Model for the simulation of coconut growth and production

In order to understand and model the performance of palms under unfavourable trophic conditions, studies were carried out under a thematic research project entitled *Development of a physiological model integrating the architectural dimension of plants to simulate coconut growth and production*, in partnership with the Vanuatu Agricultural Research and Training Centre and the Philippine Coconut Authority's Davao Centre.

Methods

Various ablation-pruning treatments were applied (figure 1):
- ablation of bunches to limit carbon sinks and simulate optimum trophic conditions,
- frond pruning to limit carbon sources and simulate unfavourable trophic conditions,
- removal of part of the root system to assess the effect of edaphic limitation or trauma on root development.

These experiments were carried out at the same time over three years on 10-year-old VRD x VTT hybrids in Vanuatu and on 25-year-old local Talls (Laguna Tall) in the Philippines.

Observations were carried out on the organogenesis and morphogenesis of the palms in response to treatments, and on photosynthesis and hydric functioning on the scale of a frond (measurement of leaf gas exchanges) and of the whole palm (sap flow measurements) depending on climatic conditions.

Three-dimensional mock-ups of coconut palms were created as a support for simulating frond lighting and carbon assimilation.

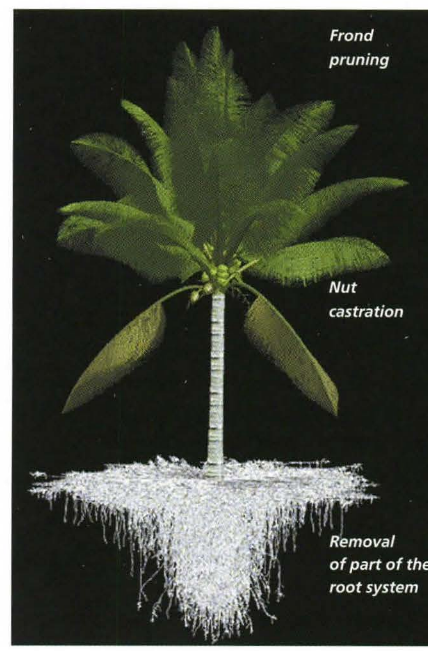


Figure 1. Treatments applied to the coconut palms.

All the results obtained served as a database making it possible to validate a simulated carbon balance based on observed growth results, and to analyse the allocation of resources for growth and production under different conditions.

Coconut palm architecture and light interception

The architecture of the palms was described in detail at the two trial sites, and was used to construct realistic three-dimensional digital mock-ups of the palms.

The digital mock-ups were positioned to reconstitute a plot in a coconut plantation and were used to simulate radiative transfers according to a MIR-MUSC model developed in earlier projects, particularly the STD3 project on *Functioning and evaluation of coconut-based intercropping systems*. The radiative simulations were validated using *in situ* radiation measurements carried out under coconut.

Changes made to the MIR-MUSC model during this project made it possible to integrate simulation of the photosynthetically active radiation (PAR) balance on a frond scale (figure 2a) and use of that balance for photosynthesis (figure 2b) and transpiration simulation, in the same software chain.

Photosynthesis and transpiration

An extensive campaign of gas exchange measurements was undertaken on fronds in Vanuatu to determine the response of leaf carbon assimilation to PAR, ambient CO_2 and temperature. These data were used to parameterize a Farquhar type model. The experimental results did not reveal any seasonal effect or frond rank effect on assimilation. Single model parameterization was adopted.

At the same time, stomatal conductance data (g_s) were used to establish a Jarvis type stomatal model integrating the effects of PAR, VPD (vapour pressure deficit) and temperature. Despite the low predictive value of the model, its integration within the assimilation model did not induce any major bias (figure 3).

Carbon assimilation was calculated on digital mock-ups (figure 2b) from simulations of frond lighting and the combined assimilation and stomatal conductance models (figure 2a). These assimilation calculations were carried out over a short time lapse of an hour or less, then integrated on a daily scale, in order to avoid bias linked to use of the mean lighting value.

