The Angiosperm Flora of Singapore 1. Introduction

RICHARD T. CORLETT
Department of Botany
University of Hong Kong
Hong Kong

EFFECTIVE PUBLICATION DATE: 15 MAR 1993

The Republic of Singapore is an independent state of 2.7 million people at the southern tip of the Malay Peninsula, 137 km north of the equator (Fig. 1). It consists of the island of Singapore and more than 50 smaller islands. The main island is 42 km by 23 km at its widest points and has an area of 574 km^2, of which more than 30 km^2 has been added by recent land reclamation (Anon, 1990). It is separated from Malaysia by shallow straits, 0.6 km wide at the narrowest point. The largest of the other islands are Pulau Tekong Besar (1,793 ha), Pulau Ubin (1,019 ha) and Sentosa (309 ha). The total land area, including all the islands, is 626 km^2.

The topography of Singapore is predominantly low, with an average elevation of only 15.1 m (Thomas, 1991). The landscape of the main island can be roughly divided into three parts. In the centre of the island is a hilly region of granite and other igneous rocks, rising to a maximum of 162 m at Bukit Timah Hill. The western, southwestern and southern region, including most of the southern islands, consists of a variety of sharply folded sedimentary rocks with northwest-trending ridges and valleys. The eastern region is relatively flat and covered in semi-consolidated deposits of sand and gravel. Low-lying coastal plains and the lower parts of river valleys are filled with recent alluvium.

Singapore's "rivers" are large streams with broad estuaries, which result from flooding of valleys incised during periods of low sea-levels in the Pleistocene. Around the coastline, cliffs and other rocky shores are of limited extent, except on some of the southern islands. Until recently, most shores consisted of mud and sand in varying proportions. Muddy shores with mangroves predominated, except along the southeast coast, which was lined with sandy beaches. Today, however, much of the coastline is entirely artificial as a result of extensive land reclamation and coastal development.

Palaeogeography

Singapore is part of the Southeast Asian extension of the great Eurasia plate and is largely unaffected by the tectonic and volcanic activity around the plate margins to the west, south and east. The regional pattern of land and sea, however, has changed dramatically many times during the last million years or so, largely as a result of changes in sea-level. During glacial periods, sea-levels were up to 200 m lower than at present, exposing most of the Sunda shelf and joining the Malay Peninsula, Sumatra, Java and Borneo into one land mass ("Sundaland"), with Singapore somewhat west of centre (Morley and Flenley, 1987). At the opposite extreme, reported Holocene sea-levels up to 5 m higher than present (Geyr and Kudrass, 1979; Pirazzoli, 1991), would have substantially reduced Singapore's land area. Glacial periods occupied much more

Fig. 1 Map of Singapore showing major roads and reservoirs. Inset map shows the geographical position of Singapore.

of the Pleistocene than interglacials, so the present geography of the region must be seen as the exception rather than the rule. Singapore is cut off from the Malay Peninsula by water less than 10 m deep at the shallowest crossing, which implies a final separation about 7,000 years ago (Pirazzoli, 1991). The sea is deeper in the Singapore Straits to the south, so Singapore would have been cut off from Riau before it was separated from the Peninsula.

The repeated alternation of glacial and interglacial periods was also reflected in the region's climate. A decrease in total rainfall and increase in rainfall seasonality during the glacial periods has been suggested for that part of the Sunda Shelf which includes Singapore (Morley and Flenley, 1987; Heaney, 1991). A pollen assemblage from middle Pleistocene Subang, 300 km northwest of Singapore, is striking for the dominance of pine and grass pollen and absence of typical rain forest taxa, suggesting a very different climate. In Singapore itself, the Pleistocene Old Alluvium, which blankets much of the eastern part of the island, seems to have been deposited under far more seasonal climatic conditions during a period of glacial low sea-levels (Gupta *et al.*, 1987). The question of glacial temperatures is more controversal. Oxygen isotope and foraminiferal data suggest a lowering of sea surface temperatures by at most 2 °C at the last glacial maximum, in the vicinity of the Sunda shelf (CLIMAP, 1981). However, this is very difficult to reconcile with evidence for much greater temperature changes at higher altitudes in the region (Walker and Flenley, 1979). Sea-level temperatures 5 °C or more below present have been suggested for near-equatorial Amazonia (Bush *et al.*, 1990) and this possibility must be considered for equatorial Asia (Liu, K.B., pers. comm.). In any case, it is clear that as little as 10–15,000 years ago and for most of the Pleistocene, Singapore would have been occupied by a vegetation and flora very different from today's and probably lacking a modern analogue elsewhere in the region.

On a longer time-scale, the phytogeography of the region has been affected by its complex tectonic history. The Malay Archipelago, as it exists today, was created by a mid-Miocene collision between Australia-New Guinea and Southeast Asia, in the vicinity of Sulawesi (Audley-Charles, 1987). There has never been a dry land connection between Australia and Southeast Asia, even at extreme Pleistocene low sea-levels, but the many islands between Sunda and Sahul (Australia-New Guinea) must have greatly facilitated floristic exchange.

Until recently, paleogeographic reconstructions of the region before convergence showed a huge gap between Southeast Asia and Australia, making earlier biotic interchange between the regions unlikely (e.g. Audley-Charles, 1981). It now appears that, not only was this gap much narrower than once believed, but the whole of Southeast Asia is made up of a series of continental fragments rifted from northeastern Gondwanaland. The dating of these events is still contentious. Even if rifting of the major fragments occurred in the Jurassic (Audley-Charles, 1987), it is unlikely that the rifted fragments carried an Angiosperm flora at the beginning of their journey north, although they may well have acted as "stepping stones" between Australia and Asia later on. If, as much of the evidence suggests, the major fragments were already welded to Eurasia by the early Mesozoic (Metcalfe, 1990), they cannot have carried angiosperms. At Gunong Belumut, 75 km north of Singapore, there is a Later Permian fossil flora of undoubted Cathaysian (i.e. tropical Eurasian) affinities, with no Gondwanic elements (Hutchison, 1989). However, other blocks that make up modern Sundaland had Gondwanic floras at this time, showing they had not yet separated from that continent. Moreover, smaller fragments apparently continued to be added to the margins of Southeast Asia during the Jurassic and Cretaceous. It thus appears that the sea between Australia and Eurasia has never been empty, although speculation on the details of the regional palaeogeography are premature at this stage.

India, which did not rift from Gondwanaland until the early Cretaceous, and then moved very rapidly north, provides another possible route for one-way transport of Gondwanic angiosperms to Eurasia. India's collision with Tibet occurred in the Eocene.

