Growth and development of true sago palm
(*Metroxylon sagu* Rottbøll)
with special reference to
accumulation of starch in the trunk

A study on morphology, genetic variation and ecophysiology, and their implications for cultivation

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Abstract

True sago palm (*Metroxylon sagu* Rottbøll) is a stout, clustering palm adapted to swampy tropical lowland conditions. Each axis in a sago palm clump flowers once at the end of its life after having amassed a large amount of starch in its trunk. Man can harvest this starch by felling the trunk, pulverizing the pith and leaching the starch out with water, and use it like other starches for food or non-food purposes. It is a staple food mainly in eastern Indonesia and in Papua New Guinea where it is harvested mostly from semi-managed stands. For establishing sago palm as a full-fledged plantation crop, desirable because of its envisaged large yield potential as a perennial, its niche habitat, and its potential as a raw material provider for bio-ethanol production, the scientific base for establishing the right felling time to harvest the starch needed strengthening.

Between October 1988 and November 1990, 27 sago trunks in the Adult Vegetative (AV) or Generative (G) phase belonging to six varieties were selected from semi-wild sago stands in the Moluccas, eastern Indonesia: 23 trunks (4 varieties) on the alluvial coastal plain near Hatusua village, Seram Island, and 4 trunks (2 varieties) on hilly terrain near Siri-Sori Serani village, Saparua Island. These trunks were felled, dissected, morphologically described and sampled for the amount and distribution of starch they contained. The leafless parts of the trunks were 4.45 to 19.65 m long, had a mean starch density of 4.6 to 254 kg/m^3 and contained five to 777 kg of starch (maximum found in a whole trunk: 819 kg).

To link starch content to age, the ages of the sampled trunks had to be estimated. To enable age estimation by counting leaf scars on the trunk, the leaf unfolding rate of 36 AV-phase palms around Hatusua (31 palms) and Siri-Sori Serani (5 palms) was monitored for varying periods between 1989 and 1992. Probably due to large variation in habitat and genetic make-up, this rate varied from 2 to 14 leaves per year (mean 7.85), rendering number of leaf scars unfit as accurate age estimator. Also trunk height proved unfit for this purpose. From monitoring 5 G-phase palms, the G-phase could be subdivided into 3 sub-phases (G1, G2, G3), recognizable from the ground by the phased development of the successive orders of inflorescence branches. By combining gathered morphological and monitoring data, a phenological scale of a model palm was composed consisting of two parallel timelines of hidden and outwardly visible events: two years after the start of the Establishment (E) phase, the first AV-phase leaf is initiated in the apical growing point, to unfold only 2.5 years later; the initiation of the first AV-phase tissues is followed 12.5 to 14.5 years later by the initiation of the first G-phase tissues, followed 4 to 5.5 years later by the shedding of fruits, and finally by a 2- to 5-year Recycling phase (name proposed here) in which the axis decays and collapses. This scale, which accounts for the large time gap between initiation of trunk parts and their becoming visible, may help to correctly time cultural measures. The 27 sampled trunks could tentatively be ranked according to physiological age into 4 AV-phase classes and 9 G-phase classes.

Since the examined palms belonged to 6 different local varieties, their relative rareness or commonness had to be established to assess the validity of the findings. Based on literature and on interviews with informants, an overview of locally recognised sago palm varieties is presented. The number of unique variety names in 32 localities in Indonesia and Papua New Guinea totalled 325, ranging from 2 (spined vs unspined only) to 34 per locality. On the basis of this survey, the Hatusua varieties were considered average. The nomenclatural category folk variety (fovar, fv.) is proposed to unambiguously name local varieties by adding to the variety name an indication of the location where, and (if known) the ethnic/linguistic group by which that name is used.

Leaf area estimation methods were devised to enable investigation of the relationship between leaf area and starch content. In the AV-phase the Total leaf area (TLA) of a sago palm axis ranged from 200 m^2 to 325 m^2, one axis having an exceptional TLA of 388 m^2. The TLA in the G-phase before fruiting mostly remained within the same range, possibly exceeding it for a short period early in that stage. The Leaf area index (LAI) of an individual axis showed an upward trend from 1 - 1.5 in the E-phase to 1.25 - 1.75 in the AV-phase, to more than 2 in the early G-phase, followed by a decrease to about 1.5 again in the late G-phase before fruiting. No fruiting palms were available for analysis. The TLA and LAI of a single trunk could not be linked to the mean starch density of its pith, nor to the total amount of starch the pith contained.

Generally, starch density in the trunk first increased with height above ground level, reached a maximum about half-way to two-thirds up the leafless part of the trunk, and then sharply dropped towards the top of the trunk. From the late AV-phase onward the maximum starch density ranged from 238 to 284 kg/m^3. The four trunks with the highest maximum starch densities, all closely around 280 kg/m^3, belonged to three different varieties, suggesting that 280 kg/m^3 may be considered the maximum starch storage capacity in the pith of any variety.
The starch distribution pattern in the leafless part of the trunk showed a tendency to evolve with age from two-tailed (density gradually increasing from base, gradually decreasing towards top) to one-tailed (density gradually increasing from base, sharply decreasing towards top). The differences in distribution pattern found strongly suggested that there must be other factors besides age and development phase affecting starch accumulation. Attempts to determine the effect of palm variety and of the environment mostly failed.

Potential yield of a model palm based on the maximum starch density of 280 kg/m^3 was estimated at 840 kg of dry starch. That this amount is much higher than generally found may partly be due to poor recovery ratios, as the results of a traditionally processed trunk demonstrated: only 47% of the starch in the processed trunk part was recovered, and if the unharvested starch present in the traditionally discarded basal and top part of the trunk is taken into account, recovery drops to 44%.

In an attempt to establish the point in time at which a sago palm starts to be a nett consumer of its own starch, the course of the energy producing and consuming capacity of an axis during its life time was modelled based on the assumption that by the end of the AV-phase the existing TLA of the axis produces just the amount of energy needed to maintain existing biomass, to keep up the normal regular growth, and to fill new trunk with starch. Using this model, assimilate requirements for building and maintaining the inflorescence and the fruits could not be met by the production capacity of the leaves plus the starch reserves in the trunk. For this modelling approach to succeed in predicting the turning point from nett production to nett consumption of starch by a sago palm axis, additional data on chemical composition of its parts and on assimilation rate are needed.

Lack of precise data on the age of the sampled trunks and lack of uniformity of their genetic make-up and growing conditions made it impossible to arrive at the sought-after detailed timetable of the evolution of trunk starch accumulation and depletion to base the right felling time of a sago palm on. The high starch density found in the trunk of a palm with half-grown fruits indicated that depletion of starch reserves by the palm itself may set in much later than generally assumed.
Once the course of starch accumulation in time in a single axis is unravelled, the next research question should be how this adds up in a clump - the actual production unit in a plantation - with axes of different age. Timing felling in such a situation should be aimed at maintaining a maximum starch accumulation rate for the plantation as a whole rather than at harvesting a maximum amount of starch per trunk.

Data sheets of each palm examined containing all primary and some secondary data, and including photographs, are appended in digital form.

Keywords: *Metroxylon sagu*, *Arecaceae*, starch crops, plant growth and development, plant morphology, inflorescence structure, electron microscopy, phenological scale, genetic variation, plant taxonomy, folk taxonomy, ethnobotany, leaf area, leaf area index, starch accumulation, starch distribution, plant ecophysiology, tropical lowlands, wetlands, traditional processing, estate cultivation, agronomy, Moluccas, Maluku.

Preface

The research reported on here was made possible by funds provided by the Netherlands foundation for the advancement of tropical science (WOTRO (grant nr. W86-085)).
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I thank the personnel of the Land Evaluation Unit and of the Soil Lab of Pattimura University, Ambon, for their assistance in using their facilities.
I would have liked to have my brother Ir Bart P. SCHUILING (Fig. 7.2b) for a permanent assistant as he proved to be a most reliable stand-in for me in the field and in the field lab during his short visit to Seram in October 1990.
For valuable comments on drafts of the section on the inflorescence morphology and development, as well as for putting sample leaflets through a leaf area meter at Lembang, West Java, 2500 km from my Seram field lab, I am indebted to Ir Lieuwe S. ANEMA, at the time (1990) lecturer of genetics at Pattimura University, Ambon, Indonesia.
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I thank Dr Rob VERDOORN for advice in an early stage of the write-up on how to statistically disentangle possible influences on sago palm's leaf unfolding rate.
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If it was not for Dr ir Egbert WESTPHAL, this thesis might well not have seen the light ever: from the time I finished my field work onward, he has friendly but incessantly inquired after the well-being of the write-up of my sago work.
Prof dr ir Paul C. STRUIK, Dr Tjeerd-Jan STOMPH, Prof Dr Ken E. GILLER, Dr ir Jan GOUDRIAAN and Ms Gon (H.H.) VAN LAAR are gratefully acknowledged for critically reviewing the manuscript of Chapter 8 and for valuable advice.
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My promotor, Prof dr ir Paul C. STRUIK, amazed me by accepting with seeming equanimity the task of trying to guide me through my final graduation, a task that a few professors before him had to give up in the face of my, let us say, thoroughness and its temporal claims.
The symposia and journals organized and/or (co-)funded by the Japanese Society for Sago Palm Studies helped me to keep up to date with the latest advances in sago palm science.
The TUPEA IT crew of Wageningen's Haarweg Building (Dorethé K., Geke V., Evert V., Jo S., Alexander v I, António V., *et al.*), started under the unconventional leadership of Mr Hans ROMBERG, is greatly acknowledged for carving out for the Plant Division the best compu admin in the whole of Wageningen University and beyond: their unbureaucratic ways made my work so much easier!
Last but not least I wish to thank Prof dr ir Michiel ‘Doctor Sago’ FLACH: if it had not been for him, I would not have been involved with the sago palm at all. We did some great sago tourism together, often in the company of, or guided by our friend JONG Foh Shoon. Over the years following my field work we went to many a sago conference together.

And my people in Hatusua village, West Seram, where I did most of the field work, what would I have done without them?: my hosts Ms Martha TUHUTERU (Usi Ata) (Fig. 7.1a) & Jance SAHUPALA (Pak Ance), my counterpart Ir Ima SEIPALLA who led us to them, my field assistants Melianus SEIPALLA (Pak Mely) (Fig. 4.10a, 4.19b), Yunus TUPAMAHU (Unu) (and

occasionally Yonky, Tinus, Pak Olop, Pak Petu), my main informant Mr Josephus TUPAMAHU (Pak Ce), and all the others I shared the good and the bad of the life in a (then) rather small and isolated village with.
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During my field work periods my home anchor was provided by my (then) partner Hetty KEIJZER (I thank her for this and for many other things) and our daughters Sarah and Nellie. And it was also during this period that two more persons came to endure my absorbedness in sago, our daughter Josje and our son Michiel. I am happy to have been able much later to show Sarah and Nellie where I was when I was not there, and to share my travel bug with Josje.

I thank all the people who shared their friendship with me during the 20 odd years that it took from the inception of this project to its completion and had to put up with sagology. To name a few: Jong FS, Lieuwe A, Willie A, Arie B, Tanja T, Tom L, Annelies L, Hanneke S, Joan L, Saar L, Juliet L, Max L, Heyta R, Erhard P, Maria W, Ellen R, Louise F, Margaret F, Martin B, Wouter G, Anthony W, Janette B, Conny A, Assia V, Santiago LR, Pablo T, Tony P, TJ & Leentje S, Maja S, Karen F, Koop W, Ton E, Gon vL, Marc M, Tom vM, Dailes N, Jochem E, Myriam A, Erica R, Ilse G, and Frank H.

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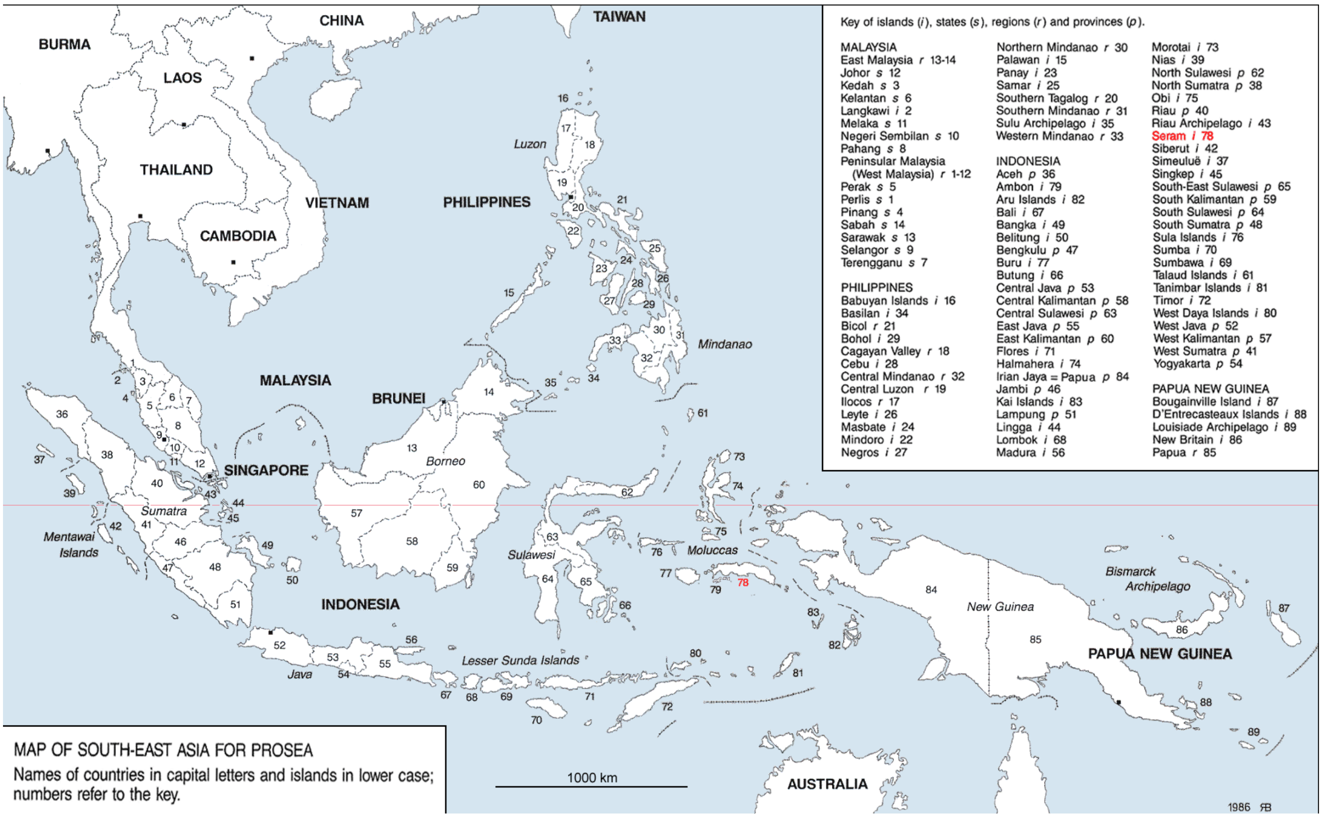
Wageningen, nov2008.

"Es ist ein Fehler, ein unsinniger Gewaltakt, wenn wir uns auf das Hier und Jetzt konzentrieren in der Überzeugung, damit das Wesentliche zu erfassen. Worauf es ankäme, wäre, sich sicher und gelassen, mit dem angemessenen Humor und der angemessenen Melancholie, in der zeitlich und räumlich ausgebreiteten inneren Landschaft zu bewegen, die wir sind. Warum bedauern wir Leute, die nicht reisen können? Weil sie sich, indem sie sich äußerlich nicht ausbreiten können, auch innerlich nicht auszudehnen vermögen, sie können sich nicht vervielfältigen, und so ist ihnen die Möglichkeit genommen, weitläufige Ausflüge in sich selbst zu unternehmen und zu entdecken, wer und was anderes sie auch hätten werden können."

Amadeu do Prado, in: Pascal Mercier 2006 "Nachtzug nach Lissabon"

"Myn moeder had veel broots, eer dat ik was gebooren,
Na myn geboorte-dag heeft s'al haar goet verlooren :
Wat vaartje wint, en moertje spaart, het kint verteert ;
Raad wat boom dat ik ben, en weet gy 't niet, zoo leert."

G.E. Rumphius 1750 (1741)
"Het Amboinsch kruid-boek, ...
- I. Boek. XVII. Hoofdst.", p.74.



Map of South-East Asia with Seram Island indexed in red.
(Source: Plant Resources of South-East Asia (PROSEA) [Multi-volume handbook]. - Wageningen : Pudoc ; Leiden : Backhuys, 1986-2003. - [adapted (original map drawn by Roel BOEKELMAN (1986))]. (Reproduced by permission))

Map of western Seram and surrounding islands with main research locations indicated in red.
(Composed and adapted from maps on p.14 and p.15 of "Atlas Maluku" (published by Landelijk Steunpunt Educatie Molukkers at Utrecht, Netherlands (1998). - 37p.). Adaptations include a correction of the location of Hatusua village and surrounding villages. Base maps used for "Atlas Maluku" may not have been up-to-date enough to accurately depict current village locations (e.g. Lohiatala (Seram) has been relocated nearer to the coast than indicated on this map).)

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[on enclosed CD]

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1 General introduction

This thesis is mainly based on field work done in the framework of a research project titled "**Distribution and use by the plant of starch stored in the trunk of the true sago palm (*Metroxylon sagu* Rottb.)**" formulated by Professor emeritus Michiel FLACH of Wageningen University. He submitted a proposal to finance this project to NWO-WOTRO (Netherlands foundation for the advancement of tropical science) in 1986. From this organization a grant was obtained in 1987 which enabled me to do field work in Indonesia and Malaysia (stationed at Hatusua village, West Seram, Moluccas, Indonesia) and laboratory work at Wageningen University from December 1987 to February 1991. Later, in January and February 1992, I made an additional sago study tour, again in Indonesia and Malaysia, which was financed with the remainder of this grant.

The idea for this research project was prompted by a lack of basic knowledge on growth and development of the sago palm in the face of increasing interest in exploiting this palm for the large amounts of starch it amasses in its trunk. The investigations were to lead, eventually, to a sound exploitation and management system of natural sago palm stands and to the development of a productive cultivation system for future sago plantations. As particularly important was considered the pinpointing of the right harvesting time.

Outline of next chapters

After a comprehensive, illustrated introduction to the various aspects of sago palm and its cultivation in Chapter 2 of this thesis, the purpose of the study is presented in detail in Chapter 3. The sago palm population chosen for the growth and development studies contained palms of various but unrecorded age, and belonged to different varieties. The issues of age assessment and genetic identity had to be addressed first and are dealt with in Chapter 4 and 5, respectively. To be able to analyse the possible role of the leaf area of a palm in the starch accumulation process, it was necessary to devise a method to estimate this area. This is done in Chapter 6. Chapter 7 is the 'core business' of this thesis and deals with the trunk starch accumulation and depletion in time. In Chapter 8 an attempt is made to explain trunk starch content by modelling the energy balance of a sago palm trunk during its life time. In the last chapter, Chapter 9, the relevance of results of my study for cultivation practice is discussed. The massive amount of primary data (including some 'raw' secondary data) is conserved for posterity in Appendices A, B and C, which, together with the photographic records, are not printed, but included in this thesis in digital form only on the enclosed CD.

Interim reports

During and after my fieldwork period I attended the recurrent International Sago Symposia organised in the region, starting with the forth one in 1990 in Kuching (Sarawak, Malaysia) up to and including the latest one, the ninth, in 2007 in Ormoc (Leyte, Philippines). These symposia helped me to stay up-to-date with the latest developments in sago research and provided part of the fora where I presented intermediate results of my studies. Preliminary versions of some sections and chapters of this thesis were made public as follows:

- A morphological study of the developmental stages of the sago palm inflorescence, which may help in establishing palm age, was presented at the Fourth International Sago Symposium (6-9aug1990 Kuching, Sarawak, Malaysia) (SCHUILING 1991a).
- A first inventory of known sago palm varieties (some 200 clones) and their characteristics, instrumental in characterizing and identifying the palms I sampled, was presented at the Fifth International Sago Symposium (27-29jan1994 Hat Yai, Thailand) (SCHUILING 1995).
- A summary of preliminary outcomes related to the original first research aim, a linking of inflorescence development stage to trunk starch content, was presented as poster (SCHUILING 1991b).

- A first attempt to explain trunk starch content by modelling the energy balance of a sago palm trunk was presented at the Seventh International Sago Symposium (27-29jun2001 Port Moresby, Papua New Guinea (proceedings not published)).
- The yield discrepancy between traditional (manual) and industrial (mechanised) starch extraction was quantified in a paper at the Eighth International Sago Symposium (04-06aug2005 Jayapura, Papua Province, Indonesia) (SCHUILING 2006).
- A full report of the additional sago study tour mentioned above was also published (SCHUILING, JONG & FLACH 1993).

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SCHUILING, D.L. 2006 "Traditional starch extraction from the trunk of sago palm (*Metroxylon sagu*) in West Seram (Maluku, Indonesia) [leaves more than half the starch unharvested]". - In: "Sago palm development and utilization : proceedings of the Eighth International Sago Symposium (8ISS) held on August 4-6, 2005, at the Auditorium of the Governor of Papua Office in Jayapura [Papua Province, Indonesia]" / KARAFIR, Y.P. ; JONG F.S. ; FERE, V.E. (eds). - Manokwari (Papua Prov., Indonesia) : Universitas Negeri Papua press, 2006. - xii,266 p. - p.189-200.

2 *Metroxylon sagu* Rottboell : an illustrated comprehensive overview of the various aspects of the sago palm and its cultivation

The overview presented here has been published as

SCHUILING, D.L. ; JONG F.S. 1996 "*Metroxylon sagu* Rottboell". - In: "Plant resources of South-East Asia 9 : plants yielding non-seed carbohydrates" / FLACH, M. ; RUMAWAS, F. (eds.). - Leiden (Netherlands) : Backhuys, 1996. - 237 p. - p.121-126.

The verbatim text as published is rendered here in black. Everything which did not appear in this original text is presented here in **bold grey** and is placed **[between square brackets]**. This includes references to figures (figures were not part of the original text), as well as notes and additions reflecting new insights since the text was published in 1996, including those resulting from the studies for this thesis and which are dealt with *in extenso* in chapters hereafter.

Metroxylon sagu Rottboell

Nye Saml. K. Danske Vidensk. Selsk. Skrift. 2: 527-528 (1783).
PALMAE
2*n* = 26

Synonyms *Metroxylon rumphii* Mart. (1845) with many varieties, designated by Beccari (1918); *M. squarrosum* Becc. (1918) with many varieties.

Vernacular names True sago palm, sago palm (En). Sagoutier (Fr). Indonesia: pohon sagu (general), pohon rumbia (general), kirai (Sundanese), lapia (Ambonese). Malaysia: rumbia (general), balau (Melanau, Sarawak). Papua New Guinea: sak-sak (Pidgin). Philippines: lumbiya. Burma (Myanmar): tha-gu-bin. Cambodia: chraè saku:. Laos: sa:kh'u: tônz. Thailand: sakhu. Vietnam: sagu.
Note: In the Indonesian-Malay language region, the word 'sagu' denotes the edible starch from the pith of any palm and each of these palms may be called 'pohon sagu' (sago tree). 'Pohon rumbia' designates one of them, namely the 'true' sago palm dealt with here, but the name is not commonly used.

Origin and geographic distribution The sago palm probably originates from New Guinea and the Moluccas but has only recently been dispersed for research beyond South-East Asia and the nearby Pacific islands. In Indonesia, the palm is now found in parts of Sulawesi, Kalimantan, Sumatra and West Java, as well as on many smaller islands with a non-seasonal climate, notably the Riau Islands, Nias and the Mentawai Islands. In Malaysia, the palm grows in Sabah, Sarawak and on the Peninsula. Some are found in Brunei and in the Philippines (Mindanao). There are large areas of sago palm in Papua New Guinea. There is also a small area in southern Thailand. Sago palm is found at least as far east as the Solomon Islands and probably the Santa Cruz Islands (species have not been identified with certainty).
The world's largest contiguous sago palm swamps and forests are found in New Guinea, totalling a roughly estimated 5-6 million ha, with 4-5 million ha on the Indonesian part of the island.

Uses The starch stored in the trunk is a staple food, notably in New Guinea. Usually, wet starch is boiled, fried or roasted **[Fig.7.1]**, alone or mixed with other foodstuffs, resulting in products of different keeping quality. In Indonesia and Malaysia, the starch **[Fig. 2.1]** is used industrially in the manufacture of cakes and cookies, noodles and kerupuk (crisps), and in the United States for custard powders. Non-food uses include sizing pastes for paper and textiles, and extender in adhesive for plywood. It is a very suitable raw material for further industrial processing, e.g. into high-fructose syrup and ethanol.

The palm has many secondary uses. Whole young trunks, pith and pith refuse are given to animals [Fig. 2.5a-b]. The 'bark' of the trunk is used as timber or as fuel [Fig. 4.13g]. Walls, ceilings and fences can be constructed from the petioles ('gaba-gaba') [Fig. 2.4]; [strips of] the fibrous outer layer of the petioles [are] used for cordage and to weave mats [Fig. 2.5e-f]. The leaflets produce one of the best ataps (roof thatch) available [Fig. 2.2], the main use of the palm in West Java. Young leaflets are made into baskets for the transport and storage of fresh (wet) starch [Fig. 2.3]. The growing point of the palm with its surrounding tissues may be eaten raw or cooked (palm cabbage) [Fig. 2.5c].

The larvae of insects feeding on the pith of the trunk, notably weevils of the genus *Rhynchophorus* [1], are eaten raw, boiled or roasted in most places where sago palm is a staple [Fig. 2.6]. A mushroom (*Volvariella volvacea* Fries) which grows on pith refuse is relished in the Moluccas [Fig. 2.5d].

Production and international trade Of the total sago palm area of 5-6 million ha, only an estimated 210 000 ha is planted. Planted areas are estimated to be 130 000 ha in Indonesia, 40 000 ha in Malaysia (mainly Sarawak and Sabah), less than 1000 ha in Brunei, 5000 ha in the Philippines, 20 000 ha in Papua New Guinea, 5000 ha in Thailand and 10 000 ha on the Pacific islands. Most sago starch is consumed locally or traded on domestic markets. It accounts for less than 3% of international trade in starches. Some of it is traded as sago pearls [Fig. 2.1g,h]: partially gelatinized kernels, 1-2 mm in diameter, obtained by forcing raw starch paste through a sieve and stirring the extruded pieces of paste on a hot-plate until hard and rounded. Sometimes, pearled starches of non-palm origin are erroneously called 'sago pearls' or even just 'sago'.

Unambiguous economic statistics are scarce. In 1992, the export of dry sago starch from Sarawak was 45 700 t (value MY$ 31 million). On Bengkalis (Riau Islands), an old centre of sago starch production, 30 mills operated in 1980 with a total output of 6600 t/year of dry starch. In the 1930s, 30 000-40 000 t/year wet starch production from the east coast of Sumatra was exported to Singapore to be refined and re-exported. The once prosperous sago-starch trade through Singapore has declined steadily since the 1950s.

Properties Purified sago starch consists of 27% amylose and 73% amylopectin. Dry starch samples from various parts of Indonesia contained water 10-17%, protein 0.31%, fat 0.11-0.25%, carbohydrates 81-88%, fibre 1.35%, ash 0.15-0.28%. A sago-based diet should be complemented with other foodstuffs to provide essential proteins, minerals and vitamins.

In Sarawak, the dry matter content [2)] of the grated whole pith (sample of 6 palms) contained: N 0.15%, P 0.046%, K 0.45%, Ca 0.24%, Mg 0.09% and starch 54%.

Sago weevil larvae from Sarawak and Papua New Guinea, weighing 3-8 g, contained: water 65-75%, protein 3-7%, fat 10-30%.

Description A medium to tall palm tree, flowering once only, andromonoecious, forming basal suckers [Fig. 2.7]. Roots spongy but with a tough central fibro-vascular strand, not extending to great depth (80-100 cm in peat soil); pneumatophores (air roots) present [Fig. 2.8]. Trunk 30-60 cm in diameter, 7-20(-25) m tall, lower part ringed with leaf scars, upper part covered with semi-persistent leaf sheaths; epidermis thin, very sclerenchymatous, surrounding the fibrous bark, 5-10 mm thick; under the bark an extremely hard layer of sclerenchymatous fibre bundles, up to 1 [4] cm thick surrounds the parenchymatous pith [Fig. 4.12, 4.13]. Leaves 18-24 in vigorous trunked palms, simply pinnate, 5-7 m long (sometimes up to twice as long); petiole very robust, widening at its base into a stem-clasping sheath; sheath and petiole unarmed or armed to various degrees with needle-like spines [3)], up to 22 cm long, arranged in transverse combs [Fig. 5.1]; leaflets up to 200 per leaf, 50-160[-200] cm x 3-6(-9)[-13] cm, often with small spines along the margins and on the midrib and sometimes with an apical, filiform appendage, margins usually valvate and reflexed. Inflorescence [Fig. 4.19] apparently a terminal panicle, 3-5(-7.5) m high and wide; first-order branches (10-)15-30, straight to curving upward, morphologically constituting separate lateral inflorescences arranged spirally on the main stem in the axils of reduced leaves or bracts with a phyllotaxy of 5/13 [Fig. 4.34], rigidly and distichously branched to the third order; the flower-bearing third-order branches spadix-like [Fig. 4.32], rust-coloured when young, darker and more red from densely packed bulging flower buds later; flowers in pairs arranged spirally, each pair consisting of one male and one hermaphrodite flower, but up to half of the buds, usually most of them male, may abort before they reach anthesis; bracts of the first to the third order smooth to spinulescent outside [Fig. 5.2]; flowers 3-merous with 6 stamens. Fruit [Fig. 4.2] a depressed-globose to obconical drupe, 3.0-5.0(-7.0) cm in diameter, covered with 18(-19) vertical rows of scales, rhomboid, pointing downwards, greenish-yellow, turning straw-coloured towards or after fruit fall; scale layer lined inside with a white spongy layer. Seed subglobose, about 3 cm in diameter, firmly embedded in shiny cream-coloured firm flesh which turns pinkish when exposed to air; testa dark brown; endosperm homogeneous, horseshoe-shaped in longitudinal section because of large chalazal cavity; seeds often fail to develop, resulting in fruits filled with the cream-coloured flesh only.

Growth and development The seed is viable as soon as the fruit is shed but may quickly lose its viability through desiccation. In the field, germinating seeds are always fully ripe (brown testa and hard endosperm inside a straw-coloured husk), and are found on damp soil or even in a thin layer of water, under conditions of high relative humidity. Seeds usually germinate within 3 weeks. Vegetative growth is divided into a rosette stage of 3.5-6 years and a trunk stage of 4-14 years, depending on palm type [4)] and growing conditions. If these conditions are optimal, leaves form at a rate of 2 per month during the rosette stage, slowing down to 1 per month during the trunk stage; longevity of adult leaves is 18-24 months. Basal suckers are formed continuously, the first ones appearing already during the first year after germination. Starch is stored in the parenchyma (pith) of the trunk [Fig. 4.12], which is gradually filled from the base upward. Maximum volumetric mass of the starch (kg per m^3 of pith) has been found to be about 190 in Sarawak, 330 in the Sepik area of Papua New Guinea, and 280 on Seram in Indonesia. During flowering and especially during fruit development, the starch is translocated towards the inflorescence. After fruits have been shed, most of the starch has disappeared from the trunk.

The generative stage [Fig. 4.3, 4.27, 4.30, 4.35, 4.36] is heralded by the 'shooting' [5)] of the main stem, forming the main flowering axis: new internodes become longer, stem diameter and leaf size decrease and rate of leaf formation increases. The development of the inflorescence is phased: first the main axis develops, then the first-order branches, subsequently the second-order branches, etc. Anthesis of a male flower lasts 1 day, of a hermaphrodite flower 1-2 days; the anthesis period for the entire inflorescence lasts 50-60 days. Within one inflorescence, most male flowers have opened (and aborted the next day) before most hermaphrodite flowers open: sago palm is largely, but not strictly protandrous. Stamens in the male and hermaphrodite flowers look the same, but the viability of pollen in the hermaphrodite flowers is uncertain.

As germinating seeds are often found where two palms close to each other have flowered simultaneously, it has been assumed that sago palm is mainly a cross-pollinator.

Recent research findings suggest that sago palm is most probably largely self-incompatible, i.e. only palms which are genetically sufficiently different are well able to fertilize each other. This, in combination with the natural vegetative propagation method of the palm, the small chance of overlap of the anthesis periods of palms, and the condition that these palms should be growing at a distance small enough to allow for the insect-assisted pollen transfer, would account for the very low percentage of seeded fruits often encountered.

A yield of 5000 (seeded or unseeded) fruits is common in Sarawak. A sample-based estimate of the number of fruit in a palm on Ternate was 28 800.

It takes about 3 years from the outwardly visible start of the generative stage to the shedding of the fruits, after which the trunk dies. So, the total life span of a sago palm ranges between 11-23 years.

In the meantime, suckers of various ages, some already with a trunk, may have developed under the parent palm. Some suckers may form trunks up to several metres away from the parent palm, after first forming a prostrate stem.

Other botanical information The distinction at species level of palms with and without spines (*M. rumphii* and *M. squarrosum* - spiny; *M. sagu* - spineless) cannot be upheld. The reduction of the number of taxa of lower order in true sago palm, however, from 21 to 4 in the latest revision of the genus, may be too drastic. For example, variation in life span, which appears to be mainly genetically determined, and which is one of the bases of the distinction of types [4)] by sago growers, is, unfortunately, not taken into account. Neither are other variations recognized, e.g. in leaf form, spine density, bark thickness, starch colour, and even starch taste.

The number of sago palm types [4)] distinguished by local sago growers increases eastwards: from 2 on Siberut island west of Sumatra and in Riau province, to 2-3 in Sarawak, to 4-5 **[up to 8]** on Ternate and Halmahera, to 5-8 **[up to 12]** in the Central Moluccas, to 10-13 **[up to 20, and even 34 in one recorded case]** on New Guinea island.

Ecology Sago palm is a tree of the per-humid tropical lowlands, occurring naturally up to 700 m above sea-level (up to 1200 m in Papua New Guinea). The best conditions for sago palm growth are an average temperature of at least 26ºC, a relative humidity of 90% and an irradiance of about 9 MJ/m^2 per day.

Natural stands of sago palm occur on swampy coastal plains, river floodplains and higher up on flat valley floors. When growing downstream along rivers, tidal influences may be part of the habitat of sago palms, and may affect the level and salinity of flood water or groundwater. Daily flooding is harmful to seedling growth, as is salinity corresponding to electric conductivities (EC) of over 1 S/m. (EC of sea water is 4.4 S/m). Occasional flooding, even with very saline water is tolerated, however. Although found on mineral, peat and muck soils, sago palm grows best on mineral soils with a high organic matter content (up to 30%).

In New Guinea, sago palms occur mainly in 4 vegetation types. Ranging from land inundated most of the year to less flood-prone lands, one may successively encounter sago palm - *Phragmites* swamp (groves of trunkless sago palms in dense stands of the reed *Phragmites karka* (Retz.) Trin. ex Steud.), sago palm swamp (dense stands of sago palms, most of them trunkless), and sago palm forest (sago palms in various stages of development mixed with dicotyledonous trees in various proportions). On peat soils that are dry most of the year, *Campnosperma* - sago palm forest (sago palms forming an understorey under a closed canopy of *Campnosperma brevipetiolatum* Volkens) can be found. The most numerous and largest trunks are found in the sago palm forest.

As the water becomes more brackish, sago palm often borders on stands of the more salinity-tolerant nipa palm (*Nypa fruticans* Wurmb).

[6)]

Propagation and planting Sago palm is mostly propagated from suckers. Rooted suckers about 1 year old with a basal diameter of 8-15 cm are severed from selected parent palms with a clean vertical cut through the runner (rhizomatous stem), leaving some 15 cm of the runner attached to the sucker to serve as food reserve **[Fig. 2.9a]**. The cut wound is sometimes rubbed with wood ash to prevent rot. Treating the wound with a broad-spectrum fungicide has been shown to increase viability of the sucker. The runner with the roots should be kept from drying out. Usually, all the leaves are cut off; sometimes the spear and all or part of the youngest unfurled leaf are left on the sucker. Before planting in the field, suckers can first be kept in nurseries, either in polythene bags, or by simply putting them in shallow water

[Fig. 2.9b], or if the water is deeper by tying them to a raft with only the runner and roots hanging in the water [Fig. 2.9c]. Usually, only about half the propagated suckers are successful. The sucker survival rate may be increased by reducing the time between cutting the suckers and putting them in a nursery, by treating them with pesticide to prevent *Rhynchophorus* attack, and by shading them in the dry season. Propagation from seed has a considerably higher rate of success but viable seeds are difficult to obtain and the heterogeneity of the offspring, e.g. spininess, is a drawback.
Suckers are planted in the field at 6 m x 6 m to 7 m x 7 m [Fig. 2.9d]. Planting depth is critical: the runner and especially the cut end should be buried to prevent *Rhynchophorus* attack and desiccation, but the shoot and especially the apical meristem inside it should be above water table (or above flood-water level), also in the wet season, to prevent rot. If necessary, the suckers are staked. Plenty of shade should be provided.
In vitro propagation of sago palms is still in the experimental stage. Plantlets have been derived from embryo culture, but micro-propagation through multiple shoot induction from sago explants has not yet been successful.

Husbandry The sucker is established as soon as the spear plus a new leaf have unfolded, normally within 3 months. Shade is then gradually removed.
Weeding is necessary until the leaf canopy has closed. Old leaves are pruned and used as mulch. One sucker is allowed to develop into a trunk every 2 years if clump spacing is 6 m x 6 m, or every one and a half years if the spacing is 7 m x 7 m. All other suckers are pruned. Thus, an annual yield of 136-139 trunks per hectare may be achieved. The water table should be no lower than 50 cm. Fertilizers are normally not used; in Peninsular Malaysia the palms grow on flood-prone river banks, the river water probably carries all the necessary nutrients. Deficiencies have been shown to reduce the rate of leaf formation and the leaf area of new leaves in seedlings.

Diseases and pests In extensive exploitation from semi-wild stands, none of the pests encountered are economically important. In intensive estate cultivation in Sarawak, however, many pests have become economically important, the most important being the larvae of the hispid beetle *Botryonopa grandis*, which attack the soft tissues of furled leaves, termites (*Coptotermes* sp.), which tunnel through the young trunk up to the growing point, and the larvae of the red-striped palm weevil *Rhynchophorus schach* (= *R. ferrugineus* var. *schach*)[7] [Fig. 2.6], the so-called sago worms, which eat away at the trunk's pith. Other pests [= Pests] reported from elsewhere include *R. ferrugineus* from Siberut (Indonesia), rhinoceros beetle (*Oryctes centaurus*) from Papua New Guinea, and nettle caterpillars (*Darna* spp.) from Java.

Harvesting To get the most starch out of one palm, it should be harvested at the peak of its starch content, which is reached during the generative stage some time between the beginning of anthesis and the beginning of fruit development. To maximize starch production per unit time, however, trees should be felled before the inflorescence emerges, when starch accumulation rate has not yet slackened. After felling, the crown is severed from the trunk and the old leaf sheaths are removed. The leaf bearing part of the trunk contains little starch.

Yield Top annual yield of dry starch from a first crop of palms of short life cycle in Peninsular Malaysia is about 25 t/ha, equivalent to 138 trunks of 180 kg each. Yields of the subsequent ratoon crops stabilize at about 15 t/ha (85 trunks of 180 kg each). Recorded production of dry starch from single 'mature' trunks in uncultivated stands range from 20-400(-800) kg. The production capacity of semi-wild stands is estimated at 50 trunks per ha per year, producing 10 t/ha, whereas good quality wild stands on the drier parts of swamps are estimated to produce 25 trunks per ha per year, yielding 5 t/ha.

Handling after harvest Processing consists of separation of bark and pith, pulverization of the pith and separation of the starch grains from the other pith constituents. Traditionally, most of the processing is done at the felling site [Fig. 2.10, 2.11]. The trunk is split lengthwise with wedges or partly debarked (i.e. the bark proper plus the outer hard layer of fibre bundles is [= are] removed). The exposed pith is pounded loose and pulverized with a hoe-like or adze-like instrument or grated with a nail-studded plank. The starch grains are leached out of the pulverized pith with water over a sieve and the starch is recovered from the slurry passing through the sieve by letting it settle. Pith starts fermenting spontaneously soon after it is pulverized, giving off an acid smell and causing irreversible staining of the starch. So starch extraction should follow pith pulverization as soon as possible.
Traditionally, only the wet starch (starch content 60%) is removed from the field. In planted stands, the trunks are usually cut into lengths of about 1 m. These logs (starch content 20-25%), weighing 80-120 kg, are rolled and floated to a central mill for further processing [Fig. 2.9e-g], a network of waterways being indispensable.

Genetic resources In Sarawak (Department of Agriculture, and Land Custody and Development Authority) and in the Moluccas, Indonesia (Makariki Experiment Station of the Coconut Research Institute at Seram Island), a start has been made with the collection of sago palm types [4)] from Eastern Indonesia and Papua New Guinea.

Breeding For estate cultivation, palm types are needed which (1) have a short life cycle (brief rosette stage and quick 'maturation') to allow an early first harvest, (2) have a high starch accumulation rate (high yield per unit time), (3) can be planted densely (high yield per unit area), (4) are responsive to fertilizers, (5) have pest and disease resistance/tolerance, and (6), especially in Sarawak, are able to grow well on peat soil.

Prospects Sago palm is one of the underexploited trees in South-East Asia. Sago starch is mainly harvested from wild or semi-wild (i.e. planted but neglected) stands. Vast areas of natural sago palm stands, in New Guinea in particular, are left unused because of the inaccessible habitat and their remoteness. Until the mid 1980s, sago palm had been cultivated regularly only in Peninsular Malaysia, especially in the State of Johor. Since about 1970, international interest in sago palm as a plant resource in equatorial swamps has increased and desk studies have demonstrated its economic viability as a plantation crop. In 1987, the development of an [= a] 7700 ha sago plantation was started near Mukah, Sarawak, on deep peat [Fig. 2.9d]. A new plantation has also been opened up in Indonesia in Riau province. New large-scale schemes exploiting natural stands have come into operation in Indonesia on Halmahera [Fig. 2.9e,j] and in Irian Jaya.
At present research is intensifying. In Sarawak, an experiment station devoted to research on growing sago palm on deep peat has been operating since 1982. Indonesia is planning to establish a sago palm research station.

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1) "notably weevils of the genus *Rhynchophorus*" should read "notably the Asian palm weevil (*Rhynchophorus ferrugineus* (Olivier)"
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2) "dry matter content" should read "dry matter".

3) A thorn is a modified branch; a spine is a modified leaf; the sharp things on the sago palm leaves are outgrowths of the epidermis and are technically called prickles (RAVEN, P.H. ; EVERT, R.F. ; EICHHORN, S.E. "Biology of plants". - 6th ed. - New York : Freeman/Worth, 1999. - xv,944p.- p.642).
Other authors use the word spine more loosely to include prickle, but they all agree about a thorn actually being a modified branch.

4) type in the meaning of variety consisting of a group of clones with similar characteristics.

5) " 'shooting' " should read " 'bolting' ".

6) According to local informants in Hatusua, West Seram, sago palm fruits are eaten by fruit bats a.k.a. flying foxes (Indonesian: *kalong* ; local language: *mursegu*). (Yonky and Tinus, at the occasion of the 2nd round of observations on sago palms marked to monitor leaf unfolding rate, 14aug1989).

7) "red-striped palm weevil *Rhynchophorus schach* (= *R. ferrugineus* var. *schach*)" should read "Asian palm weevil (*Rhynchophorus ferrugineus*)".
(See references under endnote 1.)

Figure 2.1 Starch, the main product of the sago palm.

a: **No-tech drying (sun-drying) of sago starch.** [photo nr. 92.01-203-08, Prima sago starch factory, Tanjung village, Tebing Tinggi Island, Riau Province, Indonesia mon13jan1992]

b: **High-tech drying of sago starch with an Alfa-Laval drum-drier.** [photo nr. 90.08-132-02, PPES Sago Industries, Mukah, Sarawak, Malaysia wed08aug1990]

c,d,e,f: **Bags with dried sago starch at the factory, ready for distribution to the processing industry.** [c: photo nr. 92.01-203-05, Harapan/HMM sago starch factory ; d: photo nr. 92.01-203-06, Prima sago starch factory (c,d: Tanjung village, Tebing Tinggi Island, Riau Province, Indonesia mon13jan1992) ; e: photo nr. 88.01-042-25, Mukah Sago Industries, Mukah, Sarawak, Malaysia sat16jan1988 ; f: photo nr. 92.01-209-35, Inhutani-I sago starch factory, Kao, Halmahera Island, Indonesia fri31jan1992]

g,h: **Some processed food products made from sago starch, as found in retail stores.** [photo nrs. tc-200-34 and -35, Singapore sat27aug2005]

Figure 2.2 The main secondary use of the sago palm: the use of its leaflets for roof thatch ('atap').

a,b: **Making 'atap sagu' shingles by folding leaflets over a lath of split bamboo culm and fastening them by sowing with a thin strip of split bamboo culm.** [photo nrs 90.07-123-10 and -11, Hatusua, West Seram, Indonesia sun24jun1990]

c: **Drying sago leaflet shingles. In the background are houses with gaba-gaba walls and with roofs thatched with sago leaflet shingles.** [photo nr. 88.12-074-05, Hatusua tue13dec1988]

d: **Home industry: two packs of sago leaflet shingles held together by lengths of gaba-gaba, ready to be sold.** [photo nr. 90.06-122-13, Hatusua sun24jun1990]

e: **Small-scale industry: stacks of still green sago leaflet shingles.** [photo nr. 86.03-II-31, N. of Batu Pahat, Johor State, Malaysia fri07mar1986]

f: **Putting up a sago leaflet shingle on a house under construction.** [photo nr. 89.05-085-28, Hatusua sun14-mon15may1989]

g: **Church with roof cover of sago leaflet shingles.** [photo nr. 89.08-093-26, Nolloth village, Saparua Island, Central Moluccas, Indonesia thu17aug1989]

Figure 2.3 'Tumang', containers made of sago palm leaflets for transport and storage of wet sago starch in eastern Indonesia.

a,b: **Making a tumang.** [photo nrs 90.11-145-28 and -29, Hatusua, West Seram, Maluku oct-nov1990]

c,d: **Filling a tumang with wet sago starch, and (d) a tumang filled to the rim.** [photo nrs. tc194-29 and -32, Hatusua, West Seram, Maluku thu11aug2005]

e: **A 'pikul' (load) of wet sago starch consisting of two bulging-type tumang, carried with deceptive ease.** [photo nr. 88.12-073-23, Siri Sori village, Saparua, Maluku mon05dec1988]

f: **Cone-type tumang filled to the brim with wet sago starch and topped-up with an extra cone of semi-dried starch.** [photo nr. 92.02-213-09, Saparua town, Saparua, Maluku wed12feb1992]

g: **Long-cylinder-type tumang.** [photo nr. 92.02-21-28, Tanjung Kasuari, Sorong, Papua sat08feb1992]

h: **Bulging-type tumang filled with wet sago starch, ready for transport.** [photo nr. 88.12-072-27, Siri Sori, Saparua, Maluku tue06dec1988.]

Figure 2.4 The use of the petiole-rachis ('gaba-gaba') of the sago palm leaf in the Moluccas, Indonesia.

a: **Drying gaba-gaba.** [photo nr. 88.10-067-27, West Seram oct1988]
b: **Drying gaba-gaba on the beach.** [photo nr. 90.09-139-24, Seri village, Ambon Island sep1990]
c: **Store of bamboo poles and bundles of gaba-gaba in the yard of a vendor of building materials.** [photo nr. 92.02-210-18, Ternate sun02feb1992]
d: **A house with gaba-gaba walls and a roof thatched with sago palm leaflets.** [photo nr. 88.10-067-04, Lohiatala village, West Seram sat08oct1988]
e: **School building with gaba-gaba walls and roof thatched with sago palm leaflets.** [photo nr. 90.06-119-29, Rambatu village, West Seram tue05jun1990]
f: **Boy with toy car made of gaba-gaba pith.** [photo nr. 88.11-071-10, Kairatu, West Seram tue22nov1988]
g: **Raft made of gaba-gaba roped together.** [photo nr. 90.09-138-21, Seri village, Ambon Island sat15sep1990]
h: **Gaba-gaba rafts fitted with a shelter, to be moored off the coast and used as fishing platforms.** [photo nr. 90.09-139-25, Seri village, Ambon Island 17-20sep1990]
i: **Gaba-gaba raft used in off- and on-loading goods from inter-island passenger ship.** [photo nr. 90.11-147-22, Haria, Saparua Island fri09nov1990]

Figure 2.5 Some minor secondary uses of the sago palm.

a, b: **Unprocessed pith serving as animal feed.** [photo nrs. 89.04-081-13 and -15, Hatusua village, West Seram, Maluku, Indonesia mon03apr1989]

c: **The tissues of and around the apical growing point of the stem can be eaten raw or cooked.** [photo nr. 92.01-204-10, Siberut Island, Mentawai Archipelago, West Sumatra, Indonesia fri17jan1992]

d: **'Jamur ela' (pulverized sago pith mushroom), a.k.a. the paddy straw mushroom (*Volvariella volvacea*), growing on pith processing waste.** [photo nr. 90.07-123-04, Hatusua, W. Seram, Indonesia sun24jun1990]

e,f: **Yanking strips of skin off a petiole. The strips are used as cordage.** [photo nrs. 88.09-063-02 and -03, Hila village, Ambon Island, Indonesia wed24aug1988]

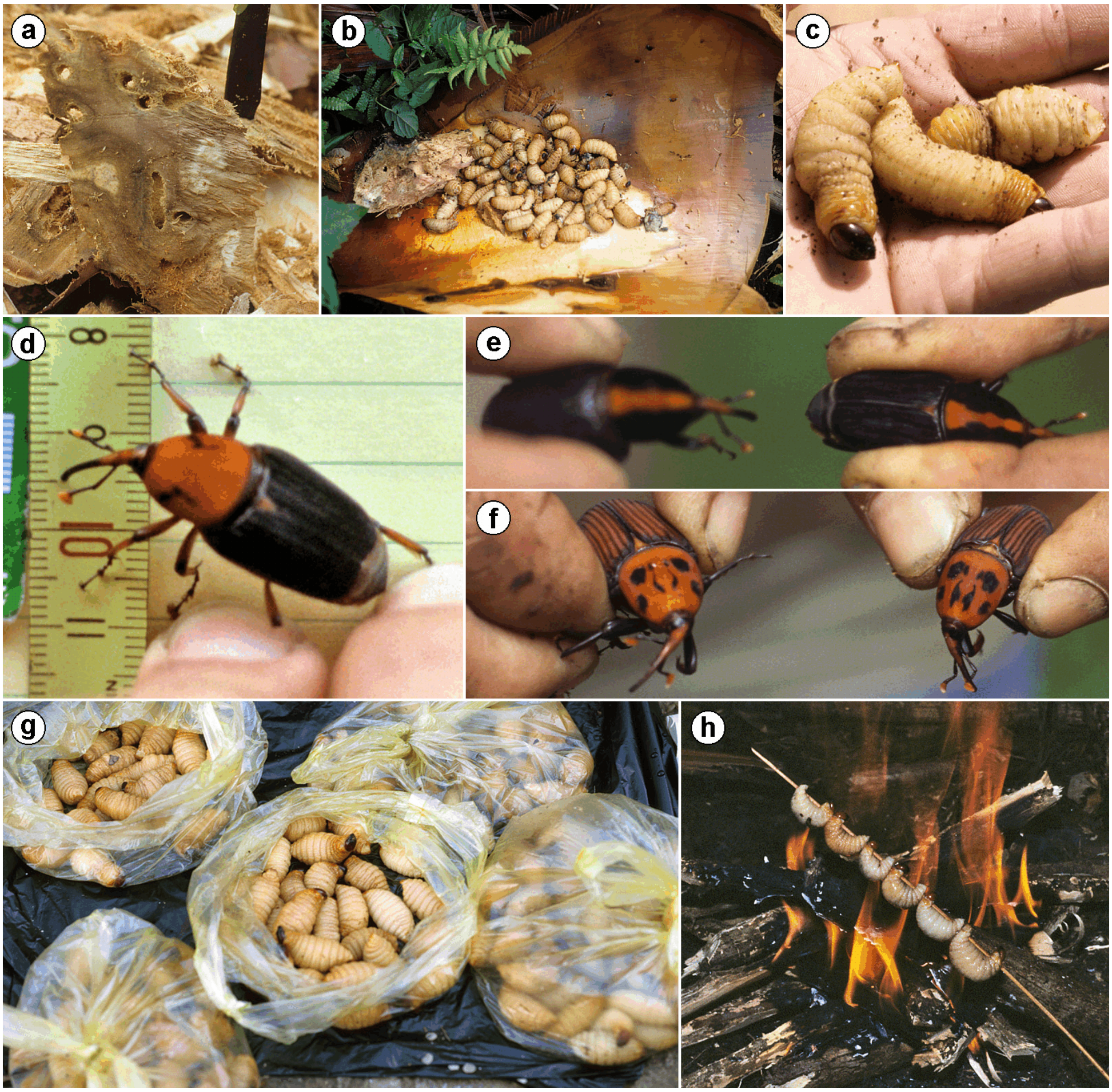

Figure 2.6 The Asian palm weevil (*Rhynchophorus ferrugineus*) in sago palm and the use of its larvae (also known as sago grubs or sago worms).

a,b: **Piece of trunk pith with tunneling holes made by feeding larvae, and inside of base of severed leaf with larvae collected from the pith.** [photo nrs. 90.11-146-10 and -09, Hatusua, West Seram, Maluku, Indonesia fri26oct1990]

c: **Showing some full-grown larvae.** [photo nr. 88.01-041-75, near Mukah, Sarawak, Malaysia sat16jan1988]

d,e,f: **Adult weevils in three different colour variations from two different locations.** [photo nrs 92.01-204-17, Siberut Island, Mentawai Archipelago, West Sumatra, Indonesia fri17jan1992 ; 92.01-205-07 and -05, Bogor, West Java, Indonesia thu23jan1992]

g: **Plastic bags with larvae for sale in the market.** [photo nr. tc-117-36, Boswezen market, Sorong, Papua, Indonesia thu25jul2002]

h: **Skewered larvae being roasted.** [photo nr. 89.06-086-35, Hatusua mon05jun1989]

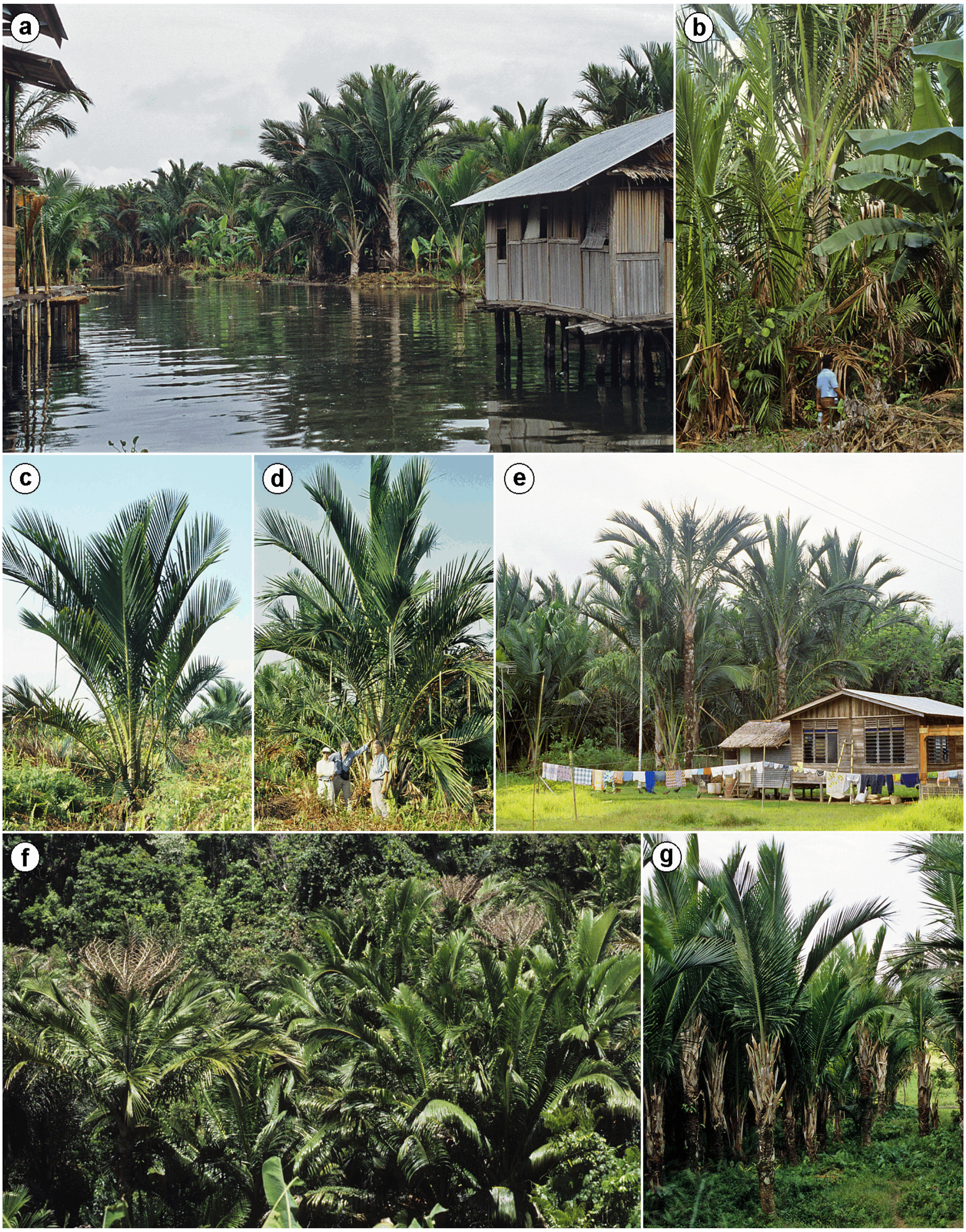

Figure 2.7 The habit of the sago palm.

- **a: Vegetative palms at various stages of development (trunked and still trunkless) at the border of a lake. (Note 'gaba-gaba' walls of the stilted house.)** (photo nr. tc-189-24, Yoboi village, Lake Sentani, Papua, Indonesia sat06aug2005)
- **b: Dense sago palm vegetation.** (photo nr. 92.01-209-34, Kao → Malifut, Halmahera Island, Indonesia fri31jan1992)
- **c: Habit of a palm 3.5 years after planting as a sucker and growing on peat soil. The palm is about to form a trunk.** (photo nr. tc-083-07, sago plantation of P.T. National Timber, Tebing Tinggi Island, Riau, Indonesia tue03jul2001)
- **d: Habit of a palm 5 years after planting as a large sucker and growing on peat soil. The palm has formed a trunk which is still hidden by the leaves (as checked by, f.l.t.r., Jong Foh Shoon, Rik Schuiling and Michiel Flach).** (photo nr. tc-083-05, [location and date as c:])
- **e: Palms at various stages of development, the tallest one clearly in the generative stage with a terminal inflorescence.** (photo nr. 86.03-II-11, near Batu Pahat, Johor, Malaysia fri07mar1986)
- **f: Bird's eye view of sago palm grove with three of the palms clearly flowering.** [photo nr. 88.10-065-31, Lohiatala village, West Seram, Maluku, Indonesia sat08oct1988]
- **g: Habit of palms mainly used as providers of leaf thatch with only about five to seven leaves left on the trunk.** [photo nr. tc-197-04, shore of Lake Tondano, North Sulawesi, Indonesia sun14aug2005]

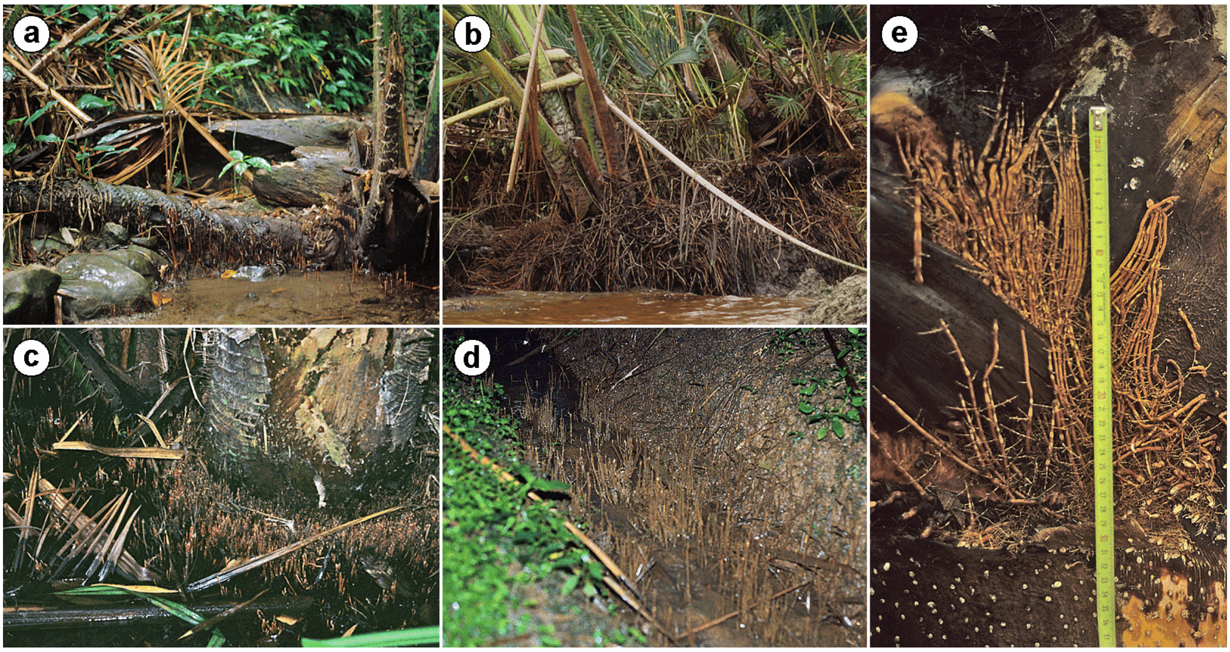

Figure 2.8 Roots and pneumatophores of sago palm.

a: **Horizontal trunk part with roots growing downwards, and pneumatophores growing upwards.** [photo nr. 90.04-114-32, Alang village, Ambon Island, Indonesia wed25apr1990]

b: **Roots exposed by water erosion.** [photo nr. tc-003-29, Tebing Tinggi Island, Riau Province, Indonesia sun15dec1996]

c: **Trunk base surrounded by pneumatophores.** [photo nr. 90.07-123-03, Hatusua village, West Seram, Indonesia sun24jun1990]

d: **Creek with emerging pneumatophores from nearby sago palm.** [photo nr. 86.03-II-26, Batu Pahat area, Johor State, Malaysia fri07mar1986]

e: **Pneumatophores growing higher up the trunk under old leaf bases (bases partly removed).** [photo nr. 92.02-215-13, Hatusua village, West Seram, Indonesia fri21feb1992]

Figure 2.9 Estate cultivation of sago palm and centralised mechanical processing of trunks.

a: **Sucker for planting.** [photo nr. tc-003-26, Tebing Tinggi Island, Riau Prov., Indonesia sat14dec1996]]

b,c: **Field nursery and floating nursery.** [photo nrs. (b) 92.01-201-25, Mukah area, Sarawak, Malaysia tue07jan1992 ; (c) tc-003-05, Tebing Tinggi Island, Riau Province, Indonesia fri13dec1996]

d: **Plantation with palms still in the trunkless establishment phase.** [photo nr. 92.01-201-35, Mukah area, Sarawak, Malaysia tue07jan1992]

e: **Rolling a log from the felling site to a waterway for transport to central processing plant.** [photo nr. 92.01-209-25, Kao area, Halmahera Island, Maluku, Indonesia thu30jan1992]

f,g: **Logs roped together to facilitate floating them to central processing plant.** [photo nrs. (f) 92.02-210-S, Kao, Halmahera Island, Indonesia fri31jan1992 ; (g) 90.08-132-06, Mukah area, wed08oct1990]

h,i,: **Feeding debarked log parts into a grinder.** [photo nrs. (h) 86.03-II-19, Batu Pahat area, Johor, Malaysia fri07mar1986 ; (i) 88.01-042-11, Mukah area, Sarawak, Malaysia sat16jan1988]

j: **Feeding log parts with the bark still on into a slicer to separate the pith from the bark.** [photo nr. 92.01-208-33, Kao, Halmahera Island, Maluku, Indonesia tue28jan1992]

Figure 2.10 Manual harvesting of sago starch in eastern Indonesia.

a-d: Splitting a sago log. [photo nrs. 90.11-148-35, -36, -24, -E, Hatusua, West Seram mon19tue20nov1990]

e-g: Pulverizing the pith of a halved log with a special hammer- or adze-like tool. [photo nrs. 88.01-045-02, Hila village, Ambon janfeb1988 ; tc-190-12, Yoboi village, Sentani, Papua sat06aug2005 ; 90.11-148-31, Hatusua, West Seram mon19tue20nov1990]

h,i: Wedges used in splitting a log, and hammer- and adze-like tools to pulverize the pith. [photo nrs. 90.11-145-34, -35, Hatusua, West Seram octnov1990]

j: Adding water to pulverized pith to wash and leach out the starch. [photo nr. 88.09-063-05, Hila village, Ambon Island wed24aug1988]

k,l: Kneading pulverized pith with water to wash and leach out the starch; the fibres and cell walls will remain behind the fine-meshed gauze filter, while the starch-laden water passes through and settles in the trough beneath. [photo nrs. 90.11-145-23, -21, Hatusua, West Seram octnov1990]

m: Scooping out the wet starch from the settling trough after the supernatant water has been drained. [photo nr. 90.11-148-29, Hatusua, West Seram mon19tue20nov1990]

n: Storing the scooped-out wet starch in containers made of sago palm leaflets. [photo nr. 88.10-065-35, Lohiatala village, West Seram sat08oct1988]

Figure 2.11 Manual harvesting of sago starch on Siberut Island, West Sumatra Province, Indonesia (17-18jan1992).

a: **Felling a trunk with an axe.** [photo nr. 92.01-204-09]

b: **Tools of the trade: axe, tools for trunk splitting and debarking, rasps for coarse pith pulverization, tools for fine pith pulverization, and a container to transport the pulverized pith to the washing site.** [photo nr. 92.01-304-26]

c: **Further pulverizing rasped pith.** [photo nr. 92.01-204-20]

d,e: **Filling a carrying basket with pulverized pith for transport to the washing site.** [photo nrs. 92.01-204-21, -23]

f: **A washing site with trampling platform.** [photo nr. 92.01-204-18]

g: **Getting water to mix with pulverized pith on the trampling platform.** [photo nr. 92.01-204-25]

h: **Trampling the pulverized pith with water to leach out the starch.** [photo nr. 92.01-204-24]

Figure 2.12 Low- and intermediate-technology in mechanical harvesting of sago starch.

a: Felling a sago palm by chainsaw (leaf remains have been removed from the trunk). [photo nr. 89.05-084-15, Hatusua, West Seram, Indonesia fri05may1989]

b: Cutting a felled and cleaned sago trunk into logs by chainsaw. [photo nr. 89.08-094-32, Hatusua sat26aug1989]

c-e: Portable rasping machine to rasp the pith off the bark of log sections in the field. [photo nrs. 88.10-065-34, Lohiatala, West Seram sat08oct1988 ; tc-194-12, and -21, Hatusua thu11aug2005]

f,g: Revolving drums lined with synthetic fine-meshed filter cloth to wash starch from pulverized pith which is fed into the drum, washing water being supplied through an axially placed pipe (f: under construction; g: in operation). [photo nrs. 90.10-143-11, Waihatu, West Seram oct1990 ; 92.01-203-07, Tanjung, Tebing Tinggi Island, Riau Province, Indonesia]

3 Purpose of study

The transition from a traditional way of exploiting sago palm starch to large-scale exploitation methods brings about the need for more precise knowledge of when, where and how the accumulation of starch in the trunk takes place. And so, the original research aims as laid down in the reasearch proposal were to elucidate

- the starch accumulation in the trunk of the sago palm as a function of time and of physiological age of the trunk.
- the influence of environmental factors on growth and starch yield.
- the influence of suckering on growth and yield of the mother trunk.
- the primary production capacity of natural stands and the dynamics of this capacity.

The rather special growth and development pattern of the sago palm makes it impossible to draw extensively from the knowledge about well-studied plantation palms such as oil palm or coconut palm in this respect. Because of the multitude of factors to be investigated which are possibly influencing sago palm growth and development, it would be particularly desirable to study sago palms of known age and of the same genetic make-up. This wish could not be met forthwith as undisturbed growth and development can only be studied in undisturbed populations, and precisely these populations are made up of genetically diverse palms of unknown age. Therefore much of the research time available had to be spent on finding out how to determine a sago palm's age and how to deal with genetically diverse sago palms as the objects of study. Indeed, part of the research aims was shifted towards these issues.

3.1 Primary question: When, where and how is starch accumulated in the trunk of a sago palm?

Since the 1970s, the interest in the sago palm as a plantation starch crop has gained momentum. In the 1980s new, large-scale plantings saw the light in Malaysia and Indonesia where before there had only been cultivation by small-holders, or even only collecting from uncultivated stands. In the 1990s some large-scale exploitation schemes of natural stands were started in eastern Indonesia.

For small-holders and collectors a maximum starch yield per trunk or per man-hour is usually the main objective. Harvesting sago starch in the traditional way is laborious: the more starch one can get by processing one trunk, the better. Therefore, traditionally a trunk is considered ready to harvest when its starch content is estimated to be at its peak, an estimation based on the interpretation of outward characters of the axis by an experienced eye.

In large-scale plantations, where returns on investments come into play, maximum yield per unit time and per unit area are the main goals. Then it becomes important to know exactly how starch accumulation develops in time. It may, e.g., be more profitable to harvest an ageing trunk which is still slowly accumulating starch and let its place be taken by a younger faster-accumulating one, than to leave the older one till it has reached its maximum starch content.

Large-scale exploitation operations of natural sago stands can only be profitable and sustainable if the development of starch accumulation in time is understood and acted upon. Clean cutting and waiting for the palms to regenerate will probably not only give disappointing yields - as many trunks will be too young to contain a worthwhile amount of starch - , but may also change the habitat and impair regeneration.

For these large-scale operations to be successful, more accurate knowledge about when, where and how starch is stored in the trunk of a sago palm is needed, but this knowledge is still largely lacking. It is the purpose of this study to fill at least part of this gap. First of all I wanted to find out the relation between the age of a palm and the amount and distribution of the starch in its trunk. Secondly, I wanted to gain insight in what drives or influences this starch accumulation.

3.2 Special traits of sago palm growth and development relating to starch accumulation

Why would sago palm deserve so much special attention? Why cannot the extensive existing knowledge of the growth and development of the commercially important oil-, coconut and/or date palm be applied directly to sago palm? This is because sago palm has two conspicuous growth and development characteristics which most palm species do not have: multiple-stemmedness and hapaxanthy (see sections 'Description' and 'Growth and development' of Chapter 2.) as shown in Figure 3.1. The exceptionality of this growth pattern is illustrated by the following résumé of the distribution of tree architectural models among palms by TOMLINSON (1990:99-100) in his excellent book "The structural biology of palms":

> "In the architectural continuum described by Hallé and Oldeman (1970) that considers all trees (see Hallé *et al.* 1978) the palms are represented by four (out of the total 23) architectural models, which provide comparative reference points at an elementary level." One of these four models is *Tomlinson's model*: "Trees with the axis branched exclusively from the base, ... i.e. all multiple-stemmed palms. Two subdivisions are recognized depending on whether the individual axes are pleonanthic ..., which is much the most usual condition, or hapaxanthic, which is rare and represented by suckering species of *Metroxylon* ..., *Raphia*, and *Eugeissona* ..."

In only about 5 per cent of all known palm species do hapaxanthic axes occur; 95 per cent is pleonanthic (TOMLINSON 1990:45). Therefore, sago palm belongs to the even less than 5 per cent of all palm species which are hapaxanthic ánd grow according to Tomlinson's architectural model.

For Tomlinson's model of tree architecture, HALLÉ, OLDEMAN & TOMLINSON (1978:118) gave the following definition:

> "This architecture results from the repeated development of equivalent orthotropic modules in the form of basal branches which are initially restricted to the epicotyledonary region of the seedling axis (the first module), and the basal nodes in subsequent axes. Inflorescences may be terminal or lateral, growth of each module is either continuous or, less commonly, rhythmic."

As mentioned above, the axes of a sago palm (also called shoots, stems or trunks) are hapaxanthic with a terminal inflorescence. Terminal in two senses: a long vegetative period is concluded by one single, relatively short generative period. This flowering and fruiting stage is the final stage in a stem's life, after which the stem dies.
In suckering palms (also called clustering, clumping or multiple-stemmed palms) like the sago palm, the plant (as defined as the biomass which has grown physically uninterrupted from a single propagule) lives on through its suckers. These suckers in turn grow out to flowering stems and produce next generation suckers.

Figure 3.1 Diagrammatic drawing of sago palm's suckering and hapaxanthic habit.
(Source: DE CASTRO-DOS SANTOS 1981:178-179 (Plate 43, Fig.3: "*Metroxylon sagu*, le sagoutier asiatique réalise le modèle de Tomlinson à article hapaxanthique (J.B. Bogor, Indonésie, 1979)."))
[Reproduction permission requested.]

> "Hapaxanthy is not synonymous with monocarpy (literally once-fruiting), which relates to the individual plant. In multiple-stemmed palms individual axes can be hapaxanthic, but continued production of new vegetative shoots, as by basal suckers, maintains the individual." (TOMLINSON 1990:307).

The growth and development pattern of the sago palm may influence its starch storage pattern. Unlike the oil palm, coconut palm and date palm, the sago palm does not have to spend its assimilates on the formation of inflorescences and infructescences for most of its life. On the other hand, the formation of suckers - a trait shared with date palm - may be a drain on the assimilates for as long as these suckers are not 'independent'.

3.3 Secondary questions to be addressed first: How to determine age and genetic identity of a sago palm?

Observations to unravel the questions put forward in the above Section 3.1 should be made in undisturbed palm populations. This is why I came to work in semi-wild (once planted, but then neglected) sago palm stands, because in plantations or managed natural stands, the chance that normal growth and development of a palm is disturbed is too great. This is because in such exploited stands

- often also leaves are regularly harvested (for thatch; see Fig. 2.2 and 2.7g), and
- suckers which are not needed for ratoon growth are often pruned.

Moreover,

- there are usually no flowering or fruiting specimens to be found in exploited stands, as the trunks are usually harvested before they reach the flowering stage, let alone the fruiting stage.

Working with palms from semi-wild stands as the object of study brings about two new problems which will have to be addressed first:

- uncertainty about the age of the observed palm;
- genetic heterogeneity of the sampled palm population.

In unmanaged stands, no planting dates are available. Therefore, the age has to be estimated from morphological characteristics. Palm trunks do not have the convenient growth rings shown by cross sections of trunks of dicotyledonous and gymnospermous trees growing in seasonal climates. Other ways to approximate age have to be devised.

The stands I had to work with clearly showed morphologically different palms, which were indeed called by different names by the local population. As sago palm propagates almost exclusively vegetatively, these folk-taxonomic categories probably represent clones or groups of clones. I had to work with all the different folk taxa in the population as no single taxon was represented with enough individuals for my research needs. As this already proved problematic enough, one also has to have an idea about the place of these taxa in the spectrum of known sago palm taxa in the world to be able to gauge the extent of the validity of one's findings for clonal groups in other areas.

Therefore, before questions about the process of starch accumulation could be answered, age determination had to be addressed first. And before conclusions about these answers were drawn, it had to be made clear how representative - genetically speaking - the observed objects were.

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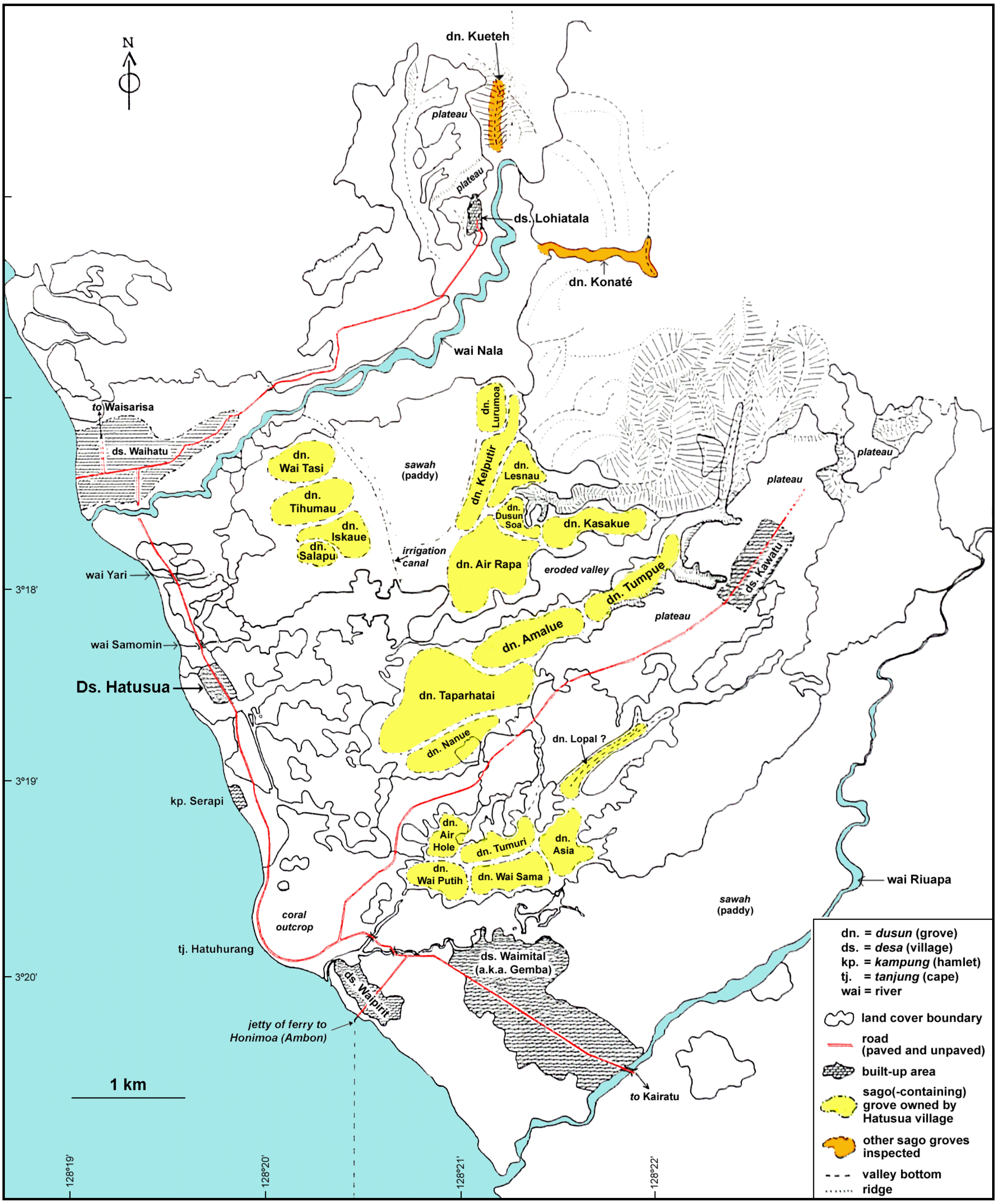

Sketch map of area around Hatusua village (Kairatu District, West Seram, Maluku, Indonesia) indicating some of the land cover and the approximate location of all sago groves (*dusun sagu*) belonging to Hatusua. Most of the sago palms destructively sampled or monitored for this study were growing in these *dusun* (the remainder in *dusun* around Siri-Sori Serani village on Saparua Island, Maluku, Indonesia).

(Base map and land cover boundaries derived from prints of aerial photographs (scale about 1 : 110,000) taken in May 1978 by the Royal Australian Air Force. Location of sago groves based on rough ground truth check and oral information by local inhabitants in 1988. Roads surveyed in 1988 on motorcycle, using the odometer to measure distance and a hand-held compass for direction. Latitude and longitude coordinates from Google Earth jan2009.)

4 Establishing the age of a sago palm: morphology and duration of developmental phases

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4.1 Relevance

Confronted with sago palm trunks of unknown age in which I wanted to investigate the influence of age on dry matter partitioning, in particular on storage of starch in the trunk, I had to devise a way to estimate that age from observable characteristics. These characteristics could only be morphological since I was not equipped to make other observations, e.g. physiological ones through chemical analyses of tissues or phloem sap.

The relationship between morphology and age in sago palm is only known in broad terms: a rosette habit with increasing number of leaves during the first few years, followed by a habit with trunk of increasing height with a more or less stable number of leaves on top during the next 5 to 15 years, and finally a tall trunk with leaves of decreasing size and a huge branched inflorescence on top. A more detailed morphological growth and development time table was needed, one with which it was possible to estimate a palm's age from morphological traits with an accuracy of at least one year. Such accuracy is needed if a recommendation for the right harvesting time based on this estimate is to be of any use in a plantation situation.

In this chapter, first it is explored what the options are for morphological age assessment in palms, noting the difference with dicot trees and gymnospermous trees. Two traits of palms which may help in this, viz. phasic development and continuity and regularity of growth, are introduced based on the work of TOMLINSON (1990).
Then the literature on the morphology, duration and growth rhythm of the developmental phases in sago palm is reviewed.
The main part of this chapter is devoted to the description of my observations on this morphology, duration and growth rhythm, mainly based on the destructive analysis of 38 mostly trunked palms, and the monitoring during a few years of 36 other trunked palms. As it could not be known beforehand which morphological features would be diagnostic of age and which ones not, some morphological details were recorded which proved not to be of use for age assessment. These details are reported here nevertheless because they are new to science.
Subsequently, relevance to age assessment of the observations is discussed in the light of existing literature and of the effects the environment may have had on the observed features.
Finally, based on all this, a new, more detailed morphological growth and development time table for sago palm is suggested.

4.2 Options for morphology-based age assessment in sago palm

Like in all monocotyledons, governing growth and development of a palm shoot (axis) is the fact that there is only one apical meristem. In general, all the cells that make up the trunk are formed in the apex: there is no secondary thickening of the trunk. There are some rare exceptions, but sago palm is not one of them:

> "It has been known since the late nineteenth century that some palms undergo a limited amount of diameter increase with age. ... The most extensive series of measurements were made by the Dutch botanist, J.C. Schoute in the early part of this century, mainly on palms cultivated at the Bogor (Buitenzorg) Botanic Gardens ... (Schoute 1912). He made repeated measurements of the diameter, at the same level, of individuals of many species over the period of his relatively short visit. His results showed that different species varied considerably in the extent to which stem diameter changed, ... There was little correlation with taxonomic group or plant size; palms with narrow stems ... as well as palms with wide stems (e.g. species of ..., *Metroxylon*, ...) showed no increase." (TOMLINSON 1990:162-163)

Thus, the age of a sago palm trunk cannot be gauged from its diameter. Nor are there any year-rings or seasonal rings in a cross section of the trunk to indicate age, as may be the case in trunks of dicotyledonous trees (such as gum trees) and gymnospermous trees (such as pine trees). If the latter types of trees are growing in a seasonal climate, the age of the tree - i.e. the age of its oldest part, viz. the base of the trunk - can be determined after felling the tree by counting the alternating rings of thick-walled and thin-walled cells visible on the transverse cut of the trunk base. Each ring of lighter thin-walled cells represents a period of fast growth (the growing season); each ring of darker thick-walled cells indicates a period of slow growth (towards the end of the growing season). In monocotyledonous trees, like palms, there is no secondary thickening of the trunk, so the age of a - felled - trunk cannot be derived from the regularity of the alternation of seasons laid down in any visible structural pattern of thickness growth of the trunk.

Other morphological characteristics to establish the age of an unknown sago palm have to be found.
The special growth and development pattern of palms in general can provide starting points for morphology-based age assessment, i.c. the traits of

- phasic development, and
- continuity and regularity of growth (no dormancy; leaves are formed one at a time).

TOMLINSON (1990:42-45) defines the five developmental phases in any palm's life as:

1. embryonic phase
   "embryonic development, from the zygote to the dormant embryo within the seed"
2. seedling phase
   "the phase involving reactivation of the embryo, its emergence from the seed and its development of a nutritional system (absorption of water and mineral nutrients, photosynthesis) independent of the food reserves provided by the seed endosperm"
3. establishment phase
   "the extended period of early development when there is gradual expansion of the seedling axis to the maximum stem diameter attained by the individual"
4. mature vegetative phase or adult vegetative phase
   "the continued extension of the vegetative axis, adding segments of fixed diameter and leaves of constant size"
5. mature reproductive phase or (adult) reproductive phase
   "the appearance of flowers (on lateral axes) and, consequently, the initiation of the ability to fruit ..."

The figure illustrating this phasic development is reproduced here (Fig. 4.1).

TOMLINSON stresses, however, that transitions are gradual:

> "To designate discrete phases in the ontogenetic development of a plant that shows a continuity of growth processes might imply that there are abrupt transitions from one state to another, with concomitant major changes in physiological processes. Most palms grow in non-seasonal or mildly seasonal climates in which gradual and ordered initiation and expansion of parts is possible. A continuous ontogeny, therefore, characterizes palms and phases of development are largely arbitrary ..."

I will use the term generative phase instead of mature or adult reproductive phase. This to avoid confusion with the reproduction of a sago palm axis through its suckers, which may take place already during the establishment phase of the axis.

As the above phase descriptions indicate, changes from one phase to the other may be physiological and/or morphological:

> "The major physiological step is from embryo to seedling, since this involves the breaking of seed dormancy; there may also be a major change to the reproductive state with the onset of flowering. Apart from increase in size, major morphological features which distinguish each

> phase include changes in the morphology of successive leaves, changes in stem diameter, and the production of flower-bearing axes." (TOMLINSON 1990:43)

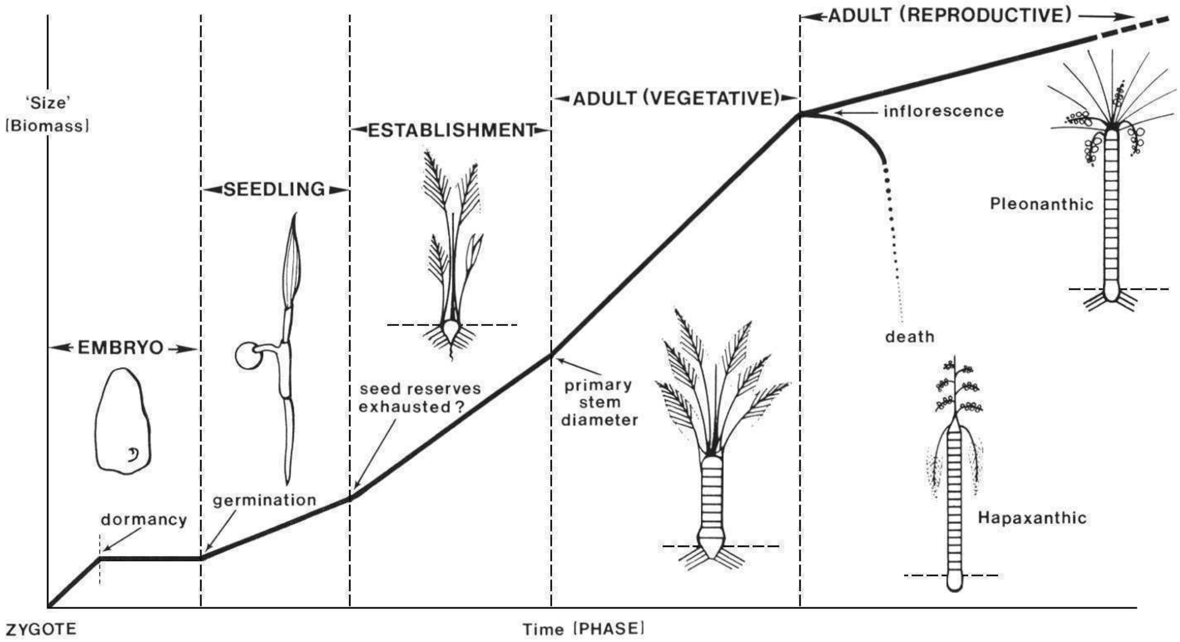

FIG. 2.1 *Phasic development in palms, represented schematically. Axes dimensions are abstract, but could be seen as logarithmic rather than linear. Articulations between phases are less abrupt than implied. Hapaxanthy versus pleonanthy represent alternatives in the adult reproductive phase.*

Figure 4.1 Phasic development of palms.
(Source: TOMLINSON, P.B. "The structural biology of palms". - Oxford (UK) : Oxford University Press, 1990. - p.42. (By permission of Oxford University Press))

I want to derive palm age from palm morphology, and then try to link the physiological processes of starch accumulation and mobilisation to the age thus estimated. Therefore, in this chapter I am only concerned with morphology and not yet with physiological processes.

Apart from the distinct developmental phases during the life of a palm axis, the unperturbable pace in which the axis grows seems to be another useful feature in estimating its age, because this continuity and regularity of growth opens the possibility to extrapolate observations made over a limited period to a longer one.
Outlining what determines the development of palm architecture, TOMLINSON (1990:41) gives as one of the characteristics that

> "growth of each axis is continuous, i.e. the apical meristem seems incapable of dormancy or rest, even though the rate of growth may fluctuate, sometimes seasonally, sometimes according to more random environmental variations."

And another:

> "Leaves are produced in a regular acropetal order with an attachment that completely encircles the stem circumference, i.e. they are borne singly at each node. Leaf number, therefore, becomes a very accessible marker for growth events."

Linking leaf number directly to age may still be not as straightforward as the above mentioned two characteristics promise, as TOMLINSON (1990:23) himself cautioned earlier in his book:

> "It is also assumed ... that age determination [in palms] is relatively easy as compared with tropical trees in general because leaf scars are obvious and more or less permanent, and that rates of leaf production can be determined over a limited period and extrapolated to the total life span of the tree. ... Great care is needed in applying extrapolated values since the rates of individual palms do vary enormously ..."

And quoting work on the arecoid palm *Archontophoenix cunninghamiana* by WATERHOUSE & QUINN (1978), TOMLINSON (1990:170-171) remarks on the "inability to make developmental inferences from comparison of different individuals."

> "...; depauperate palms will have short internodes and produce fewer leaf scars per unit time than vigorous palms. Numbers of leaf scars are therefore not a reliable method of measuring tree age (even though it is widely practiced). ... There seems to be no simple independent measure of palm age from morphology or anatomy alone, even though all the tissues at any one level are all of the same age."

4.3 Literature review on morphology and duration of the developmental phases of sago palm

What is known, in terms of morphology, about the above-mentioned phases (embryonic, seedling, establishment, adult vegetative and generative) and the transitions from one phase into the next in sago palm? And are there any published observations on the growth rate and rhythm during each phase, or on the duration of these phases?

- Embryonic phase

I know of no morphological study of the entire development from ovary to mature fruit in general, or from zygote to mature embryo in particular.
On the final part of the embryonic phase JONG (1995:122) reports that after fruits have become mature (i.e. full-grown), they undergo further ripening during which the exocarp turns from green to straw-coloured, the endosperm hardens en becomes bony, and the testa turns from not distinct, via white and slimy, to thick and dark brown.

