EcoPalm: A New Model Simulating Seasonal Variation of Oil Palm Yield

I. Day length sensitivity of flowering and competition among sinks explain bunch number.

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Abstract

Seasonal variation of fresh bunch production is difficult to explain and predict. A population scale model, EcoPalm, was developed to explain those using new physiological hypotheses. A central hypothesis was that day length influences time of flowering during a photosensitive period (PSP) at the scale of individual fronds (phytomers). The variable PSP duration between successive phytomers result in a queue of phytomers in "waiting state", which partly explains seasonal variations. The monthly, potential number of harvested bunches, based on a 100% sex ratio, and the absence of abortions and failures of fruit set, was simulated. The second hypothesis was that sex ratio, intensity of bunch abortion and bunch failure, , depend on the trophic status of a given phytomer during sensitive phases of its development, expressed through a plant-scale Index of Competition for assimilates (Ic), which is the ratio between instantaneous assimilate supply and aggregate demand. Annual demand for vegetative organ growth was assumed to be constant (stabilized growth). Bunch dry matter production was assumed to be variable. If Ic < 1 during sensitive stages of bunch development, (high competition among sinks), sex ratio was considered to be low and abortion and bunch failure high. If Ic > 1, sex ratio was high. The 3rd hypothesis was that resulting sink-source imbalances are buffered by stem carbohydrate reserves. If Ic > 1, demand was not down-sized and excess assimilates were stored (overflow model). If Ic < 1 reserves were mobilized. The model was tested on a multi-annual period in La Mé (Ivory Coast) on a control progeny, LM2T X D10D. Sensitive periods to Ic were adjusted by optimization of parameters using evolutionary algorithm method. The PSP occurs at the early stage of development of phytomer, begin 36 months before harvest (mbh) and ends 28 mbh. The sex determination is very complex and occurs during PSP. The initial sex ratio of palm population was determined by mean Ic from nearly 34 to 28 mbh and the last month a second phase increases sensitivity to low Ic. This sexualization phase ends with PSP. A first stage of abortion is founded 17 mbh (frond emergency). A second stage of abortion occurs from 10 to 8 mbh. The model shows good monthly and annual simulations of bunches number harvested by ha at La Mé station. Validations at sites in Indonesia are in progress. Other model features including simulation of oil production and impacts of drought are presented in subsequent papers.

Introduction

A major scientific challenge that has evolved during the past decade is to understand, simulate and predict the seasonal variations of bunches production in the oil palm plantations. In Ivory Coast, the monthly yield of fresh fruit bunches (FFB) vary from 0.05 to 0.2 t ha^{-1} month^{-1} in July August and September, to 2.5 to 6.6 t ha^{-1} month^{-1} in March and April for L2T x D10D material. Several consequences for oil palm industry and organization of plantations are induced by the relative level of maximum monthly production. This drove numbers of authors to try to simulate this production according to environment and climate.

Early modelling attempts simulated annual FFB production, which varied from 9 to 22 t FFB ha^{-1} year^{-1} in Ivory Coast and from 6 to 26 t FFB ha^{-1} year^{-1} in Indonesia using statistical models (Ong 1982, 1983). Dufour *et al.* (1988), showed the importance of (1) water stress at different sensitivity stages from 1 to 45 months before harvest, (2) efficient solar radiation. The second generation is represented by canopy assimilation models. OPSIM model was implemented by Van Kraalingen (1985), van Kraalingen, Breure & Spitters (1989) on the base of SUCROS model (van Keulen 1982). OPSIM run under ideal situation without any stress and had no water balance module. Dufrêne (1989) introduced a semi empirical water balance in the development of SIMPROD. In this model, growth rate of different vegetative parts can vary independently. For these two models, photosynthesis, growth and maintenance respiration as well as the carbon balance are well quantified. Partition coefficients are deduced from observations. The excess of assimilates, after partition to vegetative growth, are affected to a pool of carbohydrates and converted at the end of the year to FFB production.

Several tentative where made to modify these models to operate at monthly step (Henson 1997) and to explore alternative mechanisms explaining seasonal variation (Henson 1999). Nevertheless, seasonal variations are still now largely unexplained (Henson 2004).

The determinism of this seasonality in oil palm production is very complex. The variation of the components of carbon balance could be of less importance than the components of phenology and inflorescence development. The principal cause of variation of FFB production is the number of bunches (scale 1 to 30). In adult palm plantations there is also a smooth seasonal variation of mean bunch weight (scale 1 to 3).

Underlying hypotheses of the EcoPalm model

The EcoPalm model presented here tries to explain these variations for L2T x D10D material under Ivory Coast environment, and to determine the different sensitive phases. It breaks down phytomer development, which takes over 3 years, to different phenological phases during which yield components are set through specific processes (sexualisation, abortion, bunch dimensioning and filling). These processes constitute environment sensitive phases, affected by photoperiod or assimilate availability. Since many phytomers develop at the same time but all have different developmental stage at any given time, the simple unitary phytomer model translates into a complex system at the aggregate plant level. These are the innovative components of EcoPalm. Carbon balance which is similar to previous models and the simple water balance from SARRA-H crop model (Dingkuhn *et al.* 2003) are not presented here.

In EcoPalm, adult palm plantations (10 to 20 years old) are assumed to have constant Leaf Area Index (LAI) and constant mean annual vegetative dry matter production (VDMP). But monthly VDMP could be reduced by water stress. Annual leaf emission is thermal time driven and roughly constant for one site under tropical-humid climate but depends on genotype Assimilate demand for individual bunch filling is adjusted in several steps during phytomer development, but the filling process is assumed to take place during the month preceding harvest (bunch maturity). This is a simplification because bunches are growing during 10 months, although the last month exerts the strongest demand because of oleosynthesis.

