Durio — A Bibliographic Review

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Foreword

Under the IPGRI Project on 'Promoting Conservation and Use of Tropical Fruit Species in Asia,' much information on status of plant genetic resources has been synthesized for major (mango, citrus, rambutan) and minor (jackfruit, litchi, durian) fruits of South, Southeast and East Asia. This information gathering particularly relates to distribution, extent of diversity, status of germplasm collection, characterization, evaluation, documentation, conservation and utilization. Fifteen such reports prepared by national experts for key national programmes/countries holding rich diversity in these tropical fruits have been brought out by the IPGRI-APO; six on mango (Bangladesh, India, Indonesia, Philippines, Thailand and China), three on citrus (India, China, Japan), two each on rambutan and durian (Thailand and Malaysia), one on jackfruit (Bangladesh), one on litchi (China). Dissemination of this well synthesized information by IPGRI will promote further the conservation and use of these crop genepools.

Among the native tropical underutilized fruits of promising potential, durian assumes great importance particularly in Malaysia, Thailand and Indonesia. Global interest in this fruit is catching up fast and its commercial prospects increasing. With promising clones now available and considering the export potential of durian, more area under its cultivation has led to loss of primitive diversity and wild/semi-wild/domesticated species. Further, research and development efforts are still required to understand durian flora1 biology and physiology of fruit set, and assessing wild and domesticated primitive genepools for their usefulness in diseases/pest resistance, physiological stress and other attributes imparting better characteristics. Specific treatises dealing with studies on taxonomy, genetic diversity, flora1 biology, breeding, improvement, conservation and utilization aspects are wanting.

In the above context, the detailed synthesis provided on durian by Dr. Michael J. Brown is welcomed. It is perhaps for the first time that such a comprehensive account has been attempted on an underutilized fruit crop genepool. This publication on Durian which is a review of bibliography of about 1000 references, provides a well-synthesized information on different aspects of *Durio*. It deals with its origin, history, taxonomy of wild and cultivated species, identification, morphology of flower and fruit and other organs, its edibility, composition and uses, nutritional aspects, medicinal and toxicological prospects, seed physiology, pollination biology, ecology, forest resources, crop improvement efforts, agronomic requirements, propagation, cultivation and maintenance, post harvest technology, genetic resource and conservation.

IPGRI-APO has put in tremendous efforts to bring out this monograph suitably edited by Drs. R.K. Arora, Ramanatha Rao and A.N. Rao, and published by IPGRI Office for South Asia, Pusa Campus, New Delhi. IPGRI is happy to be able to publish this work by Dr. Michael J. Brown, as it greatly enriches knowledge on the *durio* genepools. Also, IPGRI supports the dissemination of such information on underutilized fruits, their R&D needs and above all promoting their conservation and use.

I am confident that this publication will generate further interest in this crop, and will be useful to researchers and concerned institutes to strengthen their research and development needs on durian.

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Preface

My desire to write this book grew out of an innate and deeply rooted concern to understand the durian. In the late 1980s, a vigorous search of scientific abstracts led me to believe that a bibliography on the subject would only fill 1 or 2 type-written pages; the idea that a bibliographic review resulting in a book would be necessary to fully examine the subject was unthinkable. Today, I would estimate that approximately 1200 research articles, book chapters, conference abstracts etc. have been produced which pertain to durian. At the current rate of increase, this figure will very likely double over the next 20 years. Thus, we stand at a crossroad. If our future researches are really to advance our knowledge forward, we need to come to terms with what we already know.

Despite the preponderance of information that exists on durian, numerous obstacles are present for those who wish to study them. Much of the literature presented in the bibliography of this book has never been abstracted. This, and many of the items that are abstracted, have been exceedingly difficult (and sometimes prohibitively expensive) to obtain. Thus, in many areas, a researcher cannot be reasonably expected to have discovered and read much of the pertinent background information. In numerous instances, this has led to the repetition of experiments and has stood in the way of an appropriate focus around which further research projects could be built up.

Currently, no comprehensive bibliography on durian literature exists for the researcher, which is difficult to comprehend given the economic importance of this fruit to several nations. The goal of this work is two-fold. Firstly, it is intended to remedy the information management problems just described. Secondly, it is hoped that, by means of a review, those issues which are most in need of further study will be brought to light. The diversity of research conducted has raised several very interesting lines of enquiry; while the obscurity and fragmentary nature of many studies has led to the premature acceptance of hypotheses.

The research conducted on some of the world's major crops (rice, wheat, maize, etc.) compared with that on durians is like a mountain to a mole-hill. The number of fields of scientific enquiry that have been touched upon by this mole-hill is rather staggering, and leaves me to wonder what marvels we could unearth had we the whole mountain.

In this work, great pains have been taken to give full credit to all the authors. Much time and effort have been devoted to obtaining original research articles to confirm statements and ideas presented in more general reviews. In cases where original results were published using the Imperial system of measurements, a metric equivalent is presented parenthetically. Where research on species, that are no longer taxonomically recognized, is discussed, parenthetic notes are given to help clarify their identity.

I can in no way take full credit for the massive amount of effort that went into compiling the bibliography. I wish to extend thanks to the numerous libraries and institutions without whose aid in supplying original works and/ or photocopies, this book would not have been possible: University of Guelph Library, Canada; Universiti Pertanian Malaysia Library; National Library of Malaysia; Malaysian National Agricultural Library; Management Information Systems Division, MARDI, Malaysia; University of Los Banbs Library, Philippines; Kasetsart University Library, Thailand; Thailand Institute of Scientific and Technological Research; Hunt Botanical Library, Pennsylvania; The Library of the Herbarium Universitatis Florentinae, Italy; The Library of the New York Botanical Gardens; The Library of the Jardin Botanique National de Belgique, Belgium; The British Library (Oriental and India Office Collections); Centre for Scientific Documentation and Information, Indonesia; SEAMEO-BIOTROP, Bogor, Indonesia; Forest and Nature Conservation Research and Development Centre, Bogor, Indonesia; Library of The Royal Botanic Gardens, Kew, England; Lloyd Library and Museum, Cincinnati USA; and The Solomon Islands National Library.

I am grateful to the many authors who supplied reprints of their research articles. I am indebted to the friendship and excellent library skills of Mr. David Bantroch, which greatly enhanced the scope and content of the bibliography. I am also indebted to those who graciously supplied or helped obtain copies of articles from different locations across the world: Dr. Gordon Brown, Carol Bowes, Paul d'Amboise, Peter Toorop and Dr. Andrew Powell. I also express my gratitude to the International Plant Genetic Resources Institute for supporting the publication of this work, and to Drs. R.K. Arora, V. Ramanatha Rao and A.N. Rao for editing the manuscript.

Finally, I would like to acknowledge the invaluable assistance of those who helped translate articles or parts thereof: Nusin Brown for translation of Turkish items; Aldo De Moor, Dr. Annette Nassuth and Peter Toorop for translation of Dutch and German items; Dr. Wataru Mitsuhashi for the translation of Japanese items, Chumnum Wongmanee for translation of Thai articles and my wife Nathalie Bourgouin-Brown for translation of several French documents.

Michael J. Brown

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Durio — A Bibliographic Review

Introduction

The genus *Durio* is native to South East Asia with its centre of diversity in Borneo (Mendoza 1941; Lim 1990). The genus comprises approximately 30 known species, of which only *Durio zibethinus* is cultivated for its fruits to a great extent (Lim 1990). As a rain-forest tree, it typically attains heights of 30-40 m (Tidbury 1976) and diameters of 2-2.5 m, but the cultivated varieties in an orchard, especially when grafted, grow no higher than 12 m (Malo and Martin 1979). Although relatively unknown to the western world, the durian is a valuable commodity in South East Asia, and has had a profound effect on the history and culture of that part of the world. James Low (1836) recorded that the king of Ava had fruits transported to him at Amerapoora, ‘by relays of horsemen, and by boats pulled by 40 or 50 men’. The durian fruit's reputation precedes it wherever it goes: ‘durian is to fruit what limburger is to cheese and pornography is to literature’ (Anon. 1979a).

In Malaysia, the value of durian exports alone accounted for over 40% of total fruit exports in 1989 (Ali 1993). Subhadrabandhu *et al.* (1991) state that in Indonesia, the rice harvest suffers if it happens to coincide with durian season, the harvesters being more interested in the consumption of durians than in the harvest of rice. There are quite a few recognized clones of durian, whose fruits vary in size, shape, smell, colour, texture and taste. Some clones (D2, D98, etc.) are much sought after and fetch a very high price in the market.

Although little research has been carried out in the past on durian, this trend is slowly starting to change as plans to improve the quality and consistency of durian fruits develop. This is evidenced by the success of the recent release of the first ‘hybrid’ durians in Malaysia (Othman 1991).

Studies, which have been conducted on durian, have been scattered through various disciplines including chemistry, ecology, entomology, food science, forestry, medicine, pathology, systematics and even zoology. These studies have often been published in obscure or difficult to locate publications, and not properly abstracted. Despite what can only be described as exhaustive efforts to obtain and examine every book or article that supposedly pertained to the genus *Durio*, some items were unobtainable. A fair number of erroneous or non-existent research papers have also been referenced for their relative importance. For these reasons, a comprehensive bibliography for durian is presented at the end of this work. This bibliography contains only items of which originals or copies have been obtained and examined by the author.

Taxonomic History

The durian has influenced various cultures of South East Asia for millennia, but has only been known to the western world for about 600 years. In this section, attempt is made to trace the scientific description of durian from its earliest origins to the present day. Early descriptions and knowledge were largely of a morphological and taxonomic nature. Although accounts on the effects of the fruit on human physiology abounded, our knowledge of these have expanded enormously in the last few decades and thus this aspect will be discussed in a separate section. Tracing the origins of durian research to their beginnings not only allows us to place certain information in proper historical perspective, but also an understanding of how the current taxonomic state of affairs, and perhaps much of the confusion, has arisen.

Origin of the word durian : The word durian (*Durio*) without doubt originates from the Malay word ‘duri’ which means spine (Don 1831). The word ‘zibethinus’ is a reference to the Indian civet cat *Viverra zibetha*. Don (1831) provided the following information: ‘the fruit is used as bait to entrap the civet-cat, which is very fond of it; hence the specific name’. Others have suggested that *zibethinus* refers to the smell of the fruit which is it’s (and the civet cat’s) most legendary characteristic (Hawson 1983; Watson 1984). The accuracy of this comparison is perhaps best summed up by Barrett (1912). ‘According to the specific name zibethinus, the fruit should osphresiologically remind one of the civet cat; the writer, however, after having seen and smelled live civets in Mozambique, does not concur in this idea.’ Nevertheless, the fruit is occasionally referred to as the civet cat fruit (Gamble 1881; Watt 1890; MacMillan 1909, 1912; Anon. 1952; Singh *et al.* 1983). The Latin name was coined by Linnaeus who apparently never encountered an actual specimen of a durian, and based his description entirely upon that provided in the ‘Herbarium Amboinense’ (König 1804). As Rumphius (1741) refers to the use of durian fruits to catch civet cats in his ‘Herbarium Amboinense’, it seems likely that this was the reason for the name. De Candolle (1824) also states that the name arises from the fact that civets eat durians.

De Clercq (1909) enumerated many vernacular names for durians and Heyne (1950) enumerated well over 50 names used in various parts of the Malay archipelago. Most of these are close variants of ‘durian’. Endert (1927b) suggests that the conservation of the word ‘durian’ in different native Indonesian languages probably indicates its early spread by the Malays.

Many authors give Malay vernacular names for the various species. Malay names can often be quite useful in aiding identification (Corner 1988); the taxonomy of many of the wild species of *Durio* is still in some disarray, and it is quite likely that the Malay names are more reliable in some instances. By far the most comprehensive, and probably most accurate, list of vernacular names for different species of durian are those given by Kostermans (1958b).

In this book, the word ‘durian’ will be used to refer only to *D. zibethinus*, except in its use as a forestry term. In this sense, it has historically been applied to a mixture of different species, and perhaps even related genera. Where any confusion could arise, I have endeavoured to refer to exact species. Furthermore, where the taxonomy is confusing, I have referred to species as defined in most comprehensive monograph by A.J.G.H. Kostermans (1958b) [=*sensu* Kostermans 1958b], or otherwise, as appropriate.

Durian poetry : For whatever reason, the durian has appealed to the artistic side of people for a long time. Many Malay idioms contain references to durians (Kostermans 1958b). There are also several published poems pertaining to durians (Whiteside 1914; Slate 1974; Chin 1979; Chin 1980a; Bantroch, 1995). A short story simply entitled ‘Durian’ by A.R. Roces (1949) delightfully conveys the not-so-subtle nature of durian fruits to the reader.

Historical works : The durian appeared in pre-Linnaean literature as early as the 16th century although erroneous information abounded. In 1741, Rumphius’ ‘Herbarium Amboinense’ was finally published, and provided the most thorough account of durians for over 100 years. Descriptions of durians in Linnaean works, and those that followed it, have relied almost entirely on information gleaned from this work.

The earliest European description of the durian is perhaps that of Nicolo Conti who travelled in South East Asia at the beginning of the 15th century (Bracciolini 1857). Fragoso’s ‘Discursos’ of 1572 offered a two-page Spanish description of durians ‘Doriones’. Some details about durians were also given in several works of Garcia De Orta in the late 16th century. Acosta’s (1585) ‘Trattato’ briefly described durians and contained a very stylized figure of a tree bearing fruit. Daléchamps’ (1586) ‘Historiae Generalis Plantarum’ contained a Latin description which is a near translation of the description from Acosta’s Trattato of 1585 and bears a figure of the same stylized tree. This figure was also redrawn in Boym’s ‘Flora Sinensis’ of 1656. Paludan in Linschoten (1592) published a two-page description which appeared again in one form or another in several later publications. An English translation of this work is also presented (Anon. 1851).

Dodoens (1608) published his ‘Cruydt-Boeck’ which included a German translation of Acosta’s description of durians from his ‘Trattato’ of 1585.

Pyrard (1619) stated that ‘The durion tree nearly resembles a pear tree in size; the fruit is as big as a melon. The Indians esteem this fruit to be one of the best and daintiest in the Indies. To those who are unaccustomed to it, it is disagreeable, having a stink like that of our onions, but the taste is far more excellent.’

Bauhin (1623) listed durians (duryaoen) in his ‘Pinax’, and De Bondt (1658) presented a Latin description of the physiological effects of eating durian and a drawing of the fruit which was by far the most accurate published to date. Tavernier mentioned that durians are found growing in Siam (ca. 1676), and John Ray’s ‘Historia Plantarum’ of 1693 contains a one page Latin description of durian fruits, largely copied verbatim from Acosta’s ‘Aromatum’, with a few added notes. According to Hamilton: ‘The *Durean* is another excellent fruit, but offensive to some peoples noses, for it smells very like human excrements, but when once tasted, the smell vanishes. The skin is thick and yellow, and within is a pulp like thick cream in colour and consistence, but more delicious in taste. The pulp or meat is very hot and nourishing, and instead of surfeiting, they fortify the stomach and are a great incentive to Wantonness’ (Hamilton 1727).

Rumphius’ ‘Herbarium Amboinense’ was finally published in 1741. This encyclopedic work contains several pages devoted specifically to durian fruits. Although the identity of several plants described in this work remain controversial, the plant described as ‘durioen’ in this book definitely represents *D. zibethinus* (Buchanan-Hamilton 1824). The text of the ‘Herbarium Amboinense’ was originally written in Dutch, and was published side by side with a Latin translation. No English translation ever appears to have been published. The different species mentioned by Rumphius are merely varieties. Rumphius did manage to distinguish successfully between the durian and the soursop (*Annona muricata*), which had been muddled together since the time of Garcia De Orta. Rumphius’ description included a lengthy discussion on the digestive effects of eating durian and the germination of the seeds. His description was accompanied by a very accurate plate depicting the flowers, fruit and a branch of a tree. The genus was rendered into Linnaean systematics by Adanson (1763) in his ‘Familles des Plantes’, based on Rumphius’ description in the ‘Herbarium Amboinense’.

Authority for *Durio zibethinus* : The taxonomy of durians brings to light many of the taxonomic problems. The genus *Durio,* as stated by Chevalier (1934), was created by Rumphius (1741) in his ‘Herbarium Amboinense’, and was rendered into Linnaean systematy by Adanson (1763).

The type species *Durio zibethinus* is attributed to (Murr.); J.A. Murray, however, some authors also attribute the species to Linnaeus (L.). Infrequently, other (erroneous) authorities are encountered, i.e., Chattaway (1933) referred to *Durio zibethinus* DC. De Candolle (DC.) is obviously not the correct authority as A.P. De Candolle’s Prodromus of 1824 is predated by over 50 years of valid taxonomic references to this species. Furthermore, in this work, De Candolle himself cited Linnaeus as the authority for the species. Thus, the question remains as to the correct valid authority. As there has been some confusion of this matter in taxonomic and other works, and no consensus appears to have been reached, a full investigation of the issue was warranted.

The authority L. appeared several times in early taxonomic literature. Its first appearance seems to have been in Willdenow (1800) in the 5th edition of ‘Species Plantarum’, which lists ‘*Durio zibethinus* Syst. Veg. 698.’ as a species. This is a reference to page 698 of the 14th edition of ‘Systema Vegetabilium’ of 1784 by J.A. Murray upon which *Durio zibethinus* is listed. However, this species was described several years earlier on page 581 of the 13th edition of Linnaeus’s ‘Systema Vegetabilium’ published in 1774, also edited by J.A. Murray. This 13th edition is without doubt the first ‘valid’ publication of this species, however, Willdenow’s error of accrediting the first publication to the 14th edition was copied by several future authors, and found its way into several important taxonomic works: A.P. De Candolle (1824) described ‘Durio Linn. Syst. 698. non Adans.’ in his ‘Prodromus’. George Don (1831) lists ‘Linn. Syst. 698. but not of Adans. DC. prod. 1 p. 480.’, a reference most-likely copied directly from De Candolle’s work. Furthermore, Endlicher (1840) in ‘Genera Plantarum’ cited ‘Linn. Gen. n. 698.’; and Koorders and Valeton (1895) refer to ‘*Durio zibethinus* Linn Syst. 698’. Kurz (1874) also referred to *Durio zibethinus* L. Sp. Pl. 698, however, the tree he was most likely describing was *Cullenia ceylanica*; furthermore, he describes the same species as ‘*D. zibethinus* DC.’ in his ‘Forest Flora of British Burma’ (1877).

As stated previously, the earliest valid publication on the species is that appearing on page 581 of the 13th edition of Linnaeus’s ‘Systema Vegetabilium’ published in 1774, and edited by J.A. Murray. This work has, in fact, often been cited as the first valid publication with a twist. Ridley (1922), for instance, referred to ‘*D. zibethinus* Linn. Syst. Nat. edn. xiii. 581’; and Wyatt-Smith (1953a) states that ‘*D. zibethinus* Murr. [Syst. Nat. Veg.

edn. 13, 581 (1774)]' is the earliest described species. They are both correct. They differ in that Ridley (1922) attributes this work to Linnaeus, while Wyatt-Smith (1953a) attributes the same work to Murray.

As *Durio* is not mentioned in the 12th or earlier editions of 'Systema Naturae' (later 'Systema Vegetabilium'), the only remaining question is to whom new species appearing in the 13th edition of 'Systema Vegetabilium' of 1774 should be attributed, Murray or Linnaeus. Linnaeus himself was solely responsible for these changes, and thus is the correct authority[1].

Formation of the modern concept of Bombacaceae : In early times, there was some confusion between durian and the soursop (*Annona muricata*), both of these species having spiny green fruit. Weinmann (1739) considered the durian to belong to the Castaneae as its fruit was reminiscent of the horse chestnut. Rumphius (1741) was more astute and recognized similarities between the flowers of durian and those of kapok (*Ceiba pentandra*), another Bombacaceous tree.

De Jussieu (1789) placed durian in the Capparideae, largely due to the presence of scales on the underside of the leaves, and the erroneous belief that the ovary is stipitate. König (1804) was the first botanist to examine the flowers of durian in detail. This led him to transfer *Durio* to the Malvaceae.

What is now the family Bombacaceae was originally treated as a tribe (*Bombaceae*) of the Malvaceae (Bentham 1862). This group of trees remained as a tribe of the Malvaceae consisting of three subtribes (including the *Durioneae*) in Baillon's Natural History of Plants and Maxwell T. Master's 1874 monograph. Schumann (1895) created the family Bombacaceae, elevating

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[1] According to what is unquestionably the most thorough source of information on taxonomic literature, "the botanical novelties in this [13th] edition still stem from Linnaeus and must be attributed to him. Murray acted here as editor" (F. Stafleau and R.S. Cowan 1981), Taxonomic Literature. 2nd edition. Volume 3). Yet, Farr *et al.* (1979) in the 'Index Nominum Genericorum', who attempted, after indepth research, to compile a list of valid plant genera, type species and their authorities, cites *D. zibethinus* Murray (Syst. Veg. edn. 13:581. 1774) as the type.

Murray was unquestionably the editor of the 13th edition of 'Systema Vegetabilium'; Murray received a copy of the manuscript for the 13th edition from Linnaeus in 1771, who asked him to find a publisher for it in Germany (H. Goerke 1976), Linnaeus and the Murray family, Taxon **25**(1), 15-19). Although Murray was awarded the status of Editor, his function was only to obtain a publisher for this work. Accordingly, the title page bears the Latin inscription "*Accessionibus et emendationibus novissinus manu perillustris auctoris scriptis*". Thus, the common durian is correctly referred to *Durio zibethinus* L.

the three subtribes of the former Bombaceae (*Adansonieae, Matisieae, Durioneae*) to tribal status. The genus *Durio* belongs within the *Durioneae*. These divisions have been supported by differences in leaf morphology between them. *Adansonieae* have palmately compound leaves; *Matisieae* have simple leaves with palmate venation (termed *Quararibees* by Dumont 1887); and the *Durioneae* is characterized by simple entire penninervate leaves. This system has been more or less followed to the present day, although the durian is occasionally (and erroneously) included within the Sterculiaceae; the Bombacaceae actually share more anatomical similarities with the Malvaceae (especially the genus *Hibiscus*) than they do with the Sterculiaceae.

Wild species of durian : The taxonomy of the common durian is convoluted enough, but the real confusion belongs to the wild species. Several attempts have been made to sort out the species, each in turn has in time been thoroughly reworked. The most recent monograph, and probably not the last, is that of Kostermans (1958b). Korthals (1842) introduced the new genus *Boschia* containing one species, which differed from *Durio* most significantly in having anthers that dehisced by means of pores, whereas *D. zibethinus* has anthers that dehisce by slits. Bentham and Hooker's 'Genera Plantarum' of 1862 listed one species of *Durio*, one species of *Lahia* and 2 species of *Boschia* (all of which are now considered under *Durio*). One hundred years later, Masters (1874b) recognized 7 species of *Durio* as well as *Lahia kutejensis* and four species of *Boschia*.

In 1889, Beccari produced volume three of 'Malesia' which included a monograph of the genus *Durio*. Beccari's monograph was undoubtedly the best and most thorough treatment yet produced containing lengthy descriptions and excellent diagrams. The value of this work was undoubtedly enhanced by his familiarity with field material as well as herbarium specimens. This monograph described 14 species of *Durio*, 4 of *Boschia*, 7 of *Neesia*, 3 of *Coelostegia* and *Cullenia excelsa* Wight. The genus *Lahia* was done away with and the species *Lahia kutejensis* Hassk. became *Durio kutejensis* (Hassk.) Becc., and has remained so until the present.

King (1891) described only 6 species of *Durio* (*D. zibethinus, D. lowianus, D. malaccensis, D. testudinarum, D. wrayii, D. oxleyanus* and *Boschia griffithii*) in his enumeration of the flora of the Malay peninsula. The new species *D. wrayii* King was first described in this work. Ridley (1922) enumerated 9 distinct species of *Durio* and *Boschia griffithii*.

The genus was thoroughly reworked by Bakhuizen Van Den Brink in his 'Revisio Bombacacearum' of 1924. He described 14 species of *Durio* as did Beccari, however, only 9 of these species were the same. Of the several new species enumerated by Beccari, 5 were dropped in Bakhuizen Van Den Brink's work (namely, *D. graveolens* Becc., *D. dulcis* Becc., *D. gratissimus* Becc., *D. affinis* Becc., *D sumatranus* Becc.); additionally, 5 new species were erected (*D. griffithii, D. excelsus, D. mansoni, D. ceylanicus* and *D. lowianus*). Unfortunately, Bakhuizen Van Den Brink used only herbarium specimens for the creation of his monograph and, as stated by Kostermans (1958b), many well defined species were lumped together in this work. Many specimens were also misidentified. Most of the major changes in classification described in this work have now been overturned by several authors. His grouping of the genus *Boschia* into *Durio*, however, still stands.

Corner (1939) offered a tentative scheme to untangle some of the resultant confusion, although most of his suggestions were not taken up in later works. Wyatt-Smith (1953a) unravelled much of the convoluted history surrounding the wild species of *Durio* and set the stage for Kostermans' monograph.

Kostermans' (1958b) book stands as the most recent and useful monograph of the genus. This monograph is a combination of Kostermans and Soegeng-Reksodihardjo's 1958 work on Bornean species and Kostermans' (1958a) work on non-Bornean species. This combined work describes and depicts 27 species of *Durio*. In this work, the genus is divided into two subgenera, *Boschia* and *Eu-Durio*. The subgenus *Boschia*, based on the aforementioned difference in anther dehiscence, contains 6 species while *Eu-Durio* contains the rest.

Post-Kostermans (1958b) treatment : Since the publication of his monograph, Kostermans changed his opinion on the validity of *D. cupreus* Ridl., which he had merged with *D. carinatus* Mast. [*sensu* Kostermans 1958b]. He re-erected it to species status after examining new material (Kostermans 1961). Furthermore, some of the specimens he included 'reluctantly' under *D. graveolens* Becc. in his monograph (formerly considered as *D. conicus* Becc. by Wyatt-Smith) were considered to most likely represent *D. Wyatt-smithii* Kosterm. (a new species erected by Kostermans 1958b). This is further complicated as Kostermans (1961) cites the specimen of Wyatt-Smith's (Kep. 80131) as the one which he has reconsidered. No mention of this specimen is made by Wyatt-Smith (1953a). Furthermore, the delineation of what constitutes *D. graveolens* Becc. in Kostermans (1958b) from which he now wishes to separate this species includes only *D. dulcis* (non Becc.) from Wyatt-Smith (1953a) (listed by Wyatt-Smith as a synonym of *D. graveolens* Becc.), *D. conicus* (non Becc.), and specifically not *D. conicus* Becc. *sensu* Wyatt-Smith (1953a). Although, it appears that further clarification is necessary, I am not convinced that further subjective analysis of herbarium material can add anything more to our understanding.

Soegeng-Reksodihardjo (1965) described a new species, *D. burmanicus*, which is allied to *D. oxleyanus*. This species was erected from an herbarium specimen (lacking fruit) collected in the South of Burma (now Myanmar). To date, no further information on this species has been published.

Kochummen *et al.* (1970) proposed that the species *D. macrolepis* Kosterm. consisted of a mixture of two species, namely, *D. pinangianus* (Becc.) Ridl. and *D. macrophyllus* (King) Ridl. Kostermans (1958b) separated *D. macrolepis* from the other two species based on its production of flowers at the base of the stem (cauliflory) rather than on the branches (ramiflory), which is characteristic of the other two species. Kochummen *et al.* (1970) felt that this difference was not sufficient enough to warrant the erection of a new and separate species. Further, they noted that some of the specimens included under *D. macrolepis* by Kostermans (1958b) consisted of flowers collected from ramiflorous branches (not from cauliflorous inflorescences), or flowers of which the position on the tree was not recorded. Kochummen *et al.* (1970) suggested that most, but not all, specimens of *D. macrolepis* be reassigned to *D. pinangianus* (Becc.) Ridl., the remaining known specimen being reassigned to *D. macrophyllus.*

An incomplete specimen collected from Johore, Malaysia (FRI 8677) has been described, but so far not named (Kochummen 1972). It is known as *Durio* sp. ‘A’. It bears some morphological resemblence to *D. lanceolatus* and *D. kutejensis* (Kochummen 1972).

Kostermans has recently published descriptions of two new species, namely, *D. bukitrayaensis* Kosterm. (Kostermans 1990) which bears tiny fruits; and *D. macrantha* Kosterm. which bears large edible fruits (Kostermans 1992a,b). However, from the published description and pictures (Kostermans 1992a), it is difficult to understand how *D. macrantha* differs from *D. zibethinus.*

Numerous species and varieties of durian have been named over the years, over half of which are no longer recognized. Despite this, several of these ‘defunct’ names continue to be used. This is hardly surprising considering the complexity surrounding the taxonomy. Table 1 attempts to present all the published names of species of *Durio* and their synonyms. The authority(ies) of all published names along with the date of publication have been listed. Where name changes have occurred, details are provided as far as possible. The actual details of the current composition of several species (with respect to particular herbarium specimens) is far more complex than can actually be tabulated. The relevant works for further details should be consulted. The genus *Cullenia* is also included as it has, in part, been previously included within the genus *Durio* and may well be again. As diagrams have, and still do have, a large role to play in the naming and identification of species, a list of sources for figures of plant parts for currently recognized species is presented in Table 2.

Table 1. Published species and synonyms of *Durio*

Boschia acutifolia Mast. (1874b)

  -reassigned to *D. acutifolius* (Mast.) Kosterm. (*sensu* Kostermans 1953)

B. excelsa Korth. (1842)

  -most specimens are now reassigned to *D. excelsus* (Korth.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

  -Note: *B. excelsa* [*sensu* Merrill 1921, 1929] is now *D. grandiflorus* (Mast.) Kosterm. and Soegeng. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

B. grandiflora Mast. (1874b)

  -most specimens reassigned to *D. excelsus* (Korth.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

  -some specimens reassigned to *D. grandiflorus* (Mast.) Kosterm. & Soegeng. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

B. griffithii Mast. (1874a)

  -is now *D. griffithii* (Mast.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

B. mansoni Gamble [Anon. 1908]

  -is now *D. mansoni* (Gamble) Bakh. (*sensu* Kostermans 1958a)

B. oblongifolia Ridl. (1933)

  -reassigned to *D. acutifolius* (Mast). Kosterm. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

Cullenia ceylanica (Gardn.) K. Schum. (Kostermans 1956)

  -includes part of *C. excelsa* Wight. (*sensu* Robyns 1970)

  -includes *D. ceylanicus* Gardn. (*sensu* Robyns 1970)

C. exarillata A. Robyns (1970)

  -includes part of *C. excelsa* Wight (*sensu* Robyns 1970)

C. excelsa Wight (1852)

(Contd....)

Table 1. Contd.

-is a mere synonym of *D. ceylanicus* Gardn. (*sensu* Kostermans 1958b)

-split among *C. ceylanica, C. rosayroana* and *C. exarillata* (*sensu* Robyns 1970)

C. rosayroana Kosterm. (1956)

-includes part of *C. excelsa* Wight. (*sensu* Kostermans 1956)

C. zeylanica (Gardn.) Wight ex K. Schum. (1895)

-transferred to *D. ceylanicus* Gardn. (*sensu* Bakhuizen Van Den Brink 1924a)

Durio acuminatissima [Kostermans and Soegeng-Reksodihardjo 1958]

=*D. acuminatissimus* Merr.

D. acuminatissimus Merr. (1924)

-included in *D. zibethinus* L. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. acutiminatissimus Merr. [Lim 1990]

=*D. acuminatissimus* Merr.

D. acutifolia (Mast.) Kosterm. (1953b)

-now included in *D. acutifolius* (Mast.) Kosterm. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. acutifolius (Mast.) Wyatt-Smith (1953a)

-includes *B. acutifolia* (Mast.) (*sensu* Wyatt-Smith 1953a)

-includes *D. griffithii* (Mast.) Bakh. var. acutifolius (Mast.) Bakh. (*sensu* Wyatt-Smith 1953a)

D. acutifolius (Mast.) Kosterm. & Soegeng. (1958)

-includes *D. acutifolius* (Mast.) Wyatt-Smith

-includes *B. oblongifolia* Ridl.

-includes *D. griffithii* (Mast.) Bakh. var. acutifolius (Mast.) Bakh.

D. affinis Becc. (1889)

-includes *D. malaccensis* Planch. ex Mast. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. beccarianus Kosterm. & Soegeng. (1958)

D. bukitrayaensis Kosterm. (1990)

D. burmanicus Soegeng. (1965)

D. carinatus Mast. (1874b)

-includes *D. cupreus* Ridl. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

(Contd....)

Table 1. Contd.

D. carinatus Mast. var. bintulensis Becc. (1889)

D. ceylanica Gardn. [Wight 1852]

- = *D. ceylanicus* Gardn.

D. ceylanicus Gardn. (1847)

- -includes *D. zibethinus* Moon (*sensu* Gardner 1847)
- -is now *C. ceylanica* (Gardn.) K. Schum. (*sensu* Robyns 1970)

D. conicus Becc. (1889)

- -is now *D. dulcis* Becc. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. crassipes Kosterm. & Soegeng. (1958)

D. cupreus Ridl. (1938)

- -included in *D. carinatus* Mast. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)
- -re-erected to species status (Kostermans 1961)

D. dulcis Becc. (1886)

- -reduced to *D. conicus* Becc. (*sensu* Bakhuizen Van Den Brink 1924a)
- -synonym of *D. graveolens* (*sensu* Wyatt-Smith 1953a)
- -includes *D. oblongus* Mast. (*sensu* Kostermans & Soegeng-Reksodihardjo 1958)
- -includes *D. conicus* Becc. (*sensu* Kostermans & Soegeng-Reksodihardjo 1958)

D. excelsus (Korth.) Bakh. (1924a)

- -includes part of *D. excelsus* (Korth.) Bakh. var. typicus Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)
- -includes *D. griffithii* (Mast.) Bakh. var. heteropyxis (Griff.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)
- -includes most of *B. excelsa* Korth. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. excelsus (Korth.) Bakh. var. typicus Bakh. (1924b)

- -part is now *D. excelsus* (Korth.) Bakh.; other part is *D. griffithii* (Mast.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. excelsus (Korth.) Bakh. var. grandiflorus (Becc.) Bakh. (1924b)

- -transferred to *D. grandiflorus* (Mast.) Kosterm. & Soegeng. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

(Contd....)

Table 1. Contd.

D. falcata [Stadelman 1966]

-name of no taxonomic standing

D. foetida Thunb. (1796)

-name of no taxonomic standing, synonym of *D. zibethinus* L.

D. grandiflorus (Mast.) Kosterm. & Soegeng. (1958)

-includes part of *B. grandiflora* Mast. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

-includes *B. excelsa* Korth. [*sensu* Merrill 1921, 1929] (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

-includes *D. excelsus* (Korth.) Bakh. var. grandiflorus (Becc.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. gratissimus Becc. (1889)

-is now included in *D. oxleyanus* Griff. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. graveolens Becc. (1889)

-reduced to *D. conicus* Becc. (*sensu* Bakhuizen Van Den Brink 1924a)

-includes *D. dulcis* (*sensu* Wyatt-Smith 1953a) [this inclusion not valid under Kostermans and Soegeng-Reksodihardjo 1958]

-re-erected to *D. graveolens* Becc. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. griffithii (Mast.) Bakh. (1924a)

-includes some of *D. griffithii* (Mast.) Bakh. var. heteropyxis (Griff.) Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

-includes some of *D. excelsus* (Korth.) Bakh. var. typicus Bakh. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. griffithii (Mast.) Bakh. var. heteropyxis (Griff.) Bakh. (1924b)

-a synonym of *D. excelsus* (Korth.) Bakh. with the exception of a Sumatra specimen (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. griffithii (Mast.) Bakh. var. acutifolius (Mast.) Bakh. (1924b)

-included under *D. acutifolius* (Mast.) Kosterm. & Soegeng. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. kinabaluensis Kosterm. & Soegeng. (1958)

-includes *D. kutejensis* (Hassk.) Becc. forma kinabaluensis Bakh.

(Contd....)

Table 1. Contd.