A mature fruit is depressed-globose, about 3 - 5 cm in diameter, covered with 18(-19) vertical rows of rhomboid scales, pointing downwards (Fig. 4.2c). The layer of scales (exocarp) is lined inside with a white spongy layer (mesocarp). The seed is subglobose, about 3 cm in diameter, firmly embedded in shiny cream-coloured firm flesh (sarcotesta) which turns pinkish when exposed to air ; the testa is dark brown (Fig. 4.2d left). The endosperm is homogeneous, horseshoe-shaped in longitudinal section because of a large chalazal cavity at the distal side (Fig. 4.2e top). The embryo is embedded in the endosperm near the bottom of the chalazal cavity ; it is cylindrical with a flat end towards the proximal side of the seed where there is a smaller, second peripheral cavity, and a tapering or rounded end towards the chalazal cavity (Fig. 4.2f). Seeds often fail to develop, resulting in fruits filled with the cream-coloured flesh only (Fig. 4.2d centre and right, 4.2e bottom).

SCHUILING *et al.* (1993:81) found that the diameter of fruits in which the seed did not develop is about 87% of that of seeded fruits (Fig. 4.2d). EHARA *et al.* (1998) collected 67 seeded and 14 unseeded fruits from Batu Pahat (Johor, Malaysia). On average, the seeded fruits had a diameter of 5.1 cm, a length of 4.9 cm and a fresh weight of 54 g, whereas the unseeded ones had about the same diameter (5.0 cm), were a bit longer (5.3 cm), but much lighter (36 g). (They speak about 'pollinated' and 'unpollinated' fruits, although they did not investigate the cause of the presence or absence of seeds in the fruit.)

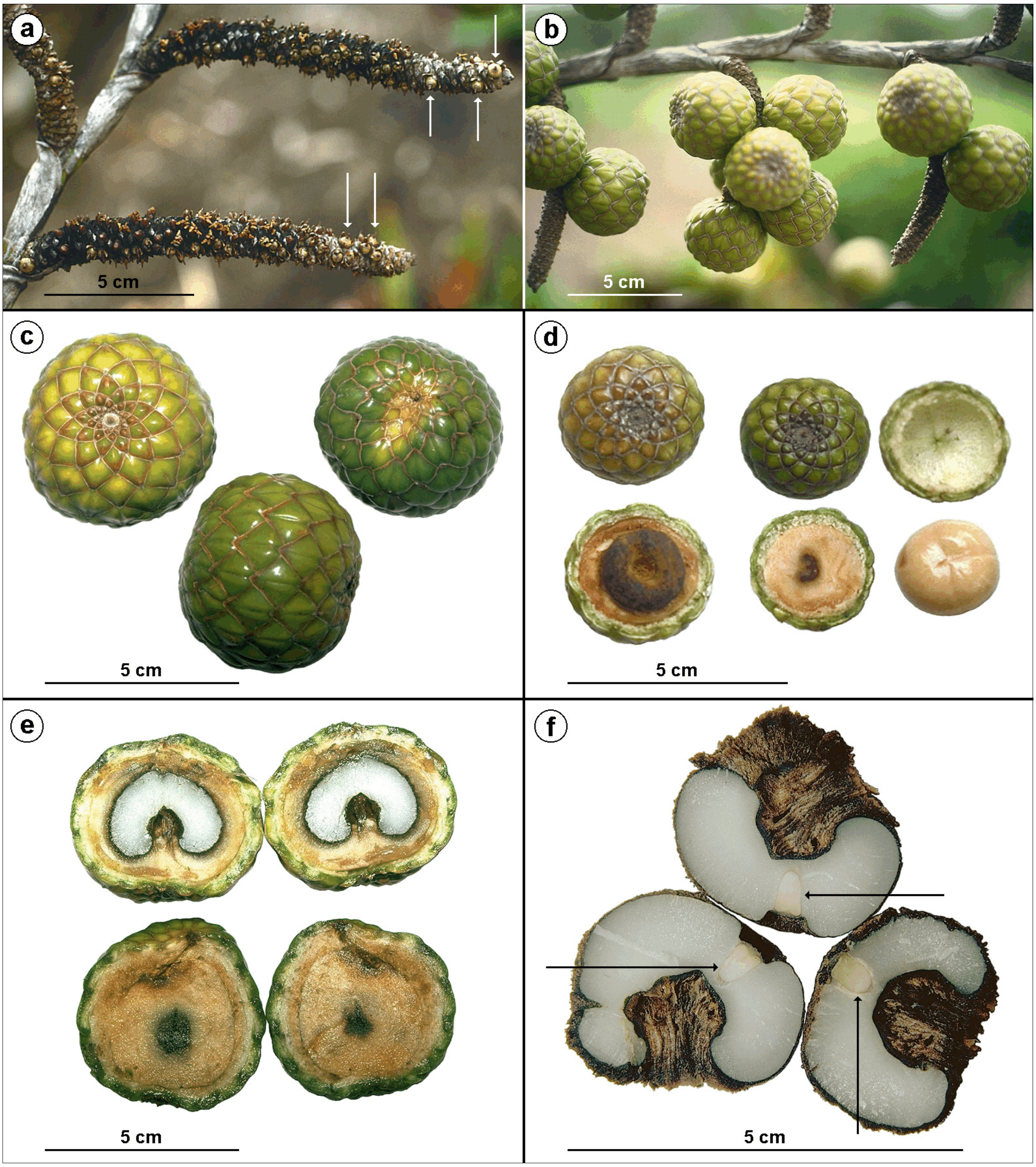

Figure 4.2 Embryonic phase of the sago palm.

a: **The zygote has been formed inside the ovary, and the ovary then starts to develop into a fruit. The arrows indicate a few of the very young fruits becoming visible on 3^rd^-order inflorescence branches.**
[photo nr. 90.08-133-02 (Dalat (Sarawak, Malaysia) thu09aug1990)]

b: **Immature fruits on 3rd-order inflorescence branches.**
[photo nr. 90.08-133-06 (Dalat (Sarawak, Malaysia) thu09aug1990)]

c: **Mature fruits in top-view (left), bottom-view (right) and side-view.**
[photo nr. jong01 (Sarawak, Malaysia 1987) (photo by JONG Foh Shoon, adapted)]

d: **Relatively small, but mature, transversely opened/cut fruits, with (left) and without seed.**
[photo nr. 92.02-210-23, variety Hange (Ternate (Maluku, Indonesia) mon03feb1992)]

e: **A seeded (top) and an unseeded fruit cut lengthwise through the middle (fruit apex pointing down).**
[photo nr. jong02 (Sarawak, Malaysia 1987) (photo by JONG Foh Shoon, adapted)]

f: **Seeds cut lengthwise through the middle. The arrows point at the embryo embedded in the endosperm.**
[photo nr. jong03 (Sarawak, Malaysia 1987) (photo by JONG Foh Shoon, adapted)]

From the germination study by JONG (1995:120-130) it is clear that in sago palm seeds it is the duration of the maturation and ripening process rather than of dormancy thereafter that determines the duration of the embryonic phase. The seeds are recalcitrant: once they are fully ripe, germination cannot be postponed by lowering humidity and/or temperature, while at the same time keeping them viable. In other words, the seeds are not storable and will die when kept in an environment not conducive to germination.

If there is no seed dormancy, the embryonic phase has the same duration as the period between female anthesis and fruit ripeness. JONG (1995:108) monitored the duration from first anthesis to last fruit fall in 5 palms in Sarawak and found an average of 20.2 months. He reports no data on the development of a single flower. Normally female anthesis in a palm lasts about 50 days (JONG 1995:97). Fruit set occurred 3 to 4 days after opening of a hermaphrodite flower (JONG 1995:94,97). How he established the time of fruit set is not made clear, but probably by the observation that the ovary had swollen.

- Seedling phase

ALANG & KRISHNAPILLAY (1986:123) made an anatomical study of sago palm seed and described germination. They state that "the blunt, distal end of the embryo encloses the embryonic initials while the tapered end of the embryo is actually the single cotyledon which grows into the endosperm during germination to form the absorptive haustorium. ... During germination the embryo expands and pushes out the region of endosperm and testa immediately above the blunt end of the embryo." This region is the operculum (Lat.: lid). EHARA *et al.* (1998) describe the outwardly visible germination process in more detail and record the sequence of root and shoot appearance, stating that "in the seedlings observed ..., the first and second leaves had no leaflets, and the third had two leaflets".
JONG (1995:128) found that, given the right humidity and temperature, 50-70% of ripe fruits germinated within 8 weeks, an inhibitory substance in the fruit husk and/or the sarcotesta probably preventing ripe seeds from germinating even sooner. ALANG & KRISHNAPILLAY (1986:123) found that if a ripe seed was divested of its fruit tissues and planted proximal end uppermost, a strong shoot and root system developed within a month of planting. They state that "the operculum, does not appear to present resistance to germination in *Metroxylon* ..." The latter observation is not in accordance with JONG (1995:125) who found that loosening the operculum did improve germinability.
I did not find any study on how long it takes for a sago palm seedling to deplete the food reserves in the endosperm.

-- Leaf unfolding rate (LUR)

Regularity of leaf appearance seems to be a feature of the sago palm right from the start. EHARA *et al.* (1998:216-217) observed that "although the time to germinate varied from one to 23 days among 15 seeds, the timing of subsequent rooting and shoot emergence were similar", and they found it "remarkable that roots and leaves emerged at regular intervals in the current experiments." They note that the first leaf emerged 12-15 days after germination - germination being recognized when the operculum is pushed up - and that "in the seedlings observed ..., the first and second leaves had no leaflets, and the third had two leaflets", but they do not state the time interval between their emergence.

- Establishment phase (E-phase)

In theory, during this stage a palm trunk hardly grows in height: internodes remain very congested, the first ones very narrow, each next one a little wider than the one on which it grows, the trunk growing into an inverted cone until the ultimate trunk diameter is reached.

Only then will a palm's trunk grow upward: the start of the Adult Vegetative phase. For a sago palm grown from seed, I did not find any documentation of actual observations of this trunk growth pattern, nor of the direct observation of the duration of this phase. The reason for the lack of studies on this subject is probably that in plantation practice sago palms are not grown from seed but from suckers.

-- Leaf unfolding rate (LUR) and duration

FLACH (1977:161, 1997:15) assumes that in the E-phase two leaves per month are formed if light conditions are optimal, because he found that this LUR was reached during the summer period in a hothouse at Wageningen University (52°N), while during the winter period the LUR was much lower. Other experiments with seedlings in these hothouses under probably sub-optimal ecological conditions showed rates of 1 leaf per 17 to 28 days (FLACH *et al.* 1986, PAQUAY *et al.* 1986).
Following the growth of 4 seedlings, FLACH (1977:161) recorded the increasing number of leaflets per leaf for a certain period. Starting with 2 leaflets on the first leaf (leaf number 1), at the end of this period the seedlings had produced 54-60 leaves (not counting, apparently, the first leaflet-less leaves), the youngest leaf having 30-33 pairs of leaflets. Linearly extrapolating to an assumed 50 pairs of leaflets on a full-grown (adult-sized) leaf, he concluded that this full size is reached with leaf number 80 to 90. At the assumed LUR of 2 leaves per month, he estimated the E-phase duration at 40-45 months.

KUEH (1995:69), reporting on fertilizer trials at the Peat Experiment Station at Stapok (Sarawak, Malaysia) from 1976 to 1988, states that from the 2nd to the 6th year after field-planting suckers, the average LUR was 15.7, 16.7, 13.7, 10.8, and 9.9 leaves per year, respectively, and that "trunk formation usually initiates in the fourth year".
JONG, doing field experiments at the Sungai Talau Deep Peat Experimental Station at Dalat (Sarawak, Malaysia), also reported on the performance of sago palms raised from suckers. In the 1st to the 4th year of growth, the average LUR was 11.1, 15.5, 14.0 and 11.8 leaves per year, respectively, the change from E-phase to AV-phase taking place 3.5 to 4 years after planting (JONG 1988).
In experiments with different sucker sizes as starting material he observed that the average LUR in the first 6 years after planting was 7.5, 10.8, 11.9, 11.8, 9.8, and 8.6 leaves per year, respectively, stating that the onset of trunk formation was after the 4th year (JONG 1995:41-42).
In these three sets of observations, LUR in the E-phase first increases, and then decreases again towards the start of the AV-phase.
In spacing experiments JONG observed that at the widest spacing (13.5 m x 13.5 m) the LUR in the first 8 years after planting was 14.9, 12.3, 11.8, 12.0, 9.9, 9.6, 10.7, and 9.0 leaves per year, respectively, stating that the first three years were the years before trunks were formed (JONG 1995:50,53).
In this set of observations, LUR in the E-phase decreases from the first year to the onset of the AV-phase.

The E-phase in palms which start as a sucker may not be governed solely by the number of leaves/nodes/internodes it takes to reach the maximum trunk diameter. In Sarawak, JONG counted the leaf scars on 20 such palms that died after fruiting and found that the number of scars on the stem part with congested internodes - which grows horizontal in suckers, at least in the beginning - differed considerably, while the number of scars on the part with the elongated internodes (the vertical part) was about the same (JONG F.S. pers.comm. 1994, in FLACH 1997:15).

- Adult vegetative phase (AV-phase)

-- Morphology

Average morphology during the AV-phase is presented in the general description of the sago palm in Chapter 2.
The variation found in the field is illustrated, e.g., by SHIMODA & POWER (1986). Surveying sago resources along the last 80- to 90-km downstream part of the Sepik River in PNG, they found that "cultivated-type" (as opposed to wild-type) trunks "at harvest time (just before flowering)" had a length of 7.9-11.8 m, with 69-93 leaf scars, 14-22 living leaves, an average internode length of 8.5-12.9 cm, and an average diameter of 37- 44 cm, an exceptionally large specimen having a diameter of 65.6 cm.

-- Leaf unfolding rate (LUR)

For the sago palm in the AV-phase, FLACH repeatedly claimed - most recently in 1997 - that 12 leaves per year are formed:

> "Healthy palms under good conditions carry approximately 24 leaves or fronds. ... Each month, one new frond appears out of the growing point, and the oldest one dies." (FLACH 1997:12)

Proof for this claim is not presented; it seems to be based on general impression rather than actual measurements.

In NPK experiments started in 1976 at Peat Experimental Station, Stapok, Sarawak, "the mean frond production for the years 1978 to 1982 was 11.78 fronds/year" (TIE *et al.* 1987:117). As they also report that "based on field observations and results obtained from Stapok and Sg. Talau Peat Research Stations" the palms would start to form a trunk after 4.5 years of growing on deep peat (starting as a sucker), probably some E-phase years are included in calculating this mean LUR.

For palms growing on deep peat in Sarawak, JONG found that the LUR dropped below 10 per year after the E-phase (JONG *et al.* 1995:82, JONG 1995:53).
KUEH (1995:69) suggested that the decrease of the LUR at the transition from E-phase to AV-phase could be caused by a shift in sink strength from leaf production to trunk and starch production.

-- Duration

It is difficult to establish the start of the AV-phase from the outside, i.e. without taking off the leaves to see what is underneath the sheaths. Also, the transition from vegetative to generative in the apical meristem does not become outwardly visible until several months later. Therefore, reports on the duration of the AV-phase that do not include any dissecting should be considered with caution. Reports that speak of the 'maturation' of the trunk rather than of the trunk becoming generative do not provide unambiguous information on AV-phase duration either. Often, by mature is meant harvestable. For example, KUEH *et al.* (1987) found that sago "reached maturity in 9-11 years" on "good mineral soils", "whereas on peat soils ... it came to maturity in 10-14 years". From TIE *et al.* (1987), who are reporting on the same investigations, it can be gathered that years from planting as a sucker is meant. This quote also illustrates that the effect of the environment is a further confounding factor in establishing the duration of the AV-phase.

FLACH (1983:16) suggested that the total number of leaves produced during the vegetative period of a sago palm axis may well be genetically determined, i.e. the same for all axes of a given clone. This in accordance with such monocots with hapaxanthic axes like banana and sisal. This would imply that by counting leaf scars on the trunk, one could establish the relative advance the axis would have made in the vegetative phase.

- Generative phase (G-phase)

-- Morphology

A well-illustrated description of the architecture of the full-grown inflorescence of *Metroxylon vitiense* and *Metroxylon sagu* is given by TOMLINSON (1971). He investigated one specimen of each, the *M. sagu* being "an old specimen ... in the lowland part of the Botanic Gardens at Lae in the Territory of New Guinea".
Features of the inflorescence shared by *M. vitiense* and *M. sagu*:

> "Flowering involves a major change in the axis. Foliage leaves are progressively reduced in size ... The uppermost series of these progressively reduced leaves have branches developed in their axils. These branches are branched obviously twice again ..., so that we may speak of first-, second- and third-order branches (ax_1, ax_2, ax_3). The third-order branches (ax_3) are the conspicuous flower-bearing parts of the panicle ... All branches bear modified leaves (bracts) throughout. These bracts are progressively reduced in size along each branch. Bracts on the main axis may be referred to as first-order bracts (subtending first-order branches) and so in order we have second-, third-, ... up to fifth-order bracts ($br_{1\text{-}5}$). The rule of branching is very simple; each bract subtends a single branch. Branches are sometimes partly adnate to their parent axis, so that the branch does not always arise directly at the node. Exceptional bracts which subtend no branch are called sterile or empty bracts and a number occur at the base of each first-order branch and again towards the end of each axis ... This unbranched basal part of the first-order branch can be usefully referred to as the peduncle, and so we may speak of bracts in this region as peduncular bracts. ... Leaves, bracts and first-order branches are spirally arranged on the main axis but bracts and branches of second and third order are distichous (two-ranked). Bracts of the fourth order are again spirally arranged." (TOMLINSON 1971:53-54)

Hereafter, the branches of successive order up to the flowers are described in detail, starting with *M. vitiense* and indicating the ways in which *M. sagu* differs. A conspicuous difference is the attitude of the ax_2, which is pendulous in *M. vitiense* and rigidly horizontal in *M. sagu*.

A description of the development of the inflorescence of *Metroxylon sagu* up to the full-grown state has been largely lacking so far; no wonder considering the poor accessibility of the inflorescence and the long time it takes from flower initiation in the growing point to the maturation of the fruits.

Some 'from the ground' observations on the development of the inflorescence were already mentioned by DEINUM & SETIJOSO (1932:107), who worked in the Moluccas as agricultural extension officers:

> "*Bij de bloeiwijze onderscheidt men drie stadia. In het eerste stadium heeft de bloemtros veel weg van een hertengewei, met dikke knoppen bezet. In het tweede stadium veranderen deze knoppen in trossen. In het derde stadium vormen de trossen weer kleine trosjes, waaraan de bloempjes ontstaan*"
> = “[In flowering, three stages are distinguished. In the first stage, the inflorescence much resembles a deer’s antler studded with thick buds. In the second stage, these buds change into spikes. In the third stage, the spikes put out small spikes again on which the small flowers grow]."

A photograph of each of the three stages illustrates their description (Fig. 4.3). They give no time table for these stages.

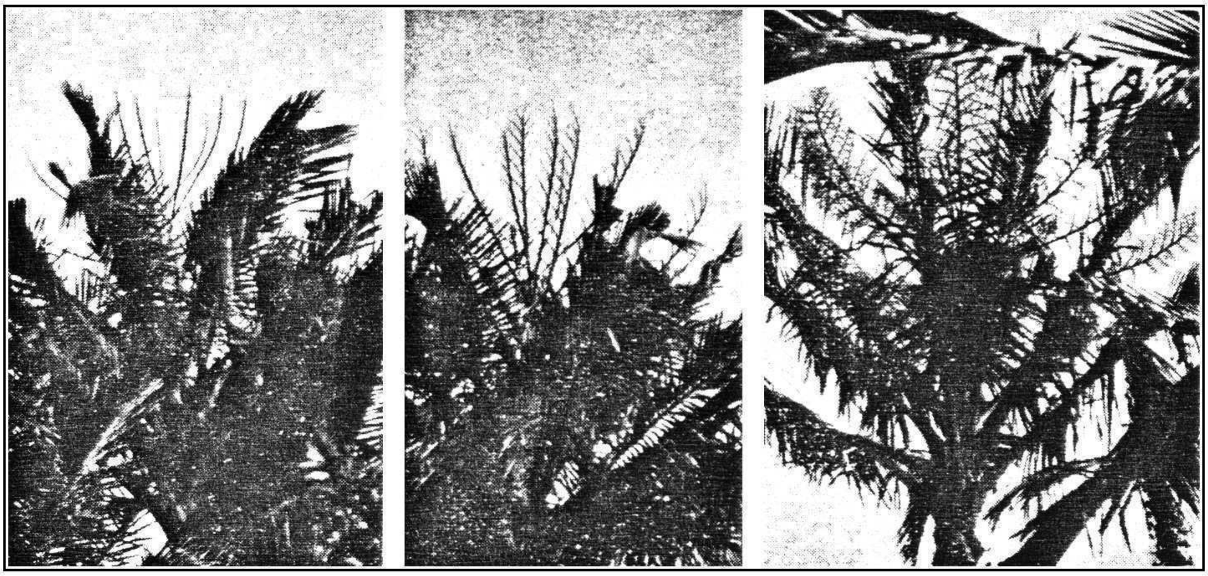

FIG. 1. BLOEISTADIA VAN DEN SAGOPALM.

Figure 4.3 Flowering stages of the sago palm. (Source: DEINUM & SETIJOSO 1932:107)

-- Leaf unfolding rate (LUR)

FLACH (1997:14) assumes that in the G-phase the "average speed of leaf formation" increases to 2 leaves per month.

-- Duration

The duration of the G-phase of the hapaxanthic axis of a sago palm may be defined as the time span between the first morphologically observable sign of inflorescence development in the apical growing point and the shedding of the last mature fruit. After this, the axis will decay and all of its tissues will eventually die. The end of the G-phase thus defined is clearly visible, but, as mentioned above, the transition from AV-phase to G-phase is not. Therefore, also reports on the duration of the G-phase that do not include any dissecting should be treated with caution. A case in point with a particularly vaguely indicated start of the G-phase is the sago palm description by KIEW (1977:151) in which he states that "the development of the inflorescence to the production of the ripe fruit lasts about two years".
On the more visible last stage of the G-phase, the fruiting stage, JONG (1995:116) reports that in 5 spineless palms in the Dalat and Mukah regions of Sarawak "the duration of fruit growth from anthesis to last fruit drop varied from 19 to 23 months".

4.4 Observations on morphology and duration of the developmental phases of sago palm

Of each individual sago palm that was systematically studied, a data sheet with all the primary observations (including photographs and in some cases line drawings) was put together. Also some tables with secondary data were included. Together, these so-called Sago Palm Data Sheets form the actual record of my morphological observations. They are appended as Appendix A, B and C. In this section these observations are elucidated and summarized.

4.4.1 Materials & methods (general)

- Palms

Plant material consisted of palms in semi-wild sago palm stands on the alluvial coastal plain near Hatusua village (3º18'30"S, 128º19'45"E) in Kairatu District, West Seram, and on hilly terrain near Siri-Sori Serani village (3º35'S, 128º42'E) on Saparua Island. Details for each individual palm are given in the Sago Palm Data Sheets.

Because of the long growth cycle of the sago palm (from seed to seed in 10-25 years), monitoring a single palm's growth and development through its entire life poses a problem. During my relatively short field work period on Seram and Saparua (mid 1988 to the end of 1990, plus one week in February 1992), only short periods in individual palms' lives could be observed directly. To tackle this problem, I had to resort to making observations on different palms and trying afterwards to rank the observations into a consecutive time order, taking care that all the major developmental phases of the palm (E, AV and G) be covered. Thirty-six palms were monitored for 4 to 34 months (App. C). Thirty-eight other palms were observed destructively, 37 of them (App. A) being the same ones as used for studying the trunk starch content (Chapter 7), and an extra one (App. B) especially for the morphological study of the transition from the E-phase to the AV-phase. The destructive method allowed for very thorough morphological (including anatomical) observations.
Studying different phases of a process simultaneously on different individuals, rather than studying the process 'in real time' on one individual is often a completely valid approach to studying processes in time. In this case, where palm ages had to be estimated and palm genetic make-up - with its possible influence on growth and development rate - was not the same for all individuals studied, caution with this approach is called for.

As chance permitted, some outwardly visible characters were recorded of individual palms in other locations, namely during excursions in January/February 1992 to Siberut Island (West Sumatera) and to Halmahera (Moluccas). Where appropriate, these findings are discussed here together with those of the more systematically observed palms mentioned above.

Further details on materials and methods are given in the sections on observation results of the different developmental phases as they are more easily understood directly in combination with these results.

- Habitat

A number of environmental properties was routinely measured with each palm felled or monitored, because of their possible influence on growth and development. If any anomaly would surface, the environmental data collected could have explanatory value. (See the 'Habitat' section in each of the Sago Palm Data Sheets.)

Recorded information on vegetation type is limited to mentioning the tree species growing within a radius of about 10 to 15 m around the palm at hand as they were known to my local assistants. No formal identification of species was done.

Soil samples were taken within 1 metre distance from a sampled trunk with an Edelman soil auger of 120 cm length. Identification of horizons and textures was based on the booklet "Guidelines for soil profile description" (FAO 1977).

The salinity and acidity of the groundwater in the hole that was formed by taking out the soil sample was measured using a combined digital EC/pH meter from Eijkelkamp Agrisearch Equipment, Giesbeek, Netherlands (product nr. 18.51).

4.4.2 Observation results

No systematic observations were done on the morphology and duration of the embryonic and seedling phases of the sago palm.
If there is no seed dormancy, the embryonic phase has the same duration as the period between female anthesis and fruit ripeness, i.e. the last stage of the generative phase of an axis. On the basis of from-the-ground-observations of one tree (Fig. 4.35), the period between full extension of the whole inflorescence and shedding of all the fruits is estimated at one to one and a half year.

In Table 4.1 a general overview is presented of the morphological data gathered from 37 destructively studied palms in the E-, AV- or G-phase. The integral data of these palms are presented in Appendix A (palm numbers 01 through 37).

Table 4.1 Morphological (including anatomical) data of various folk varieties of sago palm in various developmental phases (Dev. phase) from the villages Hatusua (Seram Island) and Siri Sori Serani (Saparua Island). Palm numbers refer to the numbers in the appended Sago Palm Data Sheets ; they only reflect the chronological order in which the palms were examined.

Palm #	Variety	Dev. phase	Trunk (ax_0) height (m)				Largest trunk width (cm)	Number of AV nodes			Number of ax_1-s of inflorescence
			leafless	leaf-bearing	rachis (= ax_1-bearing)	total		leaf scars on trunk	green leaves	spear leaf + leaves inside*	
01	Ihur	E	0.00	0.00	-	0.00	-	-	2	9	-
02	Tuni	E	0.00	0.00	-	0.00	-	-	5	7+?	-
03	Tuni	G	13.15	0.00	2.50	15.65	62	144	0	-	27
04	Makanaro	G	14.40	0.00	2.00	16.40	50	100	0	-	19
05	Ihur	G	14.50	4.80	1.80	21.10	60	100	18	-	24
06	Ihur	AV	9.50	n.r.	-	n.r.	56	69	≤17	20+?	-
07	Ihur	AV	10.35	1.35	-	11.70	52	92	17	25	-
08	Samakika (3x)	AV	4;4.5;3	n.r.	-	n.r.	n.r.	n.r.	10;12;15	n.r.	-
09	Tuni	G	17.50	1.50	-	19.00	57	121	20	32+?**	?
10	Molat	AV	9.90	2.30	-	12.20	56	63	21	22	-
11	Tuni	AV	10.70	2.10	-	12.80	64	71	20	23	-
12	Tuni	AV	6.00	1.90	-	7.90	54	33	14	20	-
13	Molat	AV	8.30	1.80	-	10.10	53	53	16	19	-
14	Molat Berduri	AV	8.10	2.75	-	10.85	61	46	22	21	-
15	Tuni	AV	9.25	n.r.	-	n.r.	55	57	16	n.r.	-
16	Tuni	AV	12.05	1.60	-	13.65	60	78	19	21	-
17	Tuni	AV	7.85	2.45	-	10.30	55	43	19	24	-
18	Molat	G	4.45	3.15	1.65	9.25	54	63	17	-	18
19	Putih	AV	9.05	1.15	-	10.20	50	72	14	19	-
20	Putih	AV	8.55	1.40	-	9.95	54	54	14	19	-
21	Putih	AV	12.25	1.55	-	13.80	53	70	14	21	-
22	Tuni	AV	11.85	1.55	-	13.40	n.r.	90	21	24	-
23	Tuni	AV	15.40	1.30	-	16.70	n.r.	103	16	22	-
24	Tuni	G	16.15	1.30	-	17.45	n.r.	129	19	12***	27
25	Ihur	AV	7.65	1.90	-	9.55	59	60	21	26	-
26	Ihur	AV/G	12.85	1.40	-	14.25	57	90	21	19+?	n.r.
27	Tuni	AV	14.60	1.55	-	16.15	61	107	19	17+?	-
28	Tuni	G	14.75	5.05	2.00	21.80	61	115	27	-	27
29	Molat Berduri	G	11.70	3.95	0.35	16.00	60	101	28	-	22
30	Molat	AV?	7.60	1.45	-	9.05	51	55	16	16+?	0?
31	Molat	AV	6.95	1.50	-	8.45	48	50	16	17	-
32	Tuni	AV?	14.45	1.55	-	16.00	61	109	19	18+?	0?
33	Molat	AV?	15.15	1.60	-	16.75	64	137	? c.20	n.r.	n.r.
34	Tuni	G	15.20	4.65	2.40	22.25	62	115	25	-	27
35	Ihur	G	7.95	4.60	2.35	14.90	49	100	27	-	23
36	Makanatol	G	19.65	4.55	1.60	25.80	60	165	28	-	20
37	Ihur	G	13.60	2.25	-	15.85	63	85	24	19	19

* up to and including the smallest primordial leaf hood which can be peeled from the growing point. For various reasons this was not always possible, in which case "+?" is added to the number of leaf primordia actually seen.

** of which Sp + c.16 'real' leaves (with leaflet primordia) and - at least - 15 br_1-s (with 'top-ribbon', without leaflet primordia; G-phase inferred from that, but actual ax_1-buds not yet detected); rest damaged (uncountable) by longitudinal sectioning for S.E.M.

*** `lf-XII` and up have an ax_1-bud in their axil. Therefore, there are Sp + 11 = 12 'real' leaves, the rest - 27 - are primordial br_1-s.

n.r. = not recorded ; - = not applicable ; E = Establishment phase ; AV = Adult Vegetative phase ; G = Generative phase.

4.4.2.1 Establishment phase (E-phase)

- Morphology

As sago palm seed or seedlings were not readily available in my research area, I did not make any observations on seedlings. I only made observations on a few suckers (see Appendix B, and data sheets of Palm#01, #02 and #37 in Appendix A).
Figure 4.4 shows that the basal part of the trunk formed during the E-phase is irregularly shaped in suckers, whereas in a seedling this part is smoothly expanding from the base up.

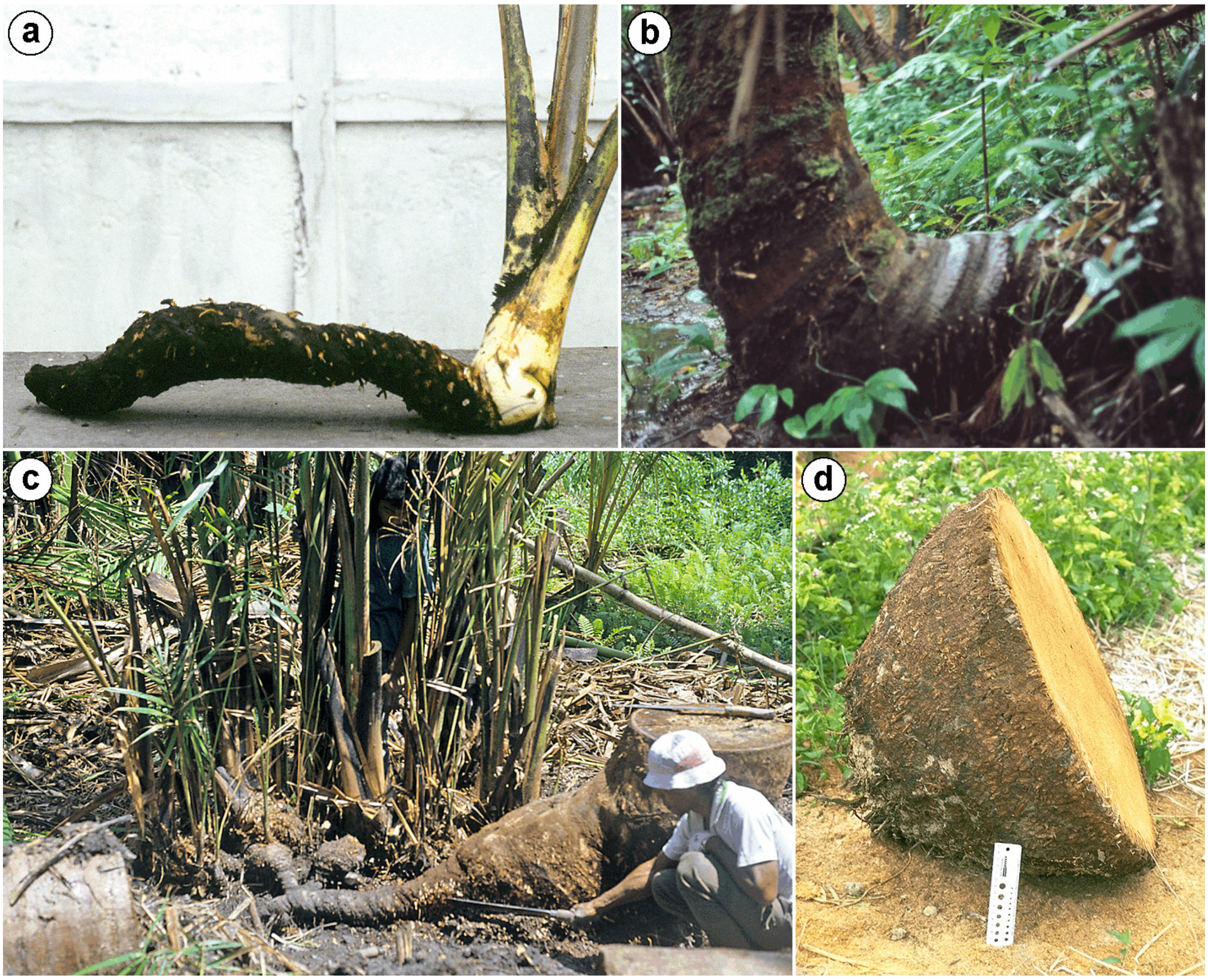

Figure 4.4 Growth and development of a palm trunk which starts as a sucker compared to a palm trunk which starts as a seedling.
a: Young sago palm sucker, roots and remains of dead leaf bases removed; whole stem horizontal.
b: Full-width trunk of a sago palm which started as a sucker; transition of horizontal to vertical trunk part.
c: Excavated base of sago palm which started as a sucker, with next generations of suckers.
d: Trunk base of a coconut palm (seedling; coconut is a non-suckering palm); excavated, all roots removed.
[a: photo nr. 88.11-069-06 (Palm#02, Hatusua, Seram mon24oct1988) ; b: photo nr. 90.04-114-33 (Alang, Ambon wed25apr1990); c: photo nr. 89.10-096-06 (Palm#18, Hatusua, Seram sat09sep1989) ; d: photo nr. tc-111-26 (Ubud, Bali thu11jul2002)]

The convex outline of a seedling trunk base as shown in Fig. 4.4-d is reached when the ratio between height increase and width increase (dh/dw) increases with each consecutive internode. As demonstrated in Figure 4.5, the outline would be straight or concave if this ratio would be constant or would decrease, respectively.

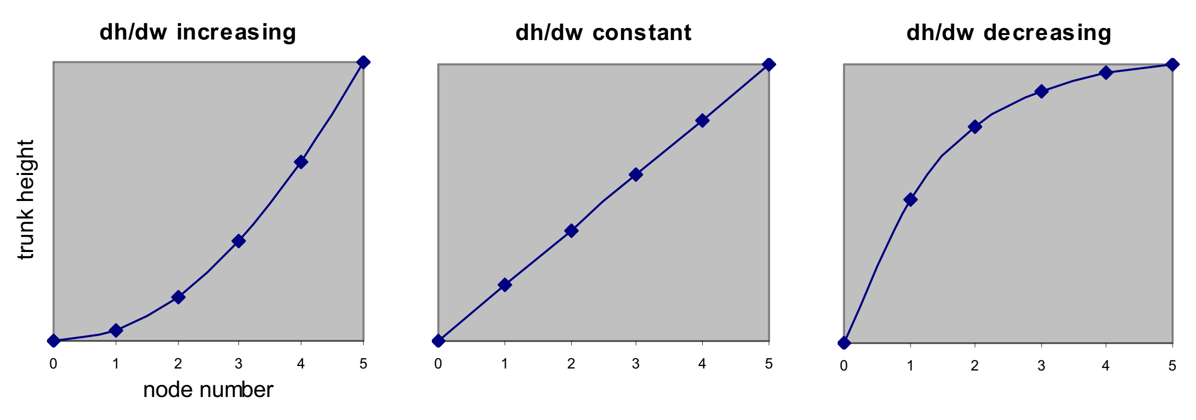

Figure 4.5 Diagramatic representation of the shape of a trunk base (the area above the curve representing the right half of the longitudinal section through the trunk base) in case the ratio of height increase to width increase would rise (left), stay constant (centre) or fall (right) with each consecutive internode.

With trunks growing from seed it may well be that the adult width is reached in a certain number of nodes/internodes/leaves. Under well-defined growing conditions, this would take a well-defined amount of time. The irregularly shaped and horizontal trunk bases of suckers seem to indicate a similarly variable number of nodes and amount of time needed to reach adult size.

The initial growth direction of a sucker may well be governed by where the strongest light is: if the mother palm is surrounded by other trees, the strongest light is above, and the sucker will grow upward; if the mother palm is free-standing, the strongest light is to the side, away from under the crown of the mother tree and the sucker will grow horizontally (see FLACH 1977:160: illustration of a free-standing clump in a paddy field with suckers grown horizontally up to several metres). Different horizontal lengths would therefore be an expression of different shade intensities during that growth phase. The question now is: are the horizontal internodes (in fact: skewed internodes (see Fig.4.4-a, -b, -c)) extra internodes, or should they be counted as in a seedling trunk? In other words: would a sucker growing from the base of a seedling mother trunk reach adult width in the same number of nodes/internodes/leaves and in the same time as the mother palm, or not?

During a revisit to the research area around Hatusua village, W. Seram in February 1992, a sago palm clump (Fig.4.6) was dissected to measure various dimensions of components of stems and leaves. The clump was of the variety Tuni and consisted of 1 axis in the early AV-phase with a leafless trunk of only 70 cm long (axis A), 2 axes without a visible trunk in the late E- or early AV-phase (axis B and C), and several suckers sprouting from these 3 axes. All observations and measurements on this clump are presented in Appendix B.
Figure 4.7 shows axis B, the biggest of the 2 trunkless axes, before and after peeling off all the green leaves. It appeared that this axis had gone from the E-phase to the AV-phase not long before. The internodes between the youngest 7 leaves were extended, whereas those between the oldest 5 were still very narrow.The transition from narrow to wide internodes is quite abrupt.

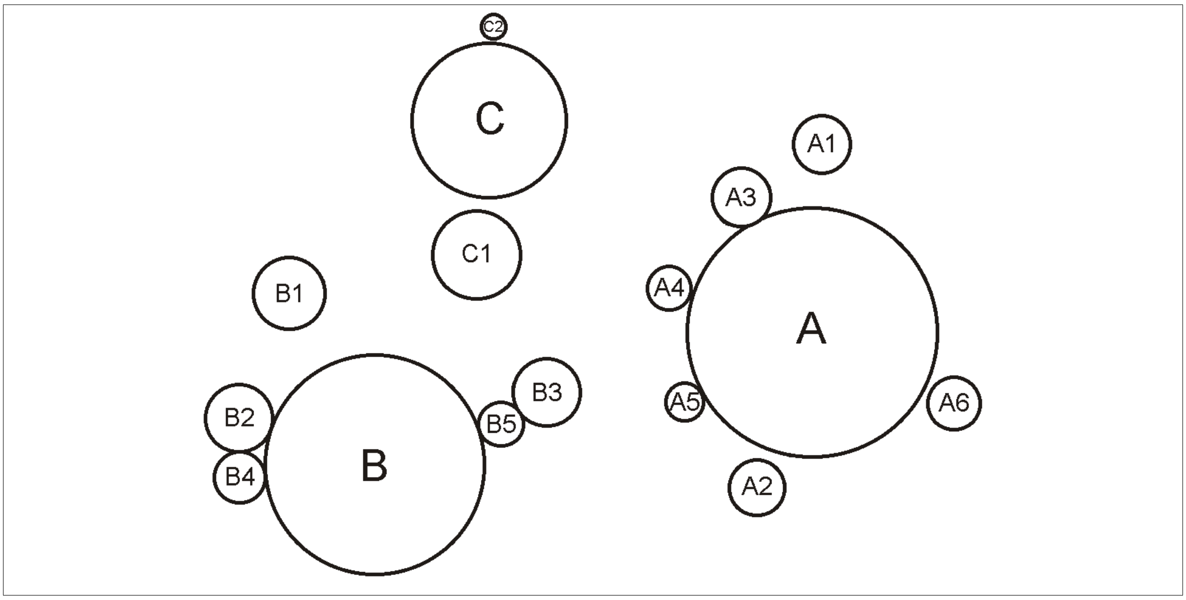

Figure 4.6 Diagramatic overview of the position of the axes (approximate ground level diameter including leaf bases as seen from above) of an actual sago palm clump (variety Tuni) with 3 main axes (A, B, C) and the suckers sprouting from them (A1, ..., A6 ; B1, ..., B5 ; C1, C2). The smaller, next-generation suckers which are sprouting in turn from the latter are not drawn.

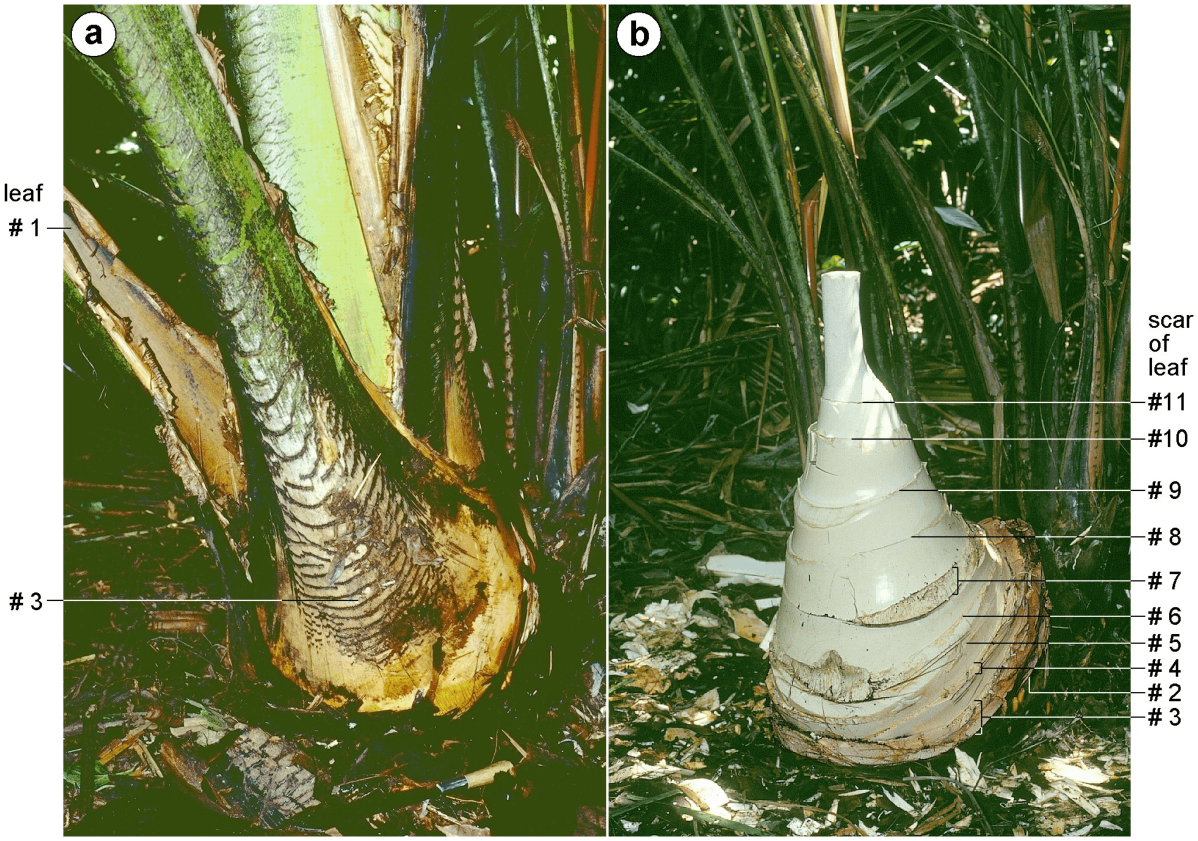

Figure 4.7 A sago palm sucker (variety Tuni) which recently changed from the Establishment phase to the Adult Vegetative phase. a: top of the axis with sheathing leaf bases of all 11 green leaves still in place; remains of dead leaves removed. b: top of the axis with all 11 green leaves removed and base of spear leaf still in place, revealing the first 5-6 extended internodes of the axis.
[Photos: a: nr. 92.02-215-18A (fri21feb1992) ; b: nr. 92.02-215-27A (sat22feb1992). Hatusua, West Seram.]

In Table 4.2 and Figure 4.8 dimensions of the petiole-rachis and the number of leaflets of the 11 green leaves of Axis B are presented. (For rationale and method of measuring the width times height of the rachis cross section where the lowest leaflet is attached, see Section 6.1 and Figure 6.2.) While number of leaflets and cross section dimensions level off to a maximum soon after the E- to AV-phase transition, total leaf length still steadily increases. Note that the leaf length increase is solely caused by rachis length increase.

Table 4.2 Dimensions of the petiole-rachis and the number of leaflets of the green unfolded leaves of a sago palm sucker (variety Tuni) which recently changed from the Establishment phase to the Adult Vegetative phase.

Lf #	Length (m)			Nr of lts			width (cm) × height (cm) of TS pt/rc at lowest lt (cm^2)
	sh+pt	rc	Total	L	R	Total	
lf-01	4.46	7.10	11.56	69	67	136	6.80 × 6.96 = 47.3
lf-02	4.41	7.25	11.66	69	67	136	6.91 × 6.90 = 47.7
lf-03	4.57	7.70	12.27	72	70	142	7.24 × 7.08 = 51.3
lf-04	4.67	7.87+	12.54+	72+	68+	140+	7.42 × 7.37 = 54.7
lf-05	4.61	8.49	13.10	76	73	149	7.85 × 7.79 = 61.2
lf-06	4.50	8.87	13.37	80	76	156	8.39 × 7.92 = 66.4
lf-07	4.42	8.84	13.26	84	78	162	8.09 × 7.78 = 62.9
lf-08	4.44	9.17	13.61	87	80	167	8.12 × 7.67 = 62.3
lf-09	4.54	9.21	13.75	85	82	167	8.03 × 7.66 = 61.5
lf-10	4.69	9.18	13.87	84	82	166	8.02 × 7.65 = 61.4
lf-11	4.57	9.41	13.98	85	81	166	8.02 × 7.75 = 62.2

lf = leaf ; lt(s) = leaflet(s) ; pt = petiole ; rc = rachis ; sh = sheath ; TS = transverse section.
L, R = left-hand, right-hand side of the leaf as seen from the top and the centre of the main axis (ax_0) of the sucker.
Remarks: `Lf-01` was already browning ("setengah kering").
`Lf-04` damaged at the top: measured rachis length and number of leaflets less than what it should be.

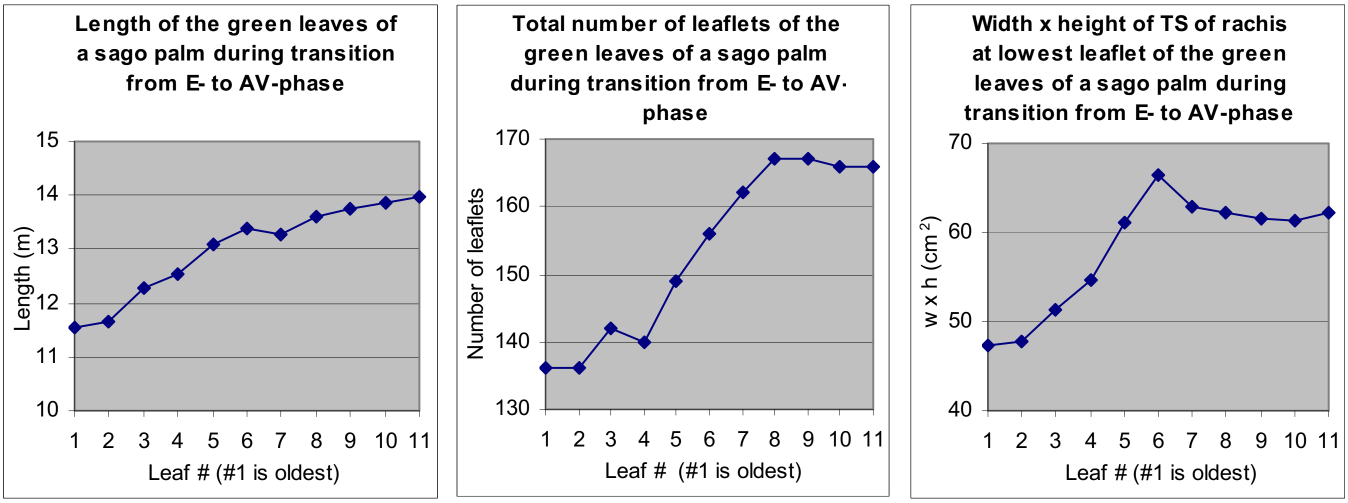

Figure 4.8 Leaf rank number of the green unfolded leaves of a sago palm sucker (variety Tuni) which recently changed from the Establishment phase (E-phase) to the Adult Vegetative phase (AV-phase) plotted against total leaf length, total number of leaflets, and width times height of the rachis transverse section (TS) where the lowest leaflet is attached.

By plotting these properties against Leaf#1 through Leaf#5 (the last leaf formed during the E-phase) and assuming linear relationships, the number of leaves needed from the start of the E-phase to arrive at this Leaf#5 can be estimated. Because of the defective tip of Leaf#4, this leaf has to be left out of the calculation of the trend in leaf length and number of leaflets. The results are shown in Figure 4.9.

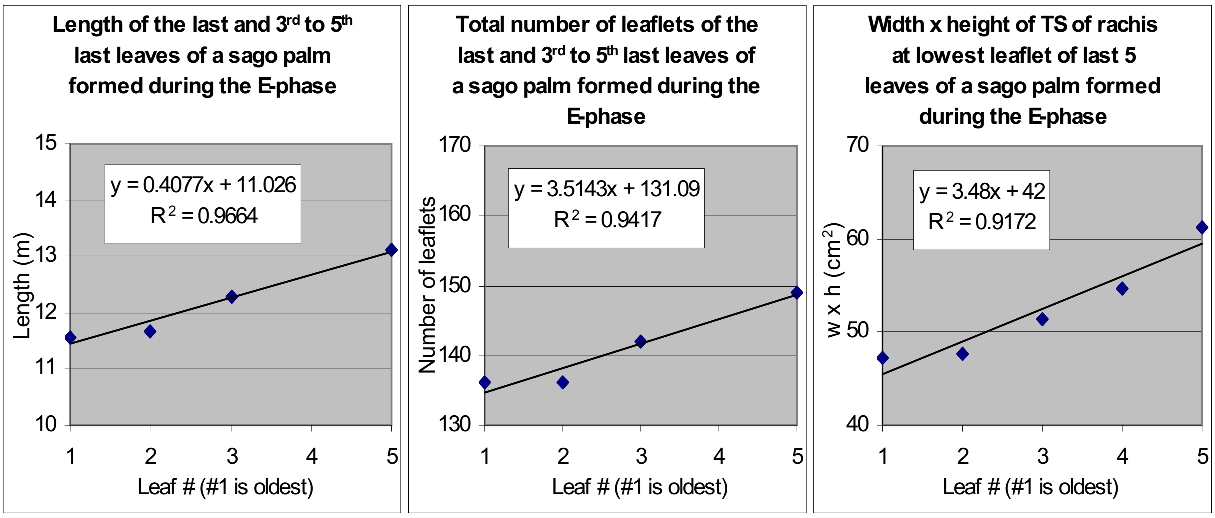

Figure 4.9 Leaf rank number of the last 5 leaves of a sago palm sucker (variety Tuni) formed during the Establishment phase (E-phase) plotted against total leaf length, total number of leaflets, and width times height of the rachis transverse section (TS) where the lowest leaflet is attached, with linear regression lines and formulas.

Leaf length (y) against leaf# (x)
$y = 0.4077x + 11.026$
$y = 0$ at $x = -27.04$
estimated total number of leaves formed in E-phase: 27+5 = 32.

Number of leaflets per leaf (y) against leaf# (x)
$y = 3.5143x + 131.09$
$y = 0$ at $x = -37.3$
estimated total number of leaves formed in E-phase: 37 + 5 = 42.

Width times height rachis cross section (y) against leaf# (x)
$y = 3.48x + 42$
$y = 0$ at $x = -12.07$
estimated total number of leaves formed in E-phase: 12 + 5 = 17.

Judging from the the coefficient of determination R^2, the first equation gives the most reliable estimate. Still, it remains to be found out whether a linear model adequately describes the above relationships.
An indication that the relationship between number of leaflets per leaf and leaf number may not be linear can be derived from the other E-phase axes observed. Palm#01 has 2 leaves, between 1 and 2 m long, both with 30 pairs of leaflets; Palm#02 has 5 leaves, between 2.5 and 3 m long, leaf#1 and leaf#5 with 19 and 18(!) pairs of leaflets, respectively; Palm#37 has 94 pairs of leaflets in its AV-phase (adult) leaves, whereas in one of its suckers the 5 youngest leaves are between 5 and 6 m long, the oldest and the youngest with 46 and 50 pairs of leaflets respectively, and in another of its suckers the 2 youngest leaves are around 12 m long, the youngest and the oldest with 75 and 74 pairs of leaflets, respectively. (With pairs of

leaflets, actually the number of leaflets on one side of the rachis is meant or - if the number on both sides was counted - the mean number of both sides.) In these observations we see that in young suckers the number of leaflets does not change, whereas in older ones with half to three quarters of the adult number of leaflets, the number of leaflets increases with 2 (one pair) per leaf. The end of the E-phase plotted in Fig. 4.9 shows an increase of 3.5 leaflets per leaf. This suggests a slowly accelerating increase of number of leaflets per leaf right up to the end of the E-phase.

- Leaf unfolding rate (LUR) and duration

No direct observations were made of the actual leaf unfolding rate during the E-phase, nor of the duration of this phase.

4.4.2.2 Adult vegetative phase (AV-phase)

- Trunk morphology

-- Number of nodes

The first node formed during the AV-phase of an axis is assumed here to be the one that ends up at the top of the axis' first visible, elongated internode above ground level. The node at ground level at the base of this internode is assumed to be the last one formed during the establishment phase. The node carrying the lowest inflorescence branch is considered as the first one formed during the generative phase of the axis. (In this context, by formation is meant initiation, and not the maturation growth thereafter.)

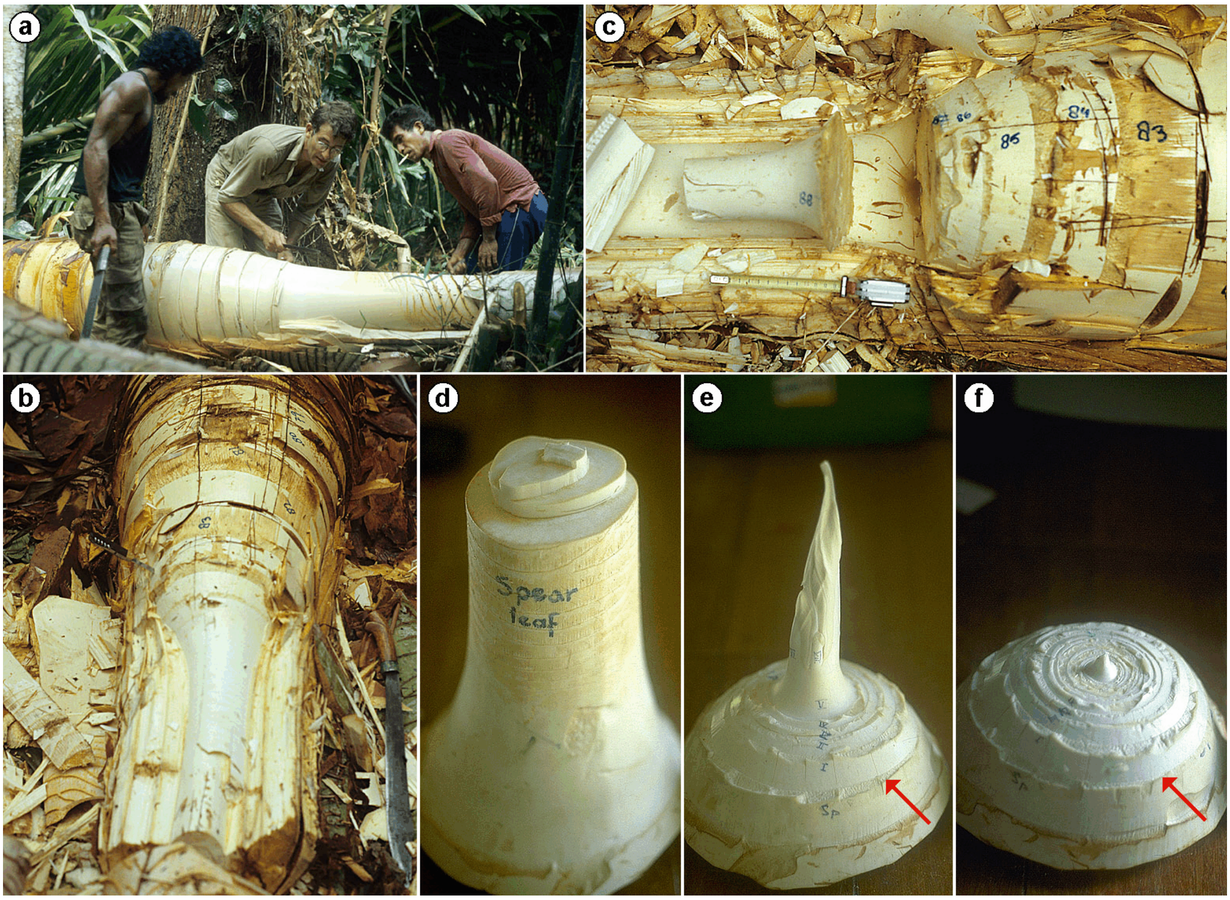

Figure 4.10 Dissecting the top of a sago palm axis.

a: Pak Olop, Pak Rik and Pak Melly inspect the top of a felled palm from which most of the green leaves have already been removed to decide where to cut to neatly remove the next leaf. Annular scars indicate where removed leaves were attached to the stem; all parts that were hidden from sunlight are whitish.

b: Top of the trunk, the enveloping bundle of leaf bases on top of it transversely cut well above where the growing point is expected to be, and the sheathing leaf bases cut away almost up to the spear leaf.

c: Top of the trunk, all the bases of the unfolded leaves removed, the tip (the base of the spear leaf with the primordial leaves and the growing point inside) severed to be taken to the field lab for further dissection.

d,e,f: Stages in the gradual removal of spear leaf and primordial leaves inside it to get to the apical growing point of the trunk. Outside diameter of the spear leaf scar (arrow) is 15.6 cm. d: top cut in such a way as to show how consecutive primordial leaves envelope each other ; e: spear + 4 leaves inside it cut away ; f: spear + 11 leaves inside it cut away. (Using a stereo microscope, 14 more primordial leaves could be discerned, bringing the total number of leaves inside the spear of this particular axis to 25.)

[a: photo nr. 88.11-071-26, Palm#07 ("Ihur", late AV), Hatusua 29nov1988 ; b: photo nr. 88.11-071-21 ; c: photo nr. 88.11-071-24 (b,c: Palm#06 ("Ihur", late AV), Hatusua 28nov1988) ; d: photo nr. 90.04-113-08 ; e: photo nr. 90.04-113-09 ; f: photo nr. 90.04-113-14 (d,e,f: Palm#25 ("Ihur", AV), Hatusua 06apr1990).]

On an axis in the AV-phase, the number of nodes formed during this phase at the time of observation was counted by adding up leaf scars, unfolded green leaves and folded primordial leaves. To establish the latter number, the trunk apex was dissected as far as possible in the field and the field lab (Fig. 4.10), the remainder with the smallest primordia preserved in FAA and further dissected later with the aid of a stereo microscope (brand: Wild; type: M7 S). If it was discovered by this dissecting that a primordial inflorescence branch was already present in the axil of a primordial leaf, the axis was declared generative and the node at hand was counted as the first one formed in the generative phase.
Thus, once an axis is in the generative phase or beyond (dead), the total number of nodes formed during its AV-phase can be established. And as there is always 1 leaf per node, this number is equal to the total number of leaves formed during the AV-phase.

In Table 4.3 the total number of leaves formed in the AV-phase is presented of all the palms for which this number could be established (with a completed AV-phase, i.e. in the G-phase or dead). This included palms from the numbered series of intensively sampled specimens in Seram and Saparua (see Sago Palm Data Sheets in Appendix A), as well as palms encountered during field trips elsewhere.
The number in "Tuni" palms (average 147, standard deviation 9.1) is consistently higher than in "Ihur" palms (average 124, standard deviation 5.5) and in any other type of palm, except for the single "Makanatol" palm observed which, with its 193 leaves, stands out far above all other palms in total AV-phase leaf number.

Table 4.3 Total number of leaves formed during the Adult Vegetative phase of a sago palm axis, ordered by variety. Palm numbers refer to the numbers in the appended Sago Palm Data Sheets ; they only reflect the chronological order in which the palms were examined.

Palm #	Variety	Number of leaves	Location
03	Tuni	**145**	Hatusua, Seram Is.
24		**160**	Hatusua, Seram Is.
28		**142**	Hatusua, Seram Is.
34		**140**	Hatusua, Seram Is.
05	Ihur	**118**	Hatusua, Seram Is.
35		**127**	Hatusua, Seram Is.
37		**128**	Hatusua, Seram Is.
18	Molat	**80**	Hatusua, Seram Is.
29	Molat Berduri	**129**	Hatusua, Seram Is.
04	Makanaro	**101**	Hatusua, Seram Is.
36	Makanatol	**193**	Siri Sori Serani, Saparua Is.
[no number (outside series)]	? (spineless)	**109**	Siberut Is., Mentawai Islands, W. Sumatera
	Sisika	**88**	near Toliwang, Kao, Halmahera Is.
		112	Sasur Tua area, Kao, Halmahera Is.
	Beka	**110**	Kao, Halmahera Is.
	Ratemu	**108**	Kao, Halmahera Is.

In Table 4.4 trunk height and number of nodes are presented of sago palms in the AV-phase, including all AV-phase palms of which the starch content was measured and of which the age still has to be estimated (of palms #06, #15, #22 and #23 no starch measurements could be taken (see Appendix A)). Assuming, as FLACH (1983:16) suggested, that the total number of leaves produced during the vegetative period of a sago palm axis is genetically determined, the relative progress an axis has made in the AV-phase can be established by the number of

Table 4.4 Height of the trunk, and number of nodes on the trunk of 5 sago palm varieties in the Adult Vegetative phase. Palm numbers refer to the numbers in the appended Sago Palm Data Sheets ; they only reflect the chronological order in which the palms were examined.

Palm #	Variety	Dev. Phase	Trunk (ax_0) height (m)			Number of nodes			
			leafless	leaf-bearing	total *	leaf scars on trunk	green leaves	spear leaf + leaves inside**	total
11	Tuni	AV	10.70	2.10	12.80	71	20	23	114
12		AV	6.00	1.90	7.90	33	14	20	67
15		AV	9.25	n.r.	n.r.	57	16	n.r.	-
16		AV	12.05	1.60	13.65	78	19	21	118
17		AV	7.85	2.45	10.30	43	19	24	86
22		AV	11.85	1.55	13.40	90	21	24	135
23		AV	15.40	1.30	16.70	103	16	22	141
27		AV	14.60	1.55	16.15	107	19	17+?	143+?
32		AV?1)	14.45	1.55	16.00	109	19	18+?	146+?
06	Ihur	AV	9.50	n.r.	n.r.	69	8-18***	20-30+?	106+?
07		AV	10.35	1.35	11.70	92	17	25	134
25		AV	7.65	1.90	9.55	60	21	26	107
26		AV/G2)	12.85	1.40	14.25	90	21	19+?	130+?
10	Molat	AV	9.90	2.30	12.20	63	21	22	106
13		AV	8.30	1.80	10.10	53	16	19	88
30		AV?3)	7.60	1.45	9.05	55	16	16+?	87+?
31		AV	6.95	1.50	8.45	50	16	17+?	83+?
33		AV?4)	15.15	1.60	16.75	137	? c.20	n.r.	-
14	Molat Berduri	AV	8.10	2.75	10.85	46	22	21	89
19	Putih	AV	9.05	1.15	10.20	72	14	19	105
20		AV	8.55	1.40	9.95	54	14	19	87
21		AV	12.25	1.55	13.80	70	14	21	105

* not including the few cm from attachment of spear leaf to top of ax_0, which was not recorded in all cases.

** up to and including the smallest primordial leaf hood which can be peeled from the growing point. For various reasons this was not always possible, in which case "+?" is added to the number of leaf primordia actually seen (and also to the total number of nodes).

*** transition from green leaves to spear leaf and folded leaves inside spear irretrievable due to damaged crown.

n.r. not recorded.

AV = Adult Vegetative phase ; G = Generative phase.

Notes on uncertainty about development phase:

1) No ax_1-s found in axils of oldest 17 leaves inside spear leaf; remainder of apex not dissected.

2) No other observations than counting the leaves actually seen could be made because the apical growing point was shattered as the trunk was felled; and it fell further apart upon opening-up the tree top.

3) No ax_1-s found in axils of oldest 15 leaves inside spear leaf; remainder of apex not dissected.

4) No outwardly visible inflorescence parts; top completely shredded upon felling.

AV nodes already formed. Therefore, comparing the number of nodes of the palms in Table 4.4 with the total (final) number of nodes formed in the AV-phase as presented in Table 4.3 may give an indication of the relative progress the former palms have already made in the AV-phase. However, only of the varieties "Tuni" and "Ihur" more than 1 dead or G-phase specimen were observed so that an average total number of AV nodes could be calculated, and the spread of the individual observations around these averages is so large that (1) the indication of relative progress for "Tuni" and "Ihur" must be inaccurate, and (2) deriving such an indication by comparison with a single observation of the total number of AV nodes (as for "Molat" and "Molat Berduri") does not seem justified at all.

If we rank the "Tuni" palms by age as estimated by number of nodes and as estimated by trunk height, we see that there are only minor shifts in rank number.

"Tuni" palm number		#12	#17	#11	#16	#22	#23	#27	#32
number of AV-nodes (% of mean total (147))		67 (46%)	86 (59%)	114 (78%)	118 (80%)	135 (92%)	141 (96%)	143+? (97+?%)	146+? (99+?%)
trunk height (m)		7.90	10.30	12.80	13.65	13.40	16.70	16.15	16.00
age ranking (1 = youngest) by ...	number of nodes	1	2	3	4	5	6	7/8?	7/8?
	trunk height	1	2	3	5	4	8	7	6

-- Trunk diameter

Trunk diameter was measured every metre on felled palms after removal of old leaf remains, from 0.5 m above ground level upwards, at least up to the oldest green leaf or to the oldest inflorescence branch, whichever came first. This was done by selecting two about 1.5-to-2-metre-long straight pieces of leaf petiole/rachis from nearby sago suckers, stripping them of leaflets if necessary, holding one of them to either side of the trunk, and checking their parallelism by measuring their distance at various heights with a measuring tape and adjusting their angle until this distance was constant (Fig. 4.11). This constant distance was taken as the trunk diameter. Thus the trunk diameter could be determined with an error of 0.5 cm or less. The measurements are presented in Table 4.5.

Figure 4.11 Removing leaf remains from a felled trunk and measuring its diameter. [photo nr.89.05-084-19 (left) and -24, Palm#13 ("Molat", AV), Dusun Air Rapa, Hatusua, West Seram, fri05may1989]

As shown in Table 4.5, trunks vary in diameter along their lengths. The largest diameter of the 31 palms in Hatusua and Siri Sori of which the diameter was measured (see Table 4.1) ranged from 48 cm to 64 cm.
During visits to other sago areas in Indonesia, 4 other palms were felled and their trunk diameter was measured in the same way from 1 metre above ground level upwards (SCHUILING *et al*. 1993:73,74,76,77). Largest diameters were: 44 cm in a spined plantation palm on Tebing Tinggi Island, Riau Province; 45.5 cm in a palm on Siberut Island, West Sumatra Province; 57 cm in a "Sisika" palm and 52 cm in a "Beka" palm, both near Kao on Halmahera Island, Maluku Province. Note that the palms measured in western Indonesia were narrower than the narrowest palms measured in the Moluccas.
In 31 out of the 35 observed palms (not in #03, #26, #35, HhS), the trunk narrows above the lowest point of observation (0.5 or 1.0 m a.g.l.); it then widens, reaching the same width as at the lowest observation point again in 25 out of these 31 palms, generally between 3 and 5 m

a.g.l.; further up the trunk, width then increases a few centimetres more in 23 out of these 25 palms, before eventually tapering towards the top.
In most cases (25 out of 35), the widest point is not in the lower half of the trunk, but in the upper half, not counting the long tapering top part in flowering trunks.
In flowering palms, the leaf-bearing part of the trunk - if leaves are still present - is clearly longer, and the trunk diameter is clearly tapering more gradually (e.g., Palms #28, #35, HhB) than in non-flowering ones (e.g., Palms #14, #25, Sib). (See Fig. 4.37 for detailed diagram of leaf-bearing trunk part of Palm #25.)
Palm #18 was an exceptional palm, all its parts being smaller than in other palms. It was standing in someone's homegarden in Hatusua village, and its smallness may have been caused by regular leaf harvesting to which it may have been subject more than the other, less accessible palms.

-- Thickness of the "wa'ah"

The so-called wa'ah is the outer layer of the trunk, consisting of a 2- to 5-mm-wide soft, fibrous cortex (covered by a smooth epidermis as long as it is still enveloped by leaf bases, the smooth surface slowly eroding away when the leaf bases are shed), and a 1- to 3.5-cm-wide layer of tough fibres (Fig. 4.12). The *wa'ah* is also what is left over after pounding the pith in traditional processing (Fig. 4.13d).
The fibre layer is actually continuous with the pith, the concentration of fibres diminishing towards the centre of the trunk. However, going from the outside in, the fibre concentration, the fibre thickness and the degree of lignification of the fibres decrease so abruptly that the outer fibre layer can easily be designated and recognised as a separate layer.

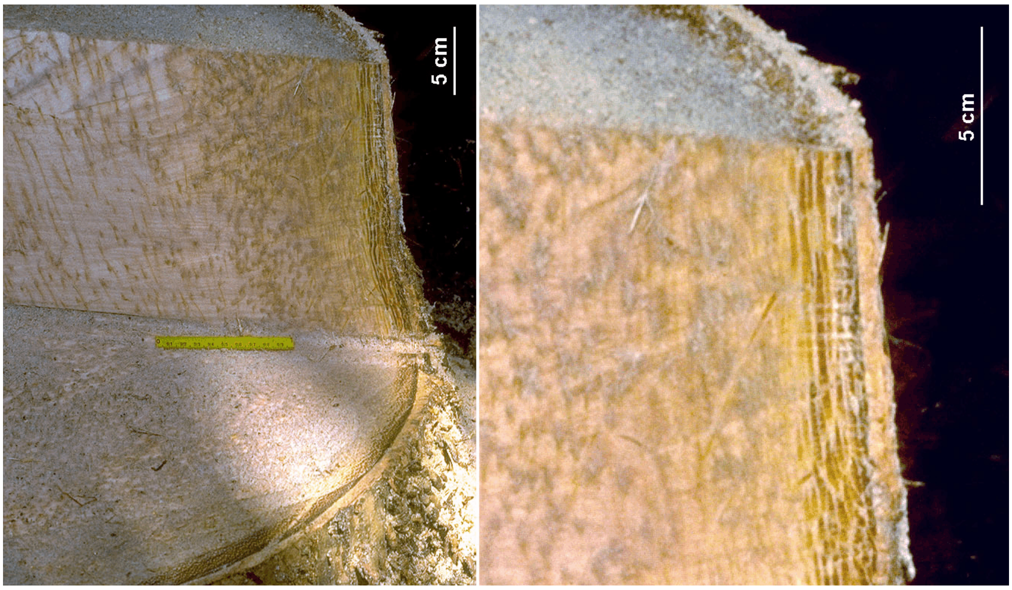

Figure 4.12 Detail of a longitudinally and transversely sawn stump of a sago palm trunk showing the position and extent of the distinct outer fibre layer between cortex and pith (on the right an enlarged part of the photo on the left).
[photo nr. 90.11-149-20, Palm#37 ("Ihur" G1), Dn Salapu, Hatusua, W.Seram, thu22nov1990]

Young fibres are yellowish. They turn blackish-brown with age, and ultimately become stone-hard: sparks may be seen flying from the *wa'ah* when a trunk is being felled with a *parang* (bush knife).

Table 4.5 Trunk diameter along the trunk of 35 sago palms. Palms numbered #03, #04, ... [etc.] are from the series sampled around Hatusua (West Seram) and Siri-Sori (Saparua) (complete data in Appendix A). Palm *Tt* is a spiny plantation palm sampled at Tebing Tinggi Is., Riau Province. Palm *Sib* is a palm sampled at Siberut Is., West Sumatera Province. Palms *HhS* and *HhB* are palms of the folk variety Sisika and Beka, respectively, sampled at Halmahera Is., Maluku Province.
Bold and underlined values indicate the largest diameter of the trunk. A checkered table cell background indicates the height at which trunk diameter equals or surpasses the diameter at 0.5 (or 1.0) m a.g.l. for the first time.
A table row reads as a graph for the length of the trunk, different table cell background colours indicating different parts of the trunk (f.l.t.r.): white = leafless; green (light grey) = leaf-bearing (from lowest leaf to spear or to lowest 1st-order inflorescence branch); pink (dark grey) = inflorescence rachis (from the lowest 1st-order inflorescence branch upward) ; hatched = beyond top of the trunk (a hatched part of a row overlapping a coloured part indicates that the exact position of the top of the trunk could not be observed).

Palm	Trunk diameter (cm) at ... m above ground level																									
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5
#03	52	58	58	**62**	61	61	60	60	54	45	-	-	-	-												
#04	**50**	41	42	44	42	42	42	40	38	35	31	-	-	-												
#05	54	50	51	51	56	57	58	**60**	58	59	59	58	59	57	50	-	-	-	-							
#06	47	-	-	-	50	52	53	**56**	55	54	-															
#07	42	39	42	48	48	46	46	46	50	**52**	51															
#09	**57**	47	49	50	51	51	51	51	51	52	53	54	54	54	**57**	56	**57**	53	42							
#10	55	49	49	52	53	53	54	**56**	**56**	**56**	**56**	50														
#11	58	52	53	56	58	61	**64**	63	63	**64**	**64**	**64**														
#12	52	49	52	53	53	52	**54**	-																		
#13	**53**	42	41	42	43	47	49	49	50	-																
#14	52	48	48	50	51	56	58	**61**	58	60																
#15	48	47	48	50	52	54	**55**	54	**55**	54	-															
#16	53	51	50	50	52	53	55	57	57	57	**60**	**60**	**60**													
#17	53	49	51	51	53	53	54	**55**	**55**	-																
#18	**54**	50	51	45	32	23	19	18	11																	
#19	48	45	45	46	48	**50**	**50**	49	48	43																
#20	**54**	48	47	47	47	48	46	47	50	-																

Palm	Trunk diameter (cm) at ... m above ground level																								
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5
#21	**53**	-	46	47	47	46	47	47	49	49	48	48	49													
#25	47	45	50	56	56	55	54	55	**59**	27																
#26	49	51	50	51	53	53	53	**57**	**57**	**57**	**57**	55	56	54												
#27	55	49	48	49	50	52	53	54	56	56	57	59	60	60	**61**	48										
#28*	56	51	51	51	53	56	59	59	59	60	**61**	**61**	**61**	60	55	47	36	33	32	32						
#29	51	46	46	46	52	59	57	57	57	**60**	57	52	44	27	-											
#30	**51**	49	47	48	49	49	49	49	42																	
#31	**48**	44	45	46	**48**	**48**	**48**	46																		
#32	55	55	52	53	52	52	54	56	57	57	58	57	58	**61**	**61**	45										
#33	51	46	50	55	60	60	63	62	**64**	**64**	62	59	56	56	47	44										
#34	52	51	51	53	54	55	55	55	57	58	60	60	**62**	61	58	53	43	35	35	34						
#35	32	34	38	40	43	**49**	**49**	45	37	27	26	25	23													
#36	44	38	40	41	45	50	53	58	56	58	58	**60**	57	57	58	56	52	-	49	43	30	25	-	-		
#37	53	49	52	54	55	58	57	57	60	**63**	62	**63**	62	58	54	34										
Tt	42	41	42	42	**44**	42	42	42	42	39																
Sib	40	35	34	35	-	38	37	40	44	**45.5**	45	30														
HhS	48	48	48.5	51	56	56	**57**	52	45	34	30.5	27	25													
HhB	45	41	38.5	39	43	48	51	**52**	**52**	48	41	31	27	25	20											

* Diameters at 16.5, 17.5, 18.5, and 19.5 m a.g.l. in Palm #28 estimated by interpolation of diameters measured at nodes.

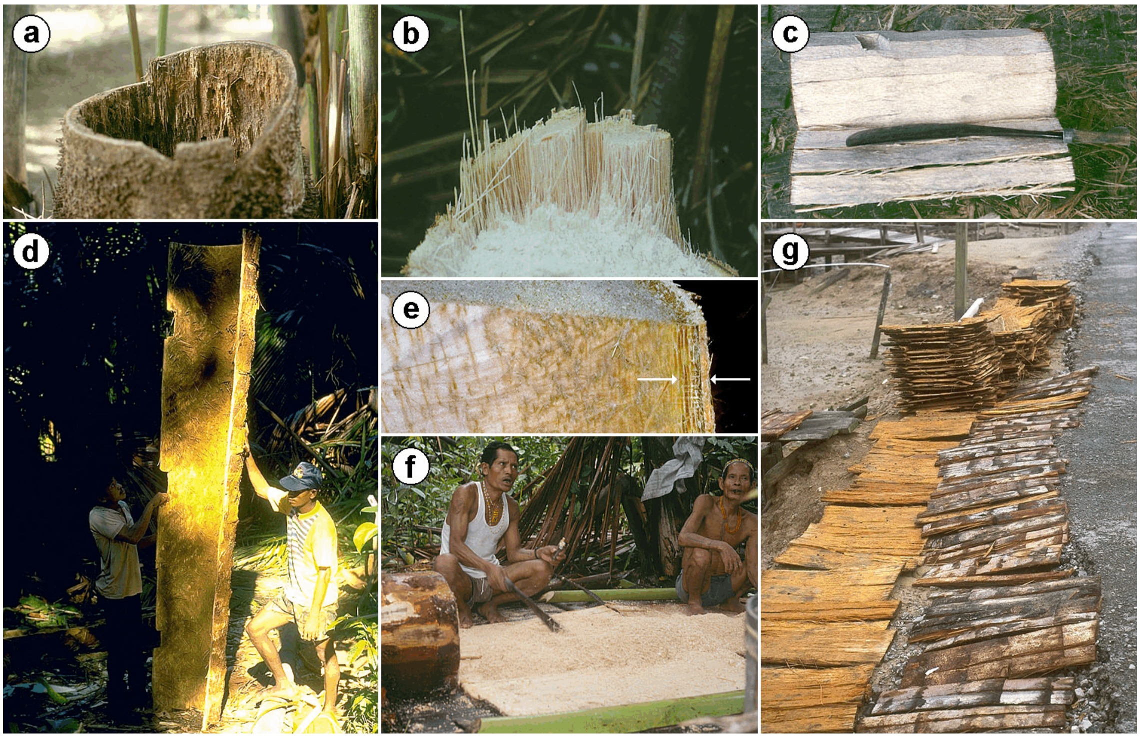

Figure 4.13 The *wa'ah* (cortex plus adjacent dense fibre layer) of the sago palm trunk.

a: Stump of trunk, *in situ*, the pith gone (harvested?, eaten by animals?), showing the remaining *wa'ah*.
[photo nr. 92.02-212-22, Tanjung Kasuari, Sorong, Papua, Indonesia, sat08feb1992]

b: Fibres ("urat") at the inside of the bark of the stump exposed as this last bit of the trunk broke off when the tree was felled.
[photo nr.89.04-082-17, Palm#11 ("Tuni", AV-phase) Dusun Salapu, Hatusua, wed19apr1989]

c: Log 'debarked' by bush knife, with part of peeled *wa'ah* still attached.
[photo nr. 88.01-042-29/30, low-input local-tech sago mill at Kampong Tabo, along Mukah River, Sarawak, Malaysia, sat16jan1988]

d: *Wa'ah* of halved log which remained after pounding out the pith. Note the notches in the rim showing where windows were hacked in the *wa'ah* of the intact log through which wedges were hammered in to split the log in halves.
[photo nr. 90.11-149-06, Palm#37 ("Ihur", G1-phase), Dusun Salapu, Hatusua, W.Seram, thu22nov1990]

e: Detail of longitudinally and transversely sawn trunk part, showing wa'ah *in situ* (between arrows).
[photo nr. 90.11-149-20, Palm#37 ("Ihur" G1-phase), Dn Salapu, Hatusua, W.Seram, thu22nov1990]

f: Pith removed from the trunk by rasping or pounding is further pulverized by bush knife, using the flattened *wa'ah* of a processed trunk part as a neat working floor.
[photo nr. 92.01-204-22, Siberut Is., Mentawai Archipelago, West Sumatra, Indonesia, sat18jan1992]

g: Drying sago palm *wa'ah* for fuel by the side of the road.
[photo nr. 90.08-133-14, Mukah, Sarawak, Malaysia, fri10aug1990]

Figure 4.14 Measuring the thickness of the *wa'ah* (in this case estimated at 2.5 cm).
[photo nr. 90.09-140-04, Palm#32 ("Tuni", AV?) at 2.5 m a.g.l., Hatusua, W.Seram, sat22sep1990]

The thickness of the wa'ah was measured, like trunk diameter, every metre on felled palms after removal of old leaf remains, from 0.5 m above ground level upwards. This was done by hacking a small window in the *wa'ah* up to where the pith starts, and measuring the depth of this window (Fig. 4.14). Thus the *wa'ah* thickness could be estimated with an error of 0.25 cm or less. The results are presented in Table 4.6.

Unlike the diameter of the trunk - which from bottom to top may first decrease, then increase, and finally decrease again - the *wa'ah* is always thickest at the base of the trunk and always gets gradually thinner towards the top.

Table 4.6 Thickness of the *wa'ah* along the trunk of 27 sago palms. The palms are from the series sampled around Hatusua (West Seram) and Siri-Sori (Saparua) (complete data in Appendix A). A table row reads as a graph for the length of the trunk, different table cell background colours indicating different parts of the trunk (f.l.t.r.): white = leafless; green (light grey) = leaf-bearing (from lowest leaf to spear or to lowest 1st -order inflorescence branch); pink (dark grey) = inflorescence rachis (from the lowest 1st -order inflorescence branch upward) ; hatched = beyond top of the trunk (a hatched part of a row overlapping a coloured part indicates that the exact position of the top of the trunk could not be observed).

Palm	Thickness of trunk "wa'ah" (cm) at ... m above ground level																									
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5
#05	3	2.5	2	2	2	2	2	2	2	2	2	2	2	2	1.5	-	-	-	-	-	-					
#06	-	2.7	2.4	2	-	-	-	-	-	-	-															
#09	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
#11	4	4	4	4	4	4	3	3	3	2.5	2	2														
#12	4	2	1.5	1.5	1	1	1	-																		
#13	3	2	2	2	1.5	1.5	1.5	1	1	-																
#14	2.5	2.5	2.5	2	1.5	1.5	1	1	1	1																
#15	3	2.5	2	1.5	1.5	1.5	1	1	1	1	-															
#16	3.5	3.5	3	3	2.5	2	2	1.5	1.5	1.5	1	1	1													
#17	2.5	2	1.5	1.5	1.5	1.5	1	1	1	-																
#18	4	2	2	2	1.5	1	1	-	-																	
#19	3	2	2	1.5	1.5	1	1	1	1	1																
#20	2.5	2	2	2	1	1	1	1	1	-																
#21	3	2	2	2	1.5	1.5	1.5	1.5	1.5	1	1	1	1													
#25	4	3.5	3	2.5	2	2	1.5	1.5	1.5																	
#26	3	2.5	2.5	2.5	2.5	2	2	2	2	2	1.5	1.5	1	1												
#27	2.5	2.5	2.5	2.5	2	2	2	2	2	2	1.5	1.5	1	1	1	-										
#28	3	3	2.5	2.5	2	2	2	2	2	2	2	1.5	1.5	1	1	1	-	-	-	-	-					
#29	3	2.5	2.5	2.5	2.5	2	2	2	1.5	1.5	1.5	1.5	1	1	-											

Palm	Thickness of trunk "wa'ah" (cm) at ... m above ground level																								
	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5	10.5	11.5	12.5	13.5	14.5	15.5	16.5	17.5	18.5	19.5	20.5	21.5	22.5	23.5	24.5	25.5
#30	2.5	2	2	1.5	1.5	1.5	1	1	1																	
#31	2.5	2	1.5	1.5	1.5	1	1	1																		
#32	3	3	2.5	2	2	2	2	1.5	1.5	1.5	1.5	1.5	1.5	1	1	1										
#33	2.5	2.5	2.5	2	2	2	2	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1	1										
#34	3	2.5	2	2	2	2	1.5	1.5	1.5	1.5	1.5	1.5	1	1	1	1	1	1	1	1	-	-				
#35	3.5	3.5	3	2.5	2	2	2	1.5	1.5	1	1	1	1	-	-											
#36	3	2.5	2.5	2	2	2	2	2	2	2	2	2	2	1.5	1.5	1.5	1.5	1.5	1.5	1	1	1	-	-	-	
#37	3	3	2.5	2.5	2.5	2.5	2	2	2	2	2	2	1.5	15	1	1										

-- *Internode length*

In Table 4.7 the mean internode length per metre along the trunk of 33 sago palms is presented. In the trunks with an (almost) complete set of measurements we see that the internode length decreases towards the top, but that in flowering palms internode length increases dramatically again towards the (developing) inflorescence, the longest internodes occurring 1 to 2 metres below the first inflorescence branch ($\mathtt{ax}_1\mathtt{-I}$). I will call that trunk part in flowering palms the bolting part of the trunk.
The initial decrease in internode length typically is from about 20 cm to about 10 cm.
In the bolting part the mean internode length is up to about 35 cm. The longest single internode measured per palm ranged from 34 cm to 45 cm, with an exceptional 30 cm in Palm #18.
Often the internode lengths in the lowest metre are on average slightly less than in the next metre.
Palm #18 and #35 were exceptional in that the initial decrease in internode length was from 10 cm to 6 cm rather than from 20 cm to 10 cm. Palm #18 was an exceptionally small palm with all its parts smaller than in other palms, whereas Palm #35 had apparently be burnt at some stage during its life (scorch marks on lowest 60 cm of trunk). Also, both these palms were standing inside the village, making them easy targets for the regular removal of green leaves (leaflets used for roof thatch, petiole/rachis used as construction material). This leaf harvesting may negatively affect internode length.

-- *Highest point of an AV trunk*

The tip (highest point) of the trunk in the AV-stage is not where the apical growing point is. As Fig. 4.10f shows (and also Fig. 4.23 and Fig. 4.24a), the apical growing point sits in a shallow depression in the truncate top of the trunk, which is according to TOMLINSON (1990:57-58) a situation common in larger palms. Previously formed primordial leaves were attached to the concentric annular dissecting scars around the apex shown in these photos, each ring a bit higher towards the rim of the depression than the ring of the next younger leaf primordium.
In Palm#11 it was observed (see Appendix A) that `lf-V` (the 5th primordial leaf inside the spear, counting inward) stood on the rim of the depression; from `lf-VI` onwards (observed up to `lf-XXII`) the leaves were attached lower than `lf-V`, i.e. inside the apical depression.
The excised top of Palm #17 from which the spear and all leaves inside it were removed (Fig. 4.15) shows that the spear leaf was attached about 3.5 cm below the tip of the trunk, and that also in this case it was about `lf-V` that was standing on the rim of the depression in which the apical growing point is located.

Figure 4.15 Excised top of a sago palm axis in the AV-phase showing the annular scars where the spear leaf (arrows) and the primordial leaves inside it were cut away.
[photo nr. 89.08-090-07, 89.08-090-08, 89.08-090-09, Palm#17 ("Tuni" AV), Hatusua, W. Seram, fri07jul1989]

Table 4.7 Mean internode length per metre along the trunk of 33 sago palms. Palms numbered #03, #04, ..., #37 are from the series sampled around Hatusua village (West Seram) and Siri-Sori village (Saparua) (complete data in Appendix A). Palm *Sib* is a palm sampled on Siberut Is., West Sumatera Province. Palms *HhS*, *HhB* and *HhR* are palms of the variety Sisika, Beka and Ratemu, respectively, sampled on Halmahera Is., Maluku Province. A table row reads as a graph for the length of the trunk, different table cell background colours indicating different parts of the trunk (f.l.t.r.): white = leafless; green (light grey) = leaf-bearing (from lowest leaf to spear or to lowest 1st-order inflorescence branch); pink (dark grey) = inflorescence rachis (from the lowest 1st-order inflorescence branch upward) ; hatched = beyond top of the trunk (a hatched part of a row overlapping a coloured part indicates that the exact position of the top of the trunk could not be observed).

Palm	Mean internode length (cm) of trunk section from ... - ... m above ground level																									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21	21-22	22-23	23-24	24-25	25-26
#03	-	-	-	-	-	-	-	-	-	10	21	34	24	-	-	-										
#04	-	-	-	-	-	-	-	-	-	-	14	30	31	20	-	-										
#05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23	38	33	25	20	-					
#07	-	-	-	-	-	-	-	-	-	-	7															
#09	-	-	22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-							
#10	17	18	18	-	-	-	-	-	-	-	-	-														
#11	-	-	21	-	-	-	-	-	-	-	-	-	-													
#13	-	-	16	-	-	-	-	-	-	-																
#14	20	18	17	17	17	17	17	15	-	-	-															
#15	19	18	17	-	-	-	-	-	-	-	-															
#16	28	24	21	20	19	19	15	13	12	11	11	10	-	-												
#17	24	18	18	17	17	17	17	16	14	13	-															
#18	9	8	7	6	6	23	28	15	8																	
#19	13	14	13	14	14	13	12	11	10	9																
#20	19	19	18	17	16	14	14	13	12	-																
#21	19	22	21	19	19	18	18	18	18	16	14	13	13	10												
#25	12	12	14	14	14	13	12	11	9	-																
#26	24	20	18	17	17	17	17	15	12	12	11	10	8	7												

Palm	Mean internode length (cm) of trunk section from ... - ... m above ground level																									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	16-17	17-18	18-19	19-20	20-21	21-22	22-23	23-24	24-25	25-26
#27	24	23	19	18	16	15	15	14	13	12	11	11	11	10	9	9										
#28	18	18	18	17	15	16	15	14	13	12	11	10	10	9	10	11	18	35	35	21	8	6				
#29	17	17	16	14	13	12	11	11	9	9	8	7	9	21	36	3										
#30	12	15	15	15	15	14	11	11	8																	
#31	15	15	14	14	14	12	11	10	7																	
#32	20	21	19	17	14	14	15	13	12	11	10	10	10	10	9	8										
#33	16	17	16	16	16	14	14	13	11	9	9	8	8	9	6	7	-									
#34	19	20	18	17	16	16	15	14	13	12	12	10	10	9	9	9	15	37	36	19	9	8				
#35	7*	6	10	9	9	8	8	6	9	31	36	24	14	10	10											
#36	18	21	18	15	17	18	13	12	13	14	14	13	12	11	11	11	9	8	7	6	9	31	34	24	-	-
#37	21	24	22	20	19	16	17	15	14	15	14	14	11	9	9	10										
Sib	18**	17	16	16	14	13	13	13	11	9	9	10	14													
HhS	17	19	18	18	16	14	11	11	9	9	21	45	36	-	-											
HhB	21**	20	19	18	16	12	12	12	11	10	7	10	22	39	21	-										
HhR	21**	23	19	19	19	18	16	15	14	13	13	11	10	12	21	28	31	30	-	-						

* number and length of internodes on first 60 cm of trunk not certain because leaf scars were hardly visible due to scorching (fire damage) of the bark.

