Interpreting some outstanding features of the flora and vegetation of Madagascar

Peter J. Grubb

Department of Plant Sciences, University of Cambridge, UK

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Abstract

Six features are covered. (1) The high endemism, which is not discussed in detail, is all-pervasive, and has resulted from the isolation of Madagascar from Africa some 125 million years ago and their present separation by 430 km. (2) The great richness in plant species (especially relative to Africa), seen particularly in the families of woody species in the wetter vegetation-types, involves both sympatry and allopatry within genera, and is explicable in terms of much less extreme drying out than in Africa during the Pleistocene and effective 'species-pumping' rather than mass extinctions during that period. (3) The abundance and species-richness of palms, pandans, tree-ferns, bamboos, and certain families of dicot trees (notably Lauraceae, Monimiaceae, Myrsinaceae and Myristicaceae) in the lowland rain forests also appears to be a result of both past and present wetness of the climate, while it is hypothesized that the low stature of most lowland rain forests, paucity of large-girth trees, and small size and sparsity of broad-leaved herbs, are a result of most rain forest soils being old and relatively nutrient-poor. (4) Within the dry evergreen forest region where rainfall is moderate (900–1600 mm yr\(^{-}\)) a sub-set of trees with fire-resistant bark seems to have evolved at sites prone to frequent ground fires, some perhaps spreading out of adjacent palm savanna on seasonally flooded sites. (5) Both the evolution of thicket rather than grassy woodland in the driest areas (300–600 mm yr\(^{-}\)), and the abundance of evergreen trees and shrubs on ordinary soils – not confined to run-on sites – are explicable in terms of there being a finite chance of rain throughout the year rather than one short wet season, coupled with relatively high values for air humidity throughout the year. The same factors probably explain the abundance and variety of succulents in the thicket; they are found throughout and not just on rocks. (6) Concerning physical defence against herbivores, the rain forests, dry evergreen forests and deciduous forests all show a complete lack of plants with physiognomic features plausibly related to browsing by extinct giant birds (a strong contrast with New Zealand), but in the semi-deciduous thicket there are many tiny-leaved, mostly non-spiny shrubs and small trees, whose dense branching and impenetrability have plausibly evolved as a defence against browsing by elephant birds. The Didiereaceae of the thicket are spiny (unlike members of the same family in Africa), and are giant analogues of the ‘ocotillo’ (Fouquieria splendens) in western North America rather than of Cactaceae; their spines appear to be protecting the leaves more than the stems against arboreal primates, spine length paralleling leaf length.

Key words: evergreenness, fire, Madagascar, plant defences, rain forest, savanna, soil fertility, species-richness, succulents, thicket

Corresponding author: Peter J. Grubb, Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK; e-mail: peterjgrubb@yahoo.co.uk
Introduction

The flora and vegetation of Madagascar are outstanding in a number of ways. Two features of the flora are almost all-pervasive: high endemicity and great species-richness. Otherwise the vegetation has many outstanding features which are likely to make unique impressions on individual plant ecologists. Four sets of features impressed me particularly during a visit in November 2001, and are treated in this paper. Firstly, the lowland rain forests are distinctive in being notably rich in palms, pandans, bamboos and tree-ferns, while also being of relatively low stature, lacking in large-girth trees, and poor in large-leaved monocot herbs. Secondly, while there is no natural savanna (apart from possible palm savanna in seasonally waterlogged hollows) the dry evergreen forest region includes a small set of trees highly adapted to fire. Thirdly, the nearly-natural vegetation of the driest part is thicket, not grassy woodland, and has a higher incidence of evergreens than the dry deciduous forest; it also has an abundance and great diversity of succulents as well as eleven species of Didiereaceae, strange tall spiny plants which are analogues of the ocotillo (*Fouquieria*). Fourthly, until a few hundred years ago there were large flightless birds which apparently ate the vegetative parts of plants and were the equivalent of the similarly extinct moas in New Zealand rather than the still-extant, fruit-eating cassowaries of north-eastern Australia and Papua New Guinea; the extent to which plants were defended against the birds has not been made clear. Contrasting with the presence of giant herbivorous birds is the total absence of the herbivorous mammal flora associated with grassland and woodland (‘savanna’) in Africa. Also, remarkably, humans reached Madagascar only in the last 2000 years.

In my experience most reasonably well-read and travelled plant ecologists are ignorant of most of the points made in the last paragraph, apart from the high endemicity which was spelled out in the classical literature (Good 1953). That issue has been covered recently by Schatz (2001) and in the volume edited by Goodman (2000), and I shall not discuss it in this paper. The great richness in species was emphasized by Guillaumet & Mangenot (1975), and the richness of the flora in general was explained by Leroy (1978) in terms of much less severe drying out in the geological past than occurred in Africa, but I believe it is still not well known, and its extent certainly astounded me when I visited the island. I shall provide a numerical comparison with eastern Africa for one functional group of plants to drive home the point.

The ignorance of the flora and vegetation of Madagascar on the part of most of the world’s plant ecologists has resulted to some degree no doubt from the difficulty and expense of getting there relative to Africa in the second half of the 20th century, but I believe it reflects also the lack of coverage in major treatments of the world’s vegetation from the time of Schimper (1903) onward. In Walter’s opus magnum, *Die Vegetation der Erde* (1964, English translation 1971), there is very little mention of Madagascar. Sadly the superb account of the flora and vegetation by Koechlin et al. (1974), summarizing the results of a long history of research, was not widely read in the English-speaking world, partly because it was published relatively obscurely and partly because it was in French. The overview in English by Koechlin (1972) appeared in an expensive book of limited circulation. More accessible summaries in English were given by White (1983) and Guillaumet (1984). Lowry et al. (1997) have provided an invaluable historical analysis of descriptive and interpretive work on the vegetation of the island; with the web version of this paper (http://www.mobot.org/MOBOT/Madagasc/vegmad1.html) there is an extended bibliography. The two volumes by Rauh (1995–1998) contain very numerous colour photos of landscapes, vegetation-types and plants, with emphasis on the drier areas. There has been widespread concern among conservation biologists about the conversion of vast areas of forest into grassland, the accompanying soil erosion, and the actual or potential loss of many species of plants and animals, and recent summaries of those issues are given in the volume edited by Goodman & Patterson (1997).

I have chosen to write about the flora and vegetation of Madagascar because they were the topics I discussed with Tim Whitmore when I was last able to see him in January 2002, soon after I had visited the island. The mixture of issues in phytogeography and ecology fascinated him. I fully accept that they represent my personal response to the vegetation, and that other topics are equally deserving of attention, such as the ecophysiology of the very various drought-resistant plants on the many rock outcrops, or the differences between Madagascar and Africa or other parts of the tropics in pollination, seed predation and seed dispersal.

I begin with a brief account of the physical features of the island relevant to the distributions of four major vegetation-types. Then I treat in turn features of interest in (1) the rain forests and high-altitude thickets, (2) the dry evergreen forests and fire-adapted woodlands, and (3) the deciduous forests and semi-evergreen thickets. I conclude with sections on physical defences and some outstanding puzzles. My accounts of the various vegetation-types are based on those of Koechlin et al. (1974), but are supported by personal experience of all the major types described apart from the high-altitude
thickets. Koechlin et al. (1974) also described the remaining vegetation-types such as those on rock outcrops, mangroves, salt marshes and other wetlands. Nomenclature follows *Flore de Madagascar et des Comores* (Humbert et al. 1936–2002), except for legumes (Du Puy 2001) and palms (Dransfield & Beentje 1995), unless otherwise indicated. Assignment to families follows Stevens (2002), except that for convenience I retain the Didiereaceae for four Madagascan genera and three African genera.

**Physical features of the island**

Madagascar is about 1570 km from north to south and – at its widest – about 560 km from east to west (Fig. 1). The closest point is about 430 km from Africa (Krause et al. 1997). The island lies between 12°30′S and about 25°32′S; in Africa this span runs from northern Mozambique to northern South Africa. There is a spine of mountains running along the eastern side of the island, with much land above 900 m altitude, but little over 2000 m. This spine intercepts the south-easterly winds which are the most frequent. As a result, shown in Fig. 1, the eastern strip is very wet (2400 to >3600 mm yr⁻¹). Mean annual rainfall declines sharply going westward across the mountains (2400 down to 1600 mm yr⁻¹), and it falls further across the lower lying land toward the west coast, especially toward the south-west (1600 down to 600 mm yr⁻¹). A relatively narrow strip on the south-western and southern sides is yet drier (600–300 mm yr⁻¹). At sea level the mean temperature of the coldest month is >25 °C at the northern tip, >20 °C in the south-eastern corner, and c. 20 °C in the dry south and south-west (Donque 1972; Koechlin 1972). The mean of the hottest month is 25–28.5 °C along the eastern side from north to south, and 27–28 °C in the dry south and south-west.