Sensitivity to day length: EcoPalm simulates potential bunch number assuming 100 % sex ratio (all female) and absence of inflorescence abortions. Potential bunch number per month depends on the frequency of leaf (phytomer) initiation, corresponding to 1 plastochron. Plastochron is assumed to be constant in terms of thermal time and translates into constant phyllochron (time elapsing between emergence of two successive leaves). This, in fact, is a simplification because drought is known to delay leaf appearance and expansion, and effect that is subsequently compensated during recovery.

Assuming that organ production rate is a measure of development rate, it is possible to evaluate from Henry (1957) the base temperature (*Tbase*) equal to 16.25 °C. But Ferwerda (1977) showed that Tbase might be could be lower. So optimal values are search by optimization. The thermal time between the initiations of two successive phytomers (plastochron) is calibrated on the basis of observed, mean, annual leaf emissions and the thermal time computed from climate and the cardinal temperatures as described above. We found a plastochron of 234 degree days. The seasonal variation of temperature induces a slight variation of number of leaves initiated every month.

The exact time of leaf initiation is unknown, but it occurs before the youngest leaf primordia, visible by dissection and electron microscopy. It occurs at rank -50 to -60, corresponding to 50 to 60 plastochrons before leaf appearance (Corley and Tinker 2003). Thus, leaf initiation can be estimated to happen on average 48 to 50 months before harvest.

The number of bunches harvested per month is sometimes much higher than the maximal number of leaves (or phytomers) that can be initiated per month. We explain this phenomenon by a photoperiod sensitive phase (PSP) during inflorescence development, which delays floral initiation if day length is unfavorable. This sensitivity would operate at the phytomer level and not the whole plant level. Consequently, the total duration between leaf initiation and flowering of the inflorescence on the same phytomer would vary according to day length during PSP. Thus, in a given month, the number of

flowering inflorescences can be smaller or larger that the phytomer number developed per month, but these differences even out at the scale of a year (accordion principle). In fact, during peak periods of bunch maturity (ca. 5-6 months after flowering), several bunches of different rank can be harvested in one month. The same phenomenon is observed for photoperiod sensitive cereals if planted at different sowing dates but flowering at the same time (Dingkuhn & al., 2008). This concept was confirmed for oil palm in field studies by Legros & al.(2009). The peaks of harvest frequency induced by the accordion effect are observed in April-March in the northern hemisphere and in October-November in the southern hemisphere, which is in accordance with the photoperiodic assumption.

The index of internal competition (Ic) among all sinks competing for a common source characterizes the trophic status of the plant. It induces sexualisation of inflorescences and their facultative abortion at a later stage. The general EcoPalm concepts are close to those described for the EcoMeristem model (Luquet & *al.*, 2006) developed for cereals, which simulates organogenetic processes as they interact with assimilate supply. In EcoPalm, the various sinks are maintenance respiration (Rm), vegetative growth and the associated growth respiration (Rg), the growth of the inflorescences and bunches and the Rg, the latter being particularly high during the oil synthesis. The ratio of assimilate Supply / Aggregate Demand is measured with a state variable called *Ic* (index of internal competition). Values of *Ic* lower than one trigger adaptive adjustments in plant organogenesis and morphogenesis, resulting in phenotypic plasticity. In EcoPalm, only the inflorescence and bunch sink are assumed to be plastic. Three types of adjustments can occur with assimilation deficiency. (1) Initial sex ratio decrease resulting in more male, unproductive inflorescences; (2) abortion of inflorescences during sensitive phases; and (3) the individual bunch weight may be below its potential or even results in bunch failure in extreme cases.

Storage of assimilates When *Ic* is higher than one, the excess assimilates are reversibly stored as reserves. In turn, assimilate deficiency (*Ic < 1*) is partially compensated by reserve mobilization, associated with a cost coefficient for mobilization and transport.

The potential demand for reproductive growth is the product of potential bunch weight with the number of bunches that are filled in one month. If there is assimilate deficiency during fruit filling, reserve mobilization buffers some of the deficit but bunch yield decreases to some extent, depending on the choice of coefficients for the management of carbon reserves.

Description of EcoPalm model

The model operates with two time steps, daily and monthly. The water balance and the carbon balance are implemented at daily time step using daily meteorological data as input. Phytomer initiation and phenology are also simulated at daily resolution. For all other processes, namely the growth of organs and the dynamics of the carbon reserve, the model works with monthly aggregation (sums or averages). The model is executed between two dates of simulation that must be many years apart and fall within the adult lifespan of a population. Six years of meteorological data inputs are needed situated before period to be simulated because the model, with its many internal feedbacks, needs to attain equilibrium before yield simulations become meaningful.

In a previous model version (Combres et al., 2006), all Ic-sensitive phases of phytomer development had a fixed duration of one month and Ic was computed at month step. In the model version presented here (EcoPalm V3), sensitive periods can begin and end any day, and Ic averages are computed between these two dates (fig. 2). The PSP duration is driven by day length including civil twilight. All other development processes are driven by thermal time.

Phenology

The time between the frond initiation and the harvest of the associated bunch is nearly 4 years. During this period the positioning of sensitive phases for yield component adjustments is poorly known, although Legros et al. (2009abc) recently provided some such information and also cited other authors for circumstantial evidence.