** estimated (leaf scars not clearly visible).

\- = not observed.

- *Leaf morphology*

In Table 4.1 the number of green leaves in the observed series of palms is presented, the number in the palms in the AV-phase ranging from 10 to 22.
Here, the observed dimensions and morphological traits of a leaf in the AV-phase are summarised. Table 4.8 presents some dimensions of leaves and leaflets, and the number of leaflets per leaf.
The axis of a leaf is continuous. In young leaves the basal part is tubular and this part is called the sheath. On one side the sheath extends into the petiole and rachis, the rachis merely being the distal part of the axis where the leaflets are attached (Fig. 4.16). With age, the sheath on the side opposite to the petiole splits downward to where it is attached to the trunk, and the entire basal part of the axis is then called petiole (i.e. length of sheath equals zero).

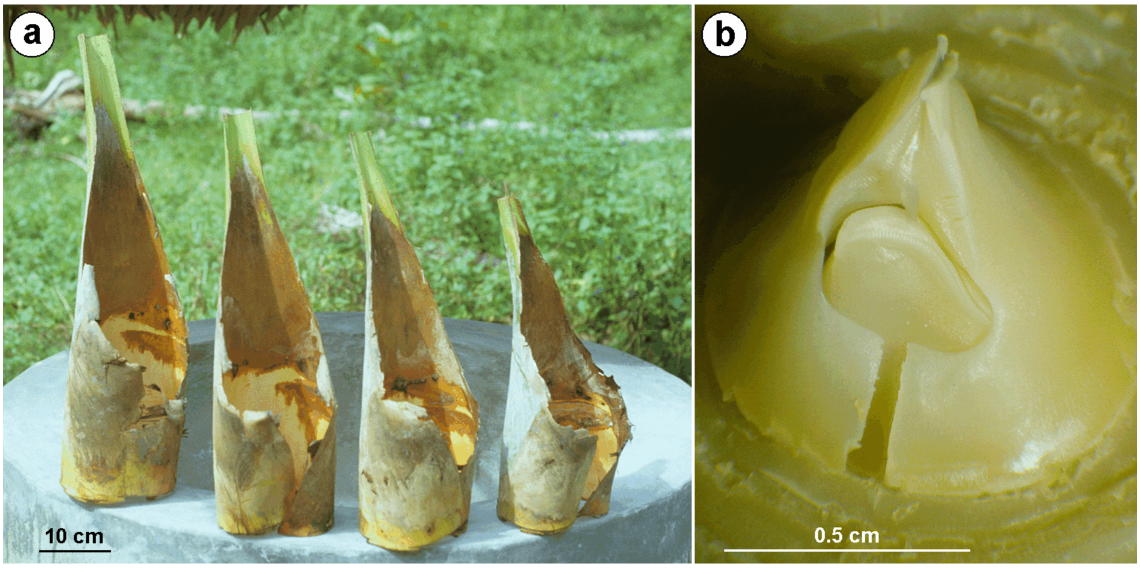

Figure 4.16 Morphology of sago palm leaves : topography of sheath, petiole and rachis.
a: Leaf bases of the youngest 4 (out of 17) unfolded leaves (in this case, the last AV-leaves) showing sheaths (cut to remove them from the trunk) extending into petioles; rachises cut off.
b: Cone of primordial enveloping leaves remaining after all green leaves, the spear-leaf and 7 primordial leaves inside the spear were cut from the trunk top; to remove the 8th primordial leaf, its sheath and base are already cut.
[a: photo nr. 89.08-092-22, Palm#18 ("Molat" G2), Hatusua, W. Seram aug1989. b: photo nr. 91.10-H-15, Palm#37 ("Ihur", Big Sucker (E-AV)), from Hatusua, W. Seram, 4nov1991, preserved in FAA.]

As already mentioned in Table 4.1, for palms #26, #30, #32 and #33 it could not be established with certainty whether their growing point was still vegetative. The top of the axes of Palm #30 and #32 was not dissected up to the very growing point, and that of Palm #33 and #26 could not be examined because it was damaged when the palm was felled. However, the internode length in these palms did not increase towards the top (see Table 4.7), indicating that these axes had not yet turned generative, at least not yet when the examined unfolded green leaves were formed. Therefore, these palms are included here as AV-phase palms.

In most palms, younger unfolded green leaves tend to have a shorter sheath-cum-petiole and rachis than older ones, while the number, length and width of leaflets and the rachis base dimension do not tend to be smaller. This seems to be in accordance with TOMLINSON (1990:48) when he states that in palms "exposure of the leaf blade does not signify complete extension of the leaf since maturation of basal parts (petiole and sheath) continue for several plastochrones after the blade expands; this is a consequence of the largely basipetal maturation of the parts of the palm leaf."

See the data sheet for Palm#27 in Appendix A for the change in length and width of leaflets from base to top in two entire leaves. For a discussion of leaf area, see Chapter 6.

In summary, among the sago palms observed, a leaf in the AV-phase has an axis of 9 to 12 m long, with an average of about 10.5 m, it has about 2 x 90 = 180 leaflets, the longest being about 1.7 m long, giving the leaf a width of about 3.5 m at its widest point.

Table 4.8 Morphological leaf statistics (range (mean) (number of observations)) of different sago palm varieties in the AV-phase from the villages Hatusua (Seram Island) and Siri Sori Serani (Saparua Island). Palm numbers refer to the numbers in the appended Sago Palm Data Sheets (Appendix A); they only reflect the chronological order in which the palms were examined. The overall extreme values in ranges and means are given in bold.

Palm #	**Variety**	**Length of axis of unfolded green leaves (cm)**			**Leaflets**			**Rachis base ****	
		sheath + petiole	rachis	total	nr per leaf [1 side]	length of longest (cm)	width of widest (cm)	width (cm)	height (cm)
10	M	299-310 (305)(2)	760-790 (775)(2)	1059-1100 (1080)(2)	86-92 (90)(4)	165-180 (173)(2)	10.2-11.4 (10.8)(2)	10.6-11.0 (10.8)(2)	10.1-10.3 (10.2)(2)
13		265-310 (292)(3)	780-813 (791)(3)	1045-1113 (1083)(3)	88-91 (89)(3)	156-172 (164)(3)	9.4-10.9 (10.0)(3)	10.3-10.7 (10.4)(3)	9.4-9.5 (9.5)(2)
30		280 (280)(1)	765 (765)(1)	1045 (1045)(1)	92* (92)(1)	176 (176)(1)	10.8 (10.8)(1)	10.2-10.4 (10.3)(6)	8.8-9.0 (8.9)(6)
31		275-285 (280)(2)	740-762 (751)(2)	1015-1047 (1031)(2)	89-92* (90)(2)	163-170 (167)(2)	10.0-10.7 (10.4)(2)	**9.3**-10.1 (**9.8**)(11)	**8.2**-8.9 (**8.6**)(11)
33		223 (**223**)(1)	**668** (**668**)(1)	**891** (**891**)(1)	**78*** (**78**)(1)	178 (178)(1)	12.6 (12.6)(1)	12.8 (12.8)(1)	10.0 (10.0)(1)
14	MB	300-**340** (**320**)(3)	825-885 (855)(2)	1125-1205 (1165)(2)	98-**98** (**98**)(2)	174-180 (177)(2)	11.6-12.1 (11.9)(2)	11.7-12.6 (12.3)(3)	10.4-10.9 (10.7)(3)
11	T	243-278 (264)(6)	774-813 (796)(3)	1017-1078 (1057)(3)	88-90 (89)(3)	160-188 (170)(4)	10.6-12.6 (11.5)(4)	12.0-12.5 (12.2)(8)	10.7-**12.5** (**11.4**)(8)
12		280-330 (313)(3)	800-855 (835)(3)	1080-1185 (1148)(3)	88-89 (89)(3)	163-169 (166)(3)	10.2-11.2 (10.8)(3)	10.4-10.8 (10.6)(2)	9.6-9.8 (9.7)(2)
15		275-305 (287)(3)	750-815 (778)(3)	1025-1120 (1065)(3)	86-87 (86)(3)	160-175 (167)(3)	10.0-11.0 (10.5)(3)	11.0-12.3 (11.6)(3)	9.9-10.8 (10.3)(3)
16		240-255 (247)(3)	720-790 (753)(3)	960-1045 (1000)(3)	89-91 (90)(3)	160-170 (163)(3)	11.8-12.6 (12.1)(3)	12.0-13.2 (12.5)(3)	10.5-11.6 (11.0)(3)
17		300-320 (310)(2)	825-**915** (**870**)(2)	1125-**1235** (**1180**)(2)	92-93 (93)(2)	170-**198** (184)(2)	11.0-11.6 (11.3)(2)	11.9-13.4 (12.7)(2)	10.5-11.7 (11.1)(2)
27		230-235 (233)(2)	741-770 (756)(2)	971-1005 (988)(2)	90-91* (90)(2)	185-192 (**189**)(2)	12.6-13.0 (12.8)(2)	12.4-13.6 (13.0)(15)	10.6-11.5 (11.0)(15)
32		251 (251)(1)	765 (765)(1)	1016 (1016)(1)	93* (93)(1)	175 (175)(1)	13.2 (13.2)(1)	12.5-13.3 (12.7)(7)	10.6-11.0 (10.8)(7)
19	P	**220**-248 (232)(3)	675-720 (693)(3)	904-968 (926)(3)	85-89* (87)(3)	**141**-156 (**147**)(3)	**9.2**-9.9 (**9.6**)(3)	9.8-10.1 (9.9)(3)	8.7-9.0 (8.8)(3)
20		256-279 (269)(3)	760-794 (773)(3)	1033-1050 (1042)(3)	83-87* (85)(3)	153-170 (162)(3)	10.2-11.3 (10.6)(3)	10.2-10.5 (10.4)(3)	9.0-9.5 (9.3)(3)
21		268-307 (288)(2)	768-815 (792)(2)	1036-1122 (1079)(2)	85-86* (85)(2)	160-166 (163)(2)	10.3-12.2 (11.3)(2)	10.1-11.2 (10.6)(2)	10.2 (10.2)(1)
25	I	247-258 (254)(4)	770-801 (787)(4)	1025-1053 (1041)(4)	93-**98*** (95)(4)	160-188 (180)(4)	11.0-**15.7** (**14.0**)(4)	12.3-**14.5** (**13.6**)(4)	10.3-11.6 (11.1)(4)
26		265 (265)(1)	760 (760)(1)	1025 (1025)(1)	93* (93)(1)	185 (185)(1)	12.9 (12.9)(1)	13.5-13.7 (**13.6**)(2)	11.1-11.2 (11.1)(2)
Overall range		**220-340**	**668-915**	**891-1235**	**78-98**	**141-198**	**9.2-15.7**	**9.3-14.5**	**8.2-12.5**
Overall mean		274 (n=45)	780 (n=41)	1052 (n=41)	90 (n=43)	170 (n=42)	11.4 (n=42)	11.7 (n=80)	10.2 (n=78)

* means of left and right side of the rachis.
** see Fig. 6.2 for the method of measuring width and height of the rachis base.
Varieties: M = Molat; Mb = Molat Berduri; T = Tuni; P = Putih ; I = Ihur.

- Leaf unfolding rate (LUR)

To monitor leaf unfolding rates, 37 undisturbed- and healthy-looking palms (axes) were selected and marked (Fig. 4.17). These palms differed in trunk height, but were all in their AV-phase judging from their outward appearances, viz. with trunk (visible or still hidden by leaf bases), but without signs of (developing) inflorescence. The palms belonged to 4 different folk varieties in 2 locations: "Molat", "Tuni" and "Ihur" palms in the area around Hatusua village, Seram, and "Putih" palms near Siri Sori Serani village, Saparua. Each palm was observed (monitored) two to five times, as opportunity and time permitted. Due to various mishaps, only 28 palms made it to their last observation with their leaves intact. One palm was killed by the felling of a neighbouring tree even before the second observation, therefore LUR data of only 36 palms could be collected. Observation intervals ranged from 4 to 15 months, the overall monitoring period from 4 to 34 months. New leaves were kept track of by marking the petiole of the youngest unfolded leaf at each observation with a streak of oil-paint (a different colour for each consecutive observation) and counting the number of new unfolded leaves above the previous marking.
As factors possibly influencing the LUR apart from the variety were observed during one or more of the observation rounds: groundwater table, degree of shading, number of dependent suckers with leaves of 4 m long or longer, visible trunk height, and total number of leaves in the crown.

All observations concerning the 'LUR-palms' are presented in Appendix C.

Figure 4.17 The selected palms were marked on a panel on the trunk cleaned of leaf remains with the letters LUR (for Leaf Unfolding Rate) in oil-paint. This to the merriment of my local assistants as 'lur' is Ambonese Malay for 'to peek' (from the Dutch word for it, 'loeren'), which well reflected our intentions with these palms.
[photo nr. 89.09-095-26. Siri-Sori Serani, Saparua 06sep1989.]

Table 4.9 gives an overview of the leaf unfolding data grouped per variety.

For further evaluation of the LUR (in leaves per year), the number of leaves unfolded as observed over a real 12-month interval (checkered columns in Table 4.9) is used, rather than an annual number calculated from a shorter or longer interval. I assume the former to be the more reliable LUR value, because it covers all yearly seasons - with their possible influence on LUR - once. Calculated rates for each of the consecutive shorter observation intervals give information on the constancy of the rate.

Table 4.10 gives an overview of the observation data on factors with a possible influence on the LUR.

Table 4.9 Leaf unfolding rate (LUR) per observation interval of trunked axes of the sago palm varieties Molat, Tuni, Ihur and Putih. The palm numbers (LUR-01 to LUR-37) only reflect the order in which suitable palms were encountered and selected for LUR monitoring.

Palm #	Leaves unfolded between ...					Leaf unfolding rate (leaves/year)					
						as *calculated* from observed interval ...				as *observed* at interval ...	
	apr89 and aug89 (4 mth)	aug89 and apr90 (8 mth)	apr90 and nov90 (7 mth)	nov90 and feb92 (15 mth)	sep89 and sep90 (12 mth)	apr89-aug89 (4 mth)	aug89-apr90 (8 mth)	apr90-nov90 (7 mth)	nov90-feb92 (15 mth)	apr89-apr90 (12 mth)	sep89-sep90 (12 mth)
Molat											
LUR-01	4	7	5	n.r.		12	10.5	8.6	--	11	
LUR-12	3	8	6	15		9	12.0	10.3	12.0	11	
LUR-13	3	4	5	11		9	6.0	8.6	8.8	7	
LUR-14	2	5	4	10		6	7.5	6.9	8.0	7	
LUR-15	2	7	5	12		6	10.5	8.6	9.6	9	
LUR-16	3	7	6	13		9	10.5	10.3	10.4	10	
LUR-18	3	5	4	9		9	7.5	6.9	7.2	8	
LUR-19	1	3	2	4		3	4.5	3.4	3.2	4	
LUR-27	1	4	3	6		3	6.0	5.1	4.8	5	
LUR-28	2	5	4	9		6	7.5	6.9	7.2	7	
Mean (sd)	2.4 (0.97)	5.5 (1.65)	4.4 (1.26)	9.9 (3.41)		7.2 (2.90)	8.3 (2.47)	7.5 (2.17)	7.9 (2.73)	7.9 (2.38)	
Tuni											
LUR-06	3	7	6	15		9	10.5	10.3	12.0	10	
LUR-07	3	8	14	2		9	12.0	24.0	1.6	11	
LUR-09	2	5	3	n.r.		6	7.5	5.1	--	7	
LUR-10	3	5	5	n.r.		9	7.5	8.6	--	8	
LUR-11	3	7	5	13		9	10.5	8.6	10.4	10	
LUR-17	4	10	8	19		12	15.0	13.7	15.2	14	
LUR-22	2	4	4	7		6	6.0	6.9	5.6	6	
LUR-23	1	2	2	5		3	3.0	3.4	4.0	3	
LUR-24	1	1	2	3		3	1.5	3.4	2.4	2	
LUR-25	2	4	4	8		6	6.0	6.9	6.4	6	
LUR-26	2	4	3	8		6	6.0	5.1	6.4	6	
Mean (sd)	2.4 (0.92)	5.2 (2.64)	5.1 (3.45)	8.9 (5.69)		7.1 (2.77)	7.8 (3.96)	8.7 (5.91)	7.1 (4.55)	7.5 (3.53)	
Ihur											
LUR-02	3	8	8	n.r.		9	12.0	13.7	--	11	
LUR-03	3	7	6	14		9	10.5	10.3	11.2	10	
LUR-04	3	7	7	n.r.		9	10.5	12.0	--	10	
LUR-05	3	7	7	n.r.		9	10.5	12.0	--	10	
LUR-20	2	5	5	11		6	7.5	8.6	8.8	7	
LUR-21	3	6	5	11		9	9.0	8.6	8.8	9	
LUR-29	1	5	n.r.	n.r.		3	7.5	--	--	6	
LUR-30	2	6	5	11		6	9.0	8.6	8.8	8	
LUR-31	1	n.r.	n.r.	n.r.		3	--	--	--	--	
LUR-32	3	5	5	12		9	7.5	8.6	9.6	8	
Mean (sd)	2.4 (0.84)	6.2 (1.09)	6.0 (1.20)	11.8 (1.30)		7.2 (2.53)	9.3 (1.64)	10.3 (2.05)	9.4 (1.04)	8.8 (1.64)	
Putih											
LUR-33					4						4
LUR-34					4						4
LUR-35					4						4
LUR-36					4						4
LUR-37					4						4
Mean					4						4

▨ = observed annual rates, as opposed to the calculated rates in the other leaf unfolding rate columns.

n.r = not recorded (e.g. because trunk was damaged, or harvested unannounced and unnoticed notwithstanding the request not to harvest it before the end of the monitoring period).

N.B. : LUR-08 not included in table because it was accidentally killed before the end of the 1st observation interval.

Table 4.10 Number of leaves and factors possibly influencing leaf unfolding rate in the sago palm varieties Molat, Tuni, Ihur and Putih.

Palm #	Ground water table *)			Shading			S3-s in clump			Visible trunk height (m) (obs1,2,3: estimated)				Total number of unfolded leaves					New leaves			
	obs1	obs2	obs3	obs1	obs2	obs3	obs1	obs2	obs3	obs1	obs2	obs3	obs5	obs1	obs2	obs3	obs4	obs5	obs1-2	obs2-3	obs3-4	obs4-5
MOLAT																						
LUR-01	0-25b	15a	0	0-1/4	n.r.	0-1/4	n.r.	n.r.	5	n.r.	n.r.	10-11	n.r.	15	17	18	19	n.r.	4	7	5	n.r.
LUR-12	35-40b	35-40b	0-25b	0-1/4	n.r.	0	n.r.	n.r.	3	n.r.	n.r.	9-10	n.r.	17	20	20	19	n.r.	3	8	6	15
LUR-13	0-25b	0-25b	0-25b	1/4-1/2	n.r.	1/2-3/4	n.r.	n.r.	1	0	n.r.	0-1	2.80	11	13	12	16	16	3	4	5	11
LUR-14	0-25b	0-25b	0-25b	1/4-1/2	n.r.	3/4-1	n.r.	n.r.	1	0	n.r.	0	2.32	13	11	14	13	15	2	5	4	10
LUR-15	28b	28b	0-25b	0-1/4	n.r.	1/4-1/2	n.r.	n.r.	2	n.r.	n.r.	3-4	4.55	14	15	17	16	18	2	7	5	12
LUR-16	0-25b	0-25b	0-25b	1/4-1/2	n.r.	1/4-1/2	n.r.	n.r.	1	n.r.	n.r.	2	3.90	14	16	16	18	22	3	7	6	13
LUR-18	0-50a	0-50a	0-25b	1/4-1/2	n.r.	1/4-1/2	5	n.r.	2	n.r.	n.r.	4	5.70	16	19	19	20	21	3	5	4	9
LUR-19	0-50a	0-50a	0-25b	1/2-3/4	n.r.	3/4-1	4	n.r.	0	n.r.	n.r.	0	c.1	10	10	11	9	9	1	3	2	4
LUR-27	0	n.r.	0	1/4-1/2	n.r.	1/2-3/4	n.r.	n.r.	0	2-3	n.r.	3-4	4.45	13	9	13	13	12	1	4	3	6
LUR-28	0	n.r.	0	1/4-1/2	n.r.	1/2-3/4	n.r.	n.r.	0	3-4	n.r.	4	5.10	14	15	15	16	18	2	5	4	9
TUNI																						
LUR-06	85b	85b	110b	0	n.r.	0	5	n.r.	3	n.r.	n.r.	8-9	9.22	17	16	18	19	19	3	7	6	15
LUR-07	30b	0	45b	0-1/4	n.r.	0-1/4	n.r.	n.r.	1	n.r.	n.r.	8-9	8.09	16	15	20	28	21	3	8	14	2
LUR-09	0-25b	10-25a	73b	0-1/4	n.r.	0-1/4	n.r.	n.r.	0	n.r.	n.r.	4	n.r.	12	11	13	12	n.r.	2	5	3	n.r.
LUR-10	0-25b	10-25a	73b	0-1/4	n.r.	1/4	n.r.	n.r.	0	n.r.	n.r.	6	n.r.	15	13	14	16	n.r.	3	5	5	n.r.
LUR-11	55b	55b	95b	0-1/4	n.r.	0	n.r.	n.r.	2	n.r.	n.r.	6-7	7.98	16	17	18	17	21	3	7	5	13
LUR-17	0-25b	0-25b	0-25b	0	n.r.	0	n.r.	n.r.	4	n.r.	n.r.	8	8.65	24	26	28	29	26	4	10	8	19
LUR-22	0-50a	0-50a	0-25b	1/2-3/4	n.r.	1/2-3/4	n.r.	n.r.	2	6-7	n.r.	8	9.05	14	12	12	14	12	2	4	4	7
LUR-23	0-50a	0-50a	0-25b	3/4-1	n.r.	3/4-1	n.r.	n.r.	0	0	n.r.	2-3	2.80	11	9	9	8	8	1	2	2	5
LUR-24	0-50a	0-50a	0-25b	3/4-1	n.r.	3/4-1	n.r.	n.r.	0	0	n.r.	0	0.00	7	7	6	7	6	1	1	2	3
LUR-25	0-50a	n.r.	0-25b	1/2-3/4	n.r.	1/2	n.r.	n.r.	0	5-6	n.r.	8	8.10	13	13	13	13	13	2	4	4	8
LUR-26	25-50b	n.r.	80-100b	1/2-3/4	n.r.	1/2-3/4	n.r.	n.r.	2	4	n.r.	5-6	5.97	12	9	9	11	12	2	4	3	8
IHUR																						
LUR-02	0-25b	15a	0	0	n.r.	0-1/4	n.r.	n.r.	3-4	n.r.	n.r.	10-11	n.r.	14	15	22	24	n.r.	3	8	8	n.r.
LUR-03	0-25b	0-25b	15b	0	n.r.	0	n.r.	n.r.	0	n.r.	n.r.	6	5.05	14	14	18	18	21	3	7	6	14
LUR-04	0-25b	0-25b	35b	0-1/4	n.r.	0	n.r.	n.r.	2	n.r.	n.r.	8	n.r.	16	18	16	22	n.r.	3	7	7	n.r.
LUR-05	0-25b	0-25b	30b	0-1/4	n.r.	0-1/4	n.r.	n.r.	1	n.r.	n.r.	8	n.r.	14	16	16	19	n.r.	3	7	7	n.r.
LUR-20	50b	50b	100-125b	1/2-3/4	n.r.	1/4-1/2	2	n.r.	1	n.r.	n.r.	6	8.05	15	15	14	15	17	2	5	5	11
LUR-21	50b	50b	100-125b	1/4-1/2	n.r.	1/4-1/2	0	n.r.	0	n.r.	n.r.	7	9.50	18	17	18	18	17	3	6	5	11
LUR-29	0-25b	0-25b	25-30b	1/4-1/2	n.r.	1/2-3/4	0	n.r.	?	2-3	n.r.	3-4	n.r.	11	10	11	n.r.	n.r.	1	5	n.r	n.r.
LUR-30	0-25b	0-25b	25-30b	0-1/4	n.r.	1/4-1/2	6	n.r.	5	4	n.r.	8	8.52	15	16	18	17	17	2	6	5	11
LUR-31	0-25b	0-25b	25-30b	3/4-1	n.r.	n.r	n.r.	n.r.	n.r.	0	n.r.	n.r.	n.r.	8	6	n.r.	n.r.	n.r.	1	n.r.	n.r.	n.r.
LUR-32	0-25b	0-25b	25-30b	1/4-1/2	n.r.	1/4-1/2	n.r.	n.r.	4	5	n.r.	6	7.42	13	15	17	17	20	3	5	5	12
PUTIH																						
LUR-33	n.a.	n.a.		1/4-1/2	0-1/4		n.r.	0		7	8			11	14				4			
LUR-34	n.a.	n.a.		0-1/4	0-1/4		n.r.	0		9	9			12	14				4			
LUR-35	90b	118b		0-1/4	0		n.r.	0		7-8	8			14	13				4			
LUR-36	90b	113b		1/4-1/2	1/4-1/2		n.r.	0		4-5	5.7			11	11				4			
LUR-37	100b	>125b		0	0-1/4		n.r.	0		5-6	6.5			14	15				4			

*) in cm above (a) or below (b) ground level. S3 = Large suckers with leaves of 4 m long and up. n.r. = not recorded
obs1 = First observation (LUR 01-17 : 12apr1989 ; LUR 18-32 : 17apr1989 ; LUR 33-37 : 06sep1989). n.a. = not applicable (no watertable found: rock
obs2 = Second observation (LUR 01-17 : 14aug1989 ; LUR 18-32 : 13aug1989 ; LUR 33-37 : 04sep1990). at 50-100 cm below ground level).
obs3 = Third observation (LUR 01-32 : 17apr1990).
obs4 = Fourth observation (LUR 01-32 : 17nov1990).
obs5 = Fifth observation (LUR 12-16,18-32 : 20feb1992 ; LUR 1-11,17 : 21feb1992). N.B.: LUR-08 is not included in table because it was accidentally killed before obs2.

LURs observed over a real 12-month interval showed a wide range of 2-14 leaves per year, although the average LUR for "Molat", "Tuni" and "Ihur" was quite similar at 7.9, 7.5 and 8.8 leaves per year, respectively. The spread of LURs in "Tuni" was the highest, in "Ihur" the lowest (standard deviation 3.53 and 1.64, respectively). The LUR of all "Putih" palms was 4 leaves per year.

Unlike all other palms observed during these periods, Palm #LUR-07 showed a remarkable 100% increase of its LUR during the observation period from April to November 1990 as compared to the preceding period August 1989 to April 1990 (not considering the very slowly growing Palm #LUR-24 for which judging one leaf folded or unfolded already made a 100% difference in the number of unfolded leaves). If we compare #LUR-07 with the two 'LUR-palms' of variety Tuni with the next highest LURs during the April - November 1990 period, viz. #LUR-06 and #LUR-17, we see that in mid April 1990, these 3 palms had about the same visible trunk height and no outward signs of a developing inflorescence. By mid November 1990, #LUR-06 and #LUR-17 had about the same number of unfolded green leaves as 7 months before, but #LUR-07 had 40% more leaves.
During a revisit of the research area around Hatusua 15 month later in February 1992 (the 5th observation round) #LUR-06 had turned generative showing first-order inflorescence branches, #LUR-07 had turned generative showing third-order inflorescence branches, while #LUR-17 was still vegetative (Fig. 4.18).

Figure 4.18 Crown details of 3 sago palm axes of variety Tuni used to monitor leaf unfolding rate, (f.l.t.r.) Palm #LUR-06, Palm #LUR-07, and Palm #LUR-17, photographed on fri21feb1992.
[f.l.t.r. photo nr. 92.02-215-06A, 92.02-215-05A, and 92.02-215-02A. Hatusua, Seram.]

As trunks in the generative phase are known to have a higher LUR than in the vegetative phase, it can be concluded that the high LUR in Palm #LUR-07 during the April to November 1990 period was related to the nearness of the appearance of the inflorescence, whereas the appearance of the inflorescence in Palm #LUR-06 was still too far off during this period to cause an increased LUR then. The relatively high LUR of Palm #LUR-17 must be unrelated to a nearing generative phase.

4.4.2.3 Generative phase (G-phase)

More exact knowledge of how the morphology of the inflorescence changes in the course of its development and of the duration of each developmental stage will contribute to a more precise estimation of how far in time a generative axis of a sago palm encountered in the field has progressed, at least in the generative phase of the axis' total life span.

Among the dozens of sago palms felled for the various purposes of my research, there were several palms with inflorescences. These inflorescences varied from primordial to full-grown. By putting the various developmental stages encountered in the right order, I could arrive at a comprehensive picture of the morphological development of an inflorescence. A chance hit was the encounter in one of the palms of very early stages of the first anatomically visible structures of the generative phase: buds of the ax_1-s, measuring a mere 1 to 2 mm long and wide, in the axils of the still primordial bracts near the growing point. One such bud will eventually grow into a 2 - 4 m long branch, itself branched again, with a total dry weight of 2.5 - 5 kg.

First the morphology of a full-grown inflorescence is described, taking varietal differences into account. Then the development of the inflorescence branches of consecutive orders is 'followed' from the very early stages onward, illustrated by macroscopic, light-microscopic and electron-microscopic photographs. Finally, observations on the duration of the consecutive stages of inflorescence development are presented.

- Morphology of developmental stages within the G-phase

-- Structure of the full-grown inflorescence

The inflorescence of a sago palm emerges at the top of the trunk above the crown of leaves (Fig. 4.19), a so-called suprafoliar inflorescence, as different from the interfoliar inflorescence in e.g. oil-, coconut and date palm, and from the infrafoliar inflorescence in e.g. betelnut palm.

Figures 4.20 - 4.22 show the branching structure of the mature inflorescence of the sago palm. I based the nomenclature of its composing parts on the one used by TOMLINSON (1971): The central inflorescence stalk or rachis, which is the tapering extension of the trunk, is called main axis or ax_0; the first-, second-, and third-order branches are called ax_1, ax_2, and ax_3, respectively, the ax_3-s being the flower-bearing rachillae; a bract growing on an ax_0, ax_1, ax_2, or ax_3 is called a first-, second, third-, or fourth-order bract, respectively, or in short a br_1, br_2, br_3, or br_4. I have indicated the position of a component on the main axis or a branch by a Roman numeral; thus, e.g. br_3-IV would be the fourth-lowest (= fourth-oldest) third-order bract on the second-order branch at hand.

The transition from complete leaf to bract is gradual along the main axis as it passes into the inflorescence rachis: the number of leaflets per leaf deminishes until only a sheath apically tapering into a long, thin ribbon is left (see also Fig. 4.27a and c). The first ax_1-s may spring from the axils of leaves which still have a few leaflets on them (Fig. 4.30a). For simplicity reasons, I will call a leaf-like organ with an ax_1 growing from its axil a (first-order) bract, irrespective of the presence or absence of leaflets.
As the ax_1 develops, it pierces through its subtending bract (Fig. 4.27c and d).

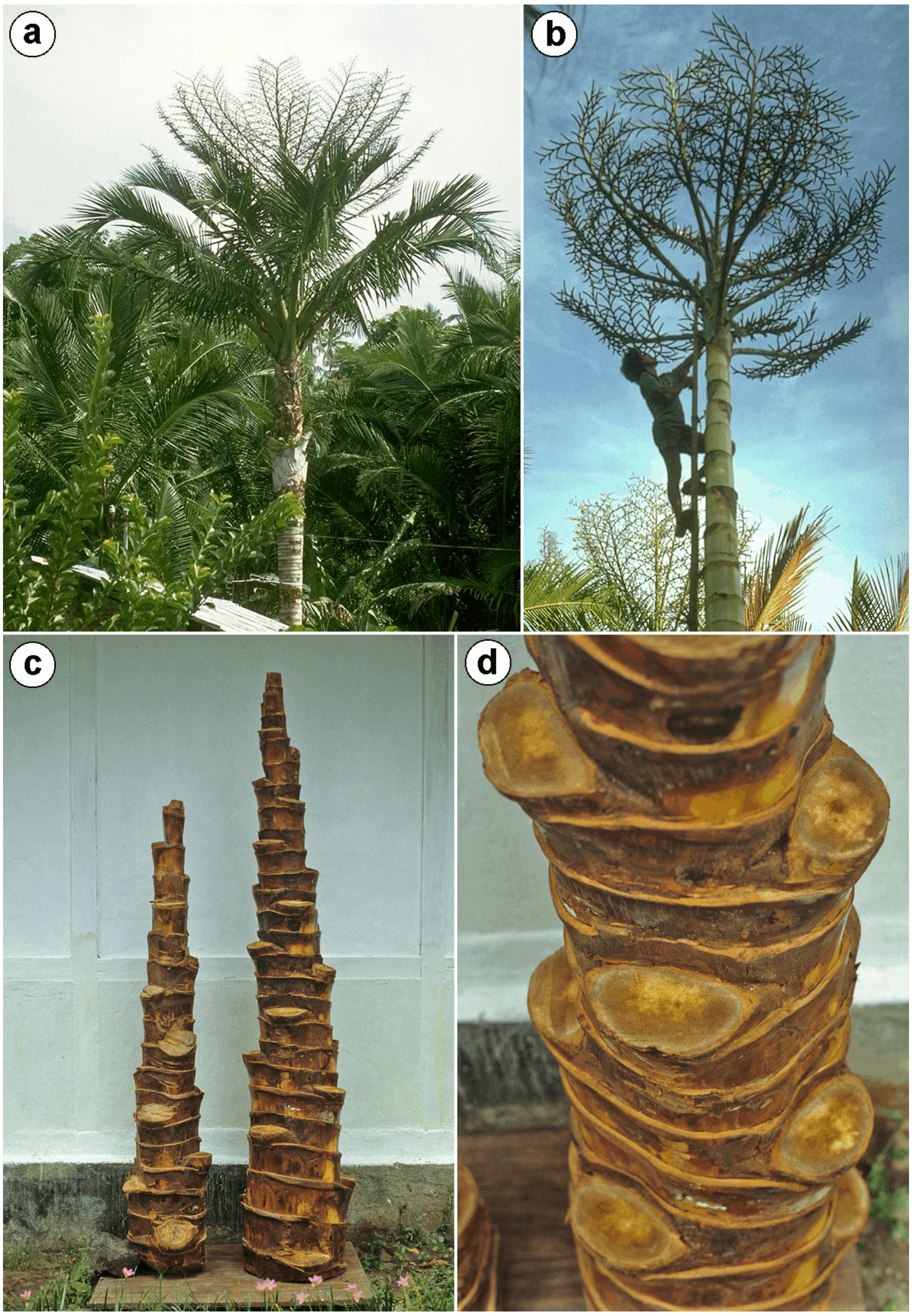

Figure 4.19 The terminal, suprafoliar inflorescence of sago palm, full-grown.

a: trunk in the original state, with leaves.

b: trunk from which all leaves were removed, showing the tapering top part with long internodes (whitish because they were covered by leaf bases).

c: two dried trunk tops, the rachises (ax_0-s) of the inflorescences, from which all bracts and inflorescence branches were removed, (also) illustrating occurring size differences between palms (rachis on the right is 182 cm long).

d: close-up of rachis shown on the right in photo c: .

[Photos: a: 90.11-147-21, by side of the road from Passo to Poka, Ambon Island, 08nov1990 ; b: 89.08-092-19 (Palm#18, "Molat"), Hatusua, W.Seram, jul1989.) ; c, d: 88.12-074-19, 88.12-074-21 (Palm#05, "Ihur"), Hatusua, W.Seram thu15dec1988.]

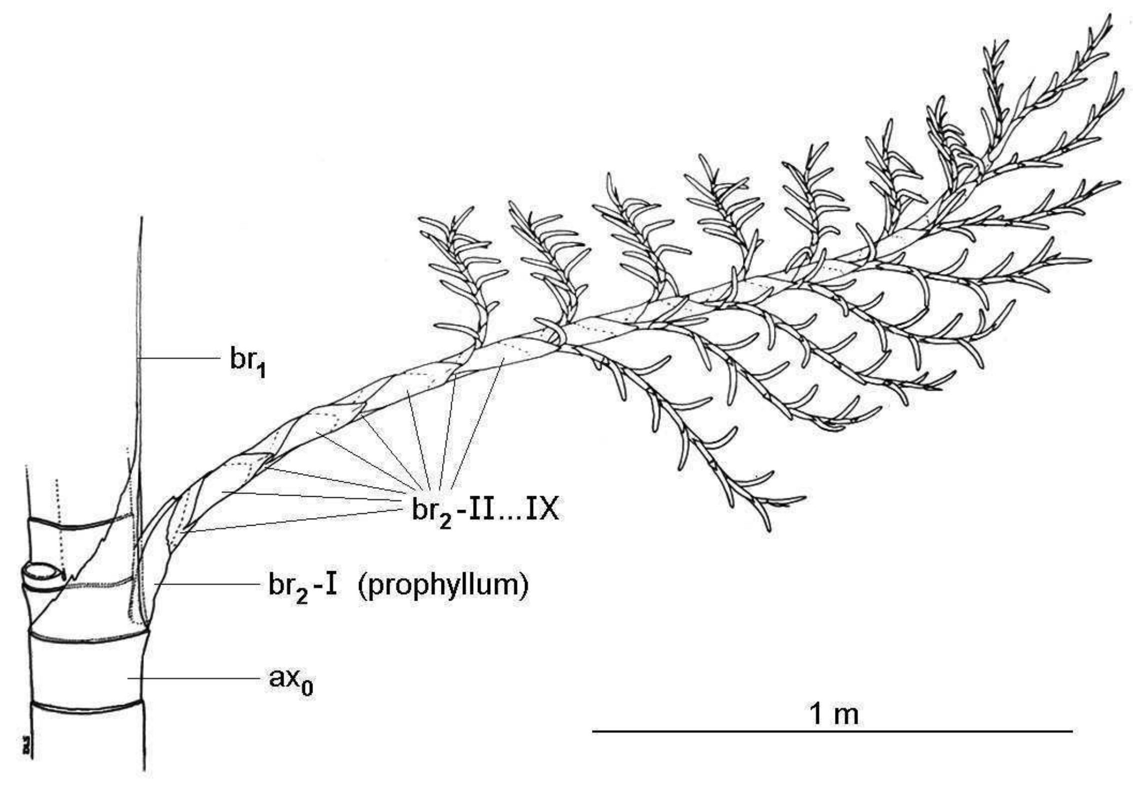

Figure 4.20 A first-order inflorescence branch (ax_1) and its attachment to the main axis (ax_0). (br_1, br_2 = first-, second-order bract).

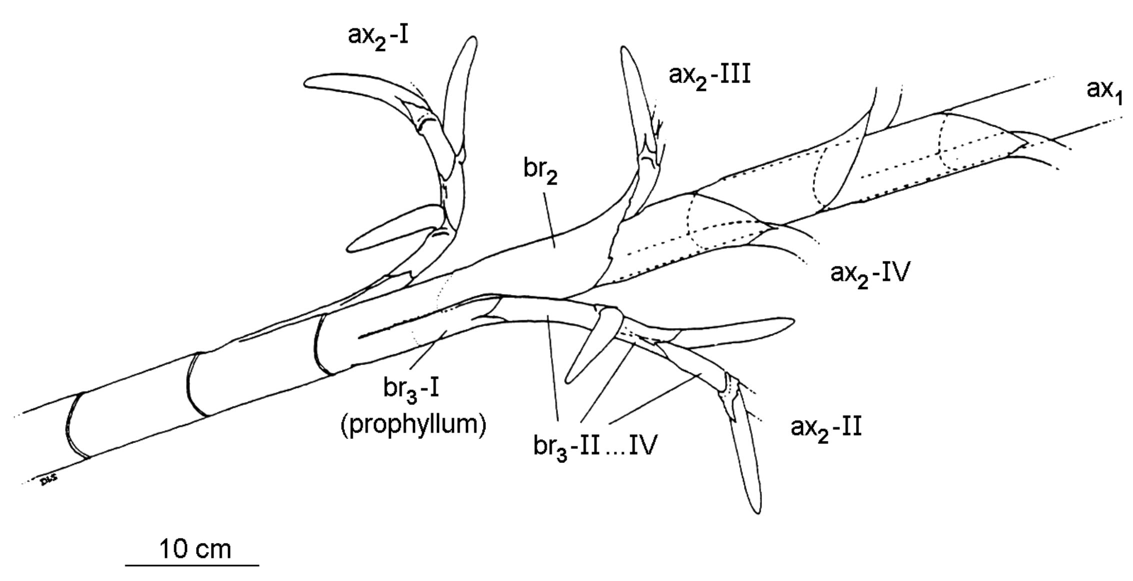

Figure 4.21 Part of a first-order inflorescence branch (ax_1) showing the attachment and two-ranked positioning of the second-order branches (ax_2-s). (br_2, br_3 = second-, third-order bract).

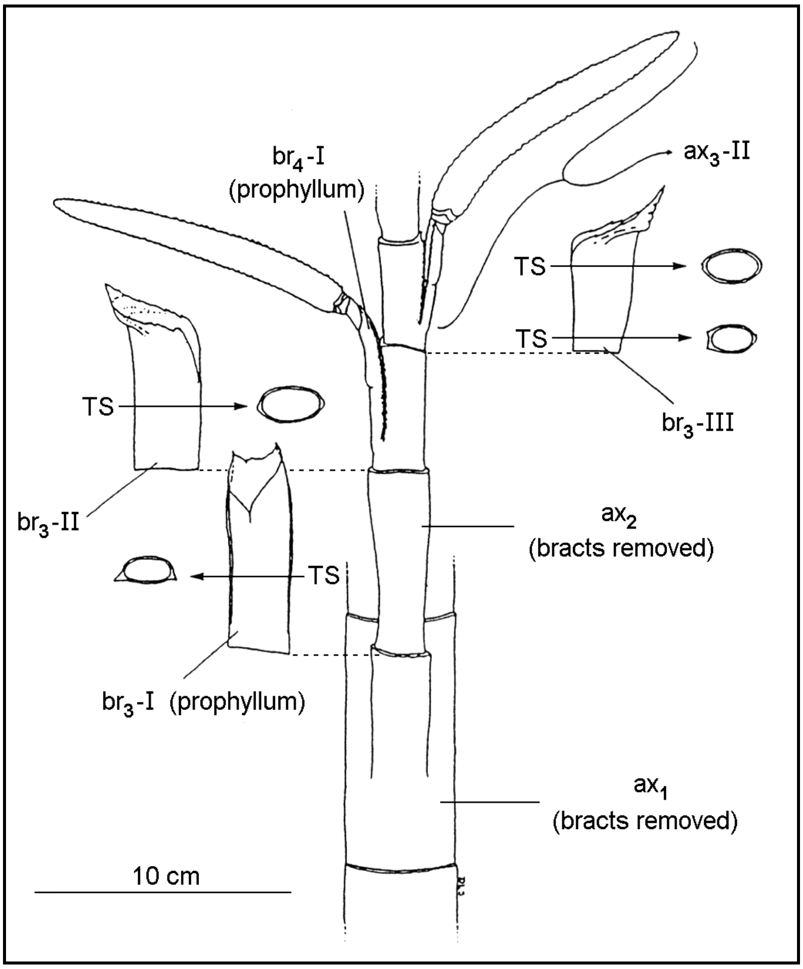

Figure 4.22 Basal part of a second-order inflorescence branch (ax_2) showing the first two third-order branches (ax_3-I, -II). (TS = transverse section)

In Table 4.11 some statistics are presented of the inflorescences of the sampled sago palms ordered by variety.

Table 4.11 Length of rachis (ax_0), number and length of first-order branches (ax_1-s), and number of second-order branches (ax_2-s) per ax_1 in inflorescences of sago palms of various varieties.

Palm #	Variety	Length of ax_0 (cm)	Number of ax_1-s	Length range of ax_1-s (cm)	Number of ax_2-s per ax_1
18	Molat	165	18	134 - 288	7 - 16
03	Tuni	250	27	205 - 410	14 - 23
24	Tuni	n.r.	27	n.r.	n.r.
28	Tuni	n.r.	27	n.r.	16 - 26
34	Tuni	239	27	242 - 415	15 - 25
05	Ihur	182	24	215 - 443	13 - 26
35	Ihur	235	23	186 - 366	13 - 21
29	Molat Berduri	n.r.	22	n.r.	n.r.
04	Makanaro	200	19	n.r.	n.r.
36	Makanatol	160	20	184 - 305	13 - 18

n.r. = not recorded, e.g. when not yet full-grown.

-- The first anatomically visible symptoms of flowering initiation

If all the leaves of a sago palm are removed from the trunk, both the green unfolded ones and the white folded and primordial ones, the 'naked' apex of a trunk in the vegetative phase looks different from one in which flowering initiation has taken place. In the latter the lengthening of the internodes apparently starts at an earlier stage, resulting in a conical apex, as opposed to a truncate one with a shallow depression in the middle at the very top in the vegetative phase (Fig. 4.23). TOMLINSON (1990:55) also suggested that an "elongation of the subapical region" in *Metroxylon sagu* "may represent the transition to inflorescence in this hapaxanthic palm."

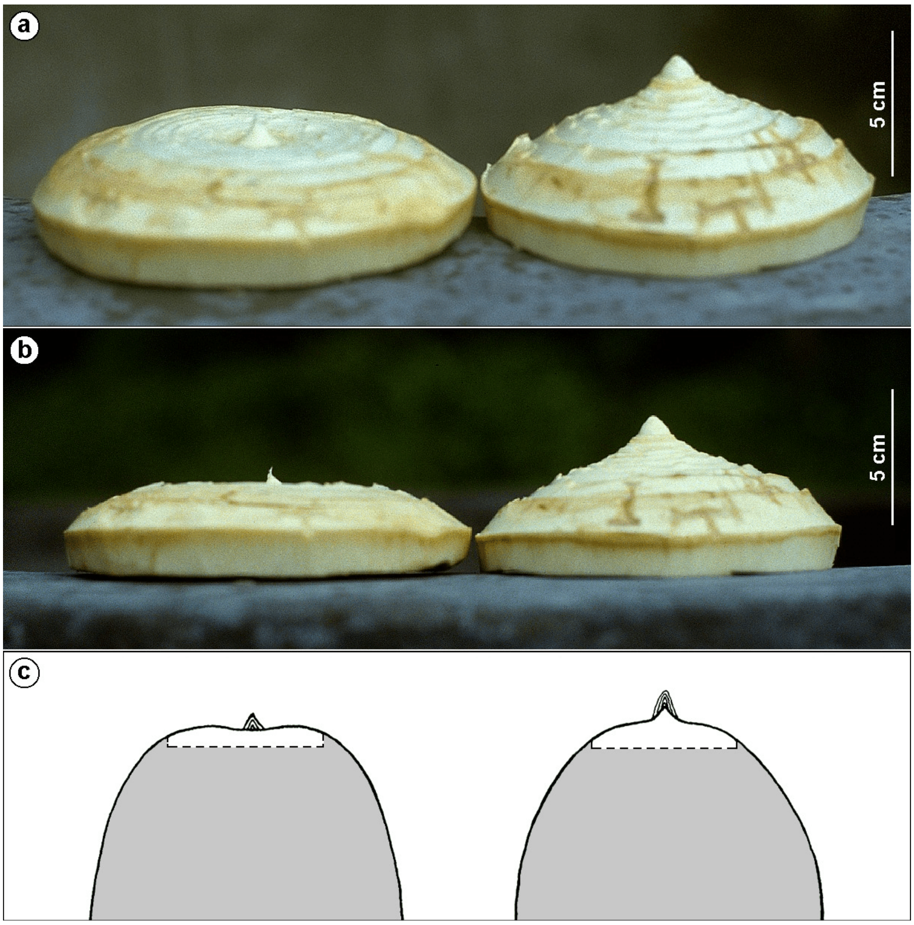

Figure 4.23 Trunk apex of a sago palm in the vegetative phase (left) and in the generative phase (right). The leaves developing on the apices have been removed until the differences in apex shape became clearly visible. The annular scars show where the removed leaves were attached.
a: oblique top view showing the depression in the vegetative apex on the left.
b: lateral view.
c: diagrammatic longitudinal sections through the trunk tops showing which parts were cut out for the photographs.
Left: Palm #23 ("Tuni", AV-phase). Right: Palm #24 ("Tuni", G1-phase).
[a: photo nr. 89.09-095-05. b: photo nr. 89.09-095-04. Hatusua, 27aug1989.]

-- The different morphology of leaf primordia after flowering initiation

A bract on the ax$_0$, in the axil of which an ax$_1$ develops, lacks leaflets and shows a tip extended into a thin, threadlike, but rather stiff appendage where a normal foliage leaf has its petiole and rachis (see Fig. 4.27a). Observing these bracts in their very early developmental stages and comparing them to normal leaves in similar stages reveals that the appendages of the former are not simply homologous to the petioles/raches of the latter. Figure 4.24 shows the difference. The terminal extensions are visible as ribbon-like appendages in the young bracts already (Fig. 4.24b,c,d), a feature lacking in the young foliage leaves (Fig. 4.24a).
In a full-grown inflorescence, however, one can also often observe that the bracts subtending the lower ax$_1$-s do have some 'remaining' leaflets (although often many of them are contorted or not fully-extended), their number per bract decreasing towards the top of the ax$_0$ (Fig. 4.30a). This suggests a gradual transition from petiole/rachis to threadlike appendage. Further study of the developmental morphology of the leaf/bract would be needed to clarify the transition from foliage leaf to bract and to determine whether the observed threadlike appendage is homologous to the petiole/rachis, or not.

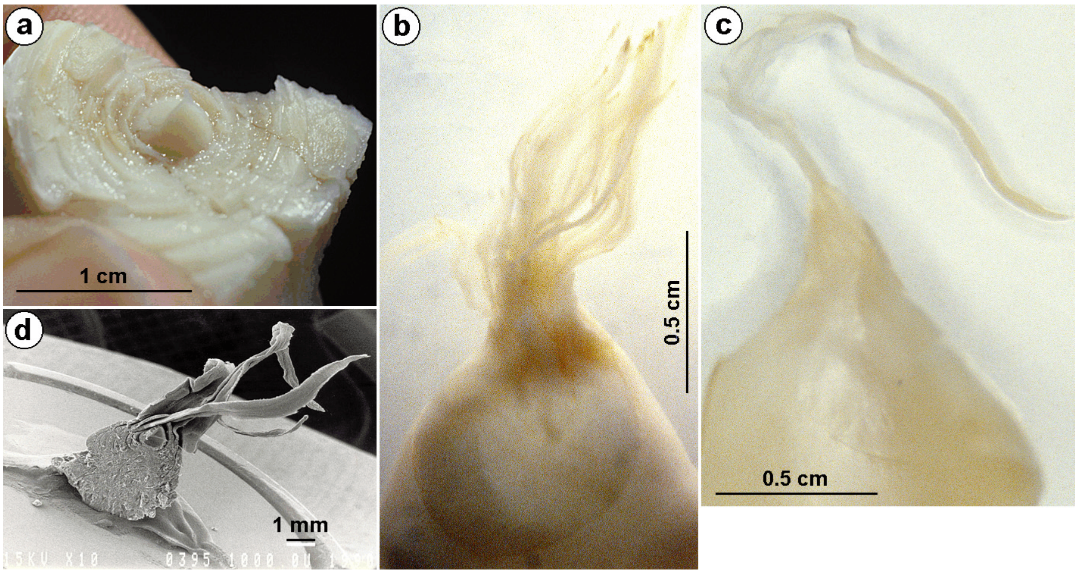

Figure 4.24 Primordial leaves/bracts at the shoot apex of a sago palm before and after flower initiation.

a: apex before flower initiation showing the remaining cone of leaf primordia after the spear-leaf and 17 leaves inside it were removed.

b: apex after flower initiation showing ribbon-like appendages at the tips of the primordial leaves/bracts (spear-leaf and 13 leaves/bracts inside it removed).

c: bract after flower initiation: adaxial side of top part of 13th primordial leaf/bract inside spear-leaf.

d: scanning electron micrograph of longitudinal section of apex after flower initiation (spear-leaf and 26 leaves/bracts inside it removed).

[a: photo nr.89.02-A-12, Palm#07 ("Ihur", AV-phase). b,c,d: photos nr.90.02-D-16, 90.02-D-15, 90.02-SEM-395, Palm#24 ("Tuni", G1-phase). a,b,c: material preserved in 70% ethanol or FAA ; d: photo by Felix THIEL wed28feb1990.]

-- Development of the first-order inflorescence branch (ax$_1$)

Figure 4.25 shows a bud of an ax$_1$ at a very early stage of development as seen through a light microscope. Figure 4.26d shows the same bud as seen with the aid of a scanning electron microscope (s.e.m.), essentially providing the same information, only with infinitely more contrast.

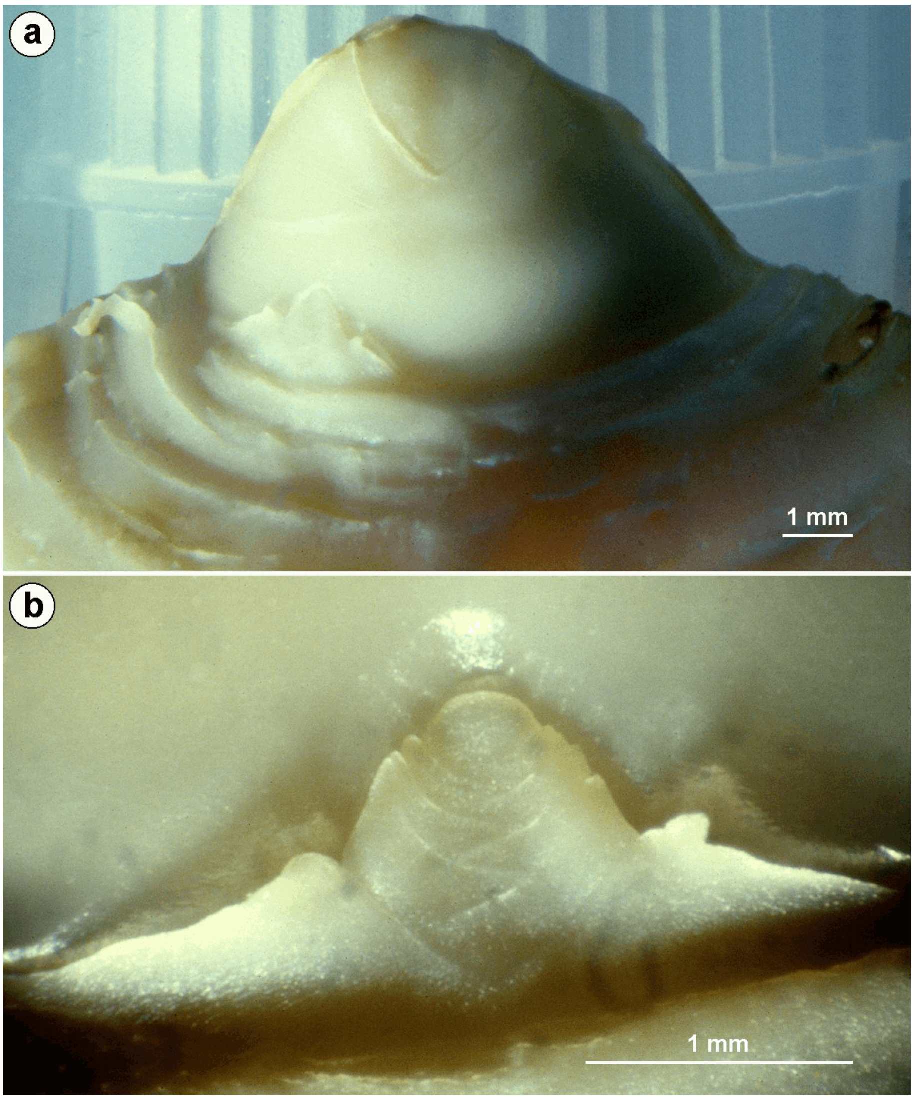

Figure 4.25 The bud of a first-order inflorescence branch in the axil of lf-XIV (spear leaf plus next 14 leaves inside it removed) as seen through a light microscope after fixation/preservation in 70% ethanol.
a: overview, showing its position on the apex.
b: close-up, showing the folds of the second-order bracts.
[a: photo nr.90.02-D-25. b: photo nr.90.02-D-27. Palm#24 ("Tuni", G1-phase)]]

Figure 4.26 shows s.e.m. pictures of ax$_1$ buds from one palm in ascending order of development, the younger ones found, of course, further inside the stacked cone-shaped primordial bracts nearer to the vegetation point.

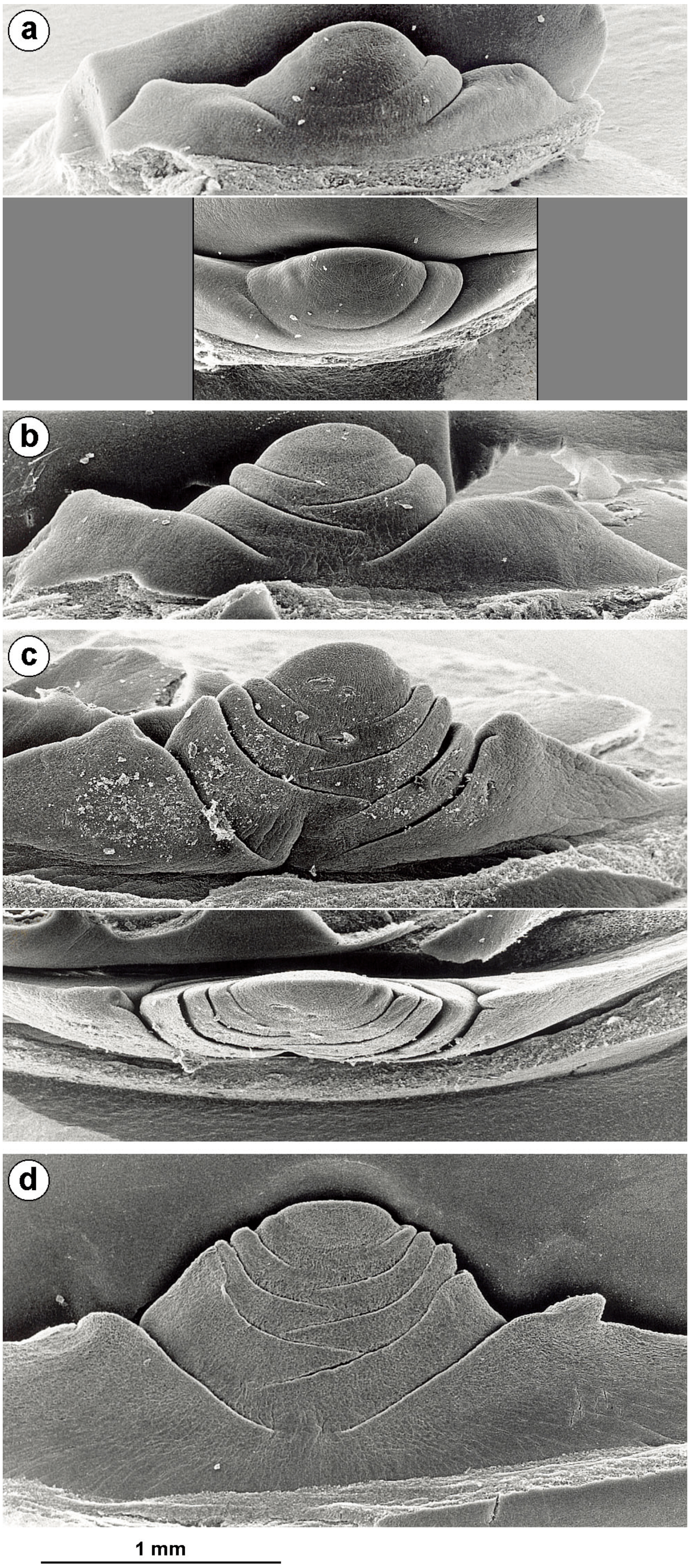

Figure 4.26
Scanning electron micrographs of early stages of ax$_1$-s (first-order inflorescence branches) of one sago palm, showing the increasing number of bracts/bracteal folds that become visible as development proceeds.

- **a: bud of ax$_1$-XIV (14th-oldest ax$_1$), found in the axil of lf-XXV ; lateral and top view.**
- **b: bud of ax$_1$-IX, found in the axil of lf-XX ; lateral view.**
- **c: bud of ax$_1$-IV, found in the axil of lf-XV ; lateral and top view.**
- **d: bud of ax$_1$-III, found in the axil of lf-XIV ; lateral view.**

[Palm#24 ("Tuni", G1-phase) ; a: photo nr. 90.02-SEM-381,382 ; b: photo nr.90.02-SEM - 376 ; c: photo nr. 90.02-SEM-384,385 ; d: photo nr. 90.02-SEM-378 ; photos by Felix THIEL wed28feb1990]

The first part of the inflorescence which emerges at the crown of the palm is the bunch of half-meter-long threadlike extensions of the tips of the first-order bracts. These bracts are sitting closely together, the internodes of the ax_0 being still un-elongated, and the ax_1-s are still hidden in their axils and invisible from the outside. Figure 4.27a shows such a young bract-covered inflorescence cut off the tree top.

When the ax_1-s grow out, they pierce through the bract in the axil of which they are growing (Fig. 4.27d). Figure 4.30a shows that these bracts can still have a few leaflets.

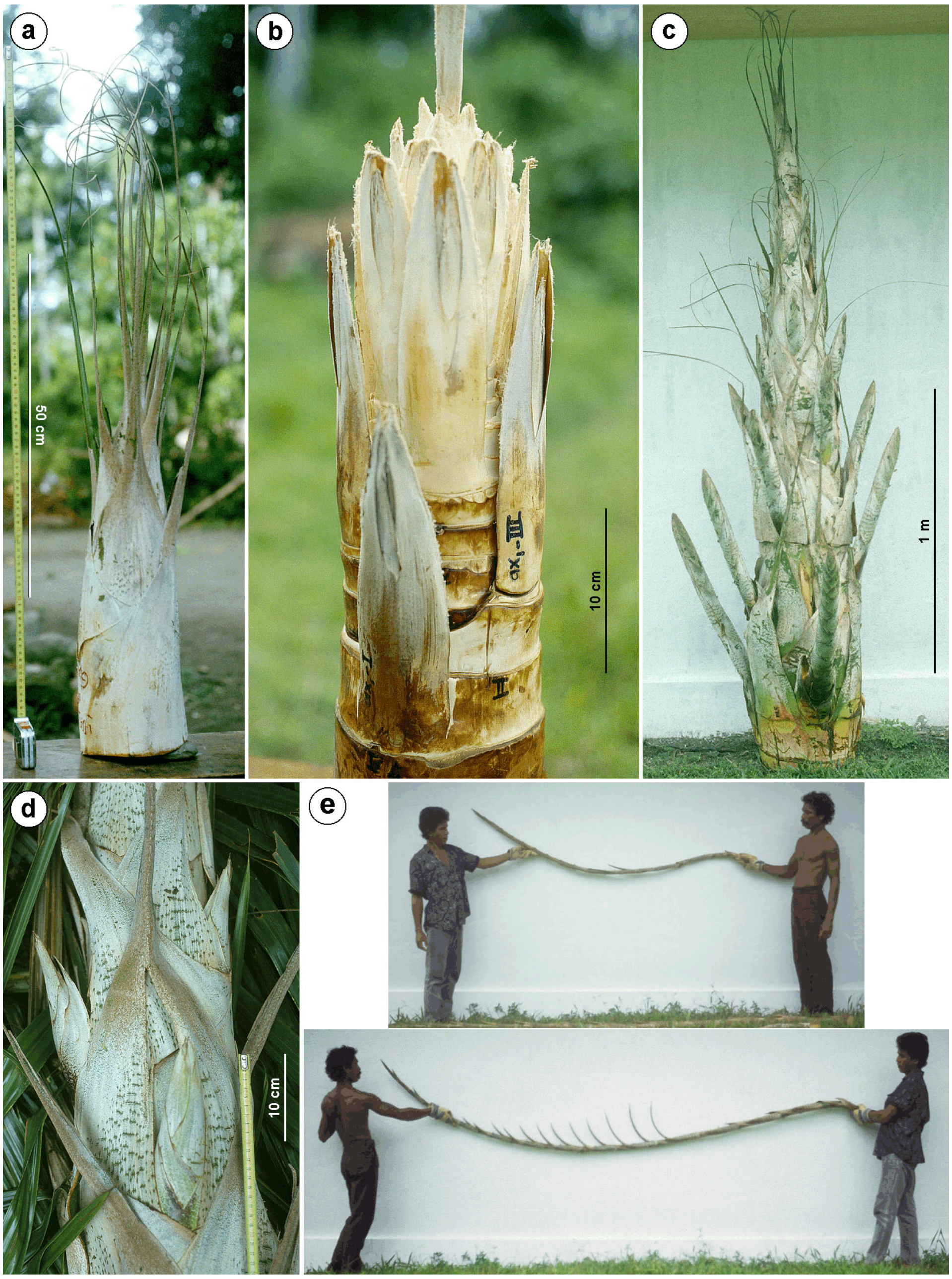

Figure 4.27 Development of the first-order inflorescence branches (ax_1-s) of the sago palm.

a: All ax_1-s still covered by first-order bracts (br_1-s).

b: Inflorescence at about the same developmental stage as the one shown in a:. All br_1-s are removed, exposing the ax_1 buds, which range in length from 5.5 cm (youngest) to 21 cm (third-oldest (ax_1-III)).

c: Inflorescence of which the main axis (ax_0) is about full-grown. The ax_1-s range in length from 20 cm (second-youngest, in the top, still completely enveloped by br_1-s) to 83 cm (second-oldest, sticking out from the base of the main axis). (NB: some lower br_1-s were removed).

d: A developing ax_1 pierces through its subtending bract.

e: Full-grown ax_1-s, viz. the first (ax_1-I , length 344 cm) and the last (ax_1-XXIII , length 205 cm) from one inflorescence, the ax_2-s already beginning to emerge.

[a: photo nr.89.09-095-14, outside series (variety?, G1), Hatusua 29aug1989 ;
b: photo nr.90.06-122-21, Palm#29 ("Molat Berduri", G1), Hatusua 23jun1990 ;
c: photo nr.90.05-116-19, Palm#28 ("Tuni", G1), Hatusua 13may1990 ;
d: photo nr.89.09-095-18, outside series ("Tuni", G1), Hatusua 01sep1989 ;
e: photo nr.90.11-147-10 (bottom) and nr.90.11-147-16 (top), Palm#35 ("Ihur", early G2), Hatusua 07nov1990.]

An ax_1 is covered in tubular br_2-s arranged distichously (in two rows) on opposite sides of it. The lower 5 to 8 bracts are empty, the top ones subtend/envelop the buds of the ax_2-s (Fig. 4.28).

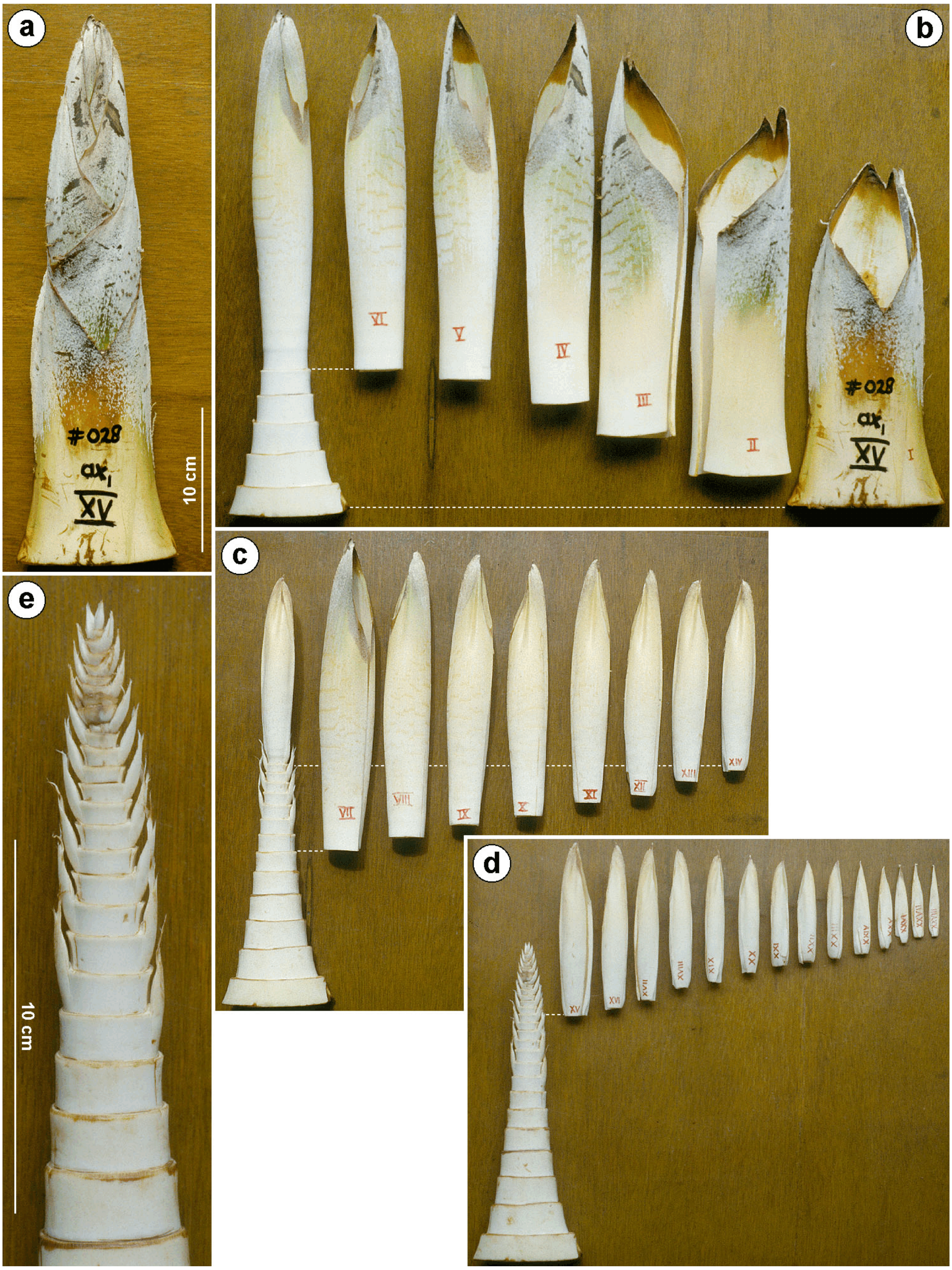

Figure 4.28 A young primary inflorescence branch (ax_1) of sago palm (a), from which all bracts (br_2-s) are successively removed (b-d), revealing the buds of the second-order inflorescence branches (ax_2-s). e: close-up of the ax_1 top stripped of all its bracts. In this case there are 28 br_2-s, the bottom 7 'empty', the top 21 covering an ax_2 bud.
[a-e: photo nrs 90.05-117-19,23,27,28,31 , Palm#28 ("Tuni", G1), Hatusua 15may1990.]

-- Development of the second- and third-order inflorescence branch (ax_2, ax_3)

Figure 4.29 shows the ax_2-s in an early developmental stage. Conspicuous are the large basal bracts, or prophylls, of the ax_2 buds in this stage, extending far beyond the tips of the other bracts.

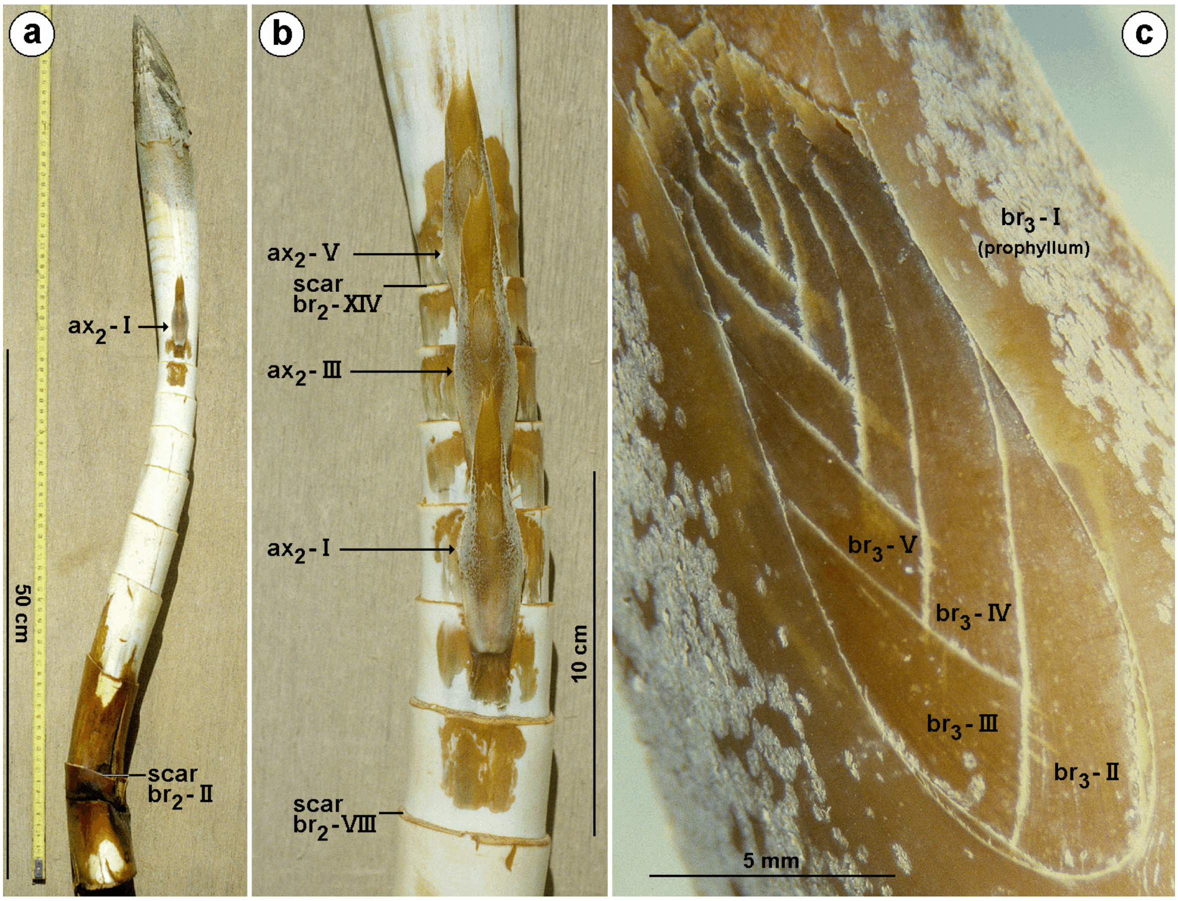

Figure 4.29 The bud of the second-order inflorescence branch (ax_2).
a: A young ax_1, seen from the side (left adaxial, right abaxial), from which nine br_2-s are removed, revealing the first ax_2 bud (ax_2-I).
b: Five more br_2-s are removed, revealing two more ax_2 buds on this side of the ax_1.
c: Close-up of part of an ax_2 bud (preserved/fixed in ethanol 70%), showing the arrangement of the third-order bracts (br_3-s), and how br_3-I, the prophyll, encases the rest of the bud at this stage.
[a, b: photos nr. 90.05-117-36 and nr. 90.05-118-04A (Palm#28 ("Tuni", G1), Hatusua 16may1990). c: photo nr. 90.07-F-08 (Palm#28 ("Tuni", G1), 25jul1990).]

The ax_2-s emerge gradually from the lowest ax_1 upward, and on each ax_1 from the base to the tip (Fig. 4.30) (see also Fig. 4.27e). The ax_2-s first grow out upwards, the further they extend, the wider the angle with the ax_1. Gradually they spread out also horizontally, alternately to either side of the ax_1.

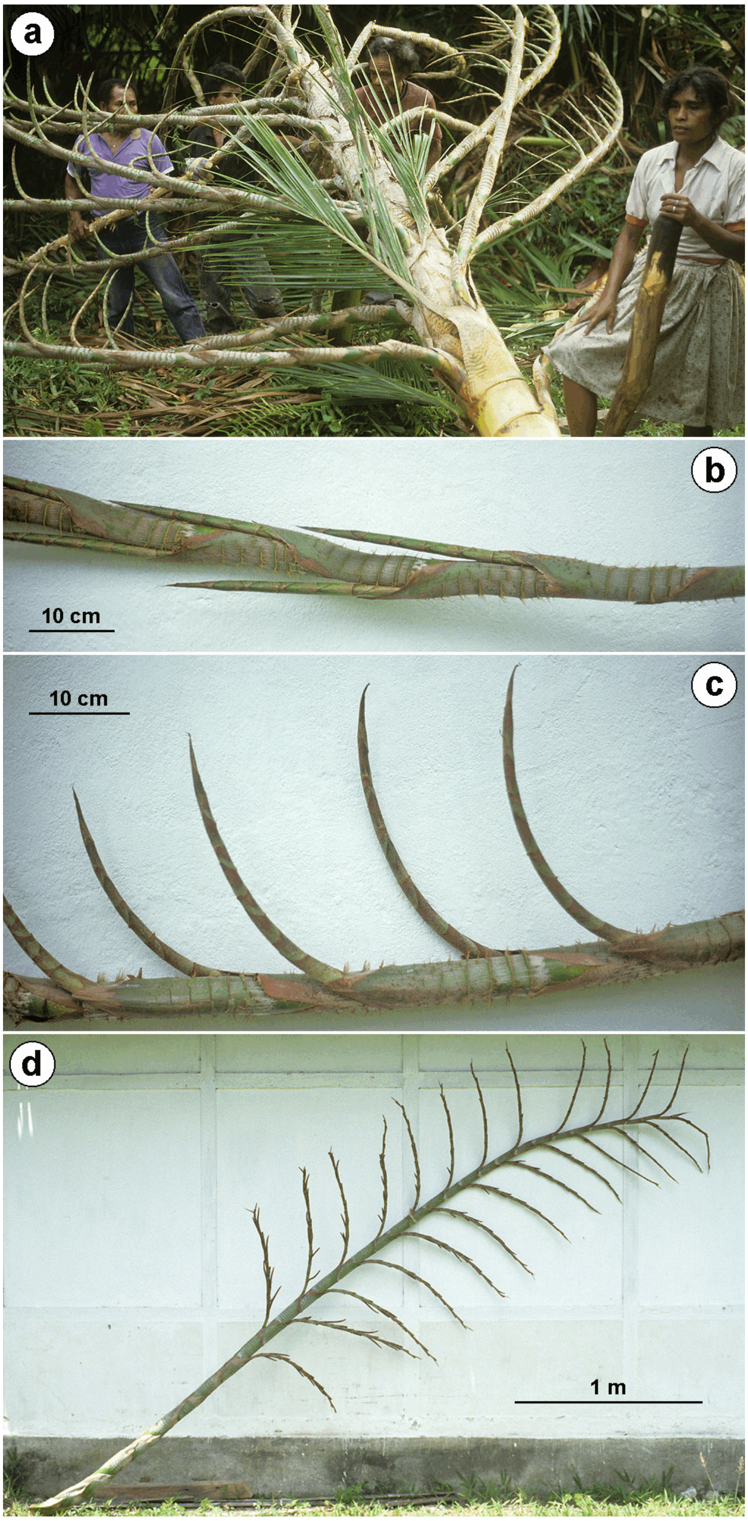

Figure 4.30 Development of the 2nd-order inflorescence branches (ax$_2$-s) of the sago palm.
a: emerging ax$_2$-s, *in situ* on 'intact' inflorescence on cut palm.
b, c: developing ax$_2$-s on top and basal ax$_1$ of same inflorescence.
d: ax$_1$ with full-grown ax$_2$-s; ax$_3$-s beginning to emerge.
[a: photo nr. 90.11-147-02 (mon05nov1990) ; b, c: photo nr. 90.11-147-18 and nr. 90.11-147-12 (wed07nov1990) ; d: photo nr 90.11-146-21 (mon29oct1990) ; a-c: Palm#35 ("Ihur", early G2) ; d: Palm#34 ("Tuni", G2) ; a-d: Hatusua, W. Seram.]

Figure 4.31 shows the ax_3 in an early stage of development. Buds of the flower-bearing ax_3-s are placed distichously on opposite sides of the ax_2. The bracts on the ax_3, the br_4-s which cover the flowers, are clearly seen to be spirally arranged on the ax_3. However, br_4-II and -III between these and the basal prophyll (br_4-I) are placed distichously on opposite sides of the ax_3 (not visible yet at the stage shown in Fig. 4.31; cf. Fig. 4.22).

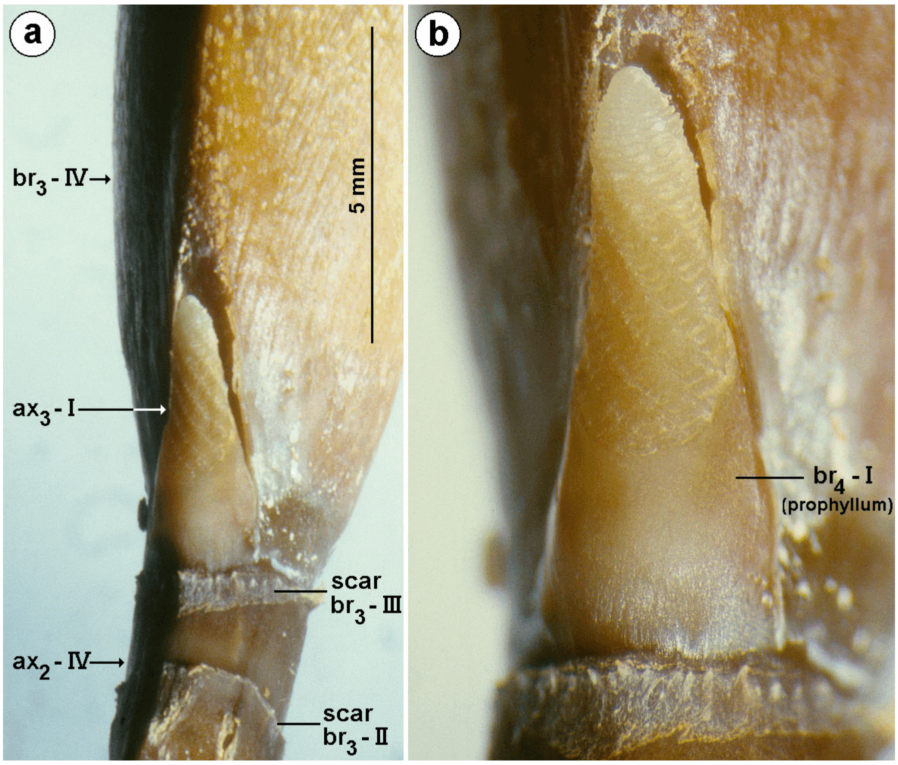

Figure 4.31 The bud of a third-order inflorescence branch, the flower-bearing rachilla (in this case the first one, ax_3-I), exposed by removal of its subtending third-order bract (in this case the third one, br_3-III). This bud sits in turn in a bud of an ax_2 (in this case ax_2-IV) the size of the ones shown in Fig. 4.29. (Preserved/fixed in ethanol 70%.)

a: Overview, showing placement of the ax_3 on the side of the ax_2 in a cavity at the base of the next br_3 up.

b: Close-up, showing the prominent prophyllum and the spiral arrangement of the br_4-s higher up which subtend the (future) flower pairs.

[a, b: photos nr. 90.07-F-15 and nr. 90.07-F-11 (Palm#28 ("Tuni", G1), 25jul1990).]

The ax_3-s emerge gradually from the lowest ax_1 upward (Fig. 4.32a), and on each ax_1 from the lowest ax_2 upward (Fig. 4.30d).

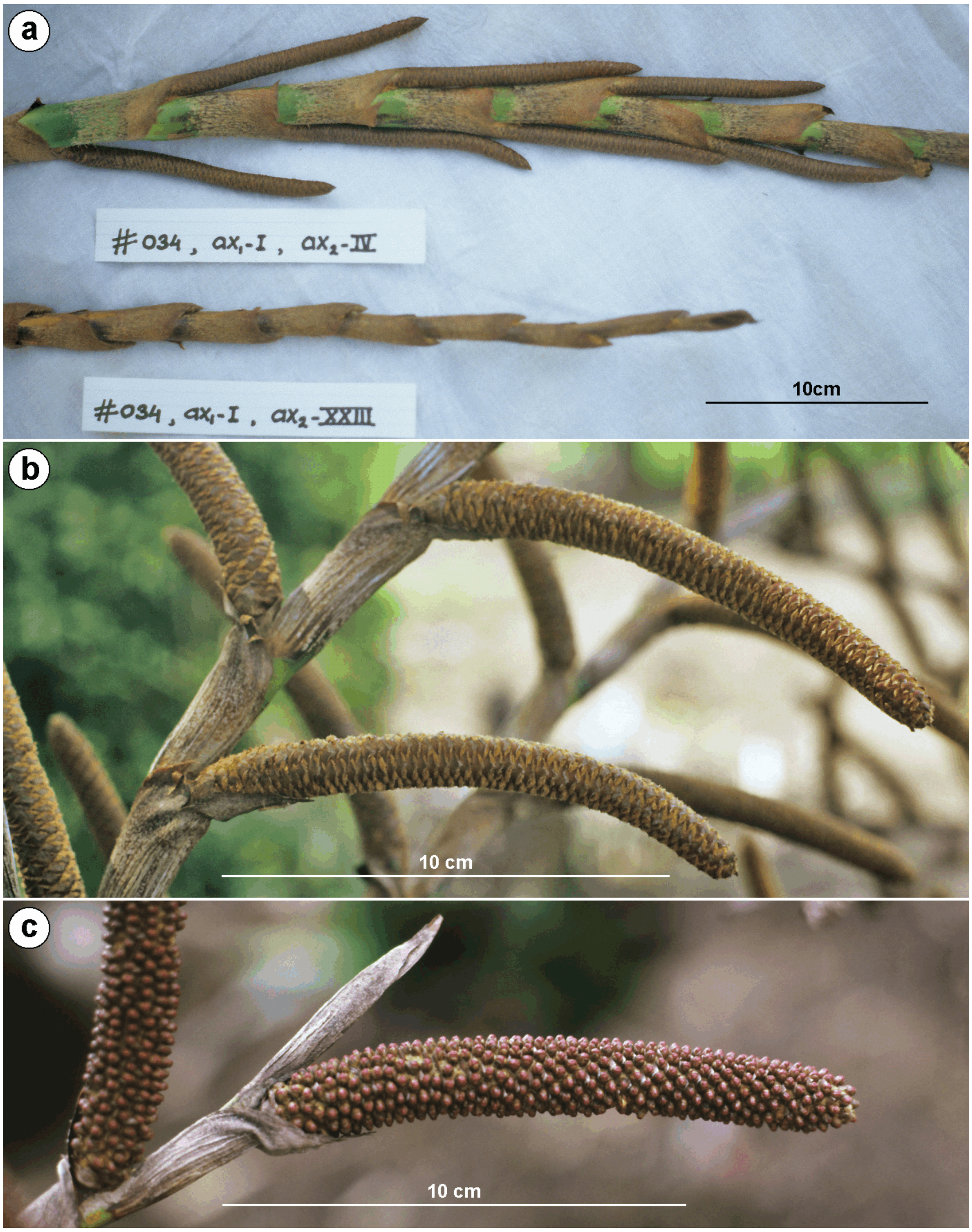

Figure 4.32 Development of the 3rd-order inflorescence branches (ax_3-s) of the sago palm.

a: development stages of the ax_3-s on the 4th and the 23rd ax_2 of the ax_1 shown in Fig. 4.30, the ones on the 23rd ax_2 still almost completely covered by their bracts.

b: full-grown ax_3-s.

c: ax_3 with flower buds which are about to open.

[a: photo nr. 90.11-146-24, Palm#34 ("Tuni", G2), Hatusua (Seram, Indonesia), 30oct1990 ; b,c: photo nr. 90.08-132-35 and nr. 90.08-132-R, outside series, Dalat (Sarawak, Malaysia), 09aug1990.]

-- Fruiting

No systematic observations were done on the morphology of the last stage of the generative phase, the fruiting stage. In the description of the embryonic phase, some aspects of the development of the fruit and seed were presented (Fig. 4.2). Figure 4.33 gives an impression of a fruiting tree.

Figure 4.33 The crown of a fruiting sago palm, most of the fruits already shed.
[photo nr. 86-3_II-33 (Batu Pahat, Johor, W. Malaysia fri07mar1986)]

- Basal bracts: the prophylls

As was shown, the bract at the base of an ax_1, ax_2, or ax_3 is shaped differently from the ones higher up; it is adaxially two-keeled, and two-lobed at the top, and is called the prophyll (TOMLINSON 1971, UHL & DRANSFIELD 1987:17). The ax_0 ends in a terminal ax_1 which bears no prophyll. The prophyll seems to be an adaptation of a (higher order) bract to accommodate to its squeezed-in position between the (lower order) bract and the on-going (lower order) axis; no such accommodation is required at the top end of a branch.
Contrary to the usual development in palms as described by UHL & DRANSFIELD (1987:17) in that "... the prophyll always completely encloses the inflorescence in early stages ..." and "... opens at different times in different genera ...", it appears that in *Metroxylon sagu* the prophyll is never completely closed.
From the s.e.m. pictures of the young ax_1 buds it is not clear which one (ones?) of the basal bracteal folds will eventually develop into the prophyllum, and how.

- Phased development

The emergence of the ax_1-s, ax_2-s, and ax_3-s is phased: the second-order branches do not emerge before most of the first-order branches of the entire inflorescence are fully extended, and the third-order branches not before most of the second-order ones are. As mentioned earlier, this phenomenon was already reported by DEINUM & SETIJOSO (1932:107).

The ax_1-s clearly emerge from the base of the rachis (ax_0) upward: the lowest (= oldest) one

may already be 1 metre long when the top (= youngest) ones may still be covered completely by their subtending bracts (Fig. 4.27c).
The development of the ax_2 buds seems to be halted until all the ax_1-s have grown to full length. They may be halted at the stage shown in Figure 4.29 (ax_2-buds on ax_1-II (second-oldest ax_1), of the inflorescence of Palm #28; length c. 7 cm), as also the biggest ax_2 buds on ax_1-X (the tenth-oldest ax_1) of that inflorescence are about the same size, whereas e.g. on ax_1-XV of the same inflorescence the biggest ax_2 buds are much smaller (Fig. 4.28e) .