D. kutejensis (Hassk.) Becc. (1889)
  - -includes *L. kutejensis* Hassk. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. kutejensis (Hassk.) Becc. forma kinabaluensis Bakh. [Wyatt-Smith 1953a]
  - -is now *D. kinabaluensis* (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. lanceolatus Mast. (1874b)
  - -reduced to *D. singaporensis* Ridl. (*sensu* Wyatt-Smith 1953a)
  - -re-erected to species status (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. lissocarpus Mast. (1874b)
  - -reduced to *D. carinatus* Mast. (*sensu* Bakhuizen Van Den Brink 1924a; Wyatt-Smith 1953a)
  - -re-erected to species status (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. lowianus Scort. ex King (1891)
  - -includes *D. wrayii* King. (*sensu* Kostermans 1958a)
  - -includes *D. zibethinus* L. var. roseiflorus Corner (*sensu* Kostermans 1958a)

D. lowii Hook. [Sutisna and Soeyatman 1985]
  - -name of no taxonomic standing, possibly *D. lowianus* Scort. ex King

D. macrantha Kosterm. (1992a)

D. macrolepis Kosterm. (1958a)
  - -specimens fractured into *D. pinangianus* (Becc.) Ridl. and *D. macrophyllus* (King) Ridl. (*sensu* Kochummen *et al.* 1970)

D. macrophyllus (King) Ridl. (1922)
  - -reduced to *D. oblongus* Mast. (*sensu* Bakhuizen Van Den Brink 1924a)
  - -re-erected and includes *D testudinarum* Becc. var. macrophylla King (*sensu* Kostermans 1958a)

D. malaccensis Planch. ex Mast. (1874a)
  - -includes *D. sumatranus* Becc. (*sensu* Kostermans 1958a)
  - -part has been removed to *D. affinis* Becc. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. mansoni (Gamble) Bakh. (1924b)
  - -includes *B. mansoni* Gamble (*sensu* Kostermans 1958a)

(Contd....)

Table 1. Contd.

D. oblongus Mast. (1874b)

D. oxleyanus Griff. (1845)

- -includes *D. gratissimus* Becc. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)
- -includes *D. griffithii* Planch. ex King. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

D. perakensis King (1891)

- -a name of no taxonomic standing, possibly *D. lowianus* Scort. ex King

D. penangianus [Kochummen and Wyatt-Smith 1979]

- =*D. pinangianus* (Becc.) Ridl.

D. pinangianus (Becc.) Ridl. (1922)

- -includes *D. testudinarum* Becc. var. pinangianus Becc. (*sensu* Kostermans 1958a)
- -includes some of *D. macrolepis* Kosterm. (*sensu* Kochummen *et al.* 1970)

D. purpureus Kosterm. & Soegeng. (1958)

D. singaporansis Ridl. [Lim 1990]

- =*D. singaporenis* Ridl.

D. singaporensis Ridl. (1922)

- -reduced to *D. oblongus* Mast. (*sensu* Bakhuizen Van Den Brink 1924a)
- -re-erected by Wyatt-Smith (1953a) as a possible synonym of *D. sumatranus*
- -retained as *D. singaporensis* Ridl. (*sensu* Kostermans 1958a)

D. singapurensis [Corner 1978]

- =*D. singaporensis* Ridl.

D. spontaneus Bakh. [Van Steenis 1949]

- -is now *D. lowianus* Scort. ex King. (*sensu* Kostermans 1958a)

D. stercoraceus Noronha (1790)

- -synonym of *D. zibethinus* L.

D. sumatranus Becc. (1889)

- -may include *D. singaporensis* Ridl. (*sensu* Wyatt-Smith 1953a)
- -synonym of *D. malaccensis* Planch. ex Mast. (*sensu* Kostermans 1958a)

(Contd....)

Table 1. Contd.

D. testudinarium Becc. [Lim 1990]
    =*D. testudinarum* Becc.
D. testudinarum Becc. (1889)
D. testudinarum Becc. var. pinangianus Becc. (1889)
    -now *D. pinangianus* (Becc.) Ridl. (*sensu* Wyatt-Smith 1953a and Kostermans 1958a)
D. testudinarum Becc. var. macrophylla King (1891)
    -lifted to *D. macrophyllus* (King) Ridl. (*sensu* Wyatt-Smith 1953a and Kostermans 1958a)
D. testudinarum Becc. var. macrophyllus King [Corner 1939]
    =*D. testudinarum* Becc. var. macrophylla King
D. wrayi [Ridley, 1922; Kostermans and Soegeng-Reksodihardjo 1958]
    =*D. wrayii* King
D. wrayii King (1891)
    -reduced to *D. lowianus* Scort. ex King (*sensu* Kostermans 1958a)
D. wyatt-smithii Kosterm. (1958a)
D. zeylanica [Worthington 1959]
    =*D. ceylanicus* Gardn.
D. zibethianus Murr. [Kanehira 1935]
    =*D. zibethinus* L.
D. zibethinus L. (1774)
D. zibethinus L. var. roseiflorus Corner (1939)
    -now *D. lowianus* Scort. ex King (*sensu* Kostermans 1958a)
D. zibethinus Moon (1824)
    -synonym of *D. ceylanicus* Gardn.
D. zibethinus Murr. (1774) improper attribution of authority = *D. zibethinus* L. (1774)
D. sp. “A” [Kochummen 1972]
    -a new, as yet un-named and incompletely known species with similarities to *D. lanceolatus* and *D. kutejensis*
Lahia kutejensis Hassk. (1844)
    -is now *Durio kutejensis* (Hassk.) Becc. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

(Contd....)

Table 1. Contd.

Neesia griffithii Planch. ex King

-is now *D. oxleyanus* Griff. (*sensu* Kostermans and Soegeng-Reksodihardjo 1958)

Currently valid species are in bold; species of dubious, controversial or unknown status are in italics, invalid species are in normal type. Dates in round brackets ( ) after a species name represent the date of publication of the species by the preceding authority. Authors and dates in square brackets [ ] represent publications in which an invalid or unrecognized name was cited either by typographical error or erroneously, or cases where the author of the first published description is not the authority.

Table 2. Sources for figures of currently valid species of *Durio* and close allies

Species	**Fruit**	**Flower**	**Seed**	**Tree**	**Leaf**
Cullenia ceylanica	LN[5]LN[13] BW[15]LN[33*]	LN[5]BW[13]	LN[13]BW[17]	BW[10]	(BW,LN)[13] BW[35]
Cullenia exarillata	LN[25]LN[33*]	LN[25]LN[33*]	LN[25]		LN[25]LN[33*]
Cullenia rosayroana	LN[33*]	LN[33*]			LN[13]LN[33*]
Durio acutifolius	LN[6] LN[15,16]C[26]	LN[4c] N[15,16]	LN[4c] LN[15,16]	BW[15]	LN[6]
Durio affinis	LN[6]LN[15,16]	LN[4]LN[15,16] LN[31*]			LN[4]LN[6] LN[15,16]
Durio beccarianus		LN[15,16]			LN[15,16]
Durio bukitrayaensis	LN[18]	LN[18]			LN[18]
Durio burmanicus		LN[28]			LN[28]
Durio carinatus	LN[4d] LN[15,16]	LN[4d] LN[15,16]	LN[4d]		LN[4d] LN[15,16]
Durio crassipes	LN[15,16]	LN[15,16]			LN[15,16]
Durio dulcis	LN[4,4b] LN[15,16]C[26]	LN[15,16]	LN[4]		LN[4,4b] LN[15,16]

(Contd....)

Table 2. Contd.

Durio excelsus	LN[12*] LN[15,16]C[26]	LN[2*]LN[12*] LN[15,16]	LN[7*]		LN[12*] LN[15,16]
Durio grandiflorus	LN[6]BW[6] LN[15,16]BW[22]	LN[6]LN[15,16]			LN[6]BW[6] LN[15,16] BW[22]
Durio graveolens	C[1]LN[4]LN[6] LN[15,16]	LN[15,16]			LN[4]LN[6] LN[15,16]
Durio griffithii	BW[14]	LN[15,16]		BW[14]	LN[15,16]
Durio kinabaluensis	LN[15,16]	LN[15,16]			LN[15,16]
Durio kutejensis	LN[15,16] LN[23]C[26]	LN[4]LN[15,16] LN[23]BW[27]			LN[4]LN[23]
Durio lanceolatus	LN[4]LN[15,16] C[26]	LN[4]LN[15,16]			LN[4]LN[15,16]
Durio lissocarpus	LN[15,16]				LN[15,16]
Durio lowianus		LN[16]			LN[16]
Durio macrantha	BW[19]	BW[19,20]	BW[19]	BW[19]	BW[19]
Durio macrolepis		LN[16]			LN[16]
Durio macrophyllus	LN[16]	LN[16]			LN[16]
Durio malaccensis	LN[4a]LN[16] LN[24*]	LN[4]BW[8] LN[16]LN[24*]		BW[8]	LN[4,4a]BW[8] LN[16]LN[24*]
Durio mansoni	LN[16,29]	LN[16,29]			LN[16,29]
Durio oblongus	LN[4]LN[15,16]	LN[4]LN[15,16]	LN[4]		LN[4]LN[15,16]
Durio oxleyanus	LN[15,16]C[26]	LN[15,16]	LN[7*]		LN[3*]LN[6] LN[15,16]
Durio pinangianus	LN[16]	LN[16]			LN[16]

(Contd....)

Table 2. Contd.

Durio purpureus		LN[15,16]			LN[15,16]
Durio singaporensis	LN[16]	LN[16]			LN[16]
Durio testudinarum	LN[4]LN[6] LN[15,16]C[26*] LN[31]	LN[4]LN[15,16]	LN[4]LN[15,16]		LN[4]LN[6] LN[15,16]
Durio wyatt-smithii	BW[16]	BW[16]			BW[16]
Durio zibethinus	LN[11] LN[15,16] LN[21]BW[30] LN[31]	LN[2]LN[4] LN[6] LN[9]LN[11] LN[15,16] LN[21]LN[34]	LN[4]	LN[11] BW[30]	LN[4]LN[6] LN[11] LN[15,16] LN[21]
Kostermansia malayana		BW[32]			

[Published diagrams of durian species: BW=black and white photo, C=colour photo, LN=line drawing. Citations with 2 superscripts indicate the same figure appears in two separate publications. An * indicates that additional clarifying information is given in the following list of sources.]

Sources for data presented in Table 2:

[1] Anon. (1986b).

[2] Baillon (1875) *Note: Figure 174 and 175 of this work are labelled *Boschia excelsa* = *D. excelsus* (Korth.) Bakh. *sensu* Kostermans (1958b).

[3] Bakhuizen Van Den Brink (1924a) *Note: According to Kostermans (1958b), Figure D (a flower) of Table 38 labelled *D. oxleyanus* is incorrect. The rest of the figures (including leaves) in the table are accurate.

[4] Beccari (1889) Changes to the classification system of Beccari by Kostermans (1958a) reflected in the above table. (a) Species described as *D. sumatranus* Becc. are now considered to be another specimen of *D. malaccensis* Planch. ex Mast.; (b) *D. conicus* Becc. is now considered to be another specimen of *D. dulcis* Becc.; (c) *Boschia acutifolia* is now considered as *D. acutifolius* (Mast.) Kosterm.; (d) *D. carinatus* Mast. is split into *D. carinatus* Mast. and *D. lissocarpus* Mast. under this scheme Table: 17 Figs. 6-7 of *D. carinatus* are called *D. lissocarpus* Mast., and Table: 17 Figs. 1-5,8-9, 18 Figs. 1-5 remain *D. carinatus.* Mast.

[5] Beddome (1869).

[6] Cockburn (1976).

[7] De Vogel (1980) *Note: Diagrams are of seedlings with attached seeds.

[8] Foxworthy (1927).

[9] Griffith (1854a) Plate 596

[10] Kadambi (1954).

[11] Köing (1804).

[12] Korthals (1839-1842) *Note: What is depicted as *Boschia excelsa* is now interpreted by Kostermans (1958b) as *D. excelsus* (Korth.) Bakh.

[13] Kostermans (1956), [14]Kostermans (1953b), [15]Kostermans (1958a), [16]Kostermans (1958b).

[17] Kostermans (1958c), [18]Kostermans (1990), [19]Kostermans (1992a), [20]Kostermans (1992b).

[21] Lamarck (1823).

[22] Meijer (1969).

[23] Ochse (1927).

[24] Ridley (1922) *Note: Part of the figure representing *D. malaccensis* was copied from Masters (1874b). The copied parts include the anther at the top right, and the two bottom left diagrams (longitudinal section of an ovary, and a spine bearing a peltate scale). According to Kostermans (1958b), of these 3 copied diagrams, only the anther belongs to *D. malaccensis* Planch. ex Mast.

[25] Robyns (1970).

[26] Setiadi (1991) *Note: The photo of *D. testudinarum* is captioned ‘Durian kura-kura’.

[27] Soegeng-Reksodihardjo (1962), [28]Soegeng-Reksodihardjo (1965).

[29] Sprague (1915).

[30] Stanton (1966).

[31] Wettstein (1935) *Note: Figure 3 on page 806, showing the flower of *D. affinis*, is copied from volume III, Table 24 of Beccari’s Malesia of 1889. This diagram was also copied by Kostermans 1958b, appearing as part of Fig. 28.

[32] Whitmore (1990).

[33] Wight (1852) *Note: This figure is titled *Cullenia excelsa* Wight. which, according to Kostermans (1958b), is equivalent to *Durio excelsa* Gardn.=*Cullenia ceylanica* (Gardn.) K.Schum. However, Kostermans (1956) and Raizada (1957) consider Wight’s figures to be drawn from a mixture of specimens of *C. ceylanica* and *C. rosayroana*, most of them being *C. rosayroana* with the exception of the fruit depicted in figures 14-16 which are probably *C. ceylanica.* More recently, Robyns (1970) has described a new species *Cullenia exarillata* A. Robyns. which he claims is what is depicted in Wight’s original figures, the interpretation of Kostermans (1956) and Raizada (1957) being in this regard erroneous.

[34] Winkler (1905).

[35] Worthington (1959).

Keys to the species : As numerous new species have been described in the last 50 years, and major reworking of species have also occurred, keys prior to Kostermans (1958b) are now of little use. An exception to this might be Wyatt-Smith (1953a), whose key to 19 species, based mainly on floral characteristics, is largely in agreement with the classification of Kostermans (1958b). Kostermans (1958b) presents a key in his monograph based largely on floral characteristics. Soegeng-Reksodihardjo (1962) provided keys to six edible species based on floral, fruit or vegetative characteristics.

Kochummen (1972) presents two keys to 10 species of *Durio*, one based on leaf characteristics, and the second on flower and fruit characteristics. Cockburn (1976) has published a key to 12 species based on leaf and fruit characteristics.

Future taxonomic work : Despite all the taxonomic work which exists on the genus *Durio*, it is quite clear that much remains to be clarified. Some of the wild species are known only from very little and incomplete herbarium specimens. For example, *D. crassipes* Kosterm. & Soegeng. is only known from one herbarium specimen, consisting of a few flowers which are missing the epicalyx (Kostermans 1958b). Some species have not been collected in many years and may have already been extinct. An examination of the various treatments of the genus, which have been published, reveals that the major cause of the collapse of old species and the erection of new ones is the subjective decision as to how physically different two herbarium specimens have to be in order to be given different names. Further, monographing of species in the style so far established for them seems unlikely to provide more insight on the matter. It is difficult to imagine how such further taxonomic shuffling can really address the most pressing and meaningful questions that are in need of answers. Future work involving proper cladistical analysis of as many characters as can be obtained from the relevant herbarium (and other) specimens, perhaps coupled with RFLP (restriction fragment length polymorphism) mapping and isozyme analysis would be valuable. Isozymes have already proved useful in distinguishing clones of *D. zibethinus* (Salma 1993). It has also been suggested that the position and morphology of the leaf trichomes may also be of taxonomic value (Salma 1991). Furthermore, chromosome counts might be of use in addressing taxonomic questions surrounding durian. Many of the species of *Durio* are known from living specimens, thus crossing experiments are possible. The structure of many durian flowers lends itself to artificial pollination, and the life span of durian pollen has been demonstrated to be sufficiently long under appropriate conditions to allow such crossing. Some crossing experiments have been conducted and offer the exciting prospect of improved trees, especially with regard to disease resistance.

Morphology

A fair amount of morphological and anatomical information on durians has been published. The majority of this information deals with the structure of the flowers and fruits, but some information is available on the leaves, roots, wood anatomy and seeds. One of the most fascinating developments from the study of the morphology of durian fruits has been E.J.H. Corner's durian theory (Corner 1949). A full examination of this theory is well beyond the scope of this work, as much of it involves species extraneous to the topic, but as this theory is forever linked to the durian fruit, it will be briefly discussed. Additionally, the tree architecture of durian has been analyzed. The anatomy of the wood will be discussed in a later chapter in relation to the use of durian in forestry, as this is the field in which such information is most useful. As chromosome counts have often been used in conjunction with taxonomic and morphological analysis, this information is also included under this section.

Durian theory : In 1949, Corner elaborated his 'Durian Theory' which, among other things, predicted that the ancestral angiospermous fruit was large, spiny and dehiscent, bearing large seeds covered in colourful fleshy arils. This type of fruit is more or less typified by that of the durian tree (*Durio zibethinus* L.). This theory was spurred by his observations of species with strikingly similar fruit morphologies in numerous unrelated angiosperm families. These species are usually very rare, and their fruits atypical of the other more common members of the family. Through a series of arguments, he proposed it was unlikely that this peculiar fruit type had evolved independently numerous times, and more likely that it represents a relic. Several arguments have been raised against this theory, most notably by Parkin (1953) and Van Der Pijl (1952, 1955). The main points of contention are the subjectivity of Corner's observations, and the denial that rarity necessarily represents antiquity. An attempt to refute this theory was published by Datta and Biswas (1969), but their 'argument' was based on an obvious misunderstanding of Corner's theory, and thus provides neither support nor evidence against it. Corner has since expanded upon his theory (Corner 1953, 1954a, 1954b), and it has been given some support by others (Mabberley, 1974a,b; Von Teichman and Van Wyk 1991, 1994). The most objective and perhaps most useful new evidence comes from Von Teichman and Van Wyk (1991) whose use of statistical character associations revealed that 'durian fruit and seed-like' characteristics (i.e., recalcitrance, arils, pachychalazy, etc.) were significantly correlated with the occurrence of other character traits generally regarded as primitive. More recently, Von Teichman and Van Wyk (1994) have elaborated on the idea hinted at by Corner (1949) that recalcitrance (high seed moisture content and a short period of seed viability) is the ancestral state of seeds, orthodoxy (the ability to withstand desiccation) having evolved later under selection pressure. This avenue of investigation suggests that recalcitrant seeds may share morphological and physiological commonalities by descent. This concept may be of substantial importance in the understanding of recalcitrant seeds and definitely opens new lines of enquiry. However, to this date, the validity of Corner's durian theory remains in dispute, and its domain of applicability is yet to be firmly established.

Floral morphology : According to Hawkins (1986), the durian is one of the most beautiful flowering trees. The flowers do have a certain appeal (apart from their smell of sour milk). The common durian is ramiflorous (Fig. 1), and very rarely cauliflorous (Lim 1990), the flowers being borne on older branches in di- or tri-chasial cymes (Davis and Bhattacharya 1974) consisting of 10-25 (Croft 1981), 5-30 (Davis and Bhattacharya 1974) flowers. Species of durian with small fruits (*D. griffithii*) have flowers that are borne in the leaf axils (Corner 1988). In the developing flower bud, the sepaline, petaline, staminal and carpellary primordia develop acropetally and at approximately the same rate (Soepadmo and Eow 1977). The floral bud of *D. zibethinus* is completely enclosed within a bracteole which eventually splits into 2 or 3 sections near maturity.

The flowers are generally pentamerous with a fused calyx usually consisting of five lobes (Fig. 2). Some variation does occur, flowers of clone D88 occasionally have 4 petals, while those of clones D8 and D104 occasionally have 6 (personal observations). Flowers with more or less than 5 petals do not always have corresponding changes in the number of other floral parts. For example, flowers of clone D88 occasionally have 4 petals, but always have 5 staminal phalanges (personal observations). In some species of *Durio*, the sepals separate at anthesis (Kostermans 1958b), however, this is not the case in *D. zibethinus.*

Flowers normally possess five staminal groups (bearing varying numbers of filaments). To quote Van Heel (1966), 'the stamens are generally placed in concave more or less antepetalous phalanges', 'staubblattbnndel' of Winkler (1905). The filaments near the middle of the staminal phalange are longer than those on the edge (Fig. 2d). The filaments vary with respect to the degree with which they are fused with neighbouring filaments. Some filaments are connate just at the base, others are fused along almost their entire length to adjacent filaments, the number of filaments per stamen is positively correlated with floral size (personal observations). The filaments of *D. acutifolius* are apparently exceptional within the genus *Durio* in not being united into staminal phalanges. In some other species, the phalanges themselves are united more or less into a tube. The anthers are unilocular, midfixed, strongly recurved and twisted, and dehisce via a single slit (Croft 1981). According to Davis and Bhattacharya (1974), the anthers are two-celled or occasionally one-celled. An extremely detailed examination of the stamens of several species of *Durio* is presented by Van Heel (1966), and the development of the anther-wall has been described in detail by Soepadmo and Eow (1977).

The single ovary of *D. zibethinus* is superior, and normally 5-loculed. It is not stipitate as claimed in the original Latin description (Linnaeus 1774). The ovules are anatropous (Winton and Winton 1935), bitegmic and crassinucellate. The micropyle is formed by both the inner and outer integuments (Soepadmo and Eow 1977). Embryo sac development is of the *Polygonum* type, and the antipodal cells are ephemeral (Soepadmo and Eow 1977). The stigmatic surface is heavily papillate (Soepadmo and Eow 1977). There are differences in colour and shape of durian stigmas (Ochse 1961; Lye 1980). Some clones (D8, D24, D104) have 5-lobed stigmas, whereas the other clones show no trace of lobes (personal observations). Some stigmas are top shaped (D2, D88, D96) while others are broad and flat (D16, D66). Stigma shape is highly consistent within a clone. Clones D8, D66 and D104 have bright orange stigmas, whereas several clones have yellow stigmas (personal observations).

Figure 1. The common durian is ramiflorous. The flowers/fruits are borne along big branches that are capable of bearing the weight of the mature fruit.

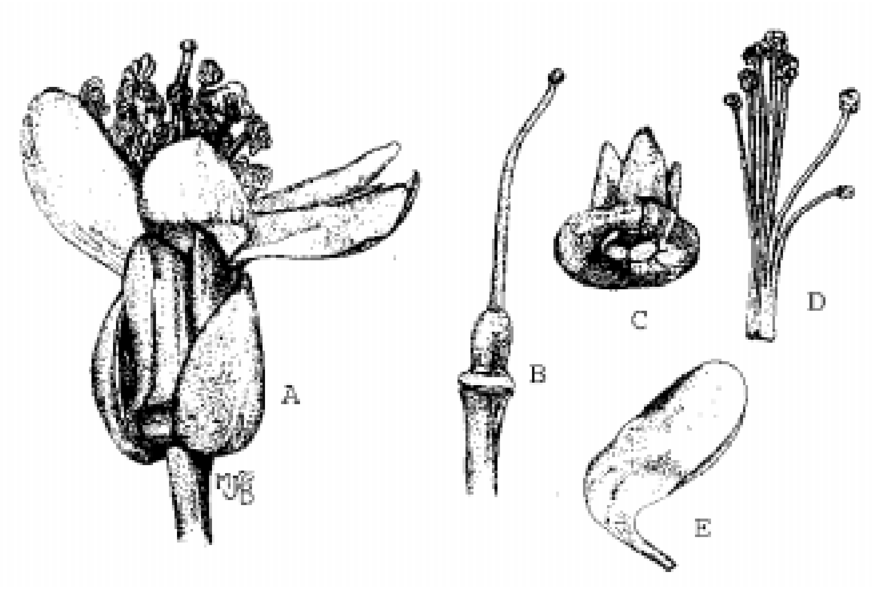

Figure 2. An open flower from D24 durian and its parts. The flower was collected in the evening of anthesis, the male and sterile floral organs abscind during the night. Figures B-E represent parts collected the next morning.

A) A mature flower, projecting from the epicalyx which normally splits into 2 or 3 sections. The sepals are fused to form a short tube with a swollen base. The 5 petals emerge through the calyx tube and reflex, exposing the numerous filaments and the stigma.

B) The gynoecium of the flower. All of the floral parts except the gynoecium have abscinded. The ovary is covered in peltate scales, the long style is often kinked in flowers from this particular clone. The stigma is also visible. The receptacle bears visible scars left from the abscision of the other floral parts.

C) The calyx of the flower. The fused sepals form a swollen base which holds the nectar produced by nectaries inside the calyx.

D) A staminal phalange consisting of 7 filaments. The filaments are connate at the base. Note that the filaments near the centre of the phalange are longer than those at the sides.

E) A petal collected from under the tree the morning after anthesis. Note that the petals are reflexed to expose the numerous filaments enclosed within them.

According to Chin and Phoon (1982), there is heterostyly between the different durian clones, however, based on evidence which is discussed in a later section of this work, this is unlikely the case. Davis and Bhattacharya (1974) note that some buds have the anthers packed in a right-handed twist while others have a left-handed twist. Likewise, the aestivation of the petals is either right- or left-handed[2].

The average nectar volume of a durian flower is 0.36 ml (Gould 1977, 1978), the caloric value of durian nectar has been calculated at 869 calories per ml (Gould 1978).

Pollen morphology : The pollen grains of durian were probably first described by Van Der Pijl (1936) who described them as 90 mm in diameter (wet), and covered in a sticky mass which stains red with Sudan III. The pollen grains are approximately spherical (Soepadmo and Eow 1977). Davis and Bhattacharya (1974) measured pollen grain size from left and right twisted flowers, and discovered that left twisted flowers had slightly, though consistently, larger pollen grains from those of right twisted flowers (see also footnote 1). According to Soepadmo and Eow (1977), the pollen grains of *Durio zibethinus* are approximately 80-150 µm in diameter, 3-4 or rarely 6 porate with a smooth and sticky exine. Davis and Bhattacharya (1974) calculated durian pollen grains to vary from 20 to 80 µm with a mean of approximately 55 µm for dry pollen and 67 µm for water soaked pollen. Erdtman (1972) states that the equatorial diameter is 50-100 µm. A study by Salakpetch *et al.* (1992) included the measurements of the equatorial and polar axes of pollen grains from four Thai cultivars. This study showed that there were slight differences between cultivars, however, the average length of both axes of all cultivars was of the order of 15 µm. I have no explanation for the much smaller dimensions provided by this study compared with those mentioned previously.

Durian pollen is binucleate when shed, and remains viable for approximately 48 hours after shedding if kept at room temperature (Soepadmo and Eow 1977). Erdtman (1972) briefly described the pollen morphology of eight species of *Durio* as 3(-4) colporate, colpoidorate, and usually suboblate with a thin sextine. According to Fuchs (1967), *D. oblongus* and *D. testudinarum* stand out among other species of *Durio* in that their pollen grains are not smooth but bluntly macropositively sculptured. The pollen grains of *Cullenia*

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[2] Davis studied thirteen species of Bombacaceous trees (excluding the genus *Durio*), and found that all bore both left and right handed flowers (Davis 1967), stamen number and pollen size in levo- and dextro-rotary flowers of Bombacaceae. Review of Palaeobotany and Palynology, 3, 133-139. Water soaked pollen grains of *Bombax ceiba* from left handed flowers had significantly bigger pollen grains, while no significant difference in size was found in the other 12 species.

are very similar to those of *Durio* (Fuchs 1967).

The pollen of D. *griffithii* is shed in thread-like chains (Ha *et al*. 1988). According to Soepadmo and Eow (1977), the pollen of *D. zibethinus* is shed singly or in clumps. The pollen of several Thai cultivars of *D. zibethinus* have been reported to be shed in clumps (Salakpetch *et al.* 1992).

Fruit morphology : There is some degree of exaggeration in the available literature as to the maximum size attained by durian fruits. It has been stated that the fruits can reach 30 cm in length, 15 cm in diameter and attain weight of 20 kg (Anon. 1975). The stated physical dimensions are more than reasonable; however, the weight is a gross exaggeration; a durian of the given dimensions and mass would have to have a density greater than that of titanium to weigh 20 kg. This possibility is negated as the specific gravity of durian fruits is known to be less than 1 (Chattavongsin and Siriphanich 1990a,b), i.e., durians float. Perhaps the claim by Everett (1968) that the fruits can weigh up to 100 pounds should remain unmentioned.

Large varieties of durian do exist, and are known as durian kepala gajah[3], and may weigh 4.5-7 kg (Ridley 1902; Chevalier 1934; Grist 1936); the size of an average durian fruit is much less. Pratt and Del Rosario (1913), for example, records the average weight of durians in their study as 2.25 kg. Coronel (1986) cites Mon Thong durians as weighing 3.2 kg. Mohamad Idris (1987) lists the average weights of fruits of several registered Malaysian durian clones, none of which exceeded 3 kg. Lim *et al.* (1992) recorded a fruit of approximately 4 kg as a result of crosses between some Thai cultivars.

Winton and Winton (1935) described 5 distinct pericarp layers as seen in cross-section: (1) an epicarp of thin walled rounded-polygonal cells, and scales; (2) a hypoderm of one or more layers of thin walled round cells; (3) fibre zone of white porous fibres; (4) mesocarp of thin walled parenchyma containing numerous oil drops; and (5) endocarp of thin walled elongated narrow celled parenchyma with occasionally sclerenchymatized walls.

Different cultivars can be distinguished to some extent by variations in fruit morphology. For example, the shape of the spines has been described for several Thai varieties (Hiranpradit *et al.* 1992a). The overall gross morphology of the fruit is useful in grading them for market (Hiranpradit *et al.* 1992). Hiranpradit *et al.* (1987) claim that fruit shape and spine morphology are

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[3] 'Kepala' is Malay for head, while 'gajah' is the Malay term for the Indian Elephant (*Elephas maximus*).

useful for characterizing durians into distinct groups, and both are highly heritable characters.

Durian fruits develop over a period of 3 to 4 months. Despite this long period of development, most of the growth occurs late in development (Fig. 3). The ovary of a durian flower is covered with peltate scales, however, spines begin to appear early in development (Fig. 3). Spineless durians are occasionally encountered. These are produced artificially by scraping the scales off the immature fruits (Mohamad Idris 1987); the bases of the scales normally develop into the spines as the fruits mature. Rodrigo (1968) claims that a naturally spineless variety of durian growing wild in Davao, Phillipines was discovered, and that fruits borne on trees grown from seeds of this fruit at the Bureau of Plant Industry Experiment Station are also spineless. I have found no other mention of these or other naturally spineless durians in the literature other than that of Coronel *et al.* (1983) who briefly mention a spineless variety from Davao.

The shape of durian fruits is affected by the presence of seeds. Locules containing unfertilized ovules tend not to develop, and thus the fruits become uneven in shape. Fruit shape greatly affects marketability and thus an understanding of pollination and its effect on durian fruit development is important for the improvement of durian.

The anatomy of the mature fruit stalk has been described by Chattavongsin and Siriphanich (1987). It consists of an outer periderm surrounding a cortex consisting of parenchyma, tannin containing cells and scleroids. The vascular tissue is contained in the centre of the stalk. Chattavongsin and Siriphanich (1987) showed that the number of cortical sclerids in the stalks of Mon Thong durians increased as the fruits matured. This study provided a useful and non-destructive method of estimating fruit maturity by measuring the stiffness of the stalk with an ‘Effigi’ firmness tester (Chattavongsin and Siriphanich 1990a,b). The mature fruit is a loculicidally dehiscent capsule (Ketsa and Pangkool 1994).

Fruit teratology : The first published description of durian teratology was in the ‘Herbarium Amboinense’ of Rumphius, in which the rare occurrence of a small durian fruit within a locule of a durian fruit was described. This occurrence was further elaborated by Joger (1814). Penzig (1921) briefly described such a fruit, and Ochse (1925-1926) provided a photograph of a specimen with a teratology similar to that described by Rumphius, which he termed ‘doerian si bakoel’. This specimen was further described by Costerus and Smith (1932). Venema (1937) provided a description and a figure of a new specimen with this teratology collected in 1933. He described it as ‘perhaps a case of median prolification with a tendency to apocarpy.'

Ridley (1902) also gave an account of a variety of durian in which an entire fruit actually developed within the ovary of a durian, 'I have met with a curious variety in which the fruit which was very large had a hole in the top and inside was another small durian complete with the spiny husk replacing the placenta of the fruit.' Ridley (1922) described 'a very small fruited variety with only one carpel and one seed'.

Rao and Singh (1964) reported that occasionally the floral meristem continued to be active after formation of all the regular floral parts resulting in the production of stamens and carpels within the ovary on the central axis of the fruit. The anthers were found to contain pollen, but none of the carpels contained mature ovules. No petals or sepals were seen to be produced. The authors noted that these anomalous structures do not take the place of previous structures, but are superfluous in nature.

A brief description of the flowers, and some scanning electron micrographs of some floral parts of *Durio zibethinus* is given by Chin and Phoon (1982), although no evidence of stamens or carpels was found within the ovaries of their specimens.

'A fruit of which the margins of the carpels with their warts and hunches at the inner-side interlock like a cog-wheel' was described by Costerus and Smith (1932).

Other teratologies : Apart from fruits occurring within fruits, petaloid stamens have also been described in durian (Winkler 1905). Soepadmo and Eow (1977) related that they had twice observed the formation of binucellate ovules. These ovules both shared a common outer integument, but each had its own inner integument.

Ovule and seed morphology and development : Inside each developing locule of a durian ovary, two alternate rows of 5-7 ovular primordia develop on the central placental column (Soepadmo and Eow 1977). The development of these primordia into ovules is described and depicted in detail by Soepadmo and Eow (1977). They also described megasporogenesis and embryosac development in detail. The initial stages of embryogenesis of *D. griffithii* have been described by Ha *et al.* (1988).

The ovules of durian are bitegmic. Although the ovule primordia of both integuments develop simultaneously, the outer integument grows faster, and overtops the inner integument and micropyle is formed by both integuments

(Soepadmo and Eow 1977).

The aril develops from the funiculus/funicular end of the ovule (Soegeng-Reksodihardjo 1962; Soepadmo and Eow 1977). In *D. zibethinus* and the majority of wild species, the aril eventually completely surrounds the seed; *D. griffithii, D. oblongus* and *D. malaccensis* have incomplete arils, and *D. singaporensis* has no aril (Kostermans 1958b).

The inner integument is eventually crushed by the developing embryo and does not persist, the cells of the outer integument develop considerably (Soepadmo and Eow 1977). The endosperm of the seed does not persist until maturity.

The major storage reserves of durian seeds are starch and protein. No lipid bodies are present in the storage parenchyma cells of mature durian seeds (Brown 1995b).

The storage protein present in mature durian seeds is unrelated to the 7S and 11S globulins common to many seeds (Charbonneau *et al.* 1991; Brown 1995b). This storage protein exists in two ungenically related forms of slightly differing electrophoretic mobility; these proteins have been termed ‘zibethinins’ (Brown 1995b).

The development of cotyledon storage parenchyma cells and the deposition of storage reserves were studied by Brown (1995b). It was shown that some of the storage protein and starch was mobilized prior to fruit dehiscence. Furthermore, the deposition of storage proteins within the vacuoles of the storage parenchyma cells during development does not seem to involve the golgi apparatus as is typical of many dicotyledonous seeds, rather the protein appears to be deposited in large swellings of the endoplasmic reticulum which presumably fuse with the vacuoles (Brown 1995b).

Some measurements of gibberellins in the seeds of developing durians have been published (Mamat and Wahab 1990, 1992).

Leaves : Durian leaves are oval-oblong in shape with an acuminate tip. The leaves of *D. zibethinus* are hypostomatic (Shanmukha Rao and Ramayya 1981). The stipules of durian leaves are sub-falcate and deciduous (Davis and Bhattacharya 1974). Durian leaves have several rather noteworthy characteristics. Rumphius (1741) noted that durian leaves have distinctly swollen petiole bases, the anatomy of which has been investigated by Funke (1931). The vascular system of durian petioles is very complex (Solereder 1908).

Clear spots occur on the upper and lower surface of durian leaves. Bottle shaped mucilaginous cells in the upper and lower epidermis of durian leaves are responsible for this phenomenon (Radlkofer 1886, 1890; Solereder, 1908). Only the narrow neck of these cells lies in the epidermal layer, the bulbous inner portion lies in the hypodermis (Radlkofer 1886). Radlkofer (1886) reported similarly constructed clear spots in the leaves of *Boschia* (now *Durio*).