Removing part of the root system did not induce any measurable drop in stomatal conductance. However, pruning lower fronds led to maintenance of stomatal conductance, and a higher level of photosynthesis than in the control during the dry season. This effect, which could be explained by the reduction in leaf areas consuming water resources, needs to be elucidated. The so-called Granier sap flow measurement method that enables overall measurement of tree transpiration, was adapted to coconut. The main difficulty consisted in evaluating the radial variability of sap conduction in the stem. Long sensors to take measurements at different levels in the stem were specially made for the study. The sap flow rate seemed to be largely constant over the entire radius. This result made it possible to precisely calculate the flow per palm and per day. The measurements taken were used to make an overall analysis of the response of palm transpiration to climatic conditions. They also made it possible to calculate the conductance of the cover, integrating overall variability in stomatal functioning on that scale. Cover conductance could be used directly in a model of plot transpiration depending on climatic conditions.

Palm growth in response to ablation-pruning treatments

The trophic regimes induced by the treatments affected both organogenesis (fronds, bunches, etc.) and growth. For example, it was necessary to take into account a period of 12 months between the initiation and emergence of fronds, then another period of 7 months for ripening. The ablation-pruning trials were therefore continued for three years, to allow the time for the coconut palms to stabilize their reserve compartments and the allocation of reserves per organ.

Aerial growth

For the nut compartment, exponential curves were obtained for the relation between dry matter and circumference in the controls, from rank 9 to rank 15 (young nuts). For the following ranks, the circumference no longer varied, unlike dry matter, which increased steadily, stabilizing from rank 20 onwards. The increase in nut dry matter could therefore be simply estimated from their circumference, their rank, the dry weight of ripe nuts, and the bunch emission rate.

Nut growth potential was attained when the sinks were reduced—limitation of the number of nuts—while leaving sources intact. The maximum potential nut weight observed was higher than normal: 55 cm circumference as opposed to 45 cm for the controls. The daily increase in the nut compart-