Human Impact

Early man arrived in southeast Asia a million or so years ago, followed by modern *Homo sapiens* at least 50,000 years ago. It seems likely that human population densities in the equatorial lowlands were low before the introduction of agriculture within the last 4,000–6,000 years but it would be a mistake to underestimate the possible impact of pre-agricultural man on the biota of the region. The arrival of *Homo erectus*, an adaptable and intelligent hunter, is likely to have affected populations of large, ground-dwelling herbivores and this impact would have extended into the forest canopy when, later, throwing spears or similar weapons were added to man's arsenal. The extinction of large herbivores would have influenced forest structure both directly, through reduced grazing, browsing and trampling, and indirectly through the loss of their role in seed dispersal. Man's use of fire – of uncertain antiquity – must have been most significant during the dryer, glacial episodes, but droughts occur even during the wet interglacials and extra sources of ignition increase the risk of fire.

The process of homogenisation of the economic and weed floras of the Old World tropics must have started early. The Malay Archipelago has been linked by a maritime trading network from prehistoric times and has had trade links with China, India and the Middle East for at least 1,500 years (Dunn, 1975). With the arrival of Europeans in the early fifteenth century and the establishment of trans-Pacific trading routes, neotropical crops and weeds also made their appearance. Maize, tobacco, chilli, peppers, papaya, pineapple and sweet potato all became established in the region before the end of the fifteenth century (Reid, 1988). In recent times, Singapore, as a port city with a large botanic gardens, may have been the point of entry to the region for many exotic plants.

Although human populations must have lived in Singapore for thousands of years, the first definite historical accounts of a settlement on the island date from the fourteenth century, when Temasek (later called Singapura) appears in Javanese, Chinese and Vietnamese records. Temasek/Singapura was probably not the great trading city described in the Malay Annals but there is archaeological evidence for a substantial settlement at the mouth of the Singapore River in the fourteenth century (Miksic, 1985). Tome Pires, who lived in Malacca from 1512–1515, says that Chinese vessels came for the "infinite quantities of the black wood that grows in Singapore" (Cortesao, 1944). Temasek went into gradual decline during the fifteenth century and the last vestiges of the settlement were burned by the Portuguese in 1613. For the next 300 years, the island disappeared from history but there is no reason to believe it was ever uninhabited.

When the British arrived in 1819, the population of Singapore island consisted of about 1,000 people. Most of these were boat dwellers: the Orang Kallang, who lived in the swamps at the mouth of the Kallang River; the Orang Seletar, who lived in mangrove areas along the north side of the island; and the Orang Gelam, in the Singapore River (Logan, 1847; Thomson, 1848). These people apparently grew no crops but may have had a significant ecological impact through their hunting and collecting activity. The remainder of the population consisted of Malays and Chinese living in a small settlement at the mouth of the Singapore River or growing gambier in the surrounding hills.

The foundation of the British colony led to a rapid and sustained rise in population. From the beginning, Singapore was primarily a trading centre, but the cultivation of cash crops also expanded and spread into the interior of the island. Many crops were grown during the nineteenth century but, except on the sandy soils of the southeast coast, where coconuts were the major crop, most of the initial clearance of primary forest seems to have been for the cultivation of gambier (*Uncaria gambir* (Hunt.) Roxb.). Gambier was grown for export to China, and later Britain, where it was used for tanning leather and as a dye. It grows best on soil newly-cleared of forest and each plantation required a roughly equal area of forest to provide firewood for boiling the gambier leaves (Jackson, 1965). The Chinese gambier growers rarely had any legal title to the ground and simply moved on when the soil was exhausted and the fuelwood supply insufficient. Abandoned plantations were invaded by the grass *Imperata cylindrica* (L.) P. Beauv. or by secondary scrub.

Gambier continued to be a major crop in Singapore until 1890, after which the area declined rapidly. By this time, little of the original forest cover remained and most surviving forest fragments had been heavily exploited for timber and firewood (Corlett, 1991*a, b*). After the departure of the gambier growers, the cultivation of other crops, particularly pineapples, increased. However, it was an entirely new crop, rubber (*Hevea brasiliensis* (A. Juss.) M.A.), which had the major impact in the first half of this century. After the first commercial plantings in the 1900s, the area expanded rapidly, reaching a maximum in 1935, when nearly 40 per cent of Singapore's total land area was under rubber plantations. After this, the area under cultivation declined sharply, except for a temporary increase in the production of food crops during the Japanese occupation (1942–45). The post-war era saw a decline in all crops except vegetables as agricultural land was increasingly lost to urbanisation and industrialisation. Today, less than 100 hectares are used for intensive vegetable cultivation while more than half the main island is urban in character.

Although heavily exploited for firewood, most of Singapore's extensive mangrove forest area survived into the twentieth century. All but a few small areas have subsequently succumbed to conversion to brackish water ponds for agriculture, systematic reclamation for building and, more recently, the barraging of all major non-urban estuaries to create freshwater reservoirs (Corlett, 1987).

Conservation

In the early decades of the colony, exploitation and clearance of the forest apparently proceeded unchecked. In 1848, however, concern about possible effects on Singapore's climate led the Governor to prohibit the further destruction of forest on the summits of hills. This prohibition seems to have been effective for Bukit Timah, at least (Corlett, 1988*b*). By 1882, when Nathaniel Cantley was commissioned to survey the forest resources of the Straits Settlements (Singapore, Malacca, Province Wellesley and Penang), concern for the climatic effects of deforestation had largely been replaced by worries about the timber supply. Cantley, reporting that only 7 per cent of the original forest remained, proposed the creation of forest reserves (Cantley, 1884). His recommendations were accepted and, eventually, about 10 per cent of the island was protected in this way (Fig. 2). Unfortunately, most of the reserve area consisted of grassland, scrub or degraded mangrove, with little good forest. In addition to the forest reserves, an area around Singapore's first reservoir (now called MacRitchie