Lamarck (1786) stated that the bottoms of the leaves and young stems are covered by scales similar to those of *Capparis*. This, among other things, led him to ally *Durio* with the *Capparaceae*. Similar parallels were echoed by Radlkofer (1884) because of similarities in flower construction, scales, and leaf folding between *Durio* and *Capparis*. A brief description of the peltate scales ‘schildharre’ of durian was first given by Bachmann (1886). Schumann (1895) described peltate scales ‘schuppe’ in *Durio*, and stellate hairs in *Adansonia*. He reported that both forms could be found in the tribe Matisieae. Some typical Malvaceous and Bombacaceous hairs are described and depicted by Solereder (1908). Salma (1991) recorded five different types of trichome morphology on the leaves of *Durio*, which can be useful in the identification of species; unfortunately, no key was given. The adaxial (upper) surface of durian leaves are smooth and apparently hairless.

Until recently, the only published description of the morphology of young *Durio* and *Neesia* leaves was that of Burger Hzn (1972), who described them both as conduplicate-induplicate; indicating that not only are the two halves of the lamina folded together lengthwise (conduplicate), but that it is the adaxial surfaces which lie against each other (induplicate). Whatley (1992) noted that the young durian leaves (20-35 mm) used in her study of plastid development were folded along the midrib. More recently, Brown (1994) showed that the leaves of *Durio* and *Neesia* share this characteristic folding. These leaves remain folded for an extended period of time, while the leaflets of other genera unfold relatively early in development. More noteworthy is the discovery that, when immature, the outer edges of the adaxial surfaces of the leaves of *Durio* and *Neesia* are rimmed with stellate hairs. These hairs differ from the stellate hairs and peltate scales of the abaxial surface in that their arms are much longer. Close examination of the adaxial leaf margin of immature folded leaves shows that the hairs intertwine to hold the two edges of the leaf together in a manner similar to that of a Velcro® fastener. Examination of adaxial leaf margins of mature leaves of *Durio zibethinus* failed to reveal the presence of these hairs, indicating that they are lost after unfolding. This mechanism appears to be a modification on an already extant theme, the leaflets of several compound-leaved Bombacaceous species examined were conduplicate-induplicately folded, but were not held together by hairs (Brown 1994). The two halves of the lamina probably separate from each other by differential growth between the upper and lower leaf surfaces.

Although one would be tempted to speculate that the covering of the abaxial surfaces of the leaves with various assorted trichomes would protect the young leaves from herbivorous insects, especially since the hairless adaxis is hidden by the induplicate-conduplicate folding, Gadug and Hussein (1987) noted that the durian carsidarid makes slits beneath scales on the underside of durian leaves.

The anatomy of leaves of *Kostermansia malayana* Soegeng has been described (Baas 1972). The most striking feature of the leaves of this species is the circular arrangement of stomata around the base of scales on the undersides of the leaves.

A very brief account of the shoot apices of several Bombacaceae including *Durio* is given by Johnson (1961). Tunica corpus zonation is apparently less pronounced in *Durio* than in other non-Durioneae Bombacaceous species.

Whatley (1992) examined plastid development during leaf development of durian and several other woody perennial tropical species. Mesophyll cells of very young durian leaves contain chloroplasts with well developed grana. Thyalkoids become more extensive and more deeply stacked as the leaves develop. The plastids of fully expanded leaves often contain starch granules. Membrane bound bodies occur in the plastids of epidermal cells.

Ashton (1978) recorded the moisture content of fresh leaves of *D. griffithii* as 63%.

Roots : Differences in root development between marcotted, inarched and seed grown trees have been noted (Polprasid 1961a). Original anchor roots were observed only in trees grown from seed or produced by inarching, but not found in trees produced by marcots. Further, the roots of marcotted trees, although well distributed, did not extend as deeply into the soil as those of the other two types (Polprasid 1961a).

D. carinatus Mast., which is endemic to marshes of Malaya, Borneo and Sumatra, forms ‘knees’ or breathing roots. These roots emerge up to 30 cm from the water and are up to 10 cm in diameter (Thorenaar 1927). Thorenaar (1927) notes that the ‘knees’ are looped, but the loop does not become fused as occurs in some other marsh tree species. The bark of *D. carinatus* is distinctively red with large pale lenticels (Kostermans 1958b).

Masri (1990) developed a method to quantify the root distribution pattern of durian trees using root length density (RLD). A study of the root distribution of durian trees (clone D24) was carried out on trees growing in different soils types (Masri 1991). Results of this study demonstrated that the RLD of budded D24 durian varies with environment and orchard management techniques. Generally, 72-87% of the RLD is found in the top 45 cm of the soil. Furthermore, 85% of the RLD was contained within the canopy radius of the tree. These results may be of use in developing ideal fertilizing strategies for durian. It has been reported that durian roots may form mycorrhizal associations (Nanthachai 1994).

Tree architecture : Durian trees are large forest trees, which can reach heights of 37 m (Foxworthy 1927), the first branch can be as much as 18-21 m off the ground (Foxworthy 1927). The trunks of most species are normally buttressed in mature specimens. Out of over 300 trees measured, an average diameter of 56 cm and a maximum diameter of 107 cm was recorded (Foxworthy 1927). Larger specimens of *Durio* often become buttressed (Soegeng-Reksodihardjo 1962). Many Bombacaceous trees are classified as having the architectural model of Massart. *D. zibethinus* has been assigned to the model of Roux (Hallé *et al.* 1978), as has *D. griffithii* (Ashton 1978). The model of Roux is characterized by having a monopodial orthotropic trunk and plagiotropic lateral branches. Roux’s model differs from that of Massart largely due to diffuse growth rather than rhythmic growth. Detailed description of the architecture of *D. zibethinus* with diagrams is presented by Buisson (1986). The orthotropic axis of durian seedlings is fast growing, producing numerous strongly plagiotropic laterals; some orthotropic laterals are also produced which eventually compete with the main axis (Subhadrabandhu *et al.* 1991).

An article by Gültekin *et al.* (1983) provides a dendrological description of what is claimed to be a specimen of *Durio kutejensis* Becc. found growing in the Cukurova region of Turkey. From the authors description of the tree, and an examination of the accompanying plates, the tree is most certainly not *D. kutejensis*, in fact, it does not belong to the genus *Durio*. The tree is most likely a specimen of the Bombacaceous genus *Chorisia* or *Ceiba*, at any rate a member of the tribe *Adansonieae* and not the *Durioneae*.

Chromosome number : Members of the Bombacaceae are characterized by high chromosome numbers (Baker and Baker 1968) with 2n=72 being very common (Baum and Oginuma 1994). It is also characteristic for the nucleolus to persist throughout the process of mitosis (Baker and Baker 1968). Durian stands out as an exception in having a diploid number of 2n=56 (Mangenot and Mangenot 1958, 1962). Datta and Biswas (1969) reported a diploid number of 2n=28 for durian. The authors attribute this difference to the sample of Mangenot and Mangenot (1958) being tetraploid. As neither groups of authors mentions the clone (if any) from which sample material was obtained, it may be that different durian clones have different levels of ploidy. To the best of my knowledge, this has never been investigated, however, it is certainly worthy of further investigation. Soepadmo (1979) reported a chromosome number of 56 in *D. zibethinus* and 60 in *D. griffithii. Cullenia excelsa* Wight [=*Durio ceylanicus* Gardn.] has a chromosome count of n=28 (Pushparajan *et al.* 1986), thus there may be variation in chromosome numbers between the species. This question never appears to have been directly addressed, but could possibly be of value in the classification of the wild species of *Durio*.

Differences in chromosome number are but one of several characteristics that distinguish the *Durioneae* from the other Bombacaceous tribes. Chromosome counts of durian are lower than those of Bombacaceous species from other tribes and closer to those found in the related Sterculiaceae, Tiliaceae and Malvaceae (Baum and Oginuma 1994), suggesting a primitive stature of the *Durioneae* within the Bombacaceae, at least in this regard.

Edibility, Composition and Uses of the Fruit

The greatest economic use of the durian is as a source of fruit, although it is also used as a timber tree. The most frequently eaten part of the durian is the fleshy aril which surrounds each seed. The aril is a fleshy outgrowth of the funicular end of the seed coat (Soepadmo and Eow 1977). The aril of *D. zibethinus* is commonly white, cream coloured or yellowish (Soegeng-Reksodihardjo 1962), or even orange (Barrett 1928). Some species have bright red arils (*D. acutifolius, D. excelsus, D. carinatus, D. graveolens*); the arils of *D. griffithii* are orange to red and those of *D. pinangianus* are pinkish (Kostermans 1958b). A great variety of studies have provided information on various chemical constituents of the fruit, from components of nutritional value to those involved in its very characteristic smell and odour.

Edibility : Of all the known species of durian, the six commonly listed as producing edible fruit are *D. dulcis, D. grandiflorus, D. graveolens, D. kutejensis, D. oxleyanus* and *D. zibethinus* (Soegeng-Reksodihardjo 1962). Several other lesser known species also bear edible fruit, such as *D. testudinarum* and *D. lowianus* (Kostermans 1958b; Ogata 1978). Fruits of the newly discovered *D. macrantha* are also edible (Anon. 1992; Kostermans 1992a,b). In addition to these species, the fruits of *D. excelsus* (Korth.) Bakh. and *D. pinangianus*

(Becc.) Ridl. may be edible (Kunkal 1984), as are the seeds of *D. carinatus* Mast., the arils of which are inedible. Kostermans (1958b) mentions that the bright red arils of *D. excelsus* (Korth.) Bakh. and the pink arils of *D. pinangianus* are tasteless, and the yellow arils of *D. lanceolatus* are almost tasteless. The fruits of *D. wyatt-smithii* Kosterm. have been incompletely described. It is possible that they are also edible as this species is very closely allied with *D. zibethinus*. Beccari (1889, 1921) described his discovery of a single tree of what he termed *D. carinatus* var. *bintulensis* Becc., which had edible fruit (*D. carinatus* itself has inedible fruit) (Endert 1927a). Kostermans has apparently made no comment on the nature or affinity of this specimen and, according to Soegeng-Reksodihardjo (1962) since Beccari's description, no tree has ever been found. It is possible that other recognized species have edible fruit as the fruit is completely unknown, or has never been described for *D. burmanicus, D. crassipes, D. kinabaluensis, D. macrolepis* and *D. purpureus.* Additionally, the mature fruit has never been collected or described for several other species.

The amount of mass that the aril contributes to the entire fruit (i.e., the amount of edible portion of a durian fruit) varies greatly with the clone or variety of fruit. Some recorded values are 30% (Adriano 1925), 19% (Abdullah and Ragab 1970), 29% (Joachim and Pandittesekere 1943), 30% (Pratt and Del Rosario 1913) and 14.5% (Intengan *et al.* 1955).

Numerous authors record that the seeds of *D. zibethinus* are also eaten after roasting (Parsons 1932b; Ochse and Bakhuizen Van Den Brink 1977; Quisumbing 1978), or boiling (Ochse and Bakhuizen Van Den Brink 1977; Quisumbing 1978; Ridley 1902). Uphof (1968) and Usher (1974) state that the almost tasteless seeds of *D. carinatus* are also eaten. According to Ochse and Bakhuizen Van Den Brink (1977), the petals of durian are occasionally consumed. Morton (1987), in a short review on the durian, states that the young leaves and shoots are sometimes eaten as greens, however, there is no original report confirming this information.

Apart from being eaten fresh when ripe, the aril is also traditionally mixed with coconut juice, sugar, rice flour and eggs to make a cake like concoction (dodol) (for recipes, see Soegeng-Reksodihardjo 1962; Coronel *et al.,* 1983; Anon. 1986b). Durian cake is now a popular contemporary commercial product (Paweenakarn *et al.* 1992). Nutritional information for durian cake has also been published (Leung *et al.* 1972; Ismail and Seow 1982; Paweenakarn *et al.,* 1992; Seow 1994). Several other commercial durian products are produced including candy and jam. The author has also encountered durian filled swiss rolls and donuts. At the present time, durians are not specifically grown for the production of processed products (Maneepun *et al.* 1994), most commercial durian products are likely produced using lower grade, damaged or surplus fruits. Unripe arils are apparently eaten after roasting by the Bataks of Sumatra (Ochse and Bakhuizen Van Den Brink 1977). Unripe arils are also recorded as being used as an ingredient in soup (Ochse 1961). The ripe arils can be prepared by fermenting them inside bamboo-joints, or earthenware vessels usually for 3 to 4 days, but in some locations up to 2 weeks (Ochse and Bakhuizen Van Den Brink 1977). The bamboo joints are either buried during this time, or suspended over a source of smoke. The following comment from Burkill (1966) would seem to adequately summarize the previous recipe: 'Apologists say that the fruit should be eaten before the garlic flavour is at all apparent. It must be added that to the depraved taste of the Besisi fermented durian pulp, obtained by burying the aril in a time of glut, appeals'. Wallace (1856, 1869) stated that durians were sometimes preserved with salt in jars or bamboo joints by the Dyaks of Borneo. In the Moluccas, fish is sometimes flavoured by smoking it above empty durian husks (Ochse and Bakhuizen Van Den Brink 1977).

According to Rambo (1988), the fruits of durian are probably the second most important source of carbohydrates for the Semang (aboriginal group from central peninsular Malaysia). Favre (1848), in describing the native Jakun, relates the following: 'For six weeks or two months, they eat nothing but durians. When the season is over, the place is abandoned until the next year.' Logan (1847) stated that the Binua of Johore actually travelled for up to two days to favourable locations for durians, at which sites they erect temporary huts, not returning to their homes for several weeks, until the last durian was eaten.

Nutritive constituents : Numerous studies have reported on the nutritive constituents of durian (Table 3). A comparison of many of the individual estimates for a particular constituent will reveal a fair amount of variation. This is in part due to the different and continually improving methods of analysis employed. However, a large part of this variation is likely due to variations between different durian fruits themselves. This is evidenced by several studies in which more than one variety of durian have been analyzed by the same method.

Table 3. Some nutritive constituents of durian fruits

Constitutent	**Fresh ripe arils of *D. zibethinus***	**Fresh arils of *D. oxleyanus***
Total ash (% of fresh weight)	1.24[2]; (1.2,1.2,1.5)[3*]; 1.2[6]; 1.11[15]; 0.8[16]; 1.24[17]; 0.8[18], 1.04[23]	3% of DW[26]
Total solids	44.50[2]	
Fibre (% of fresh weight)	(1.7,1.7,0.9)[3*]; (4.40,3.35,3.47)[4*]; 1.7[15]; 1.4[16]; 1.9[18]; 0.9[23]; 1.87[10]	5.9% of DW[26]
Moisture (% of fresh weight)	(62.8, 56.3,66.6)[3*]; (64.1,58.3,57.4)[4*]; 58.0[5]; 65[6]; 66.0[7]; 54.9[10]; 68.7[11]; 62.9[15]; 66.8[16]; 55.5[17]; 59.9[18]; 68.0[20*]; 64.2[23]; 60.6[27]	30%[26]
Protein (% of fresh weight)	2.31[2]; (2.6,3.2,0.9)[3*]; (2.33,2.58.2.81)[4*]; 2.8[5]; 2.6[6]; 2.5[7]; 2.36%[11]; 2.5[15]; 2.5[16]; 2.31[17]; 2.0[18]; 2.7[23]; 2.6[27]	7.7% of DW[26]
Nitrogen	0.211%[10]	
Carbohydrates (total) (% of fresh weight)	(29.4,34.7,23.9)[3*]; (21.33,29.32,27.81)[4*]; 34.1[5]; 27.8[6]; 25.01[11]; 30.4[15]; 28.3[16]; 36.1[18]; 28.2[23]	65% of DW[26]
Starch (% of fresh weight)	11.1[17]; 4.0[20*]	
Sugar total (% of fresh weight)	13.55[17]; (10.02, 11.14, 13.38)[19*] (11.1, 13.4)[22*]; 11.0[20*]	7.7% of FW[26]
Reducing sugars	4.79%[2]; 2.7%[11]	
Sucrose (% of fresh weight)	8.76[2]; (12.6, 19.8, 19.4)[4*]; 5.8[11]; 9.16, 10.22, 12.70[19*]; 10.2, 12.7[22*]	
Glucose	0.30, 0.51, 0.48%[19*]; 0.5,0.5%[22*]	
Fructose	(0.55, 0.41, 0.20%)[19*]; 0.4,0.2%[22*]	

(Contd....)

Table 3. Contd.

Lipid (% of fresh weight)	(2.3,2.9,4.2)[3*]; (6.29, 5.38, 7.34)[4*]; 3.9[5]; 3.2[6]; 5.00[7]; (5.1,5.2,3.8,4.2)[8*] (0.71, 0.91)[10*]; 2.10[11]; 3.1[15]; 1.6[16]; 1.2[18]; 3.0[23]	19.0% of DW[26]
Caloric value	(149, 178, 145 kcal/100g)[3*] (151.2, 176.0, 188.5 kcal/100g)[4*] 183 cal/100g[5] 128.4[11] 144 cal/100g[15] 124 cal/100g[16] 147.0 cal/100g[18] 154 cal/100g[23]	
Beta carotene	(710, 600.5, 1398.3 IU/100g)[4*]	
Vitamin A (IU per 100 g) unless otherwise noted	(-,-,1025)[3*]; (-,-,30.0)[4*]; 20[5]; trace[12]; 30[15]; 10μg/100g[16]; trace[18]; trace[23]; 3.8mg/g[24*]	
Vitamin B_1 (thiamine) (mg/100g) unless otherwise noted	(0.52, 0.67, 0.47)[3*]; (0.24, 0.36, 0.39)[4*]; 0.366[10]; 46 IU/100g[14]; 0.24[15]; 0.27[16]; 0.32[18]	
Vitamin B_2 riboflavin (mg/100g)	(0.49,0.53,0.17)[3*]; (0.07, 0.13, 0.14)[4*]; 0.172[10]; 0.20[15]; 0.29[16]; 0.28[18]	
Niacin (mg/100g)	(1.17, 1,17, 1.37)[4*]; 1.13[10]; 0.7[15]; 1.21[6]; 1.1[18]	
Vitamin C (mg/100g)	(32.5 ± 5.4)[1]; (32,43,58)[3*] (31.0, 43.3, 41.3)[4*]; 50.00[10]; 25[11]; 23.4[13]; 24[15]; 37[16]; 44.0[18]; 22.9[20*] 107[21*]	2.08 mg/100ml[26]
Vitamin E (mg/100g)	(1.50 ± 0.26)[9]	
Minerals	1.2%[5]	
Calcium (mg/100g)	(5.6, 4.5, 5.9)[3*]; (5.35,4.64,5.10)[4*]; 10[5]; 12.14[10]; 41.5[11]; 9[15]; 20[16]; 18[18]; 40[23]	0.03 % of DW[26]

(Contd....)

Table 3. Contd.

Phosphorous (mg/100g)	(27.7,28.3,19.6)[3*]; (42.0, 36.3, 36.6)[4*]; 50[5]; 65.39[10]; 40.0[11]; 44[15]; 63[16]; 56.0[18]; 44[23]	0.13% of DW[26]
Magnesium (mg/100g)	33[16]; 330[23]	0.08 µg/g[26]
Iron (mg/100g)	(1.0,1.1,0.8)[3*]; (0.80, 0.38, 0.55)[4*]; 1.0[5]; 1.13[10]; 0.9[15]; 0.9[16]; 1.1[18]; 1.9[23]; 1.1 mg/g[25]	17 µg/g[26]
Cobalt	0.4 mg/100g[16]; 0.03mg/g[25]	
Chlorine	4 mg/100g[23]	
Sodium (mg/100g)	(0.57, 0.59, 0.67)[4*]; 1[16]; 40[23]	
Potassium (mg/100g)	474.6, 431.3, 488.1[4*]; 601[16]	1.59% of DW[26]
K_2O	70 mg/100g[23*]	
SO_4	180 mg/100g[23]	
Arsenic	(0.0007, 0.0004, 0.0002 mg/100g)[4*]	
Copper	2.2 g/100g[23]; 1.0 mg/g[25]	21 mg/g[26]
Manganese	7.2 g/100g[23]; 0.81 mg/g[25]	12 mg/g[26]
Iodine	2.8 g/100g[23]	
Cadmium	<0.01 mg/g[25]	
Chromium	<0.05 mg/g[25]	
Nickel	<0.02 mg/g[25]	
Lead	<0.03 mg/g[25]	
Zinc	1.4 mg/g[25]	17 mg/g[26]
Mercury	<0.01 mg/g[24]	

(Contd....)

Table 3. Contd.

pH	7.0 ± 0.04[1]; (6.77, 6.66, 6.60)[19*]; 6.66, 6.00[22*]; 6.6[20*]
Acidity (as citric)	0.19[2]
Sugar: acid ratio	112.5[20*]
Acidity (others)	(0.09 ± 0.02 g/100g)[1]; 52.3 cc N/10 per 100 g[11]; 0.1%[20*]; 0.6, 0.8 meq/100g[22*]

Sources for data presented in Table 3:

[1] Abdullah and Ragab (1970).

[2] Adriano (1925) [Note: Data originally from Pratt and Del Rosario 1913].

[3] Anon. (1973) *Note: This original Thai article has several entries for durian, data for only three cultivars Kradum Thong, Kan Yao and Chanee are reprinted in Woller and Idsavas 1981. Only these three respectively are presented in this table.

[4] Anon. (1989b) *Note: Data on three cultivars Chanee, Mon Thong=Golden Pillow, and Ocean Petal are given respectively. Data is reprinted in Maranet (1991).

[5] Aykroyd (1963).

[6] Bauchau (1972).

[7] Berry (1980b).

[8] Berry (1980c) *Note: Data on four clones is given-D24, D2, D66, D8 respectively.

[9] Candlish (1983).

[10] Intengan *et al.* (1955) *Note: Two values for lipid are given fat and fat ash respectively.

[11] Joachim and Pandittesekere (1943).

[12] Leong (1939a), [13] Leong (1939b), [14] Leong (1940).

[15] Leung et al. (1952).

[16] Leung et al. (1972).

[17] Manas Y Cruz et al. (1939).

[18] Martin (1980) [Note: Data originally from Abdon *et al.* 1980].

[19] Niyomporn *et al.* (1984) *Note: Data on three cultivars Kan Yao, Chanee and Ruong are given respectively.

[20] Pauziah *et al.* (1992) *Note: All values are from analysis of fresh fallen mature fruits of clone D24.

[21] Phang (1976) *Note: Authors state that their result is likely artificially high.

[22] Preungvate (1982) *Note: Data on two varieties Chanee and Ruong respectively are given.

[23] Rosedale (1935) [Note: Data is reprinted in Willimot 1949.] *Note: The estimate of potassium content based on amount of K_2O is likely a gross underestimate.

[24] Speek *et al.* (1988) *Note 3.8 mg/g total carotenoid determined by spectrophotometry was reported with 1.9 mg/g as b-carotene as determined by reverse phase HPLC.

[25] Wong and Koh (1982).

[26] Wong (1992).

[27] Zanariah and Noor Rehan (1987).

The edible aril of the common durian (*D. zibethinus*) is a good source of vitamin C (Table 3), which is of the order of 33 mg per 100 g of aril (Abdullah and Ragab 1970). This is roughly equivalent to the vitamin C content of many citrus fruits. Phang (1976) estimated that durian arils contain 100 mg of vitamin C per 100 g of aril, however, he also warned that this estimate was likely inflated due to interference from mercaptans, naturally present in the aril, with his assay. This is likely a problem associated with all published estimates of the vitamin C content of durians, thus all published values are likely overestimates. Rosedale (1935) used a Guineapig bioassay to estimate the vitamin C content of durian and various other foodstuffs. He assigned an antiascorbic value to durian of 10 grams (the amount of durian necessary to alleviate the symptoms of scurvy) which was approximately only one third that of citrus fruits. This result supports the suggestion that published vitamin C contents for durian are overestimations.

The average mature fruit weighs in excess of a kilogram (Abdullah and Ragab 1970), yet the edible arils generally make up less than one third of the mass, and the seeds only about 15% (Abdullah and Ragab 1970). The aril contains about 33% carbohydrates on a fresh weight basis (Table 3), of which about one third is probably starch. The carbohydrate of durian apparently consists of mannans (Martin 1980), and an erythrodextrin, which gives a clear red colour upon reaction with iodine (Pratt and Del Rosario 1913). Two relatively old studies provided estimates of the reducing sugar content of durian arils (Table 3). These estimates (4.79 and 2.7%) grossly exceed the amounts of the two major reducing sugars (glucose and fructose, together totalling only 1% of the fresh weight at most) reported in more recent studies. These estimates of reducing sugars were in both cases produced by an unspecified copper reduction assay which strictly speaking measures total reducing substances present, not just sugars. In the case of durian, this would include mercaptans and ascorbic acid (vitamin C) which are known to be present in substantial quantities within the mature fruit. Thus, the published values for reducing sugars are large overestimates. Measurements of percentage of fructose, glucose and sucrose from ripe durian fruits, obtained by high-performance liquid chromatography (HPLC), have recently been published (Freeman and Worthington 1989).

Fresh durian arils contain 2-2.5% protein (Table 3). The total and essential amino acid composition of durian arils has also been investigated (Zanariah and Noor Rehan 1987) on a ‘per gram fresh weight’ basis. The data show that durian is a better source of all the essential amino acids than dates, peaches, oranges, mangoes, cempadak or papaya (Table 4). However, it should be remembered that durian has a much higher percentage of total protein than all these fruits.

Table 4. Amino acid composition of durian fruits

Amino acid composition (mg/100g FW)		Essential amino acids (g/16g N)	
Isoleucine	85.8	Lysine	4.8
Leucine	143	Histidine	2.0
Lysine	124.8	Arginine	2.1
Methionine	44.2	Aspartic acid	9.3
Histidine	52	Threonine	2.6
Cystine	78	Serine	3.9
Phenylalanine	78	Glutamic acid	11.9
Tyrosine	57.2	Proline	3.8
Threonine	67.6	Glycine	4.1
Valine	122.2	Alanine	8.4
		Cystine	3.0
		Valine	4.7
		Methionine	1.7
		Leucine	5.5
		Isoleucine	3.3
		Tyrosine	2.2
		Phenylalanine	3.0

Source : Zanariah and Noor Rehan (1987).

Leung *et al.* (1952) found that fresh arils are high in several B vitamins. Durians are also an excellent source of vitamin E (Martin 1978). Visetbhakdi (1988), in a brief description of durians and the economics of their production in Thailand, mentions that they are high in cholesterol; but authentic reports are lacking as to the cholesterol measurements of durian fruits.

The fruit has been examined and tested positive for thermostable anti-thiamine (thiaminase) activity (Rattanapanone 1979). Bate-Smith (1959) described the presence of caffeic acid and small amounts of leuco-anthocyanins in durians (although this was probably from an analysis of the leaves). Baldry *et al.* (1972) listed several alcohols present in the aril including ethanol, methanol and n-propanol. Wong and Tie (1995) have recently questioned the presence of ethanol and methanol. Numerous other compounds have been identified in fresh durians (Table 5). The creamy consistency of the aril is attributed to gums, pectins and hemicelluloses (Martin 1980).

Phenolic compounds have been reported in durian (tissue unknown, probably from leaves), these include flavanols and caffeic acid. Ferulic and

Table 5. Volatile compounds identified in the aroma profile of durian fruits

Volatile compound	**Source**
Acetaldehyde	1,not 3
Alkyl hydropolysulphides	2
Butan-1-ol	3
Butane-2,2-diol	3
Butanedione	3
Butyl acetate	3
Butyl propanoate	3
g-butryolactone	3
Dialkyl polysulphides	2
1,1-diethoxyethane	2,not 3
Diethyl carbonate	3
Diethyl disulphide	1,2,3
Diethyl tetrasulphide	2,not 3
Diethylthioether (diethylsulphide)	1,not 3
Diethyl trisulphide	2,3
Dimethylthioether (dimethylsulphide)	1,not 3
Cis-3,5-dimethyl-1,2,4-trithiolane	3
Trans-3,5-dimethyl-1,2,4-trithiolane	3
Dodecan-1-ol	3
Ethanol	1,not 3
Ethanethiol (ethanediol)	1,3
Ethyl acetate	1,2,3
Ethyl benzene	1,not 3
Ethyl butanoate (ethyl butyrate)	1,3
Ethyl (E)-but-2-eonate	3
Ethyl decanoate	3
Ethyl dodecanoate	3
1-(ethylthio)ethanethiol	3
Ethyl heptanoate	3
Ethyl hexanoate	3
Ethyl 3-hydroxybutanoate	3
Ethyl 2-hydroxypropanoate	3
Ethyl isovalerate	1
Ethyl methacrylate	1,not 3
ethyl(E)-2-methylbut-2-enoate	3
Ethyl 2-methylbutanoate (ethyl a-methylbutyrate)	2,3
Ethyl 3-methylbutanoate (ethyl isovalerate)	1,3

(Contd....)

Table 5. Contd.

Ethyl methyl disulphide	3
Ethyl 2-methylpropanoate (ethyl isobutyrate)	1,3
Ethyl (methylthio)acetate	3
Ethyl methyl trisulphide	2,not 3
Ethyl octanoate	3
Ethyl pentanoate	3
Ethyl propanoate (ethyl propionate)	1,3
Ethyl propyl disulphide	2,3
Ethyl propyl trisulphide	2,3
S-ethyl thioacetate	3
Heptan-1-ol	3
Hexadecane	3
Hydrogen sulphide (not due to microbial action)	1,2,not 3
3-hydroxybutan-2-one	3
4-hydroxyhexan-3-one	3
3-hydroxypentan-2-one	3
2-hydroxypentan-3-one	3
Methanethiol	1,not 3
Methanol	1,not 3
Methyl acetate	1,not 3
Methyl butanoate	3
2-methylbut-2-enal	3
2-methylbutan-1-ol	3
3-methylbutan-1-ol	1,3
Methyl hexanoate	3
Methyl 3-hydroxybutanoate	3
Methyl 2-methylbutanoate (methyl a-methylbutyrate)	1,3
Methyl octanoate	3
2-methylpropan-1-ol	3
Methyl propanoate (methyl propionate)	1,3
Methyl propyl disulphide	3
Nerolidol	3
Propanethiol	1,3
Propan-1-ol	1,3
Propionaldehyde	1,not 3
Propyl acetate	3
Propyl butanoate	3

(Contd....)

Table 5. Contd.

Propyl 2-methylbutanoate (N-propyl a-methylbutyrate)	1,3
Propyl 2-methylpropanate	3
Propyl propanoate (N-propyl propanoate)	1,3
S-propyl thioacetate	3
S-propyl thiopropionate	3
2,4,6-trimethyl-1,3,5-trithiane	3

1=Baldry *et al.* (1972), 2=Moser *et al.* (1980), 3=Wong and Tie (1995).

sinapic acids are reported absent and leuco-anthocyanins present in low amounts or absent (Bate-Smith 1959).

Fatty acids : The fresh arils of durian fruits consist of about 3-5% fat (Table 3). The exact amount of fat seems to vary between clones as does the nature of the fats themselves. The aril of the durian was first analyzed using gas chromatography by Aspiras and Tocino (1971), but no conclusions about its constituents were made. The doctoral thesis of Greve (1974) included an analysis of the fatty acid composition of durian seeds, arils and husks collected from two locations in Thailand (Table 6). Not only does the fatty acid makeup differ between these three tissues, but it differed markedly between the two varieties of durian. Most notably, 20:0 fatty acids constitute approximately 33% of the total fatty acids found in the husk (pericarp) and almost 10% of that of the seeds in Prajeen Rayong durians, but were found in negligible amounts in all tissues of Chanthaburi durians (Greve 1974); variance in the fatty acid makeup of the arils was much less between these two varieties than that found in the pericarp and seeds. Berry (1980a,b,c) reported on the lipid constituents of both the arils and seeds of durian, in particular the presence of cyclopropene fatty acids which are present in many related genera, and which may be carcinogenic (Berry 1980b). He concluded that cyclopropene fatty acids are present in the seeds in unusually high quantities, 65% of the total fatty acids in durian seed oil are cyclopropenoids (Berry 1980a). Cyclopropenoid fatty acid content was reduced, but not eliminated upon cooking. Sterculic, dihydrosterculic and malvalic acids were present in the uncooked seeds but not in the aril. Due to the toxic and perhaps carcinogenic nature of these substances, Berry (1980b) concludes that it would be unwise to ingest uncooked durian seeds. Berry (1981) compared fatty acid composition of four durian clones and linked the palmitic:palmitoleic acids ratios with taste. The lower this ratio, the higher fruits were ranked by a panel of tasters. He also noted that the degree of saturation of fatty acids varies between clones, which may influence retention of volatile flavouring compounds, and hence the flavour itself. However, at present, this relationship remains correlative rather than causative.

Smell : Although the fruits of *Durio zibethinus* are infamous for their foul smell, they apparently are not the most offensive of all the known species. Most species of *Durio* produce odourless, or nearly odourless fruits, however, the odour of the ripe (and edible) fruits of *Durio dulcis* is apparently so vile and pervasive that they can be smelled for miles (Soegeng-Reksodihardjo 1962); Kostermans (1958b) describes the smell of these fruits as 'simply nauseating'. Hayes (1957) recorded that it is believed that the smell of durian fruits can be eliminated by soaking the flesh in coconut milk overnight. I have, however, seen no recorded experiments on this procedure.

Capus and Bois (1912) described the smell of durians as alliaceous and stercoraceous. Barrett (1912) suggested that the smell might be due to sulphur compounds with some base perhaps related to butyric acid. In recent years, the exact nature of the volatile components that compose the infamous smell have been subjected to some very sophisticated analysis including mass spectroscopy, gas chromatography and ^{1}H nuclear magnetic resonance.

Stanton (1970) and Baldry *et al.* (1972) divided the smell into two distinct categories, a very strong onion-like smell (alliaceous), probably caused by thioethers; and a second fruity smell due to the presence of esters. Stanton (1966) suggested that indoles and skatols may be present in the fruit accounting, in part, for its malodorous nature. Stanton (1970) presented evidence that the arils do not release thiols, and thus thiols are not responsible for the smell. However, esters and thioethers were implicated. Baldry *et al.* (1972) analyzed durians obtained from Singapore which gave similar results, but a durian obtained from Kuala Lumpur was found to owe a large portion of its odour to thiols with minimal contribution by thioethers. The major volatile components were found to be ethanol, n-propanol and ethyl a-methylbutyrate [=ethyl 2-methylbutanoate]. This issue was further addressed by Moser *et al.* (1980) who provided evidence that durian arils do not contain thiols and that mature arils do release hydrogen sulphide, while those of immature durians do not. They also provided evidence that the release of hydrogen sulphide is not due to bacterial action in the fruit (as has occasionally been suggested), since tissue from immature arils did not yield any colonies when cultured on substrates for H_2S forming species. Martin (1978) stated that hydrogen sulphide and diethyldisulphide are responsible for the foetid odour. Durians smell more as they mature; analysis of H_2S production by 500 grams of durian at different stages of maturity produced the following results: immature durian arils produce 0.009 g H_2S, ripe durian arils 0.023 g and very ripe durian arils 0.047 g (Greve 1974).

Moser *et al.* (1980) ascribed the characteristic odour of durian to H_2S, hydrodisulphides, dialkyl polysulphides, ethyl esters and 1,1-diethoxyethane.

Indoles were not detected as was predicted by Stanton (1966). The polysulphides identified by Moser *et al.* (1980) were mainly ethyl polysulphides which apparently rarely occur in fruits. Unfortunately, Moser *et al.* (1980) obtained their durians from Thailand. Thai durians differ substantially in odour and flavour from Malay durians, the Thai durian being sweeter and considered less aromatic than Malay clones (Mohamad Idris 1987). Thus, the differences in constituents found between the study of Moser *et al.* (1980) and Baldry *et al.* (1972) may either reflect clonal differences in aroma composition or differences due to technique.