Recent authors have adopted a simplified version of the bioclimatic regions defined by Cornet (1974), as shown in Fig. 1 of Schatz (2001). The ‘humid’ region approximates to that with >1600 mm yr⁻¹ and no pronounced dry season, the ‘subhumid’ region to that with 800–2000 mm yr⁻¹ and a marked dry season, the ‘dry’ region to that with 800–1600 mm yr⁻¹ and a stronger dry season, and the ‘subarid’ to that with <800 mm yr⁻¹ and a significant possibility of rain at any time of year. The ‘montane’ region is effectively that above 2000 m altitude, and does not correspond to the normal usage of ‘montane’ in the world literature on mountain forests (cf. Grubb 1977; Whitmore 1985).

The core of the island from north to south is made of Precambrian metamorphosed basement rock, interrupted by large intrusions of granite; there is a narrow sedimentary plain to the east, and a wide one to the west (Brenon 1972). There is much limestone on the western side, and this crosses from west to east in the north. There is a characteristic ‘ruiniform’ sandstone in the Isalo National Park south-west of the centre. Volcanic deposits are scattered along the spine of the island, ranging from Cretaceous to Pliocene/Pleistocene, being younger toward the north. Quaternary dunes are extensive along the S and SW coasts; the older sands are partially decalcified and reddened. A valuable simplified map of the geology is given by Du Puy (2001). Most of the soils in the wetter part of the island are derived from acidic rocks and long leached, and therefore strongly acidic and relatively poor in available nutrients. The soils derived from the sands

Fig. 1. Isohyets for annual rainfall (cm) in Madagascar (from map 3 of Koechlin et al. 1974).
on the narrow eastern plain (carrying ‘littoral forest’) are especially poor. Those along the central strip of the island, suffering seasonal drought, have degenerated as a result of forest clearance and dominance by grass, and the worst areas show severe erosion.

Rain forests and high-altitude thickets

It is generally believed that before humans invaded the island the ‘zonal’ vegetation of the humid region and a good deal of the eastern part of the subhumid region was composed of rain forests. In the remaining vegetation the trends with altitude are those found generally on wet tropical mountains (cf. Grubb 1977). As usual, the transition from lowland to lower montane rain forest is gradual (Lowry et al. 1997); the transition from ‘medium-altitude mossy forest’ (lower montane rain forest) to ‘high-altitude lichen forest’ (upper montane rain forest) is placed by Koechlin (1972) at around 1300 m, which is the same as in NE Queensland at the same range of latitude (Tracey 1982). At about 1800–2000 m the montane forest merges into high-altitude thicket (Guillaumet 1983); in the broadest sense the thicket is reminiscent of the ‘subalpine rain forest’ of the high mountains of Papua New Guinea (Grubb & Stevens 1985), being quite species-rich, with most of the woody plants having scleromorphic leaves, some of them ericoid. It seems that this zone in Madagascar is a good deal more species-rich than the corresponding Ericaceae-dominated community of the higher East African mountains (cf. Lind & Morrison 1974).

The great species-richness of the flora

I confine myself to trees, treelets and shrubs ‘at least (4–)5 m tall, and/or with at least one vertical stem attaining 5 cm in diameter at breast height’. Schatz (2001) provides numbers of species per genus for such plants in his Generic Tree Flora. I have accepted his assignment of genera to families except where more recent research has suggested better arrangements (Stevens 2002 and references cited by him). The result is a list of 110 families. Of these five are endemic, and three are widespread non-endemic families not found in eastern Africa (Chloranthaceae, Elaeocarpaceae and Winteraceae). Of the 102 non-endemic families that are present in Madagascar and eastern Africa, I consider only the 56 found exclusively or primarily in the humid and subhumid areas, and I omit the 18 found only or primarily in the subhumid, dry and subarid areas, and the 28 which are shared fairly evenly between the wetter and drier regions. I add the Gramineae-Bambuseae, which are found mainly in the humid and subhumid areas (Dransfield 2000, 2002), and which were not covered by Schatz (2001).

I compare the numbers of genera and species in the relevant families in Madagascar with the numbers in those families in what I call ‘eastern Africa’, i.e. the area stretching from the northern border of Kenya (5°N) to Port Elizabeth in the Eastern Cape of South Africa (34°S), covered by the Flora of Tropical East Africa (Kenya, Uganda and Tanzania; Turrill et al. 1952–2002), the Flora Zambeziaca (Malawi, Zambia, Zimbabwe, Mozambique, Botswana and the Caprivi Strip of Namibia; Exell et al. 1960–2002) and Tree Floras of South Africa by Palgrave (1988) and van Wyk & van Wyk (1997). I have included only those South African species occurring east of 26°E, which passes close to Port Elizabeth. A notable feature of many genera in Madagascar is the difficulty of deciding just how many species to recognize (Koechlin et al. 1974), but the summary produced by Schatz (2001) is treated here as a proper basis for comparison with Africa.

Of the 57 families found primarily or only in the humid-subhumid regions in Madagascar, almost always in evergreen forest, 28 have ten or more indigenous species on the island, and are shown in Table 1. All of the 29 families with <10 species in Madagascar are relatively small on a world scale.

For three of the 28 families in Table 1 we cannot make a full comparison because either the Tropical East Africa account has not been published (Ericaceae) or the Zambeziaca account (Lamiaceae and Thymelaeaceae). Thymelaeaceae have fewer species in Madagascar than in eastern Africa. All of the 25 families for which we have full information have more species in Madagascar than in eastern Africa, although the difference is marginal in five cases where the quotient Madagascar/Africa is <1.5 (Annonaceae, Icacinaceae, Pittosporaceae, Rhizophoraceae and Scrophulariaceae). Most spectacular are the quotients for the Monimiaceae (43), Cunoniaceae (20), Pandanaceae (17), Arecales (14), Myrsinaceae (8.8) and Lauraceae (8.5). On a world scale all of these families are most speciose in high-rainfall areas. The median quotient is 3.2. In contrast, 8/26 families have fewer genera in Madagascar, and the median quotient for numbers of genera is 1.0. The explanation offered by Leroy (1978) for the greater richness of the flora in general in Madagascar than in Africa – that it suffered much less drying out during the Pleistocene, Pliocene and probably late Miocene – must surely be part of the explanation of the particular feature of richness in species per genus.

Examination of the recently published floras for palms (Dransfield & Beentje 1995) and legumes (Du
Puy 2001), and the check-list of orchids (Du Puy et al. 1999), as well as the older and less complete accounts of many families in the Flore de Madagascar shows that there is a great deal of allopatry in the present-day distributions of congeners. However, there are also striking instances of sympatry, for example 13 species of Diospyros on a single 0.1-ha plot (Gentry 1993). The situation is like that in the part of the Northern Hemisphere apparently least dried out in the Pleistocene, i.e. eastern Asia, where moderate drying out and isolation of populations rather than their annihilation, has led to ‘species-pumping’ (Grubb 1987; Latham & Rickleffs 1993).

Although the evolution of species-richness in Madagascar is most striking in the wetter parts, many genera in the drier parts also show the evolution of numerous, largely allopatric species. Adansonia, Aloe, Euphorbia and Pachypodium, all with distinctive growth forms, are good examples. Moreover, three of the four genera of woody plants with the most species in Madagascar span the drier and wetter parts of the island (Schatz 2001): Diospyros c. 125 spp., Croton c. 150 spp. and Dombeya c. 180 spp. (Dypsis with 137 spp., almost confined to the humid and subhumid parts, is the fourth). Thus moderate drying out seems to have favoured speciation in the drier as well as the wetter areas.

Table 1. Families of trees found in Madagascar (MAD) wholly or predominantly in evergreen forests in the humid-subhumid regions, and having ten or more species on the island: numbers of species and genera compared with those in SE Africa (SEA, Flora Zambesiaca area plus eastern South Africa), Tropical East Africa (TEA, the area of the Flora) and all eastern Africa (AEA). Definitions and sources given in the text.

<table>
<thead>
<tr>
<th>Plant families</th>
<th>Biogeographical units</th>
<th>Number of species</th>
<th>Number of genera</th>
</tr>
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<td>MAD</td>
<td>SEA</td>
<td>TEA</td>
</tr>
<tr>
<td>PTEROPSIDA</td>
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<td>–</td>
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<td>3</td>
</tr>
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<tr>
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<td>Scrophulariaceae</td>
<td>10</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Thymelaeaceae</td>
<td>14–16</td>
<td>&gt;10*</td>
<td>11</td>
</tr>
</tbody>
</table>

*Based on data for eastern South Africa, and in the Flora of Tropical East Africa account; no account for the Zambesiaca region is yet available.
–, no information available.
Structure and physiognomy of the lowland rain forests

Following on from the previous section, we see that there are four growth forms whose abundance in the lowland rain forests of Madagascar is plausibly to be explained in terms of past and present wetness: palms, pandans, bamboos and tree-ferns. Both palms and pandans are not only abundant but also strikingly diverse in mature size and in form; in contrast, in large areas of Tropical East Africa there are very few species of palms and pandans, and they are confined to topographically determined wet sites. In Madagascar several bamboo species are widespread and abundant in the lowlands, although there are certainly more species in the montane forests (Dransfield 2000); in Africa bamboos – bar one species (Lind & Morrison 1974) – are known only in montane forests. Likewise tree-ferns are confined to montane forests in eastern Africa; the other parts of the world with abundant tree-ferns in the lowlands have especially high rainfall, such as the Solomon Islands.