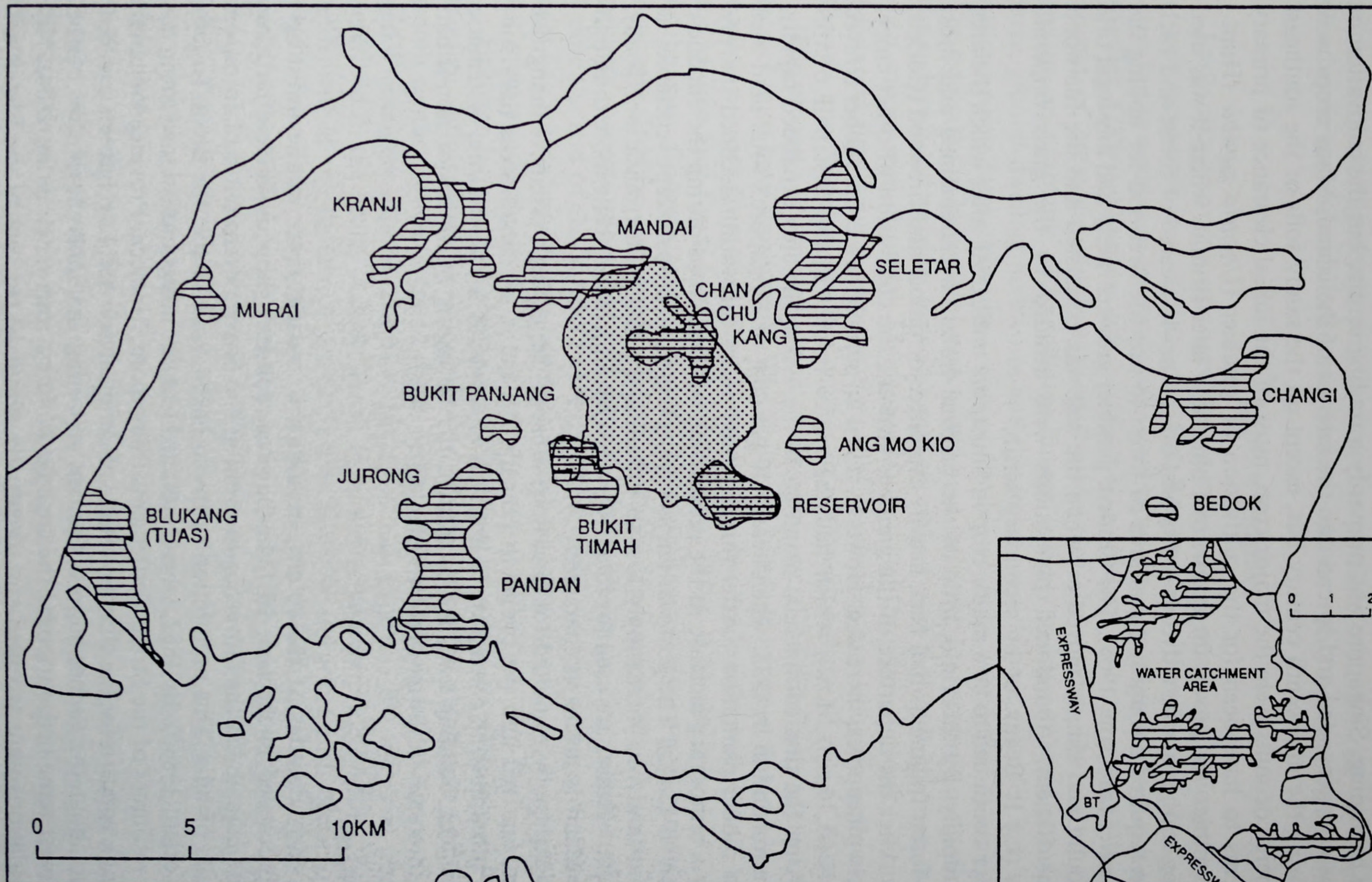

Fig. 2 Map of Singapore showing Forest Reserves in 1897 (hatched) and Nature Reserves in 1991 (dotted). Inset map of the central part of the island showing the water catchment area and Bukit Timah Nature Reserve (BT).

Reservoir), partly covered in degraded primary forest, was protected during the 1890s as a catchment.

Most of the reserves were eventually worked for timber, handed over to squatters or otherwise developed. An area of primary forest survived at Changi until 1927, when it was cleared for construction of a military base. The decline in the forest reserves coincided with an increase in the protected catchment area as new reservoirs were constructed in the centre of the island. The expanded catchment area incorporated several fragments of disturbed primary forest, including what remained of Chan Chu Kang Forest Reserve and part of the Mandai Reserve, although this latter area was later cleared for the extension of Seletar Reservoir in 1940–41.

The Forest Reserves were finally abolished in 1936 but Bukit Timah and parts of the mangrove reserves at Pandan and Kranji were placed under the control of the Botanic Gardens. In 1951, these three areas, with the entire catchment area and 4 hectares of cliff face at Labrador, became Nature Reserves. The mangrove reserves were subsequently lost to development. Today the Nature Reserve system consists of 2,795 hectares in the centre of the island, of which 81 hectares is in Bukit Timah Nature Reserve and the rest in the Public Utilities Board Catchment Area (Fig. 2). A small area of mangrove at Sungei Buloh is protected as a bird sanctuary.

Climate

Singapore is only 137 km north of the equator and has an equatorial climate. The range of mean monthly temperatures is only 25.5–27.3 °C and of mean monthly rainfall 160–300 mm. In Southeast Asia, similar climates are confined to the southern part of the Malay Peninsula, parts of Sumatra, much of Borneo and part of western Java. Elsewhere, only the island of New Guinea and parts of the central and western Amazon region have extensive areas of such climates. The botanical consequences of this extreme aseasonality are most obvious in urban areas, where the tree-lined streets are green all the year round but rarely show the massed flowering displays of other tropical cities. As discussed below, however, both seasonal and non-seasonal variations in the climate are of great significance for the native flora.

Despite its small size, Singapore also shows a surprising amount of spatial variation in rainfall. Mean annual rainfall exceeds 2,300 mm in the central part of the island and falls below 2,000 mm along much of the south coast (Chia and Foong, 1991). This spatial variation may have had a significant effect on plant distributions before the nineteenth century but its influence is now obscured by the effects of recent human impact.

A thorough review of Singapore's climate with additional references can be found in Chia & Foong (1991). Here I will only discuss features of direct botanical relevance.

Seasonality

Despite its apparent constancy, Singapore's climate is perceived by people, birds (Hails, 1987), and plants as seasonal. The time difference between the longest and shortest days of the year is only 9 minutes so photoperiod effects are unlikely, if not impossible. The long term means of air temperature, rainfall, relative humidity and solar radiation are clearly seasonal, although within a narrow range (Fig. 3). This limited seasonality is a consequence of the changes in the prevailing wind direction. The northeast monsoon prevails from November to March and the southwest (or, more accurately in Singapore, south) monsoon from May to October. During the inter-monsoon periods of April/May and October/November wind directions are variable.