Very recently, a third analysis of the aroma composition of durian fruits has been published. This study by Wong and Tie (1995) reported the presence of 63 volatile constituents (including 30 esters, 5 ketones and 16 sulphurous compounds), which contribute to the smell. More importantly, this study sheds further light on the work of Baldry *et al.* (1972) and Moser *et al.* (1980). Interestingly, this work demonstrated several differences from the earlier analyses (all the volatile compounds as yet described in durian fruits are listed in Table 6).

Wong and Tie (1995) were unable to confirm the presence of several of the volatile compounds reported in both previous studies including ethanol, methanol, ethyl methacrylate and several sulphur containing compounds. They attribute these differences to better technique, and to using ripe durians and a minimal time between harvest and analysis. There are three interesting aspects of this study, asides from a long list of new volatile components. Firstly, Wong and Tie (1995) sampled and compared the composition of fruits from three named clones, D15, D28 and D74. Not only did they show considerable differences in the total yield of volatile compounds between clones, but numerous large differences in quantities of particular volatiles exist between these clones. Some volatiles were not detectable in all of the clones. Secondly, Wong and Tie (1995) demonstrated the presence of three different a-hydroxyketones which they claim have never before been reported from an analysis of a fruit. Thirdly, these authors stated that no trace of H_2S was detectable in the aroma profile of the fruits from any of the three clones tested. This result is at variance with several previous works (Baldry *et al.* 1972; Greve 1974; Martin 1978; Moser *et al.* 1980) and is likely to be related to change in aroma composition over time during ripening of the fruit. The H_2S production increases markedly as the fruit ripens (Greve 1974). Thus, although Wong and Tie (1995) used ripe fruit, it may not have been ripe enough to produce H_2S. Apart from the study of Greve (1974), the change in aroma composition of durian fruits over time has not been examined. Such

Table 6. Fatty acid composition of durian

Tissue	Clone	Saturated unsatur-	Palmitic Palmit- ated	14:0 oletic	15:0	16:0	16:1	17:0	18:0	18:1	18:2	18:3	20:0	22:0	Dihy- drost-	Mal- valic erculic	Ster- culic	Cis vaccenic
Aril	D24[1]	1.4	4.7	0.5	<0.1	39.8	8.5	<0.1	0.8	45.8	1.8	2.7						
Aril	D2[1]	1.7	6.9	0.5	<0.1	35.9	5.2	<0.1	1.0	51.0	2.4	4.1						
Aril	D66[1]	1.8	5.3	0.8	<0.1	33.8	6.4	<0.1	0.9	48.7	2.8	7.0						
Aril	D8[1]	1.9	13.9	0.5	<0.1	32.3	2.3	<0.1	2.2	53.6	3.2	6.0						
Aril	Unknown 1[2]			0.91		34.13	7.1		1.21	42.14	7.85	5.69	<0.01					
Aril	Unknown 2[2]			0.34		28.94	5.16		1.23	5.98	3.16	2.21	<0.01					
Whole fresh seeds	Unknown[2]	82% unsaturated		0.12		12.20	1.15		1.42	8.42	6.50	11.3		1.21	2.52	15.72	38.53	
Pericarp	Unknown Thai#1[3]					30.9	4.2		1.8	52.8	4.2	4.0	<1					
Pericarp	Unknown Thai#2[3]					14.9	1.4		5.1	17.8	7.6	4.9	33.2					
Aril	Unknown Thai#1[3]					33.9	4.9		1.0	51.2	3.0	5.1	<1					
Aril	Unknwon Thai#2[3]					31.9	6.9		1.0	51.0	3.0	5.4	<1					
Seed	Unknown Thai#1[3]					26.8	8.4		3.3	38.8	5.9	3.0	<1					

(Contd...)

Table 6. Contd.

Seed	unknown Thai#2[3]		23.0	3.1		1.2	41.0	11.5	5.3	9.5					
Aril	unknown Thai[4]	0.6	31.3	3.4		2.1	(47.1, 4.3)*	1.3	7.1						8.4

Fatty acid compositon of various parts of durian fruits. Note: all values are in percent GLC peak area except for that of Shibahara *et al.* which is in % wt from GC analysis.

[1] Berry (1980c) and Berry (1981).

[2] Berry (1980b) (Unknown#1 was from a Malay durian with yellow arils, #2 was from a Malay durian with cream coloured arils).

[3] Moser *et al.* (1980) (Thai#1 was a durian from Chandburi, Thai#2 was from Prajeen Rayong.) Note: This data is originally from the thesis of Greve (1974).

[4] Shibahara *et al.* (1987) *Note: Vaules are for 18:1 n-9, n-7 respectively.

a study would be enlightening, as it is possible that the aromas of fruits from different durian clones may not just simply differ in the presence or absence or relative amounts of certain volatiles, but there may be timing differences in the production and release of these compounds that exist between clones.

Though numerous compounds have now been identified in the aroma profile of durians (Table 6), these contribute only marginally to the overall smell. The major problem that still remains is the determination of the components most responsible for the distinctive smell of durians. This is confounded by four problems. Firstly, durians from different clones appear to vary markedly in aroma composition, and the aroma composition may vary with ripeness, thus there would be no fixed 'recipe'. Secondly, of the three major published studies on aroma composition, very different conclusions regarding the major contributing compounds have been reached. Thirdly, how much a volatile substance contributes to the aroma of a fruit is not necessarily indicated by its relative abundance, some substances simply smell much more than others. Finally, all other concerns aside, the relative abundance of a compound itself is likely to be misleading, and must be interpreted with caution. Relative abundances are usually expressed as an area percentage of the total response area, taken by the response peak for a particular compound. These areas have not been corrected for differences in detector response that exist between different compounds. Thus, a compound that appears to exist ten times the quantity of another substance because its peak area is ten times greater would actually be present at the same concentration if the sensitivity of the detector to the compound was ten times greater. I could not sum up the wonderful complexities of the smell and taste of durians better than Martin (1980) who stated: 'Thus, there appear to be a wide variety of durian fruits, each combining foul, sulphurous compounds in its own delightful way...'.

Miscellaneous uses of fruit : Durian husk extracts have been studied for their suitability as aqueous binders for granules and tablets (Umprayn *et al.* 1990a,b). These authors showed that husk (pericarp) extracts are suitable for the preparation of granules and to have desirous binding properties for the manufacture of tablets (Umprayn *et al.* 1990b). The ashes of *D. zibethinus* are used to extract a dye which, in turn, is used to prepare batik dye (Kostermans 1958b). The ashes have also been used for whitening silk (Kostermans 1958b; Morton 1987). The empty husks are also used in Java as a source of fuel (Ochse and Bakhuizen Van Den Brink 1977; Morton 1987).

Medicinal and Toxicological Properties

Durians and alcohol : A common Malaysian belief is that it is harmful to drink alcohol after consuming durians. This belief dates back at least to the time of Rumphius (1741) who states that one should not drink alcohol after eating durians as it will essentially cause indigestion and bad breath. Gimlette (1929) in his 'Malay Poisons and Charm Cures' records: 'It is said that the durian fruit must not be eaten with brandy'. More recently, Croft (1981) states that '...a feeling of morbidity often follows the consumption of alcohol too soon after eating durian'. Some scientific studies have actually been conducted to investigate the validity of this belief.

For the record, there is, in fact, a published medical instance of a middle aged Indian woman dying after eating a durian and consuming alcohol (Singh 1941). In this case, the woman was admitted to hospital complaining of intense epigastric pain, and persistent vomiting. Despite attempts to save her, she died several hours after admission. Autopsy revealed fat necrosis on the peritoneum, a reddish and swollen pancreas, a swollen main pancreatic duct, and 2 pints of blood stained fluid in the abdominal cavity. It was suggested by one physician that the death was due to acute haemorrhagic pancreatitis, the ingestion of durians that morning being merely coincidental; the patient had a history of epigastrium pain and discomfort for 7 months preceding her death. A second physician concurred and added that these conditions may have been caused by alcoholism. Oddly, the opinion of the author of the report was that the ingestion of durians and the death due to acute haemorrhagic pancreatitis was not coincidental, but perhaps causative. No explanation for this opinion was presented.

Two Singaporean researchers attempted to probe the effects of durian and alcohol mixtures, in two experiments, by force feeding mice durian-alcohol homogenates containing 0.8 g durian and 10%(v/v) ethanol (Ogle and Teh 1969). Mice were fed homogenates at different times after preparation in the first experiment, controls were fed either just durian or just 10% ethanol. The alcohol-alone mice and the alcohol-durian mice behaved similarly, all had an unsteady gait. Mice fed just durian behaved similarly to untreated mice. When alcohol was administered at different times after force-feeding of durian, it was found that the sooner alcohol was administered, the fewer mice fell asleep, the lower the mean sleeping time, and the quicker the onset of sleep. The authors proposed that durian may inhibit the absorption of alcohol. Furthermore, the authors cited personal experience with persons who have consumed durians with alcohol:

'The alcohol was taken together with, or 1 to 6 hours after a durian meal. None of them felt any ill effects, except for one person who experienced discomfort from fullness of the abdomen and flatulence.' -- Ogle and Teh (1969).

In a second paper, Ogle and Teh (1971) investigated the possibility that the ill effects of durian and brandy cited by Gimlette (1929) might be due to some constituent in the brandy other than alcohol. In these experiments, mice were given homogenates consisting of 0.8 g of durian, and then fed 1 ml of 10% brandy or whisky 2, 4, or 6 hours later. Durian controls showed no ill effects, while those receiving alcohol and durian showed an unsteady gait. The authors report that those receiving alcohol after 2 hours appeared to have a more steady gait than the others. The authors again suggest that durian may inhibit the absorption of alcohol.

Techapaitoon and Sim (1973) have also investigated the effects of durian and alcohol mixtures. These experiments have corrected some of the problems present in the first study (the effects of lethal dose was studied, larger sample sizes were used, and the variety 'Koh' of durian chosen was recorded). These authors performed a series of experiments on mice and rats. In one experiment, they orally administered the lethal dose of alcohol (1 ml of 37% alcohol) to 20 mice. The authors noted that, after administering the lethal dose of alcohol, all mice subsequently died. More interestingly, in a group of mice fed the same amount of alcohol together with durian homogenate, only 11 of the 20 mice died. Furthermore, only 7 of 20 mice fed similar concentrations of Hennessey V.S.O.P. reserve brandy-durian homogenates died. Attempts to feed sleeping mice durian homogenates after feeding them the lethal dose of alcohol resulted in the deaths of all mice involved. Further experiments by the authors revealed that mice given durian together with alcohol, or immediately after, reduced the number of mice that fell asleep, and shortened the average time spent sleeping. These effects were noticed when mice were given alcohol orally or intraperitoneally. Finally, mice or rats fed durian and alcohol homogenates appeared to have a more steady gait than did alcohol controls. The experiments of Techapaitoon and Sim would appear to confirm and expand the findings of Ogle and Teh (1969, 1971).

More recently, a Thai research paper has again studied the effect of alcohol-durian mixtures on mice and rats (Nilvises and Saengsirinavin 1986). Similar results to those of the previous studies were found. Furthermore, this study revealed that similar results are obtained with durian fruits of several different clones.

Despite the important contributions to our knowledge of durians and human/mouse physiology provided by these experiments, several critical flaws are evident. And a *priori* assumption made by these authors is that the effects of durians and alcohol on humans is equivalent in mice. Mice might be less sensitive, or not sensitive at all. Ogle and Teh (1969) did, however, give some consideration to the mouse human scaling factor, thus durian doses given to mice were roughly equivalent to an adult male human consuming 6 pounds of fruit. Most importantly, all of the aforementioned experiments were lacking a control treatment in which animals were fed an equivalent mass of some food item other than durian. Thus, any effects on alcohol absorption might be due to the presence of food in the stomach, and not durian *per se.*

In considering the available evidence, experiments with mice and rats, observations of humans (by Ogle and Teh), and the recorded medical case of Singh (1941), it is fair to say that consumption of durians with alcohol has not been shown to be harmful.

It should be noted that deaths or maladies apparently do occasionally occur due to durians, but usually from being struck by one of these large spiny fruits as it falls from a tree, rather than by ingestion (Craig 1973). If the much quoted article by Wallace on durians can be relied upon, actual death by striking is in fact quite unusual:

‘When a durian strikes a man in its fall, it produces a fearful wound, the strong spines tearing open the flesh, while the blow itself is very heavy; but from this very circumstance, death rarely ensues, copious effusion of blood preventing the inflammation which might otherwise take place’ (Wallace 1856).

Medicinal properties : The effects on human physiology of the ingestion of durians has been discussed for centuries. James Low (1836) wrote: ‘He who can eat and digest a durian, and not find his liver stirred up by a host of blue imps, may well despise the anti-dispeptic precepts of a Kichener, a Sinclair or a Johnstone’. The durian fruit is often cited as having a ‘warming effect’ on the body (Rumphius 1741; Malo and Martin 1979), but this property does not seem to ever have been investigated.

Paludan in Linschoten (1579-1592) (Anon. 1851, an English translation) claimed that betel leaves when enclosed in a room with durians will cause them to rot. He also claims that a betel leaf laid upon the stomach, or eaten after eating durians will ease digestion. This belief has been echoed through several works since Paludan.

Febrifugal and anti-malarial properties : There are numerous suggestions that different parts of durian trees have been traditionally used in remedies for fevers. The juice of fresh leaves has been used as an ingredient in a lotion for fevers (Gimlette and Burkill 1930). The juice from the bark has been used to attempt to treat malaria (Panggabean 1975). Ridley (1906, 1907) states that the roots are used for treating fever, either ground up and rubbed on the body or as a decoction. According to Brown (1954), a decoction of the roots is made for fevers when the fever has lasted 3 days; also a compound is made out of the leaves and roots for fever. The most complete description of this medicinal use is a native Malayan prescription for fever, collected by Burkill and Haniff (1930): (1) Boil the roots of *Hibiscus rosa-sinensis* with the roots of *Nephelium longan, Durio zibethinus, Nephelium mutabile* and *Artocarpus integrifolia*, (2) drink the decoction, (3) also, boil the leaves of all of these species and use as a poultice. Gimlette and Burkill (1930) state, as a remedy for fever, that the leaves of *Curculigo latifolia, Gleichenia linearis, Nephelium lappaceum* and *Durio zibethinus* should be squeezed by hand, and water poured on them. The patients head should be bathed in this water for three days. Finally, in this regard, Heyne (1950) states that a concoction made from the bark of *D. oxleyanus* is used to treat malaria in Sumatra.

Although durians obviously do not cause malaria, it has been noted that many malarial infections can be traced to individuals who have stayed up, unprotected, through the night in durian orchards to collect fruit as it falls (Ponnampalam 1975).

Vermifugal properties : Hurrier and Perrot (1907), and Morton (1987) both report that durian is used as a vermifuge. De Padua *et al.* (1978) reported it to be a vermifuge, vermicide and an anthelmintic. I have, however, been unable to locate any prescription for deworming based on durians, or to find any record of what part of the plant is supposed to have this property.

Treatment of jaundice : It appears that the leaves have been used in the traditional treatment of jaundice (Brown 1954). Burkill and Haniff (1930) have recorded the following traditional prescription for the treatment of jaundice: ‘Boil leaves in water and bathe in it.’

Diabetes : An investigation of the post-prandial glucose and insulin responses of diabetes patients to 5 tropical fruits including durian revealed that the insulin response, and insulin area was the greatest after ingestion of durian.

Thus, they are not optimal food items for persons with non-insulin dependant diabetes mellitus (Roongpisuthipong *et al.* 1991). The reason for the greater effect of durian on insulin levels in the blood compared to other fruits is still unknown.

Aphrodisiac : The durian fruit is frequently claimed to have strong aphrodisiac properties, as do many foul things (Rumphius 1741; Baillon 1875; Ridley 1902; Popham 1979 and others). In fact, an often quoted Malay saying states ‘When the durians come down, the sarongs go up’. Despite the widely held nature of this belief, no experiments to determine its empirical validity have been conducted.

Miscellaneous medicinal properties : Morton (1987) states that ashes of the pericarp are taken after childbirth. The fruit is also said to be an abortivum and to improve menstruation (Kostermans 1958b). Kostermans also relates that the valves of the fruit are rubbed on the abdomen against constipation. Kostermans (1958b) and De Padua *et al.* (1978) report that durian husks are used externally to treat skin diseases. The leaves probably contain hydroxy-tryptamines and mustard oils (Stanton 1966; Morton 1987). The alleged action of durian leaves and husks in reducing swelling and aiding skin diseases may be due to the vaso-constrictor properties of hydroxy-tryptamines and bactericidal action of mustard oils (Stanton 1966).

Ridley (1902) states that durian is believed to be strengthening for children. De Padua *et al.* (1978) claim that durian is used as a general tonic, however, no specific information is given. Heyne (1950) mentions that crushed seeds of *D. oxleyanus* are used to treat sores and wounds.

De Padua *et al.* (1978) recorded the presence and relative amounts of several components in the leaves and stems of durians, which may, in part, play a role in suspected medicinal qualities. They found detectable levels of tannins in durian leaves, and abundant to very abundant amounts in the stem. Furthermore, there are detectable to abundant levels of saponins in the leaves and stems, detectable levels of fats in the leaves and stem, detectable to abundant quantities of calcium oxalate in the stem, and detectable levels of formic acid in the leaves; abundant amounts in the stem. Ashton (1964) records that leaf extracts of *D. zibethinus* and *D. graveolens* react with $FeCl_2$ causing a blue colouration, indicating the presence of tannins. Furthermore, the leaves of both species tested negative for protein precipitating compounds.

According to many authors, durian seeds contain a poisonous substance that makes one short of breath (Rumphius 1741; Kostermans 1958b; Stanton 1966). Seeds contain sterculic acid which may be responsible for this effect (Berry, 1980b).

Seeds

Mature seed constituents : The moisture content of fresh durian seeds is enumerated by Chin *et al.* (1989). The moisture content of the embryo is given as 65% (w/w) on a fresh weight basis, while the value for the 'whole seed' is only 50%. The authors do not define what is meant by whole seed, so it is unclear if this refers to the embryo and seed coat, or the embryo, seed coat, and the large fleshy aril. Berry (1980b) gave measurements of durian seed moisture as 77%, Soepadmo and Eow (1977) stated that the average moisture content of fresh seeds is 51%, Chin *et al.* (1984) listed the moisture content of freshly harvested seeds as 39%. The large variance in these estimates is likely due to differences in drying regimes. Estimates of seed moisture content of durian apparently vary greatly when the drying time and temperature is varied (Grabe 1992). Fresh durian seeds contain some small amounts of protein, 1.57% (Berry 1980b), but consist largely of starch (Table 7). Mature seeds appear to be metabolically active when shed; polysomes are evident in mature seeds and specific enzymatic activity is detectable (Brown 1995b).

Oil content is reported to be 0.5% (Berry 1980b). On the lipid constituents of both the arils and seeds of durian, it was reported that cyclopropene fatty acids including sterculic, dihydrosterculic and malvalic acids were present in the uncooked seeds but not in the aril (Berry 1980a,b,c, 1981). Due to the toxic and perhaps carcinogenic nature of these substances, it would be unwise to ingest uncooked durian seeds. It is of interest that no indication exists in the literature that durian seeds are ever eaten uncooked by any native peoples.

Culture of seeds and seed size : The seeds of durian are large. According to Troup (1921), about 1 dozen seeds weighs 454 g. I think this may be an overestimation unless the author made his calculations from a variety with unusually large seeds. From my own measurements, mature durian seeds weigh approximately 20 grams. Davis and Bhattacharya (1974) give an average weight of 12 to 15 grams from measurements made on the seeds of two fruits[4]. Chin *et al.* (1984) state that the weight of 1000 durian seeds is 14783 g (14.7 g per seed). There is a great variation in seed size within a single

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[4] These estimates include the smaller semi-aborted and full sized seeds.

Table 7. Components of durian seeds

Component	Amount and source
Moisture	(77.0%)[1*] (51.5, 51.1%)[3*]
Fat	(0.5%)[1*] (0.23%)[2*] (0.4, 0.2%)[3*]
Protein	(1.57%)[1*] (2.6, 1.5%)[3*]
Total carbohydrates	(43.6, 46.2%)[3*]
Crude fibre	(0.71%)[2*] (-, 0.7%)[3*]
Nitrogen	(0.297%)[2*]
Ash	(1.00%)[2*] (1.9, 1.0%)[3*]
Calcium	(88.80mg/100g)[2*] (17, 39mg/100g)[3*]
Phosphorus	(86.65mg/100g)[2*] (68, 87mg/100g)[3*]
Iron	(0.64mg/100g)[2*] (1.0, 0.6mg/100g)[3*]
Sodium	(3, - mg/100g)[3*]
Potassium	(962, - mg/100g)[3*]
Beta carotene equivalents	(250, - µg/100g)[3*]
Riboflavin	(0.052mg/100g)[2*] (0.05, 0.05 mg/100g)[3*]
Thiamine	(0.032mg/100g)[2*] (-, 0.03mg/100g)[3*]
Niacin	(0.89mg/100g)[2*] (0.9, 0.9 mg/100g)[3*]

Sources for data presented in Table 7:

[1] Berry (1980b) Note: data is for fresh durian seeds. [2] Intengan *et al.* (1955) Note: This data is for cooked durian seeds. [3] Leung *et al.* (1972) Note: two values are given, the first is for raw seeds (minus seed coat) and the second for cooked seeds (minus seed coat). In some instances, only one of these values is given, the missing value is represented by "-".

durian fruit, some seeds abort at different stages of development. Full sized, but flattened and completely empty seed coats may often be found inside the arils of mature fruits. Fully mature and filled durian seeds sink when immersed in water, but 'aborted' or 'partly-filled' seeds float (personal observation). Partly filled seeds can often be successfully germinated (personal observation). When mature, the seeds are non-endospermous, the endosperm becoming exhausted several weeks before fruit abscision. The endosperm remains in a free nuclear state until late in embryogeny at which time it becomes cellular (Soepadmo and Eow 1977). According to Ho (1972), there is a great deal of genetic variability in endosperm abortion in *Durio*, however, I think that he is actually referring to seed abortion. The seeds of durian are described and portrayed diagrammatically by Corner (1976) with particular attention to the vascular supply, in his encyclopedic 'Seeds of Dicotyledons'.

It has recently been possible to culture excised durian embryos (Chin *et al.* 1988). Wounded seeds exude a mucous like secretion and are highly susceptible to oxidative browning, thus, excised embryos fared best when first soaked in antioxidant, and subsequently grown on charcoal containing media, containing 1.0 mgl^{-1} NAA (α-napthalene acetic acid) or IAA (indole-3-acetic acid) and 1.0 mgl^{-1} kinetin, BAP (benzylaminopurine), or 2iP (2-isopentyladenine) (Chin *et al.* 1988). Embryos of *D. lowianus* cultured on woody plant medium supplemented with BAP produced callus (Kongnakorn *et al.* 1985). Apparently, some success in callus formation from excised cotyledonary tissue of *D. zibethinus* has also been achieved (Rao *et al.* 1982; Johri and Rao 1984), however, as of yet no literature has been uncovered on plant regeneration from such callus cultures of durian[5].

Viability : It has long been known that the seeds of durian have a short period of viability (MacMillan 1909; Main 1909a,b; Troup 1921; Chevalier 1934). The seeds of durian are now categorized as recalcitrant (Hofmann and Steiner 1989); seeds with a relatively high moisture content at maturity, which cannot withstand desiccation (Hanson 1984; Roberts *et al.* 1984), and thus have a relatively short period of viability. In durian, this is correlated with the inability to withstand chilling or freezing. The recalcitrant nature of durian seeds presents major problems in the storage of durian seeds both for commercial purposes, and for conservation. As durian is undoubtedly suffering some degree of genetic erosion (Sastrapradja 1975), research into the physiological response of durian seeds to chilling and drying is assuming a new importance.

Seeds stored at 36°C lose viability after 6 days, while surface sterilized seeds sealed in an airtight container under nitrogen can maintain viability for 32 days if the temperature is lowered to 20°C (Soepadmo and Eow 1977). Further experiments by Teng (1980) showed that fresh durian seeds, stored for 3 months on wet tissue paper at 15°C, maintained 79% germinability, although some problems with fungal infection and radicle protrusion were encountered. Storage of durian seeds at 5°C for 10 days resulted in a reduction of viability to 80%. Viability was completely lost at this temperature after 20 days of storage. Seeds stored at 15°C and 29°C maintained their viability for 20 days; however, seeds stored at the higher temperature had all germinated after 10 days. Hanson (1981) performed some preliminary drying and storage experiments on some tropical recalcitrant seeds including durian. Durian was shown to have a viability period at 27°C of 3-4 weeks; seeds stored at 15°C exhibited only 15% germination after 2 months.

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[5] Numerous attempts at tissue culturing durian seeds have been attempted by myself and Miss L. Sreedhar, in the Department of Botany, University of Guelph. Although vigorously growing callus is somewhat easy to produce, various combinations of plant growth regulators at different concentrations have proven unsuccessful in regenerating plants.

The critical moisture content of durian seeds as determined by drying over silica gel was found to be 45-50% and durian seeds lose viability at about 20% moisture (Hanson 1981). Several drying regimes were carried out by Teng (1977); 14 days of drying (to a final moisture content of 36%) reduced the percentage germination of seed from 100 to 70%. Drying for longer time periods (28 days), or to moisture contents of 23.2% or less, resulted in the complete loss of seed viability.

The moisture content at viability loss after slow and fast drying was reported as 71 and 63% respectively (Boyce 1989; Grabe 1989). These values are much higher than numerous other accounts of the minimal moisture content of viable durian seeds. The differences between this report and those of others are undoubtedly related to the exact method of moisture determination which is known to greatly affect moisture determination in durian seeds (Grabe 1992).

Hor *et al.* (1989, 1990) investigated the behaviour of durian seeds and embryos upon drying and freezing in liquid nitrogen. The critical moisture content (the value below which rapid loss of viability occurs) of durian embryos was determined to be 51.0% (Hor *et al.* 1989); 53.9% (Hor *et al.* 1990) , while that of the seed was determined to be much lower, 26%. Unfortunately, the threshold moisture content of durian embryos (the level below which there is no freezable water present) was determined to be 32%. Thus, it was not possible to lower the moisture content enough to permit successful cryopreservation without the complete loss of viability due to dehydration. Today, there is still no method for medium to long term storage of durian seeds (Lin 1992).

Morton (1987) claimed that durian seeds are rendered inviable by exposure to sunlight. This is most likely based on a statement by Malo and Martin (1979, 1980a). In their original context, they might have implied that direct sunlight would damage seeds because it raised their temperature, not because of a direct effect of light *per se.* However (Anon. 1982a) also stated, ‘germination is rapid and easily accomplished, but the vitality is short-- a few weeks or only a few hours if the seed is exposed to the sun.’ Unfortunately no data were presented in this study. These remarks are in conflict with those of Main (1909a,b) who stated that before packaging and shipping seeds, it is best to thoroughly wash them, then dry them in the sun for two or three days to help ensure viability upon arrival. It is the experience of the author that durian seeds left in a moist location on the ground, exposed to sunlight in a durian orchard, will germinate. It also seems unlikely that light would penetrate the thick opaque seed coat of durian. However, to the best of my knowledge, formal experiments on the effects of light on the viability of durian seeds have never been conducted or published.

Germination : MacMillan (1909) states that durian seeds germinate in 7 to 8 days, but no information on percentage germination was given. Durian seeds germinate very quickly, 95% germination occurring after about 10 days (Soepadmo and Eow 1977). The complete removal of the fleshy aril from the seed coat before sowing greatly enhances the rate of germination (95% germination after 3 days) (Soepadmo and Eow 1977). Ng (1975) reports 100% germination after 4 weeks, 2 weeks being necessary for 50% germination in *D. zibethinus,* and 87% germination after 3 weeks in *D. griffithii,* 1 week being necessary for 50% germination. According to Padolina (1931), 17 days are necessary for germination of *D. zibethinus,* but no record of percent germination after this time was given. As much as 94% germination has been reported for *D. graveolens* after 3 weeks, 2 weeks for 50% germination; 100% germination for *D. lowianus* after 3 weeks, 2 weeks for 50% germination; 66 and 91% germination after 6 and 3 weeks respectively for *D. oxleyanus,* 2 weeks being necessary for 50% germination (Ng and Mat Asri 1979).

The method of germination of *D. zibethinus* is unusual, and was described in detail by Rumphius (1741) in his ‘Herbarium Amboinense’. The first part of the seedling to emerge from the seed is the hypocotyl, which is thick and square in cross-section. Eventually, roots emerge from the tip of the hypocotyl, and the shoot emerges from between the petioles of the cotyledons. Oddly enough, whether germination is epigeal or hypogeal depends on the orientation of the seed when planted (Singh and Rao 1963). When the seed is planted with the micropyle oriented downwards, the germination is epigeal; upwards or horizontal, the germination is hypogeal. This type of germination has been termed false epigeal. Such a crude delineation of germination types (epigeal *vs.* hypogeal) grossly oversimplifies the processes which actually occur in this and many other species. The much more comprehensive seedling classification scheme of De Vogel (1980) further subdivides the method of germination in the genus *Durio* into two types. *D. excelsus* and some *D. zibethinus* are ascribed to the exquisitely rare Horsfieldia germination type Pseuduvaria subtype, or Hor7b, which has only been firmly documented in three other genera of flowering plants. Other species of durian; *D. acutifolius, D. dulcis, D. griffithii, D. kutejensis, D. oxleyanus,* and some *D. zibethinus* are listed as Blumeodendron type. Meijer (1968) stated (erroneously) that *Durio* is phanerocotylar (cotyledons free themselves from the testa during germination). *D. zibethinus* is most certainly cryptocotylar, as are apparently all other species of *Durio* whose germination has been described. *Durio* appears on Burtt’s list of genera with known cryptocotyly (Burtt 1991).

It has been stated that the cotyledons are shed shortly after germination, yielding no apparent advantage to the seedling (Fenner 1985); however, from personal experience, this is more true of the tropical jackfruit (*Artocarpus heterophyllus*) than for the durian. Soepadmo and Eow (1977) relate that the cotyledons shrivel and drop off within 38 days following germination, which is more in line with personal observations. A thorough morphological description of a newly emerged seedling (with diagrams) is given by Burger Hzn (1972) and De Vogel (1980).

Pollination Biology

Anthesis : Durian flowers open in mid afternoon (the flowers of some clones are reported to open as early as 2:30 PM (Tidbury 1976). Even though the flowers open, the anthers do not dehisce and release pollen until about 7:00 PM. Polprasid (1969) states that durian pollen grains function maximally at 9:30 PM. By early morning, the calyx, corolla and staminal groups have abscinded leaving just the pistil attached to the receptacle. Jamil (1966) reported that the timing of anthesis and anther dehiscence varies by several hours between clones, but no data were presented. Attempts to pollinate durian flowers with pollen released by crushing from undehisced anthers resultd in no fruit set (personal observations). Although pollen is not functional before anther dehiscence, pollen does remain viable up to two days after anthesis when stored in a refrigerator (Coronel 1966).

Valmayor *et al.* (1965) and Coronel (1966) reported that the stigmas of durian are receptive to pollen 36-48 hours before the flowers fully open. Coronel (1966) reports that hand pollination of 36-48 hours before anthesis flowers by surgical removal of the outer floral parts leaving just the pistil, results in a greater percent fruit set than hand pollination of fully mature flowers. Razak *et al.* (1992) have shown 87.5% receptivity of D24 durian stigmas 10 hours before anther dehiscence with 42.1% receptivity remaining 24 hours after anthesis (receptivity was estimated by measuring percentage fruit set). Salakpetch *et al.* (1992) found that stigma receptivity in some Thai cultivars began 24 hours pre-anthesis, receptivity remaining high until noon the day after anthesis, after which it rapidly declined. Shaari *et al.* (1985) reported that receptivity was reduced to approximately 50% by noon the day after anthesis. Jamil (1966) has suggested that the period of stigma receptivity varies considerably between clones. Salakpetch *et al.* (1992) showed that pollen viability also varies between clones in a study with 4 Thai cultivars, viability ranged from 77 to 93% two days after anthesis.

Natural pollinators : Today, durian trees are generally regarded as bat pollinated, although Beccari (1889) was of the opinion that birds could be pollinators.

The first suggestion of bat pollination of *Durio* is that of Beccari in his book 'Malesia' (1889) who records *Macroglossus minimus* Geoffr. visiting the flowers. This account apparently did not make a big impression for it was not until over 40 years later, that Boedijn and Danser (1929) noted a flock of bats visiting a durian tree, their activity causing the shedding of numerous stamens and calyxes. Although they didn't observe or demonstrate actual pollination of flowers by bats, they postulated that this may have been the case. Interestingly enough, the affinity of flying foxes for the nectar of durian flowers must have been common knowledge, an account of their feeding is given in an illustrated tour guide to the Federated Malay States first published in 1910 (Harrison 1910a). Van Der Pijl (1936) conclusively demonstrated that durian flowers have typical bat pollinated flower morphology, and that the visitation of flowers by bats does indeed cause fruit set; he also raised strong arguments against birds as possible pollinators. As birds have not been shown to visit durian flowers during the time when pollen has been released, they are unlikely natural pollinating agents.

Baker (1969) witnessed pollination by an unnamed species of bat and by an unnamed species of hawkmoth. However, this was on a single specimen growing in the Honduras, far from its native home. Van Der Pijl (1941) has recorded bats visiting durian flowers, in the case of *Durio zeylanicus*[6] he notes that the flowers are also squashed and entirely eaten by bats.

Soepadmo and Eow (1977) documented the visitation of *Durio zibethinus* flowers by three species of bats (*Eonycteris spelaea, Cynopterus brachyotis,* and *Pteropus vampyrus*). Their observations were also supported by analysis of bat guano for pollen grains. Start and Marshall (1977) calculated that pollen of *D. zibethinus* and *D. graveolens* makes up 3.4% of all the pollen grains extracted from samples of bat guano taken from Batu Caves in Kuala Lumpur, which are inhabited by *Eonycteris spelaea*. Soepadmo (1979) reported bat pollination of *Durio zibethinus, D.graveolens, D. malaccensis* and *D. oxleyanus* by *Eonycteris spelaea, Macroglossus maximus* and *M. minimus*. Whitmore (1990) states that the flowers of the related *Kostermansia malayana* are also bat pollinated.

Although bats definitely pollinate durian trees, flying foxes (*Pteropus vampyrus*) have often been thought to be responsible for destroying many young flowers (Anon. 1953a; Browne 1955). In fact, in the early part of this century, it was recommended that '...if you have a gun you are hereby requested to shoot as many of him [*Pteropus vampyrus*] as possible, for he is a bitter

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[6] He may be referring to *Durio ceylanicus* Gardn. which has now become in part *Cullenia ceylanica* (Gardn.) K. Schum. (see Table 1).

curse...' (Harrison 1910a). Gould (1977), in his study of foraging behaviour, suggested that the damage to durian flowers by flying foxes is negligible, and rather than a nuisance, they are important pollinators. Gould (1978) investigated the foraging behaviour of bats on durian flowers with reference to *Parkia* and *Musa* flowers, and proposes that access to nectar is restricted by the shape of the flower, which encourages sporadic foraging in some bats. This presumably favours outcrossing, while favouring territorial behaviour in flying foxes. Soepadmo and Eow (1977) via several pollination experiments, estimated that about 45% of successful pollination was contributed to by natural pollinators.

Mardan and Zainal (1986) studied the effects of excluding bats as pollinators of durian flowers by the use of wire mesh cages. Bat excluded treatments yielded significantly lower fruit set, suggesting bats were responsible for 39% of the total number of successful pollinations in the study. No significant effect on the abortion rate of developing fruits was found due to bat exclusion. Furthermore, these authors report visitation to flowers by the bee species *Apis dorsata*, *Apis cerana* and stingless bees of the genus *Trigona*. Only *A. dorsata* was seen to forage for nectar in flowers at night. Ferrazzi (1995) also claims that the bee species *A. dorsata, A. cerana* and *A. melifera* pollinate durian flowers in Thailand.

To some extent, nocturnal moths (Soepadmo and Eow 1977) and other insects (Jamil 1966) may also be natural pollinators of durian, although this is not well documented. Jamil (1966) reported that at least 10 insect species visit durian flowers, and probably affect pollination. Unfortunately, there is no record as to the time of these visitations (if they occur during the day, they may well precede anther dehiscence), or of the species involved.

