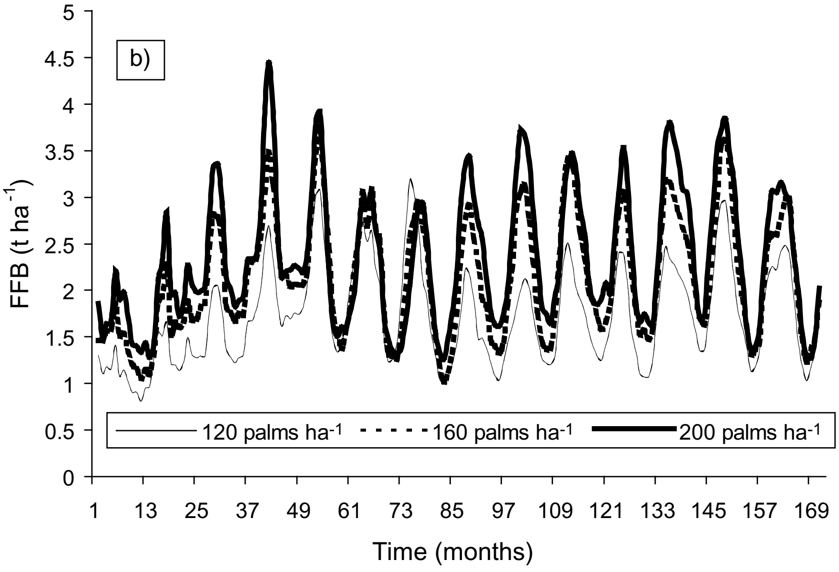


Figure 2. Monthly variation from 1988 to 2001 in: (a) mean fresh fruit bunch (FFB) production in the density trial compared with mean yields in Peninsular Malaysia (PM) and Sabah and (b) monthly variation in FFB production in the individual density treatments. Data in (b) are running means (n=3).

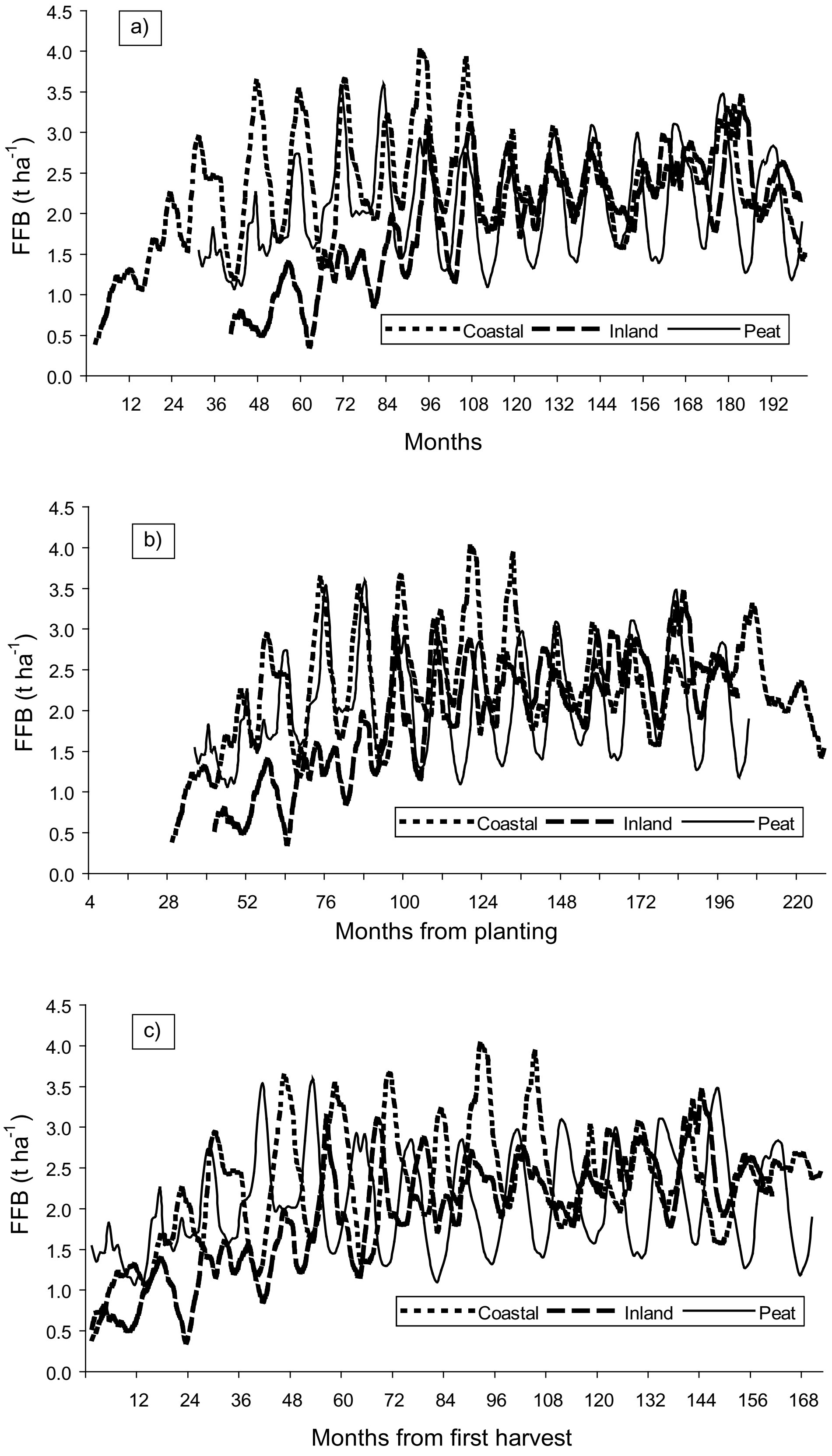


Figure 3. Monthly variation in fresh fruit bunch (FFB) (t ha^{-1}) for coastal, inland and the peat density trial (mean of all densities) sites plotted (a) in real time, (b) with planting dates approximately synchronized and (c), with first harvest times synchronized. Data are running means (n=3).