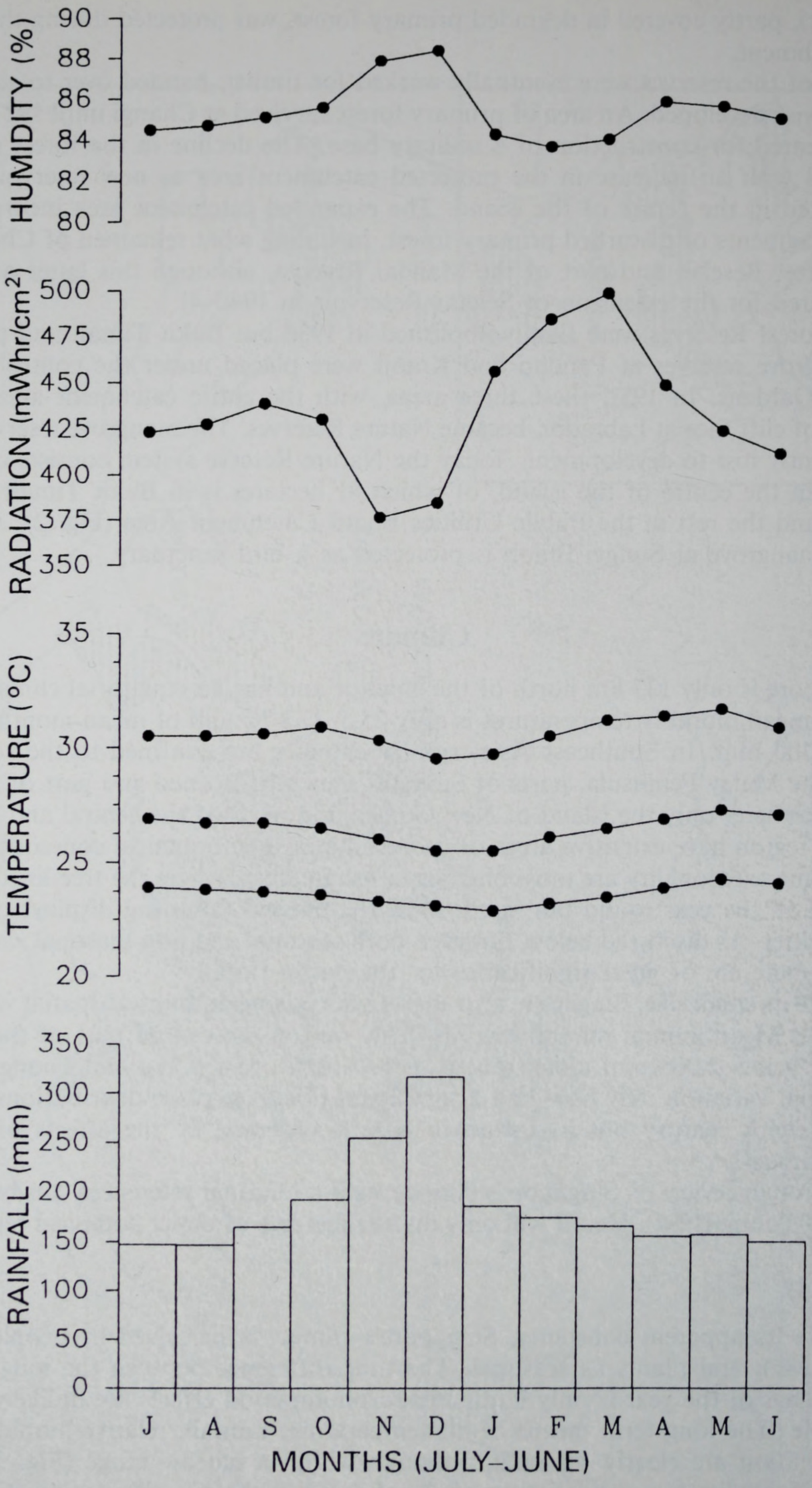

Fig. 3 Annual variation in the long-term means for humidity, solar radiation, temperature and rainfall for Paya Lebar, Singapore. Note that the time scale is from July to June so that the major annual climatic change appears in the centre of the graph.

November and December are generally cooler, wetter and cloudier than other months. The solar radiation maximum is in February/March, which is also the period most prone to long dry spells. The month with the lowest mean rainfall, however, varies in different parts of the island. The hottest months are May and June. The most striking climatic change in most years is between the cloudy, wet period at the beginning of the northeast monsoon in November/December and the relatively drier and sunny period towards the end, in February/March (Fig. 3). The strength of this contrast is obscured in long-term averages because the precise timing varies from year to year but, in most years, it is the most significant interruption to the uniformity of the climate.

A single annual community-level flowering peak — around April — has been reported from several lowland forest sites in the Malay Peninsula (Ng, 1988), presumably triggered by this change. Corner (1988) suggests that there is often a second, weaker, flowering peak later in the year, triggered by a second, less predictable, dry period. There is no quantitative evidence for this but two annual peaks of leaf flushing have been described at some sites. Clear annual (e.g. *Campnosperma auriculatum* (Bl.) Hook. f.) or biannual (e.g. *Fagraea fragrans* Roxb.) flowering periodicities are fairly common in the Singapore flora.

The absence of regular seasonal climatic extremes must make non-seasonal extremes more easy for plants to detect. It is not surprising, therefore, that irregular climatic events that do not follow an annual cycle are of at least equal botanical significance in Singapore. Some of these climatic cues occur with a frequency greater than annual. The sudden drop in temperature caused by daytime thunderstorms is known to provide the trigger for already-formed flower buds to complete their development in certain orchid species (e.g. *Dendrobium crumenatum* Sw.) and the angsana tree (*Pterocarpus indicus* Willd.). Several other species which flower synchronously several times per year (e.g. *Rhodamnia cinerea* Jack, *Timonius wallichianus* (Korth.) Valeton) presumably have a climatic trigger for floral initiation.

Other climatic extremes occur with less than annual frequency. Many forest species show supra-annual reproductive cycles which may have climatic triggers. At irregular intervals of 2–10 years, the reproductive activity of many species coincides in a massive burst of flowering followed by an equally striking fruiting peak. The cue for this dramatic mass-flowering is certainly climatic but the precise event responsible is still uncertain. Dry weather (Foxworthy, 1932; Medway, 1972), increased daily sunshine hours (Ng, 1977), and a drop in minimum temperature (Ashton *et al.*, 1988) have all been suggested. All three suggested triggers tend to occur together near the beginning of the year and may be associated with the El Niño-Southern Oscillation Event (Ashton *et al.*, 1988). A mass-flowering event in Singapore in 1987 (Corlett, 1990) followed an exceptionally dry and sunny February, but there was no significant drop in minimum temperature. The consequences of this supra-annual pattern of forest phenology for the common, basically frugivorous, monkey, *Macaca fascicularis*, are described by Lucas & Corlett (1991).

Climatic extremes may act as constraints as well as triggers but this effect is not obvious in Singapore. The extreme minimum (19 °C, in January 1934) and maximum (35.8 °C, in April 1979) temperatures recorded on the island differ little from the annual extremes. Hailstorms are rare and the longest recorded dry spell was 32 consecutive days in February and March, 1970. Singapore is well outside the typhoon belt but during the south monsoon short-lived squalls, known locally as 'Sumatras', can cause damage to isolated trees.

Microclimates

Few plants experience the "raw" climate recorded at standard meteorological stations. For the majority, climatic means and extremes are modified by the presence of other plants and non-living structures. The contrast between the microclimate near the forest floor and that above the canopy or in a large clearing is well-documented (Whitmore, 1990). Most of Singapore's native flora must have been adapted to spending all or part of its life cycle in the cool, damp shade of the forest understorey. The only exceptions would have been canopy epiphytes, gap specialists and coastal species. Most of Singapore is now one huge, permanent clearing so the dominance of exotics and coastal species among both the planted and spontaneous flora is not surprising. Outside the forest, there is also a marked rural-urban contrast in microclimate (Singapore Meteorological Service, 1986), attributed to heat stored in urban structures, but the botanical significance of this is unknown.

Geology and Soils

Geology

The geology of Singapore has recently been reviewed by Thomas (1991) and a geological map of the island is available (PWD, 1975). Only a brief summary is given here.