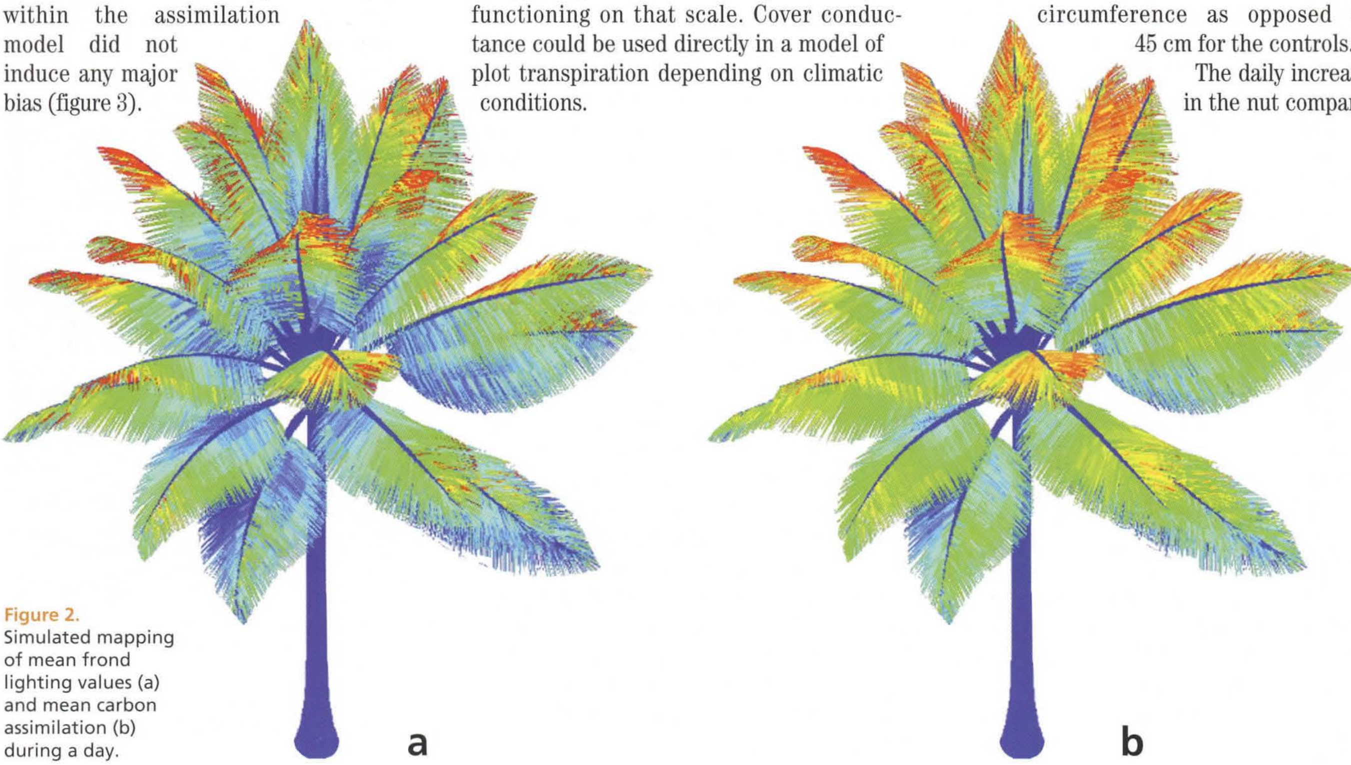


Figure 2.
Simulated mapping of mean frond lighting values (a) and mean carbon assimilation (b) during a day.

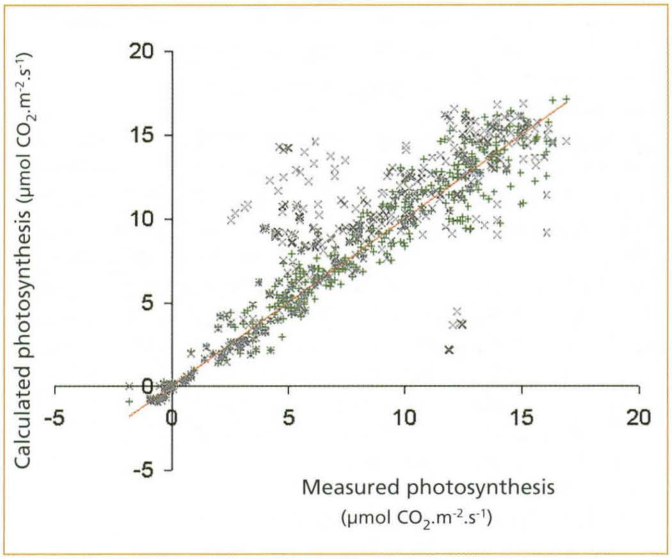


Figure 3. Comparison of measured leaf photosynthesis with that simulated by a Farquhar model. The simulations were carried out with measured (+) or calculated (x) stomatal conductance.

ment was relatively constant in Vanuatu (300 $g.d^{-1}$ of dry matter on average), with moderate fluctuations and two seasonal peaks. On the other hand, in the Philippines, the coconut palms were affected by a major drought caused by El Niño and bunch growth declined substantially (170 $g.d^{-1}$ of dry matter on average).

In terms of male or female flowers, sink suppression led to a substantial and rapid increase—only 4 to 6 months after castration—in the number of flowers. The number of flowers per bunch was proportional to castration intensity, with the largest number of flowers occurring after severe castration.

In additioning, root removal and frond pruning had a depressive effect on the number of flowers.

The frond emission rhythm did not vary much from one treatment to the next, though there was a slight increase in the castrated palms (15.5 $fronds.year^{-1}$ as opposed to 14 $fronds.year^{-1}$ in the controls).