Koechlin et al. (1974) emphasized three features of the lowland rain forest which I hypothesize to be an evolutionary result of low availability of limiting mineral nutrients in most of the soils. The largest trees are not very tall (few >30 m) and have relatively small girths (few much >1 m). As expected in a forest with not many large-girth trees, the stem density is notably high (Gentry 1993; Lowry et al. 1997). The third feature is a paucity of tall, broad-leaved monocot herbs. The paucity of these herbs in terms of biomass (most species confined to gaps and not >0.5 m tall) is paralleled by a paucity of species, compared with Tropical East Africa (Table 2), a striking contrast with the richness in species of woody plants documented in Table 1.

In Africa, Australia and South America forest height commonly parallels soil fertility (Hall & Swaine 1976; Tracey 1982; Coomes & Grubb 1996; Richards 1996). The position in SE Asia is confused by the super-plants of the Dipterocarpaceae which make very tall forests on some poor soils, but otherwise the correlation is also found there (Whitmore 1985). Vigorous growth and diversity of herbs are commonly associated with higher soil fertility in both tropical and temperate vegetation (Grubb 1987; Coomes & Grubb 1996). Determination of foliar nutrient concentrations could be useful first test of the nutrient-shortage hypothesis.

Madagascan rain forests are notable for the abundance and diversity of Dracaena species. There is some parallel in Africa, but the extremes are greater in Madagascar, as illustrated by the undescribed species found in forest on rocky ridges on the Masoala Peninsula with little branched stems up to c. 12 m tall and leaves c. 2 m long and 10 cm wide (Fig. 2).

Damage by cyclones is a major feature in the dynamics of the forests, and one notable plant to benefit from the gaps is the ‘Travellers’ Palm’, Ravenala.

Table 2. Comparison of species-richness in families of broad-leaved perennial monocotyledonous herbs found in lowland rain forests in Madagascar and in Tropical East Africa. Information has been taken from Flore de Madagascar et Comores, Flora of Tropical East Africa, Thistleton-Dyer (1902) and Agnew (1974).

<table>
<thead>
<tr>
<th>Plant families</th>
<th>Madagascar</th>
<th>Tropical East Africa</th>
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</thead>
<tbody>
<tr>
<td>Anthericaceae</td>
<td>1 (Chlorophytum)</td>
<td>3 (Chlorophytum)</td>
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<tr>
<td>Araceae</td>
<td>4 (Arophyton)</td>
<td>19 (Amorphophallus 3, Anchomanes 2, Arisaema 5, Callospis 1, Gonnatopus 4, Stylochiton 3, Zamioculcas 1)</td>
</tr>
<tr>
<td>Commelinaceae</td>
<td>4 (Commelina 2, Pollia 1, Pseudoparis 1)²</td>
<td>11 (Aneilema 4, Commelina 4, Fioscopa 1, Palisota 1, Pollia 1)</td>
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<tr>
<td>Costaceae</td>
<td>0</td>
<td>7 (Costus)</td>
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<tr>
<td>Dioscoreaceae</td>
<td>1 (Tacca)</td>
<td>1 (Tacca)</td>
</tr>
<tr>
<td>Marantaceae</td>
<td>2 (Halopegia, Marantochloa)</td>
<td>5 (Ateleida, Marantochloa, Megaphrynnum, Sarcophrynnum, Trachyphrynnum)</td>
</tr>
<tr>
<td>Musaceae</td>
<td>0¹</td>
<td>1 (Ensete)</td>
</tr>
<tr>
<td>Poaceae (tribes Olyreae, Phareae, Streptogyne &amp; Oryzeae)</td>
<td>2 (Leptaspi, Olyra)</td>
<td>4 (Leptaspir, Maltebrunia, Olyra, Streptogyne)</td>
</tr>
<tr>
<td>Zingiberaceae</td>
<td>5 (Alautandra²,²)</td>
<td>18 (Aframomum 15, Renealmia 3)</td>
</tr>
</tbody>
</table>

¹ All but the Callospis and Zamioculcas die back seasonally, so are found in rain forests with a dry season.
² Other species in these genera, and five other genera are present in Madagascar, but are found at open, non-forest sites.
³ Ensete perrieri confined to deciduous forests.
⁴ Plus 2–3 undescribed species (G. Schatz, pers. comm., March 2003).
⁵ Aframomum angustifolium and Hedychium peregrinum are treated as being introduced.
madagascariensis (Strelitiziaceae) with leaves like those of a banana plant and a woody stem up to c. 30 m tall (Hladik et al. 2000). Its seeds, a few mm across and hard-coated, persist in the soil awaiting gap-formation (Koechlin 1972).

Dry evergreen forests and fire-adapted woodlands

It is commonly believed that before the intervention of humans dry evergreen forest occupied much of the western part of the subhumid region, though this has now been deforested singularly completely over vast areas. Most remnants of this vegetation-type occur on the western scarp of the central mountains (above c. 800 m), but there are a few within the central mountainous area. The stands that appear to be least disturbed consist of small-trunked trees rarely >12 m tall with small leaves – mostly microphyll sensu Raunkiaer (Thomasson 1977). The canopy lets through a good deal of light to the undergrowth of shrubs and sub-shrubs, often dominated by Erica and Helichrysum. There are few climbers and very few epiphytes.

The version of the ‘dry evergreen forest’ encountered most often now is in fact a woodland, i.e. the trees are at some distance from each other (Fig. 3). The trees belong to a small sub-set of species in the forest. The overwhelming dominant is usually the tapia tree, Uapaca bojeri (Phyllanthaceae, formerly Euphorbiaceae). Like the four Asteropeia spp. and the deciduous Dicoma incana also found in this kind of woodland, it has thick, fissured, fire-resistant bark (Fig. 4). There is often little other than grass beneath the trees. A few extensive stands of Uapaca are found within the major mountainous area, e.g. on both east- and west-facing slopes near the main north-south road for about 13 km some 20 km south of Antsirabe. The persistence of such stands is possibly due to the use of a silkworm (Boroceras madagascariensis) which lives on the Uapaca.

Like the drier facies of the montane rain forests and high-altitude thickets to the east, the dry evergreen forest is flammable after dry spells, and is likely to have been set alight by lightning strikes, at a guess every 50–100 years. There are certainly remains of charcoal in peat formed well before the arrival of humans 1500–2000 years ago (Burney 1997). Presumably many of the species sprouted after occasional fire.

What is striking about the Uapaca and Asteropeia is that they are resistant to frequent ground fires rather than periodic crown fires, i.e. they are like Pinus palustris rather than like P. rigida among pines (cf. Burns & Honkala 1990). Uapaca and Asteropeia do resprout as
juveniles, and multi-stemmed trees are seen, but they are not recorded as resprouting from the crowns. I saw crowns of *Uapaca* that had been partially burnt and killed in the previous year, and these had not resprouted. It seems likely to me that these trees evolved as the dominants of sites within the dry evergreen forest landscape that were subject to relatively frequent ground-level fires. One possibility is that *Uapaca* and its associates were dominant on slopes immediately above natural savannas with the palm *Bismarckia nobilis* in hollows where the soils are waterlogged in the wet season, but the grasses dry out thoroughly in the dry season. This scenario is suggested by what can be seen at present immediately south-west of the Isalo National Park (Fig. 5). Nowadays the *Bismarckia* savanna here is probably burnt yearly, and it has almost certainly lost some woody elements, just as can be seen still happening in *Mauritia flexuosa* savanna at remote sites in the northern Amazon (Coomes & Grubb 1996).

The replacement of relatively species-rich dry evergreen forest by species-poor *Uapaca* woodland over wide areas parallels the replacement of *Marquesia*-dominated dry evergreen forest in Zambia by *Brachystegia* woodland as a result of burning (Trapnell 1959; Lawton 1978). The replacement of *Uapaca* woodland by grassland under a regime of annual burning is also paralleled in Zambia.

**Deciduous forests and semi-deciduous thickets**

**Deciduous forests**

The received view is that before humans arrived deciduous forests occupied most soils in the whole of the ‘dry’ region, the northern part of the ‘subarid’ and some fraction of western part of the ‘subhumid’ region. Today

![Fig. 4. The base of a forked-trunk *Uapaca bojeri* with thick, fissured bark and a basal burn-scar, providing evidence of recovery by sprouting.](image)

![Fig. 5. Frequently burned savanna with the palm *Bismarckia nobilis*, a little south-west of the Isalo National Park, showing in the distance *Uapaca bojeri* woodland on slopes immediately uphill of the savanna.](image)

![Fig. 6. A line of ‘coniferoid’ *Pandanus* along a seasonal water course persisting in a landscape where deciduous forest on soils not subject to periodic inundation has been totally replaced by grassland through frequent burning.](image)
remnants occur in a discontinuous band along the western side of the island from the northern end, and merge into semi-deciduous thicket in the south. Most of the land they are believed to have covered formerly is now occupied by grassland with or without scattered trees or shrubs ("savanna"). In the gently rolling country west of the Isalo National Park, we see along the courses of seasonal streams and rivers that run through an otherwise deforested landscape lines of amazing ‘coniferoid’ Pandanus (section Acanthostyla), with a crown shape like that of a Christmas tree, Picea abies (Figs. 6 & 7; see also Stone 1970, and Rauh 1995–1998, p. 74). Apparently a trunk structure that involves the phloem in being deeply buried inside, away from the transient high temperatures of grass fires, enables the tree to survive such fires in the manner seen commonly for palms, also for Ravenala (Koechlin et al. 1974) and sometimes for tree-ferns, as in Papua New Guinea (cf. cover of Grubb & Stevens 1985).