The PSP is assumed to begin when the accumulated thermal time from frond initiation reaches a critical value (*PrePPTT*). In the same way, the duration from the end of PSP to harvest time (bunch maturity) is set my by another critical value of accrued thermal time (*PostPPTT*). To compute the duration of PSP the model uses a very simple sub-model developed for short-day plants. Every day, if

day length (DL) is superior to a critical day length (*CritPP*), we calculate the effective photoperiod (*PPeff*) as $PPeff = Max\left(0.0001; f(DL) - f(CritPP)\right)$ The development speed (V) is the reciprocal of effective photoperiod $V = \dfrac{1}{PPeff}$.

The end of PSP (corresponding to. panicular initiation of cereals) arises when the accumulation of the daily speeds reaches a threshold (*PPThreshold*). The PSP calculation has four parameters that need to be calibrated s: *PrePPTT, CritPP, PPThreshold, PostPPTT*.

In a pre-run, the model assumes each day of the simulation like a day of frond initiation (large plot scale) and computes for each one the dates of beginning and end of PSP (fig.1) and the date of potential harvest (for female inflorescence). All of them are grouped by harvest month. For each harvest month the model determines the initiation period from the first to the latter leaf initiation date, and the PSP duration from the first day of beginning to the latter day of PSP end (fig. 2).

The cumulated thermal time during the initiation period divided by plastochrone give a number of fronds per ha (according to palm tree density) able to reach the harvest stage a same month. It's the potential number of bunches (*PNB*) if all inflorescences were female and if there were no abortion.

In the same way the model computes the dates of beginning and end of each sensitive phase to Ic (fig.1). Each one if characterized by two threshold of cumulative thermal time (1) from frond initiation (or end of PSP if after) to the beginning of the phase (*Ici DDS*) (2) from beginning to end of the phase (*Ici TTD*). Like for PSP all the dates are grouped for one harvest month and the model select the first date of beginning of the phase and the last date of end of the phase. Ic is computed between this two dates. Four sensitive phases of inflorescence and bunches development could be simulated. The first one determines the initial sex ratio. The three others further reduce the sex ratio or cause abortions of entire female inflorescences if carbohydrate supply during the sensitive phase is poor (low Ic). It is important to note that sensitive phases are implemented phytomer specifically, for many phytomers developing at the same time but having different developmental stage; and that Ic-induced adjustments of yield components during the sensitive phases impact on actual assimilate demand much later at the time of filling.

From the first day of simulation to nearly 4 years, the model is unable to simulate PNB because it takes almost 4 years for a phytomer to terminate its development. But it is necessary to approximate PNB to estimate Ic (chicken-and-egg problem). For this reason, simulations must start 6 years before the period under study, initially using default values for missing information, enabling the simulation process to gradually generate physiological equilibrium and appropriate response to climatic variation. This inconvenience is the nature of a system that has internal feedback loops involving long (multi-annual) lags.

Algorithms for Ic impacts on yield component

Comparative performance studies of different algorithms indicated that Ic should not impact proportionally on a process (e.g., Ic = 0.5 causing 50% abortions) or through a broken-stick law as frequently used by modelers, but through a power law (using parameter *IciWF* as exponent) that can assume concave, linear or convex responses depending on the parameter value. Each sensitivity phase has a new parameter *IciWF*.

The initial sex ratio *(ISR)* could be decrease (*$Ic_1 < 1$*) or increase (*$Ic_1 > 1$*) from a mean value (*$Ic_1 = 1$*). It is simulated as $ISR = A * Ic_1^{Ic1WF} + B$

ISR, multiplied with the potential bunch number (PNB) for the month, sets the initial number of female inflorescences. Thereafter, during the three other Ic-sensitivity phases, the number of effective female inflorescences is further reduced by applying an Ic-dependent coefficient less than 1 calculated using a similar principle. The survival rate (*S_i*) is $S_i = min(1, Ic_i)^{IciWF}$ and the abortion rate is $AR_i = 1 - S_i$

The final number of bunches (*NB*) harvested in a given month is therefore:

$$[NB = PNB * ISR * S_2 * S_3 * S_4]_{month}$$

Components of Ic

Ic has four components (1) the gross supply (GS) from photosynthesis (2) the demand for maintenance respiration (MR) (3) the vegetative growth demand (GD) that includes Rg, and (4) the reproductive demand (RD) including Rg. They are all expressed in kg CH_2O ha^{-1} day^{-1} In the simulation process data for these 4 components are stored for each day. This permits calculating assimilate demand during bunch filling from the phytomer's history using the following equation

$$Ic_i = \frac{\sum\limits_{beginningdate}^{enddate} GS}{\sum\limits_{beginningdate}^{enddate} MR + \sum\limits_{beginningdate}^{enddate} GD + \sum\limits_{beginningdate}^{enddate} RD}$$

GS is computed from solar radiation (Rs) converted in photosynthetically active radiation (PAR). PAR absorption is computed from Beer's law with constant leaf area index (LAI) and extinction coefficient from Dufrêne (1989). This absorbed PAR is converted in kg CH_2O with a conversion rate coefficient (ConvRate). This potential GS is adjusted downwards under water deficit conditions using a calculated coefficient cstr that is a function of the fraction of transpirable soil water (FTSW). GS thus is:

$$GS = 0.48 * Rs * \left(1 - \exp\left(-0.41 * LAI\right)\right) * ConvRate * cstr$$