The centre of the main island is underlain by the Bukit Timah Granite. This consists of acid igneous rocks, ranging from granodiorite to true granite, dated to the early-middle Triassic (230–205 Myrs B.P.). Other granites of similar or more recent age outcrop at Changi Point, Pulau Sekuda and Pulau Ubin. The Gombak Norite outcrops in a restricted area on the west of the Bukit Timah Granite, around Bukit Panjang and Bukit Gombak. It consists of basic igneous rocks ranging from norite to gabbro and is older than the Bukit Timah Granite. Most of the southern, south-western, and western part of the main island, and most of the southern islands, are underlain by a variety of sharply-folded sedimentary rocks termed the Jurong Formation. These include conglomerates, sandstones, siltstones and mudstones. They are younger than the Bukit Timah Granite: probably of upper Triassic to early or middle Jurassic age (230–180 myrs B.P.).

Much of eastern Singapore and a part of the northwest is covered in semi-consolidated alluvial sands and gravels, with some silt and clay. This deposit, called the Old Alluvium, is predominantly granitic in provenance and seems to have been deposited in a braided river environment during the more seasonal climate of one or more of the Pleistocene cold stages (Gupta *et al.*, 1987). Holocene deposits of various types cover low-lying coastal areas and fill the lower parts of river valleys. These include beach sands and gravels deposited during the Holocene sea-level maximum (ca. 5,000 B.P.) and a variety of other marine, estuarine and alluvial gravels, sands, muds and peats.

Soils

The soils of Singapore were classified into 24 series and mapped by Ives (1977) and have recently been reviewed by Rahman (1991). Unfortunately, soil classifications produced by soil scientists, principally for agricultural purposes, often seem to have little predictive value for ecology, particularly in the tropics. This is probably because many ecologically important features of a soil are destroyed by cultivation. A soil can be cleared of its vegetation cover, suffer severe compaction, have its organic matter oxidised, its nutrients leached, and its surface layers eroded, without changing its position in the classification. Moreover, Singapore's continuous high temperature and rainfall, and the resulting intense weathering and leaching, have resulted in soils with similar properties on a range of different parent materials. Extreme parent materials, such as limestone and ultrabasic rocks, do not occur in Singapore.

Most soils in Singapore can be described as sandy clay loams and have a bimodal particle-size distribution. All are acidic, with a low cation exchange capacity and low to very low concentrations of available nutrients. All except those under the small areas of primary forest have undergone at least one agricultural cycle and much of Singapore is covered in soils which, whatever their taxonomic position, are characterised by extreme soil degradation as a result of nineteenth and early twentieth century agricultural practices. Over large areas the original soil has been removed, buried or drastically altered by construction activity. A variety of different fill materials have been used for the extensive reclamation of land from the sea, including clayey subsoil from inland construction projects and marine sand dredged from the sea bed. Sand fill resembles natural coastal deposits but clayey fill, after compaction to ensure stability, results in a soil that is completely structureless, poorly aerated and drained, and very low in fertility.

Six of the ten soil orders in the United States Department of Agriculture (USDA) Soil Taxonomy have been recognised in Singapore (Rahman, 1991). The largest area is covered in Ultisols. These are found on granite, on the fine- and mixed-grained sedimentary rocks of the Jurong Formation, and on the Old Alluvium. Soil development is greatest on well-drained, level ground over granite and least on the Old Alluvium, where some of the less-developed soils may be better classified as Inceptisols or Entisols (Rahman 1991). Inceptisols are also found on some of the coarse-grained, resistant rocks of the Jurong Formation. Soils over granodiorite and the more basic igneous rocks typically develop into Oxisols. The soils on recent alluvium are mostly Entisols, although of widely varying properties. Other soil types of relatively minor extent occur near the coast, including highly organic Histosols formed under freshwater swamp forest, Spodosols (podzols) on old beach deposits, and the distinctive Sulfaquents under mangrove.

Biogeography

This account of the biogeography of Singapore's flora is based on the species list of Turner *et al.* (1990), with distributional data from regional floras, principally the Flora Malesiana, Tree Flora of Malaya, Flora of Thailand, Flore du Laos, du Cambodge et du Vietnam, and the Flora of Australia, supplemented, where possible, by data from more recent monographs. This data has a number of obvious limitations, apart from its incomplete taxonomic coverage. Most serious is the undercollection of much of the region around Singapore, particularly Riau, Sumatra and Kalimantan. There is also the problem of non-coincidence of biogeographical and political boundaries. In the region under consideration here, the clearest examples are the Malaysia-Thailand border, which is somewhat south of the northern limits of much of the Malesian flora, and the island of Palawan, which is biogeographically Bornean but politically part of the Philippines. Thus "Thailand" or "the Philippines", unqualified, in a description of a species distribution, are not very helpful to the biogeographer.

Takhtajan (1986) places Singapore in the Malesian Subregion of the Malesian Region of the Paleotropical Kingdom. The Malesian Subregion is further divided into five provinces, with Singapore in the Malay Province. However, the suggested differences between the Malay Province and the adjacent Sumatran and Kalimantan Provinces are minor. Indeed, at the species level, the most striking feature of Singapore's flora is its broad distribution. The question of possible Singapore endemics is probably best left until **after** this Flora is completed, but they are undoubtedly very few, if any. Even among the inland rain forest flora – the plants most likely to have restricted distributions – only 15 per cent of the 730 species for which I could obtain reasonable data are apparently confined to the Malay peninsula (including peninsular Thailand and, in a few cases, peninsular Burma or the Riau Archipelago). A further 50 per cent of forest species occur more widely in the everwet "core" of Sundaland (Sumatra, Borneo and West Java). The remaining third of the species are even more widespread, extending northwards into continental Asia (21 per cent), or eastwards through Malesia towards Australia (14 per cent). The wide distribution of most Singapore forest species is no doubt the result of the unexceptional nature of the physical environment and Singapore's position near the centre of the Sunda shelf. It does suggest, however, that whatever the effects of full-glacial aridity on the vegetation of the region, continuous rain forest was re-established on Sundaland *before* rising sea-levels created major barriers to dispersal.

It is important to point out that the Singapore populations of widespread species are still of conservation value because of the likelihood of ecotypic variation at the margins of the range. Moreover, deforestation to the north and south of Singapore is rapidly restricting the range of species that were widespread ten or twenty years ago.

As might be expected, the coastal flora is much more widely distributed. *Caesalpinia bonduc* Roxb. and *Thespesia populnea* (L.) Correa are effectively pantropical while a number of species range from East Africa to the western Pacific (e.g. *Bruguiera gymnorrhiza* (L.) Lamk., *Excoecaria agallocha* L.). These extremely wide ranges presumably reflect both the tendency to seawater dispersal in the coastal flora and the relative uniformity of the coastal environment.