The deciduous forests have disappeared most completely from the clayey soils, and the most extensive remnants are on limestone, with others on sand. The remnant forests vary greatly in height (8–30 m), depending on soil depth and degree of access to subsoil water, but in most areas the canopy is generally 12–15 m tall, with occasional emergents. They are less rich in species per unit area in small plots than the rain forests (Abraham et al. 1996). Although the forests are overwhelmingly deciduous, some non-succulent evergreens are to be found virtually throughout. The dominant leaf size is microphyll sensu Raunkiaer (Thomasson 1977). Climbers, some thick-stemmed, can be common, but vascular epiphytes are rare (mostly orchids). On limestone particularly there are distinctive herbs that die back in the dry season, e.g. in Amorphophallus, Begonia, Carlolyphon, Colletogyne and Dorstenia. Even the leaves of the giant herb Ensete perrieri die back at that time.

Bottle-trees and other kinds of succulent are widespread, providing in fact a complete overlap at the generic level with the thicket (Table 3 below). The tallest of the Adansonia species, A. grandidieri which reaches 30 m, occurs over large areas, and is sometimes left when the rest of the forest is cleared. In the southern forests, there are two species of the highly distinctive Didieraceae, otherwise confined to the semi-deciduous thicket.

Deciduous forests extend southward into the thicket area, forming gallery forests along rivers and streams; Tamarindus indica is often common, and may be native.

Semi-deciduous thickets

This is the most distinctively Madagascan of all vegetation-types on the island (Figs. 8 & 9). It is normally 2–6 m tall, occasionally 10 m, and reduced to <1 m on the wind-blasted Cap Ste Marie (southern tip of the island). It is characterized by impenetrability, resulting in general from the close spacing of the woody plants and in particular from the presence of many shrubs and small trees with closely spaced branches and in most cases very small leaves, and by the lack of a herb layer, whether of grasses or forbs. The densely branched shrubs are discussed in detail toward the end of this article (p. 146). I insist on the term ‘semi-deciduous thicket’ rather than ‘deciduous thicket’ used by some recent authors, because the community contains an appreciably higher density of evergreens (whether with succulent or scleromorphic leaves) than the deciduous forest.

There is a huge variety of succulents ranging from leaf-succulents such as Aloe and Kalanchoe spp. via tall ‘bottle trees’ such as Adansonia spp. to vines with

Fig. 7. The crown of an isolated ‘coniferoid’ pandan.
very swollen stems and/or roots such as *Adenia* and *Cyphostemma* spp. Particularly characteristic are the tree *Euphorbia* spp. with broad, much-branched crowns composed of relatively slender, unarmed, cylindrical succulent stems, quite different from the various ‘candelabra’ *Euphorbia* spp. of Africa with their fat, ridged and spiny shoots. Keraudren (1961) suggested that the stems being slimmer in the Madagascan species reflected the less drying conditions, but that cannot be right as most of the shrubby *Euphorbia* spp. found in very dry semi-desert or desert in Namibia (cf. p. 146) have relatively slender shoots. The variety in the form of the shoots and trunk bark of Madagascan *Euphorbia* spp. has been documented by Humbert (1927), Leandri (1966) and Rabesandratana (1984). It is important to emphasize that the succulents of the thicket occur on plain flat or sloping ground, not just on sites with fissured rock. That is a big contrast with the large variety of succulents found under 250–550 mm yr\(^{-1}\) in northern Namibia; for beautiful accurate paintings of many succulents in situ on rocky hills in that area see Craven & Marais (1992).

Most characteristic of the semi-deciduous thicket are the Didiereaceae, composed of four genera and eleven species in Madagascar, and regarded as endemic until 2000 when three genera of tall-growing Portulacaceae in S, C and NE Africa were transferred; for convenience I follow this usage, although Stevens (2002) has absorbed the Didiereaceae in this wider sense into his Portulacaceae. Two species transgress into deciduous forest, two species commonly reach a height of only 1.5–2.0 m, and two have much branched crowns, but they are essentially a family of

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### Table 3. Comparison of the genera present as succulents or as related specialized life-forms in three semi-arid areas. Genera in underlined type are represented in only one of the three areas.

<table>
<thead>
<tr>
<th>Thicket in S &amp; SW Madagascar</th>
<th>Thicket in NE Kenya</th>
<th>Woodland and rock outcrops in N Namibiaapatosep</th>
<th>Emergents with very spiny non-succulent stems</th>
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<tbody>
<tr>
<td><em>Alluaudia</em>, <em>Alluaudiopsis</em>, <em>Decaryia</em>, <em>Didierea</em></td>
<td>None, but non-emergent, non-spiny</td>
<td>None, but non-emergent, non-spiny 'Didiereaceae' present at semi-desert edge to north and south (Ceraria)</td>
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<tr>
<td><strong>Trees with succulent ultimate shoots</strong></td>
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<tr>
<td><em>Euphorbia</em> (shoots slender, unarmed)</td>
<td><em>Euphorbia</em> ('candelabra' type; shoots thick, ridged, spiny)</td>
<td><em>E. tirucalli</em> (shoots slender; unarmed); <em>E. virosa</em> with thick ridged spiny stems to 2 m</td>
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<td><strong>Bottle-trees</strong></td>
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<td><em>Adansonia</em>, <em>Commiphora</em>, <em>Cyphostemma</em>, <em>Didierea</em>, <em>Operculicarya decaryi</em>, <em>Pachypodium</em></td>
<td><em>Adansonia</em>, <em>Cyphostemma</em>, <em>Delonix</em>, <em>Moringa</em>, <em>Operculicarya decaryi</em>, <em>Pachypodium</em></td>
<td><em>Adansonia</em>, <em>Cyphostemma</em>, <em>Moringa</em>, <em>Pachypodium</em>, <em>Sesamothamnus</em>, <em>Sterculia</em></td>
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<td><strong>‘Marginal bottle trees’</strong></td>
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<td><em>Givotia</em>, <em>Gyrocarpus</em>, <em>Jatropha</em>, <em>Operculicarya hypnoides</em>, <em>Uncaria</em></td>
<td><em>Givotia</em>, <em>Gyrocarpus</em>, <em>Jatropha</em></td>
<td><em>Gyrocarpus</em></td>
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<td><strong>Stem succulents &lt;2 m tall</strong></td>
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<td><em>Adenia</em>, <em>Euphorbia</em>, <em>Sarcostemma</em>, <em>Senecio</em></td>
<td><em>Adenia</em>, <em>Euphorbia</em>, <em>Sarcostemma</em>, <em>Senecio</em></td>
<td><em>Devalia</em>, <em>Euphorbia</em>, <em>Hoodia</em>, <em>Sarcostemma</em>, <em>Senecio</em>, <em>Stapelia</em></td>
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<tr>
<td><strong>Leaf succulents</strong></td>
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<tr>
<td><em>Aloe</em>, <em>Kalanchoe</em>, <em>Xerococcus</em></td>
<td><em>Aloe</em>, <em>Kalanchoe</em>, <em>Sansevieria</em></td>
<td><em>Aloe</em>, <em>Crassula</em>, <em>Kalanchoe</em>, <em>Sansevieria</em></td>
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<tr>
<td><strong>Root or rhizome succulents</strong></td>
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<tr>
<td><em>Adenia</em>, <em>Ceropogia</em>, <em>Corallocarpus</em>, <em>Cyphostemma</em>, <em>Dioscorea</em>, <em>Dolichos</em>, <em>Karimbolea</em>, <em>Kedrostis</em>, <em>Odosicens</em>, <em>Peponium</em>, <em>Seyrigia</em>, <em>Toxocarpus</em>, <em>Trocheometeria</em></td>
<td><em>Adenia</em>, <em>Cephalopentandra</em>, <em>Ceropogia</em>, <em>Coccinia</em>, <em>Corallocarpus</em>, <em>Cyphostemma</em>, <em>Dioscorea</em>, <em>Dolichos</em>, <em>Gerrardanthus</em>, <em>Kedrostis</em>, <em>Momordica</em>, <em>Peponium</em>, <em>Pyracantha</em>, <em>Trocheometeria</em></td>
<td><em>Adenia</em>, <em>Coccinia</em>, <em>Corallocarpus</em>, <em>Cyphostemma</em>, <em>Dioscorea</em>, <em>Kedrostis</em>, <em>Momorrica</em>, <em>Trochemeria</em></td>
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2. *Uncaria*, confamilial with *Sesamothamnus*; comes in next group.
3. Formerly separated as *Kleina* or *Nottonia*.
4. Within Madagascar *Sansevieria*, as traditionally defined, is native only in the NW; the genus is included in *Dracaena* by Stevens (2002).
tall, minimally-branched plants which emerge above most other plants in the community. The primary shoots of most Madagascan species develop countless persistent spines, very firm and sharp (Fig. 10); their morphological nature is not entirely certain (Stevens 2002). All along the major axes, even when these reach 10 cm thick, there are groups of small, somewhat succulent leaves at the bases of the spines; these leaves fall in the driest periods. The major axes are not like those of Cactaceae; they have a central core of xylem which is either solid (e.g. *Alluaudia procera*; P.J. Grubb, pers. observ.; see also Rauh 1995, p. 59) or composed of plates of tissue alternating with air spaces (e.g. *Didierea madagascariensis* in Cliché 79 of Koechlin et al. 1974; *Alluaudia adscendens* on p. 70 of Rauh 1998). The bark is thick, say 2.0–2.5 cm thick on a stem of diameter 10 cm (P.J. Grubb, pers. observ. on *Alluaudia comosa* and *A. dumosa*; Rauh 1995, p. 59 for *A. procera*, and Rauh 1998, pp. 54 & 70 for *A. adscendens* and *Didierea madagascariensis*). Functionally these Didiereaceae are most closely related to the Fouquieriaceae, best known through the ocotillo (*Fouquieria splendens*), but composed of eleven species in Mexico and the USA with varying heights and degrees of trunk development (Hendrikson 1972). I have traced no published description of the root systems of Didiereaceae, but that of *Fouquieria splendens* is shallow and wide (Cannon 1911); within the Madagascan thicket *Commiphora monstruosa* and *Operculicarya* spp. are shallow-rooted (Koechlin et al. 1974, p. 269). While the Didiereaceae often dominate the appearance of the thicket, it is not clear how far the plants effect ecological dominance over plants of other growth-forms, e.g. by root competition.