Early ovary abscission *vs* premature fruit drop : The efficiency of fruit-set of durian is quite low. Only 5.4% of hand pollinated flowers of 3 durian trees (clone D8), cross-pollinated with pollen from D24, produced fruits which persisted on the tree until maturity (personal observations). This is very close to the result of 5% reported by Soepadmo and Eow (1977) after artificial pollination experiments. Mardan and Zainal (1986) reported that bat exclusion had a significant effect on fruit set but that the percentage of mature fruits finally produced compared to the number of flowers produced was less than 3 percent, regardless of exclusion of bat pollinators. Namuco (1978) reported that ovary abscision was high 4 days after anthesis, especially in self-crosses of a known self-incompatible tree; all self-crosses had abscinded by the tenth day. Premature fruit abscission, however, persisted up to the 9th week of development in cross-fertilized fruits. Similarly, Shaari *et al.* (1985) (data reprinted in Razak *et al.* 1992) showed that the ovaries of unpollinated flowers of clone D24 had all abscinded by two weeks after pollination. Self crosses of clone D24, however, resulted in initial ovary growth, but all fruits abscinded by the 4th week after pollination (Shaari *et al.* 1985). These studies imply two things. Firstly, that premature fruit drop (which occurs later in development) is an independent process to early ovary abscission caused by selfing, or lack of pollination. Secondly, they also suggest that self-incompatibility is probably not due to the inability of pollen to germinate or pollen tube abortion. If this were the case, it would not be expected that ovaries of selfed flowers would stay on the tree significantly longer (2 weeks) than those of unfertilized flowers, which was the case in the study of Shaari *et al.* (1985).

Self-incompatibility : It has been known for some time that some durian trees are self-incompatible (Coronel 1966); although crossing and selfing tests with named clones have been conducted (Jamil 1965), no details seem to have been published. This is unfortunate as such information would be useful in determining good clonal mixtures for orchards and for the production of better clonal material in the future. The Malaysian clone D99 has been shown to be self-compatible (Zainal Abidin and Nik Masdek 1992). Clone D24 (Shaari *et al.* 1985), and the Thai cultivars Gumpun and Luang (Lim *el al.* 1992) have been demonstrated to be self-incompatible. However, compatibility information for the many other clones/cultivars is not available.

The hermaphroditic flowers of the wild species *D. griffithii* have been shown to be self-incompatible (Ha *et al.* 1988). However, Tinggal (1993) states that the uniformity in fruits from different individuals of the wild species *D. kutejensis* suggests that the species is probably very homogeneous and self-compatible. As for *D. zibethinus*, there are several possible physiological explanations that can be put forward to explain self-incompatibility.

Heterostyly : Chin and Phoon (1982) claimed that there is heterostyly between different durian clones, although they presented no evidence for this statement. My personal observations (unpublished) of the stylar lengths of different durian clones show a lack of distinct size groupings between clones. Lye (1980) described several differences in stylar morphology that apparently exist between clones, but he did not mention stylar length. The study of Shaari *et al.* (1985), as mentioned previously, showed that unfertilized ovaries abscinded much earlier than did those of selfed flowers of a self-incompatible clone. Heterostyly would not explain this observation. Personal observations, and the work of Lye (1980) have shown that there is definite heteromorphy in stigma and styles between clones. Despite these differences in stylar morphology, selfed pollen has been shown to germinate on the stigmas of selfed flowers (Namuco 1978). Furthermore, pollen grains collected from fallen staminal phalanges will germinate after storage at room temperature for 48 hours, thus stigmatic exudate is not strictly necessary for germination. Thus, it seems unlikely that stigmatic heteromorphy contributes to or is associated with self-incompatibility mechanisms.

Mechanisms of self-incompatibility : There are two other schools of thought regarding the mechanism of self-incompatibility in durian. Firstly, Shaari *et al.* (1985) stated that incompatibility is due to pollen tube arrest at the base of the stigma; however, their claim is based on a previous research paper that could not be located for examination. Furthermore, their own data shows quite clearly that selfed ovaries abscind more slowly than do those of unfertilized flowers which suggests that at least the early stages of seed development are occurring in selfed ovaries. The only supporting evidence that I am aware of for the pollen tube arrest hypothesis is the observation by Soepadmo and Eow (1977) that the length of pollen tubes produced *in vitro* is dependent on sucrose concentration in the medium. While an incompatibility mechanism based on differential pollen tube growth due to varying levels of available sucrose is conceivable, it would not explain the results of Shaari *et al.* (1985).

Empirical evidence : Namuco (1978) showed that self-crossed pollen from a known self-incompatible tree actually germinated on the stigma, and that fertilization and initial endosperm development occurred. Unfortunately, the growth of the pollen tube through the style and actual syngamy was not observed in Namuco's study, which would have added further weight to his conclusions. However, his observation of zygotes and initial endosperm development is strong circumstantial evidence that these processes did occur, especially since there is no evidence that durians can produce seeds parthenogenically. Thus, a second hypothesis regarding self-incompatibility invokes early endosperm or embryo abortion as a mechanism rather than pollen tube arrest. Namuco's conclusions also support and explain the data of Shaari *et al.* (1985). Namuco (1978) showed that seed development started in the selfed flowers of an unnamed durian clone, but all selfed ovaries had abscinded by 10 days after pollination. Lim *et al.* (1992) reported that selfed fruits of two Thai cultivars (Gumpun and Luang) aborted within 3 weeks, unfertilized flowers, however, aborted after only 2 days. Thus, several independent studies show a timing difference between the abscision of unfertilized ovaries and selfed ovaries, which does suggest a difference between the two events; further, the exact timing of these events may vary between clones.

If durians have evolved under selective pressures favouring outcrossing, it is possible that several mechanisms of self incompatibility are exploited, perhaps even in addition to the two mechanisms suggested previously. Different mechanisms may function to different extents in various clones. This is somewhat supported by the varied times taken for fruit abortion using trees of different clonal origins as mentioned above. Further, Lim *et al.* (1992) state that, while selfings of the Thai cultivars Gumpun and Luang resulted in abscision within three weeks, selfings of the cultivar Kob resulted in mishapened fruit. Thus, there appears to be degrees of compatibility between clones rather than a strict compatibility/incompatibility relationship. Again, this is easier to explain by what must be a continuously varying trait such as the timing of embryo or endosperm abortion than by a simple two state phenomenon such as pollen tube arrest.

As previously mentioned, Jamil (1966) reported differences in the timing of anther dehiscence between clones. Ridley (1922) even reported encountering specimens of *D. zibethinus* upon which only male flowers were produced, the female parts being aborted; although this is definitely not the case with clones such as D24 as discussed above. Much research (Valmayor *et al.* 1965; Coronel 1966; Salakpetch *et al.* 1992) indicates that the stigmatic surface is receptive to pollen long before the anthers dehisce, thus stigmas would be open to pollination on the day of anthesis before their own pollen was released. Together, these observations suggest that varied mechanisms to promote outcrossing, and prevent self-fertilization are exploited in durian. Thus, although self-incompatibility in one durian tree (clone unnamed) reported by Namuco (1978) was likely due to either embryo or endosperm developmental arrest, other mechanisms may also be at work. Durian reproduction may be even more complex than can be explained by a simple compatible/incompatible system; some research has hinted that crosses using pollen from different clones result in different percentage fruit drops (Jamil 1965; Polprasid 1969). More research on the mechanism(s) of self and inter-compatibility in durian is needed. This is likely an area that will provide interesting and rewarding results.

Premature fruit drop : As mentioned above, premature fruit drop occurs after all abscissions due to a lack of fertilization or self-incompatibility. Yaacob *et al.* (1978) suggested that it may be due to some physiological disorder within the aborted fruits; however, pathology may not be necessary to explain this phenomenon. The number of harvestable fruits is not necessarily correlated with the number of successful pollinations above some basal level. As previously mentioned, the fruit set of durian flowers is quite low (Soepadmo and Eow 1977; Mardan and Zainal 1986). Other authors have reported very high percentage fruit set using artificial pollination (Valmayor *et al.* 1965; Coronel 1966). The discrepancy between these high values and the low values previously described probably lies in the number and distribution of flowers pollinated. Durian trees produce large number of flowers, but owing to the large size of a mature durian fruit, it is undoubtedly impossible for all flowers produced to develop into mature fruits, even if the fruits are all healthy. Polprasid (1969) noted that trees with more flowers had a lower percentage fruit set. Thus, even if all flowers on a tree are suitably pollinated, the tree must, and apparently does, have some mechanism to selectively abort some of its excess fruits. The study of Chandraparnik *et al.* (1992) showed that trees treated with paclobutrazol and thiourea had a more even distribution of flowers throughout the canopy, and had a larger number of developing fruits at 5 weeks after pollination as compared to control trees.

There is likely an upper limit to the number of mature fruits which can be produced, this number being much lower than the total number of flowers produced. Thus, artificial pollination above this limit is not useful. Future studies on percent fruit set of durian and the effect of the distribution of these fruits on the tree are necessary to define the limits of fruit set; this is likely to vary between clones. Clones with highly desirable fruits are frequently very poor bearers (Hassan n.d.). The possibility that this situation might be even slightly ameliorated by chemical spray at appropriate times, or by strategic hand pollination with pollen from particular clones remains open to investigation.

Manipulating premature fruit drop : The biochemical mechanism(s) behind the abortion of immature fruit is/are unknown, but may involve gibberellins (GA) (Mamat and Wahab 1990, 1992). Application of GA (largely GA3 with traces of GA1, GA4 and GA7) to fruit stalks of 6 weeks old fruits reduced percentage fruit drop, endogenous GA levels (measured as GA3 equivalents) of durians have also been shown to decline during fruit maturation (Mamat and Wahab 1992). Application of GA to trees has been shown to inhibit early flowering. The use of paclobutrazol (a suppressor of GA production) increases the number of inflorescences per branch, the percent branches that are flowering, and the overall number of flowers per tree (Chandraparnik *et al.* 1992).

Leaf flushing : Durian trees typically produce a flush of new leaves 3-8 weeks after anthesis (Salakpetch *et al.* 1992). Leaf flushing in durian is thought to contribute to premature fruit abscision and hence decrease percentage fruit set. To test the validity of this assumption, and the capacity of plant growth regulators to delay the onset of leaf flushing, foliar sprays of several substances were tested on mature durian trees (Punnachit *et al.* 1992). 2500 ppm mepiquat chloride (300 g/20 l), KNO_3 and 2500 ppm daminozide, and (500 g/20 l) low nitrogen (0-52-34) foliar fertilizer were found to be effective in delaying flushing, while GA3 and Multigold^{â} (a foliar fertilizer) stimulated flushing. KNO_3 treatment resulted in much higher retention of immature fruits on the trees until maturity, and an overall increase in the average weight of mature fruits. Additionally, an increase in the flesh to fruit weight ratio and an increase in the number of aborted seeds over control trees was found using this treatment. Cultar^{â} (paclobutrazol) has previously been shown to reduce leaf flushing in durian (Kittichontawat 1988). Kittichontawat (1988) demonstrated that although paclobutrazol did not affect fruit set, soluble solids and the percentage of fruit set or seeds and the overall fruit weight increased by such a treatment.

Salakpetch *et al.* (1992), in an experiment to probe source-sink relationships, sprayed mature trees with 5 different treatments (0-52-34 fertilizer, glucose-humic acid, 250 ppm Cultar^{â}, 500 ppm Cultar^{â} and controls). All the chemical treatments caused an increase in the number of harvestable fruits per tree over the controls. The glucose-humic acid treatment, chosen to increase the size of the source of nutrients, caused a 54% increase in harvestable fruits. The low nitrogen fertilizer which was meant to suppress leaf flushing, and thus reduce competition for nutrients, did increase the number of harvestable fruits, however, a higher number of deformed fruits were produced, and thus marketable value was not increased. Treatments with Cultar^{â}, a GA inhibitor which retards foliage and fruit growth, were intended to prolong development and hence reduce competition for nutrients. Treatments at both concentrations resulted in an increased harvest and marketable yield. Voon *et al.* (1992) reported the highest increase in harvestable fruits over control treatments in Chanee durian from foliar sprays of 1000 ppm Cultar^{â} in the early season. Application of Cultar^{â} in the late (normal) season produced only a minor increase in yield (at 250 ppm), and actually decreased yield of harvestable fruits at higher concentrations.

Species which feed upon durians : Some researchers have provided information regarding the species of animals which naturally feed upon durian fruits. Hubback (1941) reported that elephants trample the fruits and then eat the orangutans fed on durians (Wallace 1869; Davenport 1967; Shetford 1985). Rijksen (1978) records that orangutans also eat the fruit of *Durio oxleyanus*, which constitutes an ‘esteemed’ food item of the orangutans of Ketambe. Orangutans have developed behaviours to aid in the plucking, carrying and opening of durian fruits (Rijksen 1978). Corner (1964) enumerates rather graphically several species of animals which feed upon durian. According to Barrett (1912), wild pigs eat durian fruits. A species of Philippine flying squirrel (*Sciuropterus mindanensis*) is known to feed on the fruits of *D. zibethinus* (Rabor 1939). Gardner (1847) recorded that monkeys eat the seeds of *Durio ceylanicus* Gardn. [=*Cullenia ceylanica* (Gardn.) K. Schum. *sensu* Kostermans].

Kostermans (1953b) states that most of the fruits of wild species of durians are lost by damage from squirrels, monkeys, tupais and hornbills. Hawkins (1986) claims that durians are eaten by elephants, tigers, deer, rhinoceros and monkeys. Watson (1984) claims the fruit is even attractive to the domestic cat.

Natural dispersal of seeds : Ridley (1894) speculated on the dispersal of several durian species by bears, birds (especially hornbills) and even turtles. *D. zibethinus* is perhaps dispersed by bears. The wild bear, *Helarctos malayanus*, is known not only to eat fallen fruits, but even to climb trees to obtain durians (Ridley 1894). Ridley further speculated that *D. oblongus* seeds are dispersed by birds, as it is native to Singapore where there are no bears. Ridley related that upon feeding a fruit of this species to a wild bear (*Helarctos malayanus*), it ate the arils with great gusto but refused to eat the seeds. An unnamed *Durio* species [Ridley described it as having small red arils=*D. graveolens*?] is probably dispersed by hornbills. This sentiment is echoed by Browne (1955): ‘I well remember being seen out of a durian grove by a tiger.’ Whitmore (1990) said: ‘Tigers are notorious for their passion for durians’. Rutten (1939) reported the germination of durian seeds in elephant faeces, but none became established.

Meijer (1968) noted that the fruits of the cauliflorous *D. testudinarum*, which bears fruits at the base of the tree, are widely believed by natives to be eaten by tortoises. Ridley (1894) recorded that this species is known in Borneo as the tortoise durian.

The seeds of *D. oxleyanus* are severely damaged by orangutans in attempts to open the fruit (Rijksen 1978). Rijksen (1978) suggests that the sun-bear and tigers are probably the main dispersers of seeds of this species.

Fruiting Seasons

Maturation of buds : The floral buds take up to 5 months to become mature fruits. In my experience, mature fruits of clones D8 and D24 require 95-110 DAP (days after pollination) to mature. D99 requires only 95-100 days (Zainal Abidin and Nik Masdek 1992). Mon Thong durians are harvested 120-130 DAP (Chattavongsin and Siriphanich 1990a). Durians typically have two seasons during the year, a major and a minor one. The same trees do not necessarily bear fruits in both seasons (Browne 1955).

Several authors have recorded, for various locations, the months in which durian trees typically flower and fruit (Table 8). The maturation of durian fruits is traditionally indicative of the end of the dry season (Dove 1985).

Floral buds are produced well in advance of flowering and are usually dormant for at least one year, the breaking of bud dormancy is facilitated by cool nights (Ong and Lee 1981). Some floral buds do, however, develop from initiation to anthesis without interruption by a dormant state (Subhadrabandhu *et al.* 1991). Occasionally, floral initials can revert back to vegetative growth (Subhadrabandhu *et al.* 1991).

D. griffithii has synchronized flowering, although some individuals produced small numbers of flowers asynchronously (Yap 1980).

Table 8. Durian seasons in different geographic areas

Country/province	Flowering/fruiting season
Malaysia	
Sabah	Fruiting August to December, peak in October (Davenport 1967)
Sarawak	Main fruiting season January-March (Mohamad Idris 1987)
Peninsular	Main fruiting season June-August (Mohamad Idris 1987)
Peninsular	Two fruiting seasons June-July, August (Anon. 1982b)
Penang	Fruiting June-August (Low 1836)
Jambu Rias, Pahang	Flowering in April (major) and August (minor), fruiting August and February. The major fruiting season harvest in one year was 266.6 kg/hectare in February and 2269 kg/hectare in August (Chiow 1976).
Philippines	
Mindanao and Sulu	Flowering May-June, fruiting August-November (Rodrigo 1968; Galang 1955)
Los Banos	Flowering February, fruiting July to August (Namuco 1988)
Davao City	Flowering January to May, fruiting May-September (Pascua and Cantila 1991)
Indonesia	Flowering June-September, fruiting October-February (Rodrigo 1968)
Cambodia	Flowers in January, fruits in May (Chevalier 1935)
Sri Lanka	Flowering March-April, fruiting July to August (MacMillan 1909; Parsons 1932b)

(Contd....)

Table 8. Contd.

Thailand	Fruiting April-July (Visetbhakdi 1988)
Nonthaburi	Peak of the fruiting season is June 10-15 (Chimprabha 1964)
India	
Burliar Research Station	Fruiting July to September (Naik 1949)

Environmental effects on flowering : Watson (1984) stated that flowering is not photoperiod or temperature responsive in equatorial regions. However, the diurnal temperature range 23 months before harvest is the major climatic stimulus for flower induction (Ong and Lee 1981). A 10-14 days dry period was found to be necessary for the induction of flowering (Chandraparnik *et al.* 1992).

Pascua and Cantila (1991) reported that rainfall has a significant effect on the flowering of durian in the Philippines. The flowers emerge during or immediately after the driest months. Salafsky (1994a) notes that 'trees apparently will not flower without a prolonged period of warm dry days (or associated cool clear nights)'; in his study on the effect of El niño oscillation events on rural Indonesian agriculture.

Manipulating seasonality : Durians are only available during short day periods of the year. Attempts have been made to alter the timing of flowering to spread out the season and, therefore, make durian fruits more readily available throughout the year. Zainal Abidin *et al.* (1986) have suggested several ways of reducing the effects of seasonality on the price and availability of durians. They recommend exploiting differences in fruiting seasons that exist in different regions of Malaysia, as well as some useful characteristics of some Malaysian clones; for example, the ability of some clones to fruit twice a year and the use of early mid and late producing clones to extend the season. Previous and unobtainable work cited in Chandraparnik *et al.* (1992) has apparently shown that ethephon, daminozide, NAA (a-napthalene acetic acid), or fertilizer application are unsuccessful in inducing early flowering in durian; GA3 application has an adverse effect on early flowering. Chandraparnik *et al.* (1992) investigated the effect of foliar sprays of paclobutrazol (Cultar®), a suppressor of gibberellin (GA) production, on early flowering and fruit production on the Thai variety Chanee. They found that increasing concentrations of paclobutrazol positively affected the number of flowers produced per tree. Flowering of treated trees (using the highest concentration of paclobutrazol) began up to 43 days before that of control plants. However, the number of harvestable fruits produced, and average fruit weight was negatively affected by this treatment, treated trees also took 2 extra weeks to mature fruits. Thus, even at the highest concentrations of paclobutrazol used, a maximum of one month advance on mature fruit production over untreated trees was gained due to the extended developmental time. Chandraparnik *et al.* (1992) also investigated the effects of foliar sprays of thiourea on previously paclobutrazol treated trees. A somewhat linear relationship between the concentration of thiourea and the number of flowers produced was shown. Flower density was increased up to 400% over control trees, and the distribution of inflorescences throughout the tree was found to be more even than in the control treatment. The average number of fruits per tree at 5 weeks after anthesis was significantly increased, however, no indication of the effects on the numbers, size or quality of harvestable fruits was given. Lin (1992) proposed an irrigation forcing model to delay the production of durian inflorescences. This model has not been field tested.

Ecology, Origin and Distribution

Durio species are found growing in lowland and hill primary forests in Malaysia, up to 1000 m, at a density of not more than 3-4 trees per hectare (Soepadmo and Eow 1977). Durians (species not named) were recorded at a density of 3.7 trees per 40 ha in Ulu Kelantan forest, Malaysia (Whitmore 1990). Foxworthy (1916) states that 1.07% of the forest trees of the East coast of Borneo are *Durio* sp. based on an examination of almost 690 ha. In 1967, durian made up approximately 1 tree per 2.6 per km^2 in Sabah (Davenport 1967). The relative density of *D. griffithii* Mast. at Bukit Sebelah in Sumatra is recorded at 4.16 tree/ha (Mukhtar *et al.* 1990). *Durio* sp. tree densities of 4.4, 3.0 and 2.2 trees per hectare are recorded at Pasoh Forest reserve, Taman Negara and Krau games reserve respectively (Soepadmo 1979).

A map of the distribution of durian in Thailand is given by Kishimoto and Polprasid (1976), and a map of the suitability of different regions of peninsular Malaysia for the cultivation of durians can also be found (Anon. 1982b).

D. carinatus is an important species in peat swamp-forest of eastern Malaysia (Whitmore 1988), and Corner (1978) listed it as a fresh water swamp species. Additionally, Corner (1978) stated that *D. singapurensis* [=*D. singaporensis*] is common in fresh water swamp forests, and *D. griffithii* and *D. graveolens* occur in hillock-forests of this ecosystem. Corner also recorded the 2 related species *Coelostegia griffithii* and *Kostermansia malayana* as fresh water swamp forest trees; for the former, he estimated a frequency of 2 large trees per hectare while the latter was a dominant species with up to 30 large trees in 2 hectares.

Sutisna and Soeyatman (1985) examined a logged-over peat swamp forest, five years after logging, in 3 locations in Eastern Sumatra, Indonesia; Suakandis (Jambi Province), Sei Teban (Riau province), and Sei Lalan (South Sumatra province). In this study, *D. carinatus* was found at a density of 100.0 sapling stage individuals/hectare, 9.2 pole stage/hectare, 10.3 tree stage/hectare at Suakandis, no individuals of this species were recorded at the other two locations. *D. lowii* (the authors most likely mean *D. lowianus*) possibly was present only at Sei Lalan, measurements of number of individuals per hectare are 21.43 sapling stage/hectare, 10.29 pole/hectare and 1.86 tree stage/hectare.

Centre of diversity : Mendoza (1941) concluded that the centre of diversity of the genus was Borneo. About 20 of the approximately 30 recognized species are found in Borneo, 15 of which are endemic. There are 11 species which are found in Peninsular Malaysia and 5 of it are endemic. Only two recognized species are endemic to Myanmar. Thus, although the genus most probably originated in Borneo, it does seem to have spread up the Malay peninsula before all contemporary species had evolved. The centre of diversity of the genus is not in dispute, however, opinions abound on whether *D. zibethinus* is native or introduced to regions outside Borneo. Furthermore, there is some debate as to whether this species actually exists anywhere in the wild, or whether it is the descendant of some wild species.

Wild form of *Durio zibethinus* : Popeno (1920) stated that J.D. Hooker did not think that the natural distribution of *D. zibethinus* extended to the Malay peninsula, and furthermore that Hooker suspected that *D. malaccensis* might be the wild form. Although both these statements appear in ‘The Flora of British India’ by J.D. Hooker, they appear in chapter 26 on the Malvaceae written by M.T. Masters. Regardless of who made these claims, Kostermans (1958b) states, without explanation, that ‘Hooker’s suggestion that *D. malaccensis* is the wild form of *D. zibethinus* is, of course, entirely wrong.’ It should be mentioned, however, that there has been tremendous confusion as to what exactly constitutes *D. malaccensis.*

Van Steenis (1949) suggested that a species he discovered in Southern Sumatra (*D. spontaneus* Bakh.) is the closest wild ally of *D. zibethinus.* Kostermans (1958b), however, does not recognize *D. spontaneus* Bakh. as a valid species, rather he includes this specimen under *D. lowianus* Scort. et King. Although this species bears fruits similar to *D. zibethinus,* Kostermans does not speculate on a close affinity between the two species; rather, he opines that his newly erected species *D. wyatt-smithii* Kosterm. is perhaps the wild ancestor of the cultivated durian (Kostermans 1958b). Soegeng-

Reksodihardjo (1962) states that the ‘wild form’ of *D. zibethinus* need not be one of the extant wild species.

Some debate exists over the question of whether *D. zibethinus* is native or introduced to the Malay peninsula. Both Masters (1874a) and Ridley (1922) thought it unlikely that this species was actually native to the peninsula. As stated previously, the centre of diversity of the genus *Durio* is definitely Borneo. However, many wild species of *Durio* are, in fact, found on the Malay peninsula, some of them exclusively.

There has also been some debate as to whether durians exist naturally in the Philippines, or have been introduced. Wester and Barrett (1912), and Wester (1916b, 1921) recorded *D. zibethinus* as confined to Mindanao and the Sulu archipelago in the Philippines. Merrill (1926) listed *Durio* as a genus represented only by introduced species in the Philippines, and Van Steenis (1933) listed *Durio* as a non-native of the Philippines. Mendoza (1941) thoroughly examined this issue, and claimed that *D. zibethinus* occurs naturally on Mindanao and the Sulu archipelago as well as Palawan. Mendoza further concluded that durian occurs only as an introduced species in the Visayas and Luzon. Additionally, Mendoza recorded the discovery of a wild species (*D. testudinarum*) growing naturally on the island of Palawan, further strengthening his claim of endemism. Mendoza (1941) hypothesized that durians became indigenous due to a land bridge that connected Palawan with Borneo during the pleistocene era. Vendivil and Reynoso (1983) recently reported another wild species, *D. graveolens* Becc. growing along a river in a secondary forest in Palawan.

Durio zibethinus in the wild : Van Steenis (1949) believed that *D. zibethinus* has never actually been found in the wild, and Whitmore (1990) regarded *D. zibethinus* as completely unknown in the wild. Kostermans (1958b), on the other hand, stated that *D. zibethinus* is probably wild in Sumatra and Borneo. This and the question of its being native or introduced to certain regions share one property in common, i.e., both questions are undoubtedly impossible to answer. Aboriginal peoples have aided in the propagation of durian (knowingly or unknowingly) by eating, trading and discarding the seeds of the fruit, probably for millennia. As it can never be ascertained whether a tree growing in a forest grows there because of the actions of these people or not, such arguments are purely semantic, and can provide little on any useful information or insight.

Attempts at introduction : Durian trees can tolerate temperatures up to 46°C in parts of Thailand and India (Watson 1984), but growth becomes limited below 22°C, and temperatures below 10°C cause premature leaf abscission (Watson 1984). Although found in Borneo, much of Indonesia, Peninsular Malaysia, Thailand, Southern Myanmar and a few islands in the Philippines, durians were never introduced into New Guinea, probably because Malay and Indonesian traders never settled in New Guinea (Knight 1980). In more recent times, durian has been grown at the Lowlands Experimental Station in Papua New Guinea (Bettencourt *et al.* 1992), and successfully grown in the Solomon Islands at the Dala Experiment Station (8.5° South latitude) (Anon. 1968). Durian has also been grown on the Island of Ponape in the Kolonia Botanic Gardens (7°N) (Kanehira 1935). In the Philippines, it is found mostly in Mindanao and the Sulu Archipelago (5-10° N), but it has fruited in Laguna and Quezon provinces (Galang 1955). Recently, durian has been introduced and successfully cultivated in Northern Australia, however, it can only be grown in this country north of 17° (Watson 1993).

There are two species from Myanmar of *Durio*, however, *D. zibethinus* is probably found there only through introduction. Gamble (1881) states that it is wild in South Tenasserim, but it is cultivated as far North as Moulmein. According to Knight (1980), it can only grow in Tenasserim (the southern most part of Myanmar), but it cannot grow above 16°N in Myanmar. Durian apparently formed forests in Lower Tenasserim from 14°N southwards (Kurz 1877; Gamble 1972). Further, in the 'Report on the Settlement Operations in the Amherst District 1891-1892', the durian is believed to have been introduced into the Amherst district of Myanmar from seeds planted from a fruit washed up on the shore from a wrecked cargo ship in the 1700s (Anon. 1893).

Durian was introduced into Britain as a greenhouse curiosity in 1825 (Anon. 1849), but has never flowered or fruited in Europe. MacMillan (1908) stated that a few young trees were once grown in Syon House Gardens near London, and were apparently presented as a gift to Queen Victoria. The 29th edition of the Official Guide to the Royal Botanic Gardens and Arboretum, Kew Gardens (1885) lists durian as part of the collection.

According to Soegeng-Reksodihardjo (1962), the first trees to fruit outside Asia were grown in Dominica from seedlings shipped from Kew Gardens in 1884. A tree introduced to the botanic gardens at St. Aroment in Dominica (15° N) grew vigorously and fruited after about 10 years (Anon. 1894).

Durian has been grown in several locations in and about India. Firminger and Burns (1918) gave the following diagnosis of attempts to grow durian in Calcutta: 'they have never risen to more than 1 metre in height, when they have uniformly died off, the climate of that latitude being quite unsuited to them'. However, Firminger also recorded that trees grown from seed had reached heights of 2 metres after three years at the Burliar Experimental Gardens at the base of Nilgiri mountains at an elevation of 760 m in southern India (11° N). Some research on vegetative reproduction by grafting has since been carried out at Burliar (Khan and Sambashiva Rao 1952). Durian has also been introduced into Port Blair in the Andaman Islands (12° N) (Parkinson 1923).

In Sri Lanka, the Peradeniya Botanic Gardens has/had trees over 40 m tall (MacMillan 1909). Additionally, *Durio ceylanicus* Gardn. 'is found in Wooded hills near Galle in the Southern Province, but little above the sea level, and very common in forests in the Central province at an elevation of about 3000 feet (910 m). Flowers in May'—Gardner (1847).[7]

There have been some attempts to introduce durian into the West Indies and the Americas. Durian has been planted at the Botanical Gardens in Trinidad (Pascoe 1882); however, 'only one plant exists in the St. Clair Experiment Station...It does not seem readily amenable to the Trinidad conditions of climate' (Freeman and Williams 1928). Bailey (1914) stated that durian has been successfully introduced into Jamaica, however, I have been unable to locate any other information or confirmation regarding this. Baker (1969) reported a single mature tree growing in the botanical gardens at Lancetilla, in the Honduras.

Durian was described as 'at home' in the Canal Zone Experiment Gardens (9° N) in Panama (Allen 1941). Attempts have been made to introduce durian to southern Florida (Green and Koopman 1978). According to Knight (1980), the USDA has made four attempts to introduce durian into southern Florida, all of which failed. It is not just the temperature extremes of southern Florida that prevent its introduction, but the peculiar [coralline] high pH limestone soils are not suitable for its cultivation (Lee 1985). An interesting exception is an account of frost damage suffered by various ultra-tropical trees in Florida during the 1989 winter (Whitman 1990) (I mention this study since information on the effects of freezing on durian trees is very scarce). In December 1989, the night temperature dropped to 0°C on two consecutive nights. A single specimen of *D. graveolens*, covered with 63 shade cloth, survived the frost and lost only 45% of its foliage. A very lucky tree indeed.

A few trees are found in Hawaii, and many bearing trees in Zanzibar (Morton 1987). Durian is mentioned in Neal's 'In Gardens of Hawaii' (1965) and a small germplasm collection exists in Hilo (Bettencourt *et al.* 1992).

Finally, in this respect, I relate the following amusing anecdote regarding the introduction of durian to South America: 'They say people in the South Pacific Islands will almost kill each other, or will divorce their wives (one at least) to get a durian; but when I took one from Lancetilla and left it in the bedroom of a friend, he rushed across the hall that night and said, 'Come over

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[7] The species to which Gardner refers is probably what is now termed *Cullenia ceylanica* (Gardn.) K. Schum. (see Table 1).

here and help me hunt; there must be a dead rat in my room but I can't find it' — Popenoe (1956).

Clones

Clonal selection and hybridization : To date, well over 100 different Malaysian clones of durian have been registered (Lim 1990), which are distinguished mainly by fruit characteristics; probably more than 200 Thai durian cultivars are recognized (Hiranpradit *et al.* 1987, 1992) (300 according to Malo and Martin 1980a,b). Polchart (1952) tabulated 129 local varieties from the Dhonburi area of Thailand alone. Fruits of the more desirable clones are sought after and fetch a higher price in the market place (Fig. 3). Polprasid (1981) described the use of local durian contests in Thailand to make known local cultivars and maximize accessions of good durian germplasm. Thai durians have been divided into six groups based on fruit morphology (Hiranpradit *et al.* 1987); a detailed analysis of leaf, aril and spine morphology and fruit shape were also provided. An itemized list of criteria for assessment of varietal desirability has been established to aid the identification and collection of new clones (Hiranpradit *et al.* 1992).

Despite the numerous Thai cultivars that have been identified, only four (Chanee, Kradum, Mon Thong, Kan Yao) are grown on a commercial scale (Subhadrabandhu 1993). Clones or varieties of other durian species have not been produced or characterized. Clonal selection of durian began as early as 1922 (Hasan and Yaacob 1986). Unfortunately, clones with very high quality fruits (e.g. D2) are often not high yielding, while those which are prolific yielders (e.g. D24) have lower quality fruits (Hassan, n.d.). Hassan (n.d.) has suggested a mixture of clones is good practice in a durian orchard to compensate for good clones being sparse bearers, and for the fact that many durian clones are self-incompatible. The following clonal mixture is suggested: 60% D24, 25% D16, 5% each of D10, D8, D2 (Hassan n.d.). Kwok-Kong (1974) suggests essentially the same ratio with the substitution of 5% D7 for 5% D10. Two planting systems described by Zainal Abidin (1991b) make use of a clonal mixture of 50% D24, 30% D99, 20% D98/D114. A row planting system and some data on the growth and productivity of several different durian clones grown at the experimental orchard at the Universiti Pertanian Malaysia are given by Yaacob *et al.* (1978). Efficiency indices of several individuals of three clones have been published (Hasan and Yaacob 1986).

Natural hybrids between *D. zibethinus* and *D. graveolens* are known (Soegeng-Reksodihardjo 1962). Soepadmo and Eow (1977) suggested that red-tinged flowers of *D. malaccensis* reported by Heaslett (1972) may have belonged to a hybrid between *D. malaccensis* (normally white flowered) and *D. lowianus* or *D. pinangianus* (pink or red flowered).

Artificial hybridization of *D. zibethinus* with several wild species (*D. graveolens, D. oxleyanus, D. kutejensis*) has been attempted to improve fruit quality (Hambali *et al.* 1989). These authors reported no fruit set in crosses between *D. zibethinus,* and *D. oxleyanus, D. oxleyanus* and *D. graveolens* or between *D. zibethinus* and *D. kutejensis*. Interspecific crosses between *D. zibethinus* and *D. graveolens* yielded viable seeds. Subhadrabandhu *et al.* (1991) have recommended that attempts be made to hybridize *D. zibethinus* with *D. acutifolius* and *D. griffithii* as both these wild species flower more reliably than *D. zibethinus.*

A durian hybridization program was started in Malaysia in 1967. Hybrids of 11 clones of *D. zibethinus* have been made and are being evaluated (Chan 1992). In 1992, Zainal Abidin *et al.* reported on the success of the first commercially-produced clonal hybrid trees which show, among other traits, improved disease resistance.

Clonal identification : The clonal propagation of durian has become widely

Figure 3. Durian fruits of clone D2 and D24 for sale by the street side in Kuala Lumpur. Durians of known and desirable clonal origin fetch a much higher price in the marketplace.

Figure 4. The development of a durian fruit (Clone D8). The ovary undergoes little expansion in the first month of development.

A) A fruit at 56 DAP (days after pollination), approximately 9 cm in length. The bases of the peltate scales of the ovary have developed into spines.

B) A fruit at 63 DAP. The fruit is approximately 10 cm in length and shows little change from 56 DAP.

C) A fruit at 88 DAP. The fruit is now 19 cm in length and the spines are more fully developed.

D) A fruit at 95 DAP. The fruit is now 25 cm in length and little change occurs before the fruit abscinds at approximately 100 DAP.

established; in Malaysia between 1986 and 1989 over 800 000 clonally propagated durian trees were produced for planting (Ali 1993). This increase has led to a need to positively identify clonal material as mistakes have expensive and very long-term consequences. Watson (1993), for example, reported that problems in the introduction of durian as a crop in Australia were due to the importation of misidentified clones.