The flora of man-made open sites is essentially pantropical, consisting of species of Asian origin which have now spread around the world, and exotics from Africa and the Neotropics that have become naturalised in Singapore. As is true throughout the region, the recognizably exotic component of Singapore's flora contains many more species of Neotropical origin (at least 84 species) than from Africa (14 species) (Corlett, 1988). This may reflect similarities in climate and, perhaps, agricultural systems, as well as the large number of crop and ornamental plants deliberately introduced from tropical America. Another interesting feature of Singapore's weed flora is the rarity or absence of several pantropical exotics, abundantly-naturalised in the more seasonal climates of the region (e.g. *Crassocephalum crepidiodes* (Benth.) S. Moore, represented only by a single old record) and the absence of weeds of temperate origin (Corlett, 1992*b*). The composition of the weed flora demonstrates clearly that, far from being a "greenhouse climate" in which anything can grow, Singapore's year-round high temperatures and rainfall exclude unadapted species as effectively as extreme cold or drought.

The biogeography of Singapore's flora at the genus and family levels is that of the Sunda Shelf flora as a whole. The dual origin of the regional flora from both Gondwanic and Laurasian sources has long been recognised. However, the complex geological origin of the Malay Archipelago, outlined above, probably provided a multiplicity of times and routes for interchange, making the recognition of distinct "elements" in the flora difficult. For example, the family Dipterocarpaceae shows an overwhelming concentration of living species in West Malesia (Sundaland plus the Philippines) and probably entered the region from the Asian mainland, but the global distribution of living and fossil members suggests a possible ultimate origin on Gondwanaland (Ashton, 1982). Plants of originally Gondwanic families have probably entered the region from both the south-east (after the Miocene collision between Laurasia and Gondwanaland or, earlier, via island "stepping-stones") and from the north-west (after being "rafted" northwards from Gondwanaland on India). Some taxa (e.g. the palms, of disputed ultimate geographic origin, and the Loranthaceae) have apparently entered the region from both ends (Dransfield, 1987; Barlow, 1990).

Vegetation

Primeval Vegetation

I have been unable to find any useful description of Singapore's vegetation before the late nineteenth century. Early maps and written accounts make insufficient distinction between vegetation types or only refer to small areas. It is a reasonable assumption, however, that, except for sandy beaches and steep cliffs, and the immediate vicinity of the major settlement, closed canopy forest covered the whole island in 1819. To what extent this forest had been exploited, disturbed or cleared in the past is impossible now to determine. From topography, soil patterns and late nineteenth century maps, I estimate that mangrove forest would have occupied about 13 per cent of the main island, freshwater swamp forests of various types 5 per cent, and lowland evergreen rain forest the remaining 82 per cent (Corlett, 1991*a*). The floristic composition of the rain forest must have varied considerably with soil type and topography but extensive botanical collection did not start until the 1880s, when more than 90 per cent of the forest had gone, so we have little information on this variation. The distinctive floras of the 10 ha forest remnant at Changi, cleared in 1927, and the 4 ha Gardens' Jungle, now badly degraded, suggest that much of Singapore's primeval flora may have been lost before it was collected. Even in the 1890s, Ridley could collect rain forest taxa at many sites where forest no longer exists. Known extinctions are mostly coastal, reflecting the complete destruction of the coastal forest, with the exception of some small areas of mangrove.

Primary Forest Today

Today, primary rain forest, disturbed to varying extents, is confined to the 71 ha Bukit Timah Nature Reserve (which is about two-thirds primary forest) and scattered patches of various sizes, totalling about 50 ha, in the adjacent water catchment area. Most of these primary forest remnants are in the areas of overlap between the Forest Reserves established in the late nineteenth century and the current Nature Reserve system (Fig. 2). The Bukit Timah forest has apparently never been legally exploited, at least since its first protection in the 1840s (Corlett, 1988*b*). Extensive illegal cutting of timber and firewood has, however, undoubtedly occurred at times of reduced protection. At least 840 angiosperm species (excluding non-forest weeds) have been recorded from Bukit Timah in the past century (Corlett, 1990, 1991*b*). Five families – Rubiaceae, Euphorbiaceae, Orchidaceae, Moraceae and Annonaceae – account for almost a third of the angiosperm flora. In terms of numbers of species, the Euphorbiaceae, Rubiaceae, Myrtaceae, Annonaceae and Lauraceae are the most important tree families, but the Dipterocarpaceae provides the greatest number of large tree individuals (Wong, 1987). The Rubiaceae and Palmae are the biggest climber families, ferns dominate the herb layer, and ferns and orchids account for most of the epiphytes (Corlett, 1990).

The largest primary forest remnants in the catchment area are around MacRitchie Reservoir and the Nee Soon (Yishun) firing ranges. Both areas have been protected since the late nineteenth century (as a catchment area and Chan Chu Kang forest reserve, respectively (Fig. 2)) but, before that, were probably exploited heavily. Continuity of forest cover – and thus justification for considering them "primary" – is shown by the extremely rich flora, including numerous species absent from the adjacent secondary forests. The Nee Soon area also includes about 15 ha of disturbed freshwater swamp forest, the last remnant of the much larger area studied by Corner (1978). The floristics of these other primary forest remnants have not been investigated as thoroughly as Bukit Timah, but the floras seem to be to some extent complementary.

Secondary Forest and Scrub

The rest of the central catchment area (Fig. 2) is covered in secondary forest of various ages (Corlett, 1991*c*). This area was cleared of its original forest cover by the mid nineteenth century, cultivated until exhaustion and then abandoned to lalang. Protection as part of an expanded water catchment, mostly in the period 1899–1906, did not lead to an immediate regeneration of forest because of frequent grass fires, but most of the area seems to have been under woody cover by the nineteen-thirties. Some parts have been cut or burned more recently. The oldest areas of forest (?50–80 years old) are 15–20 m tall with 35–65 species >2 cm d.b.h. in 0.1 ha plots. This tall secondary forest is dominated by members of the families Guttiferae (*Calophyllum* spp., *Garcinia* spp.), Lauraceae (*Lindera lucida* (Bl.) Boerl., *Litsea* spp.), Myrtaceae (*Eugenia* spp., *Rhodamnia cinerea* Jack), and Elaeocarpaceae (*Elaeocarpus* spp.). It is clearly distinguished from the included primary forest remnants by its lower stature and species diversity, even canopy, poorly-developed understorey, and the complete absence of Dipterocarpaceae and other species with large, wind-dispersed seeds.

For historical reasons, tall secondary forest is confined to the central catchment area, but areas of younger secondary forest and scrub, probably all less than 40 years old, are scattered around the main island and on several offshore islands (Corlett, 1991*c*). This pioneer community is remarkably uniform, floristically, despite the wide range of rock types on which it occurs. Large areas contain less than 20 vascular plant species in total. The explanation for this relative floristic poverty must be severe soil degradation – chemical, physical or both. The dominant species is usually *Adinandra dumosa* Jack, particularly after the formation of a closed canopy has eliminated the smaller species. Transitions between the low (6–12 m), *Adinandra*-dominated forest and the tall secondary forest described above can be found in some parts of the central catchment area. Whether or not the outlying areas, if protected, will ever undergo this transition, in the absence of nearby seed sources, is an interesting question!