Climbers are common, and appear to be especially abundant alongside tracks. Among the commonest
climbers Xerocicys danguyi (Cucurbitaceae) has tough thickly succulent round leaves 4–5 cm in diameter, and Folotsia grandiflora (Apocynaceae) has succulent stems up to 2.5 cm thick. Climbers with thick succulent upright trunks (e.g. Cyphostemma corniferum) or boulder-like stems (Adenia feringalavensis), occur especially at rocky sites, where others have swollen roots (species in the same genera plus Dioscorea, Dolichos and Toxicarpus). One of the most spectacular is Odosicyos bosseri Keraudren (Cucurbitaceae) with a swollen root some 50 cm across, the top of which may be level with the soil surface, emergent or below ground (Rauh 1995, p. 117).

Epiphytes are, in general, rare. Ground-dwelling poikilohydres are also rare, though Xerophyta da-sylirioïdes occurs on some rocky sites, and the mat-forming Selaginella nivea can be common on the soil where not trampled by people or cattle.

There is appreciable variation in structure and physiognomy of the stand, but it is convenient to emphasize two main facies. On gneiss and on red Pliocene sands in the less dry part (400–600 mm yr\(^{-1}\)), there is appreciation of the stand, but it is convenient to emphasize two main facies. On gneiss and on red Pliocene sands in the less dry part (400–600 mm yr\(^{-1}\)), which lies to the south-east, toward TolanAir, the canopy is generally c. 6 m tall (Fig. 8); emergent species of Alluaudia (Didiereaceae) dominate the physiognomy, stem-succulent Euphorbia (especially E. plagiantha and E. stenoclada) are also abundant, and there is a sprinkling of bottle-trees represented by Adansonia za, Moringa drouardii and an occasional Pachypodium, a few tall aloes (especially Aloe vaombe), and various leaf succulents and evergreens amidst a wide array of shrubs and climbers. There are also what I call 'marginal bottle trees', listed as bottle trees by Koechlin et al. (1974) but hardly convincing (notably Gyrcoactus americamus), and a few tall deciduous trees that transgress from the deciduous forest and have no obvious morphological adaptations except perhaps slightly smaller leaves or leaflets than most deciduous forest trees (e.g. Cedrelopsis grevi, Rutaceae, until recently Ptaderaoylaceae).

In contrast, the thicket on the flat-bedded limestone of the low, undulating Mahafaly Plateau in the somewhat drier area (c. 300–400 mm yr\(^{-1}\)) on the southwestern side of the island, inland from Toliara, is mostly only c. 2 m tall (Fig. 9). From the air it appears that relatively undisturbed thicket remains in a long north-south belt. For most of us our detailed impression is from the road from Toliara to Isalo, which bisects the area. It is notable for its lack of the type of Didiereaceae described so far; instead Alluaudia co-mosa, a species with a densely branched, rounded crown, and spines much longer than the leaves, is characteristic though found at low density and only locally (Fig. 9). Tall succulent-stemmed Euphorbia (wholly or mainly E. onoclaud) and tall Aloe are uncommon. The occasional bottle trees are of a different Adansonia (A. rubristipa, formerly A. fony), and of Delonix floribunda (wrongly named D. adansonioides' in the literature; cf. Du Puy 2001). One major marginal bottle tree, Jatropha mahafaliensis, is locally very common.

As shown in Table 3, the genera of succulent or related plants overlap hugely with those of the thicket found in the Somalia-Masai region of White (1983), a point emphasized by Thomasson & Thomasson (1991). More surprising is the huge overlap in generic content between the succulent plants in the Madagascan thicket and those in the totally different-looking landscape (woodland plus succulents on rock outcrops) found under 250–550 mm yr\(^{-1}\) in northern Namibia, also shown in Table 3.

Among the non-succulent shrubs and small trees, the overlap between the thicket of southern Madagascar and that of north-eastern Kenya is much less strong. Considering the two areas at least 93 genera are involved (Appendices 1 and 2). Only 22 are in common, 47 are found only in the Madagascan thicket and 24 only in the Kenyan. Also striking is the fact that certain genera are hugely more speciose in one area than the other. Most notably Croton has 26 species in the Madagascan thicket and only four in the Kenyan, while Commiphora has only eight species in the Madagascan and 37 in the Kenyan. In terms of ecological dominance, the big differences between the two areas concern Acacia and Commiphora. In Kenya the dominance by these genera is so marked that the community is commonly referred to as the Acacia-Commiphora bushland or thicket. In the Madagascan thicket Acacia is not at all obvious, while Commiphora is abundant but not as dominant as it appears to be in the Kenyan thicket.
Why thicket and not grassy woodland in the driest area?
Koechlin (1972) provided the beginnings of an answer. He suggested that thicket is favoured by (a) the significant chance of rain all through the year, and (b) the notably high relative humidity all the year. The mean at 1000 hours is c. 60% (Koechlin et al. 1974, p. 244); in contrast, in the Sahel and Kalahari, it sinks to much lower values in the rainless months (Müller 1982). White (1983, pp. 47–48) pointed out that the only other area in Africa-cum-Madagascar to have thicket as the climatically determined vegetation-type is his ‘Somalia-Masai’ region which has two wet seasons each year rather than a significant chance of rain all through the year. That area is a little drier than the south and south-west of Madagascar (200–500 mm yr\(^{-1}\) rather than 300–600 mm yr\(^{-1}\)), and includes semi-desert in its driest part. Other areas with the same range of total annual rainfall (250–550 mm yr\(^{-1}\)), both north and south of the Equator, have a single short, well-defined wet season and 3–4 months with virtually no chance of rain. In these regions some kind of grassy woodland is the climatically determined vegetation-type, and thicket is confined to rocky hills, where most grasses cannot flourish. In Fig. 11 two typical climate diagrams for the Madagascan thicket are compared with one for the Kenyan thicket and one for the woodland area of northern Namibia.

Neither Koechlin et al. (1974) nor White (1983) provided an explicit mechanism, but I suggest the following. Firstly, the trees exacerbate the dryness of any dry spell by extracting water from the topsoil, and secondly the treelets and shrubs (like grasses) are generally shallower-rooted than the trees and more dependent on topsoil water. By hypothesis they cannot survive very long totally rainless spells, especially if low humidities prevail. In contrast, grasses have the ability to die back in the dry season and need almost no water then; they can endure much longer dry seasons as a routine. Once perennial grasses are dominant, they not only encourage fire which cuts back young woody plants (and selects for resprouting ability) but also exacerbate the water shortage in the dry season by their ‘wasteful’ usage in the wet season (Walter 1971; Knoop & Walker 1985).

Abundance of evergreen trees and shrubs in the thicket
Approximately 17% (33 out of 189) of species of non-succulent shrubs and small trees are evergreen (Appendix 1). Judging by the account of Koechlin et al. (1974), the proportion is much higher than in the deciduous forest to the north, but I cannot make a precise comparison. There is certainly a contrast with the much lower proportion in the deciduous thicket of NE Kenya: 8.2% (12/147; Appendix 2). Several of the evergreens in the Madagascan thicket are quite local and uncommon, but others are widespread and locally abundant (Flora).