Durian clones and varieties have been selected mainly for desirable fruit characteristics. Thus, durian varieties can often be identified by differences in fruit morphology. As mentioned previously, the shape of the spines has been described for several Thai varieties (Hiranpradit *et al.* 1992). Hiranpradit *et al.* (1987) claim that fruit shape and spine morphology are useful for characterizing durians into groups, and both are highly heritable characteristics. However, given the vast number of clones/varieties now recognized, it seems rather unlikely that all fruits could be sufficiently identified from the shape of their spines.

As mentioned above, durian clones have mainly been selected for desirable fruit characteristics, but consistent differences in the morphology of the flowers seem to exist between clones. Some of these differences have been used to distinguish between several clones (Lye 1980). Lye’s study relied mainly on stylar characteristics (5 different classes of stylar form were identified) to classify the floral buds of several durian clones. Although differences in stylar form do exist (e.g. width, degree of crookedness, etc.), the natural variance within a clone is quite large (personal observation). No indication of the variance of floral bud characteristics within a clone is given by Lye (1980). Thus, how easily clones can be distinguished in practice by floral characteristics remains to be shown. As there are clonal differences in stigmatic shape and colour, number of filaments per stamen, etc. (personal observations), the identification of clones by floral characteristics may be possible.

The use of flower characters seems more promising than spine morphology as flowers possess more characteristics that can be easily quantified than do spines. Furthermore, young durian trees will often start to flower before they are old enough to actually produce fruit (Lye 1980), so flower morphology may allow earlier identification of clones. Both the aforementioned methods could be useful in positively identifying fairly mature trees which are intended for use in the production of budwood, but would not be of use in identifying or verifying the clonal origin of batches of young grafted trees.

Recently, preliminary work on clonal identification using isozymes isolated from leaf samples, and separated by starch gel electrophoresis, has been published (Salma 1993). This preliminary work showed that 5 durian clones used in the study could be distinguished by this technique; the isozyme patterns studied were those of acid phosphatase, alkaline phosphatase and peroxidase.

Techniques such as isozyme assays and perhaps RFLP mapping would obviously be useful and very powerful tools in the positive identification of durian clones, and should be further investigated.

Nursery Care and Cultivation

Seeds : Direct sowing of seeds in the field is not recommended due to damage from rodents (Anon. 1953a). Shaharuddin (1979) has also reported large losses of germinated seeds due to rodents which eat the epicotyls. Although seedlings usually cannot survive such injuries, De Vogel recorded an instance of a seedling of *D. zibethinus* in which a ring of buds developed from a region between the cortex and the stele on a seedling whose epicotyl (including the top of the hypocotyl) had been bitten off (De Vogel 1980). If planted in a seedbed, Coronel *et al.* (1983) recommended that seeds be planted 1 cm deep with a spacing of 4-6 cm between them. Coronel *et al.* (1983) also recommended the coating of the seeds with fungicide.

Branch pruning : Some of the earliest literature on this subject recommended little or no pruning of durian trees (Parsons 1935; Mohamad Idris 1987). Coleman (1959) stated that, when growing in a jungle, the lower branches of durian trees are ‘self-pruning’, whereas orchard grown trees are pyramidal in shape with low branches. Some authors have recommended pruning of young trees to reduce wind resistance in particularly windy areas (Polprasid 1961b). The pruning of the lower branches (especially in young budded trees) to prevent infection of *P. palmivora* has also been recommended (Lee and Loh 1966; Navaratnam 1966; Tidbury 1976; Namuco 1988). Coronel *et al.* (1983) suggested that all branches lower than 2 m from the ground be removed. Zainal Abidin *et al.* (1991) have published detailed pruning instructions for durian trees. Setiadi (1991) gave considerable advice on pruning, shaping and training durian trees. In Thailand, trees are sometimes topped at 10 m (Subhadrabandhu *et al.* 1991). Flower buds and small fruitlets are also occasionally thinned to leave 1-2 fruits per inflorescence and 50-150 fruits per tree (Subhadrabandhu *et al.* 1991).

Root pruning : Very little information on the roots of durian was available until very recently. ‘The tree is very impatient of disturbance of its roots’, (Anon. 1935) however, another early report stated that cutting the roots of durian seedlings with a spade promotes the production of a fibrous root system reducing loss during transplanting (Feilden and Garner 1936). More recently, Chong (1985) suggested that the roots of durian should not be pruned to reduce circling or kinking (as commonly occurs when young trees are grown in polybags), as the trees are very sensitive to such treatment. This conflict has very recently been resolved by Ghani (1992a,b). This empirical study demonstrated that root pruning increased the growth of a fibrous root system, contributed to increased overall growth and stem enlargement, and increased survival rate of transplanted trees.

Application of fertilizer : According to Kanapathy (1976), durians do not require much fertilizer to be successfully cultivated. However, problems associated with low nutrient levels likely exist. Ding (1988) reported that up to 15% of durian trees growing in polybags in some nurseries show nutrient deficiency symptoms. Magnesium, manganese and copper deficiencies are the most common deficiencies detected in the field (Zawadha *et al.* 1993).

Chiow (1976) recorded little difference in girth measurements between manured and non-manured control plots, especially in early tree growth. However, manured trees of four different clones yielded well over 4 times as much weight in mature fruit as did controls (Chiow 1976). A manuring schedule for durian trees is presented by Hassan (n.d.). Watson (1984) stated that organic manures should actually not be used, as they are conducive to *P. palmivora* infection. In the last 15 years, numerous different fertilizer recommendations have been published for durian, most of them varying widely in their advice from completely balanced fertilizers to high nitrogen or high potassium fertilizers. For example, monthly application of 5g 6:6:6 (N:P:K) fertilizer for durian seedlings is recommended by Morton (1987). Kanapathy (1976) suggested the use of 18:11:5:2.5 for the first 5 years and 13:9:15:3 or 12:6:22:3 afterwards; a fertilizing schedule is also given in this work. Three applications annually of 15:15:15 until 5 or 6 years of age followed by a higher potash fertilizer should be used according to Mohamad Idris (1987). Woller and Idsava (1981) also recommended a balanced fertilizer for the first few years (1st year 13:13:13 at 0.5 kg/tree, 2-3 years 13:13:13 at 1.5 kg/tree), but then recommend a high phosphorous fertilizer (4-5 years 12:24:12 at 2 kg/tree). In Thailand, fertilizers are added by drip lines; 1:1:1 as flowers develop, 2:1:2 at harvest times and 1:1:1 at 4 months after harvest (Watson 1984).

Perhaps the most useful fertilizer recommendations come from various nutrient removal studies. Ng and Thamboo (1967) performed nutrient removal studies on durian fruits. They provided the following estimate of nutrients removed from the soil to produce fruits (assuming a yield of 6720 kg/ha): N

Table 9. Nutrient content of D8 durians on a percent dry matter basis (Jamil 1966)

Plant part	Nutrient content				
	N	**P**	**K**	**Ca**	**Mg**
Pericarp	0.66	0.09	1.70	0.23	0.23
Seed	1.14	0.18	1.17	0.06	0.21
Aril	1.05	0.81	1.13	0.04	0.09

16.1; P 2.72; K 27.9; Ca 1.99; Mg 3.26 (all amounts in kg/ha). Ng and Thamboo (1967) also provided estimates of the amounts of each of these nutrients in the seed, aril and pericarp of 4 different clones, on a percent dry-matter basis. Jamil (1968) reported the following results of nutrient removal studies on durian (in pounds of nutrient removed per 1000 lb of fruit): N 2.4; P 0.35; K 4.0; Ca 0.30; Mg 0.47. The nutrient content of durian fruits has also been measured (Table 9).

Results of nutrient removal studies of entire trees of different ages grown in an experimental orchard indicate that young durian trees do not need excessive amounts of fertilizer, their root system is probably not elaborate enough to take up excess nutrients, if provided (Yaacob 1983). Furthermore, after trees have become established, nutrient removal data indicated they also do not require heavy fertilization. Nutrient removal by fruits in the first two years of bearing was found to be very low (Yaacob 1983). Based on these results, Yaacob (1983) recommended the use of 2-4 kg/tree of 16:6:22:3 fertilizer per year.

What all nutrient removal studies have shown is that K is much more important than N for durians, being the major element removed by the fruits and by the tree itself, the amount of P being small in comparison. This is supported by the study of Jamil (1992c) who examined the effects of N, P and K on young durian trees. Increasing N was found to have no visible effect on plant form, increased P increased the tree height, while increased K greatly affected tree form. Thus, of the former cited fertilizer suggestions, those recommending high potassium formulations are the most valid.

Complete fertilizing schedules (and probably the most empirically derived) for durian trees from 1 to 10+ years of age are presented by Zainal Abidin *et al.* (1991) and Zabedah *et al.* (1993). Zabedah *et al.* (1993) also presented recommendations to overcome magnesium, manganese and copper deficiency.

Foliar sprays of KNO_3 and other substances during fruit development increased the overall size of fruits, the edible portion (aril) of the fruit, and seed abortion (Punnachit *et al.* 1992). These effects were presumably achieved by the reduction of competition for nutrients by inhibition of leaf flushing (Punnachit *et al.* 1992).

According to a study by Jamil (1992a), N, P, K, Cu and Zn occur as a decreasing percentage of leaf composition as leaves mature, whereas Ca, Mn and B increase in mature leaves. The study of Anuar *et al.* (1992) suggested that leaf nutrients of trees grown in wet zone area do not reflect tree phenology. Unfortunately, this study suffered from sampling problems and hence the results are limited in scope; actual data was, in fact, not presented in their paper.

A very informative investigation was carried out by Lian (1981). In this study, durian seedlings were grown in sand and selectively deprived of various nutrients. Although no fertilizer recommendations are given, a description and figures of leaves exhibiting different nutrient deficiencies are presented, which is valuable in the diagnosis of possible nutrient deficiencies in durians growing in poor soils.

Soil conditions : *D. zibethinus* is apparently suited to a wide variety of soil types (Hassan n.d.), although peat, soils with poor drainage and very sandy soils are to be avoided. Durians are suited to lateritic soils (Parsons 1932b) and have grown well on granite derived soils. Trees do better in less fertile upland soils than in more fertile marine or alluvial soils (Hassan n.d.; Kanapathy 1976). Trees do best in deep, well drained, loamy soils with a high content of organic matter (Hassan n.d.; Coronel 1986). Durian is suited to low country wet zones from sea level up to 460 m (Parsons 1932a). Although durian is tolerant of poor soils (Anon. 1953a), on stiff clays and poor soils the trees are stunted and often unproductive (Anon. 1935). *D. zibethinus* has been described as having low to moderate tolerance to flooding/waterlogging, however, durians can tolerate infrequent prolonged flooding (Maas *et al.* 1979). Durians have a low tolerance of shallow soil (depths greater than 75 cm are recommended (Maas *et al.* 1979)), a moderate tolerance of drought, moderate to high tolerance of infertile and acid soils, and may be suitable for growth on podzols (Butt and Sia 1982). Some notes on the suitability of durians to several soil types and ecological regimes are presented by Terra (1952). A ground-water salinity of less than 1000 µmhos/cm is recommended for durian (Maas *et al.* 1979).

Durian is suitable for planting on undulated or sloped land with inclines up to 35° (Hassan n.d.). Maas *et al.* (1979) stated that durian is suitable for growth on slopes up to 25°. A study of moisture requirements of young trees on steep (30°) and low (19°) slopes demonstrated that trees on steeper slopes fared less well, even with identical rainfall, to those on less steep slopes, due to the lower soil moisture reserve (Yaacob 1992). Poorer growth on steep slopes can be alleviated by mulch and irrigation (Yaacob 1992).

Water relations : Some information regarding the water relations of durian orchards in Thailand has been published. The average initial water infiltration rate of soil in durian orchards from 6 sites is estimated at 813.46 mm/h, the average constant infiltration rate at 416.67 mm/h (Wittawatchutikul and Rouysongnern 1982a). Through-fall of water through a closed canopy of durian trees in Rayong Thailand was measured to be 81.13% (Wittawatchutikul and Rouysongnern 1982c). Canopy interception of rainfall of a stand of durian trees at Tapong Nai village in Rayong is given at 47.94% (Wittawatchutikul and Rouysongnern 1983). Measurements of evapotranspiration as a percentage of rainfall for 12 continuous months is given for a durian orchard, the average for the year was 61.66% of rainfall (Wittawatchutikul and Jirasuktaveekul 1992).

Dollah *et al.* (1993) presented estimates of the daily water requirements of durian trees of different ages and in three different climatic zones. Mature durian trees require up to 360 litres of water per day. Mohd. Razi (1993) measured the rates of leaf and stem growth, and the rate of photosynthesis in greenhouse grown seedlings of clone D24 subjected to different levels of water stress. In areas with a pronounced dry season, proper irrigation of durian orchards is necessary (Subhadrabandhu *et al.* 1991).

Transplanting : Newly germinated seedlings are most successfully transplanted before the first set of leaves open (Coronel *et al.* 1983). Mulching is necessary or weeds will overcome newly planted seedlings (Mohamad Idris 1987). Seedlings are often transplanted into black perforated polyethylene bags at 3-4 weeks (Tidbury 1976). These bagged seedlings are then used as rootstocks for grafting. Durian trees are very sensitive to transplanting in the field. Survival is negatively correlated with moisture stress. Some clones are better able to withstand drought stress than others, durian clone D99, for example, was shown to withstand moisture stress substantially better than D24 (Masri 1992). Seedlings are normally planted one month before the start of the rainy season (Subhadrabandhu *et al.* 1991).

The minimum dimensions of the transplant hole should be a cube with sides of 75 cm, but larger holes are more advantageous (Hassan n.d.). The removed soil should be mixed with 12 kg of manure and replaced. The young trees can be planted one week after the hole has been prepared (Hassan n.d.). It has been suggested that organic manures may facilitate infection by *P. palmivora* (Watson 1984).

A study on the most suitable size material for planting in the field revealed that budded material of clone D24 with a stem circumference of 3 cm had 66-77% survival after one year. Saplings with smaller stem circumferences had survival rates as low as 29% (Ghani 1988). Some clones (D24 in particular) are apparently difficult to establish in orchards (Ghani 1988).

Lee and Loh (1966) recommended a spacing of 12-15 m between trees to maximize yield. A spacing of 12×12 m is common (Hassan n.d.), however, such a large spacing reduces potential yield on a per hectare basis: he recommended 10.5×10.5 m resulting in a density of 86 trees per hectare. After a few years of fruit-bearing, the trees can be thinned gradually to about 67 trees per hectare to increase yield. According to Hassan (n.d.), the four most common planting systems for durian are : square, quincunx, triangular and contour planting. Planting systems are also described by Zainal Abidin *et al.* (1991). Planting distances and other technical information for the growing of durians for budwood is given by Chong and Raziah (1993).

Intercropping : Young durian trees are sensitive to strong sunlight and should, therefore, be intercropped with other plants to provide shade (Hassan n.d.). The major concern for intercropping is that the intercrop does not harbour *Phytophthora* (Coronel 1986). It is, of course, an additional benefit if the intercrop is itself economically valuable. Bananas have been recommended for this purpose (Hassan n.d.; Hashim *et al.* 1985; Mohamad Idris 1987). Coronel *et al.* (1983) stated that newly planted trees are shaded with bananas for the first three or four years. Pineapples are also used for intercropping (Coronel *et al.* 1983). *Gliricidia* and guava have also been recommended for intercropping (Mohamad Idris 1987). Osman and Basri (1987) recommended intercropping with cocoa. Conversely, durian trees are used as shade trees for young cocoa trees (Anon. 1991a). A planting scheme for intercropping durian, cocoa and *Gliricidia* is presented by Jelani *et al.* (1992). It has been suggested that intercropping durian with cocoa can lead to increased incidence of serious pathogens such as *Phytophthora* and *Rhizoctonia*. Nawi and Mohd. (1991) have studied this claim and conclude that it is largely unfounded, any small increase in outbreaks of disease that may be associated with this intercropping can be readily controlled by improving crop management practices. Coronel *et al.* (1983) recommended that papaya and coconut should not be used to intercrop durian for reasons of disease control.

Polchart (1952) recommended intercropping with *Erythrina* which he claimed serves the dual purpose of increasing the nutrient content of the soil and aerating the soil. Conversely, durian trees have been tested for use as shade trees for coffee plantations (Sulaiman and Anuar 1987). The growth and survival of *D. zibethinus* in mixtures with seedlings of 5 other tree species on several soil types is described by Sastrapradja *et al.* (1982). A study of the economics of establishing and maintaining a durian orchard is presented by Kwok-Kong (1974).

Post-harvest Technology

Information regarding the harvesting and post-harvest processing of durian fruits is of great importance as the two factors that seriously limit the durian fruit development as a crop are its smell and its short shelf-life; both of these factors can be controlled or affected by harvest and post-harvest practices. Most of the post-harvest technology research has originated in Thailand. Although Thailand has made great strides in this area, much of the published research is difficult to obtain and is written in the Thai language, which undoubtedly limits its exploitation elsewhere. Thai research has produced valuable information in numerous areas, such as harvesting, local transport and preparation of fruits for market, methods to overcome the difficulties of export peculiar to this fruit, and detailed examination of the physiology of ripening. All of this research has provided insight into how durian's two most limiting properties can be overcome. Experiments in the physiology of fruit ripening, in particular, suggest methods to manipulate ripening which offer the prospects of greatly extending the shelf-life and limiting the undesirable nature of its smell.

Durian fruits generally fall from the trees at night (Teo 1991). In Malaysia, fruits are normally collected after they fall (Watson 1984; Mohamed 1990) as it is believed that harvesting the fruits before they are mature affects the flavour (Nanthachai *et al.* 1994). In Thailand, fruits are detached from the tree just before maturity (Watson 1984) and then allowed to ripen. A recent study by Pauziah *et al.* (1992) demonstrated that Malaysian D24 durians harvested at 105 and 110 days after anthesis and allowed to ripen had the same organoleptic properties as mature fallen fruits; however, fruits harvested too early (100 DAP) did not ripen properly. Hand harvesting immature D24 fruits increased the shelf-life to 9-11 days from that of only 3-4 days for fallen fruits (Pauziah *et al.* 1990,1992). Similar conclusions were reached in a study in the Philippines (Pascua and Cantila 1991). Thus, knowledge of the ripening process, and the exact time at which to harvest immature fruits of each particular clone or variety can be of great value in extending the shelf-life of the fruit, and yet not affect fruit quality.

Grading : Chattavongsin and Siriphanich (1987) studied the anatomy of fruit pedicels during development of several Thai cultivars of durian. The firmness of the fruit stem increases with maturity owing to a proliferation of phloem fibres during late development; hence, pedicel firmness can be used as an indicator of fruit maturity (Chattavongsin and Siriphanich 1990a,b). Experiments in estimating fruit maturity with an 'Effigi' firmness tester resulted in 85% accuracy. The degree of firmness (abundance of phloem fibres) was not found to vary between fruits of different sizes, but may be affected by the age of the tree, fruits of younger trees having stiffer stems (Chattavongsin and Siriphanich 1990a,b). This fact complicates the use of pedicel firmness measurements as practical estimates of maturity.

A comprehensive set of quality standards for three Thai cultivars has been established as well as a classification scheme for fruit shapes within these cultivars (Hiranpradit *et al.* 1992). Quality standards are also presented by Jitjumnong (1988).

Shipping and cold storage of fruit : The earliest experiments on cold storage of durian fruit are those of Cumming and Hodges (1920). Durians kept below freezing were found to be good after 4 months, but not up to the standards of fresh ones. Many of the durians had unfortunately become impregnated with the brine, which affected the flavour and preservation. The earliest recorded attempt at the cold storage and shipping of durian fruits seems to be that of Kopp (1929). A complete English translation of this French article is available (Anon. 1929). Interestingly enough, Kopp did not believe that the shipping of chilled durians to Europe held any commercial promise. Neighbouring items are at risk of being impregnated by the smell, and 'at +3°C, the smell remains weak during all the journey, to return to all its virulence during the maturation which follows the reheating' (Anon. 1929; Wardlaw 1937).

Mathur and Srivastava (1954) reported that 3.9-5.6°C and 80-90% RH were the optimum cold storage conditions for durian fruits. Weight loss and decrease in ascorbic acid content and acidity as well as increase in reducing sugar content and total soluble solids were also tabulated for various cold storage regimes.

Bauchau (1972) concluded that freezing of whole fruits is unfeasible, but that frozen arils keep their organoleptic quality for 3 months when frozen at -23°C. After longer storage, arils started losing flavour (Anon. 1960). It is reported that preliminary experiments in freezing durian arils in polyethylene bags at -22°C succeeded fairly well. Praditdoung (1986) reported that the shelf-life of intact durian arils (containing seeds) could be extended up to 30 days when wrapped in low density polyethylene and stored at 4°C. Moleeratanond *et al.* (1990) demonstrated that the quality of durian arils wrapped in plastic and kept at 2°C could be maintained for 48 days for Chanee durians, and 30 days for Mon Thong. Numerous physical data (weight loss, CO_2 buildup, etc.) were tabulated for different treatments. Romphophak and Palakul (1990), who studied cold storage of whole fruits, provided results somewhat contrary to those just described. Using Chanee durians kept at 5°C, either untreated or treated with calcium carbide, they found the pericarp of cold stored durians showed signs of chilling injury after just one week. Soluble solids in cold stored fruits remained low and did not rise even 3 days after removal to room temperature. Durian pulp remained firm while in cold storage, and became soft upon removal to room temperature. Thus, aril softening and increase in soluble solids are apparently governed by separate processes. More importantly, they reported that the palatability, scored by a panel of 6 members, was much lower for fruits stored for even 1 week than for unrefrigerated controls. No increase in palatability of refrigerated fruits occurred even after returning the fruits to room temperature for up to 3 days.

Abdullah *et al.* (1988) stated that durians can be satisfactorily stored at 10°C and 90% RH for 1-3 weeks. Pawinakan and Hiranpradit (1989) have also published some work on freezing and storage of durian arils.

Packaging : Some of the problems associated with packaging and exporting durian in Thailand (costs, containers and pests) have been examined (Anon. 1985). Surface coating of the fruit slowed ripening and helped reduce the odour (Anon. 1990). Coating material containing gibberellic acid significantly reduced internal ethylene concentrations in the fruit, improved the colour and delayed ripening. Tongdee, Suwanagul, Neamprem and Bunruengsri (1990) demonstrated that the coating of durian fruits with wax preparations extended the storage life of fruits by delaying over-ripening and reducing odour. They recommended a 1:4 dilution of SF 320 or SF 7055 coating for optimal storage. The use of surface coating extends the shelf life of durian to 2 weeks (Tongdee 1992).

The smell of durians can be successfully contained for at least 46 hours by packing them inside a double-walled corrugated cardboard box which is then shrink-wrapped with PVC film (40 mm thickness) (Swatditat and Pathomyothin 1979). Paklamjeak *et al.* (1986) investigated the best packaging method for intact ripe durian fruits. Corrugated fibreboard boxes (5.24 mm thick) with an area of ventilation of 2.5% were selected as the best type of export shipping container (Paklamjeak *et al.* 1986). Furthermore, Paklamjeak *et al.* (1986) showed that the belief that inclusion of a few basil leaves in the packing container will eliminate or absorb the odour was false, however, no other consideration was given in their study to smell containment properties of a desirable container. The design and structural features of durian export packaging containers is further elaborated by Paklamjeak *et al.* (1988, 1989).

Mohamed (1990) investigated the effects of shrink wrapping, sawdust packing and tying shut of the fruit stored at ambient temperature of 8°C. Tying the fruit shut to prevent dehiscence (a traditional method) was found to be completely ineffective at prolonging shelf-life. Shrink wrapping of durian was found to keep them fresh for approximately 4-5 weeks. It was hypothesized that shrink wrapping inhibits dehiscence by the 4 mechanisms: (1) maintains a high internal CO_2 level and hence inhibits respiration; (2) greatly slows moisture loss; (3) mechanically holds the valves together; and (4) inhibits microbial action due to the high CO_2 and low O_2 internal atmosphere.

Ripening of fruits : Measurements of CO_2 and ethylene production in ripening durian fruits have revealed that durian is a climacteric fruit (Tongdee *et al.* 1989a; Booncherm and Siriphanich 1991). The respiratory climacteric peak is higher for fruits harvested at a more mature stage (Tongdee *et al.* 1989b) and occurs later after harvest for more immature harvested fruits. In Chanee durians, the appearance of a distinct odour indicating that the fruit is ready to eat occurs one day before the respiratory peak (Tongdee *et al.* 1989b). The pH of durian fruit drops as the fruit is left to ripen (Jenie 1978); that is to say that the total acidity increases. During ripening, the aril softens and starch hydrolysis gradually occurs, this is accompanied by a rapid increase in soluble sugars (Ketsa and Pangkool 1994). Aril softening and increase in soluble solids are thought to be governed by separate processes (see section on shipping and cold storage of the fruit). As the fruit ripens, the colour of the pulp also changes. This phenomenon has not been fully explored, however, Ketsa and Pangkool (1994) suggest it may be due to the synthesis of ß-carotene. The green colouration of the husk also disappears when the fruits are ripened at low humidities (Ketsa and Pangkool 1994). Differences in the speed of ripening between clones may be due to differences in enzyme activity, notably ACC synthase and ACC oxidase (Siriphanich *et al.* 1994).

Durian fruits typically split open as they ripen. This splitting is due to the development of an abscission zone. Very little is known about structure of the abscission zone, however, the abscission zone cells are known to have tannin deposits (Sriyook *et al.* 1994). Low humidity is known to stimulate dehiscence (Ketsa and Pangkool 1994). Durians loose a lot of moisture after harvest. In one study, moisture content was shown to decrease by 21% after 9 days of storage at 30°C and 70% relative humidity, although moisture loss was lower when fruits were stored at higher humidities (Ketsa and Pangkool 1994). The majority of the moisture lost originates from the pericarp, no significant drop in moisture content of the arils was found even after 5 days at 75% RH (Ketsa and Pangkool 1994).

Effects of atmosphere : Low oxygen (O_2) concentrations affect the ripening of durian fruits. Fruits (Mon Tong variety) held in air have a typical climacteric pattern of respiration with an initial carbon dioxide (CO_2) production of 60 ml/kg/hour and a peak of 145 ml/kg/hour (Tongdee and Suwanagul 1989); ethylene production peaked at a rate of 10 µl/kg/hour. Fruits held at 10% O_2 had a peak respiration rate of only 85 ml/kg/hour with a peak ethylene production of only 3 µl/kg/hour; however, this did not delay or affect ripening. Fruits held at 2, 5, 7.5% O_2 had respiratory rates and ethylene levels that remained constant over time; the fruits did not ripen. The quality of fruit stored at 7.5% or less O_2 was slightly affected, but remained acceptable. Fruit stored at 2% O_2 failed to ripen even when returned to fresh air (Tongdee and Suwanagul 1989; Tongdee *et al.* 1990). Reduction of atmospheric O_2 levels (5 to 7.5%) was shown to cause a reduction in CO_2 and ethylene production, and delayed ripening (Tongdee *et al.* 1990); ripening resumed upon removal of the fruits to air, although this rise was non-climacteric. Storage of fruits at 10 or 20% CO_2 caused no change in ripening but the later treatment slightly lowered internal ethylene levels (Tongdee *et al.* 1990).

Plant growth regulators : CO_2 and ethylene show a parallel increase during ripening of durian fruits as shown by Tongdee *et al.* (1990) in their study on the effect of O_2 and CO_2 on ripening. Furthermore, CO_2 and ethylene production remain high after the climacteric (Tongdee *et al.* 1989a). A high ethylene level at the time of harvest (1.4 ppm) in Chanee durians indicates that ethylene actually accumulates before fruit abscission, at least in fruits of this variety (Tongdee *et al.* 1989a).

In experiments where seeds with arils were separated and isolated from the pericarp of the fruit, the bulk of respiration and ethylene production was found to occur in the pericarp (Booncherm and Siriphanich 1991). The peak of ethylene and respiration in durian arils occurred before that of the pericarp, and aril ripening still proceeds normally after its removal from the pericarp (Booncherm and Siriphanich 1991). It is, therefore, possible that the ripening of the arils stimulates the ripening of the husk in intact fruits (Booncherm and Siriphanich 1991).

Chanee durian fruit picked at 75% maturity ripened unevenly or failed to ripen. Fruits that failed to ripen only had very slight increase in internal ethylene and CO_2 concentrations (Tongdee *et al.* 1989b); the arils of these fruits remained hard after 8 days. Fruits harvested at 75% maturity, that did ripen but ripened unevenly, did show a climacteric rise in CO_2 and ethylene. The most commonly harvested stage of Chanee durians is 85% maturity. By this stage, the ripening process appears to have already commenced (Tongdee *et al.* 1989b).

In a somewhat contradictory study, Cheyglinted (1993) reported that Chanee durian fruits harvested at 75% maturity did undergo a climacteric rise in ethylene production and respiration even though they either failed to ripen or ripened abnormally. Normal ripening could be induced in these fruits upon treatment with 1000 or 2000 ppm ethephon (Cheyglinted 1993). These experiments with ethephon suggest that the failure of harvested immature fruits to ripen is due not to lower endogenous ethylene levels *per se,* but to a lower sensitivity to ethylene. Immature fruits require a level of ethylene higher than that found endogenously within the fruit to elicit proper ripening. This is supported by Ketsa and Pangkool (1994) who stated that ethylene application promoted the dehiscence of mature durian fruits more than that of immature ones.

Ketsa and Pankool (1994) showed that internal ethylene concentrations were higher in durians stored at low humidity, they speculated that this may be caused by water stress. The increased ethylene may induce cell wall breakdown in the abscission zones and thus be responsible for fruit dehiscence; ethylene has been shown to have a greater effect than weight loss on fruit abscission, and has also been shown to accelerate fruit dehiscence (Sriyook *et al.* 1994). The application of GA3 can delay fruit dehiscence, although the mechanism is unknown (Sriyook *et al.* 1994). This finding has led to the suggestion that a GA3 and wax surface coating may be useful in delaying dehiscence during shipping of fruits (Sriyook *et al.* 1994).

Post-harvest technology : Several machines have been developed specifically to aid with the post-harvest problems associated with durian fruit. Most of this post-harvest technology has been developed in Thailand. For example, a mechanical durian cleaning machine was described by Jarimopas *et al.* (1990). This machine can wash up to 1350 kg of durian per hour.

The accurate grading and sizing of durian fruits presents problems. Manual sizing of fruits is subject to large errors (43%) (Jarimopas *et al.* 1992). Recently, a durian sizing machine has been developed which can size 1.35 tonnes of fruit per hour with an error rate of only 17% (Jarimopas *et al.* 1992).

Jarimopas and Srihawong (1991) have developed a two-cylinder, 24 HP diesel durian transporter suitable for use within orchards. The transporter is capable of carrying up to 900 kg of durians at a speed of 15.4 km/h. Several articles written in the Thai language by Jarimopas *et al.* (1987 1990) describe a similar vehicle.

In Malaysia, MARDI has developed a hand-held durian opener, known as the MAAY2 durian opener. Its design and performance are described by Sukra (1990, 1991) and Ahmad Tarmizi *et al.* (1991).

Processed food products and their packaging : Because of the extremely short shelf-life of durian fruits and their seasonality, some investigations have centred on developing and improving processed durian products. In 1972, Bauchau presented the results of some experiments with drying durian arils and improvement of packaging; evaluation and storage of durian cake has been discussed by Paweenakarn *et al.* (1992). Long term storage of durian cake at room temperature is not possible, but cake can be stored at -20°C for up to 3 years (Paweenakarn *et al.* 1992). Technical information on the preparation of durian paste from Chanee durians is presented by Sisawad *et al.* (1988). This paste has a shelf life of over six months when stored at room temperature. A process for the preparation of dried durian flakes is presented by Sinthavali and Harutaitanasan (1987). Durian flakes apparently retain the ‘good characteristic smell’ and have a long shelf life (Sinthavali and Harutaitanasan 1987).

Experiments on suitable packaging material for durian powder have been performed in order to optimize the factors of cost and protection of the delicate flavour of durian as well as containment of its more objectionable qualities. The recommended packaging is laminated aluminum foil which renders a shelf life of at least 6 months (Hanousek 1971) and possibly up to a year (Huruthaithanasan 1985). Polypropylene bags (0.1 mm thickness) are less expensive, but are only suitable for short term storage (1.5 months) (Hanousek 1971). Polyethylene is not suitable for packaging as oil from the durian can penetrate it (Hanousek 1971).

Forestry Aspects

Timber characteristics of *Durio* species and close relatives *:* What is commonly referred to as 'durian' in the timber industry includes wood from more than just *D. zibethinus*. In fact, it often includes other related genera. For example, the species listed as 'durian' are by Keith (1947): *Boschia griffithii* Mast. [=*Durio griffithii* (Mast.) Bakh. *sensu* Kostermans 1958b], *Durio zibethinus* Murr. and *Durio* spp. Menon (1959) also listed *Coelostegia griffithii* Benth., *D. lowianus* Scort. ex King, *D. malaccensis* Planch. [=*D. malaccensis* Planch. ex Mast. *sensu* Kostermans 1958b], *D. oblongus* Mast., *D. oxleyanus* Griff., *D. testudinarum* Becc. var. *macrophyllus* King [=*D. macrophyllus* Ridl. *sensu* Kostermans 1958b], *D. wrayii* King [=*D. testudinarum* Becc. *sensu* Kostermans 1958b] and *Neesia altissima* Bl. Martawijaya and Kartasujana (1981) listed *D. carinatus* Mast., *D. oxleyanus* Griff. and *D. zibethinus* Murr. as species under the Indonesian timber term 'durian'. Normally, wood properties listed for 'durian' pertain to a mixture of the above and perhaps other species. Some information on individual species is given.

Boschia griffithii Mast. [=*D. griffithii* (Mast.) Bakh.] : This wood is of a yellowish red colour, yields a smooth grain after machining, but is prone to attack by insects (Howard 1948). According to Keith (1947), the wood shrinks badly upon drying. The wood has a weight of 553-832 kg/m^3 (Ridley 1901, 1903); 30 pounds per cubic foot (air dry) (480 kg/m^3) (Keith 1947); and 42 lb per cubic foot (dry) (673 kg/m^3) (Howard 1948). Two values of 47 and 51.1 pounds per cubic foot at 15% moisture (753 and 819 kg/m^3) are listed by Burgess (1966). This wood is used for house building and making beams (Ridley 1901), and sometimes furniture (Keith 1947).

Coelostegia griffithii Mast. : The weight of the wood has been recorded as 713 kg/m^3 by Ridley (1901, 1903), and 705 kg/m^3 at 15% moisture by Burgess (1966). The bark of this tree is used to tan nets. The wood is hard, flexible and durable (Ridley 1901, 1903).

Cullenia excelsa Wight : [=*D. ceylanicus* Gardn.; = in part *C. ceylanica* (Gardn.) K. Schum. *sensu* Kostermans 1958b] : Numerous measurements on the strength of this wood are enumerated by Tisseverasinghe (1963). At 12% moisture, the wood weight is 513-625 kg/m^3 (Pearson and Brown 1932). The weight is recorded as 625 kg/m^3 by Tisseverasinghe (1963). The physical and mechanical properties from Pearson and Brown (1932) are: specific gravity = approximately 0.50; 18.4% moisture in untreated timber; spike pulling elastic limit = 4849 kg/cm^2; spike pulling maximum load = 9133 kg/cm^2; compression perpendicular to the grain = 1838 kg/cm^2; and side hardness = 1724 kg/cm^2.

Durio carinatus Mast. : The bark of this species is apparently used for roofing (Uphof 1968; Usher 1974). An examination of charcoal, charcoal briquets and alcohol production from different types of wood waste of *D. carinatus* is presented by Syachri (1983).

The descriptive measurements from Chu (1969) are: air dry density-average 630 kg/m^2 range 551-700 kg/m^3; fibre length - average 1.65 mm, range 1.55-1.79mm; fibre average maximal tangential diameter ave. 32.63 µm, range 30.45-34.10 µm; fibre average maximal tangential lumen ave. 25.71 µm, range 24.26-28.32 µm; fibre average maximal tangential wall thickness ave. 7.25 µm, range 5.89-9.08 µm.