The dry weight of fronds on coconut palms subjected to frond pruning increased steadily over time, as did the number of leaflets per frond. On the other hand, total frond length, and the length of the largest leaflet seemed to decrease somewhat.

Root system growth

The hefty techniques used for root system observations (large excavations, rhizotrons), made it possible to estimate coconut root biomass, along with daily, seasonal and annual growth dynamics. Average total root biomass for a 25-year-old tall coconut palm was 200 kg in the Philippines, whereas it was only 75 kg for a 10-year-old Dwarf x Tall hybrid in Vanuatu. Annual root growth was 47.8 $g.d^{-1}$ and 37.6 $g.d^{-1}$respectively.

Sectioning of the root system, each year for 3 years, in a semicircle 1 m from the palm in the Philippines and 2.5 m from the palm in Vanuatu down to a depth of 1 m, had no significant effect on the growth rate of all root types, irrespective of their distance from the stem, led to a significant increase in root emission at the base of the stem, with uniform radial distribution, and an absence of reiteration at the cut site. The different castration intensities led to a significant increase in root biomass at the foot of the stem for all root types, but did not affect root biomass changes 2.5-m from the stem.

Frond pruning did not have any effect on root biomass or root emission.

Coconut palm growth results

Figure 4 shows the distribution of annual biomass increase in coconut palms in Vanuatu and the Philippines. The importance of the nut compartment (over 50% of total allocation) and the frond compartment (30%) can be seen. Dry matter allocation to the stem and roots was much lower (under 10%). The distribution of coconut standing biomass was not similar. Indeed, the stem (37% of total biomass), frond (28%) and root (17%) compartments accounted for more than two thirds of palm biomass; these compartments must therefore contribute mostly to respiration.

Growth and production modelling

Initially, the general approach consisted in simulating carbon fixation by combining the radiative, stomatal and assimilation models. This simulated carbon fixation, minus respiration costs, was then globally compared, on a palm scale, to the carbon equivalent estimated from the biomass balances obtained from biometric observations. Once the carbon balance had been established on a palm scale, an allocation model was used to generate fixed carbon distribution to the different sink organs.

Assimilate allocation

An original assimilate allocation model was used. The model considered a source compartment (photosynthesis apparatus), sink compartments (bunches, fronds, stem, roots), and a reserve compartment functioning simultaneously as a sink and a source. Allocation from the sources to the sinks was managed by demand from the sinks—depending on the degree to which their demand was met for potential growth —and by the set of resistances reflecting their ability to compete in relation to the sources. The average rate of satisfaction for all the sinks defined the trophic status of the coconut palm, a variable that was used

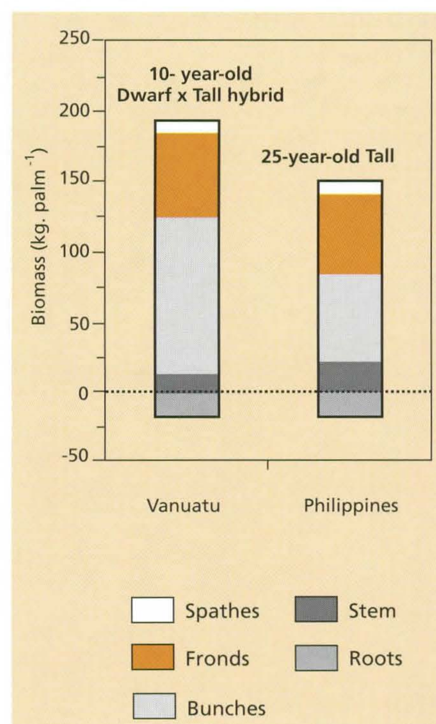


Figure 4. Mean annual allocation of dry matter per coconut palm in Vanuatu and the Philippines.

to establish an "organogenetic" model managing the formation and abortion of vegetative organs.