The evergreen leaves vary greatly in size, texture and presentation, as is nicely shown by three common evergreen tree species (4–6 m tall) in the thicket on Berenty Private Reserve near Amboasary in southern Madagascar: *Salvadora angustifolia* (Salvadoraceae, Brassicales), *Maerua filiformis* (Brassicaceae, Capparoideae) and *Mundulea stenophylla* (Fabaceae: Faboideae). The leaves of *S. persica* and *M. schinzii*, which are so widespread at rocky sites in Namibia (photos and maps in van Wyk & van Wyk 1997). Indeed, *M. filiformis* has cylindric phyllodes, the first leaves on a shoot being diminutive but showing the ovatiformal blade that is usual in the genus (Koechlin et al. 1974, p. 273). The leaves of the *Salvadora* (which are slightly succulent) are pendent,
and thus reminiscent of a narrow-leaved eucalypt; those of the *Maerua* are held at various angles from 45° up to 45° down, and are thus reminiscent of *Acacia aneura* which covers so much of central Australia. The leaflets of the *Mundulea* are parallel-sided, fibrous and mostly sub-erect, reminiscent of various Myrtaceae in the sclerophyll vegetation of Australia.

How are so many evergreens able to flourish in the thicket despite the mean annual rainfall being much lower than in the more thoroughly deciduous forest? – White (1983) suggested that the responsible factors are the same as favour the development of thicket rather than woodland – the chance of rainfall being spread through the year, and the high relative humidity – and I agree.

The same prominence of evergreens in an otherwise deciduous community, coupled with a finite chance of rain throughout the year, and a mean of about 400 mm yr⁻¹, is seen on the Peninsula de Paraguana on the northern coast of Venezuela (c. 12°N) for which a preliminary description is given by Matteucci (1987). There we find several evergreen species of *Capparis*, and one each of *Guaicam* (Zygophyllaceae) and *Jacquinia* (Theophrastaceae). Both in south-western Madagascar, and on the north-western coast of Venezuela, the evergreen trees grow on ‘zonal’ soils, and they are not concentrated – as are species of *Maerua* and *Salvadora* in northern and central Namibia – along water courses or among rocks or on land receiving water that drains off large rocks.

It is notable than in the thicket of the lowlands of the Masai-Somalian region, where the humidity is not kept especially high by a maritime influence, evergreens are generally lacking; they become prominent in the mountains where evaporative loss is reduced (White 1983). The prominence of evergreens on the north-western coast of Venezuela near sea level may reflect in part a strong cooling effect by the north-east trade winds; severely wind-pruned trees are a characteristic sight on exposed shores.

It is also possible that direct uptake of water by the shoots is involved. Koechlin et al. (1974) and Rabesondratana (1984) emphasized the abundance of dew-formation in the spiny thicket, a clear result of the prevailing high humidity. Koechlin et al. (1974, p. 276) mention specifically *Croton* and *Grewia*, as recovering turgidity after uptake from dew; both have rather soft leaves and are deciduous. Diaz (1999) has shown unequivocally for *Croton belaster* on the north-western coast of Venezuela that there is biologically significant direct uptake of water by leafy shoots from very light rains there. Whether the evergreens, which are likely to have less permeable cuticles, can take up water from dew is another question.

**Abundance of succulents in the thicket**

My hypothesis is that the factors which have led to the evolution of thicket rather than grassy woodland, and allow evergreens to be relatively abundant, also account for the abundance of succulents. However, it is necessary to consider this idea critically in relation to Walter’s interpretation of the conditions favouring an abundance and/or variety of succulents, and the need for its correction. Although I criticize his theory, I accept his use of the term ‘desert’ for areas where either there is no perennial plant present (‘extreme desert’) or (more commonly) the perennial vegetation is restricted, to sites with exceptionally favourable water supply (typically dry river beds), and his use of ‘semi-desert’ for vegetation with a diffuse cover of perennial woody plants or grasses over the landscape, even if amounts to only 1–5%.

The parts of the world to which Walter (1964, 1971) drew attention to as having abundant and/or varied succulents all have either a significant chance of rainfall spread through the whole year, e.g. much of south-western USA, the northern coast of South America, and north-western South Africa, or two rainy seasons a year, e.g. the ‘caatinga’ of NE Brazil, part of north-eastern Tanzania and the island of Socotra off the Horn of Africa. He noted that, contrary to the expectation of many lay people and beginning students who see the cactus as the ultimate xerophyte, succulents are generally poorly developed in deserts and the driest semi-deserts. They are absent from the desert and semi-desert communities of almost the whole of the largest dry area on earth today, the Sahara. His explanation (Walter 1971, p. 318–319) was based on the properties of the juvenile; he emphasized that while the adult succulents can have enormous water stores relative to their mass, and lose water very slowly during prolonged drought, that is not true of seedlings of the same species with their much higher surface-to-volume ratios. Moreover, the very slow growth of the seedlings keeps them vulnerable for a long time. For that reason supposedly they cannot regenerate where the annual amount of rainfall is always very small, or there are several absolutely dry months.

Observations in Namibia and Chile cause us to reject this approach. In Namibia succulent *Euphorbia* spp. with shoots of the order of 1 cm diameter form mound-like shrubs 2–4 m across which dominate semi-desert (with c. 125–150 mm yr⁻¹) over huge areas of gently undulating more-or-less flat-beded rocky country along the eastern side of the Namib Desert (*E. damarana* Leach in the north, and *E. gregaria* Marloth in the south; Craven & Marais 1992). Another species (*E. gummifera* Boiss.), found on sand receiving water running off outcropping rocks, forms some...
of the last stands of perennial vegetation against the extreme desert (P.J. Grubb & P.J. Carrick, pers. observ.). Yet another species (E. virosa Willd. with thick, ridged, spiny stems) is almost the only species in the ‘accidental’ vegetation (very sparse and composed of haphazardly scattered individuals) on the steep coarsely rocky slopes of the extremely dry Fish River Canyon. It is also true that cacti are found in very dry places in the Atacama Desert (Gulmon et al. 1979; Rundel et al. 1991). I should emphasize that in the case of neither the Namib nor the Atacama am I concerned with the various plants enabled to live by the fog rolling from the sea, near to the coast. I am concerned with succulents living outside the influence of the fog.

Also important is the fact that most of northern Namibia has a negligible chance of rain for 3–4 months every year (Walter & Lieth 1960–1964), and yet there we find succulent representatives of at least ten families (Apocynaceae, Asphodelaceae, Asteraceae, Crassulaceae, Euphorbiaceae, Malvaceae, Moringaceae, Pedaliaceae, Ruscaceae and Vitaceae; cf. Table 3).

A different perspective on the regeneration of succulents is needed, and is provided by Jordan & Nobel (1979). In a laboratory experiment with very young seedlings of Agave deserti they determined the impacts of the amount of water given for establishment, and the severity of a subsequent dry period. Using a mathematical model to relate the water supply in the lab to meteorological data of a conventional kind, they forecast that this species could not have established new individuals at their field site in the last 16 years. In fact the youngest plants were 17 years old. The general point is that establishment of such plants occurs only rarely, on the order of every 10–100 years, and the occurrence of exceptionally wet years which make establishment of seedlings possible is the single most important feature of the long-term rainfall regime for the plants concerned, not the distribution of rainfall in an average year.

Although the local dominance of a few species of succulent in fog-free deserts in Namibia and Chile shows that they can live under extremely low total rainfalls, and the variety of succulents in northern Namibia with an absolute dry season of 3–4 months shows that they can tolerate long dry periods on a regular basis, it is reasonable to suppose – along with Walter (1971) – that both a higher total rainfall (up to a point) and a wider spread of rainfall through the year will favour succulents. In that case, the latter factors are likely to constitute the chief explanation for the diversity as well as abundance of succulents in the semi-deciduous thicket of Madagascar, and their occurrence in the main vegetation-type rather than being restricted to rocky sites.

White (1983) emphasized that the density of succulents is not as high in the thicket of the Somali-Masai region as in that of Madagascar, and that some of the species are clearly more abundant where the rainfall is higher. Perhaps both a lower rainfall in general in the Somali-Masai thicket, and a lower mean relative humidity, are the key factors.

Physical defences against herbivores

Vegetation-types other than the semi-deciduous thicket

I deal here particularly with spines and with very densely and finely branched shrubs or small trees. My particular interest is to look for plants which were defended against the now-extinct elephant birds, and which might be analogues for ‘divaricating shrubs’ and other specialized plant types seen in New Zealand where giant flightless birds (moas) browsed until a few hundred years ago (Atkinson & Greenwood 1989). Divaricating shrubs have notably wiry or rigid stems, which branch at a wide angle and are often densely interlaced; usually their leaves are very small relative to those of non-divaricating relatives. In most species the shoots are not spiny; 15 families are involved.