TABLE 1. CORRELATION MATRICES FOR COMPARISONS OF MONTHLY FFB YIELD CYCLES BETWEEN THREE SITES [peat (the density trial), coastal and inland]

		Peat	Inland
1. Matched in real time	Coastal	0.579 ***	0.261 **
	Inland	0.200 *	-
2. Synchronized by planting time	Coastal	0.527 ***	0.290 **
	Inland	0.331 ***	-
3. Synchronized by time of first harvest	Coastal	-0.472	0.235 *
	Inland	-0.287	-

Notes: (a) Planting and first harvest dates at the sites were as follows:

Site	Planting	First harvest
Density	August 1985	March 1988
Inland	October 1985	December 1988
Coastal	October 1983	November 1985

(b) Data are correlation coefficients with levels of significance at $P< 0.05$, 0.01 and 0.001 indicated for positive correlations as *, ** and *** respectively. Yields were transformed before analysis as described in the text. The number of data pairs used for all comparisons was 161.

Cycling of FFB Yield Components

The changes in bunch number usually contribute the most to yield cycling. This is shown for the density trial in *Figure 4*. Bunch number can vary either because of variation in the number of bunches per palm or because of variation in the proportion of palms bearing bunches. *Figure 4* shows that both these contributed, although in the early years variation in bunch number per palm was the main factor.

The bunch yield components, bunch number and single bunch weight, showed the normal long-term negative correlation with bunch number declining and single bunch weight increasing with palm age (Henson and Mohd Tayeb, 2003). It is generally assumed that this inverse relationship reflects competition for assimilates, since reducing the bunch number by partial disbudding increases mean bunch weight while increasing mean bunch weight through improved pollination reduces the bunch number (Corley and Gray, 1976; Foster *et al.*, 1985; Corley and Breure, 1992). However, there is inevitably a lag between the imposing of such treatments and their effects.

However, in the short-term, as revealed following removal of the long-term trends (*Figure 5; Table 2*), bunch number and mean bunch weight were found to be positively correlated in this trial. Thus, the peaks in total yield partly resulted from the synchrony between peaks in both bunch number and weight.

At the other sites, a similar effect was observed but the correlations after removal of the trends were not significant (*Table 2*).

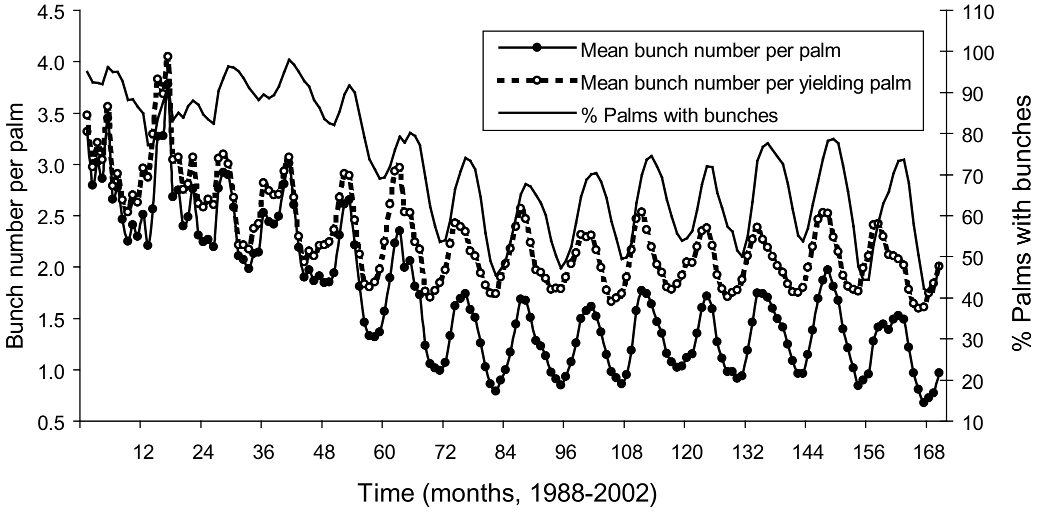


Figure 4. Monthly variation from first harvest in bunch number per palm, bunch number per yielding palm and percentage of yielding palms in the density trial. Data are running means (n=3) of all densities.

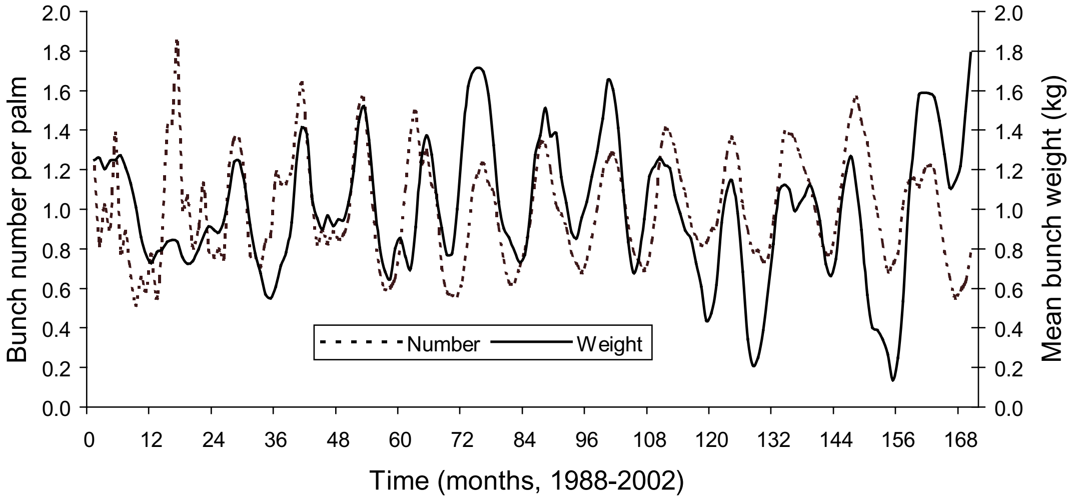


Figure 5. Monthly variation from first harvest in bunch number per palm and in single bunch fresh weight in the density trial. Long-term trends have been removed and the values for the two variables normalized. Data are means of all densities.

TABLE 2. CORRELATION COEFFICIENTS (r) AND SIGNIFICANCE LEVELS (*P*) AT THREE SITES [peat (the density trial), coastal and inland] BETWEEN BUNCH NUMBER AND MEAN BUNCH WEIGHT BEFORE AND AFTER REMOVING THE LONG-TERM TRENDS

		Peat	Coastal	Inland
Number of data pairs		170	200	161
With trend	r	-0.757	-0.796	-0.548
	P	0.001	0.001	0.001
Trend removed	r	0.403	0.049	0.085
	P	0.001	ns	ns

Note: ns = not significant at P<0.05.