Except for small areas at the back of beaches, all herbaceous vegetation in Singapore is secondary and results from recent or continued disturbance. Fire prevention and control have virtually eliminated the vast areas of lalang (*Imperata*) grassland which dominated the Singapore landscape in the late nineteenth and early twentieth century. Spontaneous herbaceous vegetation is now most extensive on wasteland awaiting development and on land newly reclaimed from the sea. Except on the poorest soils (such as land reclaimed with sand fill), this wasteland vegetation is dominated by naturalised exotic species, particularly African grasses and tropical American legumes (Corlett, 1988*a*). Exotics also dominate the weed flora of parks, gardens and other managed vegetation.

The surviving fragments of Singapore's once extensive mangrove forests all show the effects of past exploitation and disturbance (Corlett, 1987). There are few old trees and the inland margins of most patches have been destroyed by reclamation.

Moreover, land reclamation, barraging of estuaries, and developments inland have drastically changed the patterns of sediment deposition and erosion along Singapore's coastline, so even protected mangrove areas are unstable. The rich epiphytic flora recorded earlier this century has almost entirely disappeared but most of the woody flora survives.

Managed Vegetation

For most visitors to Singapore, the lasting botanical impression is not the untamed exuberance of tropical nature but the orderly rows of matching trees and neat expanses of close-mown grass. This impression has been achieved at considerable expense in money and labour, and only after many years of careful planning and experimentation (Corlett, 1992*c*). Although the final image is very Singaporean, the flora of the managed vegetation is pantropical. A continued programme of plant introductions and field trials has resulted in an exceptionally diverse park and roadside flora, with the plantings often dateable from a knowledge of past changes in the favoured tree species. The few native species that are widely planted are all coastal in origin: examples include the Pong Pong (*Cerbera odollam* Gaertn.), the Sea Apple (*Eugenia grandis* Wight), the Yellow Flame (*Peltophorum pterocarpum* (DC.) Heyne), the Sea Almond (*Terminalia catappa* L.), and the near-native Angsana (*Pterocarpus indicus* Willd.). Many early introductions were from tropical America, such as the Rain Tree (*Samanea saman* Merr.) and the Broad-leaved Mahogany (*Swietenia macrophylla* King). More recently, African Mahoganies (*Khaya* spp.) have been very widely planted, but no major tropical area is unrepresented.

Much of the diversity in the planted shrub flora is at the infraspecific level, with Bougainvillea (*Bougainvillea X buttiana* Holttum & Standley), Hibiscus (*Hibiscus rosa-sinensis* L.) and others represented by numerous cultivars. Managed grasslands, in contrast, are largely planted with one species, *Axonopus compressus* (Swartz) Beauv., propagated vegetatively and now probably the commonest plant in Singapore. Fine lawns, particularly in private gardens, are usually planted with species of *Zoysia*, while several cultivars of Bermuda Grass (*Cynodon dactylon* (L.) Pers. and hybrids) are used on golf courses.

Conclusions

Despite its small size, relatively uniform topography and recent history of massive human impact, Singapore still supports a vascular plant flora of incredible diversity. The majority of this diversity, however, is dependent on the protection of a few, small areas: most importantly, the primary forest remnants at Bukit Timah, MacRitchie and Nee Soon. Even the oldest secondary forest in the central catchment area is depauperate in comparison and its conservation significance lies more in its role as a buffer for the primary forest remnants, its importance as a habitat for vertebrates, and its potential for future floristic enrichment, by natural processes or with human intervention. Along the coast, the few remaining patches of mangrove forest, although of low floristic diversity, support an extremely rich and interesting fauna. Outside the forest, the flora, both spontaneous and planted, consists largely of pantropical species which, although often of considerable biological interest and aesthetic value, have no particular conservation importance.

The Flora of Singapore project is of major significance for plant conservation in Singapore. The availability of a modern Flora will greatly facilitate the detailed studies of species and habitats on which long-term conservation management of the flora will ultimately depend. Singapore, with its stable Government, strong economy, high education standards and well-deserved reputation for long-range planning, can and should set an example for the rest of the tropical world.

Acknowledgements

Among the many people who helped in the preparation of this paper and, earlier, during my 5 year stay in Singapore, I particularly wish to thank Dr. H.T.W. Tan, Prof. H. Keng, Mr Samsuri, Dr. P.W. Lucas, Mr D.H. Murphy, Dr. Y.C. Wee and Dr. A. Gupta.

References

Anon (1990). *Singapore: facts and pictures 1990.* Ministry of Communications and Information, Singapore.

Ashton, P.S. (1982). Dipterocarpaceae. *Flora Malesiana, Ser. I.* 9, 237–552.

Ashton, P.S., Givnish, T.J. and Appanah, S. (1988). Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mass fruiting in the aseasonal tropics. *Amer. Nat.* 132, 44–66.

Audley-Charles, M.G. (1981). Geological history of the region of Wallace's Line. In: Whitmore, T.C. ed. *Wallace's Line and Plate Tectonics*, Clarendon Press; Oxford; 24–35.

_____. (1987). Dispersal of Gondwanaland: relevance to the evolution of the angiosperms. In: Whitmore, T.C. ed. *Biogeographical Evolution of the Malay Archipelago*, Clarendon Press; Oxford; 5–25.

Barlow, B.A. (1990). Biogeographic relationships of Australia and Malesia: Loranthaceae as a model. In: Baas, P., Kalkman, K. and Geesink, R. eds. *The Plant Diversity of Malesia*, Kluwer; Netherlands; 273–292.

Bush, M.B., Colinvaux, P.A., Wiemann, M.C., Piperno, D.R. and Liu, K.B. (1990). Late Pleistocene temperature depression and vegetation change in Ecuadorian Amazonia. *Quaternary Res.* 34, 330–345.

Cantley, N. (1884). *Report on the forests of the Straits Settlements.* Singapore Printing Office, Singapore.

Chia, L.S. and Foong, F.F. (1991). Climate and weather. In: Chia, L.S., Rahman, A. and Tay, D.B.H., eds. *The Biophysical Environment of Singapore*, Singapore University Press; Singapore; 13–49.

CLIMAP (1981). *Seasonal reconstruction of the Earth's surface at the last glacial maximum.* Geological Society of America, New York.

Corlett, R.T. (1987). Singapore. *Mangroves of Asia and the Pacific*, UNDP/UNESCO; 211–218.

_____. (1988*a*). The naturalized flora of Singapore. *J. Biogeogr.* 15, 657–663.

_____. (1988*b*). Bukit Timah: the history and significance of a small rain-forest reserve. *Environ. Conserv.* 15, 37–44.

_____. (1990). Flora and reproductive phenology of the rain forest at Bukit Timah, Singapore. *J. Trop. Ecol.* 6, 55–63.

_____. (1991*a*). Vegetation: In: Chia, L.S., Rahman, A. and Tay, D.B.H., eds. *The Biophysical Environment of Singapore,* Singapore University Press; Singapore; 134–154.