- Phyllotaxis

The phyllotaxy of the bracts on the ax_0 of the inflorescence is easily determined using the implantation positions of the ax_1-s as a reference. In all cases observed this phyllotaxy proved to be 5/13. I.e. when following the imaginary spiral connecting the implantation points of consecutively formed ax_1-s (c.q. bracts) on the ax_0 starting from one such point, you have to circle the ax_0 five times before arriving at an ax_1 implanted straight above the one you started from, and this ax_1 then being the 13th one up from the start. So, consecutively formed bracts/ax_1-s are implanted on the ax_0 at an angle of an average 5/13 of a whole circle, or 138.5 °, to each other when viewed from above. Figure 4.34, especially 4.34c, illustrates this nicely: a young ax_0 from which the br_1-s are removed and the ax_1-s are cut photographed straight from above.
The spiral connecting implantation points may run either clock-wise or counter-clockwise when viewed from above.
It is interesting to note that in coconut palm, successive foliage leaves are implanted at the same angle of divergence (138.5 °), and the spiral, as seen from above, may also run either clock-wise or anti clock-wise (VON MARTIUS 1850, DAVIS & MATHAI 1975: both in OHLER 1984:22).

- Duration of developmental stages within the G-phase

The next step is to study the place of the different developmental stages on a time scale. It could well be that different sago palm varieties will show different time tables as ultimate size of the inflorescence will probably play a role: a larger inflorescence will take longer than a smaller one to complete development. Thus, the generative phase of the varieties Tuni and Ihur will probably last longer than that of Molat (see Table 4.11).

-- From-the-ground observations

To obtain some minimal data on the duration of the various stages in inflorescence development, some palms in sufficiently open terrain were photographed from the ground at irregular intervals.

In Figure 4.35 a stand of sago palms is shown with three axes in the generative phase. This stand was photographed at intervals of 2 to 7 months over an eighteen-month period.
When first photographed (photo A), the axis on the right was actually already dead or dying: a skeleton of an axis in the generative phase.
The flowering axis in the middle has its ax_1-s out on photo A, the lowest ax_2-s on the lowest ax_1-s already beginning to emerge as well. Two months later (photo B), all of the ax_2-s are out, and on the lowest ax1-s also the ax_3-s. After another two months (photo C), all the ax_3-s are out. Unfortunately, this trunk was apparently harvested between the 3rd and 4th

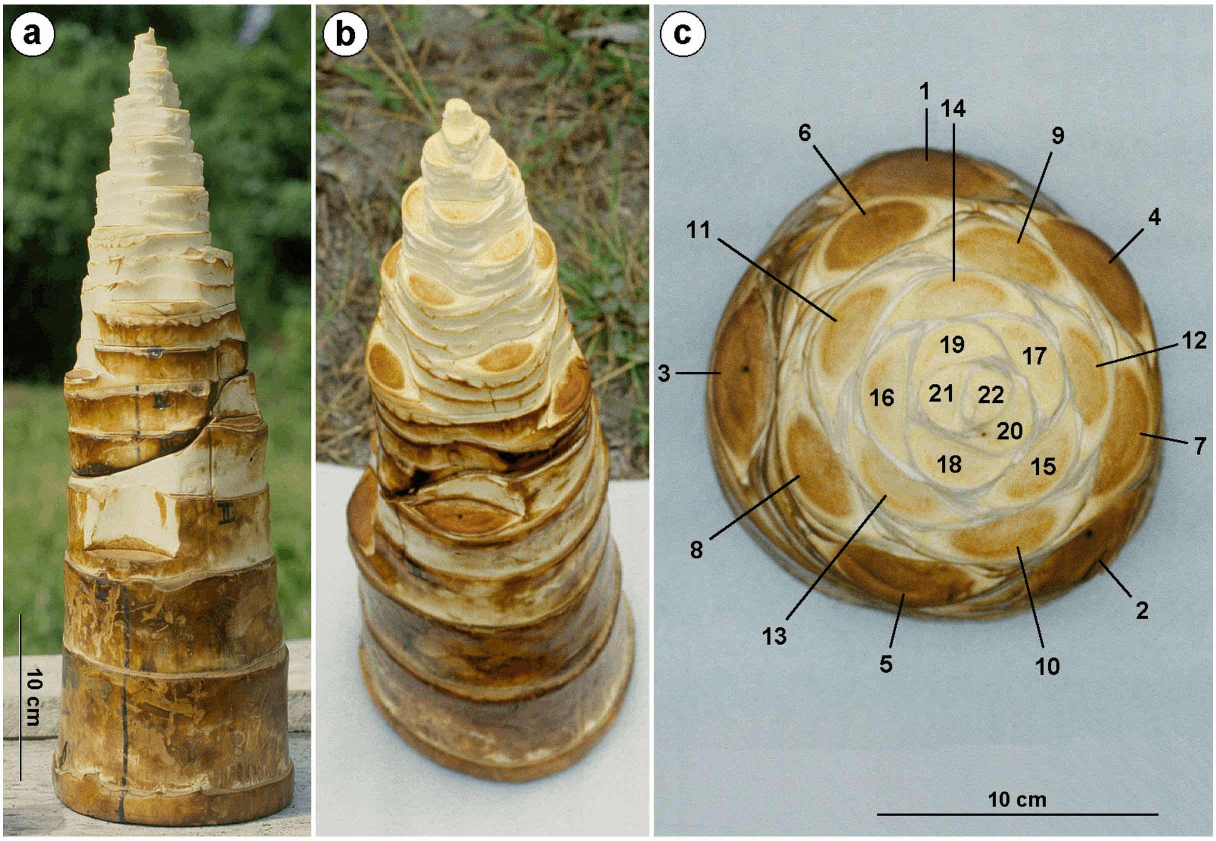

Figure 4.34 The phyllotaxis of the bracts on the main ax$_0$ and the spiral arrangement of the ax$_1$-s these bracts are subtending can be easily determined on this young inflorescence from which all bracts and ax$_1$-s were cut, leaving the naked ax$_0$. (The same ax$_0$ with the ax$_1$ buds still attached is shown in Fig. 4.27b.) The phyllotaxis here is 5/13 in a clock-wise spiral (explanation in text).

a: Lateral view of the naked ax$_0$, showing the still un-elongated internodes. (The ax$_0$ broke during felling; hence the fissure).

b: The ax$_0$ viewed obliquely from above.

c: The ax$_0$ photographed straight from above, clearly showing the placement of the successive ax$_1$-s on the stem. Consecutive numbers indicate consecutively formed ax$_1$-s.

[a: photo nr. 90.06-122-31. b: nr. 90.06-122-30. c: nr. 90.06-122-27. (Palm#29 ("Molat Berduri", G1). Hatusua, 24jun1990.)]

observation of the stand.
The trunk on the left has its third-order branches out already on photo A. Two and four months later (photo B and C), no difference in the inflorescence can be seen from this distance; the foliage has become sparser. Seven months later (photo D), the aspect of the inflorescence has changed completely: the branches have bowed out under the weight of fruit; the lowest two leaves have dropped. Two months later (photo E), some first-order branches are bending down even more; some more leaves have dropped. Four and a half months later (photo F), the fruits are apparently shed: the inflorescence looks thinner and first-order branches have veered back up; foliage is sparser again.

Fig. 4.36 shows five months of inflorescence development in another palm. In these five months the inflorescence goes from 'all first-order branches out' (a) to 'all third-order branches out' (c). In an intermediate stage three months after the first photo was taken (b), the second-order branches are seen to be not yet fully expanded and not yet perpendicular to the first-order branches.

When we combine these two series of observations, we may conclude that it takes 2-3 months for all the ax_2-s to emerge after all the ax_1-s have emerged, 2 months for all the ax_3-s to emerge after all the ax_2-s have emerged, and one to one and a half year for the fruits to mature after all the ax_3-s have emerged.

I suggest here to divide the G-phase into 3 sub-phases of which the endings are easily recognizable from the ground:

G1-phase: from initiation of the first ax_1 in the growing point to full extension of all ax_1-s.
G2-phase: from full extension of all ax_1-s to full extension of all ax_3-s.
G3-phase: from full extension of all ax_3-s to maturation (shedding) of the fruits.

G2 may be differentiated into early G2 (before any ax_3-s are visible) and late G2 (after ax_3-s have started to emerge), but from the ground this may not always be easy to see.

As the start of the G1-phase is invisible from the outside, it is not possible to observe the duration of the G1-phase directly.

A

13may1989

B

13jul1989

C

09sep1989


D

14apr1990


E

25jun1990


F

13nov1990

Figure 4.35A-F Development of the inflorescences in a stand of sago palms over an eighteen-month period. [photo nrs 89.06-086-27, 89.08-091-20, 89.10-096-08, 90.04-114-09, 90.07-123-14, 90.11-147-31 (Waipirit, West Seram)]

Figure 4.36 Development of the inflorescence of a sago palm over a five-month period.
[photo a: nr.90.06-121-13 (16jun1990) ; b: nr.90.09-135-24 (29aug1990) ; c: nr.90.11-147-21 (08nov1990). Location: Ambon Island, by side of the road from Passo to Poka/Rumah Tiga.]

4.5 Analysis

Now we have to analyse the data from literature in combination with the observed data to see whether any of the outwardly observable morphological characteristics of a sago palm axis related to age can be used reversely to establish this age with sufficient precision, i.e. with a maximum error of one year.

- Establishment phase (E-phase)

In the E-phase the only parts easily observable are the leaves. The stem is usually mostly underground and/or covered in leaf bases or roots, masking its features, such as leaf scars. Therefore, only leaf characteristics are eligible age indicator candidates, in particular the ones that progressively change with each new leaf, the most obvious ones being the length of the leaf and the number of leaflets per leaf. As the axis of the leaf is partly hidden at the base, and because it keeps extending for some time after unfolding, the number of leaflets seems the better characteristic for age assessment of a palm axis during the E-phase.

FLACH (1977:161) used this number to estimate the E-phase duration of a seedling at 40-45 months. He based his estimate on an extrapolation of an observed growth period which started at germination, assuming a leaf unfolding rate (LUR) of 2 leaves per month and a linear increase of the number of leaflets per leaf to the end-of-E-phase leaflet number of 50 pairs (see literature review in Section 4.3, E-phase, LUR).
I found a number of leaflets per leaf in the AV-phase ranging from 78 to 98 (average 90) pairs (Table 4.8). In the dissected sucker with green leaves formed in the E-phase and the AV-phase (Table 4.2), the number of leaflets levelled off at 83-84 pairs, but only 3 leaves after the transition from E-phase to AV-phase. Three leaves earlier the number of leaflet pairs was 74-75, i.e. 89% of the number on a full-grown leaf. 89% of the average 90 pairs is 80 pairs. A seedling of the AV-phase palms I observed would under FLACH's assumptions, and assuming that the number of leaflets on a full-grown leaf on a seedling axis is in principle not different from this number on a sucker axis, take 64-72 months to reach adult size. This seems unrealistically long, as most reports claim a transition to the AV-phase in the 4th year after transplanting a sucker. All the more so since a sucker may well take longer than a seedling axis to reach adult size, as I concluded from the irregular shape and direction of sucker stem bases as compared to seedling stem bases, and in accordance with the findings of variable node numbers on horizontal trunk parts compared to much less variable node numbers on the full-grown vertical parts of those trunks (JONG F.S. pers.comm. 1994, in FLACH 1997:15). Therefore, horizontal internodes may be extra internodes, accounting for extra time needed for the E-phase. Obviously, FLACH's model overestimates E-phase duration of the palms I observed. This is probably due the linear increase of the number of leaflets throughout the E-phase in his model, as opposed to the probable acceleration of this increase with time that I found.
No other estimates of E-phase duration based on morphological characters are available from literature, nor reports of direct observations of the length of this period.

How accurate could age be estimated by the number of leaflets on the youngest unfolded leaf? Assuming that the number of leaflets in a full-grown (adult, AV-phase) leaf is determined genetically, or at least mainly genetically, the ratio of actual number of leaflets in the last unfolded leaf to the number of leaflets in a full-grown leaf can be an indicator, not of axis age itself, but of relative axis age, the ratio indicating the proportion of the way to full-grownness completed. If each sago palm variety has its own mean number of leaflets in a full-grown leaf, and if the LUR during the E-phase is not constant and both LUR and the number of leaves formed during the E-phase depend on environmental factors, an empirical table composed for each situation with columns for leaf rank number, number of leaflets, and time elapsed between unfolding and beginning of palm axis growth is probably the most practical tool for age assessment based on leaflet count. If there is a different number of leaflets in each new leaf, the theoretical accuracy of the age estimate would be the inverse of the LUR.

- Adult vegetative phase (AV-phase)

In the AV-phase the easily observable parts are the stem (trunk) and the leaves. For the trunk, the outwardly visible characteristics that progressively change with time are height and number of leaf scars. The leaves do not posses such characteristics, as they remain the same throughout the AV-phase. There is a difficulty with using trunk characteristics for age assessment in the initial part of the AV-phase, because the first trunk part (i.e. the first elongated internode) becomes visible only when the last leaf formed during the E-phase (the last one that ends up at ground level) is shed, which is years after the start of the AV-phase. The trunk symptoms at the end of the AV-phase are similarly shrouded in leaf bases. The narrowing and elongation of each new internode telling that the growing point has turned generative and heralding the emergence of the inflorescence becomes clearly visible only when the last leaf attached to the top of a 'full-width' internode of 'normal' length is shed. With experience one might be able to notice the elongation of internodes beneath the leaf bases by the 'telescoping out' of the consecutive leaves attached to them. And this is indeed the method by which traditionally the nearing apparition of the inflorescence is forecast.

-- Counting nodes

In general, it takes months to years before growth and development processes that become visible in the apical growing point of an axis become visible on the outside of that axis. The wider the axis, the longer the time lag between first inner and first outer visibility. This is simply because an axis has only one apical growing point, and the wider the axis, the longer it takes for a morphological feature to 'travel' from the centre where it originates to the periphery. E.g., during the E-phase when the base of each new spear leaf (i.e. the diameter of the ring where it is attached to the stem) widens as the stem widens, the space for 'hidden' primordial leaves inside the spear increases. This is illustrated by Palm#37 (see its data sheet in App. A) in which the spear leaves of a larger and of a smaller sucker had base diameters of 10.3 cm and 4.9 cm, respectively, with 15 and 11 primordial leaves inside. In the smaller sucker it would take 11 plastochrons for the smallest primordium to become a visible spear, in the larger one this would take 15 plastochrons. Therefore, if one wants to assess the age of an axis by the number of leaves it has produced, not only the leaf scars and the green unfolded leaves should be counted, but also the spear leaf and the primordial leaves. The number of scars on a length of trunk can only tell us something about the time it took to form that particular trunk piece.

In practice, total leaf node count can only be used in a 'post mortem' age assessment of an axis, as it involves dissecting its single growing point. For age estimation of a standing axis, the number of primordial leaves has to be estimated. In Table 4.4 the number of unfolded green leaves and the number of primordial leaves (including the spear) of axes in the AV-phase are presented. For the 14 trunks for which these numbers could be established with certainty we see that, with the exception of Palm#14, the number of unfolded leaves is consistently less than the number of primordial ones. The accumulated numbers for these 14 trunks were 248 and 306, respectively. Therefore, as a rule of thumb we may estimate the number of primordial leaves including the spear leaf at 125% of the number of green leaves.

If the total number of leaves produced in the AV-phase, i.e. before the growing point turns generative, is constant (i.e. genetically fixed) for each variety, as has been suggested (FLACH

1983:16), an estimate of total number of leaves already initiated (i.e. number of leaf scars on elongated trunk part, plus number of green leaves, plus spear leaf, plus estimated number of immature leaves within the spear leaf) would give an indication of the proportion of the AV-phase already completed. How long completion would take in a given location depends, of course, on the LUR.

-- Leaf unfolding rate (LUR)

At a total of 410 leaves unfolded during a total of 627 months, the overall mean LUR can be calculated at 410/627 x 12 = 7.85 leaves per year.
The observed LURs range from 2 to 14 leaves per year, a range wide enough to doubt the validity of simply applying this overall mean to other palms for the purpose of estimating their age, and to warrant investigating what might have caused the differences in LURs.

Simple linear correlation analysis of LUR with each of the environmental and plant properties presented in Table 4.10 tells us if variation in LUR is associated with variation in these properties and gives us a first indication of which of these properties may have influenced the LUR and to what extent. In this analysis, the variety Putih is excluded because of its totally different habitat (hilly terrain vs. alluvial plain) and different observation dates. Palm #LUR-07 is excluded because its steeply increasing LUR during consecutive observation intervals indicates that this palm turned generative during the monitoring period. Palm #LUR-31 is excluded because of missing data due to the inadvertent destruction of the palm early in the monitoring period. Thus, 29 cases remained for analysis. As groundwater table the mean of observation 1 and 2 was taken, as shading the mean of observation 1 and 3. For the number of S3-size suckers and for visible trunk height, the values found in observation 3 were taken. The results -presented in Table 4.13 - show that a high LUR is associated with a low groundwater table, a low degree of shading, a high number of S3 suckers and a long visible trunk. The LUR is most strongly associated with degree of shading.

Table 4.13 Simple linear correlation between leaf unfolding rate (LUR) of sago palm and some environmental and palm properties (data from Table 4.10).

Variables	Simple linear correlation coefficient (r)	r at 5% and 1% level of significance (d.f. = 27)
LUR and ground water table	-0.51	0.37 and 0.47
LUR and shading	-0.89	
LUR and number of S3	0.59	
LUR and visible trunk height	0.66	
shading and visible trunk height	-0.68	

If LUR is a sign of vigour, the observed associations would make sense if vigour is lessened by a high water table and by heavy shading, which would be logical assumptions. A high trunk is associated with a low degree of shading, which hints at the possible cause of the positive correlation between LUR and visible trunk height. The positive correlation between LUR and number of S3 suckers would make sense if they are both signs of vigour, rather than that suckers are a drain on the vigour of the main stem.
A more rigorous analysis of causal relationships and of interactions between variables is not called for here, as an estimate of LUR during the entire axis' life is needed and the historical circumstances are unknown.

-- Age assessment by node count and LUR

I had hoped that for those varieties, for which observations on both LUR and the total number of leaves formed during the AV-phase (i.e. total number of scars on a trunk up to the lowest first-order inflorescence branch) were available, the duration of the adult vegetative phase could be estimated. Although a mean total number of leaf scars could be established for "Tuni" (147, SD = 9.1) and "Ihur" (124, SD = 5.5), the variation of the LURs observed among different trunks proved too large to base a duration estimate on. The more so because LUR probably even varies during the AV-phase of an individual axis. If the overall mean LUR of 7.85 leaves per year calculated from all observations would be considered as averaging all circumstances, the AV-phase in a "Tuni" would take on average 147/7.85 = 18.7 years, that of "Ihur" 124/7.85 = 15.8 years.
As it is not possible to estimate AV-phase duration on the basis of observed total numbers of nodes formed during that phase and LURs with an accuracy of even a few years, it is equally impossible to assess the age of a given trunk with such accuracy by counting its nodes.

-- Trunk height

The other externally visible trunk characteristic which changes with time besides number of leaf scars (nodes) is height from ground level up to where the oldest green leaf is attached. (I will call this part of the trunk the visible trunk although bases of shed leaves may still be adhering, blocking the view on the trunk proper.) As can be expected, trunk height is correlated to this number, as only one leaf is produced per node and nodes are separated by internodes. Therefore, trunk height measurement or estimation could in principle be a substitute for node count, especially in tall, standing palms in which counting all the nodes would be cumbersome. However, the data presented in Table 4.7 show that the lengths of fully extended internodes initiated during the AV-phase vary not only between palms, but also in one trunk, decreasing towards the top, typically from about 20 cm to about 10 cm. Internode length variation in combination with the variation in LUR discussed above makes height of visible trunk not a good estimator of trunk age. And only for palms of similar genotype and growing under similar conditions may height of visible trunk be a relative age indicator, i.e. a longer visible trunk probably indicating a more advanced age of the axis.

- Generative phase (G-phase)

The emergence of the inflorescence is heralded by the size of a newly emerging leaf starting to be smaller each time than its predecessor (the beginning of the transition into bracts): shorter and narrower petiole and rachis, less and smaller leaflets. Also the internodes become longer and narrower: the palm 'bolts'. The anatomically detectable beginning of the G-phase, i.e. the detectability of the first ax_1 bud in the shoot apical growing point, does not simultaneously produce these outwardly visible 'bolting' symptoms. For example, in Palm#37 (see its data sheet in App. A) the growing point had already produced at least 19 ax_1 buds, but the 24 green leaves were attached to the top of internodes varying in length from 7 to 12 cm, and leaf nr. 7 was even smaller than leaf nr. 19 (leaf nr 1. is the oldest leaf), while between the node with the youngest green leaf and the node with the oldest ax_1 bud, there were another 19 nodes (carrying the spear leaf and 18 immature leaves inside the spear). When we analyse the available internode length data from G-phase palms in which at least the first ax_1 (ax_1-I) has emerged (an indication that the internodes below the attachment point of this ax_1 have extended) presented in Table 4.14, we see that the bolted top part of the stem adjacent to the ax_1-I comprises only 14 to 17 internodes (mean 15.3; n = 8). (The lowest internode considered to belong to this part had to be at least 3 cm longer than its predecessor and the elongation had to continue from then on to the longest internode.) Therefore, at the time of

initiation of the first ax_1 bud, even some 'typical' AV trunk sections are still 'in the pipeline' to full extension before it is the turn of the 'bolting' AV trunk sections to extend and bolting becomes noticeable from the outside.
Leaf data on these G-phase palms are too incomplete to be able to estimate the duration between initiation of ax_1-I and first outwardly visible leaf symptoms.

Table 4.14 Some statistics on the 'bolted' top part of the trunk of sago palm adjacent to the inflorescence. Palm numbers refer to the numbers in the appended Sago Palm Data Sheets (Appendix A).

Palm# (development phase)	number of internodes in bolted trunk top under ax_1-I	length lowest bolted internode (length previous internode) (cm)	length longest internode (cm)	position of longest internode under node with ax_1-I
03 (G3)	14	12 (9)	36	7th
04 (G3)	17	15 (12)	34	11th / 12th
05 (G3)	16	18 (15)	40	9th
18 (late G2)	14	9 (5)	30	5th / 6th
28 (late G1)	16	14 (11)	39	8th
34 (G2)	14	14 (11)	45	7th
35 (early G2)	16	11 (8)	39	10th
36 (late G2)	15	15 (11)	40	11th

Assuming that at the moment of transition of the growing point (start of the G1-phase) the number of primordial leaves present inside the spear leaf is still equal to that of earlier stages of the AV-phase, and given the increased LUR after the transition, it would take about a year to one and a half year for all these last AV-leaves to expand and unfold and thereby expose the top of the inflorescence 'bud' (as in Fig. 4.27a). I have no observations to underpin an estimate of the time it takes from the unfolding of the last AV-leaf to the end of the G1-phase (full expansion of the rachis (ax_0) and all the ax_1-s). My guesstimate is that this will take at least one year, given the sheer bulk of the full-grown ax_0 and ax_1-s. From observing two flowering trees from the ground I estimated the duration of the G2-phase at 4 - 5 months. From observing one flowering tree from the ground I estimated the duration of the G3-phase at 1 - 1.5 year. On the basis of close observations of 5 palms, JONG (1995:116) concluded that this G3-period lasts about 1.5 - 2 years, which is undoubtedly the more accurate finding.
In conclusion, the best estimate for the duration of the G1 phase is 2 - 3 years, for that of the G2 phase 0.5 year, and for that of the G3 phase 1.5 - 2 years, which amounts to 4 - 5.5 years for the duration of the entire G-phase. Therefore, in a trunk with part or all of an inflorescence outwardly visible, the time elapsed since the initiation of the first ax_1 bud can be estimated with an accuracy of one to one and a half year.

- Summary

The quantity and quality of data on morphology and duration of the E-, AV-, and G-phase was different for each phase. This resulted in different scopes for morphology-based age assessment for these phases, i.e. the reliability / accuracy of such age assessment varies among these phases.
For the E-phase, my own morphological observations were limited and I did not make any observations of the duration of this phase. Data on duration from literature are vague for suckers and incomplete for seedlings. As a result, morphology-based age assessment during the E-phase, which is based on number of leaflets per leaf, could not be made with an error of less than one year. If the duration of the E-phase and the maximum number of leaflets for the

variety and the habitat at hand could be established beforehand, the error of age assessment based on leaflet count may only be a few months.

For the AV-phase I collected many morphological data as well as data on development rate, i.e. leaf unfolding rate (LUR). However, the LUR data showed too much variation, variation that - with the available data - could not be explained in terms of observed genetic or environmental variation, to allow for age assessment (in this case based on counting the nodes formed) with an error of one year or less. Again here, with prior knowledge of duration and maximum number of nodes formed for the variety and habitat at hand, the error of age assessment based on node count may be less than one year.

For the G-phase, own observations and data from literature on morphology and duration could be combined into a time table of sub-phases which allows for an accuracy of morphology-based age assessment within this phase of one to one and a half year.

In the next section, a time table for growth and development for all developmental phases based on these finding is proposed.

4.6 Synthesis: a new, more detailed growth & development timetable for sago palm

First a general morphological growth-&-development timetable for sago palm with the consecutive phases and their duration is proposed.
Then the age rank is estimated of the palms of which the starch content was measured. With this ranking we can try and establish the evolution of starch accumulation and depletion in time (Chapter 7).

4.6.1 A phenological scale for sago palm

Based on the static observations (dissecting felled palms) and the dynamic observations (monitoring standing palms), a time sequence of events in the growth and development of the sago palm can be established covering the entire life of a single axis, the certainty and accuracy of the time span between consecutive events varying according to the certainty and accuracy of the underlying data.

As discussed above (Section 4.5), there is a considerable time lag in a full-grown trunk between the initiation of a plant part and its maturation because of the large diameter of the trunk and the existence of only one apical growing point in the shoot from where all tissues originate. Thus, in the life of a single leaf the events that can be discerned are initiation, unfolding, reaching maximum base diameter, and shedding. Dissecting the top of a trunk in the AV-phase, viz. Palm #25 (see its data sheet in App. A.) showed that there are about 25 folded/primordial leaves and 20 unfolded (green) leaves. Of the unfolded leaves, about half had reached their maximum base diameter of about 60 cm, while the other half had base diameters gradually increasing from the 20 cm of the youngest unfolded leaf. The internode lengths between all but the top three unfolded leaves were about the same. Apparently, an internode reaches its full length much sooner than it reaches its full diameter. Figure 4.37 gives a diagrammatic representation of the top of Palm #25.
For the tentative time table I assumed a constant LUR of 10 leaves per year (i.e. a leaf plastochron of 1.2 month) during the AV-phase (prior to the final bolting period). This results in the following AV-phase events time tables:
Leaf: initiation, followed 2.5 years later by unfolding, followed 1 year later by reaching maximum base width, followed 1 year later by shedding.
Node: initiation, followed 3.5 years later by reaching maximum width, followed 1 year later by becoming visible from the outside (i.e carrying the oldest green leaf).
Internode: initiation, followed 2.75 years later by reaching maximum length, followed 0.75 year later by reaching maximum width, followed 1 year later by becoming visible.

In Table 4.15 the proposed phenological scale of a sago palm from embryo to death is presented. In this scale, the formation of suckers (basal branches) is not included. One such sucker would grow and develop according to this same scale, skipping the embryo and seedling phases.
The E-phase and the time lag between initiation and maturity of plant parts would probably be shorter for palms with narrower trunks than the ones with a diameter of about 60 cm on which this scale is based.

Table 4.15 Phenological scale of sago palm mainly based on a model axis which during the AV-phase forms 110-130 full-sized leaves at a rate of 10 per year, has a trunk diameter of 60 cm, and has 20 green unfolded leaves and 25 folded/primordial leaves.

Phase name	Hidden event			Outwardly visible event			Time since previous event
Embry-onic	fertilization of ovule						
	fruit mature			fruit full-grown, green			1.5-2 yr
	fruit ripe			fruit straw-coloured			2 m
Seed-ling	seed germinates			shoot and roots appear through pericarp			0.5-1 m
	endosperm reserves exhausted						1 m
	stem	leaf	inflor./infr.	stem	leaf	inflor./infr.	
E	starts to widen with each new node	nr. of leaflets starts to grow with each new leaf		[stem hidden by leaves]	base outer lf starts to widen ; nr. of lts starts to grow with each new lf		[none]
	Lst E-node initiated	Lst E-leaf initiated					? 2 yr
AV	1st AV-int and -nd initiated	1st AV-leaf initiated		[stem hidden by leaves]			1 m
					Lst E-leaf unfolds		29 m
					1st AV-leaf unfolds		1 m
	1st AV-int reaches max length				leaf with maximum nr. of lts unfolds		4 m
	Lst E-nd full-grown: stem reaches max width	Lst E-leaf reaches max base width					7 m
	1st AV-int and -nd reach max width	1st AV-leaf reaches max base width					1 m
				1st AV-int visible	Lst E-leaf shed		11 m
				2nd AV-int visible	1st AV-leaf shed		1 m
	Lst typical AV-nd and -int initiated	Lst typical AV-lf initiated					6.5-8.5 yr
	1st bolting AV-nd and -int initiated	1st reduced AV-lf initiated					1 m
	Lst bolting AV-nd and -int initiated	Lst reduced AV-lf initiated					17

Phase name		**Hidden event**			**Outwardly visible event**			**Time since previous event**
		stem	leaf	inflor./infr.	stem	leaf	inflor./infr.	
G	G1	1st G-nd and -int initiated ;	1st G-lf (br$_1$) initiated	1st ax_1 initiated				1 m
						Lst reduced AV-lf unfolds		11-17 m
		ax_0 full-grown					Lst ax_1 full-grown	12-15 m
	G2						1st ax_2 out	1 m
							Lst ax_2 full-grown	2-3 m
							1st ax_3 out	1 m
							Lst ax_3 full-grown	1 m
	G3			fertilization of ovule				1 m
				fruits mature			fruits full-grown, green	1.5-2 yr
				fruits ripe			fruits straw-coloured; shedding	2 m
R		death of tissues; trunk becomes hollow			decay and collapse			2-5 yr

AV = Adult Vegetative ; E = Establishment ; G = Generative ; R = Recycling (phase name suggested here).
inflor = inflorescence ; infr. = infructescence ; int(s) = internode(s) ; fr(s) = fruit(s) ; Lst = last ; lf = leaf ; lvs = leaves ; lt(s) = leaflet(s) ; m = month ; max = maximum ; nd(s) = node(s) ; nr. = number ; yr = year.
NB1: a sucker starts in the E-phase.
NB2: when a leaf is shed, it is assumed here to break off where it is attached to the trunk and reveal the underlying internode, where in reality the leaf usually breaks off near the base of the petiole, the leaf base proper adhering for some time longer .

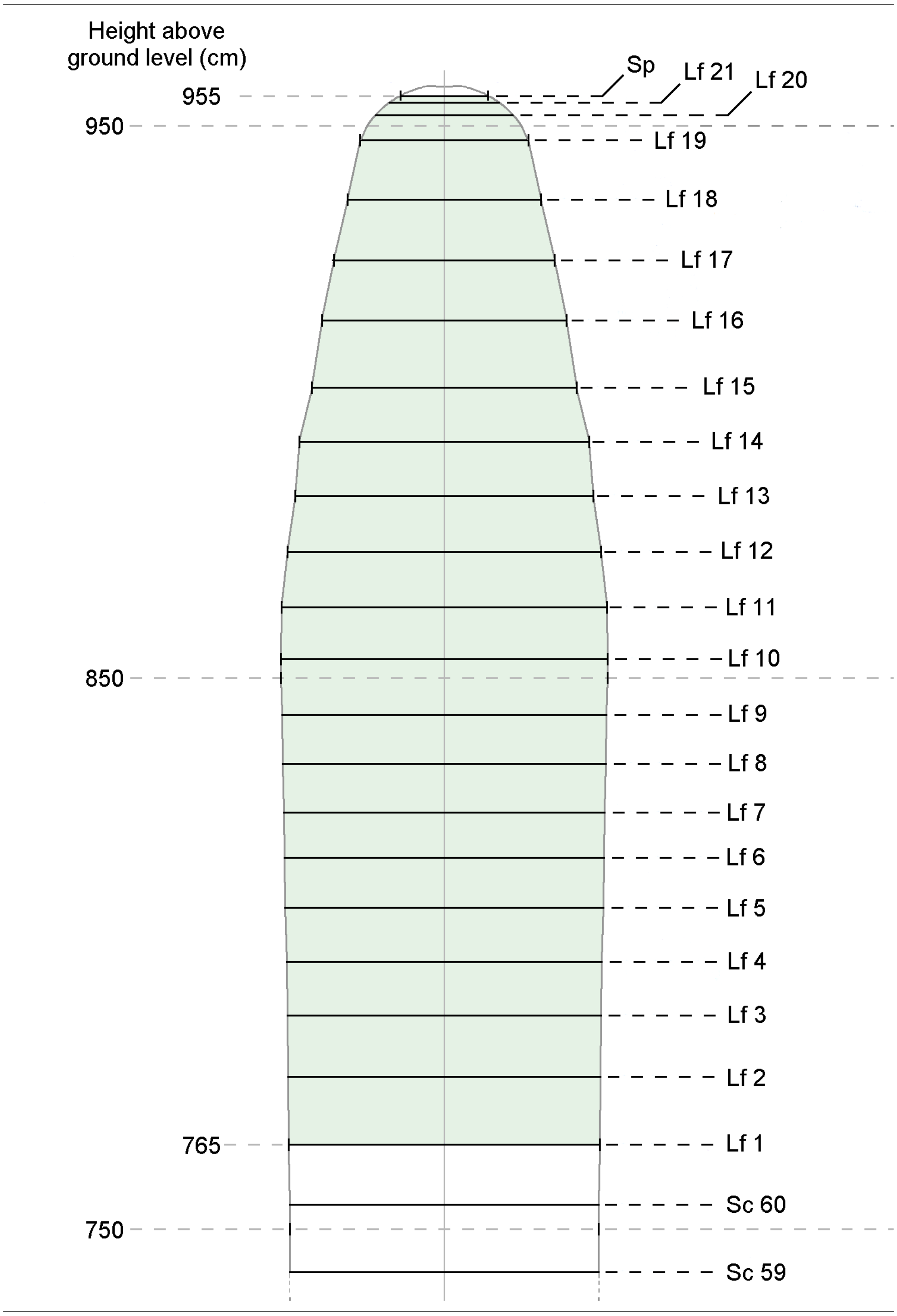

Figure 4.37 Diagram of the top of a sago palm trunk in the Adult Vegetative phase based on the observations of Palm #25 (see data sheet in App. A). Dimensions true to scale. Horizontal lines represent the nodes (places of attachment) of shed leaves (Sc), of unfolded green leaves (Lf 1, ..., Lf 21), and of the spear leaf (Sp).

4.6.2 Age ranking of observed sago palms on the basis of morphological characters

In the G-phase, the morphologically clearly trackable sequence of events in the development of the inflorescence makes it possible to rank palms - albeit not according to chronological age - according to the stage of this development (physiological age), even irrespective of the variety the palm belongs to.

In the AV-phase, any morphological indication of what part of that phase has elapsed is lacking, except for trunk height and the number of leaves formed during that phase so far. Because of the variation of internode length and of leaf unfolding rate, these indicators are only suitable for approximate age ranking. And because of the variation among the different varieties of the maximum number of leaves that is formed in the AV-phase (Table 4.3), the variety the palm belongs to has to be taken into account.

Based on the above considerations, sago palms of which the starch content was established (see Chapter 7), but of which the age was unknown, are given a tentative physiological age rank number in Table 4.16.

Based on trunk height and number of leaves formed in the AV-phase, this phase could be subdivided into 4 age classes or sub-phases only: AV early (one palm with a trunk of 7.90 m long and 67 leaves formed), AV (12 palms, trunks 8.45 m -13.80 m long, 83 to118 leaves formed), AV late (4 palms, trunks 11.70 m -16.75 m long, 134 to more than 157 leaves formed), and AV very late (one palm with a trunk of 14.25 m long and more than 130 leaves formed). The first and the last sub-phase (containing one palm of the variety Ihur each) were distinguished based on the average maximum number of 124 leaves formed during the AV-phase which was observed in this variety Ihur (Table 4.3), which make 67 and more than 130 relatively very low and very high numbers of leaves formed, respectively. Within each sub-phase, the palms are grouped by variety; the groups are not ranked by age, but the palms within each group are.

In Table 7.1 in Chapter 7, the age ranking as presented in Table 4.16 is used as the basis for the time sequencing of the observed starch densities and contents in these palms.

Table 4.16 Tentative ranking according to physiological age of the trunks of various folk varieties of sago palm from the villages Hatusua (Seram Island) and Siri Sori Serani (Saparua Island), based on trunk height, number of leaves formed in the AV-phase, and inflorescence development stage . Palm numbers refer to the numbers in the appended Sago Palm Data Sheets ; they only reflect the chronological order in which the palms were examined.

Palm #	Variety	Trunk (ax$_0$) height (m)				Number of AV leaves				Number of ax$_1$-s of inflorescence	Dev. phase	Age rank
		leafless	leaf-bearing	rachis (= ax$_1$-bearing)	total	leaf scars on trunk	green leaves	spear leaf + lvs inside*	total *			
12	Tuni	6.00	1.90	-	7.90	33	14	20	67	-	AV early	**1**
31	Molat	6.95	1.50	-	8.45	50	16	17	83	-	AV	**2 - 13**
30		7.60	1.45	-	9.05	55	16	16+?	87+?	0?		
13		8.30	1.80	-	10.10	53	16	19	88	-		
10		9.90	2.30	-	12.20	63	21	22	106	-		
14	Molat Berduri	8.10	2.75	-	10.85	46	22	21	89	-		
25	Ihur	7.65	1.90	-	9.55	60	21	26	107	-		
17	Tuni	7.85	2.45	-	10.30	43	19	24	86	-		
11		10.70	2.10	-	12.80	71	20	23	114	-		
16		12.05	1.60	-	13.65	78	19	21	118	-		
20	Putih	8.55	1.40	-	9.95	54	14	19	87	-		
19		9.05	1.15	-	10.20	72	14	19	105	-		
21		12.25	1.55	-	13.80	70	14	21	105	-		
33	Molat	15.15	1.60	-	16.75	137	? c.20	n.r.	157+?	n.r.	AV late	**14 - 17**
07	Ihur	10.35	1.35	-	11.70	92	17	25	134	-		
27	Tuni	14.60	1.55	-	16.15	107	19	17+?	143+?	-		
32		14.45	1.55	-	16.00	109	19	18+?	146+?	0?		
26	Ihur	12.85	1.40	-	14.25	90	21	19+?	130+?	n.r.	AV very late	**18**
09	Tuni	17.50	1.50	-	19.00	121	20	32+?**	158?	?	G1 very early	**19**
37	Ihur	13.60	2.25	-	15.85	85	24	19	128	19	G1 early	**20**
29	Molat Berduri	11.70	3.95	0.35	16.00	101	28	-	129	22	G1	**21**
28	Tuni	14.75	5.05	2.00	21.80	115	27	-	142	27	G1 late	**22**
35	Ihur	7.95	4.60	2.35	14.90	100	27	-	127	23	G2 early	**23**
34	Tuni	15.20	4.65	2.40	22.25	115	25	-	140	27	G2	**24**
18	Molat	4.45	3.15	1.65	9.25	63	17	-	80	18	G2 late	**25**
36	Maka-natol	19.65	4.55	1.60	25.80	165	28	-	193	20	G2 very late	**26**
05	Ihur	14.50	4.80	1.80	21.10	100	18	-	118	24	G3	**27**

* up to and including the smallest primordial leaf hood which can be peeled from the growing point. For various reasons this observation was not always possible, in which case "+?" is added to the number of leaf primordia actually seen.

** of which Sp + c.16 'real' leaves (with leaflet primordia) and - at least - 15 br$_1$-s (with 'top ribbon', without leaflet primordia; G-phase inferred from that, but actual ax$_1$-buds not yet detected); rest damaged (uncountable) by longitudinal sectioning for S.E.M.

br = bract ; lvs = leaves ; n.r. = not recorded ; Sp = spear leaf ; - = not applicable .

E = Establishment phase ; AV = Adult Vegetative phase ; G = Generative phase.

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5 Identifying sago palm varieties

<u>Glossary</u>

variable	- able to vary.
variability	- ability to vary.
variation	- the extent to which or the range in which a thing varies.
to vary	- to exhibit a range of values for a structural or physiological character.
variety	- something differing from others of the same general kind.
diverse	- composed of distinct or unlike elements or qualities.
diversity	- the condition of being diverse.

In this chapter the extent is investigated to which certain varieties of sago palm I studied are representative of the species sago palm as a whole. First it is discussed how diversity may come about, and how scientific taxonomy deals with this diversity. Then the existing diversity in all areas where the species occurs (South-East Asia and nearby Pacific islands) is explored. As first-hand observation of this diversity was beyond the scope of this study, it had to be based on the experience of informants and on existing reports thereof. That is when one comes up against folk taxonomy and its trickeries. A suggestion is made for a nomenclature of locally recognised and named varieties, positing the term folk variety (fv). An overview of folk varieties of sago palm found across its distribution is followed by an extensive description of the fvs in my main study area, Hatusua village (West Seram, Maluku, Indonesia) and by an attempt to scientifically verify claimed defining features of the leaflet blade. Local and global variation in sago palm are then analysed, and the chapter closes with conclusions about the validity of the results of my sago palm studies based on the results of this analysis.

5.1 Relevance

I wanted to study growth and development of sago palm under natural circumstances. These circumstances can be found where sago palm occurs naturally. Generally, natural populations are not genetically homogeneous. This heterogeneity proved to occur also in the semi-wild sago palm stands around the villages of Hatusua in West Seram and of Siri Sori Serani in Saparua where I took my sago palm samples. To be able to better evaluate the outcomes of my studies, I had to know how special or how common among all sago palms in the world the specimens I studied were. Therefore, I had to know more about the genetic variation of the sago palms within the sampled populations, as well as of genetic variation of sago palm in general.

Knowledge of the genetic variation of sago palm is of interest not only to those who try to find out the inner workings of a sago palm, but also to (sago) palm taxonomists and breeders. The first step in establishing genetic variation is finding out which varieties local people distinguish. This local people's perception of variation may also be of interest to ethnobotanists, linguists, and historians.

5.2 Hypotheses on sago palm variation

Because sago palm propagates itself vegetatively and is also propagated mainly vegetatively by man, each new genotype has the potential of being perpetuated and of becoming (locally) recognized and named as a separate variety.

Fruits with viable seeds are not very common. During my three-year field work in the sago forest of Hatusua, West Seram, I have not seen a single seedling. ALANG & KRISHNAPILLAY (1986:122) already reported that "fertile fruit was only found where there were two or more fruiting palms in close proximity to each other." It has been suggested therefore that sago palm is an obligatory cross pollinator: flowers can only produce viable seed if pollinated with pollen from another tree which is not of the same clone. This has been confirmed by the selfing and crossing experiments of JONG (1995:115-116). This means that such a flowering tree of a different genotype has to be in the vicinity, which may be a rare occasion in an area where trees are regularly harvested before the anthesis of the flowers.
The presence of seeds in fruits is sometimes attributed to environmental factors such as soil conditions. In Tebing Tinggi District of Riau Province, Indonesia, it was said that on clay soil 10% of the sago fruits contained a seed, whereas on peat soil there are no seeded fruits (SCHUILING *et al.* 1993:18). Also, some varieties are claimed to produce seeds easier than others (see Table 5.1, column 'Other characters', under PNG - East Sepik Province - Imb(u)ando and - Saniyo-Hiyowe, and Table 5.2), but seed-producing varieties appear to be a minority among the varieties present in a given location. An extreme example of this are the varieties distinguished by the Foi people of PNG's Southern Highlands Province: of the 34 recognized varieties, only one variety "grows readily from seed", while all other varieties are planted from suckers (FRENCH 2006), an indication that only this one variety produces fertile seeds.

- Official taxonomy

The sago palms *s.l.* , *i.e.* all the taxa in the genus *Metroxylon*, can clearly be divided into clustering palms and solitary palms. The sago palms *s.s.*, also called the true sago palms, all belong to the clustering palms. Therefore, only a true sago palm can propagate itself - and is usually propagated by man - by means of its basal offshoots, a.k.a. suckers. This propensity for vegetative propagation makes it likely for any changes in this palm's genome to become permanent. And this has led to disputes among plant taxonomists about the number of taxa of true sago palm to be distinguished. The most taxa were distinguished by BECCARI (1918). He recognized 3 species of clustering, *i.e.* true sago palms, *viz.* the *Metroxylon sagus* described by ROTTBØLL in 1783 (although ROTTBØLL called it *M. sagu*, without the final *s*), the *M. rumphii* described by VON MARTIUS in 1845, and a species described by himself, the *M. squarrosum* from East Seram. Below species level he described 3 botanical varieties of *M. sagus*, and 7 botanical varieties with 6 sub-varieties of *M. rumphii*. Of the 7 botanical varieties referable to *M. squarrosum* which he received from Buitenzorg (now Bogor) Botanical Garden with their local names (and therefore included in Table 5.1. on folk varieties below (under Indonesia, Maluku, eastern Seram, Waru village)), he himself said that they were (p.180:) "barely distinguishable ... from a systematic point of view". The distinction between '*M. sagus*' and the other two *Metroxylon* species is mainly that '*M. sagus*' is devoid of needle-like prickles (commonly called spines in sago palm literature) on the leaf sheaths and elsewhere. In later sago literature, *M. squarrosum* is hardly mentioned anymore, probably because it only occurs in eastern Seram, but the distinction into two species, *M. sagu* Rottbøll (or often with the erroneously suffixed *s*, *M. sagus*, and/or Rottbøll transcribed to Rottboell) and *M. rumphii* Martius, on the basis of the absence or presence, respectively, of spines was widely and uncritically adopted. It had been known since long, however, that both armed and unarmed sago palm seedlings are obtainable from the same mother plant. In 1873(!) SCHEFFER & HOLLE already reported on this mixed offspring phenomenon, albeit in Dutch, stating that the unspined variety found in Java, Indonesia, is

> (p.398): "*... het meest door uitloopers ... voortgeplant, terwijl men uit de zaden veelal de gedoornde variëteit verkrijgt* [... most often propagated by suckers ... , while from the seeds for the most part the thorned variety is obtained]."

In 1895 H.N. RIDLEY reported, quoting a Mr BAMPFYLDE in Sarawak [1] :

> (p.62): "The genus *Metroxylon*, to which the sago palms belong, contains about six species, ...
> The following is a list of species:
> *M. Sagus*, Rottb. - The smooth sago, ...
> *M. Rumphii*, Martius. - The spiny sago, ..."
> (p.64): "Mr. BAMPFYLDE states that the spiny and smooth sago palms produce the same quantity and quality of sago, and that the plants grown from seeds of either kind taken from the same tree come up some spiny and others smooth, though suckers of either kind keep true, ...".

More recently, also FLACH (1977:159) reported a similar observation, as did ALANG & KRISHNAPILLAY (1986:123) and RAUWERDINK (1986:178). On this and other convincing grounds, RAUWERDINK (1986) reduced all three true sago palm species distinguished by BECCARI to synonymy (*Metroxylon sagu* Rottboell) in a revision paper of the genus which - as he put it - "may contribute towards an eventual monograph of *Metroxylon*". RAUWERDINK also rejected BECCARI's great number of infra-specific taxa, because they were based on fruit shape and size, a character which RAUWERDINK showed to be unreliable. He claimed his own infra-specific classification based on spine length into only four taxa to be more reliable, because spines do not grow with age as fruits do. At the same time he reduced the rank of infra-specific taxa distinguished on the base of this spinescence because of the above-mentioned observation of mixed offspring from seed:

> "The taxonomic rank of the taxa in *M. sagu* should be low. The fact that a spiny palm may produce spiny and spineless seedlings indicates that it is heterozygous for this character and may produce embryos of at least two genotypes. The classification forma should apply to these taxa rather than variety or subvariety." (RAUWERDINK 1986:179)

The revision and further study of solitary palm species of the genus *Metroxylon* has since been taken up by Will MCCLATCHEY (e.g. 1996, 1998).

Further investigations into the relationship between existing varieties of *M. sagu* were boosted by the developments in molecular taxonomy. The unrelatedness of differences in spininess and differences in genome has been demonstrated in studies using isozyme analysis for genetic characterization of sago palm varieties (e.g. HISAJIMA *et al.* 1995, MIFTAHORRACMAN *et al.* 1998). KJAER *et al.* (2004) used the Amplified Fragment Length Polymorphism (AFLP) technique to investigate the genetic structure of 76 *M. sagu* individuals collected from 7 locations across Papua New Guinea and tried to correlate genetic variation with morphological variation and spatial separation. They concluded that variation in vegetative morphological characters, particularly the presence or absence of spines, is not correlated to underlying genetic variation, that genetic and geographical distances are generally linked, and that their study supported the taxonomy of RAUWERDINK (1986), recognizing only one species of *M. sagu* in PNG. EHARA *et al.* (2002) had reached the same conclusions for 38 individuals collected from 22 locations from West Sumatra to PNG using Randomly Amplified Polymorphic DNA (RAPD) analysis for genetical characterization.

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[1] Actually, the author (RIDLEY) is not mentioned with the article, but HEYNE (1950:337) refers to the article as "*de monographische bewerking van* Ridley, *voorkomend in* Agricultural Bulletin of the Malay Peninsula 1895, bl.62.". Henry Nicholas RIDLEY may have been the editor of the journal. In the introduction to the first issue of 'The Agricultural Bulletin of the Federated Malay States' of August 1912 it is said that he used to be the editor of the 'Agricultural Bulletin of the SS and FMS'. The mentioned Mr BAMPFYLDE is quoted hereafter in the same article (p.65) as "Mr. A.C. BAMPFYLDE"; he may be the same as the second author of the book:
BARING-GOULD, Sabine & BAMPFYLDE, C.A.A. "A history of Sarawak under its two white rajahs, 1839-1908". - London : H. Southeran & co., 1909. - xxiii,464 p.
The quote may even come from this book.

5.3 Observations: known varieties of sago palm

- Folk taxonomy

The variability of sago palm seems great judging from the large number of names for locally distinguished varieties (lexical polytypy). However, the genetic distance between distinguished varieties does not need to be big because - as argued above - these varieties are probably clones and clones can be distinguishable already by a few and/or small differences only. And if these differences coincide with different uses by local users, their consolidation into a named local variety becomes even more likely. As ELLEN, who studied the Nuaulu people of south central Seram, put it, it may be more accurate to view locally distinguished sago palm varieties "as a means of expressing a range of interlinked characters of morphology and practical use that in a particular area are sufficiently stable for recognizable differences to be widely shared and so represented in a population" (ELLEN 2006:284-5). This practical use may even take a form seemingly contradictory to the aforementioned in having a function as just being different, as TOWNSEND (2003:9,7) who studied the Sanyo people of the upper Sepik area in Papua New Guinea points out: They "attempt to maintain diversity for the sake of diversity ... in order to have alternative varieties of sago for mourners ... " "Out of grief, the chief mourners will avoid eating the variety of sago that they were eating when their loved one became ill and died."

- Folk variety (fovar, fv)

What then should a locally distinguished variety be called (so I can use the name without causing confusion for my purpose of interpreting the results of my growth & development studies) if it is most probably a group of similarly-manifesting clones for which it makes sense for a group of users to distinguish it from other sago palms: in other words, a functional category rather than a cladistic evolutionary category?

It is evident that the term 'variety' as such is too ambiguous, as in the strict sense it designates a botanical, natural variety (shortened to var.), a sub-species category in the scientific cladistic evolutionary sense. Also cultivar has this ambiguity, as this term implies a cultivated variety or variety arisen from cultivation, but in the strict sense designates a variety arisen from intentional, institutional breeding, registered and legally protected as such.

ELLEN (2006:269) chose the term 'landrace'. A landrace presupposes some measure of intentional selection in a crop population, resulting in a recognizable but genetically diverse population adapted to a specific region (land). While indeed some of the varieties ELLEN described meet these criteria, the rareness of sexual reproduction in sago palm would usually defy such selection. Moreover, like the term cultivar, it does not accommodate for named and recognized wild, unmanaged varieties.

In the case of sago palm, the botanically most accurate name for a locally distinguished variety would probably be 'clone-group'. However, as long as we are not sure about the genetic origins of the category, I prefer and suggest the term 'folk variety' as a reminder of the category's not exlusively botanical origin. This can be shortened to fovar and fv., by analogy with the customary abbreviation of cultivation variety to cultivar and cv. By the same analogy, all elements of the folk variety name should start with a capital letter, and if used without the folk variety epithet the name should be enclosed in quotation marks. I suggest to use double quotation marks to distinguish a folk variety name from a cultivar name (for which single quotation marks are in use), and to emphasize its quoted character (as opposed to the invented character of a cultivar name). After the folk variety name, an indication of the location and - if known - the ethnic/linguistic group where and by which the name is used should be added between brackets. The local variety Tuni I studied could thus be identified as *Metroxylon sagu* Rottbøll fv.Tuni (Hatusua, W.Seram, Indonesia) or *M. sagu* "Tuni" (Hatusua, W.Seram, ID); the variety Honamo recognized by the Foi people mentioned above as *M. sagu*

Rottb. fv. Honamo (Southern Highlands, PNG : Foi). Nomenclatural rules similar to the ones in use for cultivars could be devised to facilitate 'lumping', 'splitting' and other revisions of folk varietal taxonomy.
There are palm researchers who have used the term 'folk species', e.g. BYG & BALSLEV (2003:38.): "Species distinguished are "folk species", i.e., plant groups regarded as separate entities by local residents." This term implies an uncertainty with the researcher/observer about a plant's identity on the species level, which I find improbable, as unknown taxa of this magnitude would have found eager taxonomists to name them as soon as they would have been discovered.
The terms 'farmer's variety' and 'traditional variety' are also often used for a locally distinguished variety. 'Farmer's variety' presupposes exclusive usage, or selection by farmers; 'traditional variety' may be confused with a cultivar which has been in use since long, and/or imply nonmodernity. The term 'folk variety' merely, and correctly, implies a category name in use by people (for whatever reason) not representing - although possibly coinciding with - a cladistic evolutionary category. I suggest to define the term 'folk variety' precisely as such, i.e in line with what its name implies; and not just for sago palm, but for any organism.

- Identification of Indonesian varieties

On the grounds discussed above, the common practice in Indonesia of identifying varieties distinguished outside the Ambon-West Seram area with the varieties inside it, viz. with Tuni, Ihur, Molat, Makanaru and Duri rotan, or worse, directly with the different botanical taxa on the species level often attributed to these Ambonese- West Seramese varieties , viz. *Metroxylon rumphii*, *M. sylvestre*, *M. sagus*, *M. longispinum*, and *M. microcanthum*, respectively, (e.g. BADAN KOORDINASI... 1991, for East Seramese varieties; PASOLON *et al.* 2002, for Southeast Sulawesian varieties), should be rejected. JUDI *et al*. (1988:14,49) and SUNARA MARTADIWANGSA *et al*. (1989:34) also use the Ambon-West Seram names for local varieties in eastern Seram and in Halmahera Island, respectively, but at least they call these names pinned on them *nama perdagangan* (trade names), not botanical names. In agronomic studies of the sago palm, if distinguishing varieties is important, local variety names should be adhered to.
No doubt, this tendency to refer varieties back to the five above-mentioned ones is rooted in the first pre-Linnean analytical description and western-scientific naming of the variation in true sago palm by RUMPHIUS (1741). He based his descriptions on what he saw in the Ambon-West Seram area, providing Latin binomials for local varieties. Plant taxonomists after him have always referred any new scientific names back to his scientific names, contributing to the impression of wide validity and applicability of RUMPHIUS' categorization of the true sago palm, where in reality he had only - but aptly - classified the limited number of folk varieties found in a very limited area.

- An overview of folk varieties

Table 5.1 presents an overview of folk varieties of sago palm with some of their discriminating characters, based both on existing (often anthropological) literature and on my own interviews with local informants. The second column presents the alleged botanical names and/or Ambon-West Seram area folk variety synonyms discussed above.
The reports referenced in this overview are clearly of different quality, some being the result of quick surveys, others of many years' (participating) research. The longer one stays in a certain location, the more detailed the information one is usually able to extract, not lastly because one may become more able to put the right questions (see e.g. the second interview in the section on folk varieties of Hatusua below, and SCHUILING (1995:45-48)). The more detailed information often includes a more detailed categorization of the local sago palm population, i.e. more named locally recognized sago palm varieties.

Table 5.1 Folk varieties of sago palm as recognised at different locations, with some of their characteristics (entries in alphabetical order of location). Stressed syllable in variety name underlined if known. Qualitative and comparative descriptors apply to varieties in same entry (same location from same reference) only. The total number of varieties recognised per entry is given at the end of the entry line.
ax_2, ax_3 = 2nd-, 3rd-order inflorescence branch ; bark = *wa'ah* (outer trunk layer incl. adjacent fibre layer) ; comb = transverse series of spines ; lf = leaf ; lvs = leaves; lt(s) = leaflet(s) ; pt = petiole ; rc = rachis ; sd = seed ; sh = sheath(s) ; spi = spine(s) ; S = sucker ; S1 = sucker with overall height not exceeding 1.2 m ; S2 = sucker with leaves between 1.2 and 4 m long ; S3 = sucker with leaves longer than 4 m ; yld = yield ; # = rank number (highest/biggest/best to lowest/smallest/worst).

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Indonesia, Jawa ; area: north coast **Central Java**. (ENKLAAR VAN GUERICKE 1873)							5
Kersula, Rembulung, Tembulu, Bulu, Rajang bungkoan (best lts for weaving mats).							
Indonesia, Maluku ; area: probably **Ambon** Island. (TUPAMAHU 1909:105-106)							5
Putih a.k.a. Tuni (putih = white; tuni = true)		cultivated		+	young lvs whitish	pith whitish	considered best variety
'Merah a.k.a. Ihor (merah = red)		cultivated		+ ; longest (20 cm)	lf and lts longest		
Molat		cultivated		-			
Rotan (rotan = rattan)		neglected		+ ; fine/thin		internodes long as in rattan palm	low-yielding
Makanaro		neglected		+ ; fine/thin			low-yielding
Indonesia, Maluku ; area: **Ambon** Island and western **Seram** Island. (sagu (Malay), lapia (Ambonese) = sago palm) (RUMPHIUS 1750 (1741):75-76)							5
Tuni (tuni = true)	*Sagus Genuina*	cultivated		+ ; intermediate length, in thick rows	lts 4.5 ft long, 4-5 fingers wide ; best for thatch	pith harvestable up to G1 phase	most abundant, most cultivated and planted ; 2nd-best flour
Duri rotang a.k.a. Luli-uwe (rotang = rattan) considered sub-taxon of Tuni				+ ; short, dense, stiff as in rattan		pith harvestable up to flowering	many in Hoalmoal peninsula, Seram; not in Ambon.
Ihur a.k.a. Ihul	*Sagus Silvestris*		highest trunk; infructescence smaller than of Tuni.	+ ; more, denser, but shorter than in Tuni		highest; pith harder and taking more effort to pound than in Tuni, harvest-able up to start of fruiting	mostly in Seram, hardly in Ambon; ax_3s not perpendicular to ax_2s, sometimes pointing forward, longer than in Tuni.
Macanaru a.k.a. Macanalo a.k.a. Macanalun	*Sagus Longi-Spina*		trunk thinner than in Tuni	+ ; longest, not dense	lts darker, narrower, thinner and more wrinkled than in Tuni ; lvs less usable for thatch and gaba-gaba	thinner than in Tuni; pith harvestable up to flowering	yld less than Tuni

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Molat a.k.a. Parampuan (parampuan = woman)	*Sagus Laevis*			-	lts with sharp tips	pith harvestable up to just before ax_1s emerge	flour best, most used for papeda, lempeng made from it not durable **)
Indonesia, Maluku ; area: **Bacan** Island. (TEAM PROYEK P3.S.B.P.E. (SAGU) BPPT & UNPATTI 1981/1982:4-6)							6
Sike	*M.rumphii* Mart.			+			
Pulutan	*M.sylvester* Mart.			+			
Tirus	*M.sylvester* Mart.			+			
Licin	*M.sagus* Rottb.			-			
Ngani	*M.longispinum* Mart.			+			
Soang	*M.microcanthium* Mart.			+			
Indonesia, Maluku ; area: **Bacan** Island. (COLLINS & NOVOTNY 1991:129) (In Bacan Malay, "*ambulung* is a generic term for sago tree" ; "at least seven kinds of sago are distinguished".)							7+
Duri puti, Licing, Pulutang, Nggani, Sike, Soang, Tirus							
Indonesia, Maluku ; area: **Bacan** Island, **Labuha** District, **Amasing** village. (own survey/interview 15-16feb1994)							9
Sike, Pulutan, Soang, Ngganing, Tirus, Tirus mandiole, Tajang, Licing, Duriputi.							
Indonesia, Maluku ; area: **Halmahera** Island. (CAMPEN 1884:9)							7
Toppo Bohekka				+ ; length c.5 cm		excellent, very white starch	high-yielding ; most wanted
Soang				+ ; length 1 cm		very high quality, reddish starch	very high- yielding ; common on **Bacan**, rare on Halmahera.
Bawah				-		starch often reddish, good quality	much sought after
Toppo Nau a.k.a. Nau				+ ; length 15 cm		white starch	yld judgeable from trunk shape: cone-shaped → high, reversely cone-shaped → low
Hangee Bohekka				-			
Hangee				-	lvs paler than in Hangee Bohekka		
Bawah Namalau				[?]		many hard fibres	low-yielding ; least wanted
Indonesia, Maluku ; area: **Halmahera** Island. (FORTGENS 1909:90-91)							5

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Sisika Ma Dutu (= true spine)	Ihur		height rank 1	+ ; on pt 10 cm long	gaba-gaba use rank 1	up to 10 'vadem' long	yield #1
Halimè	Tuni			+ ; on pt 5 cm long		up to 7 'vadem' long	
Sòama				+ ; on pt 2 cm long			
Sirigi	Molat			-			
Bawehe				-			
Indonesia, Maluku ; area: **Halmahera** Island, **Galela** District, **Limau** village ; ('tano' means 'sago palm'). (YOSHIDA 1980)							**8**
Sika				+ ; long			
Yafa				+ ; short			
Seho Ma Tano				-	green band on back pt-rc in S stage		
Roku Ma Amo				-	brown band on back pt-rc in S stage		
Roku Ma Amo Pusu				-	brown band on back pt-rc in S stage		
Sirigi				-	black band on back pt-rc in S stage		
Bobarai				-	black band on back pt-rc in S stage		
Kuweso				-	brown band on back pt-rc in S stage		
Indonesia, Maluku ; area: **Halmahera** Island, **Kao** District. (SCHUILING *et al.* 1993:39,42)							**5**
Ratemu				+			yield #1
Beka				-			yield #2/3
Bawes				-	lts longer & narrower than in Beka		yield #2/3
Sisika		wild		+			yield #4
Balala			large var. of Ratemu	+			
Indonesia, Maluku ; area: **Saparua** Island, **Siri Sori Amalatu** village (formerly Siri Sori Serani village). (SCHUILING *et al.* 1993:56, SCHUILING 1989:15-17)							**5**
Molat		planted		-	lts hard, tips upright	pith soft	fell-ripe at *jantung***** stage

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Sagu Merah	Ihur	planted		+ ; in S2 lt margin and upperside midrib with spinules on distal 2/3	lts soft, tips drooping		fell-ripe at *sirih buah****** stage
Sagu Putih	Tuni	planted		+ ; narrower than in Samakika	lts tips upright		
Makanatol		planted		- ; in S2 lt margin smooth, lt midrib upper side with spinules on distal half	lts soft, tips drooping ; pt & rc yellowish green	pith hard ; flour pinkish	fell-ripe at *sirih buah****** stage ; unseeded fruits have three fleshy parts
Samakika		planted		+ ; broader than in Sagu Putih, length in S2: 4 cm		lf bases remain after lvs shed	pounding young tree causes itching
Indonesia, Maluku ; area: eastern **Seram** Island, **Waru** village. (BECCARI 1918:162,180-182. *))							**7**
[Woi]	*M.squarrosum* Becc. var. *Kilwoi*			-	pt intensely green		
[Lasi]	*M.squarrosum* Becc. var. *Killasi*			-	pt gray		
[Karua]	*M.squarrosum* Becc. var. *Kilkarua*			+ ; long, thick	pt intensely green		
[(L)atan(kirkie)]	*M.squarrosum* Becc. var. *Kilatan* or *Kilatankirkie*			+ ; short, thick	pt long		
[Kour]	*M.squarrosum* Becc. var. *Kilkour*			+ ; length medium	pt white		
[Tafuk]	*M.squarrosum* Becc. var. *Kiltafuk*			+ ; length medium, thin	pt green		
[Kikir]	*M.squarrosum* Becc. var. *Kilkikir*			+ ; short			
Indonesia, Maluku; area: eastern **Seram** Island. (JUDI et al. 1988:49)							**18** [see *)]
(=Molat): Baing, Wakano, Tn [?], Lasi/Kelasi, Lahanda [?] ; (=Tuni): Kelada, Kuratuku ; (=Ihur): Kelanggan, Uleu, Kelantan, Anggan, Tafok, Keltafok ; (=Makanaru): Furkeh, Valwel ; (=Duri rotan): Anggan Silan, Duri Hitam, Kelkikir, Uleu [also identified as "Ihur"] ; (=Suanggi): Kelkour, Kour, Korua.							
Indonesia, Maluku; area: eastern **Seram** Island. (BADAN KOORDINASI PENANAMAN MODAL....[LOUHENAPESSY et al.] 1991:4)							**12**
Uleu	Tuni / *M.rumphii* Mart.	semi-wild		+			

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Fallwel	Ihur / *M.silvester* Mart.	semi-wild		+			
Tanil	Molat / *M.sagu* Rottb.	semi-wild		-			
Wakan	Duri Rotan / *M. microcanthum* Mart.	semi-wild		+			
Lalada	Makanaru / *M. longispinum* Mart.	semi-wild		+			
Maf	Molat / *M.sagu* Rottb.	semi-wild		-			
Kuriatuku	Tuni / *M.rumphii* Mart.	semi-wild		+			
Anggan	Ihur / *M.silvester* Mart.	semi-wild		+			
Kelantan	Ihur / *M.silvester* Mart.	semi-wild		+			
Furkeu	Makanaru / *M. longispinum* Mart.	semi-wild		+			
Kanaki	Duri Rotan / *M. microcanthum* Mart.	semi-wild		+			
Baiing	Molat / *M.sagu* Rottb.	semi-wild		-			
Indonesia, Maluku ; area: south central **Seram** Island, **Nuaulu** people ; ('hatane' (> 'hata') = sago palm, 'nuni' = spine) (ELLEN 2006:269-271)							**11**
[Hata] Nuni Mane (mane = soft)				+ ; moderately short, in continuos combs	lt crisp ; sh clinging	very soft pith ; light bark, color as Nasinane.	
[Hata] Nuni Nasinana (nasi = blood ; nanae = delicious)				+ ; moderate to long, in continuous combs	sh clinging	red pith ; light bark	otherwise same as Nuni Weri
[Hata] Nuni Uakane				+ ; fine, in continuous combs	sh clinging		
[Hata] Ai (ai = tree)	[Sagu] Molat			-		very white pith ; girth 160 cm	reproduces both vegetatively and sexually

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
[Hata(ne)] Umena	[Sagu] Putih			+ ; short, in broken horizontal groups	sheaths do not drop off cleanly → much water retained in adhering stubs.	fresh clean and white pith, almost as Hata Ai ; thin rough surface with much moss growth ; girth 123 cm ; bark 1.5 cm, thicker than Sekane	requires more work for same yield
[Hata] Napaune				+	sh drop off cleanly	reddish pith ; smooth bark (1-1.5 cm) ; girth 138 cm	otherwise almost same as Ai
[Hata] Nuni Metene (metene = black)				+ ; black, in continuous combs across lf sh; spi clusters webbed at base ;	sh not clinging	dark bark	
[Hata] Nuni Tamnone				+ ; short, fine, hard, in almost continuous parallel combs		girth 204 cm ; bark 1-1.5 cm	
[Hata] Nuni Msinae (msinae = red)	[Sagu] Merah			+ ; long (some 22 cm), hard, in clusters, with red blotches at base	sh moderately clinging	white pith ; girth 155 cm ; bark 2 cm	
[Hata] Nuni Ueri				+ ; numerous, long, fine, in continuous parallel combs	sh clinging	dirty pith ; girth 126 cm (flowering) ; bark 1 cm	not as large as other varieties but grows quickly (7-9 yrs) ; good taste
[Hata] Nuni Sekane (seka = clean)				+ ; small numbers of moderate spi in continuous parallel combs; on young pt orange, short and thick	sh variably clinging	bark 1 cm, thinner than Umena, light color	
Indonesia, Maluku; area: western **Seram** Island, **Hatusua** village.							**7**
Ihur, Tuni, Molat Licin, Molat Duri Putih, Molat Duri Merah, Makanaru Duri Putih, Makanaru Duri Hitam (descriptions: see section 'Folk varieties of Hatusua ...' below)'.							
Indonesia, Maluku; area: western **Seram** Island, **Lohiatala** village. ('pia' means 'sago' in Alune language)							**3**
(Pia) Lubosu	Tuni			+			
(Pia) Libule	Ihur			+			
(Pia) Sane	Molat			-			
Indonesia, Maluku; area: western **Seram** Island, **Piru** village. (own survey/interview 24feb1994)							**5**

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Ihur				+ ; length #1; density #2	base narrow, normal colour; pt widt #3; thatch suitability #3; gaba2 ***) suitability #3/4	width #3; height #3; bark thickness #3; int short; pith hardness #2	time till harvestable #4; yld #2 (70%)
Tuni				+ ; length #3; density #3	base wide, whitish; pt widt #2; thatch suitability #1; gaba2 suitability #1	width #1; height #1; bark thickness #1; int length #1; pith hardness #1 (hardest)	ability to fruit #1; number of seeds per inflorescence #1; time till harvestable #5; yld #1 (70-100%)
Molat				-	base wide, whitish; pt widt #1; thatch suitability #4; gaba2 suitability #5 (pt too soft)	width #2; height #2; bark thickness #4; int length #2; pith hardness #5	time till harvestable #1 (shortest); yld #3 (50-60%)
Duri Putih				+ ; length #4; density #4	base narrow, normal colour; pt widt #5; thatch suitability #5 (lts too thin); gaba2 suitability #3/4	width #5; height #5; bark thickness #5; int short; pith hardness #4	time till harvestable #2; yld #5 (25%)
Makanaru				+ ; length #2; density #1	base narrow, normal colour; pt widt #4; thatch suitability #2; gaba2 suitability #2	width #4; height #4; bark thickness #2; int short; pith hardness #3	time till harvestable #3; yld #4 (30%)
Indonesia, Maluku ; area: **Sula** Islands ; ('saa' [sa'a] means 'sago'.). (own survey/interview 14feb1994)							2
(Saa) Sua ('Sua' means 'Sula')				-			
(Saa) Hoipopa				+			
Indonesia, Maluku ; area: **Ternate** Island, **Kastela** village. (SCHUILING *et al.* 1993:46-47)							4
Hange		planted		-		white flour	
Topo Baca(ng)		planted	larger than Topo Biasa	+ ; length in S2: 10 cm	2nd/3rd best thatch	whitish trunk; white flour	
Topo Biasa (biasa = normal)		planted		+ ; length in S2: 5-6 cm;	best thatch	reddish flour	
Soang		planted		+ ; length in S2: 1-2cm	2nd/3rd best thatch		
Indonesia, Papua ; area: **Arso** District : social group: **Kerom** tribe. (MAMBRASAR *et al.* 1984:8)							5
Nafta		planted		+	pt greenish-grey		

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Nangwiramsyah		planted		+ ; large, long; bunched closely together		shorter and with smaller diameter than in Nafta	
Nawaris		planted	usually very closely bunched	+		small, thin	yld usually high
Nakor		wild	usually grows in bunches in thick jungle	+ ; long, widely spaced	pt grayish		more vigorous than previous 3 fvs
Nawam		planted	usually grows singly rather than in bunches	-			
Indonesia, Papua ; area: **Manokwari**. (AURI & ABDURROHIM 1988)							**3**
Witime	*M.rumphii* Mart.			+			
Wimama	*M.microcanthum* Mart.			+			
Ananggemo	*M.sagus* Rottb.			-			
Indonesia, Papua ; area/social group: **Marind-anim** ; ('dah' means 'sago'). (WIRZ 1922:vol.1:94)							**10**
[Dah] Aritir , [Dah] Boi , [Dah] Bor , [Dah] Eviapatin , [Dah] Juka , [Dah] Kumu , [Dah] Tad , [Dah] Towah , [Dah] Wiprá , [Dah] Wiriba . [no characteristics given.]							
Indonesia, Papua ; area: **Salawati** Island, **Duriankari** village. (SCHUILING *et al.* 1993:51)							**10**
Fok		planted		+			15 yr to maturity; seldom fruits
Fok Surare		planted		+ ; combs closer and whiter than in Fok			15 yr to maturity
Snang (or: Hsnan)		planted		+			15-20 yr to maturity; seldom fruits
Nesek Lege		planted		+		thin bark	20 yr to maturity; lf sh remain long
Keta		planted	like Nesek Lege	+		bark thicker than Nesek Lege	
Kla (see Fig. 5.1a)		planted		+ ; length in S2-S3 to 20cm		soft bark and pith	
Kuf Bra		planted		+	lf bases blueish at fell ripeness ; lf sh not adhering long	bark white-grey in tall trees	

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Snang Kwi		planted	like rattan palm; tall	+			inland
Katun		planted		-			
Mda		wild		+ ; longest	most durable thatch	thickest bark	fruits often
Indonesia, Papua ; area/social group: **Sentani**. (MAMBRASAR *et al.* 1984:7-8).							**23**
Bara Biasa		planted		+ ; along entire pt		pith reddish, fibrous; bark extremely hard	
Bara Habou		planted		+		pith soft, whitish; bark thin	
Roondo		planted		+	margin fine spiny	pith soft; bark thin	abundant flowers
Manno Biasa		wild	gows in compact clusters	+ ; large, long		pith red; bark hard; tall, thin	
Manno Okhu		wild	similar to Manno Biasa	+		shorter than Manno Biasa	
Rurana		planted		+ ; long		pith soft, whitish; fibres few	
Ebesung		planted	similar to Rurana	+ ; marks/traces only			
Yakhalobe		planted		+ ; traces only	pt extremely long	pith whitish	
Mongging		planted		+ ; long	margin fine spiny	pith whitish, extremely soft; fibres few	
Hobelea		wild		+ ; long, large, extremely hard		pith tough	
Pui		planted		+ ; long, very hard, sprouting from single base		pith extremely hard	
Yeba Hombokhleu		planted		-		large, tall, smooth; pith whitish, less-fibrous; bark hard.	yld high
Yeba Honsai		planted		-		large, tall, smooth; pith reddish, less-fibrous; bark hard	
Folo		planted		-	pt long; lvs point downwards	pith soft, white; bark soft	starch w/ high binding strength; greatly preferred

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Hobolo		planted		-	pt short	pith soft; bark soft	
Epung Yeba		planted		-		pith reddish, rather soft; bark hard	
Oskhulu		planted		-		pith whitish, soft; bark soft	
(spineless): Wani, Hili, Yokhuleng, Yakhe, Pane, Nandia (Folo). [no characteristics given.]							
Indonesia, Papua ; area: **Sentani** Sub-District, **Kehiran** village. (MIFTAHORRACHMAN *et al.* 1998).							**20**
(spiny): Manno, Phara, Ruruna, Phui, Ebesung, Yaghalobe, Rondo, Habela, Phara Waliha ; (spineless): Follo, Wanni, Phane, Hilli, Yebha, Hobolo, Yoghuleng, Fikhela, Yakhali, Osoghulu, Rena.							
Indonesia, Papua ; area: **Sentani** District, **Maribu** village : social group: **Moi** ; ('debet' means 'sago', 'kutu' means 'spine'). (KENTIN SRI SUDARMI 1996 ; SURTINA 1997).							**19**
(spineless [all names preceded by 'Debet']): Yeglum, Kluyo, Embiam Ibakley, Embian Unit, Demisba, Banu, Daysiyabu, Wani, Maranggra ; (with inconspicuous spines): [Debet] Srom (4 types) ; (with conspicuous spines): [Debet Kutu] Swayplen, [Debet Kutu] Blub, [Debet Kutu] Yakali, [Debet Kutu] Dundu, [Debet Kutu] Menggeng, [Debet] Mamakutu.							
Indonesia, Papua ; area: **Sorong**, **Seget** District. (SCHUILING *et al.* 1993:48)							**2**
Wijinik				+			
Wijiniksan				-			
Indonesia, Papua ; area: **Sorong**, **Tanjung Kasuari** village. (SCHUILING *et al.* 1993:54)							**2**
Borek				+			
Senaf (see Fig. 5.1d)				-			
Indonesia, Papua ; area: **Waropen**. (FLACH 1997:40-42)							**4**
Mai (wild) = Nduanda (planted)				+			trunk age at flower initiation 6-7 yr (type Mai2) or 9-10 yr (type Mai1or Nduanda).
Ndosa (wild) = Sakambai (planted)				+			trunk age at flower initiation 9-10 yr
Farei				+ ; short, soft			trunk age at flower initiation 6-7 yr
Umbeni				-			6 yrs from planting as large S to sd formation ; = Moluccan "Molat"?.
Indonesia, Riau ; area: **Pulau Tujuh** archipelago, **North Natuna** Islands, **Bunguran** (**Natuna Besar**) Island ; ('rumbia' means 'sago palm'). (VAN HASSELT & SCHWARTZ 1898:453-454).							**2**
(Rumbia) Duri		planted		+			preferred for planting because spi repel boars
(Rumbia) Bamban or .. Bemban		planted		- ; practically spineless			yields more than Duri

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Indonesia, Sulawesi Tenggara. (DINAS PERTANIAN TANAMAN PANGAN SULTRA 1987, in CHALIMIE 1989)							**4**
Roe		semi-wild and planted					
Rui		semi-wild and planted					
Runggumanu		semi-wild and planted					
Baruwila		semi-wild and planted					
Indonesia, Sulawesi Tenggara ; social/ethnolinguistic group: **Tolaki**. (PASOLON *et al.* 2002)							**4**
Roe	Molat / *M.sagu* Rottb.						
Runggumanu	Tuni / *M.rumphii* Mart.						
Rui	*M.micracanthum* Mart.						
Baruwila	white sago						
Indonesia, Sulawesi Utara ; area: **Bolaang**. (JASPER 1908:2)							**4**
Monulom			large			wide trunk	
Kawu							with aerial roots
Duri				+			
Kalè				+			
Indonesia, Sulawesi Utara ; area: **Minahasa**. (JASPER 1908:2)							**4**
Karimenga				-			
Kerèttan					lvs very long	wide trunk	
Kolai					pt long		
Susulahan				+			
PNG, East Sepik Province ; area/social group: **Imbando** village. (VAN KRAALINGEN 1984)							**16**
Wakar 1		wild		+ ; length up to 20 cm in S2			yld rank 1 wild var.
Wakar 2		wild		+; length up to 20 cm in S2			yld rank 2 wild var.

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Wakar 3		wild		+; length up to 20 cm in S2			yld rank 3 wild var.
Wakar 4		wild		+			yld rank 4 wild var.
Ketro		planted		+ ; long	lts drooping		preferred for planting ; sterile
Anum		planted		+ ; long			highest yld of all ; sterile
Nago		planted		+ ; long			sterile
Waipi		planted		+ ; short to long			sterile
Makapn		planted		+ ; short			sterile
Ambutrun		planted		-	lf tip bending down		sterile
Awirkoma (awir = white)		planted		-	pt white ; lts stiff		low-yielding ; sterile
Koma		planted		-	lts stiff		low-yielding ; sterile
Kaparang, Kangrum, Ninginamé, Mandm.							
PNG, East Sepik Province ; area/social group: **Imbuando** (= **Imbando**) village. (RAUWERDINK 1985)							**17**
Wakar-true		wild		+ ; not too many	black color on sh and pt	trunk big	sds fertile ; yld good ; growth slow
Wakar-cru		wild		+ ; not too many	white color on sh and pt	trunk may be big	sds fertile ; yld low ; may grow slow
Mandènum		wild		+ ; very long	black color on sh and pt	no trunk formation	sds fertile ; rare
Ketro		mostly planted		+ ; long, many	black color on sh and pt	trunk big	sds usually sterile ; yld very good ; growth slow
Anum		mostly planted		+ ; long, many	white color on sh and pt	trunk big	sds usually sterile ; yld very good ; growth fast on dry ground, slow on wet ground
Ninginamé		mostly planted		+ ; long, not too many	black color on sh and pt	trunk big	sds usually sterile, but also fertile ; growth slow
Nago		mostly planted		+ ; long, many	white color on sh and pt	trunk big	sds usually sterile ; yld very good ; growth slow
Moiap		mostly planted		+ ; long, not too many	white color on sh and pt with greenish central band	trunk big	sds usually sterile ; yld good ; growth slow

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Makapn		planted		+ ; short, few	green color on sh and pt with distinct central band	trunk big	sds sterile ; yld medium ; growth slow on dry ground, fast on wet ground
Waipi		planted		+ ; short, few	green color on sh and pt with distinct central band	trunk not big	sds sterile ; yld medium ; growth fast.
Kangrum		planted		+ ; short, not too many	black color on sh and pt	trunk big	sds sterile ; yld good ; growth slow
Mandm		planted		+ ; short, few to hardly any	white or green color on sh and pt with distinct central band	trunk not big	sds sterile ; yld medium ; growth slow on dry ground, fast on wet ground
Ambutrum		planted		-	green color on sh and pt, sometimes with distinct central band, sometimes with small knobs at sh base	trunk big	sds sterile ; yld good ; growth slow
Koma-true		planted		-	black color on sh and pt	trunk not big	sds sterile ; yld low ; growth fast
Kaparang		planted		-	black color on sh and pt with distinct central band	trunk big	sds sterile ; yld good ; growth slow
Oliatagoe		planted		-	white color on sh and pt, with small knobs at sh base	trunk small	sds sterile ; yld low ; growth slow
Awirkoma		planted		-	white color on sh and pt, with small knobs at sh base	trunk small	sds sterile ; yld low ; growth slow
PNG, East Sepik Province ; area/social group: **Saniyo-Hiyowe** ; (nau = (more) domesticated ; yapai = wild, less domesticated) (TOWNSEND 1974:221, 2003)							**15**
Yapai		wild		+ ; long, many		some tall, some short at maturity	most common ; in poorly-drained areas ; lowest-ylding ; produces seeds
[Nau] Tavariyo		domesticated		+ ; long, not many (i.e. none on upper pt, widely spaced on base of pt)		very tall at maturity	in better-drained areas ; one of the two most commonly worked
[Nau] Piyarei		domesticated		+ ; short, not many		tall at maturity	
[Nau] Tarei		domesticated		+ ; short		short at maturity	one of the two most commonly worked
[Nau] Wa'aro		domesticated	big crown	+ ; short		short at maturity	

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
[Nau] Wopi		domesticated		+ ; short	lvs droop	short at maturity	like Tarei except for lvs
[Nau] Wourei		domesticated	small crown	+ ; short		fat trunk, short at maturity	
[Nau] Iyou		domesticated		+ ; long, many		short at maturity	
[Nau] Te'erei		domesticated		+ ; very short,many	pt erect	short at maturity	
[Nau] Meri		domesticated		+ ; short	pt erect	short at maturity	
[Nau] Sa'i Apou		domesticated		+ ; short		tall at maturity	
[Nau] Siye		domesticated		-		tall at maturity	rare
[Nau] Pavi Nau		domesticated		+ ; few		tall at maturity	rare
[Nau] Saperi		domesticated		-		short at maturity	rare
[Nau] Yapuwei		domesticated		+ ; short, few		very tall at maturity	rare
PNG, Gulf Province; area/social group: **Purari** delta, **Koravake** village, **Baroi**. (ULIJASZEK & PORAITUK 1983:583)							**12**
Havea		propagated		+		slender; tall on well drained soil	most used for starch
Pakeava		propagated		+		fat; tall on well drained soil	2nd most used for starch
Opai		propagated		+		medium girth; tall	4th most used for starch
Kauapa		propagated		+		medium girth; tall	3rd most used for starch
Kairi-kairi		propagated		+		medium girth; tall	
Aiameri		propagated		+		fat; short; fibres hard	difficult to process due to hard fibres
Kaivei		propagated		+		slender;medium height	
Avei		propagated		+			
Pirika		propagated		+			
Calai		propagated		+			
Bauma		propagated and wild		-		medium girth on well drained soil, fat on poorly drained soil; tall on well drained soil	5th most used for starch
Ikipa		propagated and wild		-		medium girth; short	
PNG, Middle Sepik ; area/social group: **Sawos** ; ('no' or 'nau' means 'sago'.). (SCHINDLBECK 1980:75-78,90-91)							**15**

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Nono				+			yld/m3 rank 2
Weno				+			yld/m3 rank 6
Mawakweno				+			
Ngikusetnau				+			rare; yld/m3 rank 7
Tepmangalano				+			rare; yld/m3 rank 8
Mbonono				+			rare; yld/m3 rank 11
Nokwalu		wild		+ ; many, extremely long		narrow, not very long	not used for starch; yld/m^3 rank 10
Kwasengak		wild		+ ; many, extremely long		narrow, not very long	only used for palm heart, grubs; yld/m^3 rank 13
Asano				+			yld/m^3 rank 1
Arinau				+			yld/m^3 rank 3
Tono				+			yld/m^3 rank 4
Wamasano				+			yld/m^3 rank 5
Walalino				+			rare; yld/m^3 rank 9
Mbareno				-			yld/m^3 rank 12; rare
Ngapalano				+			
PNG, Southern Highlands Province ; area/social group: **Foi**. (FRENCH 2006)							**34**
Honamo		planted				fat ; white starch	slow maturing ; best variety
Yora		planted	many suckers			fat ; tall ; tough bark/ fibres ; yellow starch	early maturing ; 2nd-best variety
Bisu		planted	many suckers	+ ; long		narrow ; brown starch	early maturing
Karu'u		planted		+ ; short		tough bark/fibres ; red starch	
Sau		planted		+ ; short	lt very thin, long	fat ; white starch	
Nei		planted		-		white starch	
Miare		planted				red starch	
Kagia		planted, sown		+ ; long		very tough bark/ fibres ; red starch	poor quality
Yugi		planted		+ ; long	lt long	very tough bark/ fibres ; yellow/red starch	

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Huubi		planted				fat ; white starch	
Wabari		planted				red starch	
Sesa'abo		planted		+ ; few		very tall; white starch	
Aburi		planted		+ ; short or medium			used for grubs
Kwe'eraro		planted				hard bark ; red starch	starch of good taste
Igiba		planted		+		red or white starch	
Gage		planted	like Kagia	+			
To		planted	like Kagia	+			
Bare		planted		+ ; medium			
Kenege		planted		+ ; "seasonal"		very large, tall	
So		planted			lt smooth		
Sgewi		planted	like coconut	-			
Koofe		planted	like Karu'u	+ ; short	pt/rc short		yield low
recorded without characteristics (all planted): Fana, Hebo, Ibutau, Fana'iu, Gininimu, Wasego, Enemano, Farabo, Ikina, Yamo, Hai, Gosega.							
PNG, West Sepik ; area/social group: **Abrau**. (KELM & KELM 1980:118-120)							**12**
Auraiye		partly planted, partly wild		-			
Tekoune		only planted					common
Reipe		only planted			very long lvs [=lts?]		
Kalme		wild and planted				long trunk	
Koro		wild and planted	vigorous growth		long lvs		common
Wamu.		wild and planted	very large		lvs and lts different from those of all others		
Ipomku		wild and planted	large; similar to Tekoune and Wamu				
Komki		wild and planted				large	
Iya Yumo		wild and planted	similar to coconut palm			very long trunk	
Warpe		only planted					rare

Name	Alleged bot. name and/or Ambon - W. Seram fv synonym	Cultivation status	Habit	Leaf characters		Trunk characters	Other characters
				spines	other		
Wanyamo		wild		+ ; long			only felled for rearing sago grubs
Pekrei						small	only felled for rearing sago grubs
PNG, West Sepik ; area/social group: **Kwieftim**. (KELM & KELM 1980:118-120)							**20**
Pautem, Arowam, Wofrou, Nowan, Kasi, Miteka, Ma'ip, Nitikna, Napan, Mar, Tuaitam, Iwonko, Amkuir, Koaro, Yan, Pasu Äknu, Mesäni, Sekir, Nakir, Mau'ur. [no characteristics given.]							

*) BECCARI listed the local names with the prefix 'Kil-' attached, as retained in his botanical variety names. Assuming that 'kil' means sago (HEYNE (1950:330) mentions 'Kèla' as a word for sago palm in Waru language), and comparing the names to other reports on local varieties in eastern Seram, I tentatively omitted the prefix 'kil' from all of BECCARI's local variety names.

**) papeda, lempeng: see Fig 7.1 .

***) gaba-gaba = petiole plus lower part of rachis, used dried and stripped of leaflets to construct walls, ceilings, and - because of its low bulk density when dry - rafts.

****) *jantung* stage = just before emergence of the 1st-order inflorescence branches. *****) *sirih buah* stage = 3rd-order inflorescence branches have emerged.

- Folk varieties of Hatusua village (West Seram, Maluku, Indonesia)

--Narrative

I interviewed probably the most experienced and observant sago processor in Hatusua village (see box below), although rivalries between families would probably prevent unanimous agreement on this among the villagers. I often asked him scraps of information while working with him in the sago forest. Twice I interviewed him more formally, the first time on thu20jul1989 when he was 48, the second time on tue22feb1994 when he was 52 using a questionnaire.

INFORMANT
Name: Josephus TUPAMAHU (alias: Pak Ce).
Residence: born and raised in Hatusua
Education: SD (Sekolah Dasar (Elementary School)), STN (Sekolah Teknik Negeri (State Technical School)).
Occupations: 50% sago processing, 25% carpentry, 25% sugar palm tapping, and a bit of fishing and looking after his garden plot (*kebon*).
Over 40 years of experience in sago processing.

--- 1st interview, 20jul1989

(In italics quotes from Mr Tupamahu's description in Ambonese Malay-flavoured Indonesian, followed between square brackets by my 'free hand' translation which may contain clarifying additions by me enclosed in round brackets.)

There are four main *jenis* [varieties] in Hatusua's sago forests: **Ihur**, **Tuni**, **Makanaru** and **Molat**.

On **Ihur**:
Tumbuhnya [Habit]: suckers stay close to mother trunk.
Suckers: young ones look like Tuni; they may be reddish (therefore, reddishness of suckers is not a distinguishing characteristic between Ihur and Tuni).
Trunk: *wa'ah paling tebal* [bark with outer fibre layer very thick/thickest].
Spines: *duri panjang* [spines long], *kemerah*^{2}*-an* [brownish].
Leaflet: thin, wide and long, with thin, long spinules on the margin; *tulang daun agak kecil* [leaflet midrib rather thin]; suitable for *atap* [thatch] as it is thin but strong, not breaking as easily when folded as Molat or Tuni.
Leaf: *dahan mengkilat* [petiole shiny], *ber-garis2 sedikit* [a bit striped]; in young palm (5 metre), leaves look like Tuni; when older, *pelepah agak putih-kemerah2-an* [sheaths are somewhat reddish-white]; when the palm is about *masak tebang* [fell-/harvest-ripe], the sheaths are not as white as of the other varieties.
Fruits: *buahnya jarang* [fruits seldom/sparsely].
Tepung [Starch]: *kalau diolah warnanya merah* [reddishly coloured when processed]; settles quicker than Tuni; *serat banyak* [many fibres].
Yield: *hasil banyak* [yield is high]; *sirih buah, isinya tetap vol* [at 3rd-order inflorescence branches are out, the (trunk's) content is still at its maximum]; when only 2-3 leaves are left on the tree, yield is past its maximum.

On **Tuni**:

Tumbuhnya [Habit]: *seperti Ihur, tapi kadang^2 merayap sampai 1 m dari pohon induk* [as Ihur, but sometimes (suckers) creep up to 1 m from the mother tree].