Durio dulcis Becc. : An analysis of wood from this species is given by Sudradjat (1980). The wood is listed as having a specific gravity of 0.73. Cellulose accounts for 50.9% of the oven dry weight of the wood, 36.7% is accounted for by lignin, 14.6% pentosan and 1% ash. Cockrell (1942) listed the specific gravity of the wood of *D. conicus* Becc. [=*D. dulcis* Becc. *sensu* Kostermans and Reksodihardjo 1958] as 0.60.

Durio kutejensis (Hassk.) Becc. : The only published information on wood of this species comes from Burgess (1966) who listed the weight of the wood as 599 kg/m^3 at 15% moisture.

Durio ?lowianus Scort. ex King : The weight of wood from this species was listed as 657 kg/m^3 air dry (Desch 1941).

Durio malaccensis Planch. ex Mast. : The weight of wood from this species was listed as 705 kg/m^3 air dry (Desch 1941).

Durio ?oblongus Mast. : The weight of wood from this species was listed as 657 kg/m^3 air dry (Desch 1941).

Durio oxleyanus Griff. : According to Kumarasamy and Burgess (1956), *D. oxleyanus* rated extremely well with respect to resistance to splitting when nailed. The wood shrunk 3.0% radially and 4.0% tangentially when dried, and was very susceptible to attack by powder-post beetles (Burgess 1966). The specific gravity of the wood is 0.57 (Cockrell 1942). 'Green' wood at 87% moisture had a specific gravity of 0.50, while wood dried to 16% moisture had a specific gravity is 0.53 (Shukla and Rajput 1988).

The weight of the wood was listed at 753 kg/m^3 air dry by Desch (1941) and 755 kg/m^3 by Ridley (1901, 1903). A value of 610 kg/m^3 at 15% moisture was listed as the mean weight of 10 specimens by Burgess (1966).

The physio-mechanical properties of this wood presented by Shukla and Rajput (1988) were: weight at 15% moisture = 610 kg/m^2; modulus of rupture = 751 kg/cm^2; modulus of elasticity = 119500 kg/cm^2; maximum height of drop impact bending = 161.0 cm; maximum crushing strength in compression parallel to grain = 398 kg/cm^2; fibre stress at elastic limit in compression perpendicular to grain = 42 kg/cm^2; and side hardness = 363 kg.

Durio testudinarum Becc. : The wood of this species is recorded as having an air dry weight of 692-710 kg/m^3 (Desch 1941). According to Burgess (1966), the weight is 660 kg/m^3 at 15% moisture.

Durio zibethinus L. : The wood of this species is a dull red brown colour with a hard grain, yielding an uneven rough surface. It is liable to warp and unsuitable for export (Howard 1948). The wood is straight grained and moderately heavy (Keith 1947). The wood has a specific gravity of 0.42 (Cockrell 1942). The weight is listed as 481 kg/m^3 (air-dried) by Keith (1947); 545 kg/m^3 air dry by Desch (1941) and Howard (1948); 570 kg/m^3 at 15% moisture by Burgess (1966); and 645 kg/m^3 by Ridley (1901, 1903). The wood is suitable for general construction (Keith 1947).

Durability of 'Durian' timber : Durian wood is not very durable (Jackson 1957). Durability tests have been conducted on the wood. In burying experiments, durian wood pieces were all destroyed after 1.5 years, the first pieces destroyed after only 6 months (Foxworthy and Woolley 1930). The wood of *D. zibethinus* is known to be highly susceptible to damage by termites (Martawijaya and Sumarni 1978) and moderately susceptible to attack by powder-post beetles (Menon 1957; Anon. 1964). Durian wood is also susceptible to marine borers (Burgess 1966). Fortunately, durian wood readily absorbs preservatives, which helps compensate for its natural lack of durability; absorption levels of up to 96 kg/m^3 was obtained with a mixture of creosote and diesel oil (Anon. 1964; Burgess 1966). Durian wood is normally free from defects except for sponginess of the pith (Thomas 1952, 1979).

Uses of 'Durian' timber : Durian wood is used for making clogs in Sarawak (Foxworthy 1921; Thomas 1952, 1979; Anon. 1964). It is also used for light construction, cheaper grades of furniture (Thomas 1952, 1979; Anon. 1964) and temporary construction work (Foxworthy 1909). Durian wood is recommended for non-impact tool handles (Lim 1988) and cigar boxes (Martawijaya and Kartasujana 1981). Durian wood makes satisfactory plywood (Thomas 1952, 1979). Studies of the gluability of durian plywood have been conducted by Tsai (1975); the wettability of wood veneers of durian with different adhesives has also been studied (Wang 1975), as has the bonding

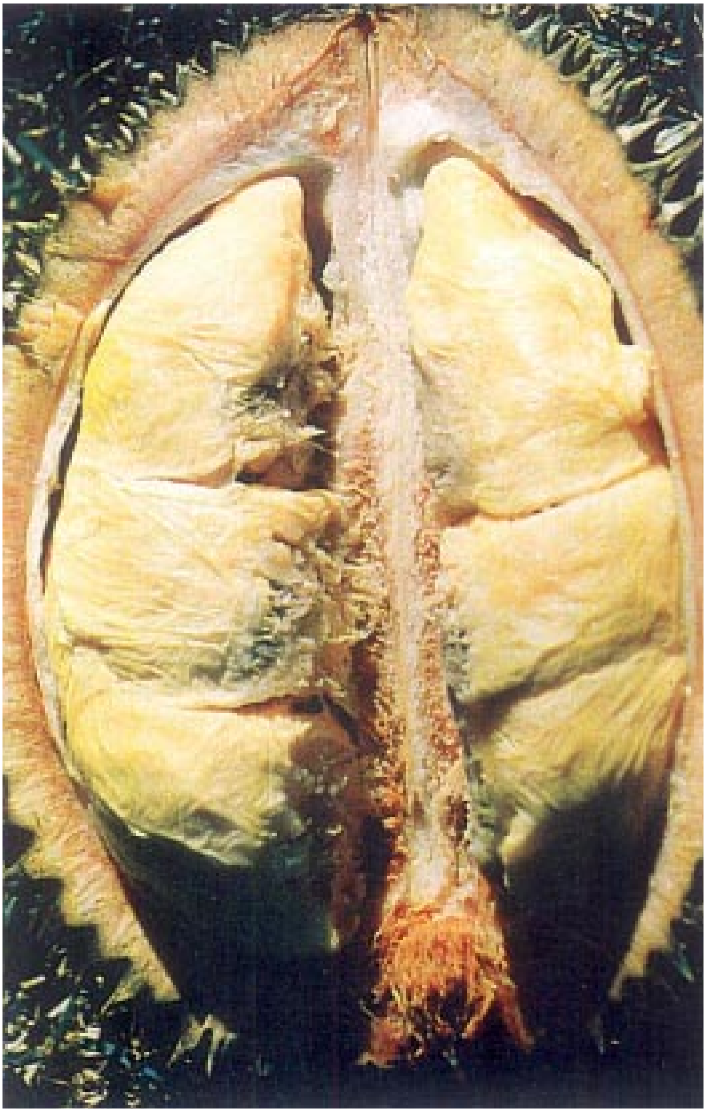

Figure 5. The inside of mature fruit of *D. zibethinus.* Two of the five locules are visible. The seeds are covered within the fleshy yellow arils which surround them and fill the locules.

strengths of different adhesives (Wang 1977; Taki 1986). Tensile tests have been conducted on plywood made from durian (Kitamura *et al.* 1982).

The properties of wood wool board manufactured from *D. zibethinus* have been described (Sulastiningsih *et al.* 1987). Durian wood has been investigated for its suitability as a substrate for the growth of oyster mushrooms (*Pleurotus ostreatus*) by Suprapti (1987). Out of 11 woods tested, durian was found to rate second only to *Hevea* wood in terms of yield of oyster mushrooms per kilogram dry weight of substrate.

Studies of pitching problems of tropical woods including durian were examined by Tachibana *et al.* (1976). Durian wood pulp causes additional pitching problems after bleaching as large amounts of residual resin in the fibres cause discolouration.

Properties of 'Durian' timber : Durian wood has approximately 100% moisture when felled. To dry it from green to air dry under cover in Malaysia takes 2 to 2.5 months for 1.25 cm boards and 3.5 to 4 months for 3.8 cm boards (Thomas 1952, 1979). Durian wood shrinks badly when dried (Foxworthy 1921). The shrinkage of the wood is estimated at 3.0% radially and 4.0% tangentially (Anon. 1964).

The weight of wood labelled as 'durian' varies considerably as it consists of several species. Some representative published values for 'durian' are 577 kg/m^3 (Foxworthy 1916); 465-625 kg/m^3 (Foxworthy 1921); 481 kg/m^3 air dry (Keith 1947); and 527-753 kg/m^3 air dry (Menon 1959).

The density of wood of different durian species also differs, some are sinkers (Anon. 1953a). Nevertheless, estimates of the specific gravity of 'durian' wood have been published. The air dry specific gravity of durian is 0.57+/-0.02, the oven-dry specific gravity is 0.63+/-0.02 (Ma and Chen 1981). Numerous physical properties of 'durian' at 12% moisture have been measured by Ma and Chen (1981). They are fibre stress at elastic limit = 789+/-71 kg/cm^2, modulus of rupture = 1372+/-61 kg/cm^2, modulus of elasticity = 167 200+/-18 200 kg/cm^2, absorbed energy in toughness = 0.82+/-0.06 kg+m/cm^2, compression parallel to the grain = 716+/-13 kg/cm^2, shear strength on tangential surface = 118+/-23 kg/cm^2, shear strength on radial surface = 113+/-15 kg/cm^2, hardness of end surface = 6.44+/-0.82 kg/mm^2, hardness of tangential surface = 2.07+/-0.27 kg/mm^2, hardness of radial surface = 1.91+/-0.23 kg/mm^2, at 17.93% moisture cleavage in radial direction = 37+/-2 kg/cm, and at 18.02% moisture cleavage in tangential direction = 29+/-2 kg/cm

Wood anatomy : The wood anatomy of *Durio* has been examined in some detail by several authors (Bargagli-Petrucci 1904; Moll and Janssonius 1906; Cockrell 1942; Menon 1959). The wood anatomy of *D. lowianus* is described in a Japanese paper (Anon. 1966). According to Menon (1959), there is silica in the wood parenchyma of *B. griffithii* Mast. [=*D. griffithii* (Mast.) Bakh. *sensu* Kostermans 1958b] and *C. griffithii* Benth.; *D. grandiflorus* is also siliceous (Burgess 1966). No silica is present in *D. oxleyanus, D. testudinarum, D. zibethinus* or *Neesia altissima*. There are crystals in chambered parenchyma strands in all 'durian' save *B. griffithii* Mast. [=*D. griffithii* (Mast.) Bakh. *sensu* Kostermans 1958b] (Menon 1959). Vertical traumatic intercellular canals are present (Metcalfe and Chalk 1957). Mucilage cavities are present in the pith of *Durio, Coelostegia* and *Boschia* (Solereder 1908).

The wood contains diffuse vessels with no definite arrangement. About 10% to less than 50% of the vessels are solitary, the remainder are found in radial pairs or groups of up to 10 (Menon 1959). There are normally less than 4 vessels per mm^2. The vessel members are 300-1200 µm in length (Cockrell 1942). The maximal vessel diameter (tangential) is 220-370 µm (Menon 1959). Vessels are further characterized by the absence of tyloses and simple perforation plates (Menon 1959). The vessel walls are 3-9 µm in diameter (Cockrell 1942)

There is no storied parenchyma in *Durio*, and the fibres have simple or indistinctly bordered pits, equally numerous in radial and tangential walls (Metcalfe and Chalke 1957). Furthermore, the fibres are in radial rows, non-libriform, occasionally semi-libriform, 20-40 µm in diameter, 900-3000 µm long, the walls are 3-8 µm thick, and pits are restricted to the radial walls (Cockrell 1942). Chu (1969) described the fibres of *D. carinatus* Mast; he listed the average maximal tangential diameter of these fibres as 30.45-34.10 µm, the average maximal tangential lumen as 24.26-28.32 µm and the average maximal tangential cell wall thickness as 5.89-9.08 µm.

Growth rings are distinct, and are delineated by denser fibrous tissue at the outer margin (Cockrell 1942). The sapwood of durian is white or pale yellow-brown, while the heartwood is brown to deep brown (Anon. 1964).

Both uni- and multi-seriate rays are present in the wood. Measurements of medullary ray elements from several durian species are tabulated by Bargagli-Petrucci (1904). The xylem rays of *Durio* are characterised by the presence of tile cells (rows of narrow upright cells that resemble tile work when viewed in radial section). Tile cells typically occur in certain members of the Malvales. These tile cells are grouped into two types. The first type are the *Durio* type tile cells, these are about the same height as the procumbent ray initials, as is typical in the genus *Durio* and 17 other genera in the Malvales (Manchester and Miller 1978). Additionally, there exists the *Pterospermum* type of tile cell, in which the tile cells are two to several times higher than the procumbent initial cells. This type of tile cell is found in approximately 30 Malvalceous genera (Manchester and Miller 1978). The development of *Durio* type tile cells has been described by Chattaway (1933). Resin is abundant in procumbent cells of durian, but rare in tile cells. The tile cells often contain crystals (Chattaway 1933). *Durio* type tile cells are found in all members of the *Durioneae* except *Camptostemon* and *Maxwellia* (Metcalfe and Chalk 1957). A study of fossilized eocene wood revealed the earliest known existence of tile cells, these being of the *Pterospermum*, or an intermediate *Pterospermum-Durio* type. No known fossil woods with *Durio* type tile cells are known, however, based on the mode of development, Manchester and Miller (1978) speculated that the *Pterospermum* type may have arisen from the *Durio* type.

Forsaith (1915) claimed from a study of anatomical features of the Malvales that the primitive condition in this order included diffuse parenchyma and aggregate rays; characters that are only possessed currently by the genus *Durio.* Thus, from an anatomical point of view, Forsaith (1915) claimed that *Durio* has the most primitive wood structure in the Malvales. After a study of wood anatomy of the Bombacaceae, Metcalfe and Chalk (1957) concluded that the *Matisieae* are more closely related to the *Durioneae* than is the *Adansonieae.*

Major Diseases, Parasitism and Associated Organisms

The major diseases of durian have been extensively covered in an excellent book by T.K. Lim (1990), which is a valuable source of information on durian diseases. Attempt is made here to list all recorded pests, and pathogens and organisms found associated with the tree or its products (fruit and timber), and all known literature pertaining to them. Such a list is not presented by Lim (1990), and could be of value to researchers in this area. As many of these organisms are discussed by Lim (1990), this work has only been listed as a reference in cases where it is the only published mention of the organisms relationship with durian.

Bacteria

Enterobacter sp. -*stem canker* Liu (1977b); Singh (1980) *Flavobacterium* sp. -*stem canker* Liu (1977b); Singh (1980); *Pseudomonas* sp. -*stem canker* Liu (1977b); Singh (1980).

Fungi

Aschersonia -leaf fungus Singh (1980); Turner (1964, 1971); *Aschersonia placentae* B. & Br. [see also the telomorphic state *Hypocrella raciborskii* Zimm.] *-probably beneficial fungus,* Lim (1990).

Botryobasidium salmonicolor (Berkeley & Broome)Venkatarayan, Weber (1973); *Botryodiplodia theobromae* Pat. [see *Lasiodiplodia theobromae* (Pat.) Griff.& Maubl.].

Calonectria rigidiuscula (Berkeley & Broome)Saccardo (the perfect state of *Fusarium decemcellulare*) *-stem rot,* Jamil (1966); Johnston (1960); Singh (1973, 1980); Weber (1973); Wiltshire (1956a,b).

Capnodium moniliforme Fraser *-sooty mould,* Singh (1980); Turner (1964, 1971).

Cercospora sp. *-leaf spot,* Chandrasrikul (1962), Giatgong (1980), Singh (1980), Williams and Liu (1976),

Chaetomium trilaterale Chiv. *-associated with seedling dieback,* Singh (1980); Turner (1971).

Cladosporium fulvum Cooke, Tigvattnanont and Pramual (1990).

Colletotrichum sp. (Hassan n.d.) *anthracnose, root rot,* Johnston (1960), Singh (1973, 1980); Subhadrabandhu *et al.* (1991); Thompson (1939); Tidbury (1976).

Colletotrichum durionis Koorders, Coronel *et al.* (1983), Soegeng-Reksodihardjo (1962); *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. [the anamorphic state of *Glomerella cingulata* (Stonem.)Spauld & Schrenk.] *-anthracnose;* Alahakoon *et al.* (1994); Alahakoon and Brown (1994); Lim (1980); Nik Masdek *et al.* (1991); Shaji *et al.* (1993); *Colletotrichum zibethinum* (Sacc.) Petrak *-leaf damage,* Coronel *et al.* (1983), Soegeng-Reksodihardjo (1962).

Coriolus vesicolor (L. ex Fr.) Quel., Yamamoto and Hong (1989).

Corticium salmonicolor Berkeley & Broome *-Pink disease,* Anon. (1967); Chandrasrikul (1962); Coronel *et al.* (1983), Giatgong (1980), Nik Masdek *et al.* (1991); Shaji *et al.* (1993); Singh (1973, 1980); Soegeng-Reksodihardjo

(1962); Turner (1966, 1971); Vichirananda (1983); Watson (1984). Williams and Liu (1976).

Corticium solani (Prill & Delacr.) Bourd. & Galz. *-leaf spot and dieback,* Singh (1973, 1980); Turner (1963; 1971).

Corynespora cassiicola (Berk. & Curt.) Wei. - *associated with leaf blotch,* Anon. (1967); Singh (1980); Williams and Liu (1976).

Curvularia sp., Ganapathi and Chinnathambi (1993); *Curvularia affinis* Boedijn *-leaf spot,* Singh (1973, 1980); *Curvularia eragrostidis* (Henn.)J.A. Meyer [anamorphic state of *Cochliobolus eragrostidis* (Tsuda & Ueyama) Sivan.] *-fruit rot,* Lim (1990).

Diplodia sp. *-scion dieback,* Singh (1973, 1980); Soegeng-Reksodihardjo (1962); Thompson (1938, 1939); *Diplodia durionis* Sacc. & Sydow. *-die back,* Baker (1914; 1931); Chandrasrikul (1962); Giatgong (1980); Reinking (1919).

Fomes lignosus [synonym of *Rigidoporus lignosus* (Klotzsch)Imazeki] *-wood rot,* San Juan (1976).

Fusarium sp. *-root disease,* Singh (1973, 1980); Soegeng-Reksodihardjo (1962); Thompson (1938); *Fusarium solani* (Martius)Sacc., Anon. (1980b); Griffiths and Lim (1966); Jamil (1966); Weber (1973); *Fusarium decemcellulare* Brick. [see also the perfect state *Calonectria rigidiuscula*] *-stem rot,* Heath (1956) Note:*Nectria ochroleuca* and *N. haematococca* were also found to be associated, but probably secondarily, Jamil (1966), Johnston (1960); *Fusarium oxysporum* Schlecht. ex Fr., Singh (1973; 1980).

Fusicoccum sp. *-twig blight,* Chandrasrikul (1962), Giatgong (1980).

Ganoderma pseudoferreus (Wakefield) Overeen & Steinmann, Van Overeen (1925), Weber (1973).

Gloeosporium sp. *-leaf spot,* Singh (1973, 1980); *Gloeosporium zibethinum* Sacc. Anon. (1928), Chigg (1918, 1921); *-anthracnose,* Chandrasrikul (1962); Giatgong (1980).

Glomerella cingulata (Stoneman)Spauld & Schrenk. [see also *Colletotrichum gloeosporioides* the anamorphic state of this fungus] *-leaf anthracnose* and *leaf spot,* Anon. (1962); Anon. (1967); Jamil (1965); Singh (1973, 1980); Turner (1964, 1971); Weber (1973); Williams and Liu (1976).

Helminthosporium capense Thumen. [see *Spiropes capensis* (Thumen.) M.B. Ellis.].

Homostegia durionis Rac. -*black* and *brown leaf spots,* Coronel *et al.* (1983); Soegeng-Reksodihardjo (1962); Subhadrabandhu *et al.* (1991).

Hypocrella raciborskii Zimm. [the telomorphic form of *Aschersonia placentae* B. & Br.] -*probably beneficial fungus,* Lim (1990).

Lasiodiplodia sp., Ganapathi and Chinnathambi (1993); *Lasiodiplodia theobromae* (Pat.) Griff.& Maubl. (=*Botryodiplodia theobromae* Pat.), Johnston (1960); Liu (1977b); Singh (1973, 1980); Turner (1963, 1971).

Lentinus subnudus Berk., Chipp (1921).

Leptoxyphium sp. -*black crusty growths on leaves and twigs,* Lim (1989).

Macrophomina phaseoli Maubl., Watson (1984).

Marasmiellus scandens (Mass.) Dennis & Reid -*thread blight,* Singh (1980), Turner (1971).

Meliola durionis Hansf. -*black mildew, sooty mould,* Hansford (1956); Johnston (1960); Lim (1989); Nik Masdek *et al.* (1991); Singh (1973, 1980); Turner (1961, 1971).

Metacapnodium dennisii S.J. Hughes, Hughes (1976).

Mucor sp. -*fruit rot,* Lim (1990).

Myrothecium verrucaria Ditmar ex Fr. -*leaf spot,* Singh (1973, 1980).

Nectria sp. -*associated with bark rot,* Anon. (1954); *Nectria haematococca* Berk. & Br. -*stem rot,* Johnston (1960); Singh (1973, 1980); *Nectria ochroleuca* (Schw.) Berk. -*stem rot,* Johnston (1960); Singh (1973, 1980).

Oidium sp. -*powdery mildew,* Chandrasrikul (1962); Vichirananda (1983); *Oidium nephelii* Hadiwidjaja -*powdery mildew,* Giatgong (1980)

Perisporium sp. -*seedling dieback,* Singh (1980); Turner (1964, 1971)

Pestalotia sp. -*leaf spot,* Chandrasrikul (1962); Giatgong (1980)

Phomopsis sp. -*leaf spot,* Chandrasrikul (1962); Giatgong (1980); Singh (1973, 1980); Soegeng-Reksodihardjo (1962); Thompson and Lim (1965); *Phomopsis durionis* Syd. -*leaf spot of seedlings, branch* and *stem necrosis,* Liu (1977b); Nik Masdek *et al.* (1991); Singh (1973; 1980); Weber (1973).

Phragmocapnias betle (Sydow & Butler) Theissen & Sydow emend. Reynolds.

-sooty mould of leaves, twigs and *fruits.*, Lim (1989)

Phyllachora makrospora Zimm., Stevens (1921)

Phyllosticta sp. *-leaf spot, seedling rim blight,* Anon. (1967); Liu (1977b); Singh (1973; 1980); Thompson (1939); Tidbury (1976); Williams and Liu (1976); *Phyllosticta durionis* A. Zimmermann *-leaf spot, rim blight,* Chandrasrikul (1962); Coronel *et al.* (1983); Giatgong (1980); Hassan (n.d.); Soegeng-Reksodihardjo (1962); Subhadrabandhu *et al.* (1991); Weber (1973).

Phytophthora sp., Anon. (1980a); Jamil (1965); Kwok-Kong (1974); Thaveechai *et al.* (1982); *Phytophthora botryosa,* Chee and Hashim (1971); Suzui *et al.* (1979b); Tai (1971); Zentmyer and Mitchell (1986); *Phytophthora nicotianae* B. de Haan var. *nicotianae -leaf blight,* Anon. (1983); Liu (1977a,b); Pawakul and Chittanawasarn (1977a, 1977b); Singh (1980); *Phytophthora nicotianae* var. *parasitica* (d'Haan)Tucker, Suzui *et al.* (1976, 1979b), Weber (1973); *Phytophthora palmivora* Butler. *-root rot, bark rot, fruit rot, hypocotyl rot, patch canker,* Anon. (1986b); Butt and Sia (1982); Chan and Lim (1986; 1987); Chee (1969); Chee and Hashim (1971); Coronel (1986); Coronel *et al.* (1983); Ding (1988); Ganapathi and Chinnathambi (1993); Giatgong (1980); Hamilton (1975); Hassan (n.d.); Holliday (1980); Jamil (1966, 1969); Johnson (1993), Johnston, (1959), Khew (1990, 1991); Khoo *et al.* (1983); Kueprakone *et al.* (1977, 1979); Lee (1991), Lee *et al.* (1993, 1994), Lee and Loh (1966); Lee and Varghese (1974); Lim (1991); Lim *et al.* (1992); Lim and Chan (1986 a,b); Lim and Yassin (1985); Ling (1991); Meon and Varghese (1986); Navaratnam (1966); Ng and Choong (1991); Nik Masdek *et al.* (1991); Pawakul *et al.* (1977); Pawakul and Chittanawasarn (1977a; 1977b); Pupipat (1984); Roger (1951); Shaji *et al.* (1993); Singh (1973, 1980); Snowdon (1990); Soegeng-Reksodihardjo (1962); Subhadrabandhu *et al.* (1991); Suzui *et al.* (1976, 1978, 1979a, 1979b); Tai (1970, 1971, 1973); Thompson (1934, 1938); Thompson and Lim (1965); Tongdee Neamprem and Chayasombat (1989); Tidbury (1976); Turner (1960); Vichirananda (1983); Vichitranond *et al.* (1981); Watson (1984); Weber (1973); Zainal Abidin *et al.* (1992); Zentmyer *et al.* (1973); Zentmyer and Mitchell (1986); *Phytophthora parasitica* (Butler) Dastur., Kueprakone *et al.* (1977).

Placosphaeria durionis Sacc. *-leaf parasite,* Baker (1914); Reinking (1919).

Plokamidomyces colensoi Bat., Costa & Cif., Lim (1989).

Polychaeton sp. *-leaf mould and black crust of fruit,* Lim (1989).

Pyrenochaeta sp. *-leaf spot*, Johnston (1960); Singh (1973, 1980); Williams and Liu (1976).

Pythium sp. *-root rot,* Coronel (1986); Lee *et al.* (1993); Ng and Choong (1991); Nik Masdek *et al.* (1991); *Pythium complectans* Braun [synonym of *P. vexans* de Bary] *-root disease, patch canker.*, Belgrave (1939); Coronel *et al.* (1983); Johnston (1959); Meon and Varghese (1986); Pawakul and Chittanawasarn (1977a; 1977b); Roger (1951); Singh (1973, 1980); Soegeng-Reksodihardjo (1962); Thompson (1938; 1939); Watson (1984); Weber (1973); *Pythium vexans* de Bary [see also *P complectans* which is a synonym], Ling (1991); Shaji *et al.* (1993)

Rhizoctonia sp. *-leaf fall, leaf blight,* Chandrasrikul (1962); Giatgong (1980); Vichirananda (1983); *Rhizoctonia solani* Kuhn. *-leaf blight,* Anon. (1986b); Lim *et al.* (1987); Ng *et al.* (1986); Ng and Choong (1991); Nik Masdek *et al.* (1991); Shaji *et al.* (1993); Singh (1973; 1980).

Rhizopus sp., Subhadrabandhu *et al.* (1991); *Rhizopus artocarpi* Racib. *-fruit rot,* Johnston (1960); Singh (1973; 1980); *Rhizopus stolonifer* (Ehrenb. ex Fr.) Lind., Lim (1990)

Rigidoporus lignosus (Klotzsch) Imazeki [see also the synonym *Fomes lignosus*] *-white root disease,* Ng and Choong (1991); Nik Masdek *et al.* (1991); Shaji *et al.* (1993); Singh (1980); Williams and Liu (1976)

Sclerotium sp., Ganapathi and Chinnathambi (1993); *Sclerotium rolfsii* Sacc. (the sclerotial state of *Corticium rolfsii* Curzi) *-fruit rot.*, Lim and Sijam (1989a).

Scorias spongiosa (von Schweinitz) Fries emend. Reynolds., Lim (1989)

Septobasidium sp. *-felt fungus, velvet fungus,* Chandrasrikul (1962); Giatgong (1980).

Spiropes capensis (Thumen) M.B. Ellis (=*Helminthosporium capensis*) *-leaf mould,* Anon. (1980b); Singh (1980); Turner (1964, 1971)

Thanatephorus cucumeris (Frank) Donk. [telomorphic state of *Rhizoctonia solani* Kuhn.] *-leaf rot,* Singh (1980); Weber (1973); Williams and Liu (1976).

Trametes persoonii Mont. *-grows on bark of living trees,* Reinking (1919), (1920).

Trichomerium grandisporum (Ellis & Martin) Bat. & Cif. *-sooty mould of leaves, petioles and twigs,* Lim (1989).

Trichopeltheca asiatica Bat., Costa & Cif. *-black film on leaves,* Lim (1989).

Tripospermum sp. -*black colonies on leaves and fruits,* Lim (1989).

Ustulina sp. -*scion dieback,* Singh (1973, 1980).

Verticillium sp., Ganapathi and Chinnathambi (1993).

Lichens

Buellia canescens (Dicks.) DeNot. -*epiphyte,* Anon. (1980b), *Parmelia* sp. -*epiphyte,* Lim (1990)

Algae

Cephaleuros virescens Kunze. -*red rust,* Nik Masdek *et al.* (1991); Singh (1980); Vichirananda (1983); Williams and Liu (1976); *Phycopeltis* sp. -*largely harmless epiphyte*, Lim (1990); *Pleurococcus nagelii -largely harmless epiphyte*, Lim (1990); *Trebouxia* sp. -*largely harmless epiphyte*, Lim (1990); *Trentepohlia* sp., Long *et al.* (1991); *Trentepohlia aurea* (L.) Martius, Lim and Sijam (1989b); *Trentepohlia monile* De Wildeman [=*Physolinum monilis* (De Wildeman) Prinz. =*T. moniliformis* Karsten], Lim and Sijam (1989b); *Trentepohlia arborum* (C.Ag.) Hariot [=*T. bisporangiata* Karsten.], Lim and Sijam (1989b).

Ferns

Drymoglossum pilloselloides (L.)Presl. -*problematic epiphyte,* Lim (1990); *Drynaria quercifolia* (L.)J. Sm., Anderson (1966)

Angiosperms

Elytranthe barnesii -mistletoe, Sands (1924); *Ficus benjamina* L. -*strangling fig,* Anderson (1966); *Loranthus pentandrus* L. -*mistletoe,* Sands (1924).

Insects

Ambrosia beetles -damage to timber, Thomas (1952); longicorn beetle larvae, Chevalier (1934); Thomas (1952, 1979); T*ermites -damage to lumber* of *D. carinatus,* Isamanto and Sumarni (1992); *Scale insects -damage to leaves,* Chiow (1976).

Acrocercops sp. -*pest of leaves*, Yunus and Hua (1980).

Adoretus sp. -*pest of leaves,* Shaji *et al.* (1993).

Allocaridara malayensis Crawford *-pest of leaves,* Lee *et al.* (1994).

Anomala sp. *-pest of leaves,* Shaji *et al.* (1993).

Apogonia sp. *-pest of leaves,* Shaji *et al.* (1993).

Aprosterna pallida Fabr., Boonyong (1983).

Asterolecanium sp. *-leaf scales,* Anon. (1959a); Chuan *et al.* (1981); McIntosh (1951); Yunus and Hua (1980); *Asterolecanium ungulata* Russel, Lim *et al.* (1991); Long *et al.* (1991); Yunus and Hua (1980).

Batocera gultata Vollenh. *-stem borer,* Nik Masdek *et al.* (1991); Shaji *et al.* (1993); Yunus and Hua (1980).

Cacoecia machlopis Meyr. *-pest of leaves,* Yunus and Hua (1980).

Canopia sp. *-borers,* Coronel *et al.* (1983).

Carpophilus sp. *-sap beetle,* Lee *et al.* (1994); *Carpophilus floveicollis -sap beetle,* Lee *et al.* (1994).

Cephonodes ?higlas L., Chiow (1976).

Chalcoscelis albiguttata Snell. *-pest of leaves,* Yunus and Hua (1980).

Conogethes punctiferalis Guen. *-fruit borer,* Mohd. Shamsudin (1992); Nik Masdek *et al.* (1991); Shaji *et al.* (1993); Zainal Abidin *et al.* (1992).

Conopia sp. *-trunk borers, secondary infection after P. palmivora,* Navaratnam (1966); Yunus and Hua (1980).

Cremastopsyche pendulla -leaf eating bagworms, Shaji *et al.* (1993).

Cryptotermes cynocephalus Light. *-destructive wood pest,* Ismanto and Sumarni (1992); Martawijaya and Sumarni (1978).

Daphnusa ocellaris Walk. *-Hawk moth which eats durian leaves,* Ramasamy (1980).

Dichocrocis punctiferalis Walk. [=*Monogatus punctiferalis*] *-fruit borer,* Boonyong (1983); Coronel *et al.* (1983); Mohd. Shamsudin (1991); Mohd. Shamsudin and Norsiah (1990); Yunus and Hua (1980).

Drosophila punctpennis v.d. Weele., Frannsen (1936).

Erizada lichenaria Wlk. *-pest of leaves*, Yunus and Hua (1980).

Eutetranychus africanus -pest of leaves, Lee *et al.* (1994).

Hypomeces squamosus F., Shaji *et al.* (1993); Yunus and Hua (1980).

Hypoperigea leprosticta Hamps. (=*Plagideicta leprosticta*) *-durian fruit borer*; Frannsen (1936); Kalshoven (1981); Subhadrabandhu *et al.* (1991).

Idiophantis chiridota Meyr., Yunus and Hua (1980).

Indarbela flavina Mell., Yunus and Hua (1980).

Lacifer javanus Chamb., Yunus and Hua (1980).

Lyctus sp., Menon (1957).

Microtermes pallidus (Haviland), Nik Masdek *et al.* (1991); Yunus and Hua (1980).

Minthea rugicollis Walk. *-powder-post beetle*, Browne (1938) [recorded on *D. lowianus* and *D. oxleyanus*].

Monogatus puntiferalis Guen. (=*Conogethes punctiferalis* Guen.) *-durian husk borer*, Lee *et al.* (1994).

Monolepta bifasciata Hornst., Shaji *et al.* (1993); Yunus and Hua (1980).

Mudaria luteileprosa Holloway *-seed borer*, Zainal Abidin *et al.* (1992); *Mudaria magniplaga* Wlk. *-seed borer*, Lee *et al.* (1994); Mohd. Shamsudin (1992); Nik Masdek *et al.* (1991); Shaji *et al.* (1993); Zainal Abidin *et al.* (1992).

Oligonychus biharensis -pest of leaves, Lee *et al.* (1994).

Orgyia postica Walk., Yunus and Hua (1980); *Orgyia turbata* Butl., Yunus and Hua (1980).

Orthaga semialba Meyr., Yunus and Hua (1980);

Paralecanium expansum Green, Yunus and Hua (1980); *Paralecanium vacuum* Morr., Chuan *et al.* (1981); Takahashi (1939); Yunus and Hua (1980).

Phenacaspis hedyoticlis Green, Yunus and Hua (1980).

Phostria nicoalis Wlk., Yunus and Hua (1980); *Phostria xipharesalis* Wlk., Yunus and Hua (1980).

Plagideicta magniplaga Walk. [=*Mudaria magniplaga*] *-durian seed* and *fruit borer,* Anon. (1986b); Butt (1982); Hassan (n.d.); McIntosh (1951); Mohd. Shamsudin (1991); Mohd. Shamsudin and Norsiah (1990); Ng and Choong (1991); Yunus and Hua (1980).

Platypus cupulatus Chap., Nik Masdek *et al.* (1991); Yunus and Hua (1980).

Postelectrotermes militaris, Thirugnanasantharan (1987).

Pseudococcus sp., Lee *et al.* (1994).

Rhadinomerus sp., Yunus and Hua (1980).

Rhytidodera simulans -stem borer, South (1922).

Saissetia sp., Yunus and Hua (1980).

Scheloribates sp., Yunus and Hua (1980).

Seira jacobsoni (Borner), Yunus and Hua (1980).

Squamura sp. *-bark feeder,* Shaji *et al.* (1993).

Sylepta derogata F., Yunus and Hua (1980); *Sylepta bipunctalis* Warr., Yunus and Hua (1980).

Synanthedon sp., Nik Masdek *et al.* (1991); Yunus and Hua (1980).