Cycling of Frond and Inflorescence Production

The bunch number is dependent among other things on the number of fronds produced. Frond production cannot be observed directly but is inferred from the rate of frond emission. In agreement with general findings, the rate of frond emission in the density trial declined with age, first quite rapidly and later more gradually (Henson and Mohd Tayeb, 2003). In addition to the long-term decline, there can also be variation in the rate of frond emission during a year, even in the absence of a marked annual dry season as observed by Corley (1977) and Chang *et al.* (1988).

Seasonal variation in frond emission is shown for the density trial together with the variation in inflorescence and bunch numbers in *Figure 6*. The frond emission rate showed an annual cycle with peaks generally in the fourth quarter.

Anthesis normally occurs at Frond 20 or thereabouts, or about nine months after frond opening (*Table 7*). Based on anthesis at Frond 20 and the observed rates of frond emission, the actual lag could have varied from 5.8 to 10.2 months (though the mean emission rate had largely stabilized to give a lag of about 8.9 months from around the fifth year onwards of recording).

It can be seen from *Figure 6* that after lagging total inflorescence production by nine months with respect to frond emission there was generally an inverse relationship between the two. A similar trend was observed for the more restricted data set from the coastal site (*Figure 7*) and, to a lesser extent, can be deduced from the figures in Chang *et al.* (1993). Correlations obtained in the density trial using the mean data and various lag periods are given in *Table 3*.

Table 3 shows that despite expectations to the contrary, there was no positive relationship between the frond emission rate and inflorescence production using the expected lag times, and neither was there a pronounced significant positive correlation between the frond emission rate and bunch production other than for periods unrealistically close to frond emission. Chang *et al.* (1988) found a positive correlation between the frond emission rate and bunch yield lagged by 11 months. It should be noted, however, that there were two peaks in frond production per year in their trial and their monthly assessments imply a higher resolution than the quarterly assessments of the present study.

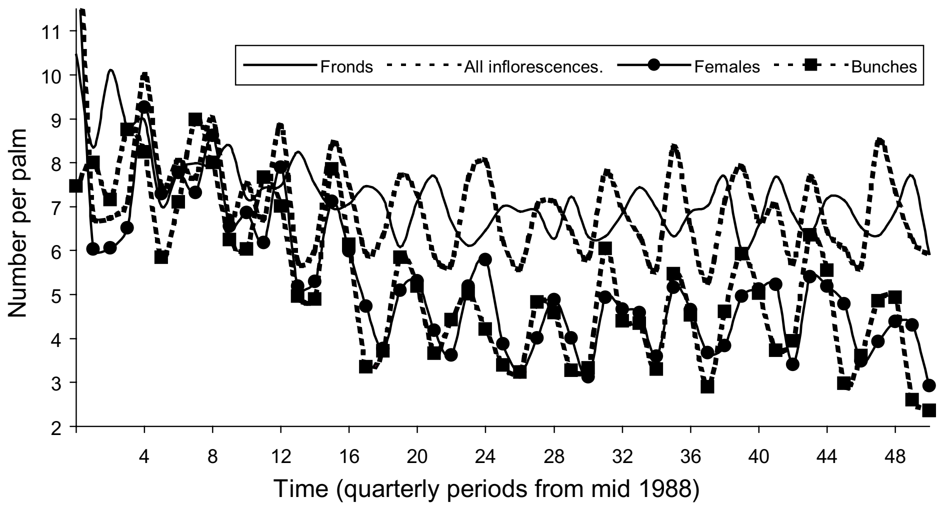


Figure 6. Quarterly variation in the density trial in frond production, total and female inflorescence numbers nine months later and bunch numbers 15 months later. Data are means for the three densities.

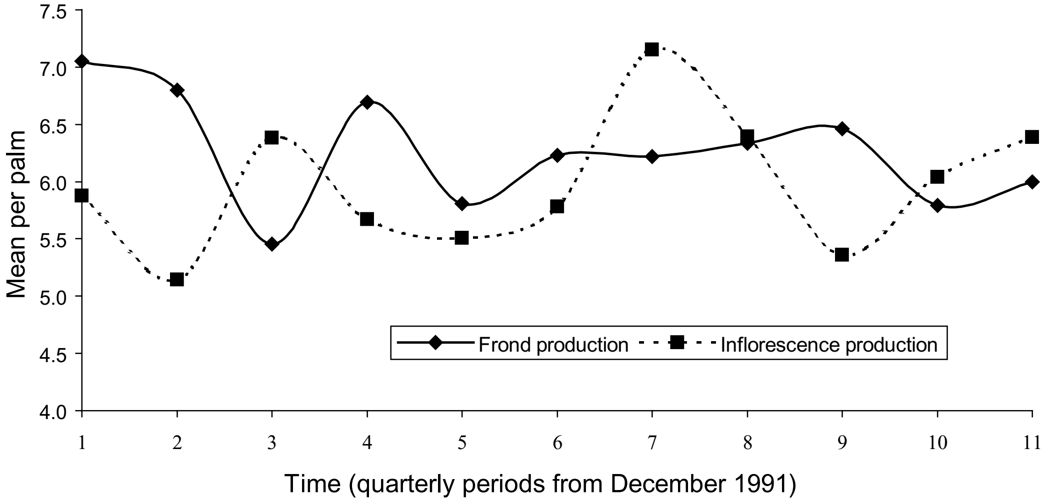


Figure 7. Quarterly variation in frond production and total inflorescence production nine months later at the coastal site.

TABLE 3. CORRELATION COEFFICIENTS BETWEEN (i) FROND EMISSION AND TOTAL INFLORESCENCE PRODUCTION, (ii) FROND EMISSION AND FEMALE INFLORESCENCE PRODUCTION, (iii) FEMALE INFLORESCENCE PRODUCTION AND BUNCH NUMBER AND (iv) FROND EMISSION AND BUNCH NUMBER

	Lag period (quarters)					
	0	**1**	**2**	**3**	**4**	**5**
n	56	55	54	53	52	51
Frond emission *vs*. total inflorescence production	0.05ns	0.35**	-0.04ns	**0.02**ns	-0.35**	0.29*
Frond emission *vs*. female inflorescence production	-0.06ns	0.18ns	-0.02ns	**0.10**ns	-0.41**	0.07ns
Female inflorescence production *vs*. bunch number	-0.06ns	0.48***	**0.33***	-0.27*	-0.33*	0.41**
Frond emission *vs*. bunch number	0.40**	-0.44***	-0.23ns	0.34*	0.28*	**-0.31***

Notes: The correlations were carried out using mean data for all planting densities after removal of the long-term trends. The significance of the correlation coefficients at $P < 0.05$, 0.01 and 0.001 is indicated by *; ** and *** respectively; ns = not significant at $P<0.05$. Correlations obtained using expected lag periods are indicated in bold. n = number of data pairs used in the analyses.