Trunk: *wa'ah nomor 2 tebalnya setelah Ihur* [bark with outer fibre layer 2nd thickest after Ihur].

Spines: long when the tree is small (sucker), short when the tree is larger; somewhat whitish; *duri pelepah sangat pendek* [spines on the leaf sheath (in trunked palms) very short].

Daun [Leaflet]: *agak pendek, tapi lebar* [rather short, but wide], *tebal* [thick] ; *duri tepi daun pendek* [spines on the leaflet margin short] ; *tulang daun* [leaflet midrib] thicker than in Ihur.

Leaf: towards harvest-ripeness of the trunk *pelepah semuanya putih* [sheaths all/totally white], *dahan licin, mengkilat kebiru^2-an* [petioles smooth, blueish-shiny].

Fruits: *buah jarang didapat* [fruits seldom found].

Tepung [Starch]: *mulai diambil, merah juga* [upon extraction it is also reddish]; *kalau diolah untuk makanan, dia jadi putih* [when processed into food, it turns white]; many fibres, a little less than Ihur.

Yield: *hasil tepung banyak* [starch yield is high]; *kalau sudah sirih buah, isinya separuh hanyut* [when the 3rd-order inflorescence branches are out, the (trunk's) content is half-gone]; yield is at its maximum when *jaga sudah pendek, belum bunting* [the leaves are getting shorter, before pregnancy (i.e. before the inflorescence is going to emerge)].

On **Makanaru**:

Ada dua jenis: Duri Hitam dan Duri Putih [There are two (sub-)varieties: Duri Hitam (Black Spine) and Duri Putih (White Spine)].

Habit: the way the suckers grow is as in Ihur.

Trunk: *wa'ah tipis* [bark with outer fibre layer thin].

Spines: *dari kecil durinya panjang sampai waktu masak tebang* [spines are long from the time (the tree) is small until it is fell-/harvest-ripe]; *pelepah* [leaf sheath (in trunked palm)]: *durinya kemerah-hitam* [spines reddish-black] (variety Duri Hitam) or *duri tetap putih* [spines always white] (variety Duri Putih).

Daun [Leaflet]: long but narrow; *duri tepi daun sama dengan Ihur* [spines along the margin the same as in Ihur]; *tulang kecil, lebih kecil dari Ihur* [midrib thin, thinner than in Ihur].

Leaf: *dahan seperti Ihur* [petiole as in Ihur]: *bergaris* [striped], *berbintik-bintik merah atau hitam* [with red/brown or black spots]; petiole *agak kecil dari Ihur* [a bit thinner than in Ihur], and *waktu kecil* [when (the tree is) young (i.e. in late establishment phase)] very long.

Fruits: *buahnya biasanya banyak, dan banyak bertumbuh* [there are usually many fruits, and many of them sprout].

Tepung [Starch]: *warna, ada sedikit mau kuning* [the colour is a bit towards yellow], *tapi putih lagi kalau diolah seterusnya* [but turns white again when it is processed completely]; fibres as in Ihur.

Yield: *kurang hasil* [yield is low]; Duri Hitam yields more than Duri Putih.

On **Molat**:

Ada dua jenis: Molat Berduri dan Molat Tidak Berduri [There are two (sub-)varieties: Molat Berduri (Spined Molat) and Molat Tidak Berduri (Unspined Molat)].

Habit: in Molat Berduri, *pertumbuhanya anakan bisa sampai tiga meter dari pohon induk* [suckers can grow up to three meters from the mother tree].

Trunk: *wa'ah tipis* [bark with outer fibre layer thin].

Spines (Molat Berduri only): *agak hitam* [blackish], few, short.

Daun [Leaflet]: *pada umumnya daunnya tebal* [generally, the leaflet is thick]; *tulang daun besar* [leaflet midrib thick]; *tepi daun seperti syilet* [leaflet margin as a gilette (razor blade)], *licin, tapi pada daun di ujungnya* [smooth, but on leaflets at the tip (of the leaf)] *tepi daun berduri juga* [the leaflet margin is also spined].

Leaf: *pelepah* [leaf sheath (in trunked palm)]: *pada waktu masak tebang putih* [white by the time (the trunk is) fell-/harvest-ripe], hence *istilah putih masak* [the term 'putih masak' (ripe

white)], in Molat Berduri, *dari kecil, warna hijau* [from/when young [?], green], *dan pada belakang warna hitam dimana tempat duri* [and on the back (abaxial) side black where the spines are attached].
Fruits: *buahnya sering ada, tapi sukar bertumbuh* [there are often fruits, but they sprout with difficulty].
Tepung [Starch]: *kalau diolah, warnanya putih, biar lama* [when processed white, even after a long time]; *serat kurang* [few fibres];
Yield: *kalau sudah sirih buah* [when the 3rd-order inflorescence branches are already out], *lebih kosong lagi daripada Tuni* [(the trunk is) even emptier than Tuni], yielding e.g. 20 *tumang* [basket made of green leaflets] instead of 40.

--- 2nd interview, 22feb1994

Generic names for sago palm:
Pohon sagu (Language: Ambon Malay) ; Pia (Language: Alune (West Seram))
Varieties known in this area:
Ihur, **Tuni**, **Molat Licin**, **Molat Duri Putih**, **Molat Duri Merah**, **Makanaru Duri Putih**, **Makanaru Duri Hitam**.
Spines
ranking according to spine features at spiniest stage (usually S3 to early trunk stage):
* spine length (long → short): Ihur→Makanaru→Tuni→Molat Duri→Molat Licin (no spines)
* density of spine combs (dense → sparse): dito

Trunk
ranking according to
* trunk width (wide → narrow): Tuni→Molat→Ihur→Makanaru.
* trunk height (tall → short): Ihur→Makanaru→Tuni→Molat.
* bark thickness (thick → thin): Ihur→Tuni→Makanaru→Molat.
* internode length (long → short): Tuni→Ihur→Makanaru→Molat.

Leaves (at adult vegetative phase of the palm)
ranking according to
* width of leaf base (wide → narrow): Tuni→Molat→Ihur→Makanaru.
* length of petiole/rachis (long → short): Ihur/Makanaru→Tuni→Molat.
* size of leaflets (large → small): Ihur/Tuni→Molat→Makanaru.
  varieties with drooping leaflet tips?: Ihur.
* whiteness of leaf base / petiole (whitest → ....):
  Tuni→Molat ; somewhat reddish in Ihur and Makanaru.
* suitability of leaflets for making thatch (high → low): Tuni→Ihur→Makanaru→Molat.
  reasons: thatch from Tuni and Ihur is more durable than that from the other two; Tuni thatch is easier to make than Ihur thatch, because the leaflet midribs of Tuni can be broken much easier when dry than those of Ihur, and Ihur leaflets are full of little spines.
* suitability of petiole/rachis for use as walling material (high → low):
  Ihur→Makanaru→Tuni/Molat.
  reasons: durability: Tuni and Molat petioles are unsuitable because the pith of the petioles easily rots.

Inflorescence
ranking according to
* ability to fruit (high → low): Makanaru→Molat→Ihur/Tuni.
* the number of fruits per inflorescence (high → low): Makanaru→others.

Timing of harvest
ranking according to
* period until harvestability (short → long): Tuni/Molat→Ihur→Makanaru.
* development stage with maximum yield (early stage → late stage):

Tuni/Molat : *bunting* stage (inflorescence about to emerge).
Ihur/Makanaru : *sirih buah merah* stage (3rd-order inflorescence branches showing reddish flower buds).

Pith
ranking according to
- * starch yield (high → low (quantity indication of wet starch yield, e.g. in *tumang* [basket made of green leaflets] (here, 1 *tumang* = c.12 kg)):
  Tuni (80 *tumang*)→Molat (70 *tumang*)→Ihur (50 *tumang*)→Makanaru (30 *tumang*).
- * pith colour (white → red): Molat→Tuni→Makanaru→Ihur.
- * starch colour (white → red): Molat→Tuni→Makanaru→Ihur.
- * starch fineness (fine → coarse): no differences.
- * storability of wet starch (good → bad): Molat→Tuni→Ihur/Makanaru.
- * ease of processing (easy → difficult): Molat/Tuni→Makanaru/Ihur.
  reasons: the pith of Makanaru and Ihur is very fibrous ("*banyak serat*").

Are there any variety preferences for specific uses of the starch? Yes:
for *sagu lempeng* (see Fig.7.1.): Ihur and Makanaru, because with the starch of these the *sagu lempeng* is done more quickly ("*cepat masak, cepat merah*" [quickly done, quickly reddish]).
for *papeda* : Molat/Tuni, because *papeda* made from their starch is tastier than that from Ihur starch. Using Ihur starch sometimes results in a bland tasting *papeda* ("*kadang-kadang rasa tawar*").

Suckering habit
ranking according to
- * tendency to form aerial suckers (strong → weak): Tuni/Molat→Ihur→Makanaru.

Combination of characteristics
- Planting: If you had an empty piece of land suitable for sago palm to grow on, which sago palm variety would you plant? (most wanted → least wanted):
  most wanted: Tuni/Molat.
  reasons: they grow quickly and they are the least spiny.
- Harvesting: If you go out into the forest to harvest a tree, which variety would you prefer to harvest? (most wanted → least wanted):
  Tuni/Molat→Ihur→Makanaru.
  reasons: yield.
  Are there any circumstances which would modify your preference?:
  Hardly. Also when there is a harvestable Ihur right near water, I would still prefer to process a Tuni/Molat further away.
- Uses: Are there any other varieties which you
  - * use only for specific purposes (e.g. rearing grubs)?:
    No. Grubs just develop quicker in a Tuni or Molat than in an Ihur or Makanaru, because the former have more starch and less fibre.
  - * use not at all?: No.

Pests and diseases: What do you know about pests and diseases?:
wild pig, '*kumbang*' [probably Rhinoceros beetle], Sexava.
Any ranking of varieties according to susceptibility to any of these?:
No. Wild pig just prefers the young shoots of the less spiny varieties.

All oral information on Hatusua folk varieties is sumarized in Table 5.2.
A similar extensive overview of the varieties recognised in Siri Sori Serani village, Saparua Island, where I sampled one variety, viz. Sagu Putih, was not made. See for the little information I did gather Table 5.1 under Indonesia, Maluku, Saparua. The variety Sagu Putih was considered to by synonymous to the variety Tuni.

Table 5.2 Folk varieties of sago palm as recognised in Hatusua (West Seram, Maluku, Indonesia) and their characteristics.
= rank number (highest/biggest/best to lowest/smallest/worst)

Name			Habit	Spines	Leaf	Leaflet	Trunk	Pith/Starch	Yield	Other characters
Ihur			skrs stay close to mother palm.	length #1, long, reddish/ brownish; comb*** density #1.	sh reddish-white in mid-AV, less white than others in G; pt shiny, striped; suitability for *gaba-gaba** #1.	bl size #1/2, wide, long, thin; w/ drooping tip; margin w/ long spinules; midrib thin, but not easily breaking when dry; suitability for thatch #2.	diameter #3; *wa'ah*** thickness #1; int length #2; max height #1.	pith and starch reddish; starch settles quicker than in Tuni; fibres many; storability wet starch #3/4.	#3, high; max in late G2; less when 2-3 lvs left on trunk.	seldom fruiting; time till harvest #3.
Tuni			skrs may creep up to 1 m away from mother palm.	length #3, long in E, short later, very short on sh in AV; whitish; comb density #3.	sh in G white; pt in G smooth, bluish-shiny; suitability for *gaba-gaba* #3/4.	bl size #1/2, wide, rather short, thick; margin w/ short spinules; midrib thicker than Ihur; suitability for thatch #1.	diameter #1; *wa'ah* thickness #2; int length #1; max height #3.	pith and starch reddish; starch after processing white; fibres many, less than in Ihur and Makanaru; storability wet starch #2.	#1, high; max in early G1, half-gone in G2.	seldom fruiting; time till harvest #2.
Molat	**Molat Licin**			no spines	sh white in G, in Molat Berduri green in E and AV w/ black spots where spi are attached; suitability for *gaba-gaba* #3/4.	bl size #3, thick; margin razor-sharp, smooth, tip w/ spinules; midrib thick; suitability for thatch #4.	diameter #2; *wa'ah* thickness #4; int length #4; max height #4.	pith white; starch white, even after long time; fibres few; storability wet starch #1.	#2, high; max in early G1, more than half-gone in G2.	often fruiting, frs seldom with viable sds; time till harvest #1 (shortest).
	Molat Berduri	**Molat Duri Putih**	skrs may creep up to 3 m away from mother palm.	length #4, short, few; slightly blackish in Duri Putih; comb density #4.						
		Molat Duri Merah								
Makanaru	**Makanaru Duri Hitam** a.k.a. **Duri Rotan**		skrs stay close to mother palm.	length #2, long E thru G; on sh in AV reddish-black; comb density #2.	sh bit reddish-white; pt shiny, striped, w/ reddish-brown or black spots, bit thinner than in Ihur, very long in late E; suitability for *gaba-gaba* #2.	bl size#4, narrow, long; margin w/ long spinules; midrib thinner than Ihur; suitability for thatch #3.	diameter #4; *wa'ah* thickness #3; int length #3; max height #2.	pith and starch yellowish- white; starch white when processed; fibres many; storability wet starch #3/4.	#4, low; max in late G2; higher in Duri Hitam than in Duri Putih.	often fruiting, frs often with viable sds; most frs per inflorescence; time till harvest #4.
	Makanaru Duri Putih			length #2, long E thru G; white; comb density #2.						

Variety name glossary: berduri = spined, duri = spine, hitam = black, licin = smooth, merah = red/brown, putih = white, rotan(g) = rattan, tuni = true.
Abbreviations: bl = blade (of leaflet) ; fr(s) = fruit(s) ; int = internode ; lf = leaf ; lvs = leaves ; lt(s) = leaflet(s) ; max = maximum ; pt = petiole ; rc = rachis ; sd(s) = seed(s) ; sh = sheath(s)/base(s) (of leaf) ; spi = spine(s) ; skr(s) = sucker(s) (S1 = sucker with overall height not exceeding 1.2 m ; S2 = sucker with leaves between 1.2 and 4 m long ; S3 = sucker with leaves longer than 4 m) ; w/ = with.
Development phases: E = Establishment phase ; AV = Adult Vegetative phase ; G1, G2, G3 = Generative phases 1,2,3 (see definitions in Chapter 4).
* gaba-gaba = petiole plus lower part of rachis, used dried and stripped of leaflets to construct walls, ceilings, and - because of its low bulk density when dry - rafts.
** wa'ah = outer trunk layer incl. adjacent fibre layer. *** comb = transverse series of spines.

- Own observations on differences between the folk varieties Ihur, Tuni and Molat

The folk varieties in the Hatusua area of which I studied the starch accumulation were Ihur, Tuni and two sub-varieties of Molat. The differences between these varieties were obvious to the experienced sago palm harvesters, but most of the claimed differences excaped me even

Table 5.3 Dry matter (DM) content of whole leaflets and specific area weight of the lamina of three folk varieties of sago palm (Molat, Tuni and Ihur) in Hatusua village, West Seram.
Leaflets were taken from palms of which the leaf unfolding rate (LUR) was monitored. Information on each individual palm is presented in Appendix C.

Molat				Tuni				Ihur			
Leaflet (LUR# - replicate)	DM content of whole leaflet (g/g)	weight (g) of standard lamina area of		Leaflet (LUR# - replicate)	DM content of whole leaflet (g/g)	weight (g) of standard lamina area of 48.7 cm^2		Leaflet (LUR# - replicate)	DM content of whole leaflet (g/g)	weight (g) of standard lamina area of 48.7 cm^2	
		fresh	dry *			fresh	dry *			fresh	dry *
01-I	0.4554	1.40	0.63	06-I	0.4852	-	-	02-I	0.4123	1.46	0.60
-II	-	1.44	0.63	-II	0.4880	-	-	-II	0.4096	1.47	0.58
-III	0.4563	1.40	0.64	07-I	0.4556	-	-	-III	0.4277	1.53	0.61
-IV	0.4322	1.36	0.57	-II	0.4550	-	-	03-I	0.4713	1.47	0.66
12-I	0.4624	1.38	0.64	09-I	0.4575	-	-	-II	0.4235	1.36	0.55
-II	0.4573	1.38	0.64	-II	0.4585	-	-	04-I	0.4534	-	-
13-I	0.3801	-	-	10-I	0.4623	-	-	-II	0.4558	-	-
-II	0.3827	-	-	-II	0.4680	-	-	05-I	0.5043	-	-
14-I	0.4182	-	-	11-I	0.4573	1.39	0.60	-II	0.5080	-	-
-II	0.3944	-	-	-II	0.4532	1.37	0.63	20-I	0.4382	1.30	0.55
15-I	0.4276	1.27	0.55	17-I	0.4759	-	-	-II	0.4444	1.29	0.56
-II	0.3861	-	-	22-I	0.4118	-	-	-III	0.4627	1.30	0.59
16-I	0.4397	-	-	-II	0.4039	-	-	21-I	-	1.37	0.61
-II	0.4436	1.40	0.62	23-I	0.4294	-	-	-II	0.4651	1.36	0.61
18-I	0.4474	1.34	0.59	-II	0.4292	-	-	29-I	0.4621	1.16	0.54
-II	-	1.25	0.53	24-I	0.4159	-	-	-II	0.4464	1.18	0.52
-III	-	1.29	0.53	-II	0.4211	-	-	30-I	0.4388	1.26	0.54
-IV	0.4340	1.29	0.54	-III	0.4017	-	-	-II	0.4422	1.21	0.53
-V	0.4469	-	-	25-I	0.4413	1.21	0.52	31-I	0.4252	-	-
19-I	0.4365	1.30	0.55	-II	0.4203	1.22	0.50	-II	0.4399	-	-
-II	0.4346	1.28	0.52	26-I	0.4176	1.29	0.51	32-I	0.4436	-	-
27-I	0.4020	-	-	-II	0.4340	1.37	0.59	-II	0.4347	-	-
-II	0.4310	-	-								
28-I	0.4243	-	-								
-II	0.4352	-	-								
-III	0.4392	-	-								
Mean	0.4290	1.34	0.58	Mean	0.4429	1.31	0.56	Mean	0.4481	1.34	0.575

* dried to constant weight at 115 ˚C.

** 10 leaf blade punches punched out with the pith auger which has an inner diameter of 2.49 cm: $10 \times \pi \times (2.49/2)^2 = 48.7$ cm^2 .

\- = not recorded.

after a few years of working with these varieties. One of the claimed differences between the leaves of these varieties was that the leaflets of Ihur were thinner than of Tuni and Molat (together with differences in durability and ease with which the midrib could be broken causing differences in suitability for use as thatch). What I could see myself was that the leaves of Ihur look somewhat scragglier than of Tuni and Molat, that the leaflet tips are drooping in Ihur and straight in Tuni and Molat (and that the upper surface of Ihur leaflets is clearly darker green than of Tuni and Molat leaflets). To see if I could substantiate these claims and quantify the observed differences, differences in thickness/stiffness of leaflets were investigated indirectly by measuring dry matter (DM) content of leaflets and specific area weight of the lamina. The observations and their statistical analysis are presented in Table 5.3, Table 5.4 and the ANOVA tables following them.

Table 5.4 Summary of Table 5.3

	Molat	Tuni	Ihur
Mean leaflet dry matter content (g/g)	0.4290 (n=23, sd=0.0244)	0.4429 (n=22, sd=0.0258)	0.4481 (n=21, sd=0.0254)
Mean lamina fresh weight (g) per 48.7 cm^2 *	1.34 (n=14, sd=0.060)	1.31 (n=6, sd=0.080)	1.34 (n=14, sd=0.115)
Mean lamina dry weight (g) per 48.7 cm^2 *	0.58 (n=14, sd=0.048)	0.56 (n=6, sd=0.055)	0.575 (n=14, sd=0.040)

n = number of observations , sd = standard deviation.

* 10 leaf blade punches punched out with the pith auger which has an inner diameter of 2.49 cm: $10 \times \pi \times (2.49/2)^2 = 48.7\ cm^2$.

Analysis of variance of leaflet DM content in three folk varieties of sago palm (data of Table 5.3).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Observed *F*	Tabular *F*	
					5%	1%
Variety	2	0.0043	0.0022	3.67*	3.14	4.96
Error	63	0.0399	0.0006			
Total	65	0.0442				

cv = 5.6% , * = significant at 5% level.

Comparing differences between DM means with Least Significant Differences:

- DM mean Molat: 0.4290 , DM mean Tuni: 0.4429. Difference: 0.0139.
  $LSD_{.05} = 0.0146$. $LSD_{.01} = 0.0253$.
  Conclusion: The DM contents of leaflets of Molat and Tuni are not significantly different.
- DM mean Molat: 0.4290 , DM mean Ihur: 0.4481. Difference: 0.0191.
  $LSD_{.05} = 0.0148$. $LSD_{.01} = 0.0256$.
  Conclusion: The DM contents of leaflets of Molat and Ihur are significantly different at the 5% confidence level.
- DM mean Tuni: 0.4429 , DM mean Ihur: 0.4481. Difference: 0.0052.
  $LSD_{.05} = 0.0150$. $LSD_{.01} = 0.0260$
  Conclusion: The DM contents of leaflets of Tuni and Ihur are not significantly different.

Analysis of variance of the specific area fresh weight of the lamina in three folk varieties of sago palm (data of Table 5.3).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Observed *F*	Tabular *F*	
					5%	1%
Variety	2	0.0049	0.0025	0.31 ns	3.31	5.36
Error	31	0.2525	0.0081			
Total	33	0.2574				

cv = 6.8% , ns = not significant.

Analysis of variance of the specific area dry weight of the lamina in three folk varieties of sago palm (data of Table 5.3).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Observed *F*	Tabular *F*	
					5%	1%
Variety	2	0.0028	0.0014	0.67 ns	3.31	5.36
Error	31	0.0652	0.0021			
Total	33	0.0680				

cv = 8.0% , ns = not significant.

The measured leaflets were not taken each from a different tree: one to four leaflets were taken from the same tree (Roman numerals in the leaflet numbers in Table 5.3). Leaflets from the same tree are most probably not as different as leaflets from different trees. In short: there must be some violation of randomness in the sampling. Randomness is probably better served by taking the average value per tree as a single observation, rather than that of each leaflet separately. The observation data grouped in this manner and their analysis are presented in Table 5.5 and the the ANOVA tables following it.

Table 5.5 Dry matter (DM) content of whole leaflets and specific area weight of the lamina of three folk varieties of sago palm (Molat, Tuni and Ihur) in Hatusua village, West Seram.
Leaflets were taken from palms of which the leaf unfolding rate (LUR) was monitored. Information on each individual palm is presented in Appendix C.

Molat				Tuni				Ihur			
Leaflets from palm # ...	Mean DM content of whole leaflet (g/g)	Mean weight (g) of standard lamina area of 48.7 cm^2 **		Leaflets from Palm # ...	Mean DM content of whole leaflet (g/g)	Mean weight (g) of standard lamina area of 48.7 cm^2 **		Leaflets from Palm # ...	Mean DM content of whole leaflet (g/g)	Mean weight (g) of standard lamina area of 48.7 cm^2 **	
		fresh	dry *			fresh	dry *			fresh	dry *
LUR-01	0.4480	1.40	0.62	LUR-06	0.4866	-	-	LUR-02	0.4165	1.49	0.60
LUR-12	0.4599	1.38	0.64	LUR-07	0.4553	-	-	LUR-03	0.4474	1.42	0.61
LUR-13	0.3814	-	-	LUR-09	0.4580	-	-	LUR-04	0.4546	-	-
LUR-14	0.4063	-	-	LUR-10	0.4652	-	-	LUR-05	0.5062	-	-
LUR-15	0.4069	1.27	0.55	LUR-11	0.4553	1.38	0.62	LUR-20	0.4484	1.30	0.57
LUR-16	0.4417	1.40	0.62	LUR-17	0.4759	-	-	LUR-21	0.4651	1.37	0.61
LUR-18	0.4428	1.29	0.55	LUR-22	0.4079	-	-	LUR-29	0.4543	1.17	0.53
LUR-19	0.4356	1.29	0.54	LUR-23	0.4293	-	-	LUR-30	0.4405	1.24	0.54
LUR-27	0.4165	-	-	LUR-24	0.4129	-	-	LUR-31	0.4326	-	-
LUR-28	0.4329	-	-	LUR-25	0.4308	1.22	0.51	LUR-32	0.4392	-	-
				LUR-26	0.4258	1.33	0.55				
Mean (sd)	0.4272 (0.0239)	1.34 (0.061)	0.59 (0.045)	Mean (sd)	0.4457 (0.0259)	1.31 (0.082)	0.56 (0.056)	Mean (sd)	0.4505 (0.0237)	1.33 (0.118)	0.58 (0.036)

* dried to constant weight at 115 ˚C.
** 10 leaf blade punches punched out with the pith auger which has an inner diameter of 2.49 cm: $10 \times \pi \times (2.49/2)^2 = 48.7\ cm^2$.
- = not recorded , sd = standard deviation.

Analysis of variance of leaflet DM content in three folk varieties of sago palm (data of Table 5.5).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Observed *F*	Tabular *F*	
					5%	1%
Variety	2	0.0030	0.0015	2.50 ns	3.34	5.45
Error	28	0.0169	0.0006			
Total	30	0.0199				

cv = 5.6% ,   ns = not significant.

Analysis of variance of the specific area fesh weight of the lamina in three folk varieties of sago palm (data of Table 5.5).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Observed *F*	Tabular *F*	
					5%	1%
Variety	2	0.0016	0.0008	0.094 ns	3.88	6.93
Error	12	0.1020	0.0085			
Total	14	0.1036				

cv = 6.9% ,   ns = not significant.

Analysis of variance of the specific area dry weight of the lamina in three folk varieties of sago palm (data of Table 5.5).

Source of variation	Degrees of freedom	Sum of squares	Mean square	Observed *F*	Tabular *F*	
					5%	1%
Variety	2	0.0014	0.0007	0.37 ns	3.88	6.93
Error	12	0.0225	0.0019			
Total	14	0.0239				

cv = 4.6% ,   ns = not significant.

From the analysis of the data may be concluded that the investigated leaflet characters are not different in the 3 folk varieties Molat, Tuni and Ihur, except for the dry matter content of leaflets which appears to be higher in "Ihur" than in "Molat". And even of this difference the statistical significance disappears when average values per tree are taken as replications rather than the values of each individual leaflet sampled (as indeed we could, since differences between trees were investigated rather than between leaflets).

Growing circumstances (e.g. degree of shadedness) of the palms sampled were probably so different that they masked variety differences in leaf characters. A study in a population with more equal growing conditions and/or with more samples per variety is needed to make a more definite statements about leaflet DM content and weight per area.

5.4 Analysis : comparing value ranges of folk variety characteristics

To see whether the varieties I studied were average or special, a list of variety characteristics could be drawn up and for each character the range and the mean of values as found among all the known varieties could be compared with the values of the varieties I studied. Candidate characters for comparison should have values which are not much influenced by the environment or by the vigour of the individual plant to avoid confounding phenotypical variation and varietal (genetic) variation. The presence or absence of spines on leaves - especially on the clearly visible petioles (Fig. 5.1) - and bracts (Fig. 5.2) appears to be universally used as a first and fail-safe criterion to discriminate between varieties. And indeed, this character is not influenced by the environment. The second most-used criterion is spine

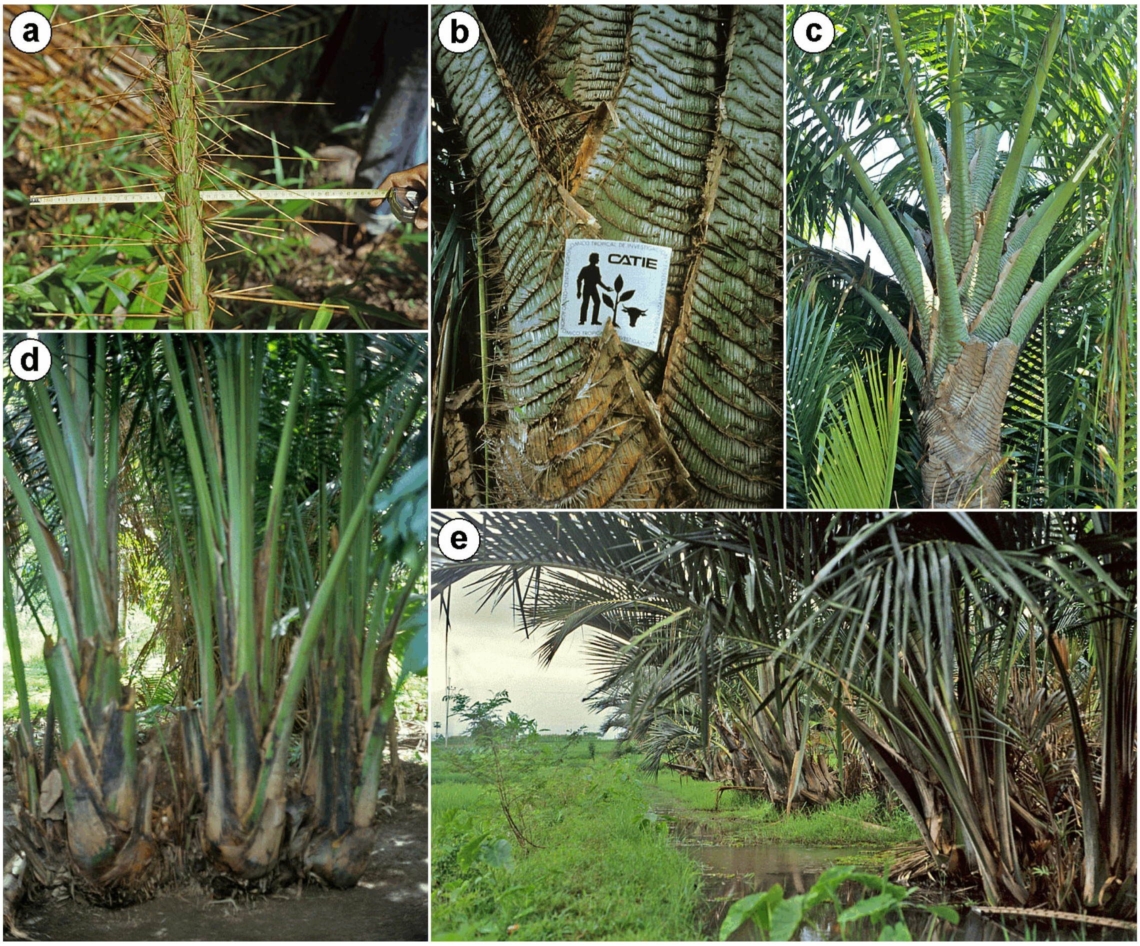

Figure 5.1 Spinescence of leaves in sago palm.

a: Detail of the petiole of a more-than-5-m-long sucker leaf of fv. Kla (Duriankari, Salawati) at 1 m above its base, showing spines of up to 20 cm long.

b: Leaf bases of a sago palm in the early AV-phase, showing closely spaced spine combs, the spines getting shorter as they are further from the base (trial in Costa Rica, variety unknown).

c: Base of crown of fv. Tuni (Hatusua, W.Seram), showing leaf bases and petioles with transverse ridges of short spines.

d: Clump of the spineless fv. Senaf (Tanjung Kasuari, Sorong), showing bases of large suckers.

e: Plantation with spineless palms, showing clumps with many suckers (trial in W. Java, Indonesia, variety unknown).

[a: photo nr.92.02-213-23, Salawati Island, Sorong, Papua, Indonesia 07feb1992. b: photo by Henk WAAIJENBERG, Guápiles, Zona Atlantica, Costa Rica, ca.1993. c: photo nr.90.11-148-19, Hatusua, W.Seram, Maluku, Indonesia 17nov1990. d: photo nr.92.02-212-23, Tanjung Kasuari, Sorong, Papua, Indonesia 08feb1992. e: photo nr.92.01-205-08, Balumbang Jaya, Bogor, West Java, Indonesia 23jan1992.]

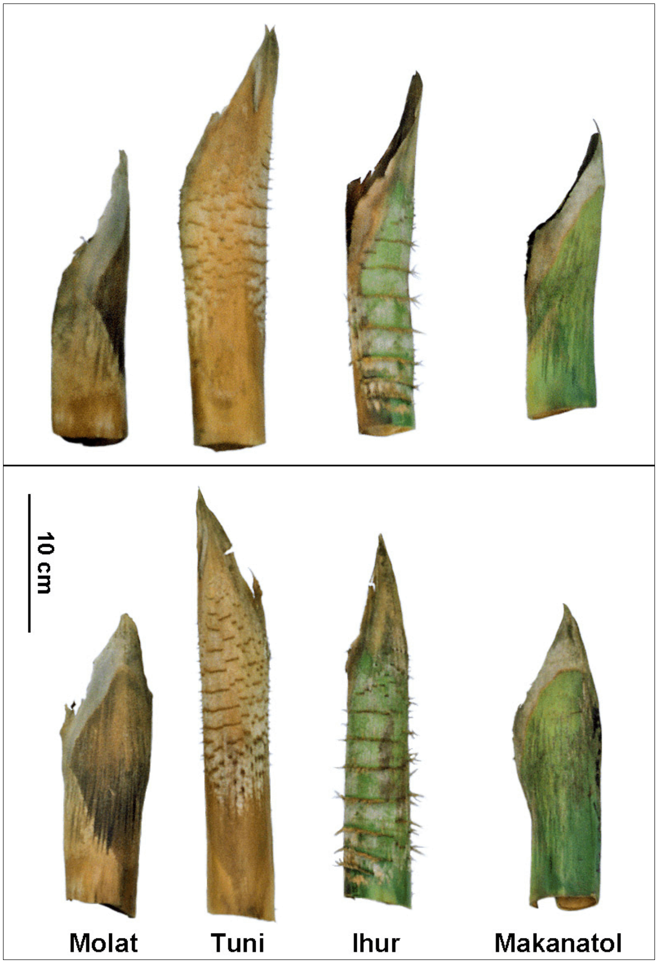

Figure 5.2 Spinescence of bracts in sago palm : second-order bracts from the inflorescences of the folk varieties Molat (Hatusua, W.Seram), Tuni (Hatusua, W.Seram), Ihur (Hatusua, W.Seram) and Makanatol (Siri Sori, Saparua), in side view (top row) and in near-dorsal view.
[photo nr.90.11-148-10 (top) and nr.90.11-148-11, 13nov1990]

length. This character is dependent on the development phase of the palm. Usually, spines on petioles are longer in the establishment phase of the palm than when it is in a later phase. Thus, petioles on suckers are usually more spiny than petioles higher up on their mother palm. The colour of the pith seems to be a criterion not influenced by either the environment or the development phase. Other criteria seem less constant, as their expressions are probably more dependent on external factors. The failed verification of claimed varietal differences in the leaflet blade could well have been attributable to light conditions preventing the expression of these differences. Other cases in point are yield level, trunk width, maximum trunk height, or any other character that may vary with plant vigour. Varieties may surely differ in potential growth, but characters depending on growth are less suitable as defining feature for varieties, unless used in combination with an indication of the growing conditions for which the criterion is valid. Also the economically interesting life cycle duration is a characteristic which much depends on growing circumstances. A related, but probably more constant characteristic is the number of nodes formed in a trunk before the first node with an inflorescence branch appears. For the varieties Tuni and Ihur which I studied, I found averages of 147 and 124 nodes, respectively (see Table 4.3). Unfortunately this characteristic was not mentioned by others in the description of folk varieties elsewhere.

The more intimate one gets with a sago-using community, the more indeed one gets to know the conditions under which variety characters are valid. Also, one gets to know more sub-varieties. E.g., the fv. Molat (Hatusua, W.Seram) was generally known as an unspined variety, but on second thought also had a spined form, which upon further inquiry could even be split up into two different forms again, one with whitish spines and one with reddish spines. Characters became fuzzier ('unspined' became 'mostly unspined') and the variety lost definition, an indication, by the way, that this folk variety Molat cannot be a single-clone variety.
It is not all fuzziness, however: the same varieties that were distinguished in the West-Seram area in the second half of the 17th century (RUMPHIUS 1750 (1741)) are still the ones recognised there 300 years later. And of these, variety Tuni is still considered to be the best variety for thatch, variety Ihur is still said to have the tallest trunk, and varieties Molat and Tuni should still be harvested at an earlier stage to obtain maximum yield than the other varieties.

In the description of folk varieties recognised in Hatusua and elsewhere, regrettably most of the characters reported on are not quantified, making meaningful comparison difficult. Moreover, different reports often use different characters to describe varieties. Here comes home to roost the fact that variety comparison was not envisaged from the beginning of my studies, its importance rather being discovered during the data processing phase.
In spite of this, and keeping the real and potential 'softness' of the data in mind, a comparison should still be made. For this the characteristics of the folk varieties recognised in Hatusua (H-fvs) as entered in Table 5.2 are used as a checklist and the characteristics that are used for both these H-fvs and for any of the other folk varieties (o-fvs) are selected. The position of the H-fvs among the o-fvs can than be evaluated by comparing the - mostly qualitative or relative - values for these characteristic.

- Spines
    - length:
        - H-fvs: long, short.
        - o-fvs: traces only; very short; short; moderately short; moderate; intermediate; medium; long; very long; extremely long; short or medium; short to long; 1 cm; 1-2 cm; 2 cm; 4 cm; 5 cm; 5-6 cm; 10 cm; 15 cm; up to 20 cm.
    - abundance/density:
        - H-fvs: spineless; spined; few.
        - o-fvs: spineless; practically spineless; spined; few to hardly any; few; not too many; not many; many; dense; close combs; in clusters; bunched closely together; widely spaced; sprouting from single base.
- Leaf
    - sheath/leaf base colour:
        - H-fvs: reddish-white in mid AV-phase; white in G-phase; green with black spots in E- and AV-phase; bit reddish-white.
        - o-fvs: bluish in G-phase; black; white; green; white or green.
    - petiole colour:
        - H-fvs: shiny and striped; bluish-shiny in G-phase; shiny and striped with reddish-brown or black spots.
        - o-fvs: with distinct central band; green band on back in E-phase; with greenish central band; brown band on back in E-phase; black band on back in E-phase; yellowish-green; intensely green; greenish-grey; grayish; gray; black; white; green; white or green.
- Leaflet
    - blade size and thickness:
        - H-fvs: narrow; wide; rather short; long; thin; thick.
        - o-fvs: long; very thin; 4-5 fingers wide; 4.5 ft long;
    - erectness:
        - H-fvs: with drooping tip.
        - o-fvs: tip upright; tip drooping; drooping; stiff.
    - margin:
        - H-fvs: smooth and razorsharp with spinules on tip; with short spinules; with long spinules.
        - o-fvs: fine spiny.
- Trunk
    - diameter:
        - H-fvs: (ranking only).
        - o-fvs: slender; narrow; thin; not big; medium; wide; fat; big; 39 cm; 40 cm; 44 cm; 49 cm; 51 cm; 65 cm.
    - *wa'ah* thickness:

    H-fvs: (ranking only).
    o-fvs: thin; thick; soft; hard; extremely hard; 1 cm; 1-1.5 cm; 1.5 cm; 2 cm.
  - ◦ internode length:
    H-fvs: (ranking only).
    o-fvs: long as in rattan palm.
  - ◦ height:
    H-fvs: (ranking for maximum height only).
    o-fvs: small; short at maturity; not big; medium; not very long; long; big; tall at maturity; very long; very tall at maturity; some short and some tall at matuity; up to 7 'vadem' long; up to 10 'vadem' long;
- Pith/Starch:
  - ◦ colour:
    H-fvs: brown; red; reddish; reddish but after processing white; red or white; yellow/red; yellow; yellowish-white but after processing; dirty; white; white.
    o-fvs: red; reddish; often reddish; pinkish; whitish; white; very white.
  - ◦ fibres:
    H-fvs: few; many.
    o-fvs: few; less-fibrous; many; fibrous; tough; hard; very tough.
- Yield:
    H-fvs: low; high.
    o-fvs: low; low to high; medium; usually high; good; high; very good; very high.
- Fruiting:
  H-fvs: seldom; often but seeds seldom viable; often and seeds often viable.
  o-fvs: seldom; often; sterile; seeds fertile; seeds usually sterile; seeds usually sterile but also fertle.
- Time till harvestable:
  H-fvs: (ranking only).
  o-fvs: early maturing; growth slow to fast depending on soil dryness; slow-maturing; growth slow; at trunk age 6-7 yr; 7-9 yr; at trunk age 9-10 yr; 15 yr; 15-20 yr; 20 yr.

Comparing the values of these variety characteristic, the values of the characteristics of folk varieties recognised in Hatusua appear to fall within the ranges of those of folk varieties recognised elsewhere. Therefore, on the basis of this comparison the Hatusua varieties cannot be diagnosed as other than average.

5.5 Variation in sago palm and the implications for my research results

Given the outcome of the folk variety characteristics analysis, viz. that the sago palm varieties I studied do not seem to reside at the extremities of the range of all known varieties, there seems to be no reason to consider the results of my studies not valid for sago palm in general. Where results are influenced by the sheer size of, e.g. trunk or leaves, they should simply be scaled down or up to apply them to smaller or bigger varieties. There is as yet no reason to assume that these results would have been qualitatively different had other varieties been studied instead.

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6 Leaf area

Abbreviations used in this chapter

- plant parts: L = leaf ; LT = leaflet ; LLT = longest leaflet (of a leaf) ; R = rachis ; RB = rachis base (i.e. where the most proximal leaflet is attached) ; C = crown.
- dimensions: L = length ; W = width ; H = height ; A = area.
  In abbreviations used to indicate dimensions of plant parts, the plant part is always named first, e.g.: LA = leaf area ; LTL = leaflet length.
- and further: SLA = single leaf area (area of one single leaf (only one surface of the constituting leaflets is counted)) ; TLA = total leaf area (summed SLA's of all the leaves in the crown of an axis) ; LAI = leaf area index ("the sum of the area of all leaves (only one surface is counted) per unit area of ground" (LOOMIS & CONNOR 1992:36)) a measure of leaf density, applicable to an individual tree, or to the canopy of a crop, c.q. stand of trees ; CPA = crown projection area (the area of the perpendicular projection of he crown of leaves on the ground).

Sago palm development phase codes

AV - Adult Vegetative.
G - Generative.
  G1 - from flower initiation to full extension of 1st-order inflorescence branches.
  G2 - from full extension of 1st-order inflorescence branches to full extension of 3rd-order inflorescence branches.
  G3 - from full extension of 3rd-order inflorescence branches to shedding of fruits.
(See Chapter 4 for detailed explanation of these different phases.)

Palm numbers refer to a series of destructively sampled sago palms, the complete data sets of which are presented in the Sago Palm Data Sheets in Appendix A.

In a study of the evolution of starch accumulation in the trunk of a sago palm, the investigation of the growth of the crown of leaves of the palm is of particular importance as the crown is the factory in which the building blocks of the starch are made. Therefore, anticipating the general presentation of observations of sampled sago palms in Chapter 7, in this chapter the data on the leaves are dealt with first.

6.1 Estimating leaf area

Definition of leaf area

I define leaf area here as the totalled one-sided surface area of the leaflets. Although the contribution of the petiole and rachis to the surface area of a leaf is not negligible, their contribution to photosynthesis is probably small, because of their small capacity for energy conversion (they are a much paler green than the leaflets (see Fig. 6.2), indicating a much smaller chlorophyll content), and because they usually have a much smaller gas exchange capacity (smaller stomata density and less parenchyma tissue) than leaflets (e.g. RAVEN *et al.* 1999:610-646).

Recorded estimator candidates

Direct measurement of the TLA of a crown was precluded by the sheer bulk of the leaflets (up to 2 m long, 160-180 per leaf, up to 28 leaves per crown) and by the lack of equipment in the field. For the area of a single leaf (SLA) an easily measurable estimator had to be devised. Estimator candidates would be properties which are likely to be proportionate to the SLA. The estimator candidates which were recorded for most of the sago palms that were sampled, are (see Table 6.3):

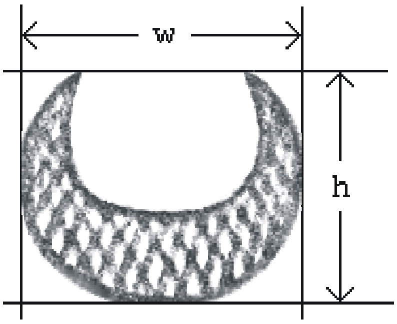


Figure 6.1 Cross section through the rachis base of a sago palm leaf, showing how its width (w) and height (h) were measured.

- length of rachis (RL)
- length of the longest leaflet (LLTL)
- width times height of the rachis base (RBW x RBH)

The latter is a measure for the strength and the conductive capacity of the leaf at that point: the larger the area of the RB cross section, the larger the number and size of the leaflets the leaf can carry and provide with water and nutrients distal to that point. The idea of relating the petiole cross section area to leaf weight and/or leaf area was explored for oil palm by CORLEY *et al*. (1971). Their example was followed by, for example, ROSENQUIST (1980) for coconut palm.

Measuring RW and RH was done as illustrated in Fig. 6.1. At first this was done with a metal measuring tape, but due to the parallax, reading of especially the height was unsatisfactory. From Palm #11 onward, measurements were done with a square vernier caliper of which I extended the beak by mounting each side of the beak with a metal ruler (Fig. 6.2). Accuracy was thus enhanced from 1 mm to 0.1 mm.

Figure 6.2 Method of measuring width and height of the cross section of the rachis base (i.e., of the petiole where the most proximate leaflet is attached).
[photo nrs. 89.05-085-08, -07, and -09, Palm#14 ("Molat Berduri", AV) *dusun* Salapu, Hatusua wed10may1989]

To determine the relationship between an SLA estimator and SLA itself, one needs some actual leaf area data, but direct measurement of the leaf area of even one whole leaf (i.e. of the area of all its separate leaflets) was impracticable for the same reasons as for measuring the TLA of a crown. Therefore, a way to estimate the area of a single leaflet also had to be devised.

Estimating the area of one leaflet (LTA)

I had the opportunity of having the actual surface area of a limited number of leaflets measured with a light-interception type area meter (at Lembang, West Java, 2500 km from my field lab). I could then determine the relationship between leaflet area (LTA) and LTA estimators based on the easily measurable length of a leaflet (LTL) and/or its greatest width (LTW) (Table 6.1).

Table 6.1 Relationship between the area of a sago palm leaflet, LTA , as measured with a light-interception type area meter, and its length (LTL) and/or greatest width (LTW).

Palm#, Leaf# *	Leaf-let# **	LTA (cm^2)	LTL (cm)	LTW (cm)	LTL x LTW (cm^2)	LTA / LTL	LTA / LTW	LTA / (LTL x LTW)
P#17, Lf#19	?20/93 ***	1467.38	178	11.6	2065	8.24	126	0.711
	?41/93 ***	1588.35	198	11.0	2178	8.02	144	0.729
P#18, Lf#1	R10/86	508.56	106	5.8	615	4.80	88	0.827
	R16/86	665.12	120	7.1	852	5.54	94	0.781
	R28/86	869.04	126	8.4	1058	6.90	103	0.821
	R37/86	932.72	141	8.3	1170	6.62	112	0.797
	R46/86	840.82	130	8.0	1040	6.47	105	0.808
	R80/86	313.48	77	5.2	400	4.07	60	0.783
	R84/86	128.48	56	2.7	151	2.29	48	0.850
P#18, Lf#2	L2/86	102.09	65	2.4	156	1.57	43	0.654
	L8/86	386.16	84	6.0	504	4.60	64	0.766
	R12/86	543.7	110	6.4	704	4.94	85	0.772
	R14/86	633.16	113	6.8	768	5.60	93	0.824
	L56/86	689.33	123	6.9	849	5.60	100	0.812
	L67/86	503.01	108	6.1	659	4.66	82	0.764
	L75/86	357.21	85	5.3	451	4.20	67	0.793
	L83/86	107.71	51.5	2.8	144	2.09	38	0.747
Average:						5.07	85	0.779

* Palm number: See data sheets of sampled palms in Appendix A. Leaf number: The unfolded green leaves are numbered from the lowest and oldest (Lf#1) to the highest and youngest.

** Leaflet number: E.g. #R2/86 is the 2nd leaflet from a total of 86 on the right hand side of the rachis (right as seen from above standing at the base of the leaf, and counted starting with the leaflet closest to the leaf base).

*** Only number recorded, not the side of the rachis at which it was attached.

From this table it is clear that LTL is not a simple LTA estimator, as the ratio of LTA to LTL ranges from 1.57 to 8.24. Nor is LTW an accurate estimator because the ratio of LTA to LTW ranges from 38 to 144 . LTL×LTW seems a much better one, as the ratio of LTA to LTL×LTW (a ratio a.k.a. the shape factor) only ranges from 0.654 to 0.850 around an average of 0.779. To better estimate this shape factor, a simple linear regression equation was determined:

$$Y = 0.7249\ X + 38.76 \qquad (n = 17,\ R^2 = 0.992) \qquad [eq\#1]$$

(Y: LTA (cm^2) ; X: LTL×LTW (cm^2))

Figure 6.3 shows this relationship graphically. The large coefficient of determination R^2 indicates that LTA may confidently be estimated by this equation in the range of the product LTL x LTW under consideration, viz. 144 - 2178 cm^2.

Figure 6.3 Area of sago palm leaflets of Palm #17 and #18 plotted against their length x greatest width, and linear regression of these properties (equation: $Y = 0.7249 X + 38.76$; $R^2 = 0.992$).

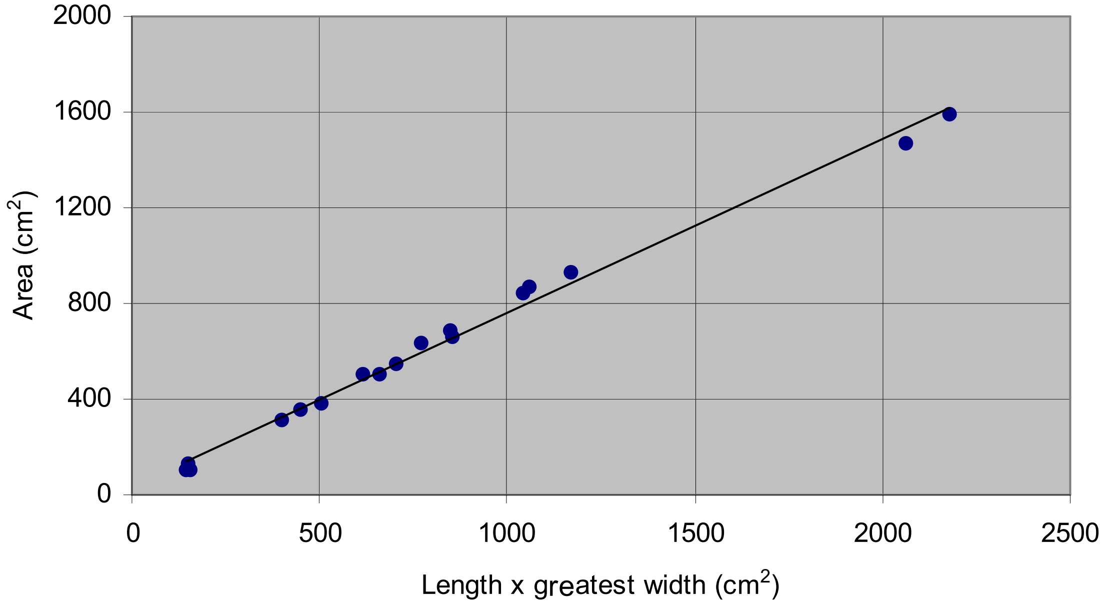
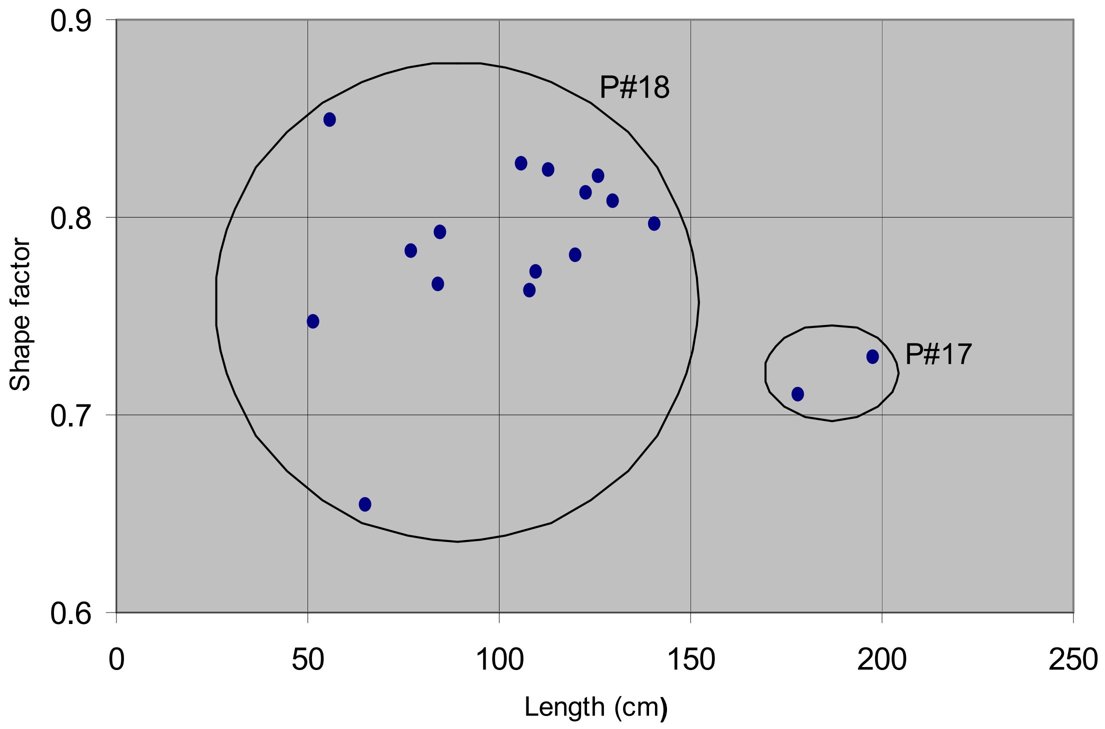


Figure 6.4 Scatter diagram of length against shape factor (area / (length x width)) of leaflets from two sago palms (P#17, P#18).



From Table 6.1 it also becomes clear that both relatively large and relatively small leaflets, or, more precisely, relative long and relatively short leaflets, have outlying values of the ratios mentioned above. This is also illustrated in figure 6.4. The two long ones are the only two leaflets from a different palm (#17) which were included in the calculation, whereas the short ones are leaflets attached towards the extremities (base and top) of the rachis.

With the outlying values of the long leaflets, genetic differences may play a role: Palm #17 belongs to the folk variety Tuni, Palm #18 to the folk variety Molat.
The outlying values of the leaflets within Palm #18 indicate that leaflets at the extremities of the rachis are more variable in shape than the longer, more centrally attached ones.

Only for leaves of Palm #18 the LTL×LTW of a sufficient number of leaflets was measured to warrant an estimate of the SLA of those leaves on the basis of summed LTA estimates. For this purpose, the variation in leaflet shape factor that may be explained by differences between palms may be excluded by using the data from Palm #18 only. This results in a regression equation which accounts for even a larger portion of the LTA variation (R^2 is slightly greater):

$Y = 0.8163 X - 12.81$ ($n = 15$, $R^2 = 0.997$) [eq#2]
(Y: LTA (cm^2) ; X: LTL×LTW (cm^2))

The range of X for which this equation is calculated is 144 - 1170 cm^2.

Finally, to check whether maybe a non-linear equation would describe the relationship between LTA and LTL better than a linear one, a power equation was fitted to the scatter diagram of LTA against LTL (using the software Microsoft Excel 97). Also the linear relationship between LTA and the squared LTL was calculated. This was done for the leaflets of Palm #17 and #18 combined, as well as for the leaflets of Palm #18 only:

$Y = 0.0218 X^{2.1561}$ ($n=17$, $R^2 = 0.9538$) [eq#3]
(Y: LTA (cm^2) ; X: LTL (cm) ; Palm #17 and #18 combined)

$Y = 0.0122 X^{2.2876}$ ($n=15$, $R^2 = 0.9454$) [eq#4]
(Y: LTA (cm^2) ; X: LTL (cm) ; Palm #18 only)

$Y = 0.0431 X + 39.209$ ($n=17$, $R^2 = 0.9737$) [eq#5]
(Y: LTA (cm^2) ; X: squared LTL (cm^2) ; Palm #17 and #18 combined)

$Y = 0.0501 X - 29.112$ ($n=15$, $R^2 = 0.9687$) [eq#6]
(Y: LTA (cm^2) ; X: squared LTL (cm^2) ; Palm #18 only)

All these equations have a smaller coefficient of determination R^2 than the equations #1 and #2 above, and therefore the equations #1 and #2 are the better LTA estimators.

Measuring length and maximum width as well as actual area of all the leaflets of seven leaves from two palms in the early trunk phase from a sago farm in Sarawak, NAKAMURA *et al.* (2005) found a very similar relationship between LTA and LTL×LTW . By assuming an Y-intercept fixed at (0,0), they arrived at the equation LTA = 0.785 (LTL×LTW) , albeit by the unnecessary circuitous route of first equalling LTA to the area of an ellipse.

Estimating the area of a single leaf (SLA)

By adding up the area estimates of all the leaflets of a leaf, the SLA of that leaf can be estimated. By this procedure, using equation #2, the SLA of Leaf#1 - #4 of Palm #18 was estimated.

> The length and greatest width of as many leaflets as possible of the four oldest functional leaves of Palm #18 were measured (as well as of sample leaflets of the remaining 13 younger leaves). The length and width of some leaflets had to be estimated themselves, because they were damaged or missing, most probably because they were eaten by the long-horn grasshopper *Sexava* sp. of which a nymph was found on a leaflet. This estimation was done by assuming a gradual change in length and width of leaflets along the length of the rachis: the missing value was estimated by calculating an intermediate value between known bordering values. As widths of adjacent leaflets proved to be more variable than their lengths[2], for width estimates the mean of three successive known widths preceding and succeeding the missing value(s) were taken to calculate the intermediate value(s).

These estimates, together with the SLA estimator candidates mentioned above, are presented in Table 6.2.

Table 6.2 Single leaf area (SLA) (as estimated by adding up leaflet area (LTA) estimates), and 3 leaf properties likely to be proportionate to SLA, (viz. length of the rachis (RL), length of the longest leaflet (LLTL) and width times height of the cross section of the rachis base (RBW×RBH)) of the oldest 4 leaves of Palm #18.

Leaf#	SLA as estimated by adding up LTA estimates (m^2)	RL (m)	LLTL (m)	RBW x RBH (cm^2)
1	10.7023	5.26	1.41	9.53 x 7.86 = 74.9
2	10.0495	4.97	1.35	9.05 x 7.68 = 69.5
3	9.7455	4.76	1.33	9.10 x 7.49 = 68.2
4	9.2919	4.59	1.32	9.15 x 7.35 = 67.3

Regression analyses of these data on single leaf area (SLA) and its possible estimators resulted in the following regression equations:

SLA (Y, in m^2) as a function of **RL** (X, in m):
$Y = 2.041 X - 0.0419$ (n = 4, $R^2 = 0.991$) [eq#7]
- idem, forced through (0,0):
$Y = 2.032 X$ (n = 4, $R^2 = 0.991$) [eq#7a]

SLA (Y, in m^2) as a function of **LLTL** (X, in m):
$Y = 14.15 X - 9.1952$ (n = 4, $R^2 = 0.929$) [eq#8]
- idem, forced through (0,0):
$Y = 7.359 X$ (n = 4, $R^2 = 0.715$) [eq#8a]

SLA (Y, in m^2) as a function of **RBW×RBH** (X, in cm^2):
$Y = 0.1662 X - 1.6816$ (n = 4, $R^2 = 0.914$) [eq#9]
- idem, forced through (0,0):
$Y = 0.1422 X$ (n = 4, $R^2 = 0.895$) [eq#9a]

Additional regression analyses of SLA data and the product of RL and LLTL resulted in the following regression equations:

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[2] A possible reason for this may be that the tops of the leaflets are at one time during ontogenesis forming the outline of the leaf blade before the blade is split up into separate leaflets: hence the almost equal length of neighbouring leaflets. With width, competition for space may play a role at some time during growth and development, space left open by a leaflet being taken by a neighbouring one, which results in a relatively narrow leaflet sitting next to a relatively wide one.

SLA (Y, in m^2) as a function of **RL×LLTL** (X, in m^2):
$Y = 0.9961 X + 3.3445$ (n = 4, $R^2 = 0.983$) [eq#10]
- idem, forced through (0,0):
$Y = 1.498 X$ (n = 4, $R^2 = 0.732$) [eq#10a]

SLA (Y, in m^2) as a function of **RL×2LLTL** (X, in m^2) (i.e. as function of length times greatest width of the entire leaf blade):
$Y = 0.4980 X + 3.3445$ (n = 4, $R^2 = 0.983$) [eq#11]
- idem, forced through (0,0):
$Y = 0.7488 X$ (n = 4, $R^2 = 0.732$) [eq#11a]

Judging by the coefficient of determination R^2, rachis length is the best estimator, at least for the tested range of lengths (4.59 m - 5.26 m). RBW×RBH, however, is by far the easiest to measure of the three estimators, especially if the leaves to be measured are in the smashed and tangled crown of a felled tree.

Judging from equation [#11a], as a rule of thumb the area of a sago palm leaf blade can be estimated at three quarters of its length times width.
This is much higher than the "between 0.5 and 0.6" as estimated by FLACH & SCHUILING (1989:279). This estimation may have "low accuracy", but was not as "illogical" as NAKAMURA *et al.* (2004:198, 2005:28) would have us believe, as it was based on the assumption that the leaflets could be considered flat and contiguous, and that both the area of a leaflet and the area within the outline of the whole leaf blade were about three quarters of the area of the rectangles that could be drawn around them: 0.75 x 0.75 = 0.56 . As shown before (Table 6.1), I found that the shape factor of a single leaflet is 0.78 on average. Therefore, to arrive at the ratio of SLA to (LLxLW) of about 0.75 I found, the ratio of the area within the outline of the whole leaf to the area of the rectangle that can be drawn around it must be much higher than the 0.75 assumed by FLACH & SCHUILING. This is probably not only because the outline is more rectangular than they thought, but also because the leaflets are roof-shaped and overlapping rather than flat and contiguous.

6.2 Leaf area of a crown in different developmental phases of the axis

Table 6.3 gives an overview of leaf dimensions that were measured in a series of destructively sampled sago palms, the complete data sets of which are given in the Sago Palm Data Sheets in Appendix A. These palms varied in, among other characters, development stage. The order in which the palms are numbered is merely chronological on sampling date. Not of all the palms sampled were leaf measurements taken (missing palm numbers in the table).

Of the 28 palms of which leaf measurements were taken, only 2 palms (#01 and #18) had all the green leaves in their crown sampled. Of another 10 palms about 1/3 to 2/3 of their leaves was sampled, mostly by measuring RBW×RBH. The remaining 16 palms had only one to four of their leaves sampled, usually one from among the older leaves, one from among the younger leaves and one leaf of intermediate age, which makes the estimation of missing data by interpolation possible. In palms of which observations were made on one leaf only (#09 and #33), crown leaf area (TLA) estimates are only possible by assuming a leaf size change from oldest to youngest similar to other palms in the same developmental phase, or proportional to the change in trunk diameter where the leaves are attached.

Table 6.3 Overview of available data for estimation of single leaf area (SLA) of sago palm leaves.
(RL = length of rachis ; LLTL = length of longest leaflet ; RBW×RBH = width times height of the rachis base.)

Palm# *	Folk variety	Develop-ment phase **	Number of green leaves	Number of leaves for which data for SLA estimation were recorded		
				RL	LLTL	RWB×RBH
01	Ihur	E	2	2	2	0
02	Tuni	E	5	4	4	0
09	Tuni	G1	20	1	1	1
10	Molat	AV	21	2	2	2
11	Tuni	AV	20	3	4	8
12	Tuni	AV	14	3	3	2
13	Molat	AV	16	3	3	2
14	Molat Berduri	AV	22	2	2	3
15	Tuni	AV	16	3	3	3
16	Tuni	AV	19	3	3	3
17	Tuni	AV	19	2	2	2
18	Molat	G2	17	17	3	17
19	Putih	AV	14	3	3	3
20	Putih	AV	14	3	3	3
21	Putih	AV	14	2	2	1
25	Ihur	AV	21	4	4	4
26	Ihur	AV	21	1	1	2
27	Tuni	AV	19	2	2	15
28	Tuni	G1	27	3	3	3
29	Molat Berduri	G1	28	0	0	16
30	Molat	AV	16	1	1	6
31	Molat	AV	16	2	2	11
32	Tuni	AV	19	1	1	7
33	Molat	AV	20?	1	1	1
34	Tuni	G2	25	2	1	11
35	Ihur	G2	27	3	3	16
36	Makanatol	G2	28	3	3	18
37	Ihur	G1	24	2	2	7

* Palm number: See data sheets of sampled palms in Appendix A.
** E = establishment, AV = adult vegetative, G = generative. See Chapter 4 for further explanation.

Below, the calculation of the TLA's of these 28 palms is presented, using SLA estimates calculated with the regression equation with the highest R^2 for which recorded leaf variables of a palm were available. If the values of these variables are outside the range for which a regression equation was calculated - as in most cases - , the corresponding equation which includes the data point (0,0) is used.

Not only mere leaf surface area determines the crown's capability to intercept light and produce carbohydrates, but also the distribution and angle of that surface in space. The Leaf Area Index (LAI) of the crown, i.e. the ratio of the TLA of the crown to the area of the crown's perpendicular projection on the ground (CPA), is a measure of this distribution and angle. For the 28 palms also this LAI is calculated.
The crown's projection area of axes in the Adult Vegetative or Generative phase can be

estimated by assuming that the lowest leaf is attached to the trunk at an angle of 45º (Fig. 6.5a) and by taking as the radius of the crown projection circle the length of the lowest leaf divided by the square root of 2 (Pythagoras) plus the trunk radius at attachment height.
In suckers (i.e. axes in the Establishment phase) leaves stand more upright than in axes in the Adult Vegetative or Generative phase. On average, the angle between the lowest leaf and the vertical is about 30º (see Fig. 6.5b). Therefore, the length of the perpendicular projection of the lowest leaf on the ground can be estimated at half the length of that leaf (planimetry). Besides, in small suckers trunk width may be ignored, and the radius of the crown projection on the ground may also be assumed to equal half the length of the lowest leaf.

Figure 6.5a The angle at which the lowest leaf is attached to the trunk can be estimated at 45º. [photo nr. 89.08-091-19, Waipirit, West Seram thu13jul1989]

Figure 6.5b The angle at which the lowest leaf of a sucker diverges from the vertical can be estimated at an average 30º. [photo nr. flach01, [loc.?, date ?]]
(Photo: Michiel FLACH)

Calculation of TLA and LAI of 28 palms

Palm #01: Establishment phase, folk variety Ihur

Leaf#	**RL (m)**	**LLTL (m)**	**SLA (Y) estimate (m^2) based on ...**		
			X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RL*LLTL (Y = 1.498 X (R^2=0.732))**
1	0.80	0.335	1.63	2.47	0.40
2	0.52	0.22	1.06	1.62	0.17
TLA (m^2)			**2.69**	**4.09**	**0.57**

Length Leaf#1: 1.83 m.
Trunk diameter where Leaf#1 is attached: negligible.
Crown projection area: π x $(1.83/2)^2$ = 2.63 m^2.
TLA (estimate based on RL): 2.69 m^2.
LAI: 2.69 m^2 / 2.63 m^2 = 1.02.

Palm #02: Establishment phase, fv Tuni

Leaf#	**RL (m)**	**LLTL (m)**	**SLA (Y) estimate (m^2) based on ...**		
			X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RL*LLTL (Y = 1.498 X (R^2=0.732))**
1	0.87	0.51	1.77	3.75	0.66
2	estimate: (#1+#3)/2		1.70	3.61	0.61
3	0.80	0.47	1.63	3.46	0.56
4	0.89	0.56	1.81	4.12	0.75
5	0.88	0.60	1.79	4.42	0.79
TLA (m^2)			**8.70**	**19.36**	**3.37**

Length Leaf#1: 2.68 m.
Trunk diameter where Leaf#1 is attached: negligible.
Crown projection area: π x $(2.68/2)^2$ = 5.64 m^2.
TLA (estimate based on RL): 8.70 m^2.
LAI: 8.70 m^2 / 5.64 m^2 = 1.54.

Palm #09: Generative-1 phase, fv Tuni

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1	7.65	1.70	126.0	15.5	12.5	17.9
2-19	estimate: (#1+#20)/2			18x13.09=235.6	18x10.56=190.1	18x15.12=272.2
20	estimate: 36.5/53 x SLA Lf#1 *)			10.67	8.61	12.33
TLA (m^2)				**261.8**	**211.2**	**302.4**

*) (See Data Sheet of this palm in Appendix A.) Trunk diameter where Lf#1 is attached, at 17.50 m above ground level (a.g.l.), is 53 cm. At 18.50 m a.g.l. trunk diameter is 42 cm, whereas Lf#20 (one leaf down from the spear leaf) is attached at about the same height as the spear leaf, viz. at 19.00 m a.g.l. Assuming the trunk diameter above where Lf#1 is attached to decrease linearly with height a.g.l., trunk diameter at 19.00 m.a.g.l. would be 53-3/2(53-42)=36.5 cm. Assuming that the SLA of a leaf is directly proportional to the trunk diameter where that leaf is attached, Lf#20 has an SLA of 36.5/53 times the SLA of Lf#1.

Length Leaf#1: 10.20 m.
Trunk diameter where Leaf#1 is attached: 0.53 m.
Crown projection area: π x $(10.20/\sqrt{2} + 0.265)^2$ = 175.7 m^2.
TLA (estimate based on RL): 261.8 m^2.
LAI: 261.8 m^2 / 175.7 m^2 = 1.49.

Palm #10: Adult Vegetative phase, fv Molat

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	assume equal to #2			16.1	12.1	15.5
2	7.9	1.65	109.2	16.1	12.1	15.5
3-20	estimate: (#2+#21)/2			18x15.75=283.5	18x12.65=227.7	18x15.65=281.7
21	7.60	1.80	111.1	15.4	13.2	15.8
TLA (m^2)				**331.1**	**265.1**	**328.5**

Length Leaf#1: 11.00 m.
Trunk diameter where Leaf#1 is attached: 0.56 m.
Crown projection area: π x $(11.00/\sqrt{2} + 0.28)^2$ = 204.0 m^2.
TLA (estimate based on RL): 331.1 m^2.
LAI: 331.1 m^2 / 204.0 m^2 = 1.62.

Palm #11: Adult Vegetative phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	assume equal to #2			16.0	12.5	21.5
2	7.85	1.70	151.3	16.0	12.5	21.5
3	8.00	1.60	135.6	16.3	11.8	19.3
4-5	estimate: (#3+#6)/2			2x16.4=32.8	2x11.8=23.6	
4	estimate: (#3+#5)/2					20.3
5	n.r.	n.r.	148.8			21.2
6	8.13	1.60	137.5	16.5	11.8	19.6
7-19	estimate: (#6+#20)/2			13x16.1=209.3	13x12.8=166.4	
7	n.r.	n.r.	139.2			19.8
8	n.r.	n.r.	128.4			18.3
9	n.r.	n.r.	138.0			19.6
10-19	estimate: (#9+#20)/2					10x19.6=196
20	7.74	1.88	137.5	15.7	13.8	19.6
TLA (m^2)				**322.6**	**252.4**	**396.7**

Length Leaf#1: 10.58 m.
Trunk diameter where Leaf#1 is attached: 0.64 m.
Crown projection area: π x $(10.58/\sqrt{2} + 0.37)^2$ = 193.7 m^2.
TLA (estimate based on RL): 322.6 m^2.
LAI: 322.6 m^2 / 193.7 m^2 = 1.67.

Palm #12: Adult Vegetative phase (early), fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	8.50	1.65	100.5	17.3	12.1	14.3
2	estimate: (#1+#3)/2			17.35	12.05	
2-13	estimate: (#1+#14)/2					12x14.7=176.4
3	8.55	1.63	n.r.	17.4	12.0	
4-13	estimate: (#3+#14)/2			10x16.85=168.5	10x12.2=122	

14	8.00	1.69	106.0	16.3	12.4	15.1
TLA (m^2)				**236.9**	**170.6**	**205.8**

Length Leaf#1: 11.80 m.
Trunk diameter where Leaf#1 is attached: 0.53 m.
Crown projection area: $\pi \times (11.80/\sqrt{2} + 0.265)^2 = 232.8\ m^2$.
TLA (estimate based on RL): 236.9 m^2.
LAI: 236.9 m^2 / 232.8 m^2 = 1.02.

Palm #13: Adult Vegetative phase, fv Molat

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1	assume equal to #2			15.8	11.5	13.8
2	7.80	1.56	96.9	15.8	11.5	13.8
3-5	estimate: (#2+#6)/2			3x16.2=48.6	3x12.1=36.3	
3-15	estimate: (#2+#16)/2					13x13.85=180.1
6	8.13	1.72	n.r.	16.5	12.7	
7-15	estimate: (#6+#16)/2			10x16.2=162	10x12.4=124	
16	7.80	1.65	97.8	15.8	12.1	13.9
TLA (m^2)				**274.5**	**208.1**	**221.6**

Length Leaf#1: 10.90 m.
Trunk diameter where Leaf#1 is attached: 0.50 m.
Crown projection area: $\pi \times (10.90/\sqrt{2} + 0.25)^2 = 198.9\ m^2$.
TLA (estimate based on RL): 274.5 m^2.
LAI: 274.5 m^2 / 198.9 m^2 = 1.38.

Palm #14: Adult Vegetative phase, fv Molat Berduri

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1-9	assume equal to #10			9x18.0=162.0	9x12.8=115.2	
1-5	assume equal to #6					5x17.4=87.0
6	n.r.	n.r.	122.4			17.4
7-9	estimate: (#6+#10)/2					3x18.35=55.1
10	8.85	1.74	135.6	18.0	12.8	19.3
11-21	estimate: (#10+#22)/2			11x17.4=191.4	11x13.0=143.0	11x19.4=213.4
22	8.25	1.80	136.9	16.8	13.2	19.5
TLA (m^2)				**388.2**	**284.2**	**411.7**

Length Leaf#1: 12.05 m.
Trunk diameter where Leaf#1 is attached: 0.59 m.
Crown projection area: $\pi \times (12.05/\sqrt{2} + 0.295)^2 = 244.2\ m^2$.
TLA (estimate based on RL): 388.2 m^2.
LAI: 388.2 m^2 / 244.2 m^2 = 1.59.

Palm #15: Adult Vegetative phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	assume equal to #2			16.6	11.8	15.5
2	8.15	1.60	109.0	16.6	11.8	15.5
3-4	estimate: (#2+#5)/2			2x16.1=32.2	2x12.35=24.7	2x16.05=32.1
5	7.70	1.75	116.6	15.6	12.9	16.6
6-15	estimate: (#5+#16)/2			10x15.4=154.0	10x12.5=125	10x17.8=178
16	7.50	1.65	133.3	15.2	12.1	19.0
TLA (m^2)				**250.2**	**198.3**	**276.7**

Length Leaf#1: 11.20 m.
Trunk diameter where Leaf#1 is attached: 0.54 m.
Crown projection area: π x $(11.20/\sqrt{2} + 0.27)^2$ = 210.7 m^2.
TLA (estimate based on RL): 250.2 m^2.
LAI: 250.2 m^2 / 210.7 m^2 = 1.19.

Palm #16: Adult Vegetative phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	7.90	1.60	125.8	16.1	11.8	17.9
2-13	estimate: (#1+#14)/2			12x15.35=184.2	12x11.8=141.6	12x18.55=222.6
14	7.20	1.60	135.0	14.6	11.8	19.2
15-18	estimate: (#14+#19)/2			4x14.9=59.6	4x12.15=48.6	4x20.5=82.0
19	7.50	1.70	153.2	15.2	12.5	21.8
TLA (m^2)				**289.7**	**226.3**	**363.5**

Length Leaf#1: 10.45 m.
Trunk diameter where Leaf#1 is attached: 0.60 m.
Crown projection area: π x $(10.45/\sqrt{2} + 0.30)^2$ = 185.7 m^2.
TLA (estimate based on RL): 289.7 m^2.
LAI: 289.7 m^2 / 185.7 m^2 = 1.56.

Palm #17: Adult Vegetative phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	9.15	1.7	124.6	18.6	12.5	17.7
2-18	estimate: (#1+#19)/2			17x17.7=300.9	17x13.55=230.4	17x19.95=339.2
19	8.25	1.98	156.2	16.8	14.6	22.2
TLA (m^2)				**336.3**	**257.5**	**379.1**

Length Leaf#1: 12.35 m.
Trunk diameter where Leaf#1 is attached: 0.55 m.
Crown projection area: π x $(12.35/\sqrt{2} + 0.275)^2$ = 254.9 m^2.
TLA (estimate based on RL): 336.3 m^2.
LAI: 336.3 m^2 / 254.9 m^2 = 1.32.

Palm #18: Generative-3 phase, fv Molat

Leaf#	RL (m)	RBWxRBH (cm^2)	SLA estimate (m^2) based on ...			
			X = RL (Y= 2.041 X - 0.0419 (R^2=0.991))	X = RL (Y= 2.032 X (R^2=0.991))	X = RBWxRBH (Y= 0.1662 X - 1.6816 (R^2=0.914))	X = RBWxRBH (Y= 0.1422 X (R^2=0.895))
1	5.26	74.9	10.7023 *			
2	4.97	69.5	10.0495 *			
3	4.76	68.2	9.7455 *			
4	4.59	67.3	9.2919 *			
5	4.45	67.2	9.04	9.04	9.49	9.56
6	4.25	63.3	8.63	8.64	8.84	9.00
7	4.19	60.4	8.51	8.51	8.36	8.59
8	4.15	59.3	8.42	8.43	8.17	8.43
9	3.80	52.2	7.71	7.72	6.99	7.42
10	3.58	43.3	7.26	7.27	5.51	6.16
11	3.15	37.7	6.38	6.40	4.58	5.36
12	2.60	28.3	5.26	5.28	3.02	4.02
13	2.17	19.6	4.38	4.41	1.58	2.79
14	1.70	15.0	3.43	3.45	0.811	2.13
15	1.30	11.1	2.61	2.64	0.163	1.58
16	0.87	6.30	1.73	1.77	[-0.634]	0.90
17	0.72	6.46	1.43	1.46	[-0.542]	0.92
TLA (m^2)			**114.58**	**114.81**	**97.30**	**106.65**

* The area of this leaf was already estimated more accurately by adding up the leaflet areas (see Table 6.2)

In the generative phase leaves become progressively smaller and are soon outside the range for which the regression equations were calculated. SLA estimates for the smallest leaves based on regression on RBW×RBH not including the data point (X=0,Y=0) even become negative.

Length Leaf#1: 6.79 m.
Trunk diameter where Leaf#1 is attached: 0.32 m.
Crown projection area: π x (6.79/√2 + 0.16)^2 = 77.3 m^2.
TLA (estimate based on RL): 114.8 m^2.
LAI: 114.8/77.3 = 1.49.

Palm #19: Adult Vegetative phase, fv Putih

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	assumed: equal to #2			14.6	10.4	12.3
2	7.20	1.41	86.5	14.6	10.4	12.3
3-8	estimate: (#2+#9)/2			6x14.15=84.9	6x10.55=63.3	6x12.2=73.2
9	6.75	1.45	85.2	13.7	10.7	12.1
10-13	estimate: (#9+#14)/2			4x13.8=55.2	4x11.1=44.4	4x12.55=50.2
14	6.85	1.56	91.4	13.9	11.5	13.0
TLA (m^2)				**196.9**	**150.7**	**173.1**

Length Leaf#1: 9.68 m.
Trunk diameter where Leaf#1 is attached: 0.45 m.
Crown projection area: π x (9.68/√2 + 0.225)^2 = 157.0 m^2.
TLA (estimate based on RL): 196.9 m^2.
LAI: 196.9 m^2 / 157.0 m^2 = 1.25.

Palm #20: Adult Vegetative phase, fv Putih

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-5	assumed: equal to #6			5x15.5=77.5	5x11.3=56.5	5x13.0=65.0
6	7.65	1.53	91.6	15.5	11.3	13.0
7-11	estimate: (#6+#12)/2			5x15.45=77.3	5x11.9=59.5	5x13.55=67.8
12	7.6	1.70	98.9	15.4	12.5	14.1
13	estimate: (#12+#14)/2			15.8	12.3	14.2
14	7.94	1.64	99.7	16.1	12.1	14.2
TLA (m^2)				**217.6**	**164.2**	**188.3**

Length Leaf#1: 10.44 m.
Trunk diameter where Leaf#1 is attached: 0.50 m.
Crown projection area: π x $(10.44/\sqrt{2} + 0.25)^2$ = 183.0 m^2.
TLA (estimate based on RL): 217.6 m^2.
LAI: 217.6 m^2 / 183.0 m^2 = 1.19.

Palm #21: Adult Vegetative phase, fv Putih

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-2	assumed: equal to #3			2x16.6=33.2	2x11.8=23.6	
3	8.15	1.60	n.r.	16.6	11.8	
4-13	estimate: (#3+#14)/2			10x16.1=161.0	10x12.0=120.0	
14	7.68	1.66	111.7	15.6	12.2	15.9
TLA (m^2)				**226.4**	**167.6**	

Length Leaf#1: 11.22 m.
Trunk diameter where Leaf#1 is attached: 0.49 m.
Crown projection area: π x $(11.22/\sqrt{2} + 0.245)^2$ = 210.1 m^2.
TLA (estimate based on RL): 226.4 m^2.
LAI: 226.4 m^2 / 210.1 m^2 = 1.08.

Palm #25: Adult Vegetative phase, fv Ihur

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1	assumed: equal to #2			15.8	11.8	18.0
2	7.80	1.60	126.4	15.8	11.8	18.0
3-11	estimate: (#2+#12)/2			9 x 15.7=141.3	9 x 12.7=114.3	9 x 19.8=178.2
12	7.70	1.85	151.6	15.6	13.6	21.6
13-14	estimate: (#12+#15)/2			2 x 15.9=31.8	2 x 13.7=27.4	2 x 22.45=44.9
15	7.95	1.88	163.8	16.2	13.8	23.3
16-20	estimate: (#15+#21)/2			5 x 16.25=81.3	5 x 13.8=69.0	5 x 23.4=117.0
21	8.01	1.87	165.5	16.3	13.8	23.5
TLA (m^2)				**334.1**	**275.5**	**444.5**

Length Leaf#1: 10.36 m.
Trunk diameter where Leaf#1 is attached: 0.55 m.
Crown projection area: π x $(10.36/\sqrt{2} + 0.275)^2$ = 181.5 m^2.
TLA (estimate based on RL): 334.1 m^2.
LAI: 334.1 m^2 / 181.5 m^2 = 1.84.

Palm #26: Adult Vegetative or Generative-1 phase, fv Ihur

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-15	assumed: equal to #...			15x...	15x...	
1-6	assumed: equal to #...					6x...
7	n.r.	n.r.	153.0			21.8
8-15	estimate: (#7+#16)/2					8x21.6=172.8
16	7.60	1.85	150.5	15.4	13.6	21.4
17-21	assumed: equal to #...			5x...	5x...	5x...
TLA (m^2)				.....	.....	.....

The top 5 leaves (#17-21) were not measured. Their SLA cannot be assumed to be equal to `Lf#16` , because in this phase leaves already begin to decrease in size towards the top. There is no simple way to estimate the SLA of these leaves. A possibility would be to assume the downward trend observed in the RBWxRBH to continue linearly to the top leaves and apply that trend to the RL. The uncertainty about the validity of this way of calculation is too great to warrant estimation of the TLA based on this calculation.

Length Leaf#1: .... (Lf#16: 10.25 m).
Trunk diameter where Leaf#1 is attached: 0.55 m.
Crown projection area: π x $(10.25/\sqrt{2} + 0.275)^2$ = 177.8 m^2.
TLA (estimate based on RL): ..... m^2.
LAI: ..... m^2 / 177.8 m^2 = ...

Palm #27: Adult Vegetative phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-12	assumed: equal to #13			12x15.6=187.2	12x13.9=166.8	
1	n.r.	n.r.	133.7			19
2	n.r.	n.r.	137.2			19.5
3	n.r.	n.r.	136.4			19.4
4	n.r.	n.r.	133.3			19.0
5	estimate: (#4+#6)/2					19.9
6	n.r.	n.r.	145.3			20.7
7	n.r.	n.r.	136.7			19.4
8	n.r.	n.r.	138.4			19.7
9	n.r.	n.r.	144.0			20.5
10	n.r.	n.r.	144.4			20.5
11	n.r.	n.r.	142.8			20.3
12	estimate: (#11+#13)/2					20.8
13	7.70	1.89	149.5	15.6	13.9	21.3
14-15	estimate: (#13+#16)/2			2x15.35=30.7	2x13.7=27.4	
14	n.r.	n.r.	145.8			20.7
15	estimate: (#14+#16)/2					21.2
16	7.41	1.83	152.1	15.1	13.5	21.6
17-19	assumed: equal to #16			3x15.1=45.3	3x13.5=40.5	
17	n.r.	n.r.	147.8			21.0
18	estimate: (#17+#19)/2					21.4
19	n.r.	n.r.	153.2			21.8
TLA (m^2)				293.9	262.1	387.7

Length Leaf#1: ... (Lf#13: 10.05 m).
Trunk diameter where Leaf#1 is attached: 0.61 m.
Crown projection area: $\pi \times (10.05/\sqrt{2} + 0.305)^2 = 172.6$ m^2.
TLA (estimate based on RL): 293.9 m^2.
LAI: 293.9 m^2 / 172.6 m^2 = 1.70.

Palm #28: Generative-1 phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-2	assume equal to #3			2x14.2=28.4	2x13.2=26.4	2x19.3=38.6
3	7.00	1.80	135.9	14.2	13.2	19.3
4-9	estimate: (#3+#10)/2			6x13.85=83.1	6x13.2=79.2	6x20.15=120.9
10	6.65	1.80	148.0	13.5	13.2	21.0
11-19	estimate: (#10+#20)/2			9x11.35=102.2	9x11.95=107.6	9x17.2=154.8
20	4.55	1.45	94.0	9.2	10.7	13.4
21-27	estimate: #20 - 3.5/10(#10-#20)			7x7.7=53.9	7x9.83=68.8	7x10.74=75.2
TLA (m^2)				**304.5**	**319.1**	**443.2**

Length Leaf#1 (assumed equal to Leaf#3): 9.28 m.
Trunk diameter where Leaf#1 is attached: 0.53 m.
Crown projection area: $\pi \times (9.28/\sqrt{2} + 0.265)^2 = 146.4$ m^2.
TLA (estimate based on RL): 304.5 m^2.
LAI: 304.5 m^2 / 146.4 m^2 = 2.08.

Palm #29: Generative-1 phase, fv Molat Berduri

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...			
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH	
						Y = 0.1662 X - 1.6816 (R^2=0.914)	Y = 0.1422 X (R^2=0.895)
1-3	assumed: equal to #4						3x18.4=55.2
4	n.r.	n.r.	129.7				18.4
5-6	estimate: (#4+#7)/2						2x19.45=38.9
7	n.r.	n.r.	144.3				20.5
8-9	estimate: (#7+#10)/2						2x20.4=40.8
10	n.r.	n.r.	142.9				20.3
11	n.r.	n.r.	137.9				19.6
12	estimate: (#11+#13)/2						19.8
13	n.r.	n.r.	139.8				19.9
14	n.r.	n.r.	136.5				19.4
15	estimate: (#14+#16)/2						19.5
16	n.r.	n.r.	138.0				19.6
17	n.r.	n.r.	126.5				18.0
18	estimate: (#17+#19)/2						17.5
19	n.r.	n.r.	118.8				16.9
20	n.r.	n.r.	113.7				16.2
21	n.r.	n.r.	100.3				14.3
22	estimate: (#21+#23)/2					12.4	
23	n.r.	n.r.	72.7			10.4	
24	n.r.	n.r.	64.3				9.1

25	estimate: (#24+#26)/2					7.4
26	n.r.	n.r.	40.2			5.7
27	n.r.	n.r.	31.5			4.5
28	n.r.	n.r.	19.2			2.7
TLA (m^2)						**447.0**

Length Leaf#1: ?
Trunk diameter where Leaf#1 is attached: 0.50 m.
Crown projection area: π x ([?]/$\sqrt{2}$ + 0.25)^2 = ? m^2.
TLA (estimate based on RBWxRBH): 447.0 m^2.
LAI: 447.0 m^2 / [?] m^2 = ?

Palm #30: Adult Vegetative phase, fv Molat

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1-9	assume: equal to #10			9x15.5=139.5	9x13.0=117.0	
1	n.r.	n.r.	89.7			12.8
2-3	estimate: (#1+#4)/2					2x12.85=25.7
4	n.r.	n.r.	90.9			12.9
5-9	estimate: (#4+#10)/2					5x13.1=65.5
10	7.65	1.76	93.3	15.5	13.0	13.3
11-16	assume: equal to #10			6x15.5=93.0	6x13.0=78.0	
11-12	estimate: (#10+#13)/2					2x13.15=26.3
13	n.r.	n.r.	91.6			13.0
14	n.r.	n.r.	92.6			13.2
15	estimate: (#14+#16)/2					13.1
16	n.r.	n.r.	90.9			12.9
TLA (m^2)				**248.0**	**208.0**	**208.7**

Length Leaf#1: ... (Lf#10: 10.45 m).
Trunk diameter where Leaf#1 is attached: 0.48 m.
Crown projection area: π x (10.45/$\sqrt{2}$ + 0.24)^2 = 182.9 m^2.
TLA (estimate based on RL): 248.0 m^2.
LAI: 248.0 m^2 / 182.9 m^2 = 1.36.

Palm #31: Adult Vegetative phase, fv Molat

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1	7.62	1.63	76.0	15.5	12.0	10.8
2-10	estimate: (#1+#11)/2			9x15.25=137.3	9x12.25=110.3	
2	n.r.	n.r.	78.7			11.2
3	estimate: (#2+#4)/2					11.6
4	n.r.	n.r.	83.9			11.9
5	n.r.	n.r.	83.9			11.9
6	estimate: (#5+#7)/2					12.2
7	n.r.	n.r.	87.1			12.4
8	n.r.	n.r.	86.4			12.3
9	n.r.	n.r.	84.5			12.0
10	estimate: (#9+#11)/2					12.4
11	7.4	1.70	89.9	15.0	12.5	12.8

12-16	assume: equal to #11			5x15.0=75.0	5x12.5=62.5	
12	n.r.	n.r.	89.2			12.7
13	estimate: (#12+#14)/2					12.5
14	n.r.	n.r.	86.1			12.2
15	n.r.	n.r.	87.2			12.4
16	assume equal to #15					12.4
TLA (m^2)				**242.8**	**197.3**	**193.7**

Length Leaf#1: 10.47 m.
Trunk diameter where Leaf#1 is attached: 0.47 m.
Crown projection area: π x $(10.47/\sqrt{2} + 0.235)^2$ = 183.3 m^2.
TLA (estimate based on RL): 242.8 m^2.
LAI: 242.8 m^2 / 183.3 m^2 = 1.32.