MR is assumed to be constant at 25 °C (*MaintResp*). It is calculated from standing biomass and biomass composition according to Penning de Vries (1989). The daily correction of *MaintResp* with mean temperature (*Tmean*) uses a Q10 = 2 law

$$MR = MaintResp * 2^{(Tmean-25)/10}$$

GD is estimated from mean growing fronds (*MGF*) using empirical values for final frond mass and duration of expansion, and similar information on trunk and root growth (Legros et al., 2009abc). Fronds grow during 7 months (from 20 to 14 mbh). The growth of fronds having a final dry weight of *FrondDW* requires 1.45 kg CH_2O per kg. Fronds constitute 52% of total vegetative growth (I. Mialet-Serra personal communication). Thus:

$$GD = MGF * FrondDW * 1.45 / 0.52.$$

RD is computed from the number of bunches (*NB*) the potential bunches fresh weight (*PotBunchFW*), water content (*BunchWC*) and the coefficient of conversion of DW to CH_2O (*TxGrResp*) particularly high because of the fruits' oil content.

$$RD = NB * PotBunchFW * BunchWC * TxGrResp$$

Experimental data

Production data come from experimental plot E70 of La Mé (Ivory Coast) research station (5.3 °N). Edaphic and climatic situation of this plot are described by Dufrêne & al (1993). Data are the mean value of 655 palm tree of the control progeny, LM2T X D10D from july 1983 to june 1992. . The plot had a population density of 143 palms ha^{-1} at planting date in 1973 Because of the subjectivity of harvest date, data were smoothened using floating averages. Smoothening method was Month = (0.5 Month -1 + Month + 0.5 Month +1) / 2. Climatic data are measured at the central meteorological station of La Mé and rain is measured near the plot E70. Data are available from 01/01/1973 to 30/06/1992.

Calibration method

The simulation platform EcoTrop that implements EcoPalm is linked with the R software (R Development Core Team 2005) using the Rgenoud package (GENetic Optimization Using Derivative) for statistical parameter optimization (W. Mebbane & J. Sekhon 2009).
The optimization interface allows selecting parameters to optimize and fixing bounds for parameters and critical state variables (i.e. phytomer maximum and minimum duration from initiation to harvest). These constraints are read by R and used by Rgenoud. Each individual of the population of parameter

values generated by Rgenoud is a vector of new values of selected parameters and is sent to Ecopalm. Ecopalm executes a simulation and send the results to Rgenoud which computes the cost function used to evaluate the fit. Between 30000 and 50000 simulations are necessary to find an appropriate and reproducible solution, requiring much computing time and power.

Five output variables are used to optimize (1) Monthly number of bunches (2) annual number of bunches (3) monthly mean bunch weight (4) monthly yield (5) annual yield. Because of different magnitude of these variables, the cost for each one is the NMSE (normalized mean square error) according to Kumar & al (1999). Rgenoud minimize the mean of the five NMSE. Optimizations were made against target files of actual production. Optimized simulation results were then compared with actual and smoothened data.

The two steps of optimization for PSP and sensitive phases
The model is parameterized to have no initial effects of sensitive phases (Ici =1) and 100% initial sex ratio. The initial number of bunches simulated is equal to PNB. A first optimization is made with only the 4 parameters of PSP and the 4 cardinal temperatures.
After the optimization of phenological parameters, the model is parameterized to have free action of Ic. The second optimization searches the parameters for the timing and intensity of Ic impacts on yield components.

Results and discussion

Positioning the PSP
Optimization of parameters for phenology gave the following values: PPcrit = 10.87 h; PPThreshold = 854; PrePPTT = 4188 degrees day; PostPPTT = 10345 degrees day; Tbase = 13.1; TOpt1 = 27.9; TOpt2 = 34.7; Tlim = 46.8 °C. The mean PSP begin 1095 days before harvest (dbh) or 36 mbh nearly 4 months after the initiation of inflorescence's meristem. It ends 826 dbh nearly 28 mbh (fig. 3). Its duration caused by seasonal day length variation varied from 275 to 320 days.

Time of sex differentiation and other sensitive phases
The time of initial sex differentiation was found to occur during PSP. It begins 34 mbh 2 months after beginning of PSP and ends 28 mbh like PSP (fig.3). At the end of sexualisation phase is included a second sensitivity phase Ic2 reducing the number of female inflorescences. This phase ends with Ic1 phase and PSP. These two sexualisation phases falling into PSP highlight the complexity of sex differentiation in oil palm.

We tried to convert the conventional industry term 'rank' into thermal time units using plastochrone, assuming mean harvest at rank 28. This was a mean value used for simplicity because bunch harvest in Ivory Coast occurred from rank 24 to rank 32.
We also tried to validate our phenological optimization results with dissections and electronic microscopy observations (Adam & al. 2005) made in Costa Rica on another genotype. The phase of differentiation of initial sex ratio begins at rank -27 with individualization of meristem's inflorescence and ends at rank -17. The second phase begins at rank -20 with initiation of spikelet bracts.

According to optimization results, a third sensitive phase acting on inflorescence abortion occurs between rank -2 and 0. This Ic3 probably represents the effect of water deficit if occurring before frond emergence

The fourth Ic-sensitive phase identified through model optimization is the well known stage of abortion 10 month before mean harvest (Legros et al., 2009abc). It begins at rank 10, when the inflorescence begins to growth and ends at rank 12 when growth becomes linear. Growth phases with very active cellular division are known to be sensitive to environment, translated in our model into variable Ic4, and thus causing phenotypic plasticity.

Outputs and performance of the model

Given the fact that the phenological parameters and parameters of timing of sensitive phases for yield components were optimized independently and without pre-conceived forcing, the results are

surprisingly coherent with the (limited) knowledge that we currently have on oil palm physiology and phenology.