Corley and Breure (1992) found that inflorescence removal led to an increased rate of frond emission, implying that high inflorescence, or later, high bunch production, may reduce frond production or emission. However, in the density trial, there was no significant correlation between frond emission and concurrent inflorescence production, while the relationship between frond emission and concurrent bunch number was significantly positive (*Table 3*). However, bunches recorded as cut at each census would have shown maximum dry matter accumulation one or two months previously and when the rate of frond emission (expressed in terms of the average time interval between successive fronds) was plotted together with concurrent BDMP, the two were well matched (*Figure 8*). Therefore, it is possible that the frond emission rate could have varied in response to the bunch load.

The lack of correspondence between frond and inflorescence production indicates that factors other than the rate of frond emission contributed to the cycling in inflorescence and bunch number.

Variation in the sex ratio (female/total inflorescence number) is commonly regarded as a prime cause of yield variation. Over the whole recording period in the density trial, a very high proportion of nodes (nearly 77%) produced female inflorescences. The percentage of females declined as the palms aged while the number of males increased (Henson and Mohd Tayeb, 2003). In addition, there were a small number of hermaphrodites that may have contributed to the final bunch number. An annual sex ratio cycle only became apparent from the eighth year after planting, as earlier there were only a small number of male inflorescences (*Figure 9*). While the sex ratio subsequently displayed annual cycles, as was also observed by Chang *et al.* (1993), this was not simply a result of reciprocal variation between the male and female inflorescences as the seasonal variation in male inflorescences was generally small.

The number of aborted inflorescences was likewise low, representing less than 5% of the total nodes. Despite the low occurrence, annual cycles in abortion were apparent with peaks in all the densities being more prominent in some years than in others (*Figure 10*). A high bunch load is associated with increased inflorescence abortion (Corley and Breure, 1992; Breure and Corley, 1992) and cycles in BDMP matched those in the abortion rate recorded nine months later (*Figure 11*).

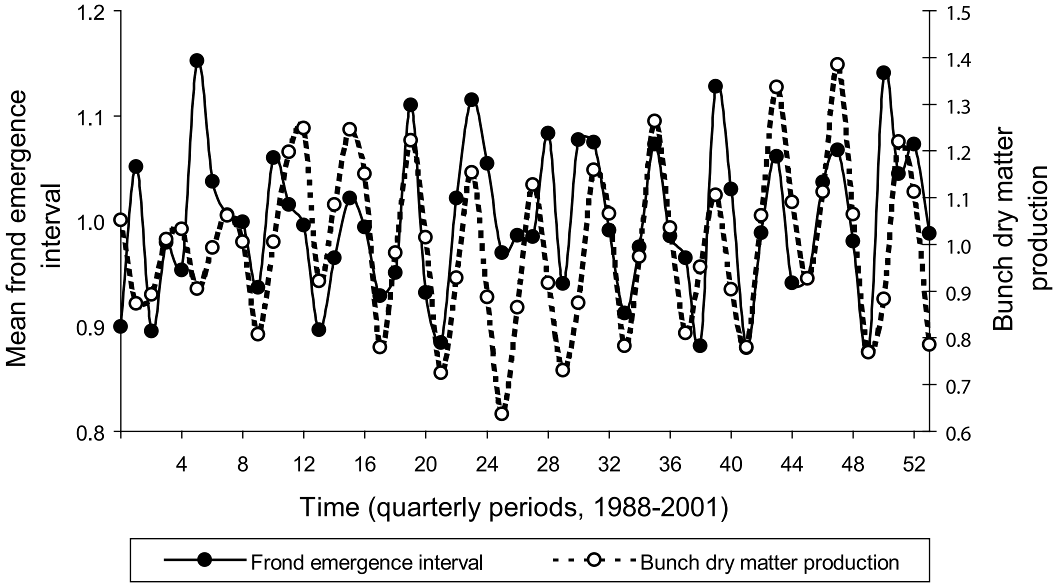


Figure 8. Quarterly variation in the density trial in bunch dry matter production and concurrent rate of frond emergence. Data, means of all densities, are with long-term trends removed and normalised with respect to the mean.

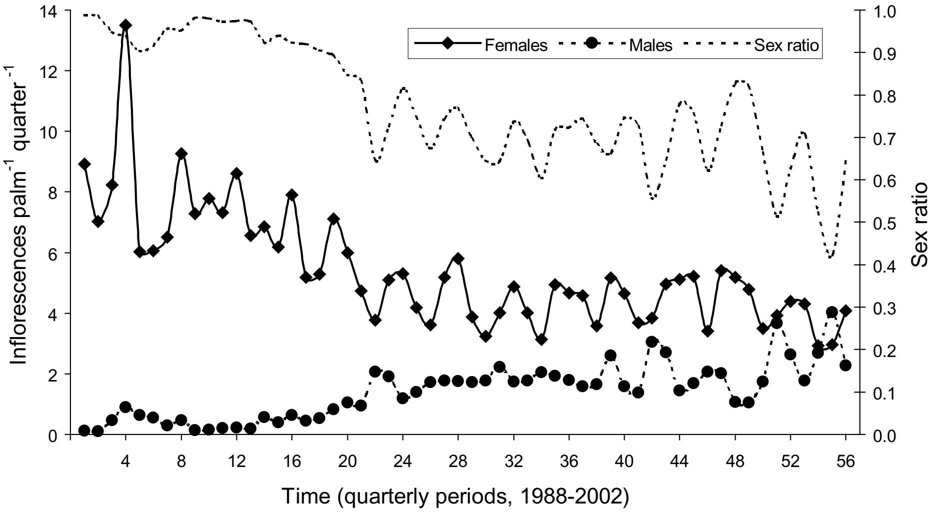


Figure 9. Quarterly variation in the density trial in female and male inflorescence numbers and in the sex ratio. Data are means for three densities.