Palm #32: Adult Vegetative phase, fv Tuni

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1-3	assume equal to #4			3x15.5=46.5	3x12.9=38.7	
1	n.r.	n.r.	132.3			18.8
2	estimate: (#1+#3)/2					19.2
3	n.r.	n.r.	137.3			19.5
4	7.65	1.75	132.0	15.5	12.9	18.8
5-19	assume equal to #4			15x15.5=232.5	15x12.9=193.5	
5	estimate: (#4+#6)/2					19.0
6	n.r.	n.r.	135.1			19.2
7	n.r.	n.r.	140.4			20.0
8-9	estimate: (#7+#10)/2					2x19.8=39.6
10	n.r.	n.r.	137.8			19.6
11-12	estimate: (#10+#13)/2					2x20.15=40.3
13	n.r.	n.r.	145.6			20.7
14-19	estimate: (#1+#3+#4+#6+#7+#10+#13)/7					6x19.5=117.0
TLA (m^2)				**294.5**	**245.1**	**371.7**

Length Leaf#1 (assumed equal to Leaf#4): 10.16 m.
Trunk diameter where Leaf#1 is attached: 0.61 m.
Crown projection area: π x $(10.16/\sqrt{2} + 0.305)^2$ = 176.2 m^2.
TLA (estimate based on RL): 294.5 m^2.
LAI: 294.5 m^2 / 176.2 m^2 = 1.67.

Palm #33: Adult Vegetative phase, fv Molat

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1-?	assume equal to #13					
13[?]	6.68	1.78	127.6	13.6	13.1	18.1
14-20?	assume equal to #13					
TLA (m^2)				.....	.....	.....

Length Leaf#1 (assumed equal to Leaf#13): 8.91 m.
Trunk diameter where Leaf#1 is attached: 0.45 m.
Crown projection area: π x $(8.91/\sqrt{2} + 0.225)^2$ = 133.8 m^2.

TLA (estimate based on RL): ? m^2.
LAI: ? m^2 / 133.8 m^2 = ?.

Because the tree was damaged during felling, too few data could be recorded for TLA calculation (see data sheet of Palm#33 in Appendix A).

Palm #34: Generative-2 phase, fv Tuni

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-2	assume: equal to #3			2x15.0=30.0	2x13.6=27.2	
1	assume: equal to #2					21.7
2	n.r.	n.r.	152.7			21.7
3	7.40	1.85	161.9	15.0	13.6	23.0
4-24	estimate: (#3+#25)/2			21x8.465=177.8		
4-5	estimate: (#3+#6)/2					2x23.2=46.4
6	n.r.	n.r.	164.7			23.4
7-8	estimate: (#6+#9)/2					2x23.25=46.5
9	n.r.	n.r.	162.3			23.1
10	n.r.	n.r.	160.1			22.8
11-12	estimate: (#10+#13)/2					2x22.15=44.3
13	n.r.	n.r.	151.3			21.5
14-15	estimate: (#13+#16)/2					2x19.8=39.6
16	n.r.	n.r.	127.2			18.1
17-18	estimate: (#16+#19)/2					2x16.3=32.6
19	n.r.	n.r.	101.9			14.5
20-21	estimate: (#19+#22)/2					2x10.65=21.3
22	n.r.	n.r.	47.9			6.8
23	n.r.	n.r.	34.3			4.9
24	estimate: (#23+#25)/2					3.4
25	0.95	n.r.	12.6	1.93		1.8
TLA (m^2)				**224.7**	-	**437.4**

Length Leaf#1 (assumed equal to Leaf#3): 9.68 m.
Trunk diameter where Leaf#1 is attached: 0.54 m.
Crown projection area: π x $(9.68/\sqrt{2} + 0.27)^2$ = 159.0 m^2.
TLA (estimate based on RL): 224.7 m^2.
LAI: 224.7 m^2 / 159.0 m^2 = 1.41.

Palm #35: Generative-2 phase, fv Ihur

Leaf#	RL (m)	LLTL (m)	RBWxRBH (cm^2)	SLA (Y) estimate (m^2) based on ...		
				X = RL (Y = 2.032 X (R^2=0.991))	X = LLTL (Y = 7.359 X (R^2=0.715))	X = RBWxRBH (Y = 0.1422 X (R^2=0.895))
1-6	assume: equal to #7			6x13.5=81.0	6x12.1=72.6	
1	n.r.	n.r.	94.6			13.5
2	estimate: (#1+#3)/2					13.5
3	n.r.	n.r.	95.2			13.5
4	n.r.	n.r.	101.0			14.4
5	estimate: (#4+#6)/2					14.7
6	n.r.	n.r.	104.6			14.9
7	6.64	1.65	104.0	13.5	12.1	14.8

8-10	estimate: (#7+#11)/2			3x13.2=39.6	3x12.3=36.9	
8	n.r.	n.r.	107.8			15.3
9	estimate: (#8+#10)/2					15.4
10	n.r.	n.r.	109.3			15.5
11	6.36	1.70	107.0	12.9	12.5	15.2
12-16	estimate: (#11+#17)/2			5x10.85=54.3	5x11.45=57.3	
12	estimate: (#11+#13)/2					14.9
13	n.r.	n.r.	102.9			14.6
14	n.r	n.r	95.5			13.6
15	estimate: (#14+#16)/2					13.2
16	n.r.	n.r.	90.0			12.8
17	4.35	1.42	82.8	8.8	10.4	11.8
18-27	estimate:#17-(10/2)(#17/11)			10x4.8=48.0	10x5.67=56.7	
18	n.r.	n.r.	77.3			11.0
19	estimate: (#18+#20)/2					9.4
20	n.r.	n.r.	54.5			7.7
21	n.r.	n.r.	44.1			6.3
22	estimate: (#21+#23)/2					5.6
23	n.r	n.r	34.5			4.9
24-27	estimate: #23-4/2(#23/5)					4x2.94=11.8
TLA (m^2)				**258.1**	**258.5**	**298.3**

Length Leaf#1 (assumed equal to Leaf#7): 8.61 m.
Trunk diameter where Leaf#1 is attached: 0.41 m.
Crown projection area: $\pi \times (8.61/\sqrt{2} + 0.205)^2 = 124.4\ m^2$.
TLA (estimate based on RL): 258.1 m^2.
LAI: 258.1 m^2 / 124.4 m^2 = 2.07.

The SLA of the youngest leaves was estimated by assuming a linear decrease to zero from the last leaf for which data were recorded.

Palm #36: Generative-2 phase, fv Makanatol

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1	6.34	1.65	108.9	12.9	12.1	15.5
2-20	estimate: (#1+#11)/2			9x12.15=109.4	9x11.75=105.8	
2	n.r.	n.r.	104.4			14.8
3	estimate: (#2+#4)/2					14.6
4	n.r.	n.r.	100.7			14.3
5	n.r.	n.r.	101.2			14.4
6-7	estimate: (#5+#8)/2					2x14.45=28.9
8	n.r.	n.r.	102.0			14.5
9	n.r.	n.r.	102.6			14.6
10	estimate: (#9+#11)/2					14.3
11	5.62	1.55	98.8	11.4	11.4	14.0
12-17	estimate: (#11+#18)/2			6x9.54=57.2	6x10.4=62.4	
12	n.r.	n.r.	95.3			13.6
13	estimate: (#12+#14)/2					13.3
14	n.r.	n.r.	90.8			12.9

15	n.r.	n.r.	83.3			11.8
16-17	estimate: (#15+#18)/2					2x10.95=21.9
18	3.78	1.28	71.1	7.68	9.42	10.1
19-28	estimate:#18-(10/2)(#18/11)			10x4.19=41.9	10x5.14=51.4	
19	n.r.	n.r.	60.5			8.60
20	estimate: (#19+#21)/2					7.42
21	n.r.	n.r.	43.9			6.24
22	n.r.	n.r.	30.8			4.38
23	estimate: (#22+#24)/2					3.56
24	n.r	n.r	19.2			2.73
25	n.r.	n.r.	17.0			2.42
26	estimate: (#25+#27)/2					1.58
27	n.r.	n.r.	5.18			0.74
28	n.r.	n.r.	1.44			0.20
TLA (m^2)				**240.5**	**252.5**	**281.4**

Length Leaf#1: 8.54 m.
Trunk diameter where Leaf#1 is attached: 0.41 m.
Crown projection area: π x $(8.54/\sqrt{2} + 0.205)^2 = 122.5$ m^2.
TLA (estimate based on RL): 240.5 m^2.
LAI: 240.5 m^2 / 122.5 m^2 = 1.96.

For the SLA estimation of the youngest leaves based on RL and LLTL it was assumed that there is a linear decrease in RL and LLTL to zero from the last leaf for which these data were recorded.

Palm #37: Generative-1 phase, fv Ihur

Leaf#	**RL (m)**	**LLTL (m)**	**RBWxRBH (cm^2)**	**SLA (Y) estimate (m^2) based on ...**		
				X = RL (Y = 2.032 X (R^2=0.991))	**X = LLTL (Y = 7.359 X (R^2=0.715))**	**X = RBWxRBH (Y = 0.1422 X (R^2=0.895))**
1-6	assume: equal to #7			6x15.7=94.2	6x13.6=81.6	
1	n.r.	n.r.	158.1			22.4
2	estimate: (#1+#3)/2					21.6
3	n.r.	n.r.	146.4			20.8
4	n.r.	n.r.	155.8			22.2
5-6	estimate: (#4+#7)/2					2x22.1=44.2
7	7.75	1.85	154.7	15.7	13.6	22.0
8-18	estimate: (#7+#19)/2			11x16.5=181.5	11x14.3=157.3	
8-9	estimate: (#7+#10)/2					2x22.65=45.3
10	n.r.	n.r.	164.0			23.3
11-12	estimate: (#10+#13)/2					2x24.05=48.1
13	n.r.	n.r.	174.2			24.8
14-18	estimate: (#13+#19)/2					5x25.4=127.0
19	8.50	2.04	182.9	17.3	15.0	26.0
20-24	assume equal to #19			5x17.3=86.5	5x15.0=75.0	5x26.0=130.0
TLA (m^2)				**395.2**	**342.5**	**577.7**

Length Leaf#1 (assume equal to Lf#7): 10.27 m.
Trunk diameter where Leaf#1 is attached: 0.58 m.
Crown projection area: π x $(10.27/\sqrt{2} + 0.29)^2 = 179.2$ m^2.
TLA (estimate based on RL): 395.2 m^2.
LAI: 395.2 m^2 / 179.2 m^2 = 2.21.

Summaries of calculations

The development of the size of consecutive leaves in a crown in the Establishment, the Adult Vegetative and the Generative phase is exemplified in Figure 6.6, which shows small leaves slowly getting larger in the E-phase, large leaves staying the same size in the AV-phase, and leaves getting quickly smaller in the G2-phase.

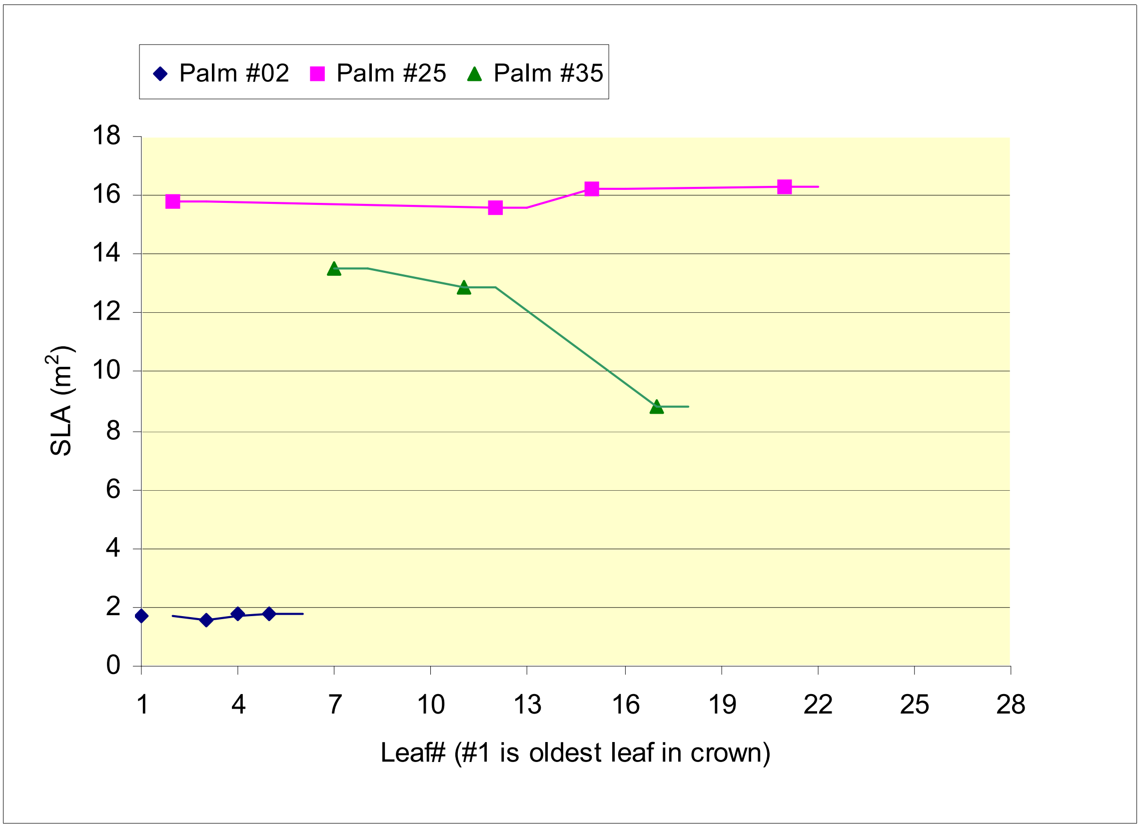

Figure 6.6 Single leaf area (SLA) of leaves in the crown of a sago palm axis in the E-phase (Palm #02), the AV- phase (Palm #25) and the G2- phase (Palm #35).

In Table 6.4 and Figure 6.7 the results of the TLA and LAI estimates are summarized. The palms for which these estimates could not be made (#26, #29, #33) are left out. The palms are ordered according to probable physiological age as presented (for the AV- and G-phase) in Table 4.16. Palm #15 ("Tuni", AV-phase), not included in Table 4.16, is ranked between Palms #17 and #11 of the same variety because it has intermediate values for height of, and number of leaf scars on the leafless trunk (see Table 4.1).

Table 6.4 Total leaf area (TLA ; estimate based on rachis lengths) and Leaf area index (LAI) per axis of various varieties of sago palms in various stages of development.

Palm#	Development phase	Folk variety	Number of green leaves	Number of leaf scars on leafless trunk	TLA (m^2)	LAI per axis
01	E	Ihur	2	n.a.	2.69	1.02
02		Tuni	5	n.a.	8.70	1.54
12	AV	Tuni	14	33	236.9	1.02
31		Molat	16	50	242.8	1.32
30		Molat	16	55	248.0	1.36
13			16	53	274.5	1.38
10			21	63	331.1	1.62
14		Molat Berduri	22	46	388.2	1.59
25		Ihur	21	60	334.1	1.84
17		Tuni	19	43	336.3	1.32
15			16	57	250.2	1.19
11			20	71	322.6	1.67
16			19	78	289.7	1.56
20		Putih	14	54	217.6	1.19
19			14	72	196.9	1.25
21			14	70	226.4	1.08
27		Tuni	19	107	293.9	1.70
32			19	109	294.5	1.67
09	G1	Tuni	20	121	261.8	1.49
37		Ihur	24	85	395.2	2.21
28		Tuni	27	115	304.5	2.08
35	G2	Ihur	27	100	258.1	2.07
34		Tuni	25	115	224.7	1.41
18		Molat	17	63	114.8	1.49
36		Makanatol	28	165	240.5	1.96

n.a. = not applicable

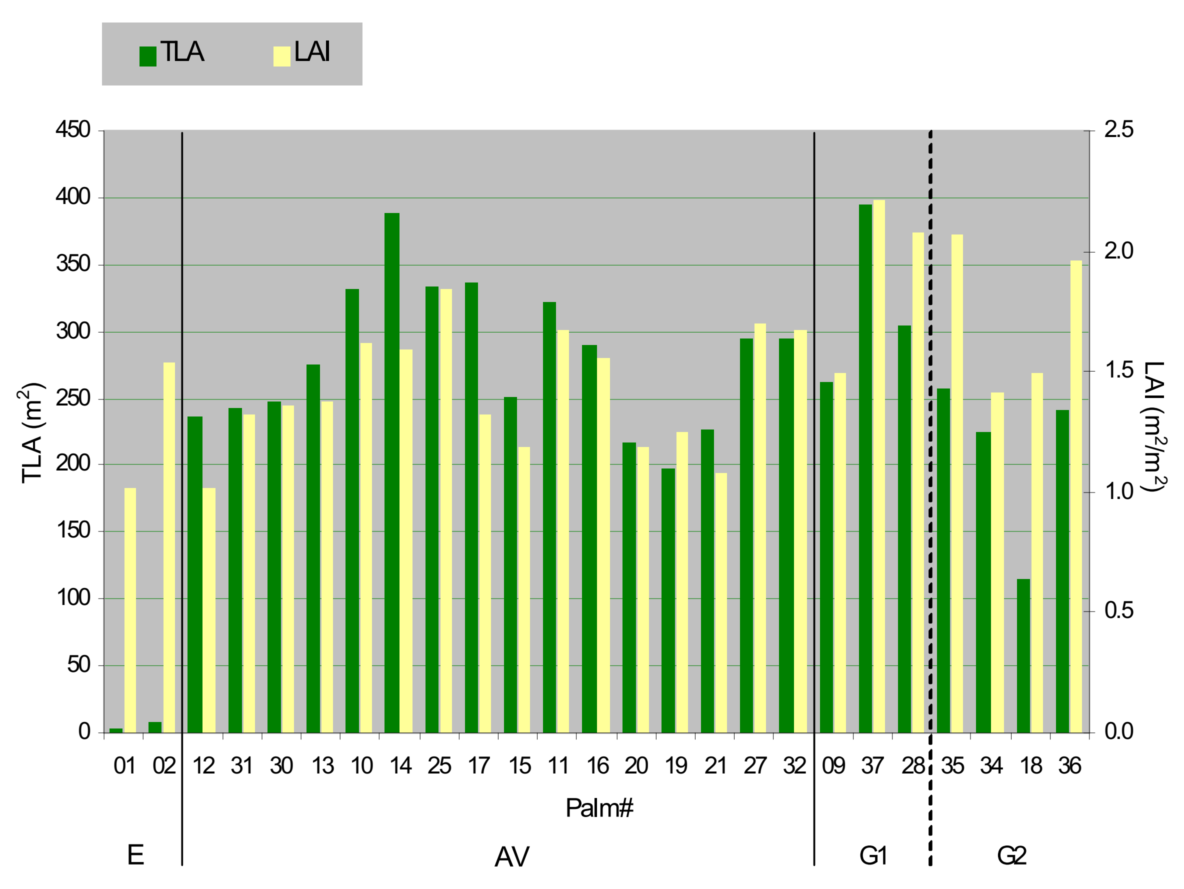

Figure 6.7 Total leaf area (TLA) and Leaf area index (LAI) of sago palms ordered by development phase (E = Establishment phase, AV = Adult Vegetative phase, G = Generative phase)

6.3 Discussion

The methodology to estimate TLA and LAI of individual axes has been explained and demonstrated. Estimation was not simple and had to be based on many assumptions. Also, most leaves of which the area was estimated by a regression equation had dimensions outside the range for which the regression equation was calculated. This is not statistically sound. I used data of relatively small leaves of a relatively small tree (Fig. 6.8) to calculate the equations because these leaves were easier to handle and the tree was better accessible than the larger ones. This now appears to have been a short-sighted decision. The relation between leaf area and other leaf properties of larger leaves still needs to be established with more accuracy.

Published findings in oil palm and coconut palm suggested that RBWxRBH would be a good estimator for SLA in sago palm, and therefore for SLA estimation I measured mostly this property . That it proved not to be the best SLA estimator for sago palm may be caused by the fact that the RB in sago palm is concave rather than triangular as in the other palms. Therefore, in sago palm leaves differences in thickness and curvedness of the RB may result in very different cross section areas where very similar RBWxRBH's are measured (and vice versa), whereas it is the cross section area which would be proportional to the SLA.

Figure 6.8 Palm #18, a relatively small sago palm with small leaves on which leaf area estimation data were based (photo shows cleaned trunk with c. 6-8 oldest green leaves already removed for sampling). [photo nr. 89.08-091-33]

The angle between the lowest leaf and the trunk in the AV-phase probably increases gradually from the E-phase's 30º in the early AV stages to 45º towards the G-phase (for it is in the early G-phase that I estimated the angle at 45º (see Fig.6.5a)). The observation that for local sago palm users an axis is nearing flowering if it is "terbuka jaga" (with open/spreading leaves (see Data Sheet Palm#37)), indicating that they were closer to the trunk before, points in the same direction. Therefore, the LAI of palms in the early stages of the AV-phase may have been underestimated.

Keeping these comments on the methodology to estimate TLA and LAI in mind, the following observations can be made.
The TLA of sago palm axes in the AV-phase shows a range of about 200-325 m^2, the only representative of variety Molat Berduri (Palm #14) exceeding this range with a TLA of about 390 m^2. The TLA in the G- phase before fruiting (G1- and G2-phase) mostly remains within the same range, possibly exceeding it for a short period early in that stage.
The development of the LAI of an individual axis showed an upward trend from between 1 and 1.5 in the E-phase to between 1.25 and 1.75 in the AV-phase, to more than 2 in the early G-phase, followed by a decrease of the LAI to about 1.5 again in the late G-phase before fruiting.
From fruiting onwards an axis will gradually shed all its leaves and TLA and LAI will drop to zero. No fruiting palms were among the sampled ones to exemplify this.
No clearer relationship between TLA or LAI and axis age could be established. Probably the genetic background and the growing circumstances of the sampled palms were too varied for the small number of palms that were sampled. That, e.g., nutrient deficiencies and low light intensities not only reduce the leaf unfolding rate, but also the leaf area of new leaves was demonstrated for sago palm seedlings (PAQUAY *et al*. 1986).

Figure 6.7 shows a parallel trend in TLA and LAI. This may be explained by the fact that in palm tree axes, with their single apical meristem and with their leaves of fairly constant dimensions, more leaf area does not normally mean larger leaves, and therefore a larger crown diameter, but more leaves, and therefore a denser crown, and hence a higher LAI. In this figure a few cases in which palms with very similar LAI's have very different TLA's strike the eye. Where this concerns palms from different phases, such as Palm #01 (E-phase) and Palm #12 (AV-phase), this is easily explained by their obvious difference in overall size while the ratio of TLA to Crown projection area (CPA) may remain about the same. The case of Palm #34 vs Palm #18, both G2-phase palms, may seem less easily explained, but has the same cause, because Palm #18 concerned, as mentioned above, an exceptionally small specimen.

Whether TLA or LAI can be related to trunk starch content will be investigated in Chapter 7.

Acknowledgement

For putting sample leaflets through a leaf area meter at Lembang, West Java, 2500 km from my Seram field lab, I am indebted to Ir Lieuwe S. ANEMA, at the time (1990) lecturer of genetics at Pattimura University, Ambon, Indonesia.

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7 Trunk starch accumulation and depletion in sago palm

Sago palm development phase codes

AV - Adult Vegetative.
G - Generative.
  G1 - from flower initiation to full extension of 1st-order inflorescence branches.
  G2 - from full extension of 1st-order inflorescence branches to full extension of 3rd-order inflorescence branches.
  G3 - from full extension of 3rd-order inflorescence branches to shedding of fruits.
(See Chapter 4 for detailed explanation of these different phases.)

7.1 Introduction

Local informants in Hatusua village (W. Seram, Maluku, Indonesia), e.g., Mr Josephus TUPAMAHU (1987, pers.comm.) with 40 years experience in exploiting sago palms for his subsistence needs, told me that young trunks as well as trunks with mature fruits contain little starch, and that old but not-yet-flowering trunks contain much starch. Apparently, (1) the trunk is not filled with starch immediately as it is built, at least not in the early AV-phase, and (2) in the G-phase the palm itself uses the starch it produced and accumulated earlier.

Local informants also told me that the top part of the trunk where the leaves are attached is usually not harvested *karena basah* (because it is wet), and that wet pith contains little to no starch. Apart from the top part, traditional sago palm exploiters usually do not process the basal part of the trunk either, leaving a stump of 50 to 75 cm standing in the field. They say it contains too little starch to make processing worthwhile. This notion may partly be inspired by the difficulty of manually processing the lower trunk part. In this part the fibres scattered in the pith are the hardest as they become more lignified with age. Also, the difficulty of felling a trunk with an axe closer to the ground than 50 to 75 cm may play a role. All in all, apparently not only does the starch content in a sago trunk depend on age and development phase of the trunk, but also the distribution of starch in a harvestable trunk is not even.

Unravelling the evolution of starch storage and distribution is the main purpose of this study, and of this chapter in particular: When and where is starch stored in the trunk of a sago palm? During the investigations it became clear that not only time drives the starch accumulation process, but also the palm's genetic make-up and its habitat. Any traditional sago exploiter would tell you so, but the extent to which this was the case - sometimes apparently even overriding age difference - only appeared in the course of time. Limited research resources (time, plant material, manpower) forced me to focus on the age factor. And even then I was limited in my choice of palms by the availability of palms of different ages in the semi-wild stands I was to work in.

In the following sections I will first review what is known about the starch accumulation process in time. Then I will present how I tried to expand this knowledge with more detail and what the results of these efforts were. In the discussion of the results, I will also discuss the influence of genetic make-up and the environment, and how this compares with what is known about these influences in literature. As an aside I will look into the possibility of linking the leaf area data found in Chapter 6 to starch content. Finally I will explore what the starch content of a typical sago trunk could be.

7.2 Literature review on trunk starch accumulation and depletion

- Palms in general

Several palm species accumulate starch in their stems:

> "At least fourteen species belonging to eight genera ... are exploited, but of these only *Metroxylon* and *Arenga* in the Old World, and *Mauritia* in the New, are of major importance as palm starch sources." (RUDDLE & JOHNSON *et al.* 1978:3.)

The depletion of this starch in the generative phase has only been described in general terms:

> "Starch accumulation in palms on a massive scale as found in *Metroxylon* is almost always associated with the hapaxanthic flowering method. ... In the hapaxanthic sago palms, starch is accumulated within the pith of the stem and is mobilised at the onset of the production of a mass of inflorescences in the axils of the most distal leaves, giving a "terminal" inflorescence state ... As flowering proceeds, the stem apex aborts and flowering and fruiting are followed by the death of the stem. ... All Southeast Asian hapaxanthic palms appear to have been used from time to time as sources of sago except for the hapaxanthic rattans, which presumably have stems too thin for starch accumulation significant for extraction." (DRANSFIELD 1977:77.)

I have not found any published information on the evolution of trunk starch accumulation, particularly in the AV-phase, in other palms than sago palm.

- Sago palm in particular

In many overview articles on the sago palm and the exploitation of its starch reserves it is stated that the trunk should be harvested before flowering because the starch content is at its peak then, and that after maturation of the fruits the starch reserves are depleted.
The statement on this matter in the article by DEINUM & SETIJOSO (1932), who were agricultural extension officers in the Moluccas during colonial times, is remarkable in that also location and quality of the starch in relation to trunk age is briefly referred to:

> "*Jonge boomen bevatten slechts aan den wortelhals een weinig meel. Kort voor den bloei is het meelgehalte in den kruin het hoogst. Wil men de sago voor sagopap gebruiken, dan velt men den boom, vóórdat de bloemtros gevormd is. Is de bloemtros reeds volgroeid dan wordt het meel grover en is dit alleen nog te gebruiken voor sagobroodjes. Is de boom uitgebloeid dan bevat het merg vrijwel geen meel meer*."
> = "[Young trees only contain a little starch near the trunk base where the roots are attached. Shortly before flowering, flour content is highest in the crown. If the sago is to be used for sago pudding, the tree is felled before the inflorescence is formed. When the inflorescence is full-grown, the flour becomes coarser and can only be used for small sago loaves. Once the tree has flowered, the pith hardly contains any flour any more]."
> (In Fig. 7.1 the two sago starch products mentioned are illustrated.)

Hereafter in the same article they explain why starch from flowering trees is not suitable to make sago pudding:

> "*Meel afkomstig van reeds bloeiende boomen is hiervoor niet bruikbaar, het bindt en stijft niet voldoende*."
> = "[Flour from trees which are already flowering is unusable for this: it does not sufficiently bind and stiffen]."
> (DEINUM & SETIJOSO 1932:109,125)

These observations or assumptions may be underpinned and generalised by the logical assumptions that

1. The amount of starch increases as long as the energy produced by the photosynthetic apparatus of the axis is more than the energy needed for the axis' maintenance and growth.

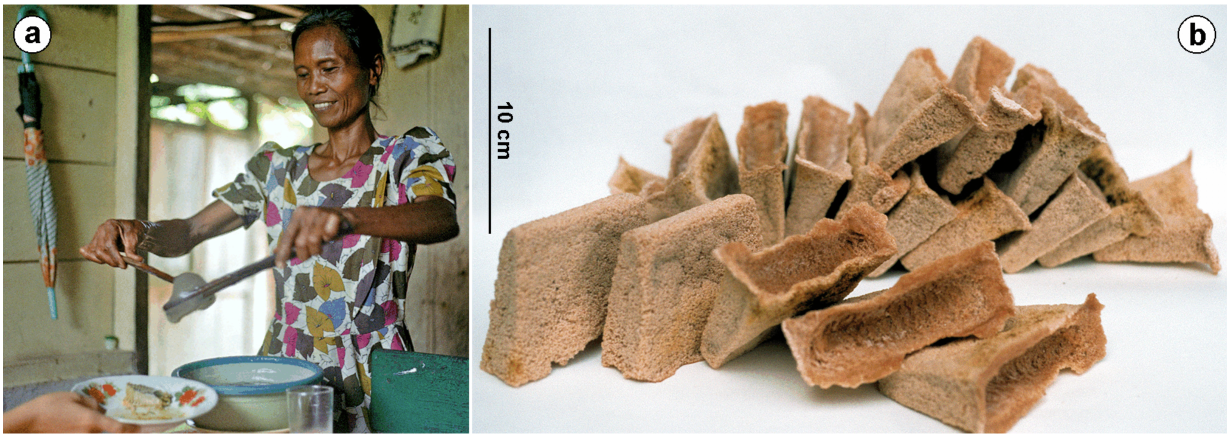


Figure 7.1 Traditional sago starch products in the Moluccas: (a) *papeda* (pudding (bland, not sweet)) and (b) *sagu lempeng* (small sago loaves).
[a: photo nr. 90.11-145-07, oct/nov1990 Hatusua, West Seram ; b: photo nr. tc-103-01, wed06feb2002]

2. As soon as the energy needed for maintenance and growth exceeds energy production, the energy reserves in the form of trunk starch will be tapped, bringing along enzymatic hydrolysis and quality degradation of the starch and decrease of starch content. This is the case when towards the end of an axis' life the enormous inflorescence has to be built and the fruits have to be filled, while the photosynthesizing surface of the axis diminishes.

I cannot explain why in young palms there would be a little starch in the trunk only near the base.

A study toward finding a simple way to assess starch content from external characters of the palm was done by VAN KRAALINGEN (1986) in the Lower-Sepik area of East Sepik Province in Papua New Guinea (see discussion in Section 7.6). He estimated the starch yield of 19 sago palms of a particular variety (viz. the highest-yielding wild variety in his study area) by sampling the pith, while some external characters of these palms which he considered likely to vary with starch yield were also recorded. VAN KRAALINGEN showed that the starch yield could only be satisfactorily estimated if sampling intensity per trunk was high (at height intervals of 0.5 or 1.0 m), because starch density (grams of dry starch per cubic centimetre of pith) appeared to vary considerably with height in the trunk. The lowest densities did not occur at the top or the base of the trunk but somewhere in between, the height where it occurred varying per palm. VAN KRAALINGEN suggested that the distribution depended on "physiological stage (i.e. flowering or not flowering)".

YAMAMOTO *et al*. (2003) studied the evolution of starch and total sugar content in the pith of sago palms growing in Sarawak, Malaysia. Concerning starch distribution, they found that in six- to eight-year-old palms the starch percentage sharply decreased from the base to the top, and from the centre to the periphery of the trunk; in older palms the distribution was more even. Maximum starch percentage was reached in 8- to 10-year old palms. Where starch percentage increased, total sugar percentage decreased, falling to 2-4% when starch percentage was at its peak. Total sugar percentage increased again during the seed-setting stage. Concerning starch accumulation in time, they found that accumulation was rapid starting 0-2 years after the onset of trunk formation, reaching maximum starch percentage at about 4 years after the onset. The percentage remained constant until flowering stage and decreased during seed-setting stage.

Only the summary, the figures and the tables of this publication are in English; the rest is in Japanese, which I cannot yet read or understand. From the English parts it is not quite clear what is meant by starch percentage (probaly weight percentage in the dry matter, as percentages of over 70 were found), nor by age ("estimated years from sucker planting or

sucker emergence"). Also the variety of sago palm used remains unknown. Moreover, the contents figures for the entire middle sections of trunks (between 90 cm from ground level to 90 cm below the node of the lowest living leaf) were lumped together. And finally, weight percentage (g starch/g pith) was (probably) used to compare starch contents, in stead of starch density (g starch/cm^3 pith), which is problematic because starch weight is not independent from pith weight.
What is clear is that they found an increase of starch percentage in the trunk pith in the AV-phase and a decrease somewhere in the G-phase, the increase being more rapid earlier in the AV-phase than later. The increase in total sugar content and the decrease in starch content during seed setting suggest that the starch is transformed into sugars to be transported from the trunk to the fruits.

All these studies confirm the sago exploiter's observations that (1) older trunks have a higher starch density than younger trunks, and that (2) starch is not, or not always, distributed evenly in the trunk. However, a comprehensive and more detailed timetable of the evolution of trunk starch accumulation and depletion, needed, e.g., to pinpoint the right time to harvest a trunk, is still lacking. Such a timetable is what I tried to establish in my study.

7.3 Observations

7.3.1 Materials & methods

Non-destructive trunk pith sampling methods were still not known. There is no method by which the rotting of the tissues around a sampling opening in the trunk could be stopped for a prolonged period. Moreover, exposed pith will always attract palm weevils (*Rhynchophorus* sp.) which will lay their eggs in the pith. The larvae hatching from the eggs will feast on the starch. Therefore, real-time monitoring of trunk starch content was impossible. Instead, a series of different palms was felled, measured and dissected; of 27 of these the trunk pith was sampled. These palms were positioned on a tentative time axis afterwards (after as many clues to their age as possible had been gathered from their external and internal morphology) to arrive at a development-in-time picture. The positioning of the sampled trunks on a time axis is discussed and presented in Chapter 4 (see Table 4.16).

With each palm felled, a number of environmental and morphological properties was routinely measured with a view to their possible influence on the starch accumulation process. See Section 4.4 for materials and methods used for these measurements.

All observations are gathered in the Sago Palm Data Sheets in Appendix A.

- Trunk pith

Taking pith samples (Fig. 7.2)

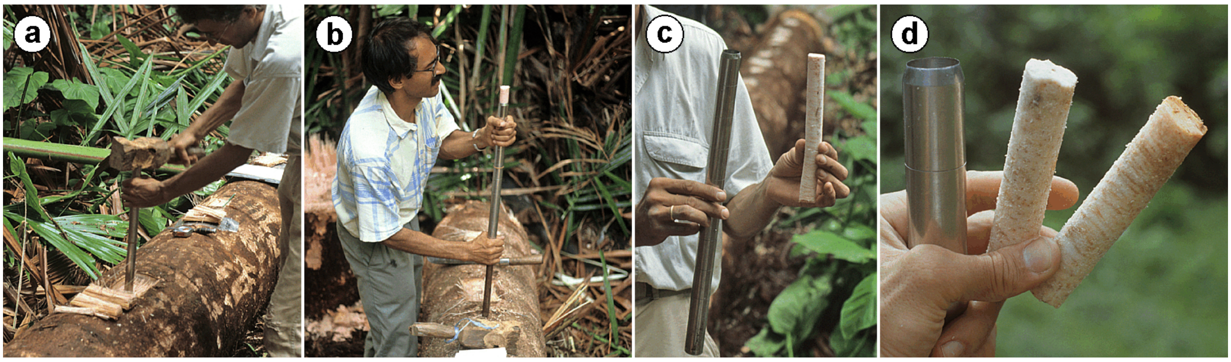


Figure 7.2 Taking trunk pith samples from a felled sago palm: a. the auger is hammered into the pith through a window opened in the *wa'ah*. b. the pith sample is pushed out of the auger with a wooden stick. c. auger and intact pith sample. d. close-up of business end of auger and of pith sample broken in two.
[a: photo nr. 90.09-140-05, sat22sep1990 ; b: photo nr. 90.10-143-04, oct1990 ; c: photo nr. 90.09-140-08, sat22sep1990 ; d: photo nr. 89.08-094-19, mon21aug1989 ; a-d: Hatusua, West Seram.]

Pith samples were taken from felled palms with an auger specially made for this purpose from a stainless steel tube, length 50 cm, outer Ø 3.2 cm, inner Ø 2.5 cm, sharpened at one end and calibrated on the outside. To be able to take the sample, a window had to be hacked first in the stone-hard, about 2-cm-thick outer layer of the trunk, a layer locally known as the *wa'ah*. Then the tube was hammered with a mallet into the exposed pith patch perpendicularly to the palm axis up to the middle of the trunk (Fig. 7.2a). Then a few mallet blows were given to the side of the end of the tube still sticking out to ensure that the complete, undisturbed sample stayed inside the auger when it was pulled out. After retracting the tube, the length and undisturbed-ness of the firm pith sample inside was checked, and if okay-ed, pushed out of the tube with a wooden stick (Fig. 7.2b). The sample was broken up into 2 to 4 pieces (Fig. 7.2d) to facilitate handling and put into polythene bags which were then closed air-tightly to prevent moisture loss.
Two replicate samples (i.e. two per window) were taken every metre along the length of the trunk (every 50 cm in one case, Palm #18, which had an exceptionally short trunk for a flowering palm), starting 50 cm above ground level and continuing at least to the point of attachment of the lowest green leaf and sometimes - in flowering axes - near to where the lowest inflorescence branch is attached.

The investigations of VAN KRAALINGEN (1983) indicate that sampling trunk pith at intervals smaller than 1 metre and sampling different depths into the trunk separately do not yield information on starch content and distribution that is significantly different from the information gathered using the above mentioned method.

Pith sample fresh-weight

In the lab, pith samples were weighed inside and together with the air-tight polythene bag they were put in in the field. Then the sample was taken out, the bag was wiped dry on the inside and weighed, and the empty bag weight subtracted from the sample-plus-bag weight to arrive at the sample fresh weight. Moisture evaporated from the sample and condensed on the inside of the bag was thus correctly included in the sample fresh weight.

Measuring pith sample volume by water displacement (under-water weighing)

Figure 7.3 Set-up for sample volume measurement by under-water weighing. The balance is placed on a small table with a hole in the top. [photo nr. 89.08-094-18, field lab, Hatusua mon21aug1989]

The firmness of the pith samples (see Fig.7.2d) enabled accurate measurements of the sample volume by under-water weighing. Because the pith is rather porous and any air spaces in the pith would be measured incorrectly as not belonging to the sample volume if these spaces are not filled with water prior to the under-water weighing, a sample piece was first immersed in water for at least one minute. The electronic balance employed (brand and type: A&D FY300) has an accuracy of 0.01 ± 0.005 g. Therefore, volume measurement would ideally have an analogue accuracy of 0.01 ± 0.005 cm^3. However, the stability of the under-water weight (i.e. its constantness during weighing or its sameness at repeated weighings) differed somewhat between palms, and in one case between samples taken at different heights in the same palm. Less firm or somewhat brittle sample pieces tended to be less stable. When the pre-soaking period was later extended, the weight stability was improved in most cases. Therefore, although in most cases the accuracy of the volume could be warranted at 0.01 cm^3 for the range of sample piece volumes of about 10-40 cm^3 at hand, in some cases the sample volume accuracy could only be warranted at 0.1 cm^3.
Especially for under-water weighing, the electronic balance has a hook underneath from which the object to be weighed is hanged (Fig.7.3). Pith samples, however, float (specific densities of pith samples ranged from 0.40 to 0.88 g/cm^3). Therefore, the connection between hook and sample had to be rigid. This was realized by using a clamp fitted with a thin but stiff piece of wire. After the pre-soaking to fill any pores, the pith sample was simply stuck onto the wire and clamped to the hook. The scales were then reset to zero, the sample piece immersed in water, giving a negative weight read-out in grams equal to the volume of the sample piece in cubic cm.

Separating starch from other non-(water-)soluble solids in a pith sample

After weighing and volume measurement, the sample was ground with a little water in a kitchen blender (brand: Philips; type: HR 1375), using the small-volume closed grinding compartment ('Mill Accessory HR 1376') coming with it (Fig.7.4a). After a few bursts to let the knives 'take' all the pieces, the sample was ground for 30 seconds.

The slurry was then poured over a 150-micron mesh sieve (soil-sample type (Fig.7.4a)). The starch was washed out of the ground pith on the sieve with ample water until the washing water passing through the sieve had become clear. The starch in the washing water was allowed to settle for some 10 minutes before the supernatant water was poured off.

Both the starch, which passed through the sieve, and the other non--water-soluble solids (fibres and cell wall material), which stayed on the sieve, were collected to be dried.

Figure 7.4 Separation and drying of starch and other non-water-soluble solids in sago palm pith samples: a. kitchen blender, and 150-micron-mesh soil sieve with partly separated ground pith sample; b. aluminium dishes with separated starch (whitish) and other non-water-soluble solids (brown) before drying; c. drying cabinet.
[a: photo nr. 89.08-094-20, tue22aug1989 ; b: photo nr. 90.05-115-28, wed02may1990 ; c: photo nr. 88.12-074-22, thu15dec1988 ; (a-c: field lab, Hatusua, West Seram)]

Dry weight of starch and other non-(water-)soluble solids

Starch and the other non-(water-)soluble solids were put in separate aluminium dishes (Fig.7.4b) and dried to constant weight in a drying cabinet (brand: Memmert (Fig.7.4c)), first at 70 ºC. If pre-dried in the sun, constant weight would usually be reached overnight; the other solids might take longer.
After weighing the dried samples, the constituents were further dried at 115 ºC, again to constant weight. With material from a sample of originally about 100 cc, this would usually take another 4 - 6 hours.

Weights after drying at 70 ºC may be used in calculating quantities of commercial interest, such as the amount of starch and other solids per unit weight or volume of fresh pith.
Weights after drying at 115 ºC are used in calculating quantities of physiological interest, such as the dry matter content of pith and the percentage of starch in total pith dry matter.
Drying moist starch directly at 115 ºC caused an irreversible gelatinization and hardening of the starch after which it was very difficult to remove the starch from the aluminium dishes. Only after most of the water had already evaporated during the drying at 70 ºC, could the starch be dried completely at 115 ºC without it gelatinizing and hardening. Other non-(water-) soluble solids were dried in the same way because it was convenient to dry them in one go with the starch.

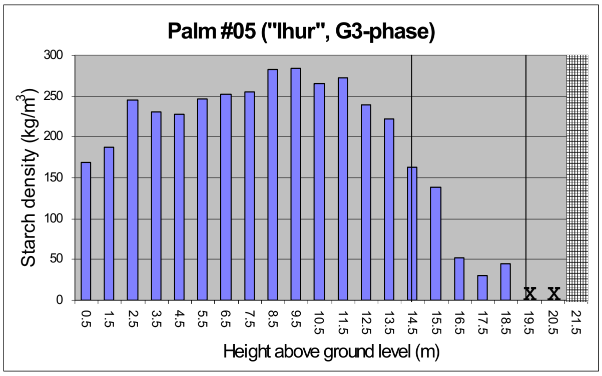
Drying to constant weight at 115 ºC, however, proved to be cumbersome and time-consuming. Therefore, the pith samples of one palm (#09) were dried in this two-phase manner very diligently and the average ratio of weight at 115 ºC to weight at 70 ºC was taken to estimate the weight at 115 ºC from that at 70 ºC for all the other palms. For starch, this average ratio was 0.959 (n=38, s=0.003), for other non-(water-)soluble solids 0.957 (n=38, s=0.002). (See Sago Palm Data Sheets, Palm #09, under Trunk pith.)

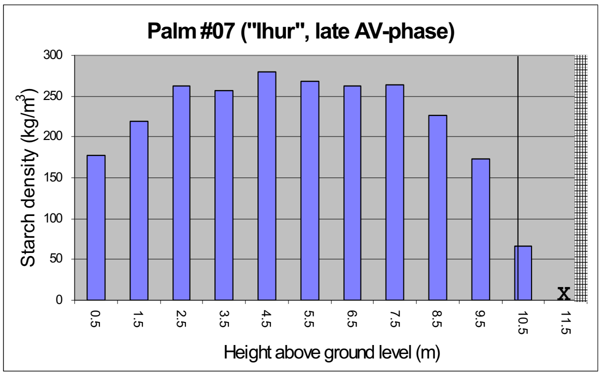
Because of the very humid air in the lab (and everywhere else in that part of the world), dried samples started attracting air moisture (and thus gaining weight) as soon as they were taken from the drying cabinet. To prevent this, a dry hot sample was transferred from the cabinet immediately to a closed polystyrene insulation box and weighed inside this box. This also prevented air turbulence caused by high temperature of the sample; this turbulance would also have affected the weighing result.

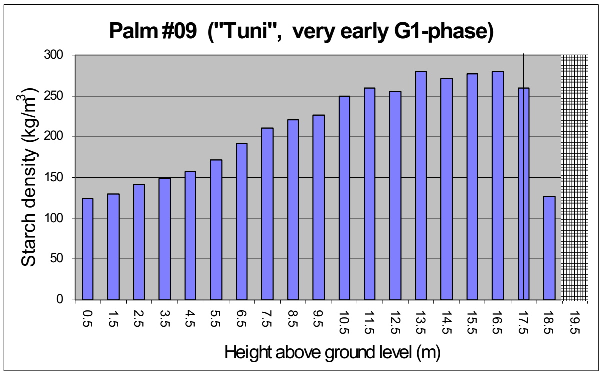
7.3.2 Results: trunk starch content and distribution in 27 palms

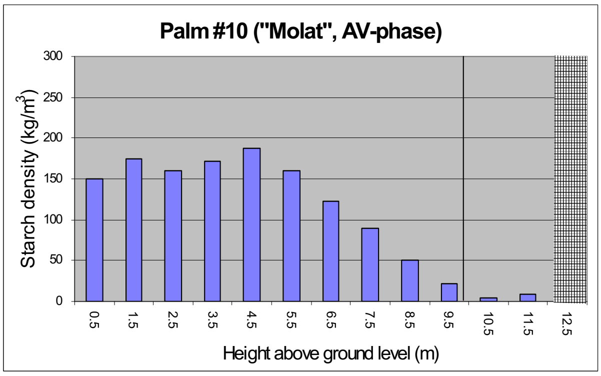
Complete series of trunk pith samples were taken from 27 palms and the starch density of the samples (kg starch per cubic metre pith) was calculated. The results are presented in Fig.7.5

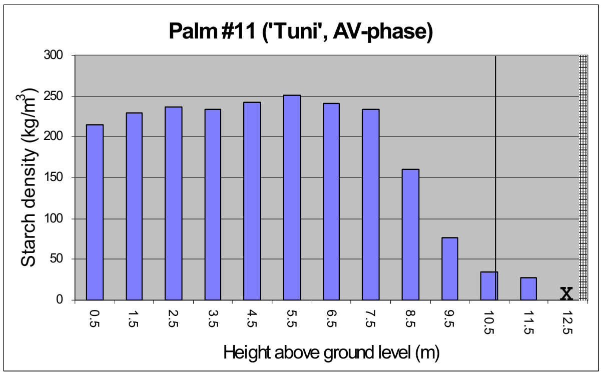
Figure 7.5 Starch density distribution in the trunk of 27 sago palms of various variety and development phase. (Palm numbers in chronological order of sampling; numbers skipped in this figure are palms sampled for other purposes only. Leaf-free, leaf-bearing, and (if applicable) inflorescence branch-bearing part of a trunk demarcated by vertical lines intersecting the X-axis at the corresponding height; total length of the trunk indicated by horizontal extent of grey part of the graph (excluding the checkered part). An X instead of a bar indicates that no observation was made at that height. NB: sampling heights in Palm #18 differ 0.5 m in stead of 1.0 m.)

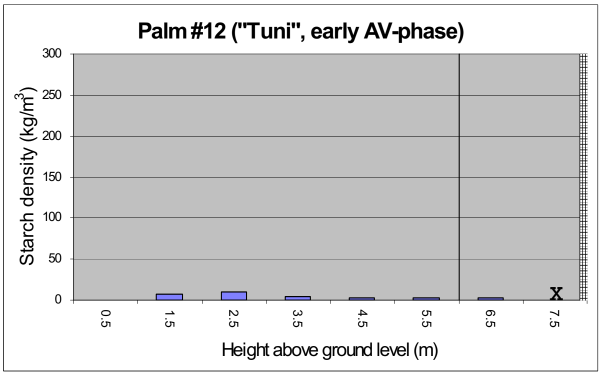

Palm #05 ("Ihur", G3-phase)

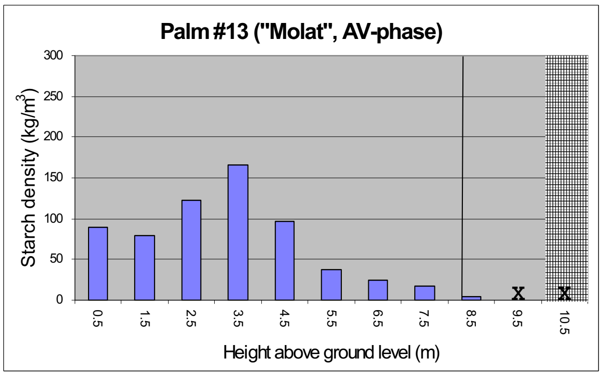

Palm #07 ("Ihur", late AV-phase)

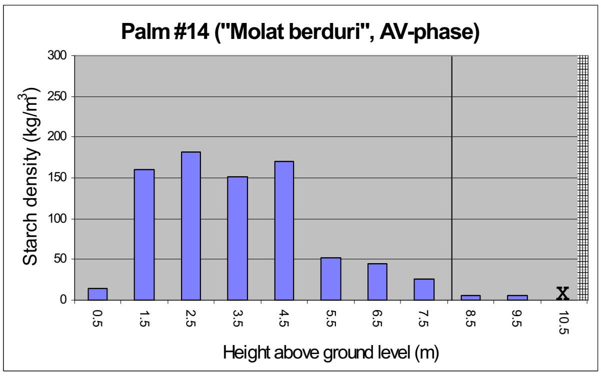

Palm #09 ("Tuni", very early G1-phase)

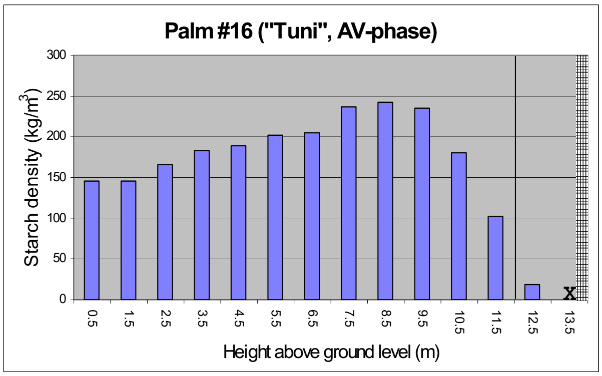

Palm #10 ("Molat", AV-phase)

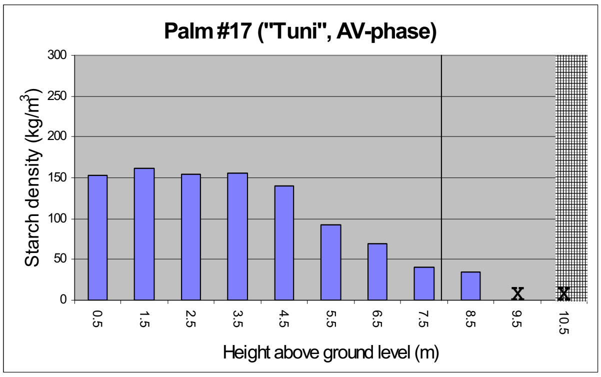

Palm #11 ('Tuni', AV-phase)

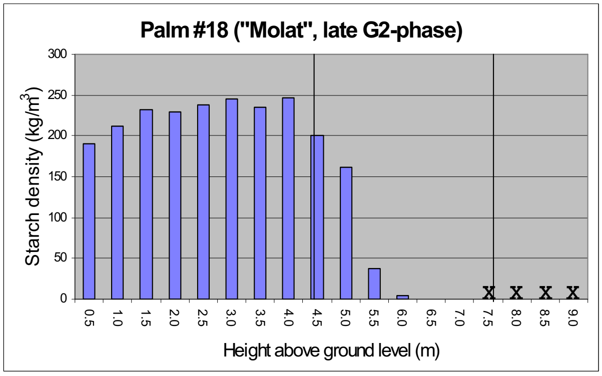

Palm #12 ("Tuni", early AV-phase)

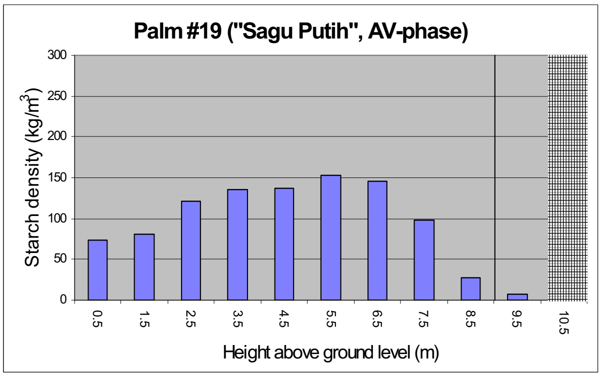

Palm #13 ("Molat", AV-phase)

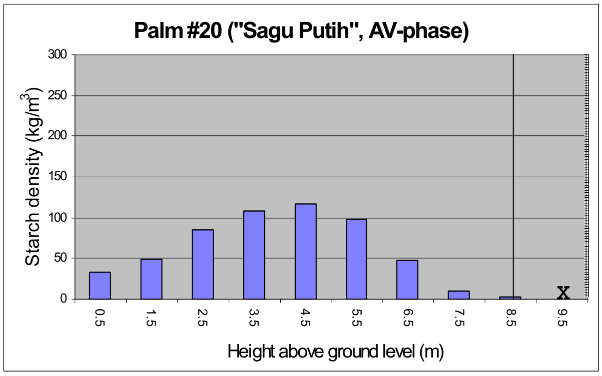

Palm #14 ("Molat berduri", AV-phase)

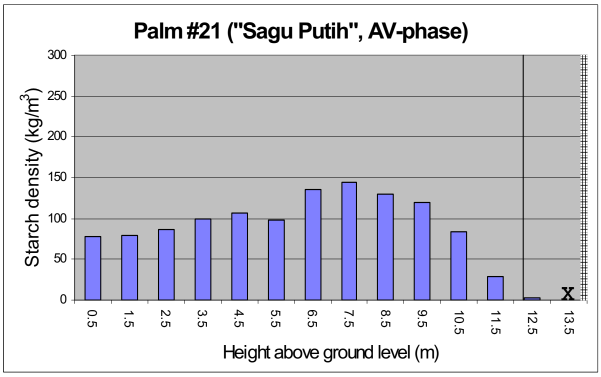

Palm #16 ("Tuni", AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
11.5
12.5
13.5
X
Height above ground level (m)

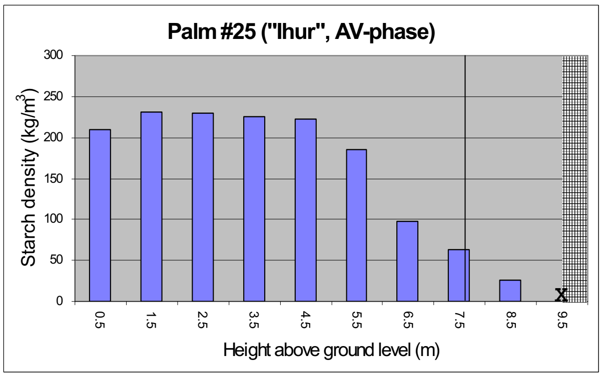

Palm #17 ("Tuni", AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
X
X
Height above ground level (m)

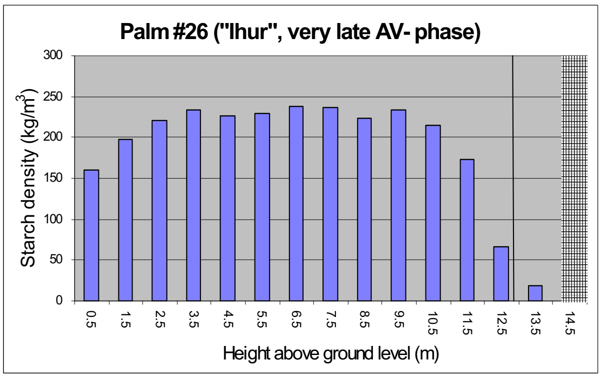

Palm #18 ("Molat", late G2-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
X
X
X
X
Height above ground level (m)

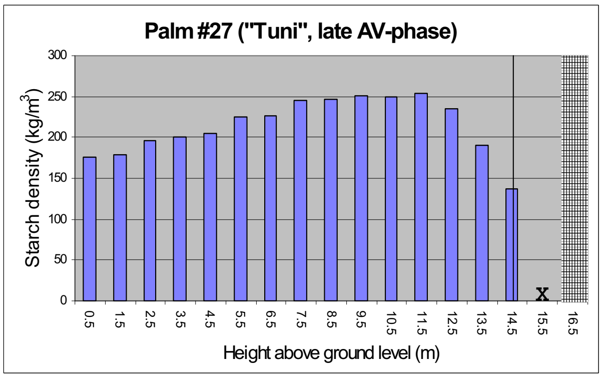

Palm #19 ("Sagu Putih", AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
Height above ground level (m)

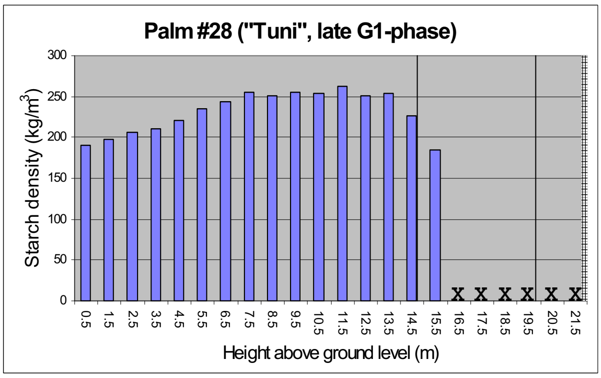

Palm #20 ("Sagu Putih", AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
X
Height above ground level (m)

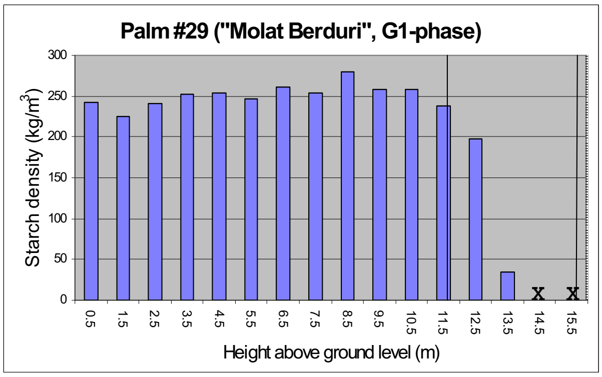

Palm #21 ("Sagu Putih", AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
11.5
12.5
13.5
X
Height above ground level (m)

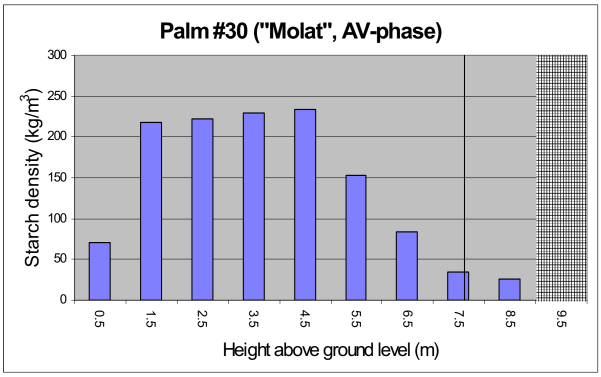

Palm #25 ("Ihur", AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
X
Height above ground level (m)

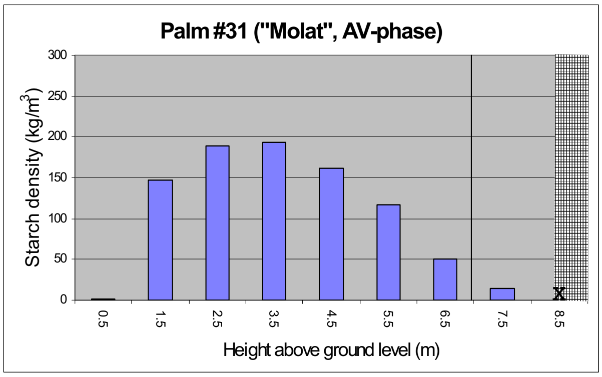

Palm #26 ("Ihur", very late AV- phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
11.5
12.5
13.5
14.5
Height above ground level (m)

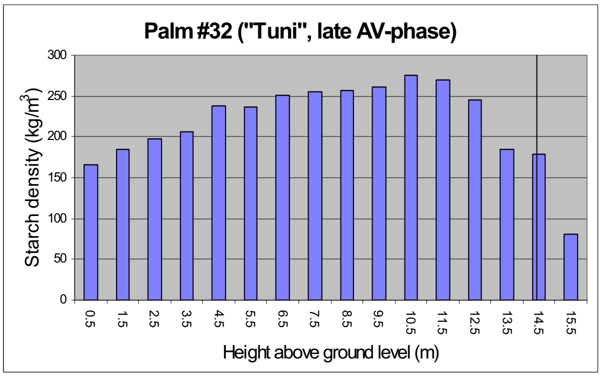

Palm #27 ("Tuni", late AV-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
11.5
12.5
13.5
14.5
15.5
16.5
X
Height above ground level (m)

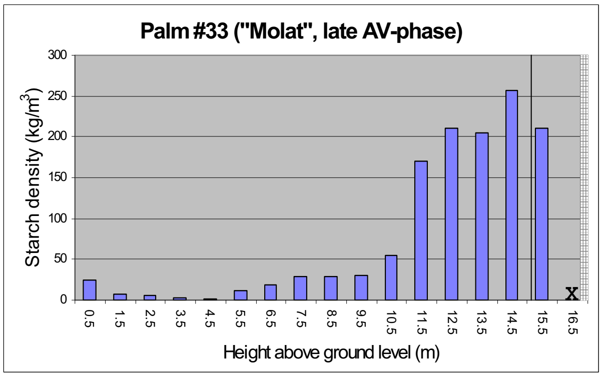

Palm #28 ("Tuni", late G1-phase)
Starch density (kg/m^3)
0
50
100
150
200
250
300
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
11.5
12.5
13.5
14.5
15.5
16.5
17.5
18.5
19.5
20.5
21.5
X
X
X
X
X
X
Height above ground level (m)

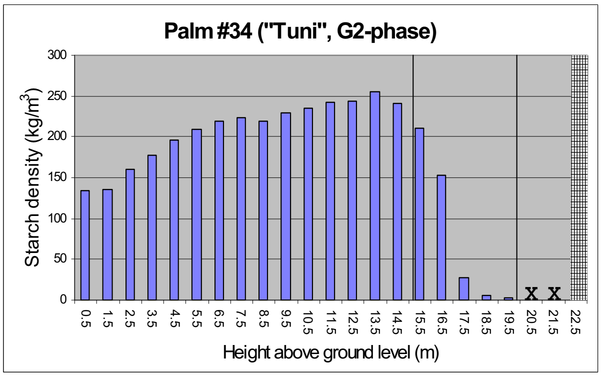

Palm #29 ("Molat Berduri", G1-phase)

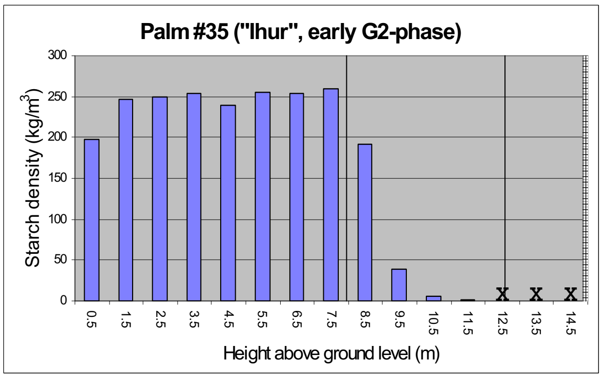

Palm #30 ("Molat", AV-phase)

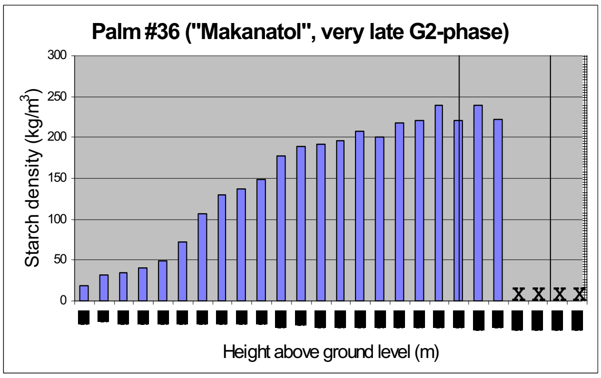

Palm #31 ("Molat", AV-phase)

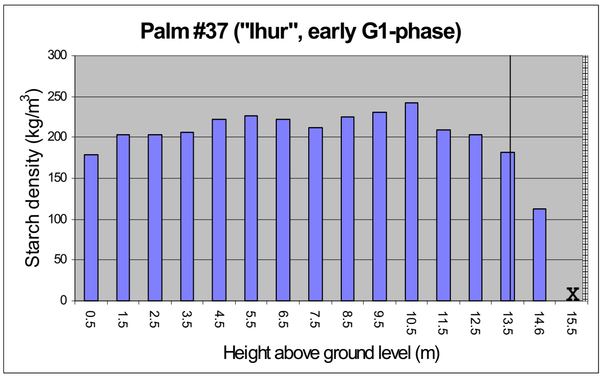

Palm #32 ("Tuni", late AV-phase)


Palm #33 ("Molat", late AV-phase)


Palm #34 ("Tuni", G2-phase)


Palm #35 ("Ihur", early G2-phase)


Palm #36 ("Makanatol", very late G2-phase)


Palm #37 ("Ihur", early G1-phase)

Note: Of Palm #33, total axis length, nor development phase could be established with certainty because the apex shattered when the trunk was felled.

When we compare the graphs in Fig.7.5, the following observations can be made:

1. Maximum trunk starch density differs per palm. In most palms it is around 250 kg/m^3, in some palms much lower.
2. With very few exceptions (Palm #13, #33), starch density in the trunk first increases with height above ground level, reaches a maximum about half way to two thirds up the leafless part of the trunk, and then sharply drops towards the top of the trunk.
3. The course of increasing and subsequent decreasing starch density in a trunk with height above ground level differs between palms, even between palms in the same development phase. Several distribution patterns, differing in the steepness of this increase and decrease, can be distinguished: from flat-topped with only one short right tail, to gently sloping with one peak and two long tails.

7.4 Analysis

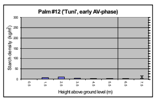
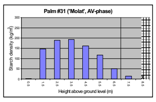
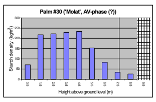
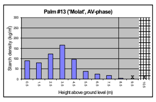
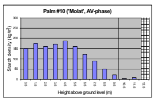
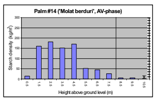
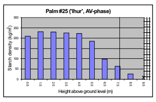
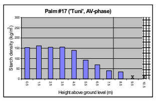
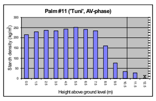
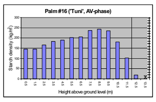
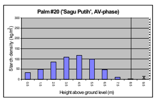
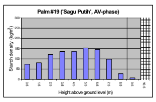
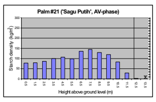
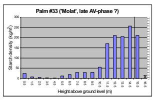
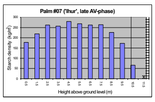
It is evident that not only age and development phase of a sago palm trunk determine the amount and the distribution of the starch it contains. The differences in distribution pattern found make it clear that there must be other factors also having a large influence, and that description of the evolution in time of trunk starch quantity and distribution is not as straightforward as I hoped it would be.

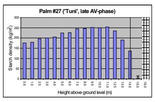
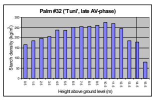
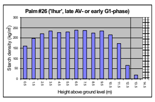
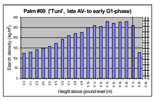
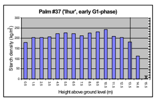
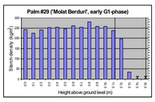
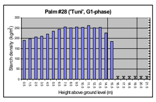
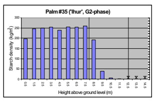
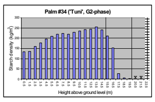
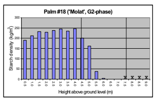
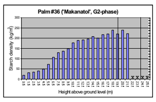
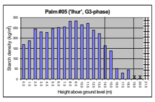
Other factors besides time possibly affecting trunk starch quantity and distribution may be internal (genetic make-up), or external (primarily availability of light, water and nutrients). The effect of differences in genetic make-up will be analysed by analysing the effect of the difference in folk variety the sampled specimen were attributed to. The effect of availability of light, water and nutrients will be analysed by analysing the effect of some indicators routinely recorded with each palm felled, viz. degree of shading, (ground-)water level, pH and salinity of groundwater, and number of suckers (see Sago Palm Data Sheets in App. A).

In Chapter 6, the total leaf area (TLA) and the leaf area index (LAI) of most of the sampled palms were estimated. The possible relationship between these indicators of the photosynthetic capacity of the trunk and trunk starch quantity and distribution will also be analysed here.

Table 7.1 shows the starch density distributions of all sampled palms arranged according to the tentative order of age and development phase as established in Chapter 4 (see Table 4.16), and to folk variety, together with TLA and LAI, and with factors possibly influencing these distributions. The mean starch density also presented in this table gives an indication of the overall filling state (which percentage of full capacity is filled) in the leafless trunk part.

Table 7.1 Trunk starch density distribution and trunk starch quantity in, and trunk height, leaf area, and some habitat characteristics of 27 sago palms ranked tentatively according to age (and grouped according to folk variety within same-age groups)

Palm #	Age group	Folk var.	Starch density distribution	Mean 1) starch density (kg/m^3)	Est. starch quant. (kg) 2)	ax$_0$ height (m) 3)	TLA (m^2) 4)	LAI 5)	Shading 6)	(ground-)Water			Nr of suckers [SBI] 9)
										level 7)	pH	EC 8)	
12	AV early	Tuni		4.64 (0.1-10.6)	5 ----- 6	6.00 ----- 7.90	236.9 (14)	1.02	0 - 1/4	0-10 cm b.g.l. (rs: flooded permanently)	6.5	0.14	S1 1-5 S2 1-5 S3 6 [7.5]
31	AV	Molat		118 (1.7-193)	125 ----- 128	6.95 ----- 8.40	242.8 (16)	1.32	1/4 - 1/2	113 cm b.g.l. (rs: flooded after showers)	6.7	0.57	S1 6-10 S2 1-5 S3 5 [7.0]
30				159 (34-234)	199 ----- 205	7.60 ----- 9.05	248.0 (16)	1.36	1/4 - 1/2				
13				70 (4.7-166)	82 ----- 83	8.30 ----- 10.10	274.5 (16)	1.38	0 - 1/4	10 cm b.g.l. (rs: flooded permanently)	5.7	0.07	S1 6-10 S2 1-5 S3 2 [4.0]
10				124 (22-187)	241 ----- 244	9.90 ----- 12.20	333.1 (21)	1.62	0 - 1/4	0-10 cm b.g.l. (n.r.)	6.7	0.17	S1 1-5 S2 0 S3 5 [5.5]
14		Molat Berduri		87 (5.1-182)	138 ----- 141	8.10 ----- 10.85	388.2 (22)	1.59	0 - 1/4	0 cm b.g.l. (flooded permanently)	6.4	0.21	S1 1-5 S2 1-5 S3 4 [5.5]
25		Ihur		185 (63-231)	246 ----- 257	7.65 ----- 9.55	334.1 (21)	1.84	0 - 1/4	50 cm b.g.l. (rs: flooded permanently)	6.5	0.23	S1 11-15 S2 1-5 S3 8 [10.5]
17		Tuni		119 (40-162)	179 ----- 187	7.85 ----- 10.30	336.3 (19)	1.32	0 - 1/4	flooded (rs: flooded permanently)	6.5	0.08	S1 11-15 S2 6-10 S3 8 [11.5]
11				192 (34-251)	452 ----- 462	10.70 ----- 12.80	322.6 (20)	1.67	0	0 cm b.g.l. (rs: flooded permanently)	6.5	0.07	S1 1-5 S2 1-5 S3 1 [2.5]
16				188 (18-242)	451 ----- 456	12.05 ----- 13.65	289.7 (19)	1.56	0	25 cm b.g.l. (rs: flooded after showers)	6.5	0.05	S1 1-5 S2 1-5 S3 6 [7.5]
20		Putih		62 (2.9-117)	86 ----- 86	8.55 ----- 9.95	217.6 (14)	1.19	1/4 - 1/2	>120 cm b.g.l. (never flooded)	n.r.	n.r.	S1 1-5 S2 1-5 S3 1 [2.5]
19				109 (6.8-153)	155 ----- 156	9.05 ----- 10.20	196.9 (14)	1.25	1/4 - 1/2	>120 cm b.g.l. (never flooded)	n.r.	n.r.	S1 1-5 S2 1-5 S3 2 [3.5]
21				96 (2.9-144)	186 ----- 186	12.25 ----- 13.80	226.4 (14)	1.08	1/4 - 1/2	10 cm b.g.l. (ds: wet, not flooded)	6.2	n.r.	S1 1-5 S2 1-5 S3 2 [3.5]
33	AV late	Molat		68 (1.7-257)	233 ----- 258	15.15 ----- 16.75	- ** (? c.20)	- **	0 - 1/4 *)	10 cm b.g.l. (rs: flooded after showers)	5.9	0.19	S1 1-5 S2 1-5 S3 0 [1.5]
07		Ihur		233 (76-280)	333 ----- 340	10.35 ----- 11.70	n.r. (17)	n.r.	0	30 cm b.g.l. (rs: flooded permanently)	n.r.	n.r.	S1 6-10 S2 1-5 S3 2 [4.0]

Palm #	Age group	Folk var.	Starch density distri-bution	Mean 1) starch density (kg/m^3)	Est. starch quant. (kg) 2)	ax_0 height (m) 3)	TLA (m^2) 4)	LAI 5)	Shad-ing 6)	(ground-)Water			Nr of suckers [SBI] 9)
										level 7)	pH	EC 8)	
27		Tuni		217 (137- 254)	645 ----- 660	14.60 ----- 16.15	293.9 (19)	1.70	0 - 1/4	80 cm b.g.l. (rs: flooded permanently)	6.6	0.07	S1 1-5 S2 1-5 S3 4 [5.5]
32				230 (166- 275)	707 ----- 746	14.45 ----- 16.00	294.5 (19)	1.67	0 - 1/4	8 cm b.g.l. (flooded after showers)	5.0	0.05	S1 1-5 S2 1-5 S3 2 [3.5]
26	AV very late	Ihur		204 (66- 238)	511 ----- 517	12.85 ----- 14.25	- ** (21)	- **	1/4 - 1/2	20 cm b.g.l. (rs: flooded permanently)	6.6	0.11	S1 6-10 S2 1-5 S3 5 [7.0]
09	G1 very ear-ly	Tuni		219 (124- 280)	685 ----- 723	17.50 ----- 19.00	261.8 (20)	1.49	0 - 1/4	40 cm b.g.l. (rs: flooded after showers)	7.5	0.20	S1 1-5 S2 1-5 S3 4 [5.5]
37	G1 ear-ly	Ihur		215 (178- 243)	646 ----- 687	13.60 ----- 15.85	395.2 (24)	2.21	0 - 1/4	17 cm b.g.l. (rs: flooded permanently)	6.5	0.33	S1 6-10 S2 1-5 S3 4 [6.0]
29	G1	Molat Ber-duri		254 (225- 280)	571 ----- 613	11.70 15.65 ----- 15.95	- ** (28)	- **	0 - 1/4	10 cm b.g.l. (rs: probably flooded permanently)	6.1	0.11	S1 6-10 S2 1-5 S3 5 [7.0]
28	G1 late	Tuni		237 (191- 262)	777 ----- 819	14.75 19.80 ----- 21.80	304.5 (27)	2.08	0 - 1/4	0 cm b.g.l. (rs: flooded permanently)	6.0	0.02	S1 1-5 S2 1-5 S3 4 [5.5]
35	G2 ear-ly	Ihur		247 (197- 260)	212 ----- 233	7.95 12.55 ----- 14.90	258.1 (27)	2.07	0 - 1/4	45 cm b.g.l. (flooded after heavy showers)	5.8	0.09	S1 21-25 S2 6-10 S3 5 [9.5]
34	G2	Tuni		213 (135- 255)	713 ----- 770	15.20 19.85 ----- 22.25	224.7 (25)	1.41	0 - 1/4	23 cm b.g.l. (flooded after heavy showers)	5.9	0.24	S1 6-10 S2 1-5 S3 4 [6.0]
18	G2 late	Molat		229 (40- 247)	151 ----- 159	4.45 7.60 ----- 9.25	114.8 (17)	1.49	0	40 cm b.g.l. (flooded after heavy showers)	6.7	0.68	S1 11-15 S2 1-5 S3 2 [4.5]
36	G2 very late	Maka-natol		153 (19- 239)	551 ----- 585	19.65 24.20 ----- 25.80	240.5 (28)	1.96	0 - 1/4	57 cm b.g.l. ([n.r.])	6.0	0.14	S1 11-15 S2 6-10 S3 4 [7.5]
05	G3	Ihur		242 (163- 284)	746 ----- 791	14.50 19.30 ----- 21.10	n.r. (18)	n.r.	0	0-20 cm b.g.l. (ds: dry)	5.8	0.51	S1 1-5 S2 1-5 S3 2 [3.5]

1) Of the pith of the leafless trunk part (i.e., estimated dry starch yield of the leafless trunk part divided by the pith volume of the leafless trunk part). Between brackets the starch density range found in samples of this trunk part; the top of this range was always also the maximum found in the entire trunk.

2) Estimated starch quantity in the leafless trunk part, and - below the dashed line - in the whole sampled part of the trunk.

3) Below the dashed line the total trunk (ax_0) height. Above the dashed line the height of the leafless trunk part, and - if not equal to the entire trunk height - the height of the leafless plus leaf-bearing part (the remainder being the ax_1-bearing trunk part).

4) TLA = Total Leaf Area (see text). Between brackets the number of green leaves on the axis.

5) LAI = Leaf Area Index per axis (see text).

6) At time of felling.

7) At time of felling. Between brackets info re rest of year (rs = rainy season (in Seram and Saparua: may-august); ds = dry season; b.g.l. = below ground level).

8) EC (= Electric Conductivity) in miliSiemens per centimetre (mS/cm).

9) SBI = Sucker Biomass Index (see text).

*) Trunk 80 cm from stump of dead tree which may have been shading this sago palm during most of its life.

**) Too few data on leaf area could be recorded for TLA and LAI calculation.

n.r. = not recorded.

7.4.1 Trunk starch content and distribution in relation to age and developmental phase

Table 7.1 shows that with respect to trunk starch content and distribution, only the early AV-phase can be clearly distinguished from the later phases: in the early AV-phase hardly any starch has accumulated at all. The mean starch density (MSD) and the maximum starch density (i.e. the high end of the range (HSD)) of the trunks, as well as the estimated quantity of starch (ESQ) they contain as presented in Table 7.1 are visualised in Figure 7.6, further illustrating this gap in starch content between early AV-phase (Palm#12) and the next (sub-) phases.

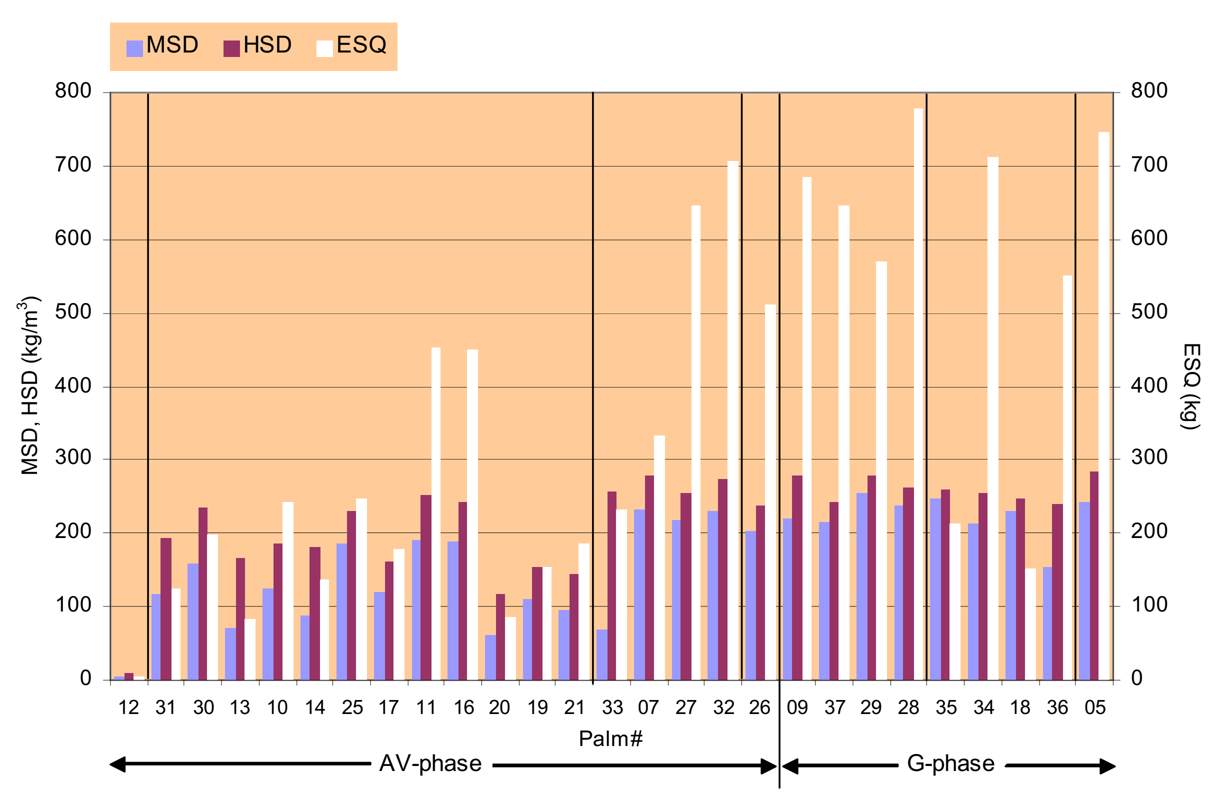


Figure 7.6 Mean starch density (MSD), maximum starch density (HSD) and estimated starch quantity (ESQ) in the pith of the leafless trunk part of 27 sago palm axes ordered by development phase and their sub-phases, as presented in Table 7.1.

After the early AV-phase the maximum starch density seems to sharply rise and then to level off at about 260 kg/m^3, whereas the mean starch density and the total amount of starch show an upward trend up until the G-phase, mean starch density leveling off at about 230 - 240 kg/m^3. Table 7.1 shows that among the palms in the AV-phase there are three palms (#20, #19, #21) which stand out with a much lower maximum starch density than the other palms, and they are the only three palms belonging to the variety "Putih". This folk variety is not represented in any other development phase. If these three palms were excluded from the calculations, maximum starch density in the AV-phase would be on average 205 kg/m^3 (with a range of 162 - 251 kg/m^3), accentuating the above observed trend in the evolution of the maximum starch density even more. However, maximum starch density, and even more so mean starch density and starch quantity, show a considerable range around the average which cannot be explained by age and development phase alone.

Especially when we consider the leafless part of the trunk only, the distribution pattern shows a tendency with progressing age and development from a two-tailed distribution (lower starch densities in both the lower and the upper part of the leafless trunk) towards a one-tailed distribution (lower starch density only in the lower part of the leafless trunk). The one-tailed distribution pattern in particular shows a wide range in the length of the tail, which age and development alone cannot account for. E.g., Palm#33 (late AV-phase) and #36 (late G2-phase) have a long thin tail, whereas Palm#29 (G1-phase) does not show a tail at all.

Depletion of starch reserves for the building of the inflorescence and the fruits may apparently set in much later than generally assumed, as shown by Palm#05 which has already half-grown fruits, but still has a very high mean starch density of 242 kg/m^3. The higher starch density towards the top shortly before flowering as reported by DEINUM & SETIJOSO (1932), was observed in some palms (#33, #27, #32), but not in others (#07, #26).

7.4.2 Trunk starch content and distribution in relation to folk variety

As we have seen in the previous section, the maximum starch density sharply rises and quickly levels off after the early AV-phase. In Table 7.2 the average maximum starch densities per folk variety for all palms beyond the early AV-phase are presented.

Table 7.2 Average maximum starch density (with range) of trunk pith in various sago palm folk varieties (fv.); only trunks in development phases beyond the early Adult Vegetative phase are included.

fv.	Molat (n=6)	Molat Berduri (n=2)	Ihur (n=6)	Tuni (n=8)	Putih (n=3)	Makanatol (n=1)
Max. starch density (kg/m^3)	214 (166-257)	231 (182-280)	256 (231-284)	248 (162-280)	138 (117-153)	239

The fv. Putih is the only variety with an average maximum starch density (138 kg/m^3) which is markedly different from that of the other varieties; even the observed range of values in "Putih" does not overlap with the range of any of the other varieties. The average maximum starch densities for the other varieties range from 214 to 256 kg/m^3.

The difference between "Putih" and the other varieties may also be caused by environmental factors as all three sampled "Putih" specimen were located on a slope on the island of Saparua, whereas all the others but one were located on flat alluvial soil on a coastal riverine flood plain on the island of Seram, the one exception being the single "Makanatol" specimen which stood on flat alluvial soil on Saparua.

The starch distribution pattern does not seem to have a strong relationship with variety. In "Molat", "Ihur" and "Tuni" two-tailed, one-tailed and hardly-tailed (homogeneous) distribution patterns occur; the two "Molat Berduri" specimens each show a different pattern. Only the three "Putih" specimens all show a two-tailed distribution, but this could also be related to a low maximum starch density as also specimens of other varieties with a maximum density of less than 200 kg/m^3 tend to have a two-tailed distribution.

7.4.3 Trunk starch content and distribution in relation to degree of shading

FLACH (1977:163) already speculated about shading as a reason for variation of the starch filling pattern in sago palm trunks:

> "Carbohydrates produced in the leaves are transported and sedimented in the "sink", i.e. trunk tissue; we may assume that for reasons of economy of transport, the starch will be sedimented as close as possible to the crown. Thus unless proven otherwise, we have to assume that

> sagopalms growing in full sunlight will fill their trunks from the base upwards immediately after the formation of such trunk parts. Palms grown in the shade would be expected to reach for full sunlight first, so that the trunks grow upwards until full sunlight is reached before they fill their trunks."

Differences among the sampled palms in starch density in the lower part of the trunk may well be explained by this effect of shading. For palms in the G-phase showing this variation, it may well be that if an axis was in full sunlight too short before it reaches the G-phase, it may never have had the chance to fill the lower part of the trunk (e.g. Palm #09, #34, #36), as would have had palms for which this period was long enough (e.g. Palm #29, #18, #35). Palm #36 would be a case in point: although it is a very tall palm (25.80 m) and - like most of the palms - at time of felling only a quarter or less of its crown area (i.e. the area of the outline of the vertical projection of the crown) overlapped with that of neighbouring tree crowns, there were even taller "Makanatol" specimens in the vicinity (see the Palm #36 data sheet in Appendix A), suggesting that Palm #36 grew up in a sago stand where young, short palms are shaded for a long time before they reach full sunlight.
The relatively tall trunk and the extremely low starch density in all but the upper few metres of Palm #33 may also be explained by severe shading during most of the palm's life as a trunk of a dead tree was standing less than 1 m away from the palm.

It remains to be established to what extent shading is a primary rather than a secondary cause of a reduced starch density. Retarded trunk growth caused by other factors may result in the vegetation in the surroundings to outgrow the sago palm and shade it.

7.4.4 Trunk starch content and distribution in relation to level, pH and EC of the groundwater

Level

Groundwater level was measured at the time of felling only. Rather than the level at a given moment, the water level history during a trunk's life time would be affecting trunk starch content and distribution. From literature (e.g. LOUHENAPESSY (1993:142)) and local informants it is known that the longer the flooding period, the less the amount of starch in the trunk. Information on the flooding history of a palm was only gathered informally by questioning the local person(s) who assisted me in felling and sampling the palm. I asked them about the water level of the palm's habitat during the year. As palms were mostly felled during the dry season (and for practical reasons almost always on a (then) dry spot), I had to rely on their knowledge and memory especially for data on the water level during the rainy season.
Among the 27 felled and sampled palms, there are three cases in which water level during the year clearly differs between palms which belong to the same age group ánd to the same variety:

1. AV-phase / "Molat": #30/#31 vs #13,
2. AV-phase / "Tuni": #11 and #16, vs #17,
3. late AV-phase / "Tuni": #32 vs #27.

Ad 1: Palm #30 and #31 (belonging to the same clump) have a much lower groundwater level at the time of felling than Palm #13, and during the rainy season the former two are flooded only after showers, whereas the latter is flooded permanently. In spite of the lighter shading and the taller trunk, Palm #13 has a much lower mean and maximum starch density than the other two.

Ad 2: Of the three "Tuni" palms in the AV-phase (Palms #17, #11 and #16), Palm #17 was standing on flooded terrain at the time of felling (actually, the palm was standing in a creek with streaming water, but could be made to fall on the dry land beside it): it has a markedly lower mean and maximum starch density than the other two.

Ad 3: Of the two "Tuni" palms in the late-AV-phase, the water level at the time of felling of Palm #32 is much higher (8 cm below ground level) than that of Palm #27 (80 cm below ground level). During the year, on the other hand, Palm #32 is flooded only after showers, whereas Palm #27 is flooded permanently during the rainy season. Palm #27 has a maximum starch density of 254 kg/m^3, Palm #32 of 275 kg/m^3, their mean starch densities being 217 kg/m^3 and 230 kg/m^3, respectively.

All three cases indicate a negative influence of prolonged flooding on starch density.

pH

In his studies on the influence of soil conditions on trunk starch yield of sago palms at about the height of their starch content, LOUHENAPESSY (1993:142) found that high soil pH was associated with low yield: A "Molat" grown on a soil with a pH of 7.4 yielded half as much as one on a soil with a pH of 5.7, and a specimen of the Moluccan folk variety Makanaru grown on soil with a pH of 7.7 yielded one sixth to half the amount of starch of specimens grown on soils with a pH between 4.5 and 5.1.

Of 24 of the 27 palms felled and sampled in my study, the pH of the groundwater was measured at the time of felling. In 22 of these 24 cases, the pH was between 5.7 and 6.7; there was 1 case with a pH of 5.0 (Palm #32), and 1 with a pH of 7.5 (Palm #09). Among these 24 there are two cases in which groundwater pH clearly differs between palms which belong to the same age group ánd to the same variety:

1. AV-phase / "Molat": #31/#30 and #10, vs #13,
2. late AV-phase / "Tuni": #32 vs #27,

Ad 1: Palm #30 and #31 (belonging to the same clump) and #10 all have a groundwater pH of 6.7, whereas Palm #13 has a groundwater pH of 5.7. The trunk of Palm #13 contains the smallest amount of starch and also has the lowest mean and maximum starch density.

Ad 2: Of the two "Tuni" palms in the late-AV-phase, Palm #27 and Palm #32 have a groundwater pH of 6.6 and 5.0, respectively. At about equal trunk lengths, the trunk of Palm #27 contains slightly less starch, and its mean and maximum starch density are slightly lower.