The warm temperate and cool temperate rain forests of New Zealand contain numerous divaricating shrubs, especially on more fertile soils and at edges, and also other unusual physiognomic types apparently defended against tall browsing birds. The tropical rain forests of Madagascar lack such plants completely. In many parts of the tropics a large proportion of the spiny plants in rain forests is made up of palms, pandans and tree-ferns; I suggested earlier that increased investment in defence by such plants can be understood in terms of the one shoot apex not being replaceable (Grubb 1992). In Madagascar the palms are notably non-spiny. Dransfield & Beentje (1995) drew attention to this point, and to the contrast with the Seychelles where many rain forest palms are spiny; they hypothesized that the key difference between Madagascar and the Seychelles was the lack of herbivorous giant tortoises on the former. In contrast to the palms, the pandans in the Madagascan rain forest all have spiny leaf margins. Eleven of the 40 tree-fern species (of which many are found only in montane forest or high-altitude thicket) are known to have spines on the trunks (3) or petioles (7) or both (1), and the figure may be higher as the trunks and petioles of several species are unknown (Flora); the percentage of species with spines may be very similar to that in Malesia (36%; Grubb 1992). There are a few shade-tolerant dicots with spiny leaves, e.g. some Plagioscyphus spp.
Sapindaceae), for which no rationale is apparent (cf. Grubb 1992).

The position in the deciduous forests of Madagascar is also as in the tropics generally. That is to say, apart from a few palms and pandans, spines are almost confined to evergreen dicots which clearly suffer an increased risk of being eaten while the deciduous plants are leafless. Some such as Diospyros aculeata and Ludia dracaenoides have a spine at each leaf apex, while others such as Euonymopsis humbertii and E. longipes (Celastraceae) and Rinorea spinosa (Violaceae) have leaves like the European holly. Just as in the case of Ilex in the Northern Hemisphere (Grubb 1992), Euonymopsis and Rinorea are represented in wholly evergreen forests by non-spiny species (E. acutifolia and E. obcuneata, and 14 Rinorea species). In Madagascan deciduous forest there also a few spiny stem-succulents, notably Pachypodium rutenbergianum, and on rocks within the forest Euphorbia ankarensis and E. pachypodioides.

**Semi-deciduous thicket**

It is remarkable that so very few of the many succulents in the thicket are spiny. All of the abundant tall Euphorbia spp. with succulent stems bar E. stenoclada, all the convincing bottle trees bar Pachypodium (Adamsonia, Combretum, Delonix, Moringa, Opercularia decaryi), and all the marginal bottle trees (Givota, Gyrocarpus, Jatropha, Opercularia byphaenoides, Uncarina) lack spines. Similarly the leaf-succulent Kalanchoe spp., the low-growing stem-succulents Senecio (Kleimia) and Sarcostemma, and the many climbers with succulent leaves, stems or roots all lack spines. Just a very few lower-growing Euphorbia spp. carry spines, as do the Aloe spp. (well illustrated by Rauh 1995–1998). Perhaps the few stem and leaf succulents with spines are particularly attractive as a result of being especially fat, water-rich and lacking in strong defences of any other sort; alternatively they may simply carry features which they evolved early on, and still show in Africa as well as Madagascar.

I suggest that the spines of the Didiereaceae are primarily protective of the leaves, not the stems. The evidence is that the length of the spines is related to the length of the leaves (Fig. 12). At one extreme there is Didierea madagascariensis which has long leaves and spines, while at the other there is Alluaudia dumosa which has leaves only in the first year of the life of a stem and is thereafter leafless with very short spines or none at all. In between we have Alluaudia fibrensis with middle-length leaves and spines. The species with leaves in the shorter range (10–20 mm long) show a variety of relative lengths of the spines, but three of the eight species fall close to the line defined by the species with longest, middle-sized and no leaves. My hypothesis is consistent with the fact that there are no spines on the tall stem-succulent Euphorbia spp., only one of which (E. antso) produces any leaves at all, and they soon fall (good photos in Rauh 1998, pp. 44 & 46). As 9/11 of the Didiereaceae in the Madagascan thicket reach mature heights of 4–6 m or more (Rauh 1963), it seems likely that the protective spines have evolved as a response to lemurs rather than elephant birds. The situation among the eleven species of the Fouquieriaceae is quite different; the data of Hendrickson (1972) show no correlation between spine length and leaf length.

The incidence of spines on non-succulent shrubs and small trees in the Madagascan semi-deciduous thicket is modest: 12% of all species (22/189). Thomasson (1975), using data from substantial assemblages of species in each of three kinds of thicket (on white sand, red sand and limestone) found a very similar mean (13%). The incidence is much higher in the thicket of NE Kenya: 31% (46/147), and the difference is statistically significant (chi-square contingency table: \( \chi^2 = 18.6, P < 0.001 \)). The difference between Madagascan and Kenyan thickets is shown clearly within particular taxa: 1/8 vs. 19/37 spiny in Commiphora, 0/28 vs. 5/12 in Euphorbiaceae, and 3/17 vs. 12/13 in Fabaceae-Mimosoideae. I return to this difference in spininess shortly.

The relationship between mean spine length and mean leaf length on short shoots in the eleven Madagascan species of Didiereaceae, based on the data of Rauh (1963); one species (Alluaudia dumosa) has no leaves on short shoots.
The thickets of the two areas are alike in that among the non-succulent shrubs and small trees there is a very high proportion of species with very small leaves (leptophylls and nanophylls): 62% (118/189) in Madagascar, and 53% (78/147) in Kenya (details in Appendices 1 and 2). For the Madagascan thicket, leaving aside the genera *Acacia* and *Dichrostachys*, which have leptophylls or nanophylls under any climate, and the closely related endemic genus *Alantsilodendron*, which always has leptophylls, the value is still high at 59% (100/170). The comparable figure for the Kenyan thicket is 49% (66/134). Thomasson (1975) found a mean of 56% for all shrubs and small trees in SW Madagascar, and no significant difference between thickets on white sand, red sand and limestone.

The possession of especially small leaves is associated with the development of impenetrable bushy crowns composed of densely branching shoots. On many species most of the leaves are borne on very short side shoots, and the leaf-clumps are scattered all through the crown. White (1983) noted the abundance of ‘small narrow leaves’, but in fact most are obovate (Fig. 13) – a good shape for minimizing mutual shading in mini-rosettes of semi-erect lvs produced on short lateral shoots. Because, as stated in one of Corner’s rules, twig diameter is closely related to mean area of lamina on the leaves borne (Corner 1949), it is possible to argue that selection has worked primarily on leaf size or on density of branching (dense branching needing slender twigs), or indeed on a combination of small leaf size and slender twigs.

If we compare leaf (or leaflet) sizes for the thicket-forming species in Madagascar with congeners in a part of Africa with a similar total annual rainfall and a striking similarity in genera present but woodland instead of thicket, i.e. northern Namibia, we see just how distinct the two areas are. In all of eight genera, for which comparisons may be made (see Appendices 1 and 3), the Madagascan species have smaller leaves.

The classical physiological explanation for having especially small leaves would be the advantage of cooling more easily (the still air layer on smaller leaves being thinner) and of reducing the problem of supplying water to the lamina edge from the base during times of extreme water shortage. Some support for this approach comes from considering species within genera along a rainfall gradient in Namibia, comparing those from rocky hills at the edge of the true desert (at about 100–125 mm yr⁻¹) with those in the woodland landscape (at 250–550 mm yr⁻¹). Of the seven *Commiphora* species found on rocky sites fringing the desert four have notably tiny leaflets: *C. kraeuseliana* 3.6 mm², *C. dinteri* 12 mm², *C. virgata* 35 mm² and *C. saxicola* 160 mm² (cf. 170–1500 mm² in ten woodland species; Appendix 3). Of the eight *Grewia* spp. in northern Namibia the only one going into semi-desert (*G. tenax*) has the smallest leaves (100 vs. 450–2800 mm²; Appendix 3).

It is hard to consider extreme lack of water as the explanation of very small leaves in S and SW Madagascar in view of the perspective put forward above for abundance of evergreens and succulents. Bearing in mind the fact that in New Zealand the evolution of very small leaves has manifestly occurred in relation to some factor other than water shortage, most plausibly herbivory, I suggest that in the Madagascan thicket small leaf size has evolved, along with dense branching, as a defence against ground-based herbivores, specifically elephant birds. Only a minority have divaricate branching in the strict sense (a kind of pseudo-dichotomy), e.g. *Terminalia divaricata* and several species of *Croton*, most notably *C. amboboombensis* and *C. menarandrae*, and only a small minority have

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**Fig. 13.** Examples of leaf form on short shoots of shrub and small-tree species of the semi-deciduous thicket: (a) *Commiphora simplicifolia*, (b) *Diospyros humbertiana*, and (c) *Terminalia divaricata* (based on drawings in *Flore de Madagascar et Comores*, Humbert et al. 1936–2002). The Scale = 10 mm.
The evolution of similarly bushy impenetrable shrubs in S and SW Madagascar and in the Somalia-Masai region shows that the design cannot have evolved specifically against elephant birds. However, I suggest that dense bushiness has evolved as a defence against medium-sized ground-based herbivores, whether birds or mammals. Moreover, the distinctive feature of the Madagascan shrubs, relative to these groups not managed better in Africa with its past (S. Dransfield, pers. comm., March 2003). How have the received record of vegetational history between moas and plants. – This question parallels the query over the significance of the huge range in nitrogen concentration, and many related properties, found elsewhere within a single functional group in vegetation ranging from semi-desert to rain forest (Grubb 2002).