The allocation model was tested with Model Maker software and used to simulate biomass distribution to the different compartments depending on the treatments applied.

In addition to biomass distribution, the model was used to simulate the buffer effect of reserves when conditions changed. For example, figure 5 illustrates how the model performed when the sources were reduced, in this case by frond pruning.

The allocation model now needs to be integrated into the AMAP software chain and coupled to the organogenetic model.

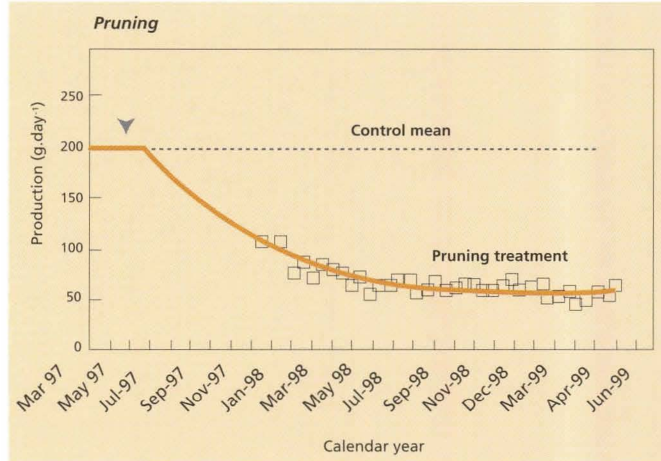


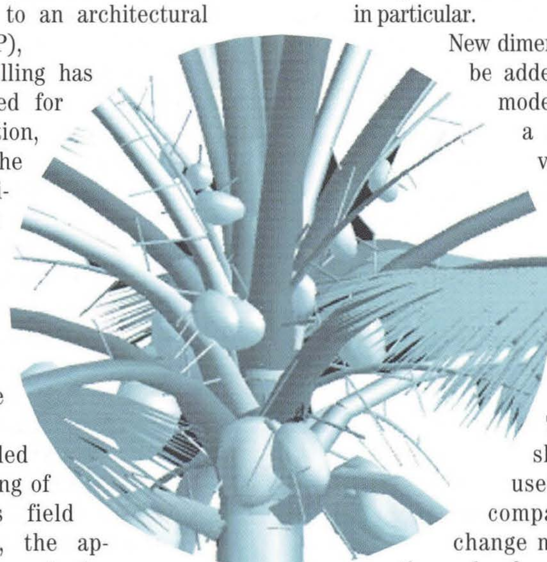
Figure 5. Coconut yields following pruning of simulated (▬) and observed (□), fronds, compared to the average yields of control palms (- - - -).

Conclusions and prospects

Our approach to coconut palm functioning is original in two ways:

- it is the first time that a functioning model including an explicit carbon balance has been coupled to an architectural mock-up (AMAP),
- original modelling has been attempted for carbon allocation, which avoids the need to attribute constant coefficients to the organs, and the rules of priority are modified depending on the organ fill rates.

This study called for the monitoring of fairly laborious field trials. However, the approach was made easier because coconut palm architecture and growth are particularly simple.



The next stage will be to validate our simulated carbon balance using measured growth results. A calibration phase may be necessary. A sensitivity analysis will be carried out.

Once this validation is complete, we shall develop this model further, by optimizing simulated production using planting density in particular.

New dimensions will have to be added to the current model, so as to give it a greater scope of validity: sensitivity to a water deficit in the soil, to fertility, etc.

This work consisted in integrating leaf gas exchanges on a plant scale. This approach should prove very useful in its future comparison with exchange measurements on the scale of a plot or the ecosystem limited to the plantation, in a carbon sequestration and water balance context. This stage could be dealt with using the turbulent fluctuations micrometeorological method currently being applied in Vanuatu.

It will then be possible to construct a new functional model from empirical relations between gas exchanges in the cover and the climate. ■

List of publications

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