No trend in the influence of groundwater pH on trunk starch content can be detected from these two cases. The only palm that was growing on soil with a groundwater pH comparable to the high pH values in the study by LOUHENAPESSY is Palm #09, a "Tuni" in the very early G1-phase: it was growing on soil with a groundwater pH of 7.5 and contained much starch, but there is no palm to compare it with.

EC

The only case in which salinity (measured as electric conductivity) of the groundwater clearly differs between palms which belong to the same age group ánd to the same folk variety, are the "Molat" palms in the AV-phase: Palms #31 and #30 (belonging to the same clump) have a groundwater EC of 0.57 mS/cm, whereas that of Palm #13 and #10 is 0.07 and 0.17 mS/cm, respectively. Any effect of these different groundwater salinity levels on trunk starch quantity and mean starch density is not clear from this case. Only the maximum starch density appears somewhat higher at the higher salinity level.

The starch distribution among the palms contrasted for these three groundwater characteristics all showed a similar two-tailed pattern, except for Palm #17 and #11. The latter two both showed a one-(right-)tailed pattern, but were contrasted for grounwater level. Therefore, an effect of these three characteristics on starch distribution pattern could not be detected.

7.4.5 Trunk starch content and distribution in relation to number of suckers

The underground part of a sago palm trunk branches, and each branch (offshoot, sucker) is in turn capable of forming next-order branches. In this way a clump is formed usually consisting of a main (mother) tree with suckers of various age and size (see photo nrs 89.10-096-01 through -06 in the data sheet of Palm #18, Appendix A). The suckers may compete with the mother tree for nutrients from the soil, and as long as their photosynthetic apparatus is not big enough or not productive enough (e.g. because of shading by the crown of the mother tree) they may draw on the mother tree for their assimilate needs. Starch content and distribution in the mother trunk may thus be affected by the number and size of suckers sprouting from its base.

VAN KRAALINGEN (1983) suggested a simple sucker size classification based on his observations in the Sepik area of Papua New Guinea:
S1= sucker with overall height not exceeding 1.2 m.
S2= sucker with leaves between 1.2 and 4 m long.
S3= suckers with leaves longer than 4 m.
I adopted this classification here to characterise the sucker biomass of a sago clump. In Table 7.1 the number of suckers in the S1 and S2 class is lumped into groups of 5 (i.e., 1-5, 6-10, etc.), whereas the exact number of S3-class suckers is given.

In an attempt to compare the degree of suckering of clumps, I calculated a Sucker Biomass Index (SBI) by counting as follows:
1-5 S1-class suckers equals 0.5 ; 6-10 S1-class suckers equals 1.0 ; etc. ;
1-5 S2-class suckers equals 1 ; 6-10 S2-class suckers equals 2 ; etc.
each S3-class sucker counts as 1.
The marks for each sucker class are added to arrive at the clump's SBI.

The SBI of the 27 felled and sampled palms ranged from 1.5 to 11.5. The average SBI was 5.67 (n = 26 (Palm #30 and #31, belonging to the same clump, were counted as one); SD = 2.46). There are three cases in which SBI clearly differs between palms which belong to the same age group ánd to the same folk variety:

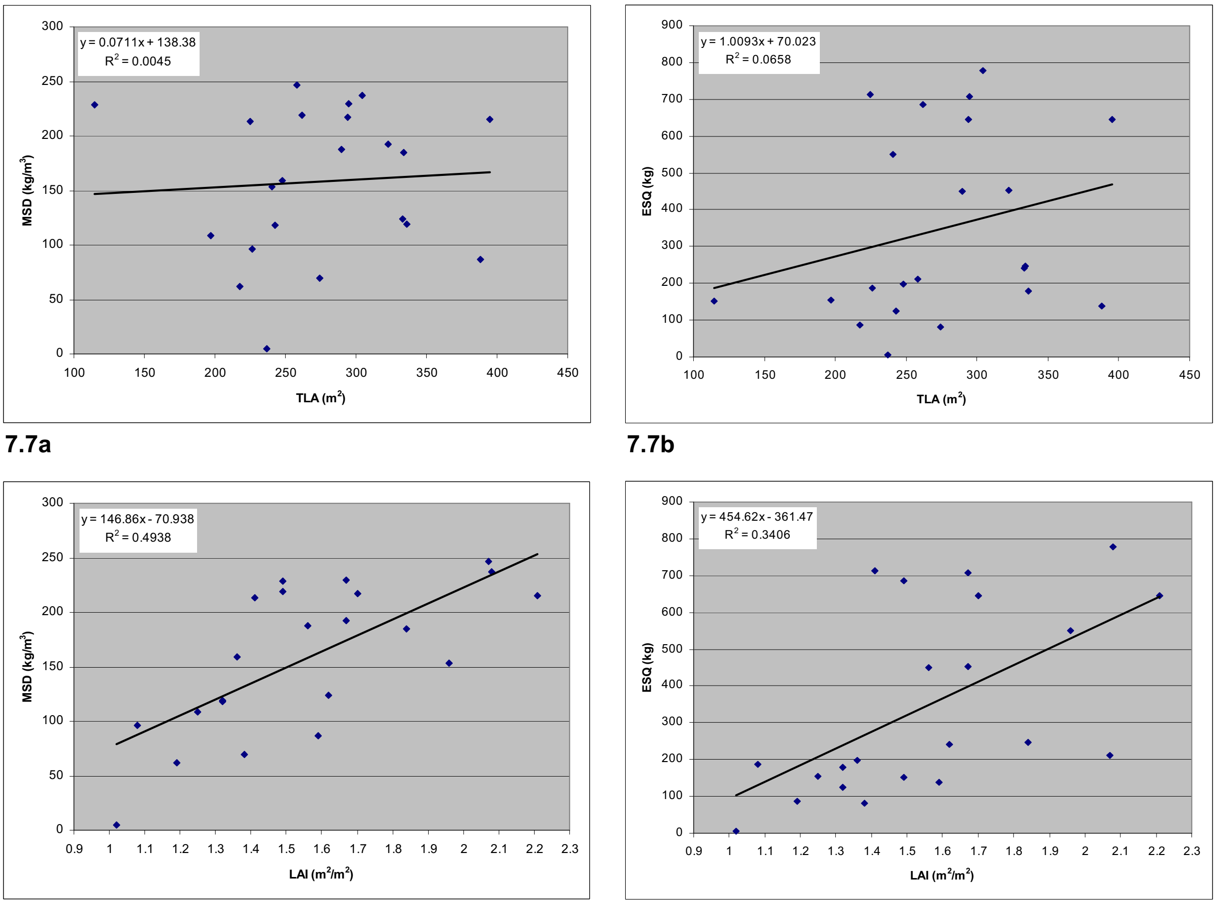
1. AV-phase / "Molat": #31/#30 vs #13;
2. AV-phase / "Tuni": #17 vs #11;
3. late AV-phase / "Tuni": #32 vs #27.

Ad 1: Palm #31 and #30 have an SBI of 7, whereas Palm #13 has an SBI of 4. The former have a markedly higher mean and maximum starch density and contain more starch than the latter.
Ad 2: Palm #17 has an SBI of 11.5, whereas Palm # 11 has an SBI of 2.5. The former's mean and maximum starch density of 119 kg/m^3 and 162 kg/m^3, respectively, are much lower than the latter's 192 kg/m^3 and 251 kg/m^3.
Ad 3: Palm #27 has an SBI of 5.5, Palm #32 of 3.5. The trunk of Palm #27 has a somewhat lower mean and maximum starch density, and contains somewhat less starch.
Case 2, and to a lesser extent case 3, appear to confirm the hypothesis of a negative effect of suckering on starch density and starch quantity, whereas case 1 shows an opposite effect. This opposite effect may be related to the overruling negative effect of a longer flooding period for the palm with the lower SBI.

All contrasted palms had a similar two-tailed or one-(right-)tailed starch distribution pattern. Therefore, any effect of the number of suckers on this pattern could not be established.

7.4.6 Trunk starch content and distribution in relation to Total leaf area (TLA) and Leaf area index (LAI) of the axis

The question I am trying to answer here is whether the amount and/or spatial distribution of green leaf surface of an axis at the time of felling can be related to the amount of starch in its pith at that time, and through this relationship perhaps help in predicting starch yield of the axis. The bar graph of Fig. 6.7 shows that palms with a similar TLA may have a dissimilar LAI, and *vice versa*. This warrants an analysis of the possible relationship of both TLA and LAI with variables of trunk starch content. As variables of trunk starch content are chosen the mean starch density (MSD) of the pith as a measure of the degree to which the capacity of the trunk's pith is filled (which may be independent of this capacity, i.e. of the size of the trunk, itself), and the estimated total starch quantity (ESQ) (which is clearly dependent on the capacity of the pith, as determined by trunk size). It is beyond the scope of this study to analyse the nature of any of these relationships (does TLA or LAI drive MSD or ESQ, or *vice versa*, is a more complex feedback system in play, or are all independently influenced by other factors and thus perhaps independent expressions of the vigour of the axis).
The relationships between TLA or LAI and MSD or ESQ are visualised in Fig. 7.7 and Fig. 7.8.



7.7a

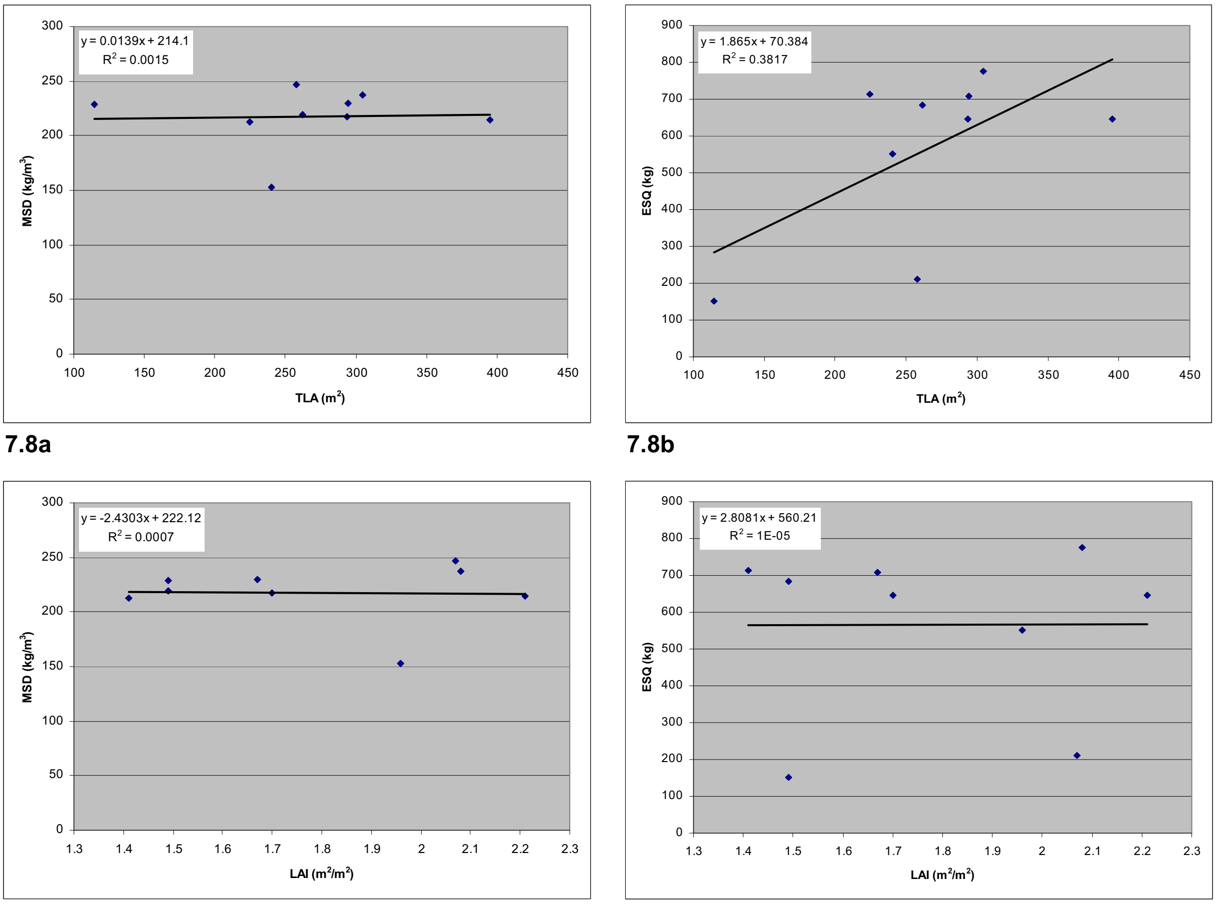
7.7b

7.7c

7.7d

Figure 7.7 Scatter diagrams of Total leaf area (TLA) and Leaf area index (LAI) of 22 early to late AV-phase and G-phase sago palm axes against the Mean starch density (MSD) of, and the Estimated starch quantity (ESQ) in the pith of the leafless part of these axes (with linear regression lines and their equations and coefficients of determination (R^2))

Figures 7.7a and 7.7b do not show that there is a correlation between the TLA of an axis and the MSD or ESQ. In these figures data of all the 22 different palms are included of which both starch content and leaf area were estimated. That no correlation was found is in accordance with the observations on an individual axis that starch accumulation has a slow start in the beginning of the AV-phase, whereas during most of the AV-phase, the number of leaves remains about the same (Table 4.10) while the increasing number of leaves towards the G-phase may be set off by their smaller size, resulting in a fairly constant TLA during most of an axis' AV- and G-phase. Any correlation that may still exist between the TLA and the MSD or ESQ of these palms is probably masked to a large extent by their difference in age and development phase. If we narrow down the sample population to include only the 9 oldest palms, viz. late AV-phase and older, however, there seems to be again no correlation between TLA and MSD, as expected (Fig. 7.8a), but the correlation between TLA and ESQ becomes stronger (Fig. 7.8b).



7.8a **7.8b** **7.8c** **7.8d**

Figure 7.8 Scatter diagrams of Total leaf area (TLA) and Leaf area index (LAI) of 9 late AV- and G-phase sago palm axes against the Mean starch density (MSD) of, and the Estimated starch quantity (ESQ) in the pith of the leafless part of these axes (with linear regression lines and their equations and coefficients of determination (R^2))

The LAI of the axes, however, which have a weak correlation with MSD and ESQ when all 22 palms are taken into consideration (Fig. 7.7c and 7.7d), seem to have none at all when the 9 oldest palms are taken only (Fig. 7.8c and 7.8d). I can neither explain why LAI would show a weak correlation with starch density and quantity where TLA does not, nor why these weak correlations would disappear when only the older palms are included in the plots.

No leaf area-based yield predictors could be derived from this study. The few weak correlations found suggest that they still may exist. Further study of the relationship between TLA and/or LAI and starch content could reveal these, but these studies should then be done with more homogeneous plant material, growing under more homogeneous conditions. Also, the influence of age and development on this relationship seems such that even for a trunk size-independent variable as MSD it is not the best option to study this relationship in a series of palms at least partly selected for differences in precisely these age and development aspects, as is the case here.

7.4.7 How can starch density differences in the pith of the trunk be interpreted morphologically?

Are differences in starch density of the pith (g starch / cm^3 pith) attributable to differences in filling percentage of the available storage capacity or to differences in the available storage capacity itself, or to a combination of both?

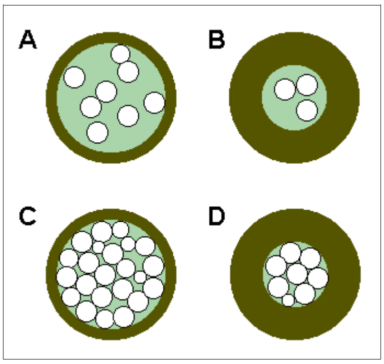


Figure 7.9 Hypothetical causes of starch density differences in a parenchyma cell in the pith of a sago palm trunk.
(See text for explanation.)

On a cellular level these possibilities are illustrated in Fig.7.9: difference in filling percentage (A and B vs C and D); difference in storage capacity (A and C vs B and D); a combination of differences (B vs C).
On the pith tissue level, capacity differences could be caused either by differences in the ratio of storage cells (parenchyma) to other cells (e.g. vessel elements, fibres), or by differences in intercellular space.
The question about the variation in starch content and distribution in sago palms should be expanded accordingly with the question: Does the space for starch granules in the pith of a sago palm trunk - in other words: the potential starch density of the pith - differ with age and/or development phase of the trunk, and do genetic and/or environmental factors affect the available space for starch granules?

It is unlikely that on a cellular level the storage capacity would vary much as the cell wall thickness of parenchyma cells is not likely to change much with age.

There may be differences on a tissue level. VAN KRAALINGEN studied sago palms in East Sepik Province, Papua New Guinea. He reported about the structure of the trunk pith:

> "At the base of the palm, many singular, almost vertical, air channels occur. They are visible with the naked eye and about 200-300 µm in diameter ... Pith samples taken at a height of 5 m have no air channels nor have pith samples from 8 m ..." (VAN KRAALINGEN 1983:45)

Larger intercellular space at the base of the trunk would cause a lower potential starch density there. Wether intercellular space differences come about with age or are laid out from the start, remains unclear. Also any differences between varieties in this respect remain to be studied.

7.5 Conclusions

1. Early on in the AV-phase the trunk may be formed without any starch being deposited in it at the same time. A case in point is Palm #12 with a leafless trunk of 6 m tall and a starch density not exceeding 11 kg/m^3.

2. From the late AV-phase onward the maximum starch density ranges from 238 to 284 kg/m^3, with an average maximum of 261 kg/m^3.

3. The 4 trunks with the highest maximum starch densities were an "Ihur" in the late AV-phase, a "Tuni" in the late-AV-to-early-G1-phase, and a "Molat Berduri" in the early G1-phase, all three with a maximum of 280 kg/m^3, and an "Ihur" in the G3-phase with a maximum of 284 kg/m^3. It seems safe to conclude that the maximum starch storage capacity in the pith of any sago palm is 280 kg per cubic metre of pith.

4. The furthest-developed trunk that was sampled (Palm #05) had half-grown fruits, but still had a uniform, high starch density in its trunk. Therefore, the evolution of starch depletion escaped being investigated in this study.

5. Lack of precise data on the age of the sampled trunks and lack of uniformity of their genetic make-up and growing conditions made it impossible to arrive at the desired detailed timetable of the evolution of trunk starch accumulation and depletion.

6. The starch distribution pattern in the leafless part of the trunk shows a tendency to evolve from two-tailed to one-tailed (i.e. left-tailed, with a decreasing starch density towards the base of the trunk). This contradicts the findings of YAMAMOTO *et al.* (2003), who found the one-tailed distribution in the younger trunks. Also the low-density dip occurring somewhere in the middle of the trunk as reported by VAN KRAALINGEN (1986) was not found here.

7. Varietal influences on starch density and distribution could not be detected. A variety with a markedly lower maximum starch density was also growing under markedly different circumstances. Further study is needed to disentangle their influences.

8. The influence of shading on starch density and distribution could not be established directly as data on the shading history rather than the shading at the time of felling are needed to find out whether there is a relationship or not. A long left tail in the starch distribution could tentatively be linked to an early AV-phase spent in the shade.

9. There is a negative correlation between the duration of flooding and trunk starch density.

10. No trend in the influence of pH or salinity of the groundwater, or of the number of suckers on trunk starch density or quantity could be detected as there were too few cases with large enough differences in PH, EC or the number of suckers in which these differences could be separated from other differences with a possible influence on trunk starch accumulation.

11. Total leaf area nor Leaf area index of a single trunk could be linked to either the mean starch density of its pith or the amount of starch the pith contains. A time series of palms, which was the study object at hand, is not the ideal population to study these relationships anyway because of the influence of age and development on these relationships.

7.6 A starch accumulation model for sago palm based on starch density evolution

As summarized in Conclusion #5 in the previous section, lack of precise data on the age of the sampled trunks and lack of uniformity of their genetic make-up and growing conditions made it impossible to arrive at a detailed timetable of the evolution of trunk starch accumulation and depletion. Figure 7.6 illustrates this lack of data and uniformity in the jagged course of the graph. If we would single out one variety - eliminating one source of (probable but still unproven (see Conclusion #7)) variability in the plant material - and make some educated guesses based on the available data, an attempt at the fomulation of a starch accumulation model describing the potential trunk starch yield in time can be made.

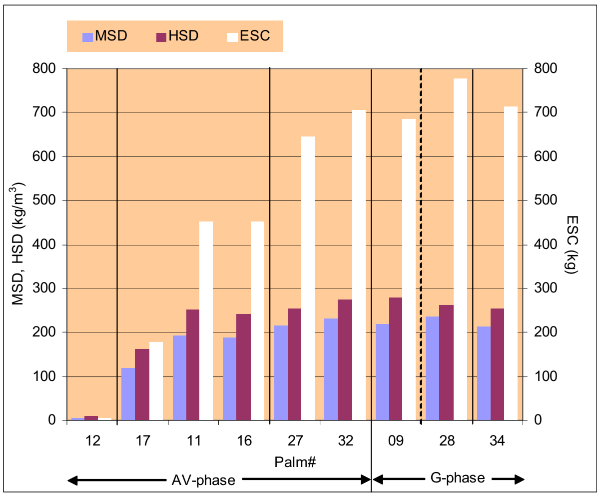


Figure 7.10 Excerpt of Fig.7.6 (q.v.) presenting the data of "Tuni" palms only.

Of the 27 palms sampled, folk variety Tuni was represented best with 9 specimens, occurring in 6 of the 13 development sub-phases distinguished. In Figure 7.10 the same data as in Figure 7.6 are presented, but now for these 9 "Tuni" palms only. These "Tuni" palm data, together with data on trunk length, are presented also in Table 7.3.

Table 7.3 Length and pith starch density of the leaf-free trunk part of 9 "Tuni" sago palms tentatively ranked by age and development phase

Palm # (Development phase)	12 (AV early)	17 (AV)	11 (AV)	16 (AV)	27 (AV late)	32 (AV late)	09 (G1 very early)	28 (G1 late)	34 (G2)
Length (m)	6.00	7.85	10.70	12.05	14.60	14.45	17.50	14.75	15.20
Mean starch density (kg/m^3)	4.64	119	192	188	217	230	219	237	213
Maximum starch density (kg/m^3)	10.6	162	251	242	254	275	280	262	255

The following assumptions are made based on the data presented in Fig.7.10 and Table 7.3.

1. Starch density throughout the leafless part of a trunk (the part that is usually harvested) eventually reaches a level equal to the maximum starch density of 280 kg/m^3;
2. This maximum starch density level is reached at the end of the AV-phase and stays at this level up to the beginning of the G3-phase;
3. At 100% of the AV-phase duration, the leafless trunk is 15 m long (disregarding the exceptionally tall trunk of Palm #09);

And because of the normally very regular growth of a trunk (see Chapter 4) it is also assumed that

4. In the AV-phase, the age of the leafless part of the trunk is linearly proportional to its length.

Based on the assumed proportionality of trunk length and age, the course of the MSD in time during the AV-phase can be investigated by plotting MSD against trunk height (Figure 7.11).

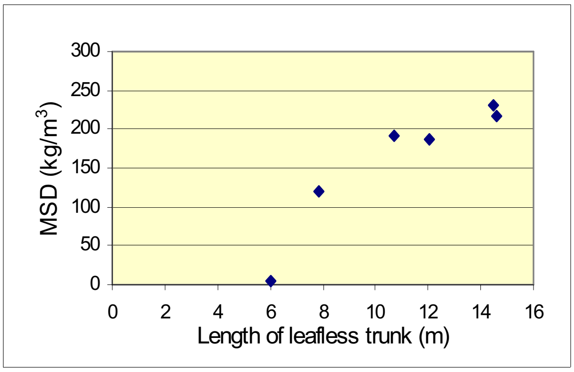


Figure 7.11 Scatter diagram of the mean starch density (MSD) in the pith of the leafless part of the trunk of AV-phase "Tuni" sago palms against the length of this trunk.

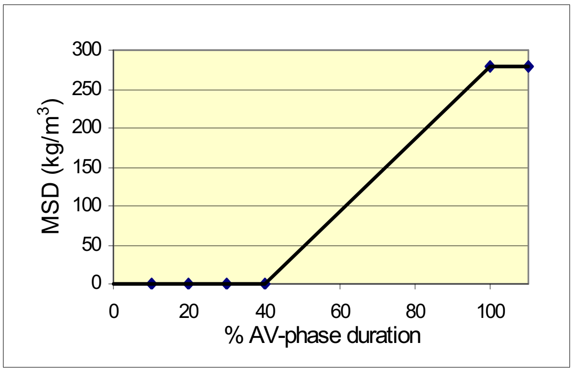


Figure 7.12 Model of the development of the mean starch density (MSD) in the pith of the leafless part of a sago palm trunk during the AV-phase.

At an assumed leaf-free trunk length at the end of the AV-phase of 15 m, a 6 m leaf-free trunk length corresponds to 40% of AV-phase time elapsed. Because at this point in time the amount of starch in the "Tuni" palm (#12) is almost zero, I take 40% AV-phase as the starting point of starch accumulation in the model. The data points in Fig. 7.11 suggest a gradual levelling off of MSD increase in time to a maximum level. For simplicity, and because of the uncertainty of the "Tuni" data points, I assume a linear increase to the maximum starch density of 280 kg/m^3 in the model. The equation for this line would thus be $Y = 280/60\ X$

For the whole AV-phase duration:

$Y = 0$ for $0 \le X \le 40$

$Y = 4.67\ (X - 40)$ for $40 \le X \le 100$

in which

Y : mean starch density (kg.m^{-3})

X : percentage of AV-phase duration elapsed.

With the MSD development taken as a given in this model, the amount of starch in the trunk solely depends on the development of the storage capacity of the trunk, i.e. of its diameter and its length. With trunk diameter not varying much during the AV-phase, the quantity of starch at a certain point in time between 40% and 100% of the AV-phase duration can be calculated as follows:

StarchQuantity = 4.67 × ((AVphaseTimeElapsed / AVphaseDuration × 100) - 40) × AveragePithDiameter × π/2 × LUR × InternodeLength × AVphaseTimeElapsed

The growth in trunk length in this formula is expressed as Leaf unfolding rate (LUR; see below) times the internode length.

As an example, the starch content development for a typical sago palm axis as it emerged from my data will be calculated. Typically, the diameter of the leafless trunk part ranges from 45 cm to 60 cm (Table 4.5). The typical thickness of the bark plus adjacent fibre layer which has to be subtracted from the trunk diameter to arrive at the pith diameter is 2 cm (Table 4.6). For convenience, 5 cm are subtracted, making the typical pith diameter range from 40 cm to 55 cm. Typical internode length of the leafless trunk part during the AV-phase would be between 10 and 20 cm (Table 4.7). The other data still needed are the duration of the AV-phase and the growth rate. The necessity of prior knowledge of these is obviously a drawback of this model. The growth rate, expressed as LUR, may vary from 2 to 14 leaves per year, with an average of about 8 leaves per year (Table 4.9). If we take an LUR of 10 leaves per year, an average of 15 cm per internode, an AV-phase duration of 10 years, and a 50-cm pith diameter, the starch accumulation during the AV-phase would develop as presented in Table 7.4. And as assumed in the above assumption #3, the starch in the leafless trunk at the end of the AV-phase will still be available for harvesting during the G-phase as long as the flowers have not opened and the fruits have not started to be formed.

Table 7.4 Development of the amount of starch in a hypothetical sago palm axis during the AV-phase

AV-phase time elapsed (year)	1	2	3	4	5	6	7	8	9	10
% of AV-phase duration elapsed	10	20	30	40	50	60	70	80	90	100
MSD (kg/m^3)	0	0	0	0	47	93	140	187	234	280
pith volume (m^3)	0.30	0.60	0.90	1.20	1.50	1.80	2.10	2.40	2.70	3.00
accumulated starch (kg)	0	0	0	0	71	167	294	449	632	840

Discussion

The amount of starch accumulated at the end of the AV-phase seems high in this example. Starch yields per trunk reported in literature are seldom this high (e.g.: a top estimated 234 kg in a sample of 19 of "the highest yielding wild type" in the study by VAN KRAALINGEN (1986) mentioned earlier). It should be kept in mind, however, that this example refers to potential starch content based on the assumption of attaining the maximum starch density recorded of 280 kg per cubic metre of pith. Also, the difference in plant material examined (relatively large trunks in my case) may play a role, or the starch extraction method the reported figures are based on (traditional versus laboratory). The latter may cause a startling difference, as the experiment with Palm #37 presented in the appendix to this chapter (Section 7.7) shows.

The model VAN KRAALINGEN (1986) devised in his study referred to in the literature review (Section 7.2) was meant to predict the actual amount of starch accumulated in a given trunk. It ingeniously incorporates environmental influences and trunk age through indices gleaned from the palm itself:

$$Y = 0.2190 + 0.0242\ K_1 - 0.0108\ K_2$$

in which

Y = starch density (dry starch in g/cm^3 pith)

K_1= real minus expected number of leaves. As it was found that the number of leaves increased by 0.048 per day from an average 12.7 after the yearly floods had receded, an expected number of leaves at the time of sampling could be calculated. Deviation from the expected number was considered proportional to palm vigour, and hence to starch accumulation capacity.

K_2= length of highest internodes (cm) [i.e. probably mean length of top 10 internodes (VAN KRAALINGEN 1983:69)]. Probably the length of the last internodes before the trunk bolts in the G-phase is meant, as VAN KRAALINGEN found that "every palm shortens its internodes to a fixed length or flowers before that".

Multiplying Y with harvestable trunk volume gives the predicted starch yield of the trunk. 76% of the yield variation was explained by this regression equation. A weakness in the equation, VAN KRAALINGEN admits, is the term K_1, because the determination of the expected number of leaves is not straightforward: it requires additional data on the local flooding regime and the starting point of the number of leaves (here 12.7) probably depends on many parameters, including palm variety. Moreover, the equation does not accommodate for a floodless situation.

Both the VAN KRAALINGEN model and the model presented in Section 7.6 try to predict starch content by predicting the starch density, after which the amount of starch is calculated by multiplying it by the harvestable pith volume. However, as the former model is a static one (time does not feature in the equation), it is not usable for predicting the dynamics of starch accumulation and depletion.

Another approach to arrive at an estimate of the starch accumulation and depletion rate is possible if one knew the energy production of a palm axis and the amount of energy needed to maintain and build its components. Evolution of size of the components during the life of an axis is presented in Chapter 4. In this chapter the evolution of the amount of trunk starch was investigated as well as the potential starch yield of a trunk. Together they give an idea of the evolution of the total biomass of a sago palm axis, and of what can be considered a standard or model sago palm. An attempt at modelling this energy production and consumption in such a model palm is presented in Chapter 8.

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7.7 Appendix

Traditional starch extraction from the trunk of sago palm (*Metroxylon sagu* Rottb.) in West Seram (Maluku, Indonesia) leaves more than half the starch unharvested *

Abstract

Efficiency of starch recovery from sago palm trunk by traditional methods in West Seram was investigated by traditionally processing one whole trunk of variety Ihur in the early generative phase and comparing the starch yield to the actual starch content of the trunk estimated by laboratory processing of pith samples. The traditionally harvested wet starch contained 41% water. Only 47% of the starch in the processed trunk part was recovered. If the unharvested starch present in the traditionally discarded basal and top part of the trunk is taken into account, recovery drops to 44%.

Introduction

Reports on sago starch production in communities harvesting the starch for subsistence needs in a traditional way often mention yields in number of traditional containers of wet starch per trunk. For researchers working on dry matter production and distribution in sago palm this information is useless if additional information is lacking not only on the volume and the weight of these containers, but especially on the dry matter content of the wet starch, and on the part of the total amount of starch in the trunk extracted by the traditional harvesting method used.
Reversely, reports on starch content of a sago palm trunk analysed by precise laboratory techniques often lack information on how that content would translate to yield in a traditional field situation.
To get an idea of what portion of total trunk starch is extracted by the traditional processing method used in most parts of the Moluccas and New Guinea, in November 1990 pith samples were taken from one whole sago palm trunk in Hatusua village, West Seram, after which the trunk was processed in the traditional way by local processors. By laboratory analysis of the pith samples and dry matter determination of the traditionally extracted wet starch, total dry starch content of the trunk and traditionally extracted dry starch yield per trunk could be estimated and compared.

This study was part of a much more comprehensive investigation into development of trunk starch content in time **. Laboratory pith extraction and analysis techniques used here were developed in the framework of this greater study.

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* Adapted from the paper presented at the 8th International Sago Symposium, 4-6 August 2005, Jayapura (Papua Province, Indonesia), which was published as

> D.L. SCHUILING 2006 "Traditional starch extraction from the trunk of sago palm (*Metroxylon sagu* Rottb.) in West Seram (Maluku, Indonesia)". - In: "Sago palm development and utilization : proceedings of the Eighth International Sago Symposium (8ISS) held on August 4 - 6, 2005, at the Auditorium of the Governor of Papua Office in Jayapura" / KARAFIR, Y.P. ; JONG F.S. ; FERE, V.E. (eds). - Manokwari (Indonesia) : Universitas Negeri Papua Press, 2006. - xii,266 p. - p.189-200.

Adaptations include 1) restoring the title, the vertically stretched photos, the 2nd footnote in Table 7.6 and some other (minor) editorial unasked-for changes, 2) adding reference to SHIMODA & POWER (1986), and 3) leaving out photos, tables and text already placed elsewhere in this thesis, and changing or adding their references in the (remaining) text accordingly.

** The palm processed here is Palm #37 (details in the Sago Palm Data Sheet on this palm in Appendix A).

Plant material

A sago palm trunk of the local variety Ihur was marked with a felt-tip pen at 0.5 and 1.5 m above ground level (a.g.l.) and then felled with a chainsaw at about 65 cm a.g.l. The palm was of a developmental stage designated by local informants as between *terbuka jaga* (= leaves opening/spreading) and *putih masak* (= mature white [stage]). The felled trunk was cleaned of leaf remains and measured. Further marks were made every metre along the trunk. The leaves, green and still folded (white), were carefully removed up to the growing point. Anatomical analysis of the apex revealed that the axis had recently turned generative as buds of inflorescence branches were found in the leaf axils from the 19th immature leaf inside the spear leaf upward (oldest leaf inside spear leaf is first immature leaf; total number of immature leaves inside spear was 37). (See SCHUILING (1991) for apex analysis method.)
Statistics of the palm are gathered in Table 7.5.

Table 7.5 Some statistics of the felled sago palm axis (see text).

Height:	ground level - attachment lf1	13.61 m
	attachment lf1 - attachment spear leaf	2.23 m
	Total	15.84 m
Nodes:	leaf scars	85
	with unfolded green leaves	24
	with folded/primordial leaves	Spear+18 = 19
	with primordial bracts and axillary ax_1-s	19
	Total	147

Transverse dimensions along axis:

Height (m) above ground level	Diameter (cm)	Thickness of *wa'ah* (bark + fibre layer) (cm)
0.5	53	3
1.5	49	3
2.5	52	2.5
3.5	54	2.5
4.5	55	2.5
5.5	58	2.5
6.5	57	2
7.5	57	2
8.5	60	2
9.5	63	2
10.5	62	2
11.5	63	2
12.5	62	1.5
13.5	58	1.5
14.6	54	1
15.5	34	1

lf1 = leaf #1 = oldest green leaf
ax_1 = first-order inflorescence branch

Laboratory starch extraction

Pith samples were taken in the way as described in the section on materials and methods of this chapter (Section 7.3.1).
Two replicate samples (i.e. two per window) were taken every metre along the length of the trunk, starting 0.5 m above ground level up to 14.5 m. At 15.5 m a.g.l. the trunk pith was so watery (indicating low, if any starch content) that no sample was drawn anymore.

The volume of the pith samples was measured by under-water weighing as described also in Section 7.3.1. Starch and other non-(water-)soluble solids in a pith sample were separated, and the starch dried as described in this same section.

Traditional starch extraction

The trunk was sawn into four 3-m-long logs and one 1-m-long log, starting at 1 m a.g.l. A log (*mot*) was then split lengthwise by hammering wedges into its side (Fig. 2.10a-d).
The exposed pith was pounded loose and pulverized with a hoe-like or adze-like instrument (*nani*) (Fig. 7.13).

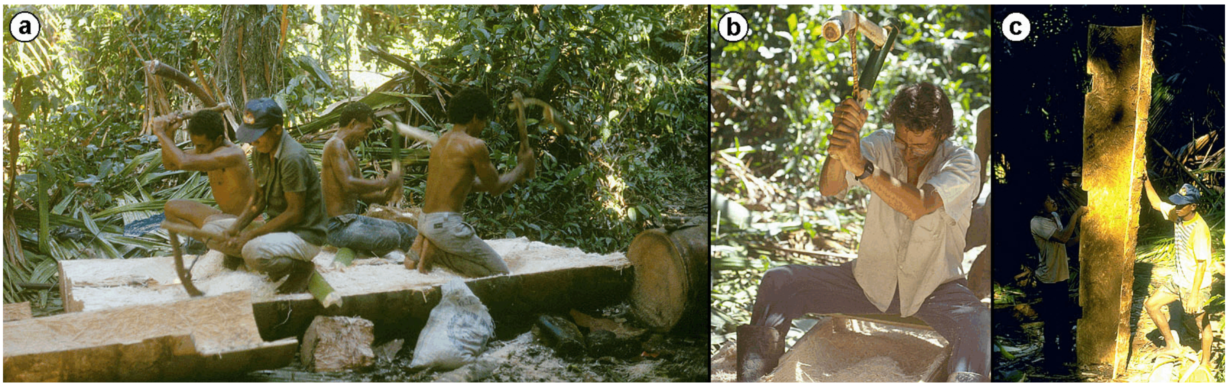

Figure 7.13 Pulverizing and removing the pith until only the *wa'ah* is left.
[a, b: photo nr. 90.11-148-31, -28 (mon19-tue20nov1990); c: photo nr. 90.11-149-06 (thu22nov1990); a-c: Hatusua, West Seram]

The starch grains were leached out of the pulverized pith with water over a sieve and the starch was recovered from the slurry passing through the sieve by letting it settle in a trough. The settled wet starch was transferred to *tumang*, baskets made of young sago palm leaflets especially for the purpose of transport and storage of the starch (Fig. 2.10j-n, Fig. 2.3).

For this study, the logs were carefully processed metre by metre so that the starch content of separate 1-metre trunk parts corresponding to trunk parts sampled for laboratory extraction could be established. The first metre (0-1 m a.g.l.) from which laboratory samples were taken, was excluded from traditional processing because it was impractical to process it. Usually the first 50-75 cm is not processed anyway because traditional processors find that it contains too many hard fibres (hard to pound) and too little starch. Also the last metre sampled for laboratory processing (14-15 m a.g.l.) was excluded as the local processors did not think it would be worth their while judging from the texture of the pith and the proximity to the top.

The nett weight (wet starch weight) of each *tumang* was recorded (Fig. 7.14a,b). Then a sample of the starch was taken from each *tumang* by inserting the stainless steel sampling tube described above (Section 7.3.1) in the centre of the *tumang* down to the bottom. Upon retracting the tube (drawing the sample), the *tumang* had to be held upside down, otherwise the sample would not stay intact inside the tube (Fig. 7.14c). The dry starch content (%) of the sample was then established by weighing the sample before and after drying to constant weight at 70 ºC. The weight of the dry starch in each *tumang* could then be estimated by multiplying the weight of the wet starch by the dry starch content of the sample.

Figure 7.14 Weighing the *tumang* and drawing a wet starch sample from it.
[photo nrs. 90.11-149-02, -03, -04, Hatusua, West Seram wed21nov1990]

Results and discussion

The results of the traditional starch extraction from the trunk part between 1 m and 14 m a.g.l. are presented in Table 7.6. The average dry matter content of the harvested wet starch can be calculated by dividing the total dry starch yield estimated on the basis of the dry starch content of each *tumang* by the total wet starch yield: 293.59/498.72 x 100 = 58.87%. Correcting the yield for the starch that could not be harvested because it was lost in sawing or taken away in laboratory samples (see note below Table 7.6) gives a total dry starch yield by traditional processing of 296.69 kg.

The results of the dry yield estimation based on laboratory starch extraction from samples representing the trunk part between ground level and 15 m a.g.l. are shown in Table 7.7. The estimated total is 687 kg; the estimated starch content of the part between 1 m and 14 m a.g.l. equals 687-31-24 = 632 kg.

Assuming that the yield estimate based on lab analysis of pith samples equals 100% of the starch actually present in the trunk, starch recovery percentage by the traditional methods equals 297/632 x 100 = **47.0%**.

Most of the unrecovered 53% of the starch actually present in the trunk must still be in the washed pulverized pith (*ampas*). This is probably due to a combination of incomplete pulverization of the pith (not every cell broke and released its starch grains) and incomplete washing-out of the starch kernels that wére released. Findings by BINTORO *et al.* (1990) point in the same direction: they investigated the feeding value of traditional sago processing waste, and still found 56.2 - 69.2 % starch (on a dry basis) in sago pith residue from which the coarse fibres had been removed.
At two locations in the Sepik River Basin, Papua New Guinea, SHIMODA & POWER (1986:102) found 28.2% and 43.1% of the starch still remaining in pulverized pith after traditional processing. As traditional processing there involved washing the pulverized pith 7 to 8 times, they attributed the loss to "incomplete crushing using traditional means".

By not processing the first (basal) metre of trunk, nor the top (14-15 m a.g.l.) part, another 31 + 24 = 55 kg of dry starch (see Table 7.7) is left in the field. If this amount is added to the unrecovered starch in the processed part, the recovery percentage by traditional methods drops to 297/687 x 100 = 43.2%. Usually the stump of the trunk that is left unprocessed is about 65-75 cm. Therefore, 25-35 cm of trunk is not accounted for in the traditional processing here. Assuming that 5 kg of starch can be recovered from these 25-35 cm of trunk, the starch recovery percentage from the whole trunk by traditional methods would be (297+5)/687 x 100 = **43.9%** of the starch estimated to be actually present in the whole trunk.

Table 7.6 Starch recovery by traditional processing methods (manual pith pounding and manual washing of pounded pith).

Mot **(height a.g.l.)**	***Tumang***		**DM content (%)of *Tumang* starch sample ***	**Dry starch per *tumang* (kg) [estimated]***	**Dry starch per *mot* (kg) [estimated]***	**Dry starch per *mot* (kg) [estimated]*, corrected ****
	#	**wet starch contents(kg)**				
1-2 m	A	14.12	59.48	8.40	15.49	15.59
	B	11.69	60.69	7.09		
2-3 m	A	12.15	59.77	7.26	15.54	15.72
	B	13.90	59.56	8.28		
3-4 m	A	14.32	60.84	8.71	17.59	17.79
	B	14.27	62.25	8.88		
4-5 m	A	11.99	57.50	6.89	22.21	22.45
	B	12.89	58.76	7.57		
	C	13.38	57.93	7.75		
5-6 m	A	12.82	58.89	7.55	24.99	25.27
	B	15.12	58.84	8.90		
	C	14.21	60.07	8.54		
6-7 m	A	12.92	58.47	7.55	19.92	20.14
	B	14.73	58.64	8.64		
	C	6.35	58.81	3.73		
7-8 m	A	13.02	59.85	7.79	25.49	25.78
	B	12.12	59.26	7.18		
	C	12.35	59.58	7.36		
	D	5.41	58.35	3.16		
8-9 m	A	14.24	58.95	8.39	31.07	31.41
	B	13.12	59.05	7.75		
	C	14.09	58.69	8.27		
	D	11.47	58.06	6.66		
9-10 m	A	13.04	58.27	7.60	26.72	27.02
	B	13.35	59.02	7.88		
	C	13.10	59.20	7.76		
	D	5.98	58.24	3.48		
10-11 m	A	13.89	59.28	8.23	32.37	32.73
	B	14.42	58.96	8.50		
	C	13.32	58.26	7.83		
	D	13.27	58.84	7.81		
11-12 m	A	13.17	58.28	7.68	25.48	25.77
	B	14.59	58.36	8.51		
	C	14.40	57.69	8.31		
	D	1.70	57.73	0.98		
12-13 m	A	12.96	57.32	7.43	21.58	21.71
	B	13.50	57.56	7.77		
	C	11.03	57.80	6.38		
13-14 m	A	13.89	58.00	8.06	15.14	15.31
	B	12.43	56.98	7.08		
TOTAL		**498.72**		**293.59**	**293.59**	**296.69**

Note: *mot* = trunk section (from Dutch *moot* = section); *tumang* = traditional wet starch container made of sago palm leaflets.
* (based on) sample(s) dried to constant weight at 70 ºC.
** Corrected upwards for the loss of pith in the 1-cm saw-cut width of the chainsaw and in the samples taken for laboratory processing (0.1% by volume) prior to traditional processing. First, 12 m of trunk were sawn off at 1 and 13 m a.g.l. sawing away 99-100 cm and 1300-1301 cm a.g.l. Then 1-metre sections were sawn through the middle of each metre mark. Finally an extra 1 m was sawn off the remaining trunk part, sawing away 1400-1401 cm a.g.l.

Table 7.7 Estimation of dry starch yield by laboratory extraction method.

Sampling height (m a.g.l.)	Height range represented by sample (m a.g.l.)	Trunk diameter (m)	Bark thickness (m)	Pith diameter (m)	Pith volume represented by sample (m^3)	Dry starch [70°C] density (kg/m^3 pith)	Dry starch [70°C] yield (kg)
			leafless trunk part				
0.5	0.00 - 1.00	0.53	0.030	0.47	0.17	178	31
1.5	1.00 - 2.00	0.49	0.030	0.43	0.15	204	30
2.5	2.00 - 3.00	0.52	0.025	0.47	0.17	203	35
3.5	3.00 - 4.00	0.54	0.025	0.49	0.19	207	39
4.5	4.00 - 5.00	0.55	0.025	0.50	0.20	222	44
5.5	5.00 - 6.00	0.58	0.025	0.53	0.22	227	50
6.5	6.00 - 7.00	0.57	0.020	0.53	0.22	222	49
7.5	7.00 - 8.00	0.57	0.020	0.53	0.22	213	47
8.5	8.00 - 9.00	0.60	0.020	0.56	0.25	225	55
9.5	9.00 -10.00	0.63	0.020	0.59	0.27	231	63
10.5	10.00 -11.00	0.62	0.020	0.58	0.26	243	64
11.5	11.00 -12.00	0.63	0.020	0.59	0.27	209	57
12.5	12.00 -13.00	0.62	0.015	0.59	0.27	204	56
13.5	13.00 -14.00	0.58	0.015	0.55	0.24	182	43
14.6	14.00 -15.00	0.54	0.010	0.52	0.21	113	24
total	0.00 -15.00				**3.31**		**687**

m a.g.l. = metre above ground level.
[70ºC] = (based on samples) dried to constant weight at 70 ºC.

Conclusions

- Only 44-47% of the starch in the trunk of a sago palm in the early generative phase is recovered by traditional Moluccan processing techniques.
- Multiply starch yield reported in kg of **wet or dry starch** obtained in the traditional Moluccan way by 0.59 x 632/297 = **1.25** or 632/297 = **2.13**, respectively, to estimate the number of kg of dry starch present in the **processed part** of the trunk.
- Multiply starch yield **per trunk** reported in kg of **wet or dry starch** obtained in the traditional Moluccan way by 0.59 x 687/302 = **1.34 or** 687/302 = **2.27**, respectively, (i.e., as a rule of thumb: by **1⅓ or 2¼**, respectively) to estimate the number of kilograms of dry starch present in the **whole trunk**, including parts traditionally not processed.
- Traditional processing methods recover less than half the starch actually present in the trunk. Therefore, to increase starch yield for traditional processors, it is probably more worthwhile to look into possibilities to improve their processing techniques than to look for higher-yielding varieties.

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8 Energy production and consumption in sago palm : modelling trunk starch content in time based on their assumed equality by the end of the vegetative phase

Abstract

During the life span of a sago palm axis part of the energy produced by the crown of leaves is stored in the trunk as starch for later use by the palm to build its terminal inflorescence and fruits. This starch is also wanted by man for food and industrial purposes who harvests it by felling the trunk. To arrive at a scientific basis for the timing of felling, the energy demand and supply during growth and development of a sago palm axis were modelled to gain insight into the development of the axis' starch production capacity. The basis for this model were field data on phenology, morphology and anatomy of semi-wild sago palms in Seram (Maluku, Indonesia), and literature data on average energy costs of production and maintenance of carbohydrate and lignin, the axis' main components. Actual light interception and photosynthesis data were not collected and do not underlie the model.

First, the energy costs were calculated for the production and maintenance of the axis in the adult vegetative (AV) phase for which many data on dry matter (DM) produced, including starch, were available. Then these costs in the establishment (E) and generative (G) phase, not taking into account any starch production, were estimated assuming that the size changes that take place in these phases occur at constant rates.

Assuming 1) that during the last year of the AV-phase the crown of leaves is at full production capacity and exactly capable of producing the energy for that year's DM production and maintenance of the axis, and 2) that there is a linear relationship between that production capacity and the crown's DM weight, the axis' production capacity in the 4-year G-phase was estimated. There appeared to be no room for starch production in the G-phase. On the contrary, the estimated production capacity fell short of demand by 65 kg glucose already in the first year of the G-phase, and at the end of the G-phase after using up all the energy stored in the trunk starch, there was even a deficit of 905 kg glucose.

As the energy production and consumption in a sago palm axis could not be matched, the scientific basis for timing the harvest could not yet be established with this model. To improve the model additional data are needed on the chemical composition of sago palm parts and on assimilation rate.

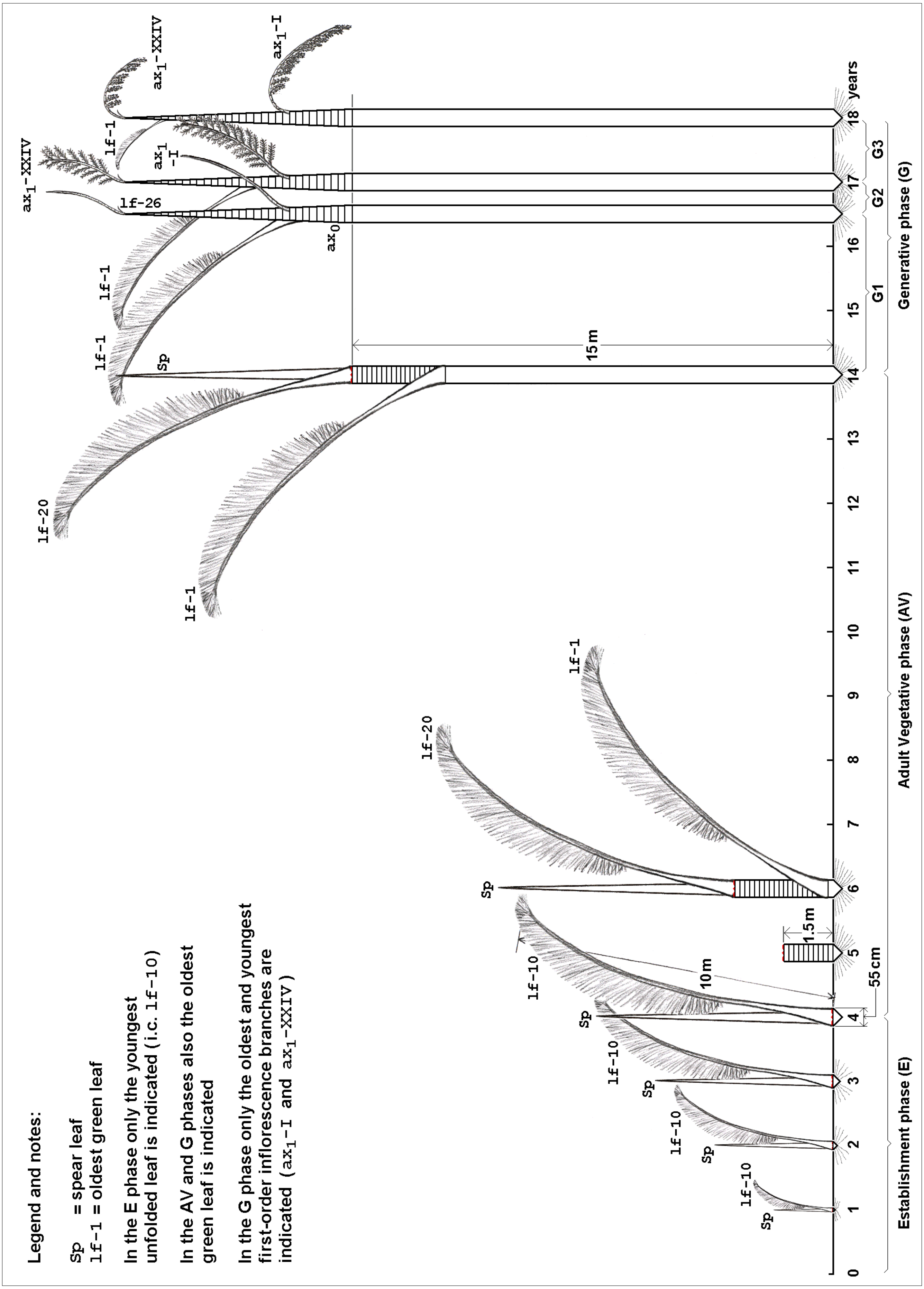

Figure 8.1 Schematic representation of the growth and development of a vigorous West-Seram-type sago palm axis. Dimensions to scale, except for those of roots.

8.1 Introduction

Sago palm (*Metroxylon sagu* Rottboell) is a suckering palm species. Each single trunk of a sago palm clump is an axis with a determinate growth habit: it dies after the terminal inflorescence has produced mature fruit 12-20 years after its inception as a sucker on the mother palm. During the life span of the axis part of the energy produced by the crown of leaves is stored in the trunk as starch. Towards the end of its life, energy from the starch is used again for the formation of the inflorescence and the fruits. This starch is also wanted by man for food and industrial purposes and is harvested by felling the trunk.

I assume here that the photosynthates produced by the leaves are needed first of all for growth and maintenance of the palm, and only when there is a surplus will these photosynthates be used to build up the starch reserve. The crown size starts at zero and grows to adult size in the establishment phase, remains constant during the adult vegetative phase and diminishes again during the generative phase towards the end of the axis' life. As the crown gets smaller in the same period as the enormous inflorescence is built, there comes a moment that the photosynthate requirement for growth and maintenance of the whole axis becomes greater than its photosynthate production capacity. From that moment on, starch reserves must be mobilized to replenish the deficit. If one wants to harvest the starch it is useful to know when this moment takes place.

Up till now, timing the harvest is usually done on the basis of external examination by an experienced sago farmer. I attempt here to establish a scientific basis for the timing of this felling by modelling the energy demand and supply during growth and development of a sago palm axis. By this modelling, insight is gained into the development of the axis' starch production capacity.

The model is based only on observations of size and composition of the parts of an axis during the axis' life time, and on literature data on what it would cost in terms of assimilates to build and maintain the axis. No actual data on the energy production side, such as light interception and CO_2-assimilation rates, were collected.

8.2 The 'model' sago palm

8.2.1 Material

Phenological, morphological and anatomical data were taken from rather heterogeneous semi-wild sago palm stands on West Seram, Maluku, Indonesia (1988-1990). These stands did not contain what one would consider standard plantation-type sago trees: of average stature and fast-maturing. However, the energy calculation concept that will be presented here does not depend on size or development rate. The field data on which most of the size parameter values of my model palm are based, are presented or referred to in Appendix 8A. The development rate values of the model palm are educated guesses based on field observations over short periods (1-3 years), on interviews with sago farmers, and on literature data.

8.2.2 Simplification of growth and development for the sake of modelling (see Figure 8.1)

To make calculations easier, the following assumptions are made, some of them obvious simplifications of the truth:

1. Sago palm forms a single trunk from seed. Thus, suckering is not taken into account.
2. Sago palm has only three development phases: a 4-year establishment phase, a 10-year adult vegetative phase, and a 4-year generative phase.
3. Phases are clearly distinguished, beginning and ending abruptly.
4. Within each phase, growth and development proceed continuously and at a constant rate. Between phases rates may differ.

8.2.3 **Description of development phases** (see Figure 8.1)

For the description of the developmental phases of the 'model' sago palm and of the accompanying size changes of its parts, the morphological terminology as in TOMLINSON (1971) is used (also used and explained in SCHUILING (1991)). E.g., ax_0 means main axis (trunk + inflorescence rachis), ax_1 means 1st-order branch of the inflorescence, etc.

<u>Establishment (E) phase</u>: 4 years.
- Trunk: Diameter increases from 0 cm to 55 cm; trunk forms an inverted cone with an estimated top angle of 90°, resulting in a trunk height of 27.5 cm.
- Leaves: Per year 10 new leaves are unfolded. Therefore 40 new leaves are built during this phase, the last one having the final adult size with a length of 10 m. The longevity of an adult-size leaf is 2 years; longevity of juvenile leaves is less (JONG F.S., pers. com. 2001). Here I assume that throughout the E-phase leaf longevity is only 1 year.

<u>Adult vegetative (AV) phase</u>: 10 years.
- Trunk: at 10 new leaves per year, and 15 cm per internode: 1.5 m trunk height increase per year, i.e. 15 m trunk height increase in the 10 years of this phase.
- Leaves: 10 new leaves are unfolded per year, therefore 100 leaves are built during this phase. The longevity of each leaf is 2 years.

<u>Generative (G) phase</u>: 4 years.
Sub-phases:
G1 (to end of growth of ax_0 and ax_1-s): 2.5 years;
G2 (to end of growth of ax_2-s and ax_3-s): 0.5 year;
G3 (to end of growth and ripening of fruit): 1 year.

- Trunk (G1 only): From diameter 55 cm to 5 cm over a trunk length of 7 m in 2.5 years.
- Leaves (G1 only): At an average 13 new unfolded leaves per year, 32 leaves are built in the G1-phase. Leaves still drop off at the same rate as in the AV-phase, therefore the number of green leaves increases during G1. Leaf size from full AV-size (length 10 m) to nothing in 33 steps (the 33rd leaf has a size of zero, i.e. it is not formed anymore).
- Inflorescence (G1): 24 ax_1-s are formed, decreasing in length from 4 m to 2.5 m, and decreasing in average diameter from 5.75 cm to 3.95 cm. [4]
(G2): At 20 ax_2-s per ax_1 on average, 24 x 20 = 480 ax_2-s are formed. And at

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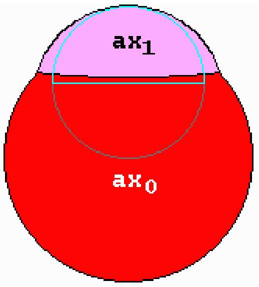
[4] Derived from inflorescence data of palm #34 (see Appendix A): the cross section of the base of an ax_1 is not round but lens-shaped with a rounder outside face and a flatter inside face, and only the circumference of the outside face was measured (about 20 cm in the lowest branches, about 12 cm in the highest). A short distance from its implantation on the main axis (ax_0) the ax_1 cross section becomes circular, tapering off to a diameter of about 2.5 cm at the top. To arrive at an average ax_1 diameter, the diameter at the base was estimated by deriving it from the area of the cross section at the base as if this area were a circle. The lens-shaped area itself was in turn estimated by assuming it to be a semicircle with a circumference of the curved side equal to the circumference of the outside face of the lens. Base ax_1 diameters were thus estimated to be 9.0 cm in the lowest ax_1, and 5.4 cm in the highest, resulting in average diameters of (9.0 + 2.5)/2 = 5.75 cm and (5.4 + 2.5)/2 = 3.95 cm, respectively.



12 ax_3-s per ax_2 on average, 12 x 480 = 5760 ax_3-s are formed. ax_2-s are 50 cm long with an average diameter of 1.8 cm; ax_3-s are 14 cm long with an average diameter of 1.4 cm.

- Fruits (G3): at an average 2.5 fruits per ax_3, the number of fruits equals 5760 x 2.5 = 14 400 fruits; average diameter 4.5 cm.

8.2.4 Roots

I have no data on sago palm root development. According to LOOMIS & CONNOR (1992:34) roots constitute about 10% of the crop biomass when soil resources are not limiting. Where water or nutrients are limiting, the root fraction may be much larger. They probably refer to an annual crop.
For this model case, I assume that soil resources are not limiting. I also assume that root production is limited to keeping up with the increase in above-ground biomass and that there is no replacement production (i.e. all roots stay alive throughout the palm axis' life). Finally I assume that only live above-ground biomass has to be catered for by the roots. Combining LOOMIS & CONNOR's 10% and my 3 assumptions, the premise for root development in the model palm is that at all time root dry matter weight equals 1/9 or 11% of the above ground dry matter weight in live material.

8.3 Energy costs of potential production

In crop production, solar energy is fixed in biomass by the process of photosynthesis. In this process CO_2 from the air is transformed into glucose (gross CO_2 assimilation). The energy stored in glucose is partly released again to keep plant tissues alive and functioning (maintenance respiration) and to convert glucose into structural plant dry matter (growth respiration). The remainder of the glucose or net CO_2 assimilation is the basis of crop dry matter increase.

Maintenance coefficient (MC)

The amount of energy needed for maintenance respiration (the maintenance costs) can be expressed in kg of glucose per kg of dry matter (DM) in living material per day. On average this so-called maintenance coefficient (MC) is 0.015 kg glucose per kg DM per day (LÖVENSTEIN *et al.* 1995:27,32), which is 365 x 0.015 kg = **5.475 kg glucose per kg DM in living material per year**. I have applied this generalized MC throughout the calculations below.

Conversion factors (CVFs)

The energy needed for growth respiration, i.e. for the biosynthesis and putting in place (transportation) of plant tissue constituents (the production costs) can be calculated by applying the appropriate so-called conversion factor (CVF) for each of the constituents. The CVF of a plant constituent is the amount of glucose (g) needed to build and put in place 1 g of that constituent. PENNING DE VRIES *et al.* (1989:61) calculated the CVFs for the constituent groups **carbohydrates (1.275)**, proteins (1.887), fats (3.189), **lignins (2.231)**, organic acids (0.954) and minerals (0.120).

Potential production

In absence of adverse environmental conditions which would limit crop growth (viz. shortage or excess of water and nutrients) or reduce crop growth (viz. weeds, pests, diseases), potential production is reached as determined entirely by the amount of available light, the prevailing temperatures and the crop characteristics (LÖVENSTEIN *et al.* 1995:10). It is this potential production that I have tried to model here for the sago palm. Therefore, I have tended to take a higher than average value in the range of observed values of production parameters as the model value, assuming higher values represent potential production better than lower ones. E.g., I assumed the internode length during the AV-phase to be 15 cm, rather than the observed average of 13.1 cm in Palm #34 (range between 8 and 20 cm, excluding outliers (see Appendix A)).

8.4 Calculations of energy costs

For a calculation of how much photosynthate is needed to build a sago palm axis on the basis of CVFs for the chemical constituents of that axis, one needs, of course, data on the amounts of those chemical constituents in the various parts of the axis.
For a calculation of how much photosynthate is needed to maintain the built-up material on the basis of a generalised MC only, one only needs to know how much of this material is alive.

8.4.1 About chemical analysis data of plant material

As mentioned above, CVFs have been published for the broad plant constituent categories carbohydrates, proteins, fats, lignins, organic acids and minerals. Unfortunately not all of these categories correspond to the ones into which plant tissues are usually analysed: apart from the usual fractions crude protein, crude fat and ash - corresponding to the CVF categories proteins, fats and minerals - analysis results may include, depending on the method used, the fractions crude fibre, nitrogen-free extract (NFE), cellulose, hemicellulose, acid detergent fibre (ADF), and neutral detergent fibre (NDF), and they may or may not include a lignin fraction. A total carbohydrate fraction corresponding to the CVF category carbohydrates is never mentioned, because analyses are usually done by persons interested in the quality of plant material for use as animal feed or as source of fibre for the paper or textile industry and a total carbohydrate fraction does not give them the quality indication they look for. The analytical methods they often use are the classical proximate analysis, a.k.a. Weende analysis (in which carbohydrate and lignin are in both the fractions NFE and crude fibre) [5], and the treatment procedures with detergents to discriminate between cell contents material and cell wall material as outlined by VAN SOEST (1967) (in which carbohydrate and lignin are in both the fraction NDF or ADF and the fraction that the detergent removes) [6].

How do these analysis data translate into CVF categories? To answer this question, one needs to recall some basic facts about the molecular composition of plant cells.

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[5] The Weende analysis was developed in the 1860s at an experimental station at Weende near Göttingen, Germany. The crude fibre fraction "is defined as the residue of plant cells after extraction by acid and alkaline hydrolysis. In the standard procedure for crude fiber determination, the sample is first boiled in dilute acid and then in dilute alkali. The acid hydrolysis removes free sugars and starch. The alkaline hydrolysis removes protein and some carbohydrates. This process also removes some hemi-cellulose and lignin; therefore, only partial recovery of fiber components is achieved. ... recovery rates: Hemi-cellulose 20-30%, Cellulose 50-80%, Lignin 10-50%."
(Internet, WWW. - URL: "http://www.rosesci.com/Products/Chemical%20Analysis/ Fibertec%20-%20Overview.htm". - (Rose Scientific Inc., Cincinnati, Ohio, USA). - access date: 25jan2003)

[6] "Neutral Detergent Fiber (NDF) — Organic matter that is not solubilized after one hour of refluxing in a neutral detergent consisting of sodium lauryl sulfate and EDTA at pH 7. NDF includes hemicellulose, cellulose, and lignin.
Acid Detergent Fiber (ADF) — organic matter that is not solubilized after 1 hour of refluxing in an acid detergent of cetyltrimethylammonium bromide in 1N sulfuric acid. ADF includes cellulose and lignin."
(Glossary of Terms for the Biomass Feedstock Composition and Properties Database. - Internet, WWW. - URL: "http://www.ott.doe.gov/biofuels/glossary.html". - (U.S. Department of Energy (DOE) National Biofuels Program). - access date: 08jan2003)

> (From RAVEN, EVERT & EICHHORN 1999:20-22,36,64) :
>
> The carbohydrate starch is the primary storage molecule in plants; it is a polymer composed by the plant of the monomer glucose. The carbohydrate cellulose is the main component of the plant cell wall; it is also a polymer of glucose, but in a different configuration. Other cell wall components include the carbohydrates hemicelluloses and - in cells that are still growing - pectins.
>
> "Cellulose molecules form the fibrous part of the plant cell wall. The long, rigid cellulose molecules combine to form microfibrils, each consisting of hundreds of cellulose chains. In plant cell walls, the cellulose microfibrils are embedded in a matrix containing two other complex, branched polysaccharides, namely pectins ... and hemicelluloses... Plant cells have been compared to reinforced concrete, in which embedded steel rods - the cellulose microfibrils - are used to strengthen the concrete - the matrix."
>
> "Lignins, unlike other phenolic compounds, are deposited in the cell wall rather than in the vacuole. Second only to cellulose as the most abundant organic compound on Earth ... The major importance of lignin is the compressive strength and stiffness it adds to the cell wall. ... Lignin also waterproofs the cell wall. It therefore facilitates upward transport of water in the conducting cells of the xylem by limiting the outward movement of water from the cells. In addition, lignin assists the water-conducting cells in resisting the tension generated by the stream of water (the transpiration stream) being pulled to the top of tall plants ..."

From the above it is clear that it is doubtful whether the structural carbohydrates cellulose and hemicellulose are still metabolically active and require much maintenance, especially when they get encrusted with the metabolically inactive lignin as the cell ages.

8.4.2 Chemical analysis data of sago palm

The only published chemical analysis of sago palm to my knowledge was that by JAMALUDDIN KASIM *et al.* (1995) who tested the suitability of sago palm leaves for paper making. They took 10 leaves from an approximately 10-year-old sago palm in Peninsular Malaysia. Unfortunately, they excluded the leaflets from their analyses. The average composition of oven-dry milled samples of the leaves was (rounded): holo-cellulose 73%, alpha-cellulose 66%, lignin 26%, pentosans 22%, 1%-NaOH solubles 32%, hot water solubles 11%, alcohol-benzene solubles 6.7%, ash 4.6%.

> Holocellulose is the total of the cellulose and the hemicellulose fractions. Alpha-cellulose is the long-fibre fraction of the holocellulose which is usable in the paper industry after the short-fibre beta-cellulose fraction has been removed with strong (17.5%) NaOH solution (BRINK & ESCOBIN 2003:390).
> "Pentosans form the major part of the difference between holocellulose and cellulose and are often indicated as hemicellulose." (BARREVELD 1993)

Apparently the material JAMALUDDIN K. *et al.* analysed contained only cell wall material as holo-cellulose and lignin - both only found in the cell wall - make up 99% of the DM. From these data we may conclude that the cell wall of a sago palm leaf stalk (including base and rachis) consists of about three quarters carbohydrate (cellulose and hemicellulose) and one quarter lignin.
For information about the ratio of cell wall DM to total DM in the leaf stalk, about the composition of the leaflets, and about other components of the axis, we have to turn to information which is available for other palms.

8.4.3 DM and chemical analysis data of other cultivated palms

Date palm

In his book on date palm products BARREVELD (1993) presents data on the composition of leaf base, leaf midrib and leaflets of the date palm with a view to their use as industrial fibrous rawstock (adapted from BUKHAEV & ZAKI 1983) (% on dry weight basis; moisture content 55-65%, 60-66%, and 38-40%, respectively):

	Frond bases	Frond midrib	Leaflets
Holocellulose	54.5	55.6	48.0
Cellulose	22.5	33.5	28.0
Lignin	27.0	21.5	28.1
Furfural	13.6	16.2	9.2
Ash	9.5-11.5	8.5-10	10.5-11.5

Furfural is a derivative of pentosans (see info on pentosans above).

The cell wall DM (vs cell content DM) may be estimated by combining the percentages of holocellulose and lignin (cellulose and furfural are contained in the holocellulose fraction) and adding half of the ash fraction (assuming that the other half is in the cell contents): 87% in leaf base, 82% in leaf midrib, 82% in leaflet.
Thus, only about 13 to 18% of the date palm leaf DM is not in the cell wall and may require maintenance. In fact none of the ash fraction requires maintenance, and therefore maintainable leaf DM in date palm is only about 8 to 14% of total leaf DM.

Oil palm

Results of studies on the nutritive value for ruminants of whole oil palm leaves (ALIMON & HAIR BEJO 1995, WONG & WAN ZAHARI 1992, MAT RASOL *et al.* 1993) are presented by ABU HASSAN *et al.* (1995?) (on dry matter basis): crude protein 4.7%, crude fiber 38.5%, NDF 78.7%, ADF 55.6%, ether extract 2.1%, ash 3.2%.
If we assume the NDF fraction (which contains the cell wall materials cellulose, hemicellulose and lignin) and the ash fraction as not requiring maintenance, maintainable leaf DM in oil palm is only 18% of total leaf DM.

ABU HASSAN *et al.* (1995?) also presented analyses for oil palm trunks (on dry matter basis): crude protein 2.8%, crude fiber 37.6%, neutral detergent fiber 79.8%, acid detergent fiber 52.4%, ether extract 1.1%, ash 2.8%.

8.4.4 Conclusions and assumptions on DM content and chemical composition of sago palm

As said before, for the calculation of the maintenance costs, an estimate of total DM and of the living portion of the total is needed.
For the calculation of the production costs I will limit the differentiation of the DM to the components **carbohydrates and lignins** since they make up by far the larger part of the DM. And as the CVFs of the left-out proteins, fats, organic acids and minerals are more or less evenly spread among the total range of CVF values, under- and over-estimation of production costs as a consequence of not taking these components into account probably levels out.

Trunk

In one year the volume of trunk tissue built by a model palm in the AV-phase is a cylinder 1.5 m long and 0.55 m wide, with a volume of $\pi r^2 h = 3.14\ (0.275\ \text{m})^2 \times 1.5\ \text{m} = 0.356\ \text{m}^3$. On the average the trunk is made-up of a 50-cm-wide cylinder of soft pith surrounded by a 2.5-cm-wide bark plus adjacent fibre layer, the compound outer trunk shell left over after pounding out the pith in traditional harvesting and known in the local vernacular as the wa'ah (Fig. 4.12, 4.13). Therefore, $r_{pith} : r_{total} = 10 : 11$, and $\text{volume}_{pith} : \text{volume}_{total} = 10^2 : 11^2 = 0.826 : 1$. The *wa'ah* is very dense, especially the stone-hard fibres closest to the bark, and in the fresh state even heavier than water (cellulose and lignin have specific gravities of 1.52×10^3 and $1.46 \times 10^3\ \text{kg.m}^{-3}$, respectively). The *wa'ah*'s DM density increases with age from 0.33 to 0.64 g/cm^3 (see Table 8.1). Here I assume that throughout the palm axis' life *wa'ah* DM density is 0.50 g/cm^3, which is 500 kg/m^3. The result is an annual ***wa'ah*** DM production of $0.174 \times 0.356\ \text{m}^3 \times 500\ \text{kg/m}^3$ = **31.0 kg**.
I assume the *wa'ah* to be **metabolically inactive** and its DM to consist of **75% carbohydrate** and **25% lignin**.

Table 8.1 DM density of the *wa'ah* (combined bark and adjacent fibre layer) along the trunk of Palm #18.

Sampling height (m a.g.l)	0.5	1.5	2.5	3.5	4.5	5.5	6.5
Wa'ah DM density (g/cm^3)	0.56	0.64	0.53	0.45	0.41	0.39	0.33

a.g.l. = above ground level

Table 8.2 Comparison of DM content of whole and ground samples of trunk pith in Palm #18 taken at 1-metre intervals along the trunk.

Sampling height (m a.g.l.)	Pith sample series A (dried as whole pith)			Pith sample series B (dried after grinding in water and discarding the water)			(Dry weight of starch + NSS in pith) to (Total DM weight in pith) ratio
	fresh weight (g)	dry weight* (g)	total DM content (weight %)	fresh weight (g)	dry weight* of starch + NSS (g)	dry starch + NSS content (weight %)	
0.5	225.4	73.06	32.4	184.53	62.21	33.7	1.04
1.5	526.4	222.91	42.3	178.52	66.59	37.3	0.88
2.5	284.5	119.37	42	185.51	69.34	37.4	0.89
3.5	416.7	176.07	42.3	163.48	59.9	36.6	0.87
4.5	357.9	137.3	38.4	110.76	39.45	35.6	0.93
5.5	453.7	114.08	25.1	57.24	8.81	15.4	0.61
6.5	376.3	67.33	17.9	42.35	4.22	10	0.56

NSS = Non-(water-)Soluble Solids. a.g.l. = above ground level
* Dried to constant weight at 115ºC.

In Table 8.2 the total DM content of pith samples of Palm #18 are compared to the content of starch and non-water-soluble solids in other pith samples of the same palm (see Appendix A). Palm #18 is relatively very short, with a leaf-free trunk of 4.45 m only. Taking into account this full-grown leaf-free trunk part only, and also disregarding the lowest part where apparently all DM is cell wall and starch, I conclude that in general 90% of the total pith DM is starch and cell wall material, and therefore that **DM in living pith cell content** is only **10% of total pith DM**.

Depending on age of the pith, pith contains - apart from starch - 0.02 to 0.07 g non-water-soluble DM (probably all cell wall material) per cm^3 (see data on derived trunk pith characteristics in Trunk pith sections of Sago Palm Data Sheets (Appendix A)) . Here I assume that throughout the palm axis' life total non-starch DM content of the pith is 0.05 g/cm^3, which is 50 kg/m^3. The result is an annual DM production of 0.826 x 0.356 m^3 x 50 kg/m^3 = **14.7 kg pith cell wall** material per axis. These cell walls consist of carbohydrates (cellulose and hemicellulose) and lignin, the lignin portion becoming larger with age. Here assume the pith cell walls to consist of **75% carbohydrate** and **25% lignin** throughout the palm axis' life.

I assume here that a vigorous palm is able to store 250 kg of dry starch per m^3 of pith (see Table 7.1). At a yearly pith production of 0.826 x 0.356 m^3 = 0.294 m^3, the dry **starch** production would be 0.294 x 250 = **73.5 kg** per year. The starch is **metabolically inactive**. At a carbohydrate CVF of 1.275 this production would cost 73.5 x 1.275 = **93.7 kg** glucose per year.

Table 8.3 Summary of estimated amounts of total DM, DM in live material, carbohydrates and lignin produced each year in the trunk of a sago palm axis in the adult vegetative phase.

Trunk part			**DM density (kg/m^3)**	**Volume (m^3)**	**DM weight (kg)**	**DM weight in live material (kg)**	**Carbo-hydrate weight (kg)**	**Lignin weight (kg)**
wa'ah			500	0.062	31	0	23.2	7.8
pith	cell wall		50	0.294	14.7	0	11	3.7
	cell content	starch	250		73.5	0	73.5	0
		other	n.e.		9.8*	9.8	9.8	0
Total				0.356	129	9.8	117.5	11.5
(Total without starch				0.356	55.5	9.8	44	11.5)

n.e. = not estimated.
* estimated at 10% of the total pith DM weight

<u>Production costs</u> At 44.0 kg carbohydrate (excluding starch) and 11.5 kg lignin per year, production costs equal (44.0 x 1.275) + (11.5 x 2.231) = 56.1 + 25.7 = **81.8 kg** glucose per year.

<u>Maintenance costs</u> Each year the <u>extra</u> DM in live material to be taken into account is half of last year's production + half of this year's production. As this production amounts to 0.34kg in year#4 (see Appendix 8B), the extra DM production to be taken into account in year#5 amounts to (0.34 + 9.8)/2 = 5.1 kg, whereas for the remainder of the AV-phase this amounts to the full 9.8 kg. At a generalised MC of 5.475 kg glucose per kg DM in live material per year, maintenance costs amount to:
year#5: (maintenance costs year#4) + (5.1 x 5.475) = 2.3 + 28 = **30 kg glucose**.
year#6 through #14: 5.475 x 9.8 kg = **54 kg glucose more than the year before**.

Leaf

An adult-size 10-m-long sago palm leaf has a dry weight of 11.5 kg [7]. At 10 new leaves per year, **annual leaf DM production** in the adult vegetative phase equals 10 x 11.5 = **115 kg**.
As sago palm resembles oil palm more than date palm and occurs in the same humid tropical environment as oil palm, I assume that the sago palm has a leaf DM distribution similar to that of oil palm, viz. 82% in the cell wall and ash fractions. Allowing for some metabolic activity in the cell wall DM when the leaf is still young, I will base maintenance respiration on a **DM content in live material** of a rounded **20%** of total leaf DM.

According to JAMALUDDIN K. *et al*. (1995) 26% of the DM of the cell wall material of a sago palm petiole and rachis consists of lignin and 73% of cellulose and hemicellulose. If the cell wall DM equals 80% of the total DM, lignin would represent about 20% of total DM. BARREVELD's (1993) data show about the same lignin percentage in date palm midrib (21.5%), but a higher percentage in the frond bases (27%) and the leaflets (28.1%). To compensate for the missing leaflet lignin data in the sago palm study, I assume here that **25% of the total DM** in sago palm leaf is **lignin**, and furthermore that the remaining **75%** is all **carbohydrate**. In actual fact there will be an appreciable amount of protein in photosynthetically active leaf tissue. The CVF of protein (1.887) is intermediate between the CVF of carbohydrates (1.275) and that of lignins (2.231), so that the omission for simplicity sake of protein production will probably have little effect on overall DM production costs.

<ins>Production costs</ins> At 75% carbohydrate and 25% lignin, production of 115 kg leaf DM costs (0.75 x 115 x 1.275) + (0.25 x 115 x 2.231) = 110 + 64 = **174 kg** glucose per year.
<ins>Maintenance costs</ins> 20 leaves have a total dry matter of 20 x 11.5 = 230 kg. At 20% of that DM metabolically active, maintenance of the crown of leaves during the full-crown period in the AV-phase (**7th to 14th year**) would cost 5.475 x 230 x 0.2 = **252 kg** glucose per year.
At the beginning of year#5, leaf DM is 102 kg, made up by 10 leaves with a longevity of 1 year (see App. 8B, Section B1.2). Therefore, at the end of year#5 the crown consists of only the 10 new leaves formed during that year, with a total of 10 x 11.5 = 115 kg DM. At an average of (102 + 115)/2 = 108.5 kg leaf DM during **year#5**, maintenance would cost 5.475 x 108.5 x 0.2 = **119 kg** glucose.
At a longevity of 2 years for the leaves formed during the AV-phase, average leaf DM during **year#6** would be (115 + 230)/2 = 172.5 kg, costing 5.475 x 172.5 x 0.2 = **189 kg** of glucose in maintenance.

Roots

During the AV-phase, DM in live trunk material increases a constant 9.8 kg per year. Leaf DM increase is 115 - 102 = 13 kg in year#5, and 230 - 115 = 115 kg in year#6, while there is no more increase during the remainder of the AV-phase. At 20% of the leaf DM in live material, the total DM increases in live material amount to 9.8 + (0.2 x 13) = 12.4 kg in year#5, 9.8 + (0.2 x 115) = 33 kg in year#6, and 9.8 kg in years#7 through #14. At a root DM weight assumed to equal 11% of the above ground DM weight in live material, the root DM production can be estimated at 0.11 x 12.4 = **1.4 kg** in **year#5**, 0.11 x 33 = **3.6 kg** in **year#6**, and 0.11 x 9.8 = **1.1 kg** in **years #7 through #14** .
It is unknown which part of the root DM produced remains metabolically active and therefore subject to maintenance respiration. In the trunk I estimated this to be 9.8 out of 55.5 kg (not

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[7] Estimate based on two entire leaves of a "Tuni" type sago palm (Palm #27) of which the dry weight was actually determined (by drying to constant weight at 115 ºC). These were the 13th and 16th leaf in a crown of 19 green leaves, the 1st leaf being the oldest. Data leaf 13: length 10.05 m, fresh weight 42.76 kg, dry weight 12.19 kg. Data leaf 16: length 9.71 m, fresh weight 41.05 kg, dry weight 10.91 kg.

counting starch), which is 17.7%, and in the leaves 20%. As root metabolic activity is probably more like that in the leaves than in the trunk, I estimate the root **DM content in live material** at **20%** of total root DM.
I also assume that the DM composition is like the one assumed in leaves (**25% lignin, 75% carbohydrate**) rather than the one estimated in the trunk (11.5 out of 55.5 kg or 21% lignin, 79% carbohydrate, not counting starch) as roots have a very tough central strand of conducting tissue that is probably high in lignin.

Production costs At 75% carbohydrate and 25% lignin, production of 1 kg of root DM would cost (0.75 x 1.275) + (0.25 x 2.231) = 1.52 kg glucose. Thus production costs would be 1.4 x 1.52 = **2.1 kg** glucose in **year#5**, 3.6 x 1.52 = **5.47 kg** glucose in **year#6**, and in 1.1 x 1.52 = **1.7 kg** glucose in **years #7 through #14**.

Maintenance costs At the end of the E-phase root DM to be maintained equals 0.068 + 0.20 + 0.32 + 0.46 = 1.05 kg (see App.8B, Sect.B1.3). During **year#5**, 0.42 kg maintainable DM is added and total maintenance costs would be 5.475 x (1.05 + (0.5 x 0.42)) = **6.9 kg** glucose.
At the end of year#5 root DM to be maintained equals 1.05 + 0.42 = 1.47 kg. During **year#6**, 0.72 kg maintainable DM is added and total maintenance costs would be 5.475 x (1.47 + (0.5 x 0.72)) = **10 kg** glucose.
At the end of year#6 root DM to be maintained equals 1.47 + 0.725 = 2.20 kg. During **year#7**, 0.22 kg maintainable DM is added and total maintenance costs would be 5.475 x (2.20 + (0.5 x 0.22)) = **13 kg** glucose.
For each of the remaining years of the AV-phase (**years #8 through #14**), maintenance cost is the cost of one-year's live root DM production of 0.22 kg higher than the year before, i.e. 5.475 x 0.22 = **1.2 kg higher**.

Inflorescence

From the dimensions of the inflorescence branches outlined above (Section 8.2.3) the volume increase of the branches that make up the inflorescence can be calculated.

Volume increase The first and lowest ax_1 has a volume of $\pi r^2 h = 3.14 \times (0.0575/2)^2 \times 4 = 0.010\ m^3$. The 24th and highest ax_1 has a volume of $\pi r^2 h = 3.14 \times (0.0395/2)^2 \times 2.5 = 0.0031\ m^3$. Assuming a linear volume decrease, total volume of ax_1-s equals 24 x ((0.010 + 0.0031)/2) = 0.157 m^3.
The total volume of ax_2-s is $480 \times \pi r^2 h = 480 \times 3.14 \times (0.009)^2 \times 0.50 = 0.061\ m^3$.
The total volume of ax_3-s is $5760 \times \pi r^2 h = 5760 \times 3.14 \times (0.007)^2 \times 0.14 = 0.124\ m^3$.

Dry matter production
The branches are stem-like structures that stand up stiffly and remain that way after they die. They probably have a higher DM density than the trunk's 55.5 kg / 0.356 m^3 = 156 kg/m^3, not counting starch. I assume here that the DM density of all the inflorescence branches equals 250 kg/m^3. At a total branch volume of 0.157 + 0.061 + 0.124 = 0.342 m^3, total branch DM production equals 0.342 x 250 = 86 kg.
Although expansion (appearance) of the ax_1-s, ax_2-s and ax_3-s is clearly phased, their production is gradual. Therefore their total DM production of 86 kg may be averaged over the combined G1 + G2 phases of three years during which all the branches are formed, i.e. **29 kg** per year (**year #15**, **#16**, **#17**).

Production costs Inflorescence branches are more woody than the trunk. Assuming that 50% of total DM is lignin and 50% is carbohydrate, the CVF for inflorescence branch tissue would be an average (0.5 x 1.275) + (0.5 x 2.231) = 1.75. This would result in an inflorescence production cost of 29 x 1.75 = **51 kg** glucose per year (**year #15**, **#16**, **#17**).

Maintenance costs At an estimated inflorescence branches **DM content in live material** of **20%** of the total inflorescence branches DM, in year#15, #16 and #17 each 0.2 x 29 = 5.8 kg of DM in live material would be produced. Each year the extra DM in live material to be taken into account is half of last year's production + half of this year's production. Thus the maintenance costs would amount to:

Year#15: 5.475 x ((0 + 5.8)/2) = 5.475 x 2.9 = **16 kg glucose**.
Year#16: 16 + 5.475 x ((5.8 + 5.8)/2) = 16 + 5.475 x 5.8 = **48 kg glucose**.
Year#17: 48 + 5.475 x ((5.8 + 5.8)/2) = 48 + 5.475 x 5.8 = **80 kg glucose**.
Year#18: 80 + 5.475 x ((5.8 + 0)/2) = 80 + 5.475 x 2.9 = **96 kg glucose**.

Fruit

Dry matter production At a radius of r (or a diameter of d), the volume of a sphere equals 4/3 πr^3 (or $\pi/6 \times d^3$). Assuming the fruit to be spherical with a diameter of 0.045 m, total fruit volume amounts to 14 400 x 1/6 x 3.14 x $(0.045)^3$ = 0.687 m^3. At an estimated DM density of 300 kg/m^3, total fruit DM weight equals 0.687 x 300 = **206 kg**.

Production costs Assuming an average CVF of 2 for fruit tissues, production would cost 2 x 206 = **412 kg** glucose.

It could make a big difference in production costs whether the fruits would be seeded or unseeded (see Fig. 4.2d and e). Not only would the total DM produced be much less in unseeded fruits than in seeded ones, also the composition would be quite different: mainly carbohydrate (CVF 1.275) in unseeded fruits, against containing a large proportion of the more 'expensive' components lignin (CVF 2.231), protein (CVF 1.887) and fat (CVF 3.189) in seeded ones. Often, a very low percentage of seeded fruit is found in sago palm for reasons outlined in the paragraph on growth and development of Chapter 2.

Maintenance costs If 50% of the fruit DM were metabolically active, fruit maintenance during year #18 would amount to 0.5 x 5.475 x (0.5 x 206) = **282 kg** glucose.

8.4.5 Results

First, the energy costs were calculated for the production and maintenance of the axis, including its starch production, in the AV-phase, because these calculations could be more based on my direct observations than in the E- or G-phase. Also, the AV-phase is the only phase in which trunk starch content was measured. Then the energy costs for the E- and G-phase, not taking into account any possible starch production, were estimated, mostly on the basis of size or weight of parts (observed or, in turn, estimated) relative to those in the AV-phase.
The calculations for the E- and G-phase are presented in Appendix 8B. Table 8.4 and Figure 8.2 summarise all calculations.

Table 8.4 Estimated annual dry matter (DM) production and its growth and maintenance costs during the life cycle of a vigorous West-Seram-type sago palm axis. (Question marks indicate the possible but as yet unknown contribution of starch to DM production and to energy costs in the generative phase.)

	Establishment phase				Adult vegetative phase										Generative phase			
year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
DM production (kg)																		
trunk (excl. starch)	0.1	0.37	1	1.9	55.5	55.5	55.5	55.5	55.5	55.5	55.5	55.5	55.5	55.5	70.4	22.6	1.9	0
leaves	16	45	73	102	115	115	115	115	115	115	115	115	115	115	118	59	8	0
roots	0.34	0.99	1.6	2.3	1.4	3.6	1	1	1	1	1	1	1	1	2	0.3	0	0
inflorescence	0	0	0	0	0	0	0	0	0	0	0	0	0	0	29	29	29	0
fruits	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	206
trunk starch	0	0	0	0	74	74	74	74	74	74	74	74	74	74	?	?	?	?
total	**16**	**46**	**76**	**106**	**245**	**248**	**245**	**245**	**245**	**245**	**245**	**245**	**245**	**245**	**219+?**	**111+?**	**39+?**	**206+?**
Energy costs (kg glucose)																		
production																		
trunk (excl. starch)	0.1	0.55	1.47	2.9	82	82	82	82	82	82	82	82	82	82	104	33.3	2.8	0
leaves	24	67	111	154	174	174	174	174	174	174	174	174	174	174	179	89	11.3	0
roots	0.52	1.5	2.4	3.5	2.1	5.47	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	3	0.5	0	0
inflorescence	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51	51	51	0
fruits	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	412
trunk starch	0	0	0	0	94	94	94	94	94	94	94	94	94	94	?	?	?	?
prod.costs excl. starch	*25*	*69*	*115*	*160*	*258*	*261*	*258*	*258*	*258*	*258*	*258*	*258*	*258*	*258*	*337*	*174*	*65*	*412*
prod.costs sub-total	*25*	*69*	*115*	*160*	*352*	*355*	*351*	*351*	*351*	*351*	*351*	*351*	*351*	*351*	*?*	*?*	*?*	*?*
maintenance																		
trunk	0	0.24	0.9	2.3	30	84	138	192	246	300	354	408	462	516	577	622	634	635
leaves	9	33	65	96	119	189	252	252	252	252	252	252	252	252	253	224	146	64
roots	0.19	0.73	2.1	4.2	6.9	10	13	14.2	15.4	16.6	17.8	19	20.2	21.4	23	24	24	24
inflorescence	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	48	80	96
fruits	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	282
maint.costs sub-total	*9*	*34*	*68*	*103*	*156*	*283*	*403*	*458*	*513*	*569*	*624*	*679*	*734*	*789*	*869*	*918*	*884*	*1101*
total costs excl. starch	***34***	***103***	***183***	***263***	***414***	***544***	***661***	***716***	***771***	***826***	***882***	***937***	***992***	***1047***	***1206***	***1092***	***949***	***1513***
costs grand total	**34**	**103**	**183**	**263**	**508**	**638**	**754**	**810**	**865**	**920**	**975**	**1030**	**1086**	**1141**	**?**	**?**	**?**	**?**

Note: The conspicuously large root DM production in year#6 is due to the large increase in leaf DM in that year. This is because no leaves die in that year since 2-year-lifespan leaves only started to be formed from the beginning of year#5. All the previous leaves were assumed to be 1-year-lifespan leaves and the last of these died already in year#5. Root DM production is assumed to relate to above-ground DM increase only. (See also text.)