The abundance and diversity of three types of plant in the Madagascan rain forests – palms, pandans and bamboos – is commonly attributed to the more secure water supply enjoyed by plants on Madagascar in the past. Yet all three groups are represented in the driest vegetation-type on the island: Ravena xerophila, Pandanus aridus St John and an undescribed bamboo (S. Dransfield, pers. comm., March 2003). How have these groups not managed better in Africa with its past and present dry climates? Did the chance of producing a drought-tolerant species depend on there being a large reservoir of biotypes in ‘safe’ moist-climate areas?

Finally, there is a huge commonality at the generic level between Madagascar and Africa in the plants of dry-climate vegetation (Table 3, Appendices 1–3). In one respect, this observation is readily compatible with the received record of vegetational history because there is believed to have been a wide range of rainfall in the tropics during the Cretaceous before Madagascar and Africa separated (Vakhrameev 1991). We have only to assume that all the relevant genera evolved early on. However, the received view is that by the early Tertiary wet climates were strongly dominant (Wolfe 1985). Where did the present-day dry-climate genera live on Madagascar then?

The flora and vegetation of Madagascar are not only of exceptional interest in themselves, but throw up serious problems for understanding of plant life on Africa and in the world as a whole.

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Some outstanding puzzles

In my discussion of the Madagascan semi-deciduous thicket I emphasized the high proportion of species with very small leaves. Equally impressive is the very wide range in lamina area, up to two orders of magnitude, found within genera with 2–26 species in the Madagascan thicket, or 2–37 in the Kenyan deciduous thicket (Appendices 1 & 2). Does this variation in leaf size contribute in some way to the maintenance of coexistence? – This question parallels the query over the significance of the huge range in nitrogen concentration, and many related properties, found elsewhere within a single functional group in vegetation ranging from semi-desert to rain forest (Grubb 2002).

The abundance and diversity of these groups not managed better in Africa with its past and present dry climates? Did the chance of producing a drought-tolerant species depend on there being a large reservoir of biotypes in ‘safe’ moist-climate areas?

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The flora and vegetation of Madagascar are not only of exceptional interest in themselves, but throw up serious problems for understanding of plant life on Africa and in the world as a whole.

References


Appendix 1. Check-list of species of non-succulent shrubs (>1 m tall) and small trees (not normally >6 m tall in thicket) in the Semi-deciduous Thicket of southern and south-western Madagascar.

Within each functional group species are ordered firstly by family, then by genus in alphabetical order, and then by increasing leaf or leaflet size. Definite bottle trees and ‘marginal bottle trees’ (cf. Table 3) are excluded. Compiled from the Flore de Madagascar et des Comores, and information given by Lourteig (1960), Capuron (1969), Kochchin et al. (1974), Leroy (1976), Rabesandrataina (1984), Dransfeld & Beentje (1995), Du Puy (2001), Schatz (2001), Mr A. Radcliffe-Smith (Flore de Madagascar et des Comores, in press; pers. comm., March 2003) for Croton; three papers quoted by Schatz (2001) for Grewia, and my own observations in Herb. Kew for Cordia, Pandanus, Turraea and the remaining Grewia spp.

The number after each species is my best estimate of the mean area of a leaf or leaflet blade (mm²) based on arithmetic means of usual upper and lower limits on length and breadth given in publications cited; for most species, area has been calculated as length x breadth x 0.67 (following Cain et al. 1956), but for linear leaves I have used simply length x breadth, and for nearly round leaves I have used

Evergreen species (33)
Acanthaceae, Acanthus decaryi 24, Barleria brevistyla* 25, B. decaryi 50, B. her 140, B. illuavidii* 250; Asteraceae, Brachylaena microphylla 600, Vernonia swingelii 40, V. mahaly 130, V. scolium 400, V. pectorialis 770, V. seyrigi 6700, V. mandarensis 7200; Bignoniaceae, Fuchsia decaryi 28, Physostegia dumetaria 14, Physostegia linearis 69; Ochnaceae, O. greveana 1200; Olacaceae, Rhopalopolis perrieri 200; Pandanaceae, Pandanus arundis 24000; Rhamnaceae, Scutia myrtina** 190; Salvadoreaeae, Azima tetracantha** 300, Salvadora angustifolia 500; Sapotaceae, Capuronid endrocy 15, Mandrense deumetaria 0.3, V. venosa 3.1.

Mimosoid Fabaceae (17, all deciduous)
A group usually leptophyllous or nanophyllous in any climate. Acacia bellula* 2, A. viguiera* 20; Albizia divaricata 3, A. maskororum, A. commiphoroides 3.7, A. atakatak**** 6.7, A. tulearensis 100; Alantsilodendron gloratana 0.3, A. pilosum 1, A. ramosum 1, A. alluaudianum 3, A. decaryanum 3.5, A. brevipes 4.8, A. humbertii 5.2, A. mahafalense 15, Dichrostachys dumetaria 0.3, D. venosa 3.1.

Other deciduous species (139)
Acanthaceae, Acanthas 24, Barleria brevistyla* 25, B. decaryi 50, B. her 140, B. illuavidii* 250; Asteraceae, Brachylaena microphylla 600, Vernonia swingelii 40, V. mahaly 130, V. scolium 400, V. pectorialis 770, V. seyrigi 6700, V. mandarensis 7200; Bignoniaceae, Fuchsia decaryi 28, Physostegia dumetaria 14, Physostegia linearis 69; Ochnaceae, O. greveana 1200; Olacaceae, Rhopalopolis perrieri 200; Pandanaceae, Pandanus arundis 24000; Rhamnaceae, Scutia myrtina** 190; Salvadoreaeae, Azima tetracantha** 300, Salvadora angustifolia 500; Sapotaceae, Capuronid endrocy 15, Mandrense deumetaria 0.3, V. venosa 3.1.

1I have omitted Capparis chrysocma as found in gallery forest rather than thicket (P. J. Grubb, pers. observ.), and Gymnosporia lineari as typical of cleared land rather than thicket (Kochlin et al. 1974).
Appendix 2. Check-list of species of shrubs (>1 m tall) and small trees (not normally >6 m tall in thicket) in the Bushland and Thicket of the Northern Province of Kenya.

Compiled from the Flora of Tropical East Africa with help from Dale & Greenway (1961) and White (1983). Conventions as in Appendix 1. The two subspecies of Commiphora holtziana are so different in leaf size that they have been treated as different species. The extent of evergreenness in Maerua spp. is unclear from the published account. This list is certainly incomplete as there is no published account of the Polygala or Solanum spp. of the area; there is no modern account of the Acanthaceae present, but all those I have traced at Kew are <1 m tall.

Evergreens (12)
Brassicaceae-Capparoideae, Boscia coriacea 720, Maerua sessilifolia 12, M. kaesneri 38, M. endlickii 50; Celastraceae, Elaeodendron aquifolium** 1600; Ebenaceae, Diopyros scabra 130, D. wajirensis** 130, D. anacardifolia 2100. Check-list of species of shrubs (>1 m tall) and small trees (not normally >6 m tall in thicket) in the Bushland and Thicket of the Northern Province of Kenya.

Mimosod Fabaceae (13, all deciduous)
Acacia tortilis spp. spirocarpa* 0.5, A. edgeworthii* 1.3, A. reficiens* 1.9, A. bussei* 2.2, A. turnbulliana* 2.2, A. stuhlmannii* 3.1, A. horrida* 3.4, A. paoli* 4.6, A. rubica* 6.9, A. condylocarpa* 61, A. mellifera* 79; Abizia amara spp. amara 4.0, Dichrostachys cinerea spp. cinerea* 3.6.

Other species (118)

Appendix 3. Species of the dry woodland landscape of northern Namibia in the same genera as shrubs or small trees in the Madagascan semi-deciduous thicket. Compiled from Palgrave (1988); calculation of lamina area as in Appendix 1.

Bignoniaceae, Rhigozum brevispinosum 38; Burseraceae, Commiphora multifluga 170; C. oblateolata 200, C. tenutepetiolata 310, C. pyracanthoides 350, C. merkeri 440, C. angolensis 450, C. africana 480, C. glaucens 540, C. molls 750, C. crenata-serrata 1500; Celastraceae, Gymnosporia senegalensis 600, G. buxifolia 670; Combretaceae, Terminalia pruniodies 250, T. sericea 1500, T. brachystemma 3200; Euphorbiaceae, Croton menyanthi 670, C. grattissimus 1500; Fabaceae, Bauhinia persians 2300; Malvaceae, Grewia tenax 100, G. flavata 490, G. retinervis 500, G. bicolor 600, G. flavescens 1400, G. schinzii 1900, G. villosa 2800; Olacaceae, Ximenia americana 300, X. caffra 600. Check-list of species of shrubs (>1 m tall) and small trees (not normally >6 m tall in thicket) in the Bushland and Thicket of the Northern Province of Kenya.