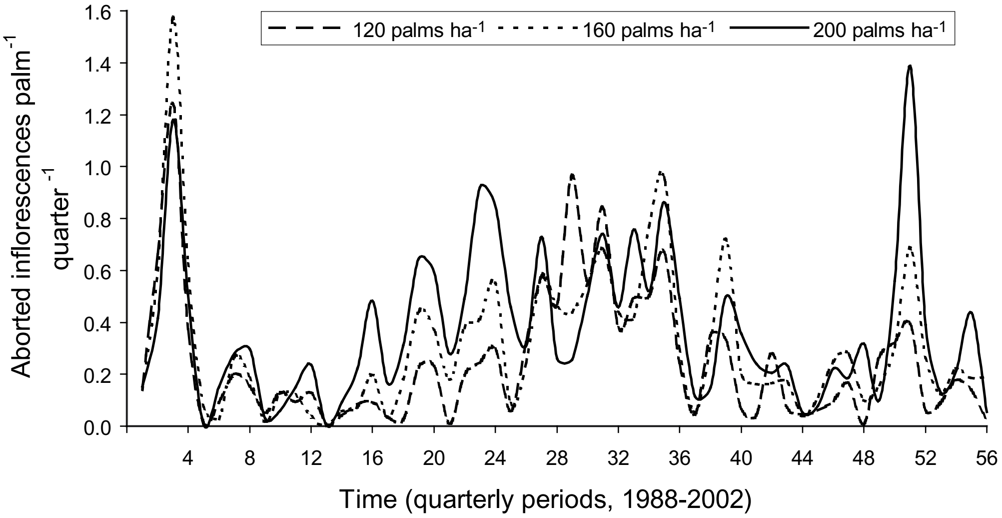


Figure 10. Quarterly variation in the density trial in aborted inflorescence numbers. Data are shown for individual densities.

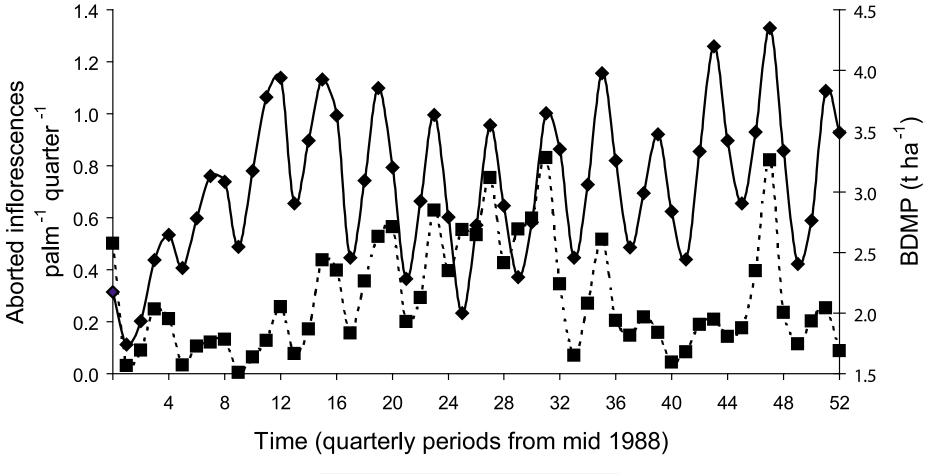


Figure 11. Quarterly variation in bunch dry matter production (BDMP) and inflorescence abortion nine months later in the density trial. Data are means of all densities.

Comparison of Peak Amplitudes

Corley (1977) and Chang *et al*. (1993) noted that the amplitude of inflorescence cycles can often exceed that of frond emission. Comparison of the cycles in frond, inflorescence and bunch production in the density trial revealed a sequential increase in deviations from the means such that variation in the amplitude of inflorescence peaks exceeded that for fronds, while variation shown by cycles in bunch production was even greater (*Table 4*). Thus, there were successive increases in cycle amplitude at each stage of the developmental process.

Rates of Development

The fact that the cycles of frond, inflorescence and bunch production differed in magnitude and timing implies that there were variable rates of development at different stages. Indeed, individual inflorescences are known to develop at different rates (Chang *et al*., 1993; 1995; Lamade *et al*., 1998). As detailed records of development at individual nodes were not taken in the density trial, it was not possible to determine the time intervals between the separate growth stages.

If the period between the emission of a frond and the anthesis of its inflorescence were constant, then the more rapid the rate of frond emission the higher would be the frond number (using the conventional numbering system with the youngest fully expanded frond labelled as 1) and the lower its position on the palm at anthesis. This possibility was checked using quarterly data from two commercial field sites (Henson and Chai, unpublished). The results (*Table 5*) show statistically significant, though weak, positive correlations. However, the slopes of the regressions were insufficient for the variation in frond emission rate to account for more than 16% to 17% of the difference in frond number at anthesis. Hence, differences in rates of inflorescence development must have accounted for the remaining variation.

The above conclusion was further confirmed by analysing the unpublished data of Chang *et al.* (*Table 6*). With this data, it was possible to directly compare the two main alternatives likely to account for variation in frond position at anthesis; namely, the rate of frond emission and the rate of inflorescence development. The results clearly show that the former had little or no influence compared with the latter, thus supporting the conclusions drawn from *Table 5*.

TABLE 4. COMPARISONS OF MONTHLY MEANS, STANDARD DEVIATIONS AND COEFFICIENTS OF VARIATION IN THE RATES PER PALM OF FROND EMISSION, TOTAL INFLORESCENCE PRODUCTION, FEMALE INFLORESCENCE PRODUCTION AND BUNCH NUMBER PRODUCTION IN THE DENSITY TRIAL. DATA ARE MEANS FOR ALL DENSITIES; n = 52

	Frond emission	**Total inflorescence production**	**Female inflorescence production**	**Bunch number**
Mean	2.41	2.42	1.86	1.72
Standard deviation	0.31	0.53	0.64	0.68
Coefficient of variation (%): raw data	12.9	21.7	34.5	39.6
Coefficient of variation (%): de-trended data	8.4	19.9	26.4	29.0

TABLE 5. RELATIONSHIPS AT TWO COMMERCIAL FIELD SITES BETWEEN THE FROND EMISSION RATE AND THE NUMBER OF THE FROND SUBTENDING THE YOUNGEST ANTHESISING INFLORESCENCE NINE MONTHS LATER. DATA WERE DERIVED FROM QUARTERLY RECORDS

		Coastal	**Inland**
A. Sample size		972	568
B. Mean frond production per year		24.9 ± 3.88	25.7 ± 4.47
C. Mean frond number at anthesis		21.7 ± 2.00	20.7 ± 2.20
D. Mean interval from frond emission to anthesis (days)		318	294
E. Regression of C on B:	slope	0.125	0.120
	intercept	18.58	17.63
	r^2	0.058	0.059