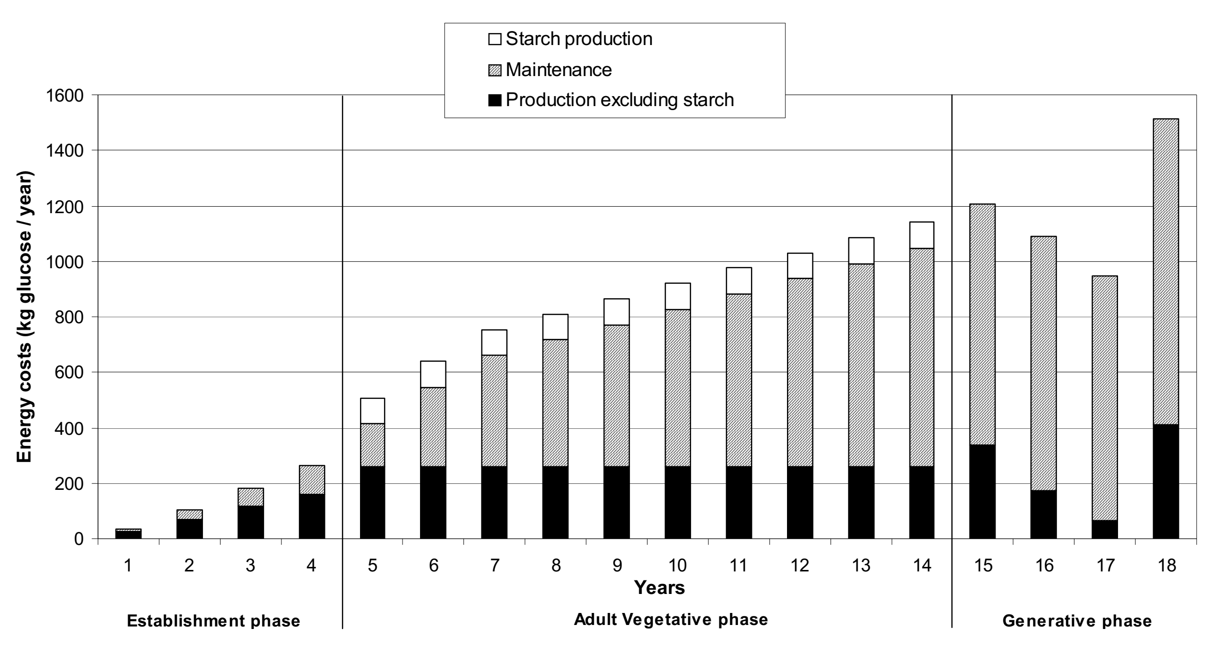

Figure 8.2 Estimated energy costs of production and maintenance of a sago palm axis throughout its life time, and of trunk starch production during the Adult Vegetative phase.

8.5 Discussion and conclusions

8.5.1 Energy consumption in time

Energy costs for production (excluding starch) plus maintenance of the sago palm axis keep rising from year#1 through year#15. The rise is sharp until full crown size is reached in year#7, and then eases off to a constant slower increase between year#7 and year#14 during which period it is mainly the trunk maintenance cost which still increases. In year#15 the rise is a bit steeper again because of the 'bolting' which takes place at the beginning of the G-phase with initially higher trunk and leaf productions, on top of the starting of the construction of the inflorescence branches. Trunk and leaf production dramatically drop during the two subsequent years, causing overall costs to fall as well. The massive fruit production during the last year gives the energy costs level a final jolt upward.

8.5.2 Energy production in the AV-phase

I have no data with which I can directly calculate energy production capacity (e.g., photosynthesis measurements). Indirectly this capacity can be derived from the energy requirement. However, as total energy requirement in the AV-phase keeps rising, while from year#7 onwards crown size remains the same, which AV year should be considered indicative of the energy production capacity of this crown?

During the last year of the AV-phase, the full crown of twenty full-size leaves is likely to be at full production capacity because during that year it is less likely to be shaded than during the earlier years of the AV-phase. The total energy requirements during the last year of the AV-phase (year#14) could thus be considered indicative of the production capacity of the full crown: capable of producing **1141 kg** glucose per year, **including 94 kg for the production and storage of 74 kg of starch in the trunk**.

8.5.3 Energy production in the G-phase

The production capacity in the G-phase can be derived from the production capacity in the last year of the AV-phase by assuming that the ratio of production capacity to total green leaf DM weight remains constant from this last AV year onward. The room for starch production during the G-phase can be investigated by further assuming that a growing palm stem is a system in which assimilates are used in the first place to build and maintain the structural vegetative dry matter and that these assimilates are used for other purposes such as trunk starch storage only if there is a surplus of assimilates. It then depends on the energy production capacity of the crown of leaves during a particular period whether there is room for starch production during that period or not.

During the first year of the generative phase, **1206 kg** of glucose are needed for growth and maintenance of the palm alone, i.e. if no starch is produced and stored. During this year green-leaf DM is on average 231.5 kg, i.e. 231.5/230 = 1.0065 times that of the year before. Glucose production capacity can therefore be estimated at 1.0065 x 1141 kg = **1148 kg**, a deficit of 1206 - 1148 = **58 kg**. This means that there is no production capacity left for starch production, and that, on the contrary, starch reserves in the trunk have to be mobilized to replenish the deficit. In the conversion of starch into transportable water-soluble sugars by hydrolysis, water is added to the molecules, so that a kg of starch is equivalent to more than a kg of glucose. On the other hand, the relocating of the sugars from the trunk to the places where the energy is needed also costs energy. Rather than quantifying these processes here, I assume that 1 kg of trunk starch can simply substitute for the energy in 1 kg of glucose. The trunk starch reserve of 740 kg would thus drop to 740 - 58 = **682 kg** during the first year of the G-phase. During the second year of the G-phase, average green-leaf DM over the year equals 205 kg, and glucose production capacity can be estimated at 205/230 x 1141 kg = **1017 kg**, while **1092 kg** are needed for growth and maintenance of the palm alone, a deficit of 1092 - 1017 = **75 kg**. The trunk starch reserve would thus drop to 682 - 75 = **607 kg** during the second year of the G-phase. During the third year of the G-phase, average green-leaf DM equals 133 kg, and glucose production capacity can be estimated at 133/230 x 1141 kg = **660 kg**, while **949 kg** are needed for growth and maintenance of the palm, a deficit of 949 - 660 = **289 kg**. The trunk starch reserve would thus drop to 607 - 289 = **318 kg** during the third year of the G-phase. During the fourth and final year of the G-phase, average green-leaf DM equals 58.5 kg, and glucose production capacity can be estimated at 58.5/230 x 1141 kg = **290 kg**, while - mainly because of the production of fruit during that year - an enormous amount of **1513 kg** are needed for growth and maintenance of the palm, a deficit of 1513 - 290 = **1223 kg**. Therefore the glucose balance at the end of the palm axis' life would come to 318 - 1223 = –**905 kg**.

The above calculations are summarised in Table 8.5.

Table 8.5 Energy balance of a sago palm axis during the generative phase.

G-phase year	Energy (kg glucose)		
	needed	production capacity	balance
#1	1206	1148	-58
#2	1092	1017	-75
#3	949	660	-289
#4	1513	290	-1223
Sub-total	4760	3115	-1645
Starch reserve			740
Total			**-905**

8.5.4 Matching energy consumption and production

The energy produced during the G-phase plus the energy stored in the trunk starch should be more than, or equal to the energy consumed during that phase, whereas in the model production plus reserve is 905 kg glucose less than consumption. Therefore, I have to conclude that with the available field data and the assumptions made about growth and development, energy consumption and production in a sago palm trunk cannot be matched, and that therefore the sought-after scientific basis for timing the harvest cannot be established yet.

According to the model, 694 kg glucose are needed for the production and maintenance of the fruits. If fruits were all unseeded, and assuming an unseeded fruit DM density of half that of the seeded fruit DM density, i.e. 150 kg/m^3, fruit DM production would be halved to 103 kg and maintenance costs to 141 kg glucose. At an CVF of 1.3 in stead of 2, production costs would drop to 1.3 x 103 = 134 kg glucose. Production and maintenance of the fruits would then total 275 kg glucose, i.e. 419 kg less then with all seeded fruits. The total glucose production shortage would still be 912 - 419 = 493 kg glucose.

On the other hand, not included in this model is the production of nectar by the flowers. This production may not be negligible (JONG 1995). Taking the nectar production into account would increase the glucose production deficit at the end of the G-phase.

The assumptions and estimates based on observed weights and dimensions of sago palm parts are probably the more accurate ones. Assumptions and estimates on the chemical composition of the various parts of the sago palm axis and of the percentage of live, maintenance-requiring material in these parts are probably far less accurate, and the model would most likely improve if they could be based on observed data as well.

Using direct observations of the assimilation rate instead of production capacity data inferred from the amount of biomass would be a logical, albeit complicated next step in improving the model. Only very few such data have been published so far and they were obtained from young leaves on young plants completely or partly grown in greenhouses in the Netherlands and Japan.
UCHIDA *et al.* (1990) experimented with 4-year-old, 1.2-m-tall palms raised inside (winter) and outside (summer) a greenhouse at Kobe University under two light regimes (natural and 80% shade): 35- to 45-days-old leaflets showed an assimilation rate levelling off at an incident photosynthetic photon flux density of about 600 μmol $^{-2}$ s^{-1} to 13-15 mg CO_2 dm^{-2} h^{-1} (at an optimum temperature of 26.0 - 27.4ºC).
Earlier, FLACH (1977:166-167) reported about experiments with young establishment-phase palms grown in a hothouse at Wageningen University: leaflets of 31 and 59 days after unfolding showed a photosynthesis rate levelling off at an irradiance of about 1.5 J cm^{-2} min^{-1} to 135 and 95 μg cm^{-2} h^{-1}, respectively (measured at 28-30ºC). Unfortunately the report does not state what substance was measured; comparing the figures with those of UCHIDA *et al*. above suggests that CO_2 assimilation was measured here also.
By extrapolating UCHIDA *et al* 's data, a first estimate of the annual assimilation capacity of an entire crown in the AV-phase can be made: 14 mg CO_2 dm^{-2} h^{-1} = 14 x 0.000001 x 100 x 24 x 365 or 12.3 kg CO_2 m^{-2} yr^{-1} . A 10-m-long leaf has an area of about 15 m^2 (see Chapter 6). An AV-phase crown of 20 leaves would have a total leaf area of 300 m^2, and the annual photosynthesis per tree would be 300 x 12.3 = 3690 kg CO_2. This translates to 30/44 x 3690 = 2516 kg of glucose (conversion factor of CO_2 to CH_2O (of which glucose ($C_6H_{12}O_6$) can be thought to be made up) on the basis of their respective molecular weights 44 and 30 (atomic weights: H=1, C=12 and O=16)). With the model, the annual energy cost in year#14 of the AV-phase is calculated at 1141 kg glucose and was assumed to tally with the production capacity

in that year. The difference in the outcomes can probably be explained by the mutual shading of the leaves in a crown resulting in sub-optimal light intensities for part of the leaves, and by the senescence of the leaves (most of the green leaves in a crown are much older than the ones used by UCHIDA *et al*.). Data on assimilation in older leaves and on light interception in a sago palm crown under field conditions are clearly needed.

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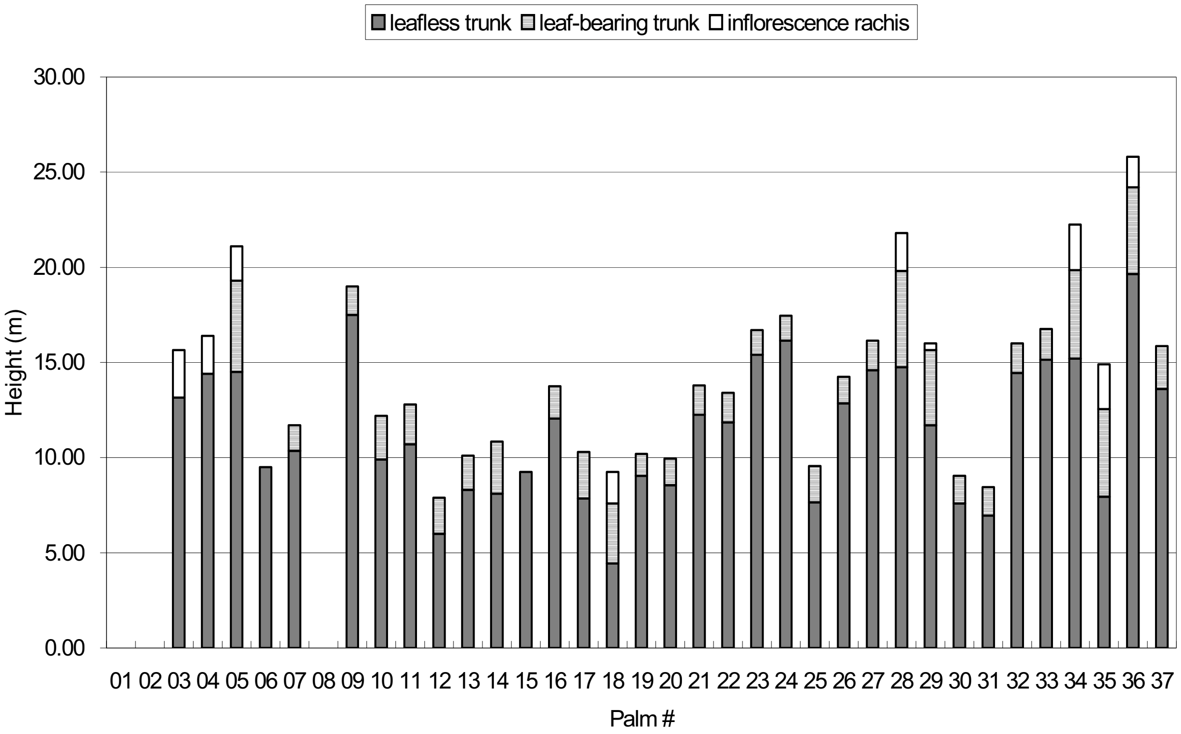
APPENDIX 8A

Height of the main axis (ax_0, i.e. trunk plus its extension into the inflorescence rachis) of all sago palms felled and sampled in 1988-1990 in Seram and Saparua (Moluccas, Indonesia).



Note 1: In a still vegetative trunk, the 'leaf-bearing' part of the trunk is measured from the node with the oldest green leaf to the node with the spear leaf; in a generative trunk from the node with the oldest green leaf to the node with the oldest 1st-order inflorescence branch.

Note 2: Palm #01 and #02 were sampled in the establishment phase, hence no trunk was present. Palm #08 was an a-typical, rare variety on Saparua Island ("Samakika") which I was not allowed to sample destructively. Of Palm #06 and #15 the parts above the leafless trunk were not observed.

Most of the dimensions of the model palm were taken from Palm #28 and #34 as these two palms, together with Palm #05, apparently represent an average stature among the 9 flowering palms sampled; the data of Palm #05 is less complete than of #28 and #34 (see the data sheets of these palms in the general Appendix A).

<<

APPENDIX 8B

Calculations of the dry matter production (kg per year) of trunk, leaves and roots, and the energy costs of dry matter production and maintenance (kg glucose per year) during the establishment and generative phase of a vigorous West-Seram-type sago palm axis (results rounded to significant number of digits). The calculation results that are (rounded and) entered in Table 8.4 are given in bold.

B1 Establishment (E) phase

B1.1 **Trunk** - E-phase

Volume increase At a constant vertical and horizontal growth rate, each year trunk height increases by 27.5/4 = 6.875 cm, and trunk diameter increases by 55/4 = 13.75 cm, and the radius by 13.75/2 = 6.875 cm. The volume of a cone equals $\pi r^2h/3$. Because in this case r = h, the volume equals $\pi r^3/3$. Thus, the trunk volumes built during the E-phase years are: (3.14 x 0.06875^3)/3 = 0.00034 m^3 in year#1 ; (3.14 x (2 x 0.06875)^3)/3 - (3.14 x 0.06875^3)/3 = 0.0027 - 0.00034 = 0.0024 m^3 in year#2 ; (3.14 x (3 x 0.06875)^3)/3 - (3.14 x (2 x 0.06875)^3)/3 = 0.0092 - 0.0027 = 0.0065 m^3 in year#3 ; (3.14 x (4 x 0.06875)^3)/3 - (3.14 x (3 x 0.06875)^3)/3 = 0.0218 - 0.0092 = 0.0126 m^3 in year#4.
Assuming, as in the AV-phase, that pith diameter equals 10/11 of the total diameter, and applying the same DM densities and constituent proportions as in the AV-phase, DM productions in the E-phase -and the part in living material thereof -, as well as the DM production costs can be calculated by multiplying the AV-phase values by the ratio of the trunk volumes produced per year. As no starch production takes place in the E-phase, the calculations have to be made with AV values from which the contribution of starch production has been subtracted. Where starch is stored in the cell in the AV-phase, there is assumed to be water in the E-phase.
Dry matter production
year#1: At a volume production of 0.00034 / 0.356 = 0.00096 times that of the annual AV-phase production , **DM** production equals 0.00096 x 55.5 = **0.053 kg**, of which 0.00096 x 9.8 = **0.0094 kg in live material**.
year#2: At a volume production of 0.0024 / 0.356 = 0.0067 times that of the annual AV-phase production , **DM** production equals 0.0067 x 55.5 = **0.37 kg**, of which 0.0067 x 9.8 = **0.066 kg in live material**.
year#3: At a volume production of 0.0065 / 0.356 = 0.018 times that of the annual AV-phase production , **DM** production equals 0.018 x 55.5 = **1.0 kg**, of which 0.018 x 9.8 = **0.18 kg in live material**.
year#4: At a volume production of 0.0126 / 0.356 = 0.035 times that of the annual AV-phase production , **DM** production equals 0.035 x 55.5 = **1.94 kg**, of which 0.035 x 9.8 = **0.34 kg in live material**.
Production costs Multiplying the above volume production ratios by the annual production cost of 81.8 kg glucose in the AV-phase gives:
year#1: 0.00096 x 81.8 = **0.079 kg** glucose.
year#2: 0.0067 x 81.8 = **0.55 kg** glucose.
year#3: 0.018 x 81.8 = **1.47 kg** glucose.
year#4: 0.035 x 81.8 = **2.86 kg** glucose.
Maintenance costs Each year the extra DM in live material to be taken into account is half of last year's production + half of this year's production: (0 + 0.0094)/2 = 0.0047 kg, (0.0094 + 0.066)/2 = 0.038 kg, (0.066 + 0.18)/2 = 0.12 kg, and (0.18 + 0.34)/2 = 0.26 kg, for years #1, #2, #3 and #4 respectively. Therefore, maintenance cost would amount to:
year#1: 0.0047 x 5.475 = **0.026 kg** glucose.
year#2: 0.026 + (0.038 x 5.475) = 0.026 + 0.21 = **0.24 kg** glucose.
year#3: 0.24 + (0.12 x 5.475) = 0.24 + 0.66 = **0.90 kg** glucose.
year#4: 0.90 + (0.26 x 5.475) = 0.90 + 1.4 = **2.3 kg** glucose.

B1.2 **Leaves** - E-phase

Dry matter production Assuming a linear increase in dry weight from 0 kg to the full-size 11.5 kg in 40 steps, each new leaf has 11.5/40 = 0.2875 kg more dry weight than its predecessor. Therefore in the first year of the E-phase (**year#1**), leaf DM produced equals 0.2875 + (2 x 0.2875) + ... + (10 x 0.2875) = 55 x 0.2875 = **15.8 kg** ; in **year#2** leaf DM produced equals (11 x 0.2875) + ... + (20 x 0.2875) = 155 x 0.2875 = **44.6 kg** ; in **year#3** leaf DM produced equals (21 x 0.2875) + ... + (30 x 0.2875) = 255 x 0.2875 = **73.3 kg** ; and in **year#4** leaf DM produced equals (31 x 0.2875) + ... + (40 x 0.2875) = 355 x 0.2875 = **102 kg**.
Production costs Applying the same DM densities and constituent proportions as in the AV-phase, the production costs in an E-phase year can be derived from the annual AV-phase production cost of 174 kg by multiplying it by the ratio of the DM production in that E-phase year to the annual DM production in the AV-phase:
year#1: 15.8/115 x 174 = **23.9 kg** glucose.
year#2:: 44.6/115 x 174 = **67.48 kg** glucose.
year#3: 73.3/115 x 174 = **111 kg** glucose.
year#4: 102/115 x 174 = **154 kg** glucose.
Maintenance costs Maintenance per year has to be counted over the average DM amount existing during that year. For year#1 this is 15.8/2 = 7.9 kg DM. Thus, leaf maintenance during **year#1** would cost 5.475 x 7.9 x 0.2 = **8.7 kg** glucose.
At a leaf longevity of 1 year, all the leaves built during a year are gone again at the end of the following year. Thus the leaf DM in the beginning of year #2 is 15.8 kg, while at the end it is 44.6 kg, resulting in an average during **year#2** of (15.8 + 44.6)/2 = 30.2 kg, costing 5.475 x 30.2 x 0.2 = **33 kg** glucose in maintenance. Similarly, maintenance during year #3 would cost 5.475 x (44.6 + 73.3)/2 x 0.2 = **65 kg** glucose, and during **year #4** it would cost 5.475 x (73.3 + 102)/2 x 0.2 = **96 kg** glucose.

B1.3 **Roots** - E-phase

Dry matter production DM in live trunk material increases by 0.0094 kg in year#1, 0.066 kg in year#2, 0.18 kg in year#3, and 0.34 kg in year#4. DM in live leaf material increases by 0.2 x 15.8 = 3.16 kg in year#1, 0.2 x 44.6 = 8.92 kg in year #2, 0.2 x 73.3 = 14.7kg in year#3, and 0.2 x 102 = 20.4 kg in year#4. Thus total above-ground DM increase in live material amounts to 0.0094 + 3.16 = 3.16 kg in year#1, 0.066 + 8.92 = 8.99 kg in year#2, 0.18 + 14.7 = 14.9 kg in year#3, and 0.34 + 20.4 = 20.7 kg in year#4.
At a root DM weight assumed to equal at all time 11% of the above-ground DM weight in live material, the root DM production can be estimated at 0.11 x 3.16 = **0.34 kg** in **year#1**, 0.11 x 8.99 = **0.99 kg** in **year#2**, 0.11 x 14.9 = **1.6 kg** in **year#3**, and 0.11 x 20.7 = **2.3 kg** in **year#4**.
Production costs At 1.52 kg glucose per kg root DM, production costs would be 0.34 x 1.52 = **0.52 kg** glucose in **year#1** , 0.99 x 1.52 = **1.5 kg** glucose in **year#2**, 1.6 x 1.52 = **2.4 kg** glucose in **year#3**, and 2.3 x 1.52 = **3.496 kg** in **year#4**.
Maintenance costs At an estimated 20% of the root DM remaining metabolically active, the production of DM subject to maintenance amounts to 0.068 kg in year#1, 0.20 kg in year#2, 0.32 kg in year#3, and 0.46kg in year#4. Each year the extra DM in live material to be taken into account is half of last year's production + half of this year's production: (0 + 0.068)/2 = 0.034 kg, (0.068 + 0.20)/2 = 0.13 kg, (0.20 + 0.32)/2 = 0.26 kg, and (0.32 + 0.46)/2 = 0.39 kg, for years #1, #2, #3 and #4 respectively. Therefore, maintenance cost would amount to:
year#1: 0.034 x 5.475 = **0.19 kg** glucose.
year#2: 0.019 + (0.13 x 5.475) = 0.019 + 0.71 = **0.73 kg** glucose.
year#3: 0.73 + (0.26 x 5.475) = 0.73 + 1.4 = **2.1 kg** glucose.
year#4: 2.1 + (0.39 x 5.475) = 2.1 + 2.1 = **4.2 kg** glucose.

B2 Generative (G) phase

B2.1 **Trunk** - G-phase

Volume increase Trunk growth ends at the end of the 2.5-year G1 phase. At a constant vertical growth rate, 7 m in 2.5 years means 2.8 m per year; a linear decrease in diameter from 55 cm to 5 cm in 2.5 years means 20 cm decrease per year. Therefore, the trunk volume built in year #15 equals a cone section 2.8 m high, 0.55 m wide at the base, and 0.35 m wide at the top; in year #16 it is a cone section 2.8 m high, 0.35 m wide at the base, and 0.15 m wide at the top; and in year #17 it is a cone section 1.4 m high, 0.15 m wide at the base, and 0.05 m wide at the top. The volume of a cone equals 1/3 x (area of base) x (height). Using this formula, trunk volumes produced were calculated to be 0.453 m^3, 0.145 m^3, and 0.012 m^3, in years #15, #16, and #17, respectively.
Dry matter production
year#15: At a volume production of 0.453 / 0.356 = 1.27 times that of the annual AV-phase production , **DM** production equals 1.27 x 55.5 = **70.48 kg**, of which 1.27 x 9.8 = **12.4 kg in live material**.
year#16: At a volume production of 0.145 / 0.356 = 0.407 times that of the annual AV-phase production , **DM** production equals 0.407 x 55.5 = **22.6 kg**, of which 0.407 x 9.8 = **4.0 kg in live material**.
year#17: At a volume production of 0.012 / 0.356 = 0.034 times that of the annual AV-phase production , **DM** production equals 0.034 x 55.5 = **1.9 kg**, of which 0.034 x 9.8 = **0.33 kg in live material**.
Production costs Multiplying the above volume production ratios with the annual production cost of 81.8 kg glucose in the AV-phase gives:
year#15: 1.27 x 81.8 = **104 kg** glucose.
year#16: 0.407 x 81.8 = **33.3 kg** glucose.
year#17: 0.034 x 81.8 = **2.78 kg** glucose.
Maintenance costs Each year the extra DM in live material to be taken into account is half of last year's production + half of this year's production: (9.8 + 12.4)/2 = 11.1 kg, (12.4 + 4.0)/2 = 8.2 kg, (4.0 + 0.33)/2 = 2.17 kg, and (0.33 + 0)/2 = 0.17 kg, for years #15, #16, #17 and #18 respectively. Therefore, maintenance cost would amount to:
year#15: 516 + (11.1 x 5.475) = 516 + 60.8 = **577 kg** glucose.
year#16: 577 + (8.2 x 5.475) = 577 + 44.9 = **622 kg** glucose.
year#17: 622 + (2.17 x 5.475) = 622 + 11.9 = **634 kg** glucose.
year#18: 634 + (0.17 x 5.475) = 634 + 0.93 = **635 kg** glucose.

B2.2 **Leaves** - G-phase

Dry matter production Assuming a linear decrease in dry weight from the full-size 11.5 kg to 0 kg in 33 steps, each new leaf has 11.5/33 = 0.348 kg less dry weight than its predecessor. At 13 leaves unfolded in the first year of the generative phase (**year#15**), leaf dry matter produced in this year equals (11.5 - (1 x 0.348)) + (11.5 - (2 x 0.348)) + ... + (11.5 - (13 x 0.348)) = (13 x 11.5) - (91 x 0.348) = **118 kg**. The next year another 13 are formed, each one with 0.348 kg less dry weight than its predecessor, dry weight of the last leaf of the previous year being 11.5 - (13 x 0.348) = 6.98 kg. Leaf dry matter produced during **year#16** thus equals (13 x 6.98) - (91 x 0.348) = **59 kg**. During year #17 the last six leaves are formed. The dry weight of the last leaf of the previous year was 6.98 - (13 x 0.348) = 2.46 kg. Therefore leaf dry matter produced during **year#17** equals (2.46 - (1 x 0.348)) + ... + (2.46 - (6 x 0.348)) = (6 x 2.46) - (21 x 0.348) = **7.5 kg**.
Production costs Applying the same DM densities and constituent proportions as in the AV-phase, the production costs in a G-phase year can be derived from the annual AV-phase production cost of 174 kg by multiplying it by the ratio of the DM production in that G-phase year to the annual DM production in the AV-phase:
year#15: 118/115 x 174 = **179 kg** glucose.
year#16: 59/115 x 174 = **89 kg** glucose.
year#17: 7.5/115 x 174 = **11.3 kg** glucose.

Maintenance costs At the end of year#14, leaf DM equals 20 x 11.5 = 230 kg. During year#15, 10 full-size leaves are shed, while 13 smaller leaves with a total DM of 118 kg are added, resulting in a leaf DM at the end of year#15 of 230 - 115 + 118 = 233 kg. Maintenance has to be counted for the average DM amount, i.e. 231.5 kg. At a DM content in live material of a rounded 20% of total leaf DM, leaf maintenance during **year#15** would cost 5.475 x 231.5 x 0.2 = **253 kg** glucose. In the same way, with a leaf DM at the end of year#16 of 233 - 115 + 59 = 177 kg, and an average leaf DM during this year of (233 + 177)/2 = 205 kg, leaf maintenance during **year#16** would cost 5.475 x 205 x 0.2 = **224 kg** glucose. During year#17, the first 10 smaller leaves are shed, while the last 6 are added. At the end of **year#17** leaf DM thus equals 177 - ((10 x 11.5) - (55 x 0.348)) + 7.5 = 89 kg. Average leaf DM during this year equals (177 + 89)/2 = 133 kg, and its maintenance would cost 5.475 x 133 x 0.2 = **146 kg** glucose.
During the final year#18, 10 more smaller leaves are shed, while no new leaves are added. At the end of year#18 leaf DM equals 89 - ((10 x (11.5 - (10 x 0.348))) - (55 x 0.348)) = 28 kg. Average leaf DM during this year equals (89 + 28)/2 = 58.5 kg, and its maintenance would cost 5.475 x 58.5 x 0.2 = **64 kg** glucose.

B2.5 **Roots** - G-phase

Dry matter production in the roots is assumed only to take place to keep up with the increase in above-ground DM in live material. Leaf DM increase is 233 - 230 = 3 kg in year#15, 177 - 233 = -56 kg in year#16, 89 - 177 = -88 kg in year#17, and 28 - 89 = -61 kg in year#18. At 20% of the total leaf DM in live material, change in leaf DM in live material would be 0.2 x 3 = +0.6 kg in year#15, 0.2 x -56 = -11 kg in year#16, 0.2 x -88 = -18 kg in year#17, and0.2 x -61 = -12 kg in year#18.

Year	#15	#16	#17	#18
Increase of DM in live trunk material (kg)	11.1	8.2	2.17	0.17
Increase of DM in live leaf material (kg)	0.6	-11	-18	-12
Increase of DM in live inflorescence material (kg)	5.8	5.8	5.8	0
Increase of DM in live fruit material (kg)	0	0	0	103
Total (kg)	18	3	-10	91

At root DM assumed to be 11% of total above-ground DM in live material, root DM production would be:
Year#15: 0.11 x 18 = **2.0 kg**.
Year#16: 0.11 x 3 = **0.3 kg**.
Year#17: 0.11 x -10 = -1.1 kg
Year#18: 0.11 x 91 = 10 kg
Instead of root DM to decrease with the diminished total above-ground DM in live material in **year#17**, and to suddenly increase again in **year#18**, I assume it to remain constant (increase of **0 kg**) after year#16. The formation and maintenance of the fruits in the last year demands such a large amount of energy, and the location of that energy sink is so much closer to the leaves than the roots, that it is unlikely that energy is still spent on the production of roots during this final stage in the life of an axis.
Production costs At 1.52 kg glucose per kg root DM (see above), production costs would be
2.0 x 1.52 = **3.0 kg** glucose in **year#15**,
0.3 x 1.52 = **0.5 kg** in **year#16**,
0 kg glucose in **year#17**, and **year#18**.
Maintenance costs At an estimated 20% of the root DM remaining metabolically active, the production of DM subject to maintenance amounts to 0.4 kg in year#15, 0.06 kg in year#16, and 0 kg in year#17 and year#18. Each year the extra DM in live material to be taken into account is half of last year's production + half of this year's production: (0.2 + 0.4)/2 = 0.3 kg, (0.4 + 0.06)/2 = 0.2 kg, (0.06 + 0)/2 = 0.03 kg, and (0 + 0)/2 = 0 kg, for years #15, #16, #17 and #18 respectively. Therefore, maintenance cost would amount to:
year#15: 21.4 + (0.3 x 5.475) = 21.4 + 1.6 = **23 kg** glucose.
year#16: 23 + (0.2 x 5.475) = 23 + 1.1 = **24 kg** glucose.
year#17: 24 + (0.03 x 5.475) = 24 + 0.16 = **24 kg** glucose.
year#18: 24 + 0 = **24 kg** glucose.

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9 Implications for cultivation ?

The investigations reported on in this thesis were prompted by plans in the 1980s to grow the sago palm on a large scale as an industrial starch crop. For a large-scale plantation to succeed, a better understanding of growth and development of this palm was needed, as cultivation practices at the time were still largely based on ill-documented knowledge of sago farmers with experience in exploiting semi-wild sago stands for subsistence. Since then, only a few sago estates have been established in Indonesia and Malaysia, but establishing new ones is back on the agenda as new interest in it was gained in recent years with the intensified search for suitable crops for bio-fuel production. Indonesia's Antara News Agency recently ran a story of which the first line read "Three domestic companies are ready to develop sago plantations in Riau and West Papua Provinces to meet demand for raw materials to make bioethanol as alternative energy, an Agriculture Ministry official said." (ANTARA 2008). It is striking that with this renewed interest, the plantation idea came full circle. One of the first serious post-colonial plantation plans were driven by exactly this idea of bio-ethanol production (DEPARTMENT OF MINERALS AND ENERGY, PAPUA NEW GUINEA 1980/1981). These plans were never realised, probably because the economic risks were deemed too high. With fossil fuel prices soaring, the economic prospects of such a factory may well have changed. The relevance for studying growth and development of the sago palm has certainly not diminished.

Since I started this research in 1988, much research on sago has been done in the region, in particular by Malaysian, Japanese and Indonesian scientists. One could wonder whether the results of my study would still have any practical value, based as they mainly are on three years of fieldwork from 1988 onward. Although much of the work done by the Asian scientists is on industrial processing and starch technology, many studies on the palm in the field have also been done. The unique combination, however, of scale, environment and accuracy of the study I have undertaken (some 40 palms in a semi-natural habitat felled and studied up to microscopy level), has yielded some unique results as well.
Working in academia gives more opportunity to, and is more geared towards in-depth, fundamental and exploratory research than working in a research institute. Stepping back and taking more distance to the subject becomes possible, seeing more unresolved problems that should be tackled first, problems most scientists had to shy away from because their employers wanted more immediately applicable results. Through circumstances like these and no doubt because of some of my personality traits, I found myself taking the time to diligently round corners that had been cut before. The results may be less immediately applicable, but their fundamentalness will probably render them a longer shelf life.

What drove me to step back from immediate applicability during my investigations may have to do with the domestication status of the sago palm. The very wide value ranges of plant variables I found (wider ranges of duration of development phases and of many sizes and weights of plant parts than recorded before, highest ever recorded estimated starch content) are reminiscent of wild plants. Other plants exploited by man that became object of scientific agronomic research may have had a long history of selection as field-grown crop behind them already. Not so in the case of sago palm. Not only is its status as crop quite recent - after always having been gathered rather than grown - , its hapaxanthy, its long vegetative phase and its cross-fertilization mode (Section 5.2) defy a quick genetic modification and selection process. CLEMENT (1992), in agreement with HARLAN (1975) considered sago palm a semi-domesticated palm species, as the only trait acted upon (selected) by human intervention is the spinyness, and "the spineless populations are maintained by management rather than long term genetic modification". There may be other selected traits, too, but the same lack of long term genetic modification will apply.

A consequence of this 'semi-wildness' is that researchers will have to describe the plant material they work with very well and establish where it stands in the spectrum of the total sago palm population before they draw any general conclusions from their work.

What direct implications for cultivation can still be derived from my study results? And how could the not immediately applicable ones contribute to better sago growing practices in the future?

9.1 Choice of variety

The first decision a sago grower has to take is which variety to plant. Although finding the best variety to grow was not an objective of my investigations, I was confronted with the diversity of the sago palm right from the start. Dealing with this diversity meant dealing with the local names for the different varieties. And stepping back here meant investigating the status of those local variety names instead of taking them for granted. I devised a method to unambiguously name locally distinguished varieties by introducing the format 'folk variety' as a way out of the hitherto very confused folk taxonomy of the sago palm (Section 5.3). This format links a local name to the place and - where applicable - to the ethnic/linguistic group using it, similar to how a scientific name is linked to its author. One of the advantages of this nomenclature is that it enables a researcher to be accurate without being pressured into erroneously identifying his plant material with named material used and published about by other students before him. The folk variety format is also 'open source', in the sense that its origin is there for everybody to see and evaluate. For example, a linguist specialising in the language of the ethnic/linguistic group name which is part of the folk variety name may expose that variety name as merely meaning 'wild', which would imply it to be a very variable variety which for many scientific questions would probably be unsuitable as the object of study. Together with a sound description and with data gathered from local informants (see description checklist and tips on interviewing in SCHUILING (1995)), using the folk variety format will enable scientists to perform the above-mentioned much-desired recording of the identity of the plant material they work with and to better advise growers on which variety to choose. As to the characteristics such a variety should have, in Section 9.3 below I will explain why the often stated desirability of 'early-maturing' is not a trait one should look for.

9.2 Timing of cultural measures

Because of the large time gap between initiation of trunk parts and their becoming visible from the outside, cultural measures to promote their growth may have to be applied earlier than expected.

In a palm representative of the population I sampled, during the AV-phase there is a 4.5-year time gap between initiation of an internode in the apical growing point and it becoming visible from the outside (Section 4.6.1). Generally, growth and development are governed by cell division (establishment of growth capacity) followed by cell expansion (realisation of that capacity). With sago palm's single apical meristem and absence of secondary meristems, there is only one division and expansion cycle, starting with a relatively short growth capacity-establishing phase. Growth stimulation measures such as nutrient application to assure the formation of wide and long internodes with ample storage space for starch, will have to be timed rightly for maximum effect during this cell division period. Reversely, the negative effects of adverse growing conditions will become visible from the outside long after the damage has already been done and curative measures taken at the time symptoms become visible will leave years worth of tissue growth unaffected. The timetable of events as presented in Table 4.15, differentiating between hidden and outwardly visible events, will facilitate the right timing of cultural measures.

9.3 Timing of harvest

It was very disappointing that in the end it proved impossible to draw the much-desired graph depicting the course of trunk starch accumulation in time. Too many factors also influencing this course came into play without it being possible to quantify and separate their influence from that of time. Only the negative correlation between the duration of flooding and trunk starch density was consistent. I had to step back and admit that more sophisticated experimentation methods would be needed to disentangle all the other factors influencing starch accumulation. What I did find, however, was that maximum starch density of the pith, in other words, the maximum capacity of pith tissue to store starch kernels in its cells, was close to 280 kg/m^3 across different varieties of sago palm and apparently independent of the other accumulation influencing factors.

Finding many trees in the generative phase which still had very much starch in their trunks and with a high mean starch density (Table 7.1), - the most extreme case being a tree with half grown fruits on its third-order inflorescence branches, with a mean starch density in its leafless trunk part of 242 kg/m^3 and containing an estimated 746 kg of starch - should put behind us for good the myth that a sago trunk needs to be harvested 'before it starts to flower' (not meaning before anthesis, but before the inflorescence becomes visible) if any good starch yield is to be obtained.
It has still escaped detection at which stage of the development of the axis the amount of starch it contains is at its maximum. An attempt at establishing it by searching for the turning point at which assimilate production capacity of the axis would equal assimilate requirements for growth and maintenance of the axis, failed (Chapter 8). In the modelling approach that was taken, assimilate requirements for building and maintaining the inflorescence and the fruits could not be met by the production capacity of the leaves plus the starch reserves in the trunk. For this approach to succeed, additional data on chemical composition of sago palm parts and on assimilation rate are needed.

Ignorance about what is really going on inside a sago palm trunk is often masked in the literature by using the word 'mature'. It is probably the subsistence farmer's term fell-ripe (Indonesian: *masak tebang*) that has transpired into scientific literature as this ill-defined term 'mature'. As is often the case, vague terms lead to vague thinking (and *vice versa*). The term 'mature' should have no place in scientific discourse about development stages of a sago palm axis. In fruit development, mature means full-grown (after which processes involving chemical substance change (as different from substance increase) lead to a stage called ripe). Whereas this holds true also for sago fruits, it has no meaning for a sago axis. Were it perhaps a defendable notion if it were to mean full-grown also in the case of an axis, this is certainly not what is generally meant by its usage in, e.g., a 'mature trunk', or 'the trunk needs 10 years to mature'. Usually something is meant like a trunk which is about at the end of the vegetative phase and which is worth felling for its starch. In fact, the main axis (ax_0) of a sago palm is full-grown no sooner or later than the end of the G1-phase when also all first-order inflorescence branches (ax_1-s) are fully extended.
In prioritizing traits for a good plantation type palm it is often stated that it should be 'early maturing'. This is better replaced by 'early accumulating', which would make it worth felling early, while not implying reaching any final best harvest time early.

9.4 By-products of this research

In looking for A, one may (also) find B. If B will ultimately have any implications for cultivation remains to be seen.
By-products of my studies are:

- More accurate and detailed morphological description of development phases:
  - first description and picture of a stem in transition from Establishment-phase to Adult

  Vegetative-phase (Fig. 4.7).
  - first description and pictures of hollow versus conical trunk apices (Fig.4.23) associated with an apical growing point before and after flower initiation, respectively.
  - first description and pictures (including s.e.m. pictures) of unknown ribbon-like appendages at the tip of primordial leaves/bracts after flower initiation (Fig. 4.24).
  - first s.e.m. pictures of primordia of first-order inflorescence branches (Fig. 4.26).
  - subdivision of the Generative phase into three sub-phases (G1, G2, G3) visible from outside from the ground (end of Section 4.4.2.3).
- Best estimator for the area of a sago palm leaf is not width times height of the main leaf axis cross section at the petiole-rachis transition (as suggested by results with leaves of oil palm and coconut palm), but the length of the rachis (Section 6.1). This is probably because in sago palm the leaf axis at this transition point is concave, whereas in oil palm and coconut palm it is triangular.
- Total leaf area per axis estimated on the basis of rachis length ranged from about 200 m^2 to 325 m^2 in the AV-phase, while Leaf area index per axis during this phase ranged from 1.25 to 1.75 (Table 6.4).
- First comparison of traditional manual versus laboratory starch extraction of an entire trunk. The comparison showed that only 47% of the starch present in the processed trunk part was recovered by the traditional method (Section 7.7).

9.5 And finally ...

For plausible reasons (Section 3.3), semi-wild sago stands came to be the object of study.
I would have probably been able to establish the right felling time under certain growing conditions better if I had studied palms in a plantation. This in spite of the drawback of the disturbing influence of inevitable sucker-pruning and harvesting-before-fruiting in a plantation situation. As it is, I tried to work from the general (wild) to the particular (plantation). I would probably have had more and better results if I had started with a case with known parameters and derived the general from the particular.

In a plantation (see Fig. 2.9) with an at least partially controlled environment and at least some degree of selection in plant material, there are, of course, better opportunities to disentangle the various influences on growth and development of the palm. In a sago plantation

- the groundwater table is usually regulated by a system of canals and water gates (the canal system doubling as a network of waterways which not only provides access to the plantation, but via which also harvested logs are extracted);
- fertilizer applications overrule soil fertility variation;
- shading is uniform, with no shading of the first generation of palms in a new plantation, and shading of the next generations (the suckers growing under the first) regulated by a strict pruning regime;
- this sucker pruning regime is in place to achieve a constant annual yield of trunks per unit area, removing the variation in number of suckers per axis;
- plant material is still a source of error although it is selected and managed to be as uniform as possible. Large quantities of suckers of exactly the same age and guaranteed from the same clone are hard to come by and therefore one makes do with suckers of similarly looking clones, at least belonging to the same folk variety. The nursery and transplanting method usually employed allows for roguing of deviant specimens.

To study growth and development of the sago palm in a sago plantation, one could start by studying them under the prevailing plantation conditions, provided that sufficient palms would be allowed to flower and fruit to be able to follow the life of an axis to the end. From the results of such a study, valid only for these particular set of circumstances, one could arrive at a more generalized growth and development model by follow-up experiments including various levels of groundwater, fertilization, and sucker pruning, and by using different varieties. For the first study, sufficient data points to establish the influence of age on starch content will probably be

obtained when palms are felled and sampled every 12 months, starting 12 months after the beginning of the 'telescoping-out' of the leaf bases indicating the start of the elongation of the first AV-internode. In the follow-up studies, this time interval can be lengthened or shortened for periods where less or more detail is required. Trunk sampling could be done in the same way as I did for the current study, including the apex analysis to check for signs of flower initiation, followed by standard factory processing of the trunk to know how laboratory starch extraction results translate to factory results. Samples of palms of different age could be obtained, of course, from a population planted at the same time by sampling them at the desired time intervals, or by selecting palms of the desired age from palms planted at different times. The number of replicates needed could be derived from the variation among trunks in starch content and distribution as found in factory extraction. Alternatively, if these data are not available, subsistence growers' knowledge on this variation could be invoked.
Once the starch accumulation rate in an axis slows down, starch yield per unit time goes down, and this then seems to be the best time to fell (harvest) the axis and replace it, or let its place be taken, by another (younger) one in which the accumulation rate has not yet slackened. In a clump, the actual production unit in a plantation, with axes of different ages and different starch accumulation rates, all these rates have to be taken into account in establishing the best felling age of the oldest axis of the clump if maximising clump starch yield per unit time is aimed for. As there may be an axis in the clump that has not reached maximum accumulation rate yet, it may well be that best harvest time of the oldest axis is not as soon as, but some time after its accumulation rate has slowed down. Moreover, in a clump the felling of the oldest axis will certainly affect the accumulation rates in the remaining ones. Establishing the right harvesting age of an axis for maximum starch yield per unit time and per unit area in a plantation under different pruning regimes is certainly one of the sago agronomists' most important next challenges.

Insight comes with hindsight. Looking back, ' watching the palm grow ' from germination to fruit shedding as a method to study sago palm growth and development is an approach which would probably have taken less time and given better results than disentangling data from parallel observations on palms of different age growing under diverse circumstances. At least in my case.

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Summary

True sago palm (*Metroxylon sagu* Rottbøll) is a stout, clustering palm adapted to swampy tropical lowland conditions. Each axis in a sago palm clump flowers once at the end of its life after having amassed a large amount of starch in its trunk. Man can harvest this starch and use it like other starches for food or non-food purposes. It is used as a starchy staple mainly in eastern Indonesia and in Papua New Guinea and mostly by exploiting semi-managed stands. For establishing sago palm as a full-fledged plantation crop, desirable because of its envisaged large yield potential as a perennial and because of its niche habitat, much of the necessary basic knowledge about the growth and development of this palm was still lacking. Especially pressing was the lack of knowledge about where and when the starch was accumulated in the trunk and when it was used by the palm itself again to build the enormous terminal inflorescence and to form and fill the thousands of golf ball-sized fruits. Making a major contribution to filling this knowledge gap is the main purpose of the studies reported on in this thesis.

In **Chapter 2** a comprehensive overview of the various aspects of this relatively unknown palm species and its cultivation is presented. The overview is illustrated with about 100 photographs taken in the course of the last two decades at all major sago exploitation and processing locations, covering main products, by-products, morphological aspects, estate cultivation, and processing using various levels of technology.

To properly analyse growth and development of the sago palm, it was deemed necessary to work with plant material that was undisturbed by human actions such as the random cutting of leaves for use as roof thatch material, or the felling of trunks before they could come to their natural end after fruiting. This led to the choice of the semi-wild (i.e. perhaps once planted but then left to grow untended) sago stands around Hatusua village on Seram Island in the Indonesian archipelago of the Moluccas as the main study material. In **Chapter 3** it is explained that this choice presented two problems that had to be addressed first, namely that of the unknown age and of the unknown genetic identity of this semi-wild plant material.

Chapter 4 deals with the first of these two issues, the age issue. As growth rings nor secondary widening occur in sago palm trunks, other age-related features had to be looked for. Therefore, 38 palms at various apparent stages of development were felled and examined. Three main developmental phases are distinguished: 1) the Establishment (E) phase, during which leaves and trunk diameter develop towards their maximum size, while trunk internodes stay unelongated, 2) the Adult Vegetative (AV) phase, during which each new trunk internode elongates, lifting the crown of leaves from the ground, and 3) the Generative (G) phase, in which the terminal inflorescence is formed. Of these selected 38 palms the morphology (including the anatomy) of the trunk, the leaves, and in particular - if present - the giant inflorescence were examined, described and illustrated (with photos and line drawings), including their ontogeny in the apical meristem of the axis. For each of these palms a data sheet with the morphological data, the photographic record, and various environmental data of its habitat was composed. (These data sheets are made available in the appendices to this thesis for reference and as data sets for future research.)
The number of leaf scars on a trunk gives an indication of age if the rate at which leaves are formed is known. Therefore, the leaf unfolding rate (LUR) of 36 palms in their AV-phase was monitored at 4- to 15-month intervals over a 4- to 34-month period. The mean rate was 7.85 leaves per year, but varied from 2 to 14. This variation could not be explained in terms of genetic variation (the different folk varieties the examined palms were attributed to) or of observed environmental variation and was too big to allow for age assessment with an error of one year or less. It was possible, however, to differentiate the AV-phase into early AV-phase and late AV-phase, as the number of leaves formed during the AV-phase is fairly constant for

each variety (147 (SD = 9.1) for variety Tuni, 124 (SD = 5.5) for Ihur). Trunk height proved unfit as accurate age indicator because also internode length varied too much, not only between palms, but also within one trunk.
Development during the G-phase was monitored in 5 palms which had inflorescences in various stages. On the basis of this, the G-phase could be further divided into 3 sub-phases (G1, G2, G3) which are recognizable from the ground by the phased development of the successive orders of inflorescence branches.
Based on the observations and on estimations derived from them, a phenological scale of a model palm is composed presenting hidden and outwardly visible events on two parallel time lines. This 'double' scale was considered necessary to account for the time lag of up to several years between the initiation of a plant part in the apical growing point and its exterior visibility. About two years after the start of the E-phase, the first AV-phase leaf is already initiated, but it does not unfold until 2.5 years later. The initiation of the first AV-phase tissues is followed 12.5 to 14.5 years later by the initiation of the first G-phase tissues, followed 4 to 5.5 years later by the shedding of fruits, and finally by a 2- to 5-year Recycling phase (name proposed here) in which the axis decays and collapses. The palms felled and examined to arrive at this phenological scale and which would be used later (Chapter 7) to study the relation between trunk starch content and age could tentatively be ranked according to physiological age into 4 AV-phase classes and 9 G-phase classes.

In **Chapter 5** the second problem posed by using semi-wild plant material is dealt with, namely its unknown genetic identity and the ensuing lack of knowledge about the relative rareness or commonness of its characteristics. The number of locally recognized varieties in the world is large. This seems logical as true sago palm propagates itself mainly vegetatively through basal offshoots (suckers) and because the production of viable seeds is rare (sago palm is an obligatory cross pollinator with a relatively very short anthesis period). Therefore each new genotype has the potential of being perpetuated and of becoming (locally) recognized and named as a separate variety. Official taxonomy has tried to capture the variation in sago palm in several species, subspecies and botanical (sub-)varieties but has now consented in lumping them into one species, *Metroxylon sagu* Rottbøll, which did away also with the particularly persistent misconception of spined and unspined sago palms belonging to different species.
The variation in sago palm is mapped based on literature and on interviews with local informants. The number of locally recognised varieties in 32 localities spread all over Indonesia and Papua New Guinea ranges from 2 (spined vs unspined only) to 34, the number of unique variety names totalling 325. In this mapping, one has to navigate by the local names given to varieties, which may be confusing as different names may be given in different localities to the same variety, and vice versa. As a way out of this ambiguity in the folk taxonomy, the nomenclatural category folk variety (fovar, fv.) is proposed in analogy to the category cultivation variety (cultivar, cv.). The proposed fovar name consists of the local variety name followed between brackets by an indication of the location where, and (if known) the ethnic/linguistic group by which that name is used (e.g., ' *Metroxylon sagu* Rottb. fv. Honamo (Southern Highlands, Papua New Guinea : Foi) ', in short notation ' *M. sagu* "Honamo" (Southern Highlands, PG : Foi) '). The common practice in Indonesia of labeling sago palm varieties found anywhere as one of the five main varieties found in the Ambon-West Seram area (Tuni, Ihur, Molat, Makanaru or Duri Rotan), or worse, directly as one of the obsolete botanical taxa on the species level with which they are often identified (*Metroxylon rumphii*, *M. sylvestre*, *M. sagus*, *M. longispinum*, or *M. microcanthum*, respectively), should be rejected. No doubt, this practice is rooted in the first pre-Linnean analytical description and western-scientific naming with Latin binomials of the variation in true sago palm by RUMPHIUS (1741), who based his descriptions on what he saw in the Ambon-West Seram area.
Claimed differences among folk varieties from around Hatusua in leaflet thickness and stiffness could not be substantiated by significant differences in dry matter content of leaflets

or in specific area weight of the lamina, probably because of the masking effect of differences in shading.
By comparing traits reported with each variety in the above-mentioned variation survey with traits of the fvs recognised in Hatusua, the Hatusua varieties cannot be diagnosed as other than average and there is as yet no reason to assume that the study results reported on in this thesis would have been qualitatively different if other varieties had been studied.

Running up to the analysis of the relation between age and starch content of sago palm trunks, the collected data on their leaves was analysed first, as the leaves represent the structural starch production capacity of the palms. In **Chapter 6** the total leaf area (TLA) and the leaf area index (LAI) of 25 axes are estimated and their relationship with age and development is studied.
As direct measurement of the TLA, i.e. of the one-sided surface area of all individual leaflets was unfeasible (160-180 leaflets of up to two m long per leaf; up to 28 leaves per crown), the possibility of estimating the area of a single leaf (SLA) by the length of its rachis (RL), the length of its longest leaflet (LLTL) and by the width times height of the cross section of its rachis base (RBW×RBH) was investigated. For reference, one needs some actual observations of the SLA, i.e. of the sum of the areas of all the constituting leaflets. As even the direct measurement of the area of all the leaflets of only a few leaves was unpracticable, it was tried to estimate the area of a single leaflet (LTA) by its length (LTL) and its greatest width (LTW). Regression analysis showed that LTA was best estimated by a linear function of (LTA×LTW), and that SLA was best estimated by a linear function of RL. As a rule of thumb, the area of a sago palm leaf blade can be estimated at three quarters of its length times width.
After a probably gradual build-up of the TLA from zero in the E-phase, in the AV-phase the TLA of 15 out of 16 sago palm axes showed a range of about 200-325 m^2, one axis having an exceptional TLA of about 390 m^2. The TLA in the G-phase before fruiting mostly remained within the same range, possibly exceeding it for a short period early in that stage.
The development of the LAI of an individual axis showed an upward trend from between 1 and 1.5 in the E-phase to between 1.25 and 1.75 in the AV-phase, to more than 2 in the early G-phase, followed by a decrease to about 1.5 again in the late G-phase before fruiting. No fruiting palms were available for analysis.

In **Chapter 7** it is attempted to reach the main objective of the investigations for this thesis: linking trunk starch content and distribution in sago palm to palm age. To this end the density and the distribution of the starch in 27 palms belonging to 6 different varieties was compared to the age rank they had been given on the basis of morphological characteristics in Chapter 4. From each palm, pith samples were taken at 1-metre intervals along the felled trunk and the starch content of each sample was measured by milling the sample, washing out the starch and drying it. Variables probably influencing starch content that were routinely measured with each trunk included degree of shading, (ground-)water level, pH and salinity of groundwater, and number of suckers .
With very few exceptions, starch density in the trunk first increases with height above ground level, reaches a maximum about half-way to two-thirds up the leafless part of the trunk, and then sharply drops towards the top of the trunk.
Early on in the AV-phase the trunk may be formed without starch being deposited in it at the same time, as a palm with a 6-m-long leafless trunk and a starch density not exceeding 11 kg/m^3 illustrates. In most palms the maximum trunk starch density reached is around 250 kg/m^3. From the late AV-phase onward this maximum ranges from 238 to 284 kg/m^3, with an average of 261 kg/m^3. The four trunks with the highest maximum starch densities, all closely around 280 kg/m^3, belonged to three different varieties, suggesting that this is the maximum starch storage capacity of the pith of any sago palm. The furthest-developed palm that was sampled had half-grown fruits, but still had trunk pith with a uniform, high starch density, indicating that depletion of starch reserves by the palm itself may set in much later than

generally assumed. The course of increasing and subsequent decreasing starch density in a trunk with height above ground level differs between palms, even between palms in the same development phase. Several distribution patterns, differing in the steepness of this increase and decrease, can be distinguished: from flat-topped with only one short right tail, to gently sloping with one peak and two long tails. The starch distribution pattern in the leafless part of the trunk shows a tendency to evolve with age from two-tailed (density gradually increasing from base, gradually decreasing towards top) to one-tailed (density gradually increasing from base, sharply decreasing towards top). The differences in distribution pattern found make it clear that there must be other factors besides age and development phase that have a large influence on starch accumulation. Attempts to determine the influence of palm variety and of the environment on this mostly failed: varietal influences could not be detected; the influence of shading could not be established directly as data on the shading history rather than the shading at the time of felling are needed, although a long left tail in the starch distribution could tentatively be linked to an early AV-phase spent in the shade; prolonged flooding has a negative influence on starch density; no trend in the influence of pH or salinity of the groundwater, or of the number of suckers could be detected. Total leaf area and Leaf area index of a single trunk could not be linked to either the mean starch density of its pith, or the total amount of starch the pith contains.
Lack of precise data on the age of the sampled trunks and lack of uniformity of their genetic make-up and growing conditions made it impossible to arrive at the desired detailed timetable of the evolution of trunk starch accumulation and depletion.
Based on the data of the variety of which the most specimens were sampled (Tuni), and on the found maximum starch density of 280 kg/m^3, a simple model of potential starch accumulation in time was constructed, in which the accumulated amount of starch depends on the percentage of the AV-phase already elapsed. By this model, a typical palm axis as it emerged from the sampled palms would reach a maximum dry starch yield of 840 kg. That this amount is not generally reached may not only be due to a lower maximum starch density or to smaller trunk dimensions, but also to the starch extraction method employed. To illustrate the latter, the efficiency of starch recovery from sago palm trunk by traditional methods in West Seram was investigated by traditionally processing one whole trunk of variety Ihur in the early G-phase and comparing the starch yield to the actual amount of starch in the trunk estimated by laboratory processing of pith samples. The traditionally harvested wet starch contained 41% water. Only 47% of the starch in the processed trunk part was recovered. If the unharvested starch present in the traditionally discarded basal and top part of the trunk is taken into account, recovery drops to 44%.

In an attempt to establish the point in time at which the palm starts to be a nett consumer of its own starch, the course of the energy producing and consuming capacity of an axis during its life time was modelled (**Chapter 8**). Underlying this model is the assumption that by the end of the AV-phase these capacities are in balance, meaning that the then existing total leaf area of the axis produces just enough energy in the form of photosynthates to cover the energy required to maintain the then existing biomass, to keep up the normal regular growth, and to fill new trunk with starch. Average dimensions, growth rate and development rate of the more vigorous palms as found in the plant material studied for this thesis were applied to the model palm as they were thought to be the better representatives of good growing conditions and thus of potential growth and development. During the G-phase, the total leaf area of the crown diminishes, thereby reducing the energy-producing capacity of the axis, while maintenance costs of the trunk stay high, the massive inflorescence has to be built, and finally the fruits have to be formed and filled. From the estimated chemical composition of the various palm components and from their building and maintenance costs in terms of kilograms glucose produced by the leaves, and taking into account the gradual change in size of trunk and leaves, the course of the energy balance during the G-phase was calculated. A deficit of 905 kg of glucose by the end of the axis' life resulted from these calculations: using this model, assimilate requirements for building and maintaining the inflorescence and the fruits could not be met by the production in the leaves plus the starch reserves in the trunk. For this modelling approach to succeed in predicting the turning point from nett production to nett consumption of starch by a sago palm axis, additional data on chemical composition of its parts and on assimilation rate are needed.

In the final chapter, **Chapter 9**, the applicability of the research findings is discussed. The relevance for studying growth and development of the sago palm, evident in the 1980s when large scale plantations were planned, has not diminished now that new plantations are back on the agenda as providers of starch for bio-fuel (ethanol) production. The main part of the study was done from 1988 to 1990, but the results are still valuable today because of the unique combination of scale, environment and accuracy of the study (some 40 palms in a semi-natural habitat felled and studied up to microscopy level). The results may be less immediately applicable, but their fundamentalness will probably give them a longer shelf life.
Exploratory and in-depth study of genetic identity and morphology was prompted by the large variation found in these respects, which is probably related to the fact that human selection in sago palm has hardly led to lasting genetic modification, and which is why sago palm is considered as only semi-domesticated. The study of genetic variation led to the introduction of the taxon 'folk variety' (fovar, fv) which allows researchers to unambiguously name the plant material they work with and to better advise growers on which variety to choose. The study of sago palm's morphology led to the formulation of a phenological scale which accounts for the large time gap between initiation of trunk parts and their becoming visible from the outside, facilitating the correct timing of cultural measures.
The multitude of factors other than time influencing trunk starch accumulation, and the impossibility to disentangle these influences with the chosen methods and plant material made it impossible also to pinpoint the best harvesting time. Finding many trees in the generative phase with trunks still containing very much starch and with a high mean starch density proved that a sago trunk does not have to be harvested before the inflorescence emerges. The ill-defined term 'mature' in relation to trunk development should be avoided, and in prioritizing traits for a good plantation palm the characteristic 'early maturing' is better replaced by 'early accumulating', which would make it worth felling early, while not implying reaching any final best harvest time early.
It is argued that establishing the best felling time would probably have been possible if palms in a plantation had been studied, step by step developing more generally valid results by controlled variation of the growing circumstances, in stead of palms in semi-wild stands in which the influences of the varied circumstances had to be disentangled.
And once the course of starch accumulation in time in a single axis is unravelled, the next research question is how this adds up in a clump - the actual production unit in a plantation - with axes of different age and in which the felling of one (the oldest) axis will affect the accumulation in the remaining ones. Planning and methodology of this follow-up research should be such, that the results of the study would be available before a sago palm axis has the chance to complete an entire life cycle, as different from the research reported on in this thesis.

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Samenvatting

De echte sagopalm (*Metroxylon sagu* Rottbøll) is een robuuste, uitstoelende palm die aangepast is aan de omstandigheden van het tropische laaglandmoeras. Elke as in een sagopalmstoel bloeit één maal aan het eind van zijn leven nadat hij een grote hoeveelheid zetmeel in zijn stam heeft opgehoopt. De mens kan dit zetmeel oogsten en het net als zetmeel uit andere bronnen gebruiken voor voeding en voor andere doeleinden. Als hoofdvoedsel wordt het voornamelijk gebruikt in oostelijk Indonesië en in Papoea Nieuw Guinea, en dan meestal gewonnen uit extensief beheerde bestanden. Om de sagopalm als volwaardig plantagegewas te vestigen, wat wenselijk is vanwege het voorziene hoge opbrengstpotentieel van dit overblijvende gewas en vanwege zijn niche habitat, ontbrak nog veel van de benodigde basiskennis over de groei en ontwikkeling van deze palm. Nijpend was vooral het gebrek aan kennis over waar en wanneer het zetmeel in de stam werd opgehoopt en wanneer het weer door de palm zelf werd verbruikt om de enorme eindstandige bloeiwijze te bouwen en de duizende vruchten ter grootte van een golfbal te vormen en te vullen. Een belangrijke bijdrage te leveren tot het vullen van deze kennisleemte is het voornaamste doel van de onderzoekingen waarover in dit proefschrift wordt gerapporteerd.

In **Hoofdstuk 2** wordt een volledig overzicht gegeven van de verschillende aspecten van deze relatief onbekende palmsoort en de teelt ervan. Dit overzicht is verlucht met ongeveer 100 foto's die in de loop van de laatste twee decennia zijn genomen op alle belangrijke locaties waar sago wordt geëxploiteerd en verwerkt, en tonen hoofd- en bijproducten, morfologische aspecten, plantagegewijze teelt, en verwerking op veschillende technologische niveaus.

Om de groei en ontwikkeling van de sagopalm op de juiste manier te kunnen analyseren, werd het noodzakelijk geacht om met plantenmateriaal te werken dat niet was verstoord door menselijk handelen zoals het willekeurig afsnijden van bladeren voor het gebruik als dakbedekkingsmateriaal, of het vellen van stammen voordat zij aan hun natuurlijke einde konden komen na de vruchtdracht. Dit leidde tot de keuze van half-wilde (d.w.z. wellicht ooit geplante maar daarna ongemoeid gelaten) sagobestanden rond het dorp Hatusua op het eiland Seram in de Molukse archipel in Indonesië als het voornaamste studiemateriaal. In **Hoofdstuk 3** wordt uitgelegd dat deze keuze twee problemen met zich meebracht die als eerste moesten worden behandeld, namelijk dat van de onbekende leeftijd en van de onbekende genetische identiteit van dit half-wilde plantenmateriaal.

Hoofdstuk 4 behandelt de eerste van deze twee problemen, het leeftijdsprobleem. Aangezien sagopalmstammen groeiringen, noch secundaire diktegroei vertonen, moest naar andere leeftijdsgerelateerde kenmerken worden gezocht. Te dien einde werden 38 palmen in verscheidene, duidelijk van elkaar verschillende ontwikkelingsstadia geveld en onderzocht. Drie hoofdontwikkelingsstadia worden onderscheiden: 1) de Vestigingsfase (*Establisment* (E) fase), gedurende welke de bladen en de stamdiameter zich ontwikkelen tot hun maximum grootte, terwijl de internodiën van de stam ongestrekt blijven, 2) de Volwassen Vegetatieve fase (*Adult Vegetative* (AV) fase), gedurende welke elk nieuw staminternodium zich strekt en daarmee de bladerkroon van de grond tilt, en 3) de Generatieve (G) fase, waarin de eindstandige bloeiwijze wordt gevormd. Van deze 38 geselecteerde palmen werden de morfologie (inclusief de anatomie) van de stam, de bladen, en in het bijzonder de reusachtige bloeiwijze - indien aanwezig - onderzocht, beschreven en geïllustreerd (met foto's en lijntekeningen), inclusief de ontogenie ervan in het apicale groeipunt van de as. Voor elk van deze palmen werd een lijst met gegevens (*data sheet*) samengesteld met daarin de mofologische gegevens, de foto's die van de palm werden genomen, en verscheidene milieu-gegevens over de habitat van de palm. (Deze *data sheets* zijn voor naslagdoeleinden en als data sets voor toekomstig onderzoek beschikbaar gemaakt in de appendices van dit proefschrift.)

Het aantal bladlittekens op een stam geeft een indicatie van de leeftijd mits de snelheid waarmee bladen worden gevormd bekend is. Daartoe werd de bladontvouwingssnelheid (*leaf unfolding rate* (LUR)) gevolgd in 36 palmen in de AV-fase met tussenpozen van 4 tot 15 maanden over een periode van 4 tot 34 maanden. De gemiddelde snelheid was 7,85 bladen per jaar, maar varieerde van 2 tot 14. Deze variatie kon niet worden verklaard in termen van genetische variatie (de verschillende volksvariëteiten waartoe de onderzochte palmen werden gerekend) of van waargenomen variatie in milieu, en was te groot om de leeftijd mee te kunnen vaststellen met een fout van één jaar of minder. Het was echter wel mogelijk om in de AV-fase een onderscheid te maken tussen vroege AV-fase en late AV-fase aangezien het aantal bladen dat tijdens de AV-fase wordt gevormd voor elke variëteit vrij constant is (147 (SD = 9,1) voor variëteit Tuni, 124 (SD = 5,5) voor Ihur). Stamlengte bleek ongeschikt als nauwkeurige leeftijdsindicator omdat ook de internodiumlengte teveel varieerde, niet alleen tussen palmen, maar ook in één stam.
De ontwikkeling gedurende de G-fase werd gevolgd in 5 palmen die bloeiwijzen hadden in verscheidene stadia. Op basis hiervan kon de G-fase verder verdeeld worden in 3 sub-fasen (G1, G2, G3) die van de grond af herkenbaar zijn aan de gefaseerde ontwikkeling van de opeenvolgende orden van vertakking van de bloeiwijze.
Gebaseerd op de waarnemingen en op daarvan afgeleide schattingen is een fenologische schaal van een modelpalm samengesteld die verborgen en aan de buitenkant zichtbare gebeurtenissen weergeeft op twee parallelle tijdlijnen. Deze 'dubbele' schaal werd als noodzakelijk beschouwd om rekenschap te geven van het tijdsverschil van tot enige jaren tussen de aanleg van een plantendeel in het apicale groeipunt en het aan de buitenkant zichtbaar worden daarvan. Ongeveer twee jaar na het begin van de E-fase wordt het eerste blad van de AV-fase al aangelegd, maar dat ontvouwt zich pas 2,5 jaar later. De aanleg van de eerste weefsels van de AV-fase wordt 12,5 tot 14,5 jaar later gevolgd door de aanleg van de eerste weefsels van de G-fase, 4 tot 5,5 jaar later gevolgd door de vruchtval, en tenslotte door een 2- tot 5-jarige Recycling-fase (naam hier geponeerd) gedurende welke de as vergaat en ineenstort. De palmen die werden geveld en onderzocht om tot deze fenologische schaal te komen en die later (Hoofdstuk 7) zouden worden gebruikt om de relatie tussen het zetmeelgehalte en de leeftijd van een stam te bestuderen, konden onder voorbehoud worden gerangschikt naar fysiologische leeftijd in 4 AV-fase klassen en 9 G-fase klassen.

In **Hoofdstuk 5** wordt het tweede probleem dat het gebruik van half-wild plantenmateriaal met zich meebrengt behandeld, namelijk de onbekende genetische identiteit ervan en het daaruit voortvloeiende gebrek aan kennis over de relatieve zeldzaamheid or algemeenheid van de eigenschappen van het materiaal. Het aantal lokaal gekende variëteiten in de wereld is groot. Dit lijkt logisch aangezien de echte sagopalm zichzelf voornamelijk vegetatief voortplant d.m.v. basale scheuten (*suckers*) en omdat de productie van kiemkrachtig zaad zeldzaam is (sagopalm is een obligate kruisbestuiver met een relatief korte periode van bloei (anthesis)). Daarom heeft elk nieuw genotype de potentie om te worden bestendigd en (lokaal) te worden erkend als een aparte variëteit met een afzonderlijke naam. De officiële taxonomie heeft geprobeerd de variatie in sagopalm te vangen in verscheidene soorten, ondersoorten en botanische (sub-)variëteiten, maar er is nu consensus over de samenvoeging daarvan tot één soort, *Metroxylon sagu* Rottbøll, waarmee ook werd afgerekend met de bijzonder hardnekkige misvatting dat gestekelde en ongestekelde sagopalmen tot verschillende soorten zouden behoren.
De variatie in sagopalm is in kaart gebracht op basis van literatuur en van interviews met lokale informanten. Het aantal lokaal erkende variëteiten op 32 plaatsen verspreid over heel Indonesië en Papoea Nieuw Guinea loopt uiteen van 2 (alleen gestekeld vs. ongestekeld) tot 34, met in totaal 325 unieke variëteitsnamen. Bij dit in kaart brengen moet men afgaan op lokale namen die aan variëteiten worden gegeven, wat verwarrend kan zijn aangezien aan dezelfde variëteit op verschillende plaatsen verschillende namen kunnen worden gegeven, en vice versa. Als uitweg uit deze dubbelzinnigheid in de volkstaxonomie wordt naar analogie

van de categorie 'cultivation variety' (cultivar, cv.) de categorie volksvariëteit (folk variety (fovar, fv.)) voorgesteld. De voorgestelde fovarnaam bestaat uit de lokale variëteits-naam gevolgd door een tussen haakjes geplaatste aanduiding van de lokatie waar, en (indien bekend) de ethnische of taalkundige groep door wie die naam wordt gebruikt (bv., '*Metroxylon sagu* Rottb. fv. Honamo (Southern Highlands, Papua New Guinea : Foi)', in korte notatie '*M. sagu* "Honamo" (Southern Highlands, PNG : Foi)'. Het algemene gebruik in Indonesië om waar dan ook aangetroffen sagopalmvariëteiten te bestempelen als een van de vijf voornaamste variëteiten die in het Ambon-West Seram gebied worden aangetroffen (Tuni, Ihur, Molat, Makanaru of Duri Rotan), of erger, direct als een van de verouderde botanische taxa op soortsniveau met wie deze vaak worden geïdentificeerd (respectievelijk *Metroxylon rumphii*, *M. sylvestre*, *M. sagus*, *M. longispinum*, of *M. microcanthum*), moet worden verworpen. Ongetwijfeld is deze praktijk geworteld in de eerste pre-Linneïsche analytische beschrijving en westers-wetenschappelijke naamgeving met Latijnse binomialen van de variatie in de echte sagopalm door RUMPHIUS (1741), die zijn beschrijvingen baseerde op wat hij zag in het Ambon-West Seramse.
Geclaimde verschillen tussen volksvariëteiten uit de omgeving van Hatusua in dikte en stijfheid van de blaadjes konden niet worden gesubstantieerd door significante verschillen in droge stofgehalte van de blaadjes of in gewicht per eenheid oppervlakte van de bladschijf, waarschijnlijk vanwege het maskerende effect van verschillen in beschaduwing.
Door vergelijking van de kenmerken die werden opgegeven bij elke variëteit in het boven-genoemde variatie-onderzoek met de kenmerken van de fvs die in Hatusua worden onderscheiden, konden de Hatusua variëteiten niet als anders dan gemiddeld worden gediagnostiseerd, en er is vooralsnog geen reden om aan te nemen dat de onderzoeksresultaten gerapporteerd in dit proefschrift kwalitatief anders zouden zijn geweest als andere variëteiten waren bestudeerd.

In de aanloop naar de analyse van het verband tussen leeftijd en zetmeelinhoud van sagopalmstammen werden eerst de verzamelde bladgegevens geanalyseerd; de bladen vertegenwoordigen immers de structurele zetmeelproduktiecapaciteit van de palmen. In **Hoofdstuk 6** worden het totale bladoppervlak (TLA) en de *leaf area index* (LAI) van 25 assen geschat en hun verband met leeftijd en ontwikkeling bestudeerd.
Omdat het ondoenlijk was de TLA, d.w.z. van het éénzijdige oppervlak van alle individuele blaadjes, direct te meten (160-180 blaadjes van tot twee meter lang per blad; tot 28 bladen per kroon), werd de mogelijkheid onderzocht om de oppervlakte van een enkel blad (SLA) te schatten aan de hand van de lengte van de rhachis (RL), de lengte van zijn langste blaadje (LLTL), en de breedte maal de hoogte van de dwarsdoorsnede van de rhachisbasis (RBW × RBH). Als referentie heeft men enkele werkelijke waarnemingen van de SLA nodig, d.w.z. van de som van de oppervlaktes van alle samenstellende blaadjes. Omdat zelfs het directe meten van de oppervlakte van alle blaadjes van slechts enkele bladen slecht uitvoerbaar is, werd gepoogd de oppervlakte van een enkel blaadje (LTA) te schatten aan de hand van zijn lengte (LTL) en zijn grootste breedte (LTW). Regressie-analyse toonde aan dat LTA het beste geschat werd door een lineaire functie van (LTA×LTW), en SLA door een lineaire functie van RL. Als vuistregel kan de oppervlakte van een bladschijf van de sago palm geschat worden op driekwart van zijn lengte maal breedte.
Nadat de TLA in de E-fase waarschijnlijk geleidelijk vanaf nul was opgebouwd, vertoonde de TLA van 15 van de 16 sagopalm-assen in de AV-fase een spreiding van ongeveer 200-325 m^2; één as had een uitzonderlijke TLA van 390 m^2. De TLA in de G-fase vóór de vruchtzetting bleef grotendeels binnen dezelfde grenzen, hoewel het mogelijk is dat hij er vroeg in die fase korte tijd bovenuit kwam.
De ontwikkeling van de LAI van een individuele as vertoonde een opwaartse trend van tussen 1 en 1,5 in de E-fase tot tussen 1,25 en 1,75 in de AV-fase, tot meer dan 2 in de vroege G-fase, gevolgd door een afname tot ongeveer weer 1,5 in de late G-fase vóór de vruchtzetting. Er waren geen vruchtdragende palmen voor analyse beschikbaar.

In **Hoofdstuk 7** wordt getracht de voornaamste doelstelling van het onderzoek voor dit proefschrift te realiseren, namelijk een verband leggen tussen de hoeveeheid en de verdeling van zetmeel in de stam van een sago palm en de leeftijd van die palm. Daartoe werd de dichtheid en de verdeling van het zetmeel in 27 palmen behorende tot 6 verschillende variëteiten vergeleken met hun plaats in de leeftijdsrangschikking die zij op grond van morfologische kenmerken in Hoofdstuk 4 hadden gekregen. Van elke palm werden uit de gevelde stam om de meter mergmonsters genomen, en het zetmeelgehalte van elk monster werd gemeten door het monster te vermalen en het zetmeel er uit te spoelen en te drogen. Variabelen die waarschijnlijk van invloed waren op de zetmeelinhoud en die stelselmatig bij elke stam werden gemeten waren o.a. de mate van beschaduwing, het (grond-)waterpeil, de pH en het zoutgehalte van het grondwater, en het aantal basale zijscheuten.
Bijna zonder uitzondering neemt de zetmeeldichtheid in de stam eerst met de hoogte boven de grond toe, bereikt een maximum op ongeveer de helft tot twee derde van het bladloze gedeelte van de stam, en neemt dan naar de top van de stam toe scherp af.
Vroeg in de AV-fase kan de stam worden gevormd zonder dat er tegelijkertijd zetmeel in wordt afgezet, zoals wordt geïlllustreerd door een palm met een 6 m lange stam en een zetmeeldichtheid die niet boven de 11 kg/m^3 komt. In de meeste palmen is de maximale zetmeeldichtheid die wordt bereikt ongeveer 250 kg/m^3. Vanaf de late AV-fase ligt dit maximum tussen de 238 en 284 kg/m^3, met een gemiddelde van 261 kg/m^3. De vier stammen met de hoogste maximum zetmeeldichtheid, alle dicht rond de 280 kg/m^3, behoren tot drie verschillende variëteiten, wat suggereert dat dit de maximale zetmeelopslagcapaciteit is van het merg van sagopalm in het algemeen. De verst ontwikkelde palm die werd bemonsterd had halfvolgroeide vruchten, maar had nog altijd stammerg met een uniform hoge zetmeeldichtheid. Dit wijst er op dat het verbruik van de zetmeelreserves door de palm zelf misschien veel later inzet dan algemeen wordt aangenomen. Het verloop van met hoogte boven de grond toenemende en daarna afnemende zetmeeldichtheid in een stam verschilt tussen palmen, zelfs tussen palmen in dezelfde ontwikkelingsfase. Verscheidene verdelingspatronen, verschillend in de steilte van deze toe- en afname, kunnen worden onderscheiden: van een verdeling met een vlakke top en één korte staart aan de rechter kant, tot een verdeling met glooiende hellingen, één top, en twee lange staarten. Het verdelingspatroon van de zetmeel in het bladloze deel van de stam tendeert met de leeftijd te evolueren van een twee-staartige (dichtheid neemt vanaf de basis geleidelijk toe, en naar de top geleidelijk af) naar een één-staartige (dichtheid neemt vanaf de basis geleidelijk toe, en naar de top scherp af). De verschillen in verdelingspatroon die gevonden werden, maken duidelijk dat er naast leeftijd en ontwikkelingsfase nog andere factoren moeten zijn die een grote invloed hebben op de zetmeelaccumulatie. Pogingen om de invloed van palmvariëteit en van het milieu vast te stellen, zijn grotendeels mislukt: variëteitseffecten konden niet aan het licht worden gebracht; de invloed van beschaduwing kon niet direct worden vastgesteld omdat daarvoor eigenlijk gegevens over de beschaduwingsgeschiedenis nodig zijn en niet over de beschaduwing op het tijdstip van vellen, hoewel een lange staart aan de linkerkant van de zetmeelverdeling met enige aarzeling kon worden toegeschreven aan een in de schaduw doorgebrachte vroege AV-fase; langdurige inundatie heeft een negatieve invloed op de zetmeeldichtheid; er kon geen trend worden bepaald in de invloed van de pH of het zoutgehalte van het grondwater, of van het aantal basale scheuten. De TLA en de LAI van een individuele stam konden niet in verband worden gebracht met de gemiddelde zetmeeldichtheid in het merg van die stam, noch met de totale hoeveelheid zetmeel die het merg bevat.
Gebrek aan nauwkeurige gegevens over de leeftijd van de bemonsterde stammen en gebrek aan uniformiteit van hun genetische samenstelling en van hun groeiomstandigheden maakten het onmogelijk om tot de gewenste gedetailleerde tabel te komen van het verloop in de tijd van de opslag en het verbruik van het zetmeel in de stam.
Op basis van gegevens over de variëteit waarvan de meeste exemplaren waren bemonsterd (Tuni) en van de gevonden maximale zetmeeldichtheid van 280 kg/m^3 werd een eenvoudig model samengesteld van de potentiële zetmeelaccumulatie in de tijd waarin de hoeveelheid

geaccumuleerd zetmeel afhangt van het percentage van de AV-fase dat verstreken is. Volgens dit model zou een typische palm-as zoals die uit de palmen die bemonsterd werden valt af te leiden een maximum droge zetmeelopbrengst bereiken van 840 kg. Dat deze hoeveelheid niet algemeen gehaald wordt, valt misschien niet alleen toe te schrijven aan een lagere maximum zetmeeldichtheid of aan kleinere stam-afmetingen, maar ook aan de gebruikte zetmeelextractiemethode. Om dit laatste te illustreren, werd de efficientie van de zetmeelwinning uit een sagopalmstam door middel van traditionele methoden in West Seram onderzocht door een hele stam van de variëteit Ihur in de vroege G-fase op traditionele wijze te verwerken en de zetmeelopbrengst te vergelijken met de werkelijk aanwezige hoeveelheid zetmeel in de stam geschat aan de hand van mergmonsters die in het laboratorium verwerkt werden. Het traditioneel geoogste, natte zetmeel bevatte 41% water. Slechts 47% van de zetmeel in het deel van de stam dat verwerkt wordt, werd er uit gehaald. Als de zetmeel die aanwezig is in het traditioneel niet verwerkte onderste en bovenste deel van de stam wordt meegerekend, zakt dit percentage tot 44.

In een poging het tijdstip vast te stellen waarop de palm een netto consument wordt van zijn eigen zetmeel, werd het verloop van de energieproductie- en consumptie-capacitiet gedurende het leven van een as gemodelleerd (**Hoofdstuk 8**). Aan dit model ligt de aanname ten grondslag dat deze capaciteiten aan het eind van de AV-fase in evenwicht zijn, dat wil zeggen dat de dan bestaande totale bladoppervlakte precies genoeg energie in de vorm van fotosyntheseproducten levert om de energiebehoefte te dekken voor het onderhoud van de dan bestaande biomassa, voor het in stand houden van de normale regelmatige groei, en voor het vullen van nieuwe stam met zetmeel. Voor de modelpalm werden de gemiddelde afmetingen, groeisnelheid en ontwikkelingssnelheid van de meest levenskrachtige palmen onder het plantenmateriaal dat voor dit proefschrift bestudeerd werd gebruikt, omdat deze palmen geacht werden goede groeiomstandigheden, en derhalve potentiële groei en ontwikkeling, het beste te typeren. Tijdens de G-fase neemt het totale bladoppervlak van de kroon af, waarmee ook de energie-producerende capaciteit van de as minder wordt, terwijl de onderhoudskosten van de stam hoog blijven, de enorme bloeiwijze moet worden gebouwd, en tenslotte de vruchten gevormd en gevuld moeten worden. Aan de hand van de geschatte chemische samenstelling van de verschillende palmcomponenten en van hun bouw- en onderhoudskosten in termen van kilogrammen door het blad geproduceerde glucose, en rekening houdend met de geleidelijke verandering in grootte van stam en bladen, werd het verloop van de energiebalans gedurende de G-fase berekend. Een tekort van 905 kg glucose aan het eind van het leven van de as was het resultaat van deze berekeningen: volgens dit model konden aan de vraag aan assimilaten voor de bouw en het onderhoud van de bloeiwijze en de vruchten niet worden voldaan door de productie in de bladen plus de zetmeelreserves in de stam. Wil men er met deze modelleer-benadering in slagen het keerpunt van netto productie naar netto consumptie van zetmeel door een sagopalm-as te voorspellen, dan zijn er meer gegevens nodig over de chemische samenstelling van de palmdelen en over de assimilatiesnelheid.

In het laatste hoofdstuk, **Hoofdstuk 9**, wordt de toepasbaarheid van de onderzoeksresultaten besproken. De relevantie van het bestuderen van de groei en ontwikkeling van de sago palm, evident in de tachtiger jaren van de vorige eeuw toen grootschalige plantages werden gepland, is niet minder geworden nu nieuwe plantages weer op de agenda staan als zetmeelleveranciers voor de productie van bio-brandstof (ethanol). Het grootste deel van het onderzoek werd verricht van 1988 tot 1990, maar de resultaten zijn ook nu nog waardevol vanwege de unieke combinatie van schaal, milieu en precisie van het onderzoek (een veertigtal palmen in een half-natuurlijke habitat, geveld en bestudeerd tot op mikroskopisch niveau). De resultaten zijn misschien minder direct toepasbaar, maar door het fundamentele karakter ervan zijn ze waarschijnlijk wel langer houdbaar. Aanzet tot verkennend en diepgaand onderzoek van de genetische identiteit en van de morfologie was de grote variatie die hierin werd gevonden, wat waarschijnlijk verband houdt met het feit dat menselijke selectie in sagopalm nauwelijks geleid heeft tot duurzame genetische verandering, wat ook de reden is waarom sagopalm als slechts half-gedomesticeerd beschouwd wordt. De bestudering van de genetische variatie leidde tot de introductie van het taxon '*folk variety*' (fovar, fv) dat onderzoekers in staat stelt om op ondubbelzinnige wijze het plantenmateriaal waarmee ze werken te benoemen en om telers beter te adviseren over de te kiezen variëteit. De bestudering van de morfologie van de sagopalm leidde tot de formulering van een fenologische schaal die rekening houdt met de lange tijd die verstrijkt tussen het aanleggen van stamonderdelen en het aan de buitenkant zichtbaar worden daarvan. Deze schaal kan helpen bij de timing van teeltmaatregelen.

De veelheid van faktoren, afgezien van de tijd, die de accumulatie van zetmeel in de stam beïnvloeden, en de onmogelijkheid om deze invloeden met de gekozen methoden en het gekozen plantenmateriaal te ontrafelen, maakten het onmogelijk om het beste oogsttijdstip vast te stellen. De vele bomen in de generatieve fase die werden aangetroffen met stammen met nog zeer veel zetmeel en een hoge zetmeeldichtheid, toonden aan dat een sagostam niet hoeft te worden geoogst voordat de bloeiwijze verschijnt. De slecht gedefinieerde term 'rijp' met betrekking tot de ontwikkeling van een stam dient te worden vermeden, en bij het bepa-len van de meest gewenste kenmerken voor een goede plantagepalm kan de eigenschap 'vroeg-rijpend' beter vervangen worden door 'vroeg-accumulerend', wat hem vroeg de moeite waard om te vellen zou maken, zonder te ïmpliceren dat er een uiteindelijk te bereiken best oogsttijdstip is dat hij vroeg bereikt.

Er wordt gesteld dat het bepalen van de beste tijd om de palm te vellen waarschijnlijk mogelijk was geweest als palmen in een plantage waren bestudeerd, waarbij stap voor stap meer algemeen geldende resultaten waren ontwkkeld door gecontroleerde variatie van de groeiomstandigheden, in plaats van palmen in half-wilde bestanden waarbij de invloeden van de gevarieerde omstandigheden moesten worden ontward.

En als eenmaal het verloop van de zetmeelaccumulatie in de tijd in een enkele as ontrafelt is, is de volgende onderzoeksvraag hoe de optelling uitvalt in een stoel - de feitelijke productie-eenheid in een plantage - met assen van verschillende leeftijd waarbij het vellen van één (de oudste) as de accumulatie in de resterende assen beïnvloedt. De planning en de methodologie van dit vervolgonderzoek zouden zodanig moeten zijn dat de resultaten van de studie beschikbaar komen voordat een sagopalm-as de kans heeft om een complete levenscyclus te voltooien, anders dus dan van het onderzoek waarvan in dit proefschrift verslag wordt gedaan.

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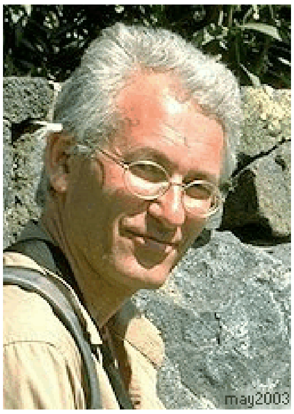
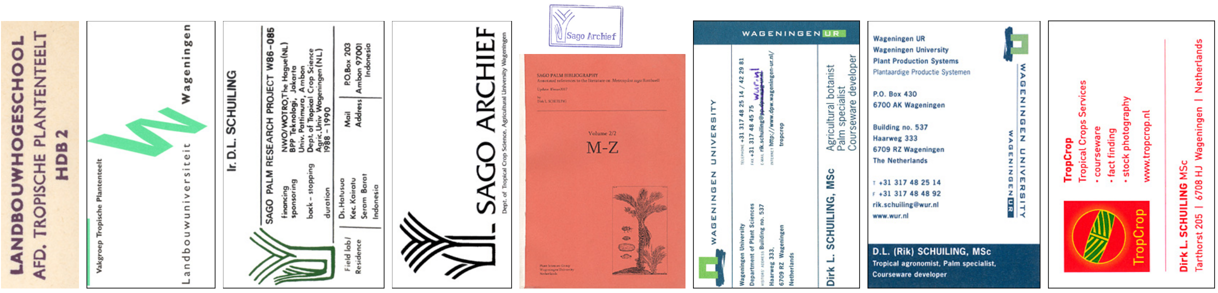
Curriculum vitae

Dirk Leopold ('Rik') SCHUILING was born on the 2nd of June 1953 in Voorschoten, Netherlands. The successive stationings of his father, an officer in the Dutch navy, made him spend his childhood in Rotterdam, Sorong (Papua Province, Indonesia (then Netherlands New Guinea)), Huisduinen and again Voorschoten, before he moved to his current domicile Wageningen in 1971. He enjoyed secondary education (gymnasium β) at the Gemeentelijk Lyceum in Den Helder and the Rijnlands Lyceum in Wassenaar, and tertiary education at Wageningen University (then called Landbouw Hogeschool), majoring in entomology and tropical crop science. Field exploits during his studies included a 2-month tobacco harvesting period in Ontario, Canada and an 8-month research internship studying a pest in rice at the Maros Agricultural Research Institute (S. Sulawesi, Indonesia). They also included some one and a half year of extra-curricular but all the more formative travelling in the Americas, North Africa, Asia and Australia. After graduation from Wageningen in 1984, he was assistant horticulturist at Brawijaya University (Malang, Java, Indonesia) in 1986 in a NUFFIC inter-university cooperation project. In 1988 he embarked on a study of the sago palm funded by NWO-WOTRO for which he was stationed on Seram Island (Moluccas, Indonesia) and which ultimately resulted in this PhD thesis. Before and after this study he was employed by Wageningen University in various capacities including that of assistant lecturer, librarian, lecturer and educational software developer. From 1996 he has also been teaching a short course in tropical crops at the Leuphana University (Lüneburg, Germany), and more recently at ISARA (Lyon, France). Currently he is self-employed, running his own company TropCrop - Tropical Crops Services, which offers courseware, teaching, fact finding and photo stock in the field of tropical crops.





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