_____. (1991*b*). Singapore. In: Collins, N.M., Sayer, J.A. and Whitmore, T.C., eds. *The Conservation Atlas of Tropical Forests: Asia and the Pacific,* Macmillan; London; 211–215.

_____. (1991*c*). Plant succession on degraded land in Singapore. *J. Trop. For. Sci.* 4 (2), 151–161.

_____. (1992*a*). The ecological transformation of Singapore: 1819–1990. *J. Biogeogr.* 19, 411–420.

_____. (1992*b*). The naturalized flora of Hong Kong: a comparison with Singapore. *J. Biogeogr.* 19, 421–430.

_____. (1992*c*). The changing urban vegetation. In: Gupta, A. and Pitts, J., eds. *Physical Adjustments in a Changing Landscape: the Singapore Story,* Singapore University Press; Singapore; 190–214.

Corner, E.J.H. (1978). The freshwater swamp forest of South Johore and Singapore. *Gard. Bull. Sing. Suppl.* 1, 1–266.

_____. (1988). *Wayside Trees of Malaya.* Malayan Nature Society, Kuala Lumpur.

Cortesao, A. (1944). *The Suma Oriental of Tome Pires: an account of the East, from the Red Sea to Japan, written in Malacca and in India in 1512–1515.* Hakluyt Society, London.

Dransfield, J. (1987). Bicentric distribution in Malesia as exemplified by palms. In: Whitmore, T.C. ed. *Biogeographical Evolution of the Malay Archipelago,* Clarendon Press; Oxford; 60–71.

Dunn, F.L. (1975). *Rain-forest collectors and traders: a study of resource utilization in modern and ancient Malaya.* Malayan Branch, Royal Asiatic Society, Kuala Lumpur.

Foxworthy, F.W. (1932). *Dipterocarpaceae of the Malay Peninsula,* Malayan Forest Records 10, Forest Department, Kuala Lumpur.

Geyr, M.A. and Kudrass, H.R. (1979). Sea-level changes during the late Pleistocene and Holocene in the Straits of Malacca. *Nature* 278, 441–443.

Gupta, A., Pitts, J., Rahman, A. and Wong, P.P. (1987). The Old Alluvium of Singapore and the extinct drainage system of the South China Sea. *Earth Surface Processes and Landforms* 12, 259–275.

Hails, C. (1987). *Birds of Singapore,* Times Editions, Singapore.

Hutchison, C.S. (1989). *Geological evolution of South-east Asia* Clarendon Press; Oxford.

Heaney, L.R. (1991). A synopsis of climatic and vegetational change in Southeast Asia. *Climatic Change* 19, 53–61.

Ives, D.W. (1977). *Soils of the Republic of Singapore,* New Zealand Soil Survey Report 36, New Zealand Soil Bureau; New Zealand.

Jackson, J.C. (1965). Chinese agricultural pioneering in Singapore and Johore, 1800–1917. *J. Malay. Branch Roy. As. Soc.* 38, 77–105.

Logan, J.R. (1847). The Orang Biduanda Kallang of the River Pulai in Johore. *J. Indian Archipelago and East Asia* 1, 299-302.

Lucas, P.W. and Corlett, R.T. (1991). The relationship between the diet of *Macaca fascicularis* and forest phenology. *Folia Primatologica* 57, 210-215.

Medway, Lord. (1972). Phenology of a tropical rainforest in Malaya. *Biol. J. Linn. Soc.* 4, 117-146.

Metcalfe, I. (1990). Allochthonous terrane processes in Southeast Asia. *Phil. Trans. R. Soc. Lond.* A 331, 625-640.

Miksic, J.N. (1985). *Archaeological research on the "Forbidden Hill" of Singapore: excavations at Fort Canning, 1984.* National Museum, Singapore.

Morley, R.J. and Flenley, J.R. (1987). Late Cainozoic vegetational and environmental changes in the Malay Archipelago. In: Whitmore, T.C. ed. *Biogeographical Evolution of the Malay Archipelago,* Clarendon Press; Oxford; 50-59.

Ng, F.S.P. (1977). Gregarious flowering of dipterocarps in Kepong 1976. *Malay. For.* 40, 126-137.

_____. (1988). Forest Tree Biology. In: Earl of Cranbrook ed. *Malaysia.* Pergamon Press; Oxford; 102-125.

Oxley, T. (1847). Gutta Percha. *J. Indian Archipelago and East Asia* 1, 22-29.

Pirazzoli, P.A. (1991). *World atlas of Holocene sea-level changes,* Elsevier; Amsterdam; 114-115.

Public Works Department (1975). *Geology of the Republic of Singapore,* Public Works Department; Singapore.

Rahman, A. (1991). Soils. In: Chia, L.S., Rahman, A. And Tay, D.B.H., eds. *The Biophysical Environment of Singapore,* Singapore University Press; Singapore; 89-133.

Reid, A. (1988). *Southeast Asia in the age of commerce, 1450-1680.* Yale University Press, USA.

Ridley, H.N. (1900). The Flora of Singapore. *J. Roy. As. Soc. Str. Br.* 33, 27-196.

Singapore Meteorological Service (1986). A study of the urban climate of Singapore. In: Chia, L.S., Lee, H.C., Rahman, A., Tong, P.L. and Woo, W.K., eds. *Proceedings, The Biophysical Environment of Singapore and its Neighbouring Countries,* Geography Teachers' Association; Singapore; 50-76.

Takhtajan, A. (1986). *Floristic Regions of the World,* University of California Press, California.

Thomas, G.S.P. (1991). Geology and Geomorphology. In: Chia, L.S., Rahman, A. and Tay, D.B.H., eds. *The Biophysical Geography of Singapore,* Singapore University Press; Singapore; 50-88.

Thomson, J.T. (1848). Remarks on the Seletar and Sabimba tribes. *J. Indian Archipelago and East Asia* 1, 341-351.

_____. (1850). General report on the residency of Singapore drawn up principally with a view to illustrating its agricultural statistics. *J. Indian Archipelago and East Asia* 4, 41-77, 102-106, 134-143, 206-219.

Turner, I.M., Chua, K.S. and Tan, H.T.W. (1990). A checklist of the native and naturalized vascular plants of the Republic of Singapore. *J. Sing. Nat. Acad. Sci.* 18, 100–130.

Walker, D. and Flenley, J.R. (1979). Late Quaternary vegetational history of the Enga District of upland Papua New Guinea. *Phil. Trans. Roy Soc. B.* 286, 265–344.

Wang, G. (1958). The Nanhai trade. *J. Malay. Branch Roy. As. Soc.* 31, 1–135.

Whitmore, T.C. (1990). *An Introduction to Tropical Rain Forests*, Clarendon Press; Oxford; 99–102.

Wong, Y.K. (1987). Ecology of trees at Bukit Timah Nature Reserve. *Gard. Bull. Sing.* 40, 45–76.