TABLE 6. RELATIONSHIPS BETWEEN (a) FROND NUMBER AT ANTHESIS AND FROND EMISSION RATE AND (b) FROND NUMBER AT ANTHESIS AND DAYS FROM FROND EMISSION TO ANTHESIS

a) Frond number at anthesis and frond emission rate

A. Mean frond number at anthesis	18.19 ± 2.33
B. Mean frond production per year	28.01 ± 11.28
C. Regression of A on B: slope	0.004
intercept	18.08
r^2	0.0004 (ns)

b) Frond number at anthesis and interval (days) from frond emission to anthesis

A. Mean frond number at anthesis	18.19 ± 2.33
B. Mean interval (days) from frond emission to anthesis	250.6 ± 34.6
C. Regression of A on B: slope	0.375
intercept	8.79
r^2	0.309***

Note: Data were derived from records made at 10-day intervals on 20 palms at an inland site near Serdang, Selangor from 1989 to 1993*; n=1524; significance level is indicated: ns = not significant at *P*<0.05; *** = significant at *P*<0.001.

Source: * Original data sourced from Chang, K C.

External Control of Yield Cycling

The environmental factor most likely to give rise to yield variation in the lowland tropics is the soil water supply, as evident from the pronounced yield cycles usual in regions with severe and regular annual dry seasons. Even the generally much less severe dry periods in Southeast Asia can affect yields (Turner, 1977) with marked yield declines following drought exhibiting lags consistent with effects on inflorescence abortion and sex ratio. Statistical models (*e.g.* Chow, 1988; 1991;1992; Dufour *et al.*, 1988) that incorporate rainfall as a variable affecting short-term yield variation have frequently demonstrated statistically significant relationships using lag periods consistent with the impact of drought at physiologically sensitive stages. However, while drought events of sufficient intensity undoubtedly affect yields and may impact on yield cycles, they do not explain the regular annual cycles such as seen in the present study where drought as such was absent and palms had the benefit of a continuous water supply from the near-surface water table. Furthermore, yield cycles are still apparent even when a good soil water supply is maintained by irrigation (*e.g.* Chan *et al.*, 1985; Chang *et al.*, 1988; Kee and Chew, 1993; Foong and Lee, 2000).

It is probable that factors associated with dry conditions other than the soil water supply, such as high temperature, high atmospheric vapour pressure deficit and high evaporation rate, might be involved in yield cycling. Such factors would correlate with rainfall. Thus, although rainfall and soil water supply in the density trial were generally not limiting, there were regular annual fluctuations in rainfall and in the depth of the water table (Henson and Mohd Tayeb, 2003). In this trial, as well as at the coastal site referred to previously (which also had a permanent water table within rooting depth), there were significant positive correlations between yield and the concurrent depth of the water table (*Figure 12*). Both the rainfall and water table depth showed regular though inverse annual oscillations that either matched or mirrored the yield peaks.

Similarly, annual variations occur in solar radiation and evaporation rates. *Figure 13* shows that it is possible to match such variations quite well to those of annual yield using appropriate lags. While these relationships may not be causal they do demonstrate that annual climatic changes of sufficient magnitude and regularity do occur which could drive or entrain the yield cycles. However, the nature of the yield-determining process(es) affected by such external factors remains unclear.