Tenaphalara malayensis Crawford., Boonyong (1983); Braza and Calilung (1981); Gadug and Hussein (1987); Hodkinson (1983); Shaji *et al.* (1993); Tigvattnanont and Pramual (1990); Yunus and Hua (1980).

Tetranychus fijiensis Hirst., Lee *et al.* (1994); Yunus and Hua (1980).

Tirathaba mundella Walk., Yunus and Hua (1980); *Tirathaba ruptilinea* Hamps., Frannsen (1936).

Tonica terrasella Wlk. *-fruit borer,* Lee *et al.* (1994); Mohd. Shamsudin (1991); Mohd. Shamsudin and Norsiah (1990); Mohd. Shamsudin (1992); Nik Masdek *et al.* (1991); Zainal Abidin *et al.* (1992).

Tyrophagus putrescentiae (Schrank); Yunus and Hua (1980).

Xyleborus cordatus Hag., Yunus and Hua (1980); *Xyleborus declivigranulatus*

Sch., Yunus and Hua (1980); *Xyleborus ferrugineus* (F.), Yunus and Hua (1980); *Xyleborus formicatus* Eichh., Boonyong (1983); *Xyleborus similis* Ferr., Yunus and Hua (1980); *Xyleborus testsceus* Wlk [=*X. perforans* Wall.], Yunus and Hua (1980).

Zeuzera sp. *-borers.*, Polchart (1952); *Zeuzera coffeae* Nietn. *-stem borer*, Coronel *et al.* (1983), Nik Masdek *et al.* (1991), Yunus and Hua (1980).

Nematodes

Helicotylenchus sp., Fong and Poh (1970); Sidam and Yuen (1992); Singh (1973).

Macroposthonia sp., Sidam and Yuen (1992).

Meloidogyne sp., Sidam and Yuen (1992).

Pratylenchus sp., Sidam and Yuen (1992); *Pratylenchus coffeae* (Zimmerman)Filipjev & Schuurmans Stekhoven *-hypocotyl rot*, Giatgong (1980).

Radopholus sp., Fong and Poh (1970); Singh (1973).

Rotylenchulus reniformis Lin. & Ol., Sidam and Yuen (1992).

Tylenchorhynchus sp., Sidam and Yuen (1992).

Xiphinema sp. *-attack roots*, Ng and Choong (1991); Sidam and Yuen (1992).

Other animals

Squirrels can be a nuisance in durian plantations (Butt 1982). For instance, a fruit loss of 15.6% was attributed to squirrels in one season (Chiow 1976). Ithnin (1992) has examined the distribution of several rodents in mono- and inter-cropped durian orchards. These include three species of squirrel (*Callosciurus canisep, Callosciurus nigrovittatus, Callosciurus notatus*) and one species of rat (*Rattus tiomanicus*). Squirrel populations were found to be higher in durian plantations intercropped with cocoa. Rat populations were unaffected by intercropping. The three squirrel pests of durian are also mentioned by Nik Masdek *et al.* (1991). Shaji *et al.* (1993) remark that *C. notatus* can be controlled in durian orchards by placing metal shields around the base of the tree, or by the use of poisoned bananas. Oei-Dharma (1969) states that rats, boars and bears are problem animals in Indonesia. Rats are also known to cause damage to stored fruit awaiting shipment (Lee *et al.* 1994). Snails have been listed as a pest of durian leaves by Shaji *et al.* (1993).

Hyperparasitism in durians : Several cases of hyperparasitism have been reported on durian. In these instances, durian parasites are themselves parasitized. One such case is that of the fungus *Gliocladium roseum* Banier., which is a parasite of the durian parasite *Phytophthora palmivora* Butler. (Lim and Chan 1986b). *P. palmivora* is the causal organism of several durian diseases and is probably its major pathogen. *G. roseum* penetrates and destroys the chlamydospores of *P. palmivora.* Although this system immediately suggests a form of biological control for *P. palmivora* related durian diseases, Lim and Chan (1986b) stress that much comprehensive study is needed before this system could be exploited as a method of control. Unfortunately, I have not come across any further work in this area.

The scale insect *Asterolecanium ungulata* is an economic pest of durians. Damage done by this insect often leads to secondary infection of the tree. Lim *et al.* (1991) described the natural control of this pest by the fungi *Aschersonia placenta* and *Hypocrella raciborskii.* More information on this ‘microbial pesticide’ is presented by Ibrahim *et al.* (1993).

A most spectacular case of hyperparasitism of *D. zibethinus* is related by Sands (1924). Mistletoes are parasites of many tropical trees. They can even be found parasitizing other mistletoes. Sands (1924) reported a specimen of *D. zibethinus* upon which was growing *Elytranthe barnesii.* This mistletoe was being parasitized by another mistletoe (*Viscum articulatum*), which, in turn, was being parasitized by another (*Loranthus ferrugineus*).

Vegetative Propagation of Durians

Although durian seeds are viable and trees have historically been grown from seed, durians are now preferably propagated asexually by grafting, seeds being used for the production of rootstocks. Seeds of the cultivar Chanee are used to produce rootstocks for grafting in Thailand (Subhadrabandhu *et al.* 1991). The major problems with direct sowing of seeds are that the genetic makeup of the trees is unknown, and the emerging seedlings are susceptible to predation by rodents. Seeds are now generally grown in a nursery in polybags to produce material for grafting (Hassan n.d.).

Asexual reproduction of durian trees by grafting offers three main advantages over trees produced directly from seeds. Firstly, the genetic nature of the tree is known and can be controlled. This is desirable as fruit quality, size, time of flowering, length of time to maturity and fruitfulness of trees varies widely between clones. Secondly, grafted trees are generally smaller in stature than are trees produced from seed and some clonal material (e.g. D99).

Consequently, more grafted trees can be planted per hectare of land and the fruits are produced closer to the ground. Thirdly, grafted trees start bearing fruits at an earlier age than do trees raised from seed.

The disadvantages of vegetatively propagated material are likewise three-fold. Vegetative propagation is much more labour intensive, different grafting methods have varying degrees of success, and durian trees are sensitive to transplanting; budded durian trees frequently suffer 50% mortality (Feilden and Garner 1936). Thus, it is preferable to keep trees in the nursery for extended periods after grafting to increase the success of transplanting. Because of the great advantages to be gained by asexual propagation, much research has been conducted in this aspect of durian cultivation.

Etiolated shoot method : The etiolated shoot method is a type of layering in which shoots are produced from partially buried branches. Some early work on asexual propagation focused on the etiolated shoot method of propagating durian (Lambourne 1935), which showed some success (Anon. 1935). Analysis of results obtained using this method are published (Lambourne 1935), but the technique does not appear to be very promising. The removal of some of the bark from the shoot has been shown to promote faster root formation in durian (Feilden and Garner 1936).

Double root system : ‘Three legged’ durian trees are created in Thailand (Boonbongkarn 1960). Using this technique, the stems of a few seedlings are grafted onto a more mature tree. This is done after the tree has reached 1-1.5 m in height. The resultant tree has more than one root system, is better able to obtain food and water, and can withstand stronger winds (Boonbongkarn 1960). Old durian trees with declining productivity can apparently be revitalised by grafting a young shoot onto the trunk, and then removing the original stem (Boonbongkarn 1956). Ahmad and Ghani (1990) have noted that this technique is occasionally used on *D. zibethinus* to induce rapid flowering.

Preliminary attempts have been made to graft durian scions onto multiple rootstocks simultaneously (Zabedah *et al.* 1992; Zabedah 1993). These experiments were carried out to investigate the possibility of creating more vigorous planting material with a higher survival rate. Initial results indicated that double and triple grafted material grew more vigorously and had higher fruit set than grafted plants with single rootstocks (Zabedah *et al.* 1992; Zabedah 1993).

Approach grafting : Success with approach grafting of durian trees has been reported using 6-8 months old seedlings (Chua and Teoh 1973). Up to 100% success was reported by Chua and Yong (1978), however, success of graft was higher using older (8-10 months) rootstocks, and an extended time before cutback. Baga Kalie (1979) described a technique for simple splice approach grafting of durian. Baga Kalie and Anwarudin (1980) compared results of simple splice approach grafting and tongued approach grafting of durian; these two techniques were found not to differ significantly in success rate. The highest rate of success was achieved using 8.5 months old rootstocks. An approach grafting technique for grafting seedlings onto branches of mature trees is presented by Zainal Abidin *et al.* (1991). In Thailand, bagged rootstocks are also grafted onto branches of mature trees by inarching (suckle grafting) (Subhadrabandhu *et al.* 1991).

Inarching : Early experiments with inarching (a modified form of approach grafting) of durians were carried out at the Burliar Research Station in India; a success rate of 100% was obtained from inarches made in October, 80% success in November, the success rate of inarching in other months varied from 20 to 60% (Khan and Sambashiva Rao 1952). Furthermore, these authors noted that the graft union took an inordinate amount of time to form. Although inarching durians requires minimal skill, it is laborious, and is not recommended for large scale propagation (Coronel *et al.* 1983). This method of grafting has the disadvantage of requiring larger plants and thus is more expensive (Coronel 1986).

Top grafting : The effects of scion length for top grafting has been investigated using four Thai cultivars of durian (Anwarudin and Sunarjono 1987). Scions of 2, 3 and 4 nodes length were tested; no significant difference in graft take was found. Some durian varieties were found to top graft more easily than others. Rootstocks of different ages have also been tested to discover the most suitable age. No significant difference in suitability was found in rootstocks aged between 1.5 and 3 months (Anwarudin *et al.* 1987).

The wedge (cleft) grafting experiments of Chua and Yong (1978) were not very successful with a maximum of 39% success using 6 months old rootstocks. However, Chong (1985, 1992b) also investigated the success of cleft grafting in 5 clones of durian at different rootstock ages. Chong reported high rates of success (up to 100%), even with 5 weeks old rootstocks in all clones tested. The technique is depicted diagrammatically by Chong and Chai (1986), and is also described in detail by Chong (1992a). It differs from the original technique of Chua and Yong (1978) in that the shoot was bagged, and the plant was well watered for several weeks to ensure the scion received high humidity. Cleft grafting has apparently become a popular technique for commercial propagation of durian in the Philippines (Coronel 1986) as it is fast and requires comparatively little skill.

Bimantoro (1982) described a method of cleft grafting durian scions onto one month old durian seedling hypocotyls, avoiding having to grow and mature rootstocks to the one year old seedling stage. Using this method, parts of the leaves of the scion are removed to reduce transpiration, and the grafted plant is covered by a plastic bag to maintain high humidity. Sunarjono and Jawal (1985), and Sunarjono (1988) described the grafting of durian scions to the epicotylar and hypocotylar regions of seedling rootstocks. The highest success rate was reported for epicotylar grafting (Sunarjono 1988).

Hasan and Inoue (1989) investigated inlay grafting of durians, a modified form of cleft grafting, which allows the joining of a scion with a rootstock having a much greater diameter. This technique was investigated using 2.5 years old bagged rootstocks, and scions of different clonal origins. The effects of the number of leaves on the scions was also studied. The grafts were covered in polyethylene bags as described in Bimantoro (1982). When all leaves were removed from scions, inlaying had a 100% success rate, the best rate of success being obtained from two leaved scions in which the leaves had been cut in half. There was large difference in success rate between different clones; D2 and D7 had adequate success rates but the technique is unfortunately unsuitable for propagating D24 which is one of the most desirable clones (Hasan and Inoue 1989).

Budding techniques : Wester (1914c) reported on the shield budding of durian using the inverted-T method. A success rate of 100% occurred when leaf blades of the budwood were removed from the petioles before grafting, so that a good leaf scar had formed when the petioles had abscinded. If the above treatment was not carried out, bud decay occurred.

Budding experiments using the modified Fokert method resulted in 90% success during the rainy season, but only 40% during the dry season (Magielse and Ochse 1931). Feilden and Garner (1936) reported that the modified Fokert method was used in Java employing one year old non-petioled budwood.

Naik (1949) stated that inarching experiments met with 50% success, but there was no success in shield budding; however, he did not describe his shield budding technique. Wester (1918) provided the following instructions regarding shield budding of durian: ‘Use non-petioled, fairly mature, but not old and hard budwood; cut the bud 2.5 to 3.5 cm long; age of stock at point of insertion of bud unimportant’.

Belgrave (1939) reported that bud patches from previously ring-barked branches are superior for grafting than bud patches from non-ring-barked branches. It is important to note that buds will fail to unite if they become wet (Sankhariksha 1968; Coronel *et al.* 1983).

Sankhariksha (1968) reported low success using several budding techniques, however, these results were attributed to the fact that the rootstocks were not actively growing at the time of grafting. This report did, however, demonstrate that plastic wrap yielded a higher percentage of 'takes' than did traditional budding tape.

Bud grafting experiments with durian have showed that a high percentage success can be obtained. Younger rootstocks are preferable (in this case 4 months) (Chua and Yong 1978). Coronel (1986) stated that patch budding is the least popular method used in the Philippines due to the complexity of the technique, and the need for more mature plant material. Commercial bud grafting of durian has been practised in Malaysia since at least 1954 (Dickinson 1959); according to Hassan (n.d.), bud grafting is the most common form of durian propagation practised in Malaysia.

Other asexual propagation techniques : A side grafting technique for durian is described pictorially by Yong-Ho (1988); this technique requires the use of 5-6 months old bagged rootstocks. I have found no published information on success rates using this technique. Very little information on marcotting of durians is available (Coronel *et al.* 1983); marcotting can be accomplished but it is not recommended. An investigation on the formation of roots on stem cuttings of durian has been published (Hasan and Dodd 1989). Two years old durian seedlings were found to readily form adventitious roots when the stems were cut, dipped in IBA and a fungicide, and planted.

Very little work on the tissue culture of durian has been published. Some success with shoot tip culture of *D. lowianus* has been reported. Although durian tissue can be made to callus, no report of its regeneration has been published.

Grafting to other species : Experiments have been carried out at the Burliar Fruit Station to graft *D. zibethinus* scions onto *Cullenia excelsa* rootstocks (Anon. 1953b). Grafting onto *Cullenia excelsa* rootstocks in India has been reported by Sundararaj *et al.* (1970). Tidbury (1976) tabulated results of grafting experiments onto rootstocks of this species at the Burliar Research Station. These results showed that approach grafts to *C. excelsa* rootstocks averaged much greater growth than did grafts to *D. zibethinus* rootstocks. Grafting to *C. excelsa* also contributed to earlier flowering. Unfortunately, no record of actual success rates of grafts to *C. excelsa* rootstocks were uncovered in the available literature.

As early as 1934, Chevalier recommended grafting *D. zibethinus* scions to rootstocks of one of several wild species including : *D. graveolens, D. dulcis, D. carinatus* and *D. gratissimus* Becc. (now *D. oxleyanus* Griff. *sensu* Kostermans 1958b). Hamilton (1975) and Ding (1988) suggested attempting to graft *D. zibethinus* onto rootstocks of other durian species which may be resistant to *Phytophthora palmivora* in order to provide resistance against this important pathogen. In this regard, it should be noted that the work of Tai (1973) showed that several clones of *D. zibethinus* also differ in their susceptibility to infection by *P. palmivora.*

In their review, Malo and Martin (1979) stated that *D. zibethinus* grafts well onto *D. malaccensis.* More recently, Pupipat (1984) has reported that the resistance originally possessed by *D. malaccensis* roots to *Phytophthora* has since broken down, and that grafting on this species is now useless as a preventive measure.

Pawakul and Chittanawasan (1977a,b) reported that *D. lowianus* is a suitable stock for grafting *D. zibethinus.* Furthermore, they demonstrated that *D. lowianus* is more resistant to the pathogen *P. palmivora* than *D. zibethinus.* Thus, these authors recommended grafting *D. zibethinus* scions onto rootstocks of this species as a disease control measure. Watson (1984) and Subhadrabandhu *et al.* (1991) stated that *D. lowianus* and *D. mansoni* have resistance to *P. palmivora* when used as rootstocks. Tinggal (1993) suggested that *D. testudinarum* may be tolerant to several soil-borne diseases including *Phytophthora*, and that it would make excellent rootstocks for grafts with *D. zibethinus.* However, no results of the success of grafts with this species have been published.

Songpol (1987) described the results of grafting scions from 8 species of durian to *D. zibethinus* rootstocks. Scions differed greatly in their ability to take, *D. lowianus* and *D. kutejensis* had the highest percentage of takes (approx. 75%) while intraspecific grafts of *D. zibethinus* cv. Chanee showed only 33% success after 1.5 months. After one year, *D. graveolens* scions showed the highest percentage of takes (approx 70%). Scions of different species were also shown to vary in the increase in diameter of the graft union stem diameter, stem length and number of nodes produced.

Grafting to rootstocks of *D. mansoni* may have a dwarfing effect on the tree (Subhadrabandhu *et al.* 1991) as the rootstock and the scion thicken at different rates, however, a low percentage of graft occurs.

Although frequent claims are made that grafts of *D. zibethinus* scions to rootstocks of other species could be useful in overcoming diseases of economic importance, it seems unlikely that this would hold true in practice, especially since such grafted trees would need to be planted in large numbers to significantly overcome the economic effects of the disease. The broken resistance of *D. malaccensis* stands as an example of the futility of this simplistic approach (Pupipat 1984). Grafting to other species could perhaps become a useful tool to produce trees of smaller stature, trees which bear fruit at an earlier age, and possibly grafted seedlings with a greater survival rate upon transplanting. Future research on inter-specific grafts would do well to concentrate on these objectives.

Advanced planting material : In order to overcome the problems of establishing grafted seedlings in an orchard, especially when no or little irrigation is provided, the use of 'Advanced Planting Material' is recommended (Zainal Abidin *et al.* 1992). Such material consists of grafted seedlings allowed to reach 15-18 months in the nursery before planting. This material significantly increases the survival rate of trees. Kamariah and Mohammad Isa (1992) have presented some evidence that planting material with a girth of less than 2 cm has a significantly higher mortality rate. Another major advantage to using advanced planting material is the shortening of the time trees take in the orchard before they bear fruit. Normally, grafted durian trees take 6-7 years before they flower, advanced planting materials can flower after 3.5-4 years of growth in the orchard (Zainal Abidin *et al.* 1992).

'Hybrid' Durians : Durian hybrids (clonal) have become a valuable and desirable new commodity. Three clones, MDUR 78, 79 and 88, have been released by MARDI, and are the products of experimental crosses between *D. zibethinus* clones D10 and D24 (Zainal Abidin *et al.* 1992; Zainal Abidin 1993). These 'hybrid' clones show combinations of desirable fruit and tree characteristics including a natural increase in shelf-life of the mature fruits, desirable shipping characteristics, and the trees bear fruits at a relatively early age (Zainal Abidin *et al.* 1992).

Economics and Prospects for Development

A description how durian fruits were locally grown and marketed in Malaysia in 1954 is provided by Wilson (1954). Today, this account is more of historical value than of relevance to modern durian economics. More recent information on strategies to develop durian as a domestic and export crop in Malaysia has been published (Ali 1993; Hamid 1993; Lim 1993). Also, a study of the preferences of Malaysian consumers for durian fruits has recently been published by Syed Abdillah *et al.* (1993). An excellent description of the marketing of durian fruits in different ASEAN nations is provided by Alim *et al.* (1994).

There is little immediate possibility of successfully developing durian as a crop outside Austral-Asia. The durian has no prospects for development as a crop in Western Australia (Boughton *et al.* 1983; Hawson 1983), and is unsuitable for growth in the Mediterranean (Galán Saúco 1994). Durian is, however, suitable for growth in Northern Australia (35 hectares were planted as of 1990), however, durian can only be grown north of 17^o S (Watson 1993). Watson (1993) stated that the demand for fruit is great enough that the hectarage could easily be tripled. The major problem with its introduction into Australia has been the planting of unsuitable clones due to misidentification. Chadha and Pareek (1988) have suggested that durian is worthy of consideration for development in India.

In 1987, Malaysia had almost 40 000 hectares under durian cultivation (Hasan 1989), whereas Thailand had 84 500 hectares under cultivation with a production of 222 000 tonnes (Subhadrabandhu 1992) (a figure approximately double the recorded tonnage in 1983).

Although durian may be unsuitable for growth outside Austral-Asia, the potential for valuable export markets certainly exists. Malaysian trade statistics for 1988 showed that durian already accounts for over 40% of fruit exports (Karim 1992). Although, currently most exported durians end up in Hong Kong (Wurdack 1985), the possibility of developing other overseas export markets remains open (Ito and Hamilton 1990). Japanese import statistics (Kitagawa *et al.* 1990) show that imports of durians into Japan almost tripled during 1986-1988. Although export markets for fresh durians certainly exist, Nichols (1992) has suggested that durian might be better promoted in the form of processed products.

The cultivation of durian is a rapidly growing enterprise as the following statistics will show. Thailand is undoubtedly the worlds largest producer of durian, thus several statistics on their production are available (Watson 1984; Visetbhakdi 1988; Paweenakarn *et al.* 1992). The main durian growing regions of Thailand are the provinces of Rayong and Chanthaburi (Subhadrabandhu 1992; 1993). In 1985, Thailand produced 167 800 metric tonnes of durian fruits, of which 9800 tonnes were produced for export (Paweenakarn *et al.* 1992). In 1989, 89 927 ha were planted with durian with a total production of 486 644 tons [494 430 tonnes] (Subhadrabandhu 1993). The export potential for Thai durians has been steadily growing; exports almost tripled over the 6 years period from 1981 to 1987 (Visetbhakdi 1988); 7 million baht worth of durians were exported to Canada alone in 1986, over twice the amount of longan and pomelo exports to Canada combined in the same year.

According to Watson (1984), Indonesia is the second largest producer of durian fruits with a total production of 157 000 tonnes (Circa 1975). However, the second largest producer of durians today is more likely Malaysia. In 1962, 14 025 ha were under durian cultivation in Malaysia (Jamil 1965). However, in 1972, only 8296 ha were under cultivation. Durian cultivation has been steadily increasing since the 1970s with 31 225 ha reported in 1985, 49 820 ha in 1989 (Ali 1993). The annual production of durians in Malaysia in 1991 was 250 000 tonnes (Zainal Abidin *et al.* 1992). Johore is the major durian growing state in Malaysia (Lim 1990), accounting for 32% of the total durian hectarage in the country (Alim *et al.* 1994). Furthermore, durian currently occupies the largest area under cultivation in Malaysia of any fruit tree species (Jamil 1992c).

A thorough description of the economics of production and marketing of processed durian products in the Philippines is presented by Lisondra (1984), but few published statistics on durian acreage in this country have been encountered. Durian is a relatively minor crop in the Philippines, most likely owing to its limited distribution. In 1977, only 1080 hectares of durian were grown in the Philippines with a total production of 6048 tonnes (Coronel *et al.* 1983), however, in 1985, 1900 hectares of durians existed with a total production of 14 992 tonnes, which represents more than a doubling of production in less than ten years.

Nichols and Christie (1993) state that development should concentrate on germplasm conservation and development of efficient production and post-harvest technology. Setefarzi *et al.* (1991) state that the biggest problem to be overcome is the lack of profitability which springs from a lack of technology, knowledge and high investment costs.

Significant genetic erosion within the genus *Durio* has already been reported (Sastrapradja 1975), especially in Malaysia, Thailand and Indonesia, where clonal varieties have become popular. Hasan (1989) stated that within Malaysia, durians should be the first priority in development. Karim (1992) suggested that different flowering seasons of different clones should be exploited on a national plantation scheme to spread the durian season. This idea is thoroughly discussed by Zainal Abidin *et al.* (1986) (see section on manipulating seasonality). Karim (1992) also suggested that research is needed to reduce the gestation time of the fruit. Pietrzyk (1992) has stated the need for the creation of cDNA libraries for durian and other Malaysian fruits.

Genetic Resources and Conservation

The issue of plant genetic resources conservation is one that hardly needs introduction. In recent years, concern has arisen that the genetic variability of many of the world's most widely grown crops (i.e. wheat, corn, rice) have succumbed to some degree of genetic erosion. Mere popularity of a crop does not ensure the maintenance of genetic diversity necessary for the creation of future varieties, in fact it often produces the opposite effect: those who grow crops are usually interested in increasing their productivity by replacing old and perhaps poorer yielding varieties with new ones.

Although we have very little first hand knowledge of the degree to which durian is threatened by an erosion of genetic resources, it is quite reasonable to suppose that genetic erosion is a very real problem. The majority of durian species are endemic to Borneo which is suffering from intense deforestation. Very little, if any, information is available on the natural genetic variability that exists within durian. For *D. zibethinus*, it is tempting to guess that genetic variation is high, based on the large number of clones now catalogued, however, the amount of variability that exists in any of the wild species of durian is simply unknown. RFLP analysis and isozyme studies are methods which could very easily be applied to answering this queston. Research efforts in this direction would not be prohibitively expensive and would certainly be worth the investment. Such knowledge would aid in estimating the extent, if any, of the problem and provide empirical evidence that remedial action is requried.

Conservation of genetic resources, especially for plant such as durian, needs to be approached holistically in order to achieve desired results. For this reason, this section appears at the end of this work, so that it may draw upon the wealth of knowledge that does exist on durians that has been discussed so far. There are several unique problems that surround the genetic conservation of *Durio*. Firstly, durian cannot be grown with any success outside the humid tropics, limiting sites for the collection of varieties. The durian is not held in great esteem in most of the world (excepting South East Asia), nor is it terribly well suited for growth in other tropical areas of the world. The genus is unsuited for conservation in traditional seed banks as the seeds have a very short period of viability. Some studies have been conducted on cryopreservation of seeds (see section on viability) but no success has yet been achieved. Growing plants in a 'living germplasm' collection has advantages over conventional seed bank storage, but as all members of the genus are large trees, maintaining large numbers of accessions is costly and not always practical. A diverse range of genetic resources to draw upon is crucial for this genus, as it is a crop that has undergone very little domestication and one which has a large potential for improvement. The genetic resources of the common durian are threatened, to some extent, apart from deforestation, due to the new 'improved' clones themselves. The proliferation of popular varieties has led to considerable genetic erosion as less popular non-clonal trees are replaced (Sastrapradja 1975). This is a particular problem in Indonesia, Malaysia, Thailand and Vietnam (Smith *et al.* 1992).

The wild species of *Durio* present another and perhaps larger challenge for genetic conservation. *D. zibethinus* faces the dilution of its gene pool by the large scale planting of genetically identical clones. By comparison, all of the wild species are quite rare, some are in danger of extinction and a few may already be extinct. It is claimed that a *D. macrantha* tree growing in Bogor (a newly described species with edible fruit) may be one of the last living specimens (Anon 1992). Smith *et al.* (1992) stated that several wild species are threatened by logging. Although admittedly not much is known about the genetic diversity of most of the wild species, erosion has been documented for *D. kutejensis* (Sastrapradja 1973b). The genetic resources of the wild species are equally, if not more, valuable than those of *D. zibethinus* for three reasons. Firstly, some of these species do have potential as fruit tree crops themselves. Although not grown anywhere near the scale of *D. zibethinus,* several other species are cultivated. *D. kutejensis* is cultivated in the eastern part of Kalimantan and *D. oxleyanus* is in rare instances cultivated in some Bornean villages (Soegeng-Reksodihardjo 1962). At least a dozen of the known species have edible fruits (see section on edibility), although the majority of these have never been cultivated. Some of the these wild fruits may actually be superior in quality to those of many of the clones of *D. zibethinus*. Secondly, there is evidence that some of the wild species may have higher resistance to some of the major durian pathogens (*Phytophthora* in particular). Hamilton (1975) has already called for the investigation of resistant rootstocks to *P. palmivora* from other durian species. There is interest in not only using wild *Durio* species as rootstocks for *D. zibethinus* (as *Phytophthora* is a root disease), but in producing true hybrid trees. Thirdly, the possibility of producing hybrid trees opens the door to improvement possibilities far beyond resistance to pathogens. Several *Durio* species are so closely related to *D. zibethinus,* they most likely do, or have already been shown to hybridize with it. Possibilities thus exist for altering the size of the tree, time of flowering, reducing the age to first flowering, affecting seasonality, increasing yield, improving the flavour, smell, colour, texture and size of the fruits.

Wild rootstocks were rather recently held to be the solution to

Phytophthora infections, however, attempts to implement this as a solution by mass planting of grafted trees have not only failed, but destroyed the resistance that originally existed in *D.malaccensis* (Pupipat 1984). The key in maintaining diversity in *Durio* and successfully using it, while avoiding similar misfortunes, lies in a multifaceted approach to durian improvement. Perhaps a three pronged approach such as the following is a solution.

There is a role that can be played by seed bank type institutions. Although the seeds of durian cannot be stored conventionally, successful cryopreservation may, with research, be achieved. Even better would be the production and cryopreservation of callus. In my experience, durian callus is relatively easy to produce, and it seems a more likely candidate for surviving cryopreservation than do the seeds. What is so far lacking is not a method for callus production, but rather a method of regenerating plants from callus. Attempts to regenerate durian callus have so far been unsuccessful, but very few attempts have been made. Developing methods for the successful preservation of durian germplasm may simply be a matter of informing researchers that this is a problem that needs attention. Much research on durian has been carried out in several ASEAN nations, however, much repetition exists. A combined effort of the ASEAN nations is a key to surmounting this problem and perhaps to increasing awarenss of genetic resource erosion of durian as well as identifying those areas of research most in need of attention.

Germplasm collections of trees (not necessarily the most popular clones) are of great value. Collection of durians in this manner has already begun. Chang and Lee (1975) stated that Singapore has carried out some collection and conservation of *D. zibethinus* (although the extent of this remains unknown). Attempts to collect and preserve genetic variability in 3 species of *Durio* in Indonesia have been reported (Anon. 1979b).

Several collections of considerable size already exist (Table 10). The MARDI germplasm collection, one of the largest collections of *Durio* in the world, consisted of about 40 trees in 1975 (Arasu 1975) but now contains almost 400 accessions (Chan 1992). However, such collections are not in themselves the entire answer. These collections need to be supplemented by the preservation of large tracts of forest in areas where wild species are naturally found (Lamoureux 1975). Reforestation could even be exploited to these ends as durian trees have been recommended for such purposes (Djober 1953). Furthermore, some consideration needs to be given as to which materials need to be collected, especially in the case of the wild species. Hopefully, this manuscript has provided some insight into this matter.

In utilizing genetic resources for the improvement of durian, we need

Table 10. Durian germplasm holdings at different locations

Country	Location	Accessions No. *(D. zibethinus)* species)	Accessions No. (other *Durio*	Source
Australia	Darwin, N.T.	10		1
Guadeloupe, France	CIRAD	2 Thai, 1 Indonesian		2
Indonesia	Bogor (Agricultural University)	86 advanced Indonesian cultivars		2
	Bogor (National Biological Institute)	?	?	2
	Lembang	20 advanced Indonesian cultivars		1,2
Malaysia	Kuala Lumpur	310 (including other species)		1
	Penang (Relau Agricultural Centre)	Two collections: 25 varieties (mainly from Penang) and 40 varieties (from other Malay states)		4
	Sabah (Department of Agriculture)	75 clones	*D. dulcis* (1) *D. graveolens* (3) *D. kutejensis* (4) *D. oxleyanus* (5) *D. testudinarum* (2) *Durio* sp. (1)	6
	MARDI	122 accessions in the breeders' collection and 394 accessions in the MARDI-IBPGR germplasm collection		3

(Contd....)

Table 10. Contd.

Papua New Guinea	Lowlands Agri. Experimental Station	1		2
Philippines	Los Banos	97 advanced cultivars +others		1,2
	Location unknown	200 accessions		5
Taiwan	Chiayi Agri. Experiment Station	1		2
Thailand	Bangkok	68 Thai		1,2
	Chanthaburi	504 (500 advanced Thai, 4 old Philippines)	*D. graveolens* (102) *D. kutejensis* (14) *D. malaccensis* (5) *D. mansoni* (158) *D. oxleyanus* (8) *Durio* spp. (36)	1,2
USA	Miami, Florida	16		1
	National Clonal Germplasm Repository Hilo, Hawaii	6 advanced Thai lines		1,2

Sources for data presented in Table 10:

[1] Anon. (1986a).

[2] Bettencourt *et al.* (1992).

[3] Chan (1992).

[4] Murad *et al.* (1993).

[5] Smith *et al.* (1992).

[6] W.W.W. Wong (1993).

to ask the question of exactly what is meant by improvement. If improvement entails increased resistance to pathogens and diseases, increased productivity, decreased seasonality and increased number of cultivars, then improvement means diversity, not homogeneity. Thus, plans for 'improvement' that involve the use of genetic resources for the mass production of new clones/hybrids/grafts are not actually improvement, but the opposite, and may exacerbate the problems they allegedly are trying to solve. This hardly means that the genetic diversity of a genus such as *Durio* cannot be used for improving durians in various ways, indeed it should, but actual improvement requires some foresight as to the consequences of actions.

The ability to improve durians by providing new flavours for those who wish to eat them, spreading out the season and coping with pathogens lies in diversification of the materials that are planted. This is perhaps more crucial for durians than for annual crops as the risks of monoculture have more long-term effects (5-7 years to start up a new orchard).

As discussed above, durians are generally outcrossed, and the nature of the parent trees may affect the degree of fruitfulness. Clones vary in their susceptibility to pathogens as do the varied species. Durians also vary greatly in their flavour, size and desirability. For these reasons, the most intelligent approach to designing orchards should be carefully planned diversity; to their credit, this appears to be the approach taken by MARDI (Chan 1992). A diversity of rootstocks, a diversity of clones, a diversity of hybrids, and a diversity of species, and in this way the numerous and varied advantages of different trees can all be exploited and the varied disadvantages diluted. This approach also offers the real possibility of extending the durian season and thus increasing availability and profitability. It is easy to see how this approach could limit the effect of pathogen outbreaks. The exploration of as yet uncultivated (or barely cultivated) species offers the potential for entire new markets.

In conclusion, much has been discovered and written about the mysterious durian fruit, but so much more remains to be achieved. I hope this review has helped to identify and polarize those areas which are in need of further clarification. While we strive to accomplish new goals through our many varied researches, I would remind the reader of the poignant words of Alfred Russel Wallace who, in my estimation, has written the most profound words about man's relationship with this noble fruit.

"Poets and moralists, judging from our English trees and fruits, have thought that there existed an inverse proportion between the size of the one and the other, so that their fall should be harmless to man. Two of the most formidable fruits known, however, the Brazil Nut (Bertholletia) and the Durian,

grow on lofty trees, from which they both fall as soon as they are ripe, and often wound or kill those who seek to obtain them. From this, we may learn two things: first, not to draw conclusions from a very partial view of Nature; and secondly, that the trees and fruits and all the varied productions of the animal kingdoms, have not been created solely for the use and convenience of man" — Wallace (1856)

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The following bibliography consists of over 1000 references (largely of a scientific nature) pertaining to durian. The bibliography consists only of items of which an original or a facsimile has been examined by the author. Much of the research conducted on durian has been published in extremely obscure and difficult-to-obtain books, journals, conference proceedings and reports. As these materials have often never been abstracted, the need for a comprehensive bibliography is even more pressing. This bibliography attempts to present detailed (non-abbreviated) citations for all items, to aid others in identifying and obtaining copies of these works. The bibliography also contains parenthetic notes [square brackets] which have been added to provide additional information, such as the language of publication, what portions of the work (if any) are written in English, where possible an English translation of non-English titles and/or information on published translations of works. The date(s) following the author's name(s) represent the actual date of publication (as far as is known). This occasionally deviates from the dates printed on the work, especially for older works, annual reports, etc. Explanatory notes are given as appropriate. To accommodate to the realities and limitations of obtaining copies of scholarly works, and the severe limits imposed on research by modern copyright legislation, the pages pertaining specifically to durian in long works and/or works in which durian forms only a small and discreet portion of the whole are noted at the end of references, when appropriate. Attempts are made to clarify the identity of species where the current taxonomic identity has changed from that used in the publication. Although exhaustive attempts were made to fully identify and give credit to all authors responsible for each publication, this is often difficult or impossible to accomplish. All works, to which no actual person could be attributed authorship (including publications of institutes, associations, etc.), are listed chronologically as anonymous. I apologize in advance to the authors of what I estimate to be approximately 150 research articles on durian not included in this bibliography. Despite exhaustive efforts, copies proved impossible to locate or examine.

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