The number of days between sensitive phases and the beginning of the harvest month is not constant because of changes of temperatures (fig.3). The variation could be as large as 2 months for phases after PSP and 5 months for those before (i.e. Initiation). This explains partially the variability of bibliographic results expressed in month before harvest.

The simulated, potential number of bunches (Fig. 4) was lower than the actual bunch number harvested only during 2 months out of 108 months (April 1987 and May 1991). But predicted potential bunch number was on all months higher than the observed, smoothened values. Probably the two cases of apparent underestimation of potential bunch number was due to inaccurate montly yield data, resulting from shifts in harvest date from one month to the next due to organizational constraints as they frequently occur on plantations. se two peaks are over estimated by transfer from one month to the other. In April 1987 plot E70 had higher number of bunches than neighbouring, similar plots. In 1991 April was the lowest observation in the 9 years and May the highest. Thus, in both cases, sampling artefacts are more likely to be blamed than the model. In fact, May is not the normal peak of production in Ivory Coast (April). The initial sex ratio showed large variations and must be close to 1 in April 1987 to simulate this peak (Fig. 5).

The model's simulations showed a good agreement with observations on monthly bunch number harvested (Fig. 4). The amplitudes of variation between months were generally well simulated. Nevertheless, there was a tendency to underestimate bunch number at the beginning of the simulation and to overestimate it the last 3 years. Perhaps the production of palms 19 years old began to decline due to age. This trend is particularly clear when comparing inter-annual, 12-month cumulated data and the corresponding simulated production (Fig.6)

Discussion

Despite many simplifications (i.e., constant LAI and fruit filling in one month) the simulation of monthly and annual variation of the number of harvested bunches was in good agreement with observed data. Although the model remains to be validated with independent data (which are hard to get by for an identical genotype), the ability of the model to simulate accurately both intra-l and inter-annual trends of bunch production is a significant result that was previously not achieved with other models.

The new hypothesis of photoperiod sensitivity of flowering in oil palm contributed much to this advance. Related experimental research published by Legros et al. (2009abc) provided further support for this hypothesis, based on different environments in Indonesia.

Physiological processes involved in source-sink relations and sink-sink competition for carbohydrates are complex. Our model's state variable Ic appears to be a suitable yet simple approach. However, it involves simplifications that are not necessarily accurate, namely the assumption that in a large and complex plant such as oil palm the daily assimilate reserve acts like a single pool, without preferential destinations caused by topological proximity. But it seems that our hypothesis of assimilate restrictions (be they caused by drought, variable solar radiation or periods of high internal demand) acting on adjustments of yield components is working well. This was demonstrated by the identification of reasonable timing of sensitive phases for sex determination and abortions obtained through a neutral optimization process.

The model gives a better understanding of the very complex phenology and sex determination of palms. It's also interesting to see how a given environmental stress can impact on production variations happening many months later, due to the long developmental lags in the physiological feedback loops. Again, this is consistent with Legros et al. (2009abc). This observation may open opportunities for predictive applications of the model because yield is in part pre-determined by growth history (principle of structural memory in a perennial plant that is accessible to simulation).

We did not present here other model calibrations for different biological materials, which show large genetic variation in parameter values that may be of interest to breeders.

Further papers will follow presenting EcoPalm's capacity to simulate oil yield, drought effets on phenology and yield, and genetic diversity in parameter values. Further research and model development is also planned to capture long-term phenology of the crop including the juvenile stage and production decline in ageing plants. More research are needed about thermal time, modality of action of day length and sensitivity to Ic.

Conclusion

This new, simple model of oil palm introduces several new hypotheses on the phenological and physiological causes of inter-annual rhythms of production and inter-annual variation of it. These hypotheses seem to have the potential of significantly advancing modelling and functional understanding of this complex crop. Data availability, both on environment (including climate) and the crop itself, is a major constraint in this research.