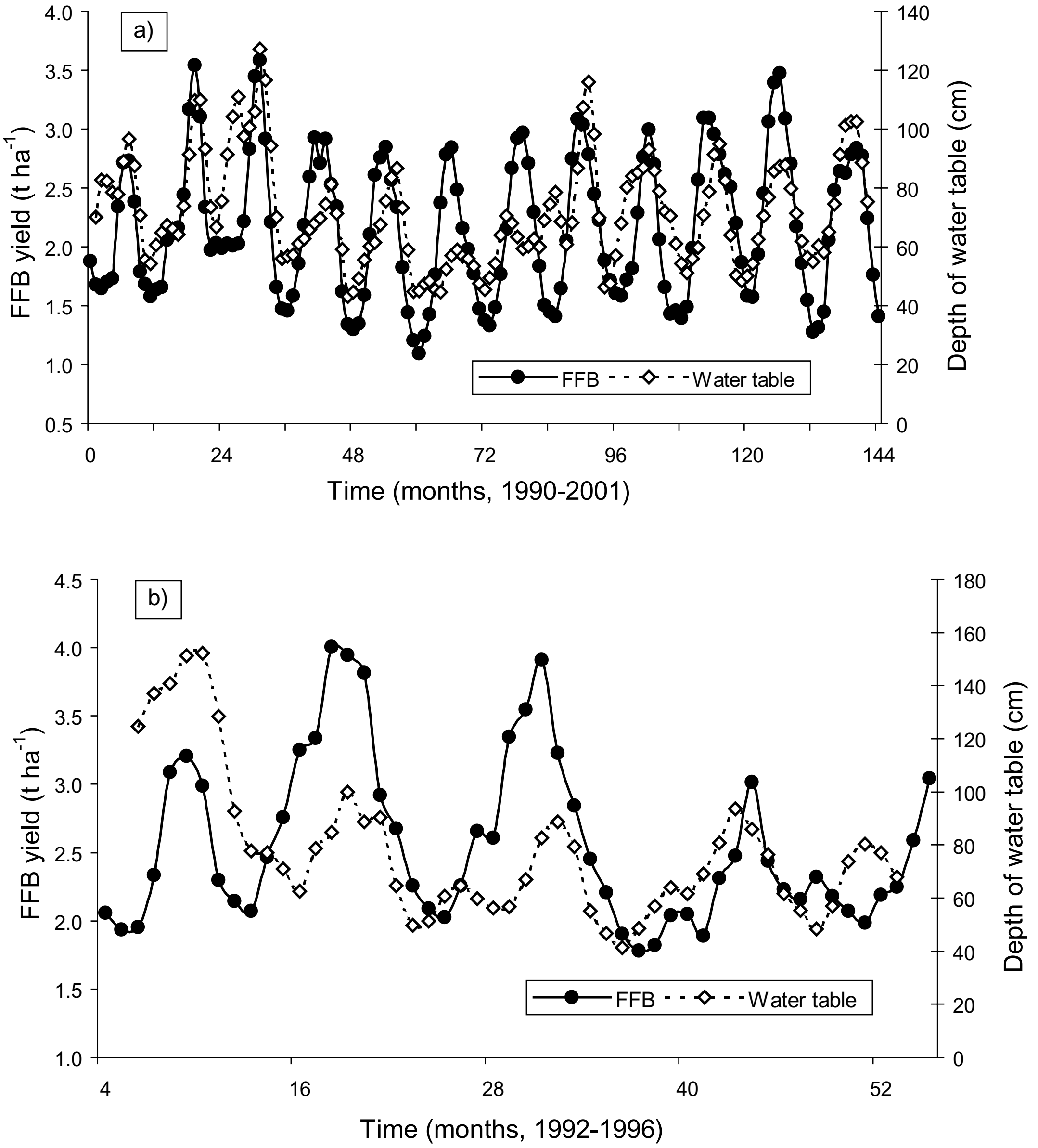


Figure 12. Monthly variation in fresh fruit bunch (FFB) yield per hectare and water table depth (both as running means; n=3; (a) for palms in the density trial (means for all densities) and (b) for palms on a coastal site. For (a), the coefficient of correlation between FFB yield and water table depth was 0.64, significant at P<0.001, while for (b) the correlation was 0.312, significant at P<0.05.

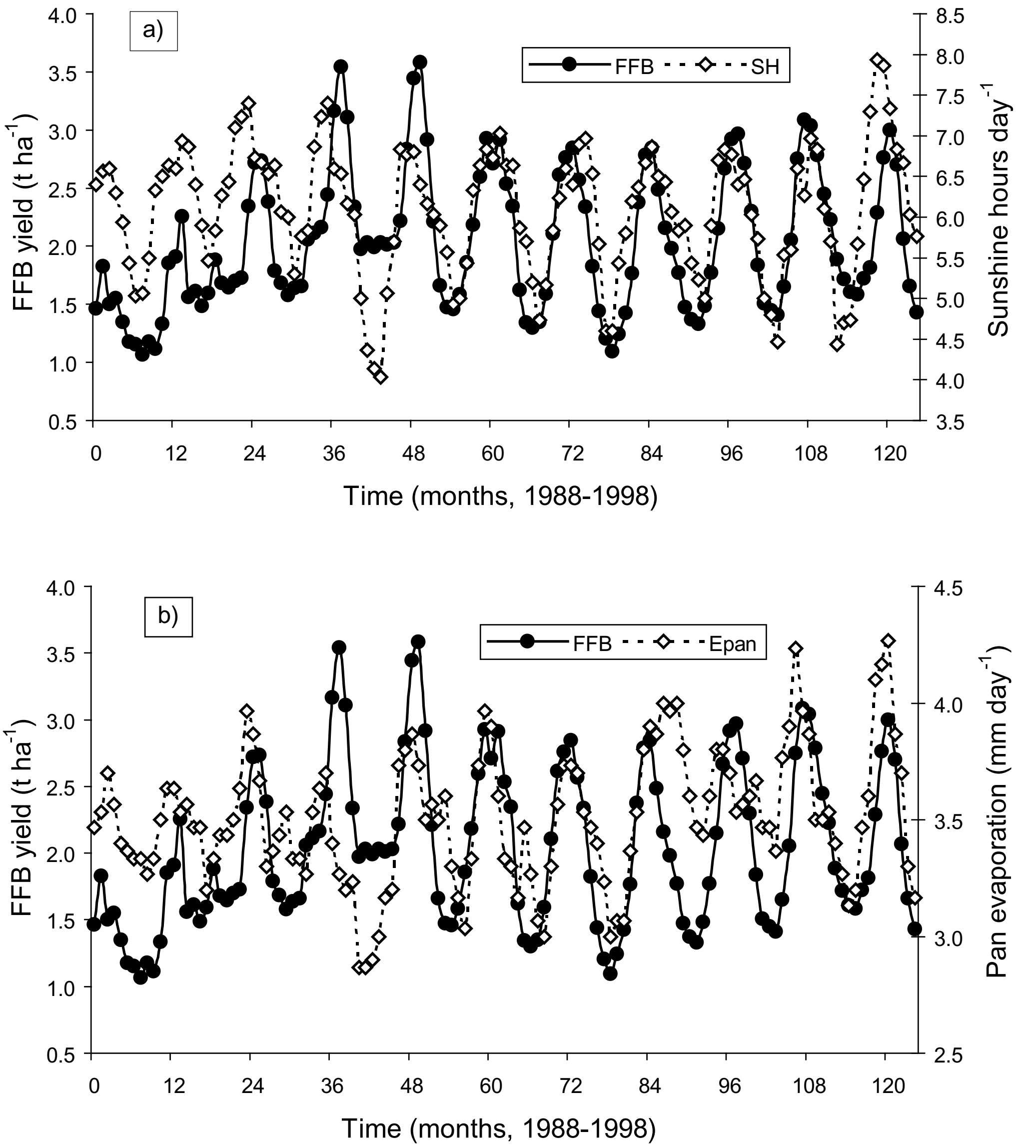


Figure 13. Monthly variation in fresh fruit bunch (FFB) yield per hectare for palms in the density trial and (a) mean daily sunshine hours (SH) three month earlier, and (b) mean daily pan evaporation (Epan) three months earlier. All data are running means (n=3). SH and Epan data were recorded at Hilir Perak, approximately 10 km from the trial site. For (a), the coefficient of correlation between lagged FFB yield and SH was 0.557, while for (b) the correlation between lagged FFB yield and Epan was 0.487. Both correlations were significant at P<0.001.

Endogenous Control of Yield Cycling

Yield cycling in oil palm has also been viewed as a manifestation of internal feedback mechanisms whereby a current high yield leads to a future low yield and *vice versa*. The prevailing bunch load (fruiting activity or BDMP) may regulate sex differentiation, abortion and future bunch development influencing both the number and mean weight of subsequent bunches. There is both experimental and statistical support for this idea (*e.g.* Corley, 1977; Chow, 1988; Corley and Breure, 1992; Breure and Corley, 1992).