Acknowledgements

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Figures

Fig 1: Determination of the dates of beginning and end of each sensitive phase for each day of simulation. Beginning date is computed from date of initiation if Ic is before PSP and from date of end of PSP if later.
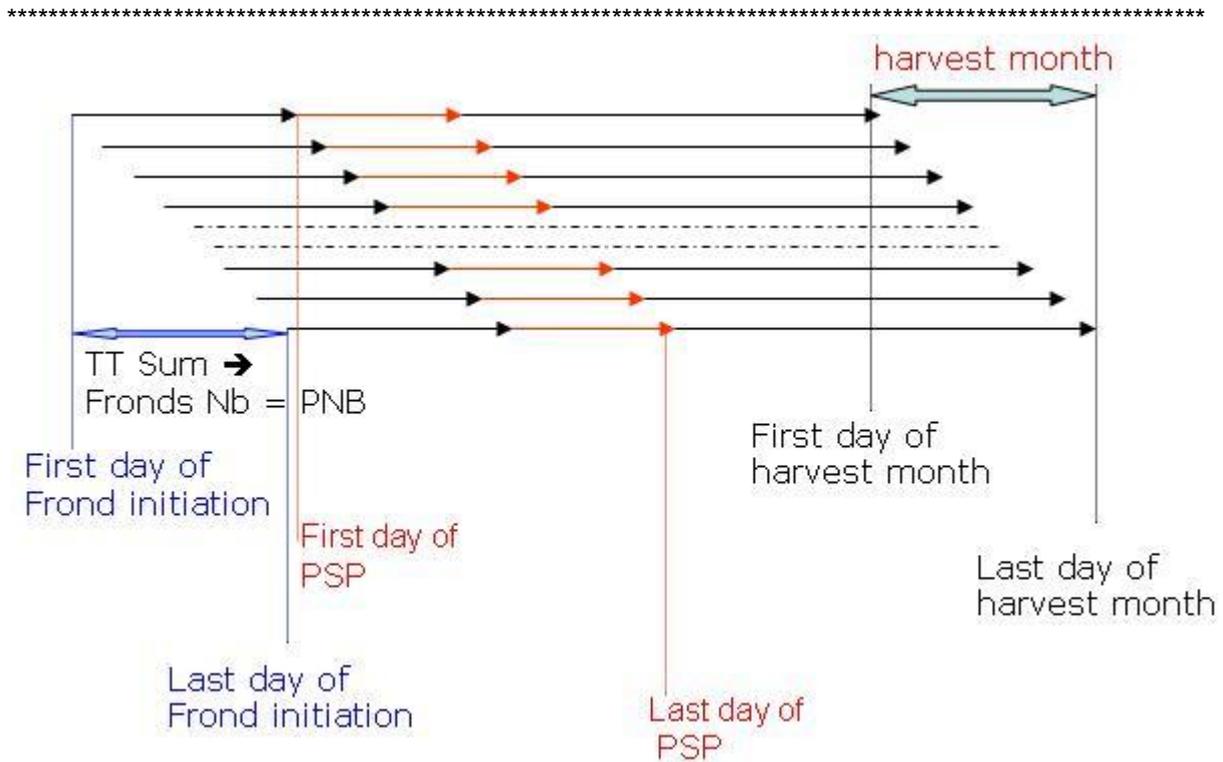