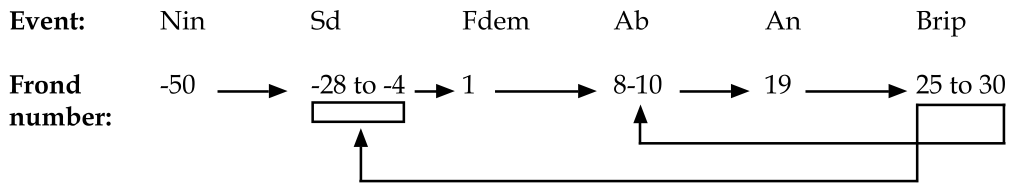
While such a mechanism could result in perpetual cycling, there are problems reconciling the annual yield cycles found with the much longer lag periods likely to arise from internal feedback loops (*Table 7*). Using the most probable timings suggested by Corley and co-workers, an abortion-controlled cycle would have a full (peak-to-peak) cycle length of around 16 months while a cycle dependent on changes in the sex ratio would have a full cycle length of at least 30 months. Furthermore, the length of such cycles would be expected to alter as the palm ages and the frond emission rate gradually declines. Such cycles would need to interact and overlap to give rise to annual peaks. Although the phase of the yield cycle can be shifted following treatments such as disbudding (presumed to operate via bunch load), such phase shifts are transient and apparently *reset* by external factors.

TABLE 7. (a). STAGES IN OIL PALM INFLORESCENCE DEVELOPMENT AND POSTULATED INTERNAL NEGATIVE FEEDBACK LOOPS

	Developmental events					
	Node initiation (Nin)	**Sex determination (Sd)**	**Frond emission (Frd em)**	**Abortion (Ab)**	**Anthesis (An)**	**Bunch ripening (Brip)**
Frond number	-50	-28 to -4	1	8 to 10	19	25 to 30
Months before bunch maturity	40	18 to 29	15	10 to 11.5	5.5	2.5 to 0

	Feedback loops	
	Inflorescence sex determination	**Inflorescence abortion**
Probable half-cycle length (months)	15 to 27	7.5 to 8.5
Full cycle length (month)	30 to 54	15 to 17

TABLE 7. (b) DIAGRAM OF POSTULATED FEEDBACK LOOPS



Notes: Development times, in months, assume that two nodes are initiated per month. Cycle lengths are calculated assuming that negative signals originate from developing bunches starting around Frond 25. Based partly on Corley *et al.* (1995) and Jones (1997).

The abortion rates (*Figure 10*) were generally too low in the density trial (their annual peaks varied from 1.6% to 13.2% of total inflorescences) to have influenced the yield cycling and although any changes in the sex ratio would have contributed to yield variation, the annual yield peaks were apparent (*Figure 2*) well before any sex ratio cycles (*Figure 9*).

It was hoped that by examining the cycles of different plantings, it might be possible to evaluate the relative importance of environmental as opposed to internal regulation of the cycles. The results of this approach (*Table 1*) were not conclusive though the time of first harvest did not appear crucial for the development of the subsequent cycles. More such comparisons are needed, preferably involving adjacent areas of the same materials planted at different times of the year.

CONCLUSION

There seems to have been little progress made in understanding the nature of yield cycles in oil palm since the review of Corley in 1977. Major conclusions reached by Corley and later at a joint PORIM/ MPOGC meeting in 1985 (Anon, 1985) are still largely valid today. These, and additional findings can be summarised as follows:

i) oil palm yield normally exhibits an annual cycle with one major peak and trough per year;

ii) the yield cycles in West Africa are largely a response to the severe dry season;

iii) yield cycles still occur in regions lacking a dry season, even at sites with abundant rainfall and in locations with a continuous ground water supply;

iv) consistent with (iii) is the finding that irrigation does not eliminate, nor greatly reduce, yield cycles;

v) meteorological variables other than rainfall also display annual cycles and so could potentially regulate the yield cycles;

vi) the phase of yield cycles can be shifted by treatments such as frond removal or disbudding (inflorescence removal) though the effects are often transient;

vii) the phase of cycles can vary with both location and planting material;

viii) while there is evidence for internal control of future yield by the current yield, the annual cycles are too regular to be accounted for solely on this basis;

ix) interaction between the internal and external factors with the latter *entraining* the endogenous cycles is often suggested but we are still no further forward in understanding the mechanisms or identifying the external controlling factor(s); and

x) variation in the rates of frond emission and in inflorescence and bunch development could account for yield cycles independently of, or in concert with, cycles in abortion rate and sex ratio.

The data presented support the idea that variation in the inflorescence development rate plays an important role in yield cycling. This was realized by Corley (1977) and has since been confirmed in detailed studies (Chang *et al.*, 1993; 1995; Lamade *et al.*, 1998).

Corley (1977) and Chang *et al.* (1995) suggested that yield cycles may be related to the incidence of abortion periods. From their results, abortion appears to be a culmination of a progressive slow-down in inflorescence growth, while following an abortion phase there is a *flush* in growth of anthesising inflorescences. The latter phenomenon could largely explain the peaks in inflorescence numbers. Even in the absence of abortion or with abortion at low levels, as in the present trial, so-called sub-abortive periods could occur (Chang *et al.*, 1995) during which growth slows but the inflorescences survive. These could lead to similar, though perhaps less extreme changes in inflorescence peaks. By postulating an annual cycle in inflorescence development rate it was possible, using a simple model, to reproduce essentially the yield cycles seen at Teluk Intan (Henson, 2004). Again, however, the extent to which, and how, internal versus external factors control such behaviour remains an open question.

Further effort is thus required to resolve these long standing issues. The nature of the environmental signal(s) controlling the cycles is difficult to resolve simply from correlation exercises. This is firstly because most, if not all the climatic variables [*e.g.* rainfall, radiation, temperature, atmospheric vapour pressure deficit (VPD)], are themselves interrelated and tend to exhibit similar annual variation and cycles. A study of some integrative measure of the environment which imposes stress on the palm rather than the individual climatic variables may be more useful. One example is the evapotranspiration (ET) rate which depends on, and so reflects, changes in radiation, temperature, VPD, wind speed and rainfall. While pan evaporation, which is recorded at many meteorological stations, can be used as a proxy for this, it is only an approximation for actual ET. A more refined approach is to use the ratio between actual and potential evapotranspiration (ET/PET). Low ET/PET ratios indicate greater stress, as the palm is increasingly unable to meet the atmospheric demand for water vapour. Unfortunately, determination of this ratio requires detailed on site measurements while the limitations of the correlative approach would still remain.

Finally, simulation modelling is an additional tool for achieving better understanding of yield cycling. However, previous mechanistic models (Gerritsma, 1988; Jones, 1997) had limitations and did not account fully for the observed trends.

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