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Fig 2: all the dates of beginning and end of sensitive phases are grouped for one harvest month i.e. for PSP phase. The potential number of bunches is computed from the sum of thermal time from beginning to end of frond initiation for this harvest month.
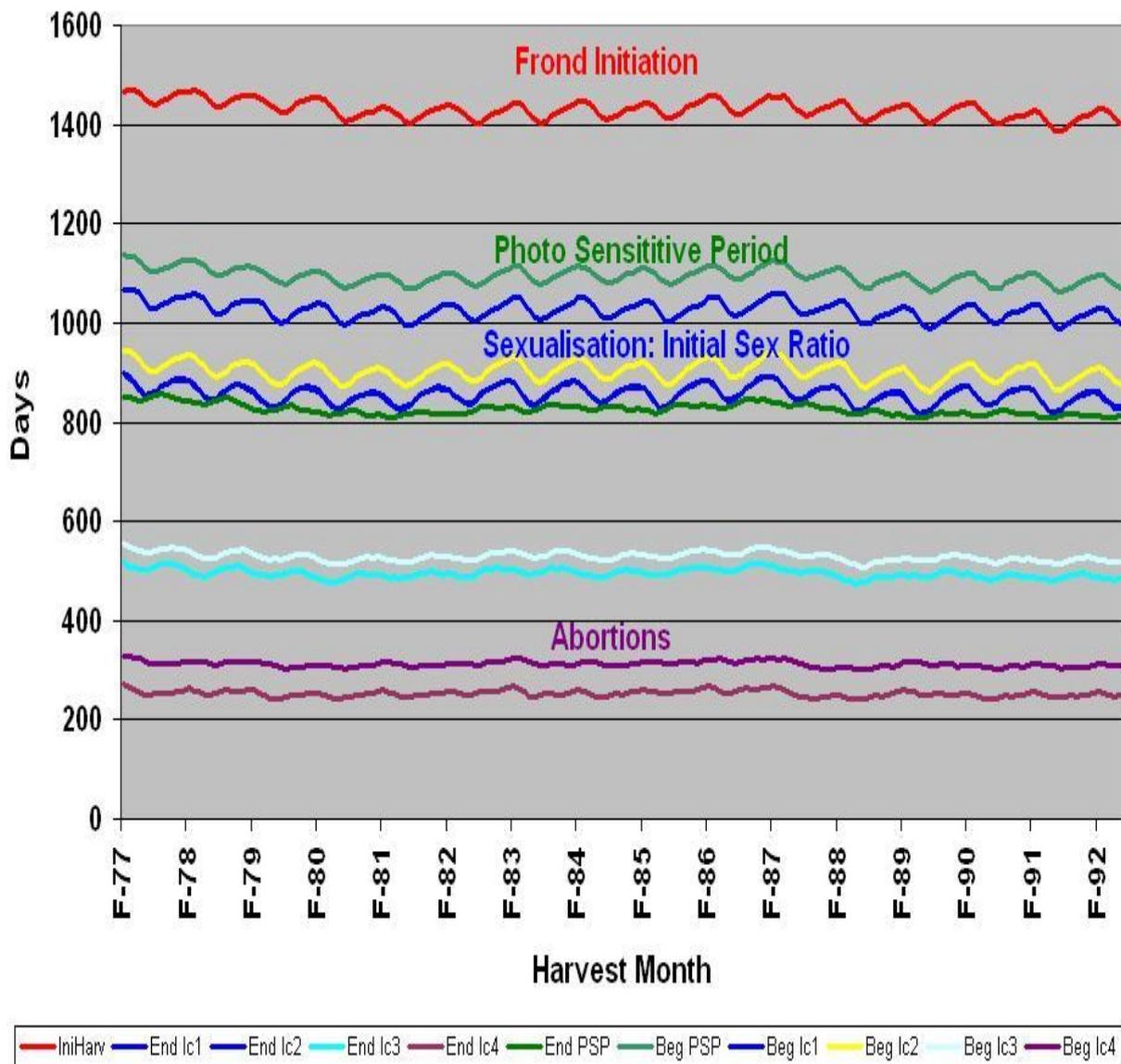
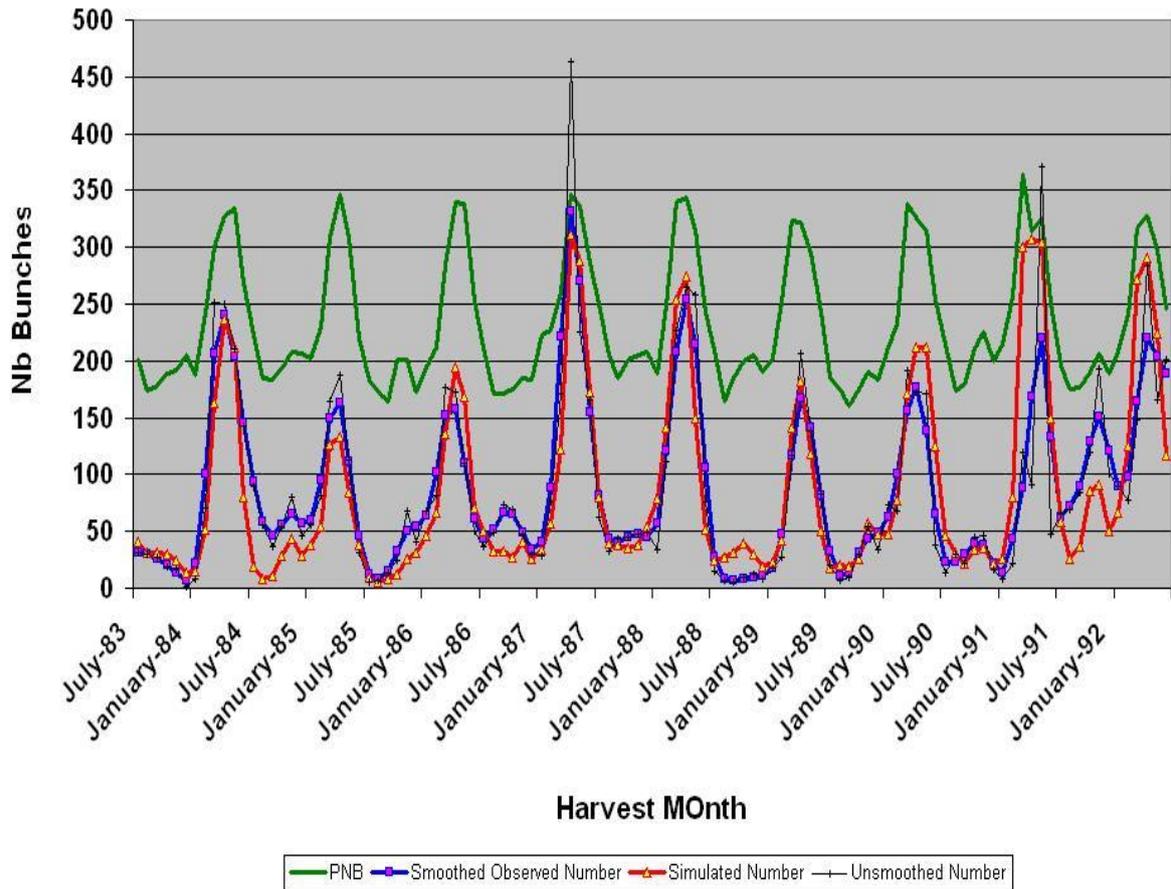Fig 3: Time between sensitive phases and first day of harvest

Fig 4: Potential number of bunches (PNB, green) number of simulated bunches (red) number of harvested bunches (blue and black)
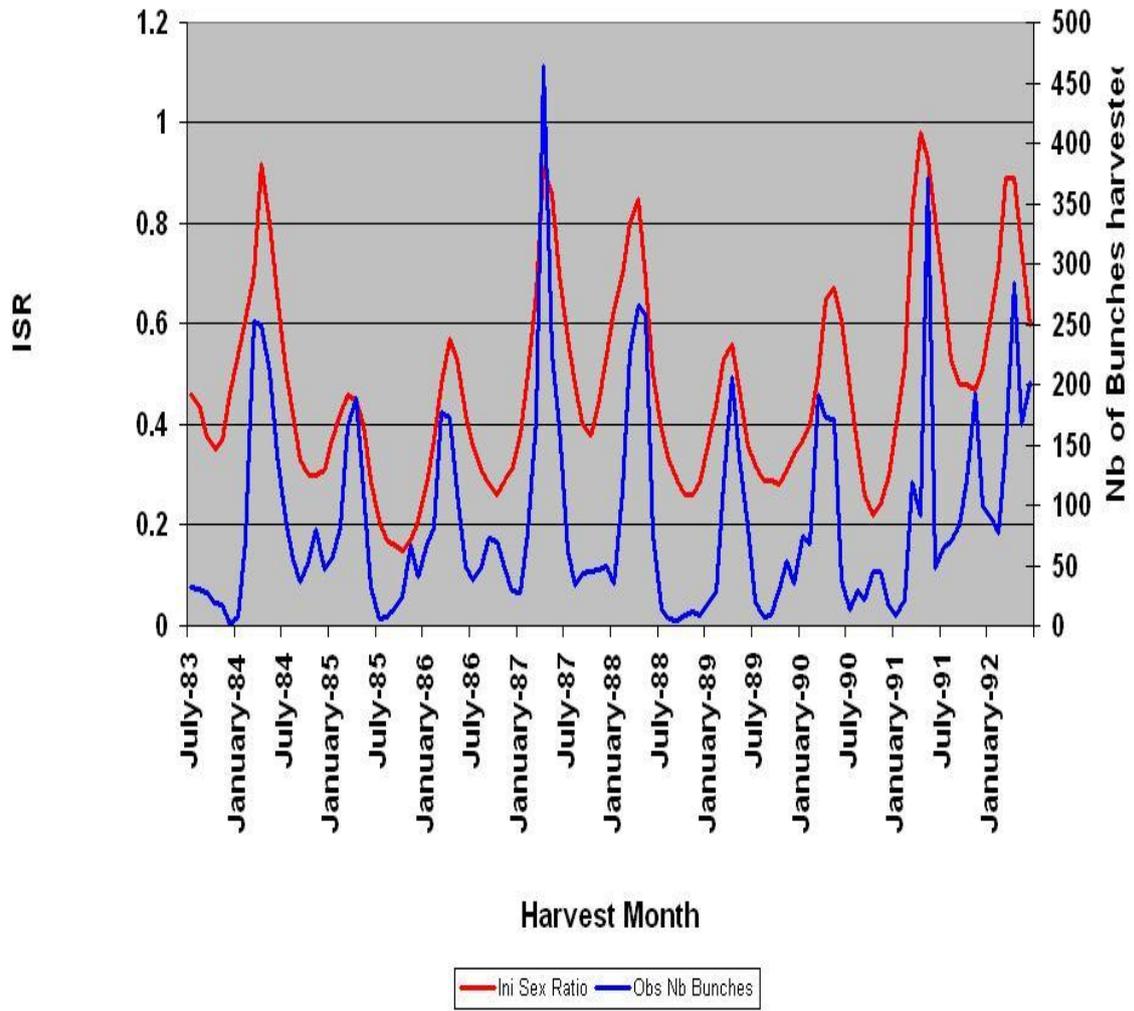
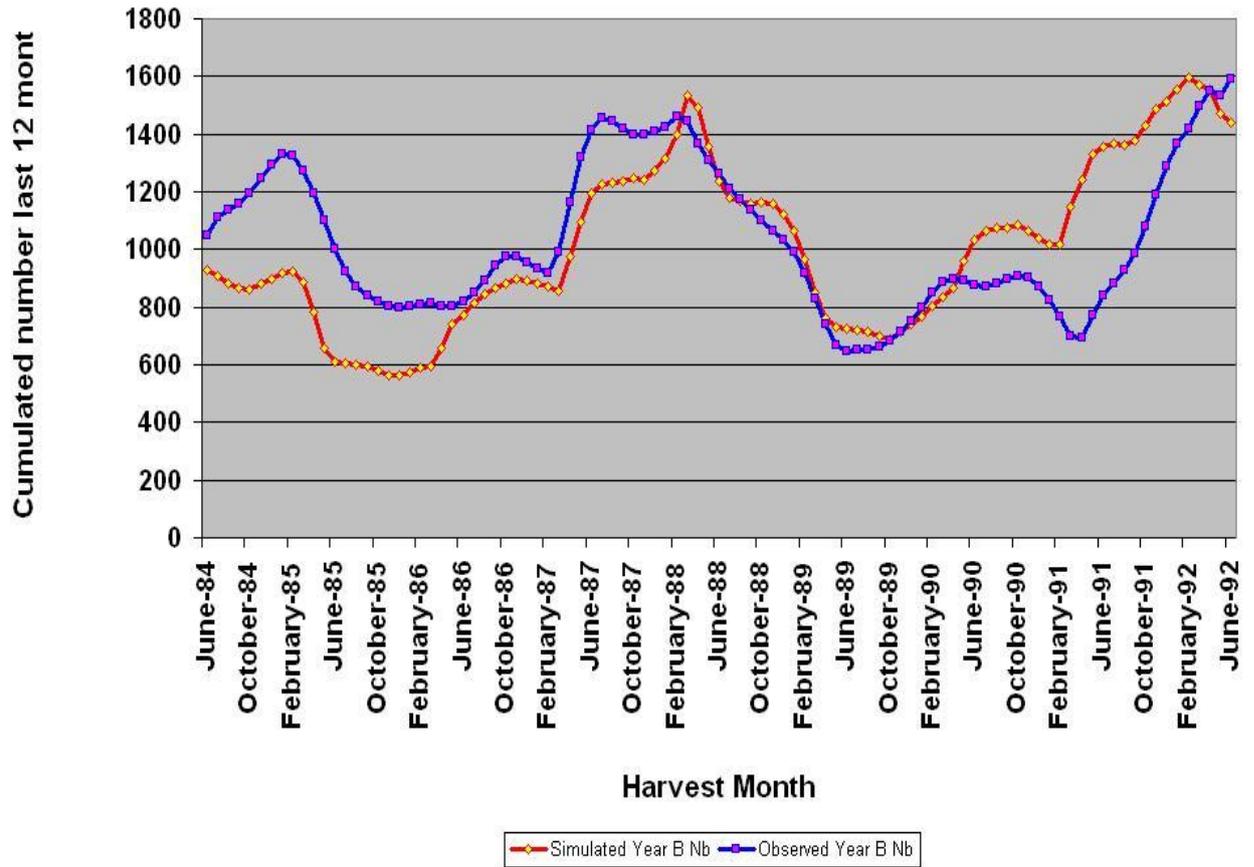Fig 5: Evolution of initial sex ratio (ISR) and number of harvested bunches

Fig 6: 12 months production of bunches simulated and observed