Tropical forest types



China Tropic of Cancer Taiwan Myanm India Bangladesh Thailand Vietnam Wester Ghat Cambodia Brunei Malaysia Sri Lanka Singapore Borneo New Guinea quator Papua Sulawesi Sumatra New Guinea Kalimantan Indonesia Do da co Java Australia Iropic of Capricorn

Principal rain forest areas: reconstruction of original extent



Moist forest types: determined by water regime, soils and temperature

Climate	Soil water	oil water Soils		Elevation		Forest formation	
Seasonally Strong annual dry shortage		nual				Monsoon forests (various formations)	
	Slight annual shortage					Rain forests: Semi-evergreen rain forest	
Everwet	Dryland		Zonal	L	owlands	Lowland evergreen rain forest	
(pernumid)			(ultisols)	-	(750) 1200–1500 m	Lower montane rain forest	
				Mountain	(600) 1500-3000 m (3350) m	Upper montane rain forest	
					3000 (3350) m to tree line	Subalpine forest	
			Podzolized sands	Mostly lowlands		Heath forest	
			Limestone	Mostly lowlands		Forest over limestone	
			Ultrabasic rocks	Mostly lowlands		Forest over ultrabasics	
	Water table high (at	Water able salt- salt- water east beriodi- ally) Inland fresh- water Eutrophic (muck and mineral) coils				Beach vegetation Mangrove forest Brackish water forest	
	periodi-		Oligotrophic peats			Peat swamp forest	
	(cany)		=Permanently wet		Freshwater swamp forest		
			initieral) sous	P	eriodically wet	Freshwater periodic swamp forest	

Those shown bold are discussed in the text

Annual litter decomposition rates



The litter decomposition rate scaled to unity when the mean annual temperature is zero and the precipitation does not limit the decomposition.

Plant soil C and litter pools distribution



either due to high production of litter, or low depletion rates, or large share of dever decomposing wood on intal litter production. The total amount of the global litter pool as presented by this map accounts to 168 × 10* 1 dry matter.

Tropical decomposition: plant matter disappears in <1 year

Forest locality	Altitude (m)	Litterfall (t ha ⁻¹ yr ⁻¹)	Litter standing crop (t ha ⁻¹)	Turnover coefficient (k _L)	Time (wks)
Malava, Pasoh	10	6.3	1.7	3.6	14
Malava Penang	_	5.4	5.1	1.1	47
New Guinea	100	7.3	5.0	1.5	35
Sarawak	225	5.4	3.2	• 1.7	31
Ghana	150	7.4	3.0	2.5	21
Niceria	250	4.7	1.0	2.8	19
Brazil	45	6.1	4.0	1.5	35
Panama	150	7.0	2.8	2.6	20

Table 2.13 Leaf litterfalls and turnover coefficients for selected tropical forests (after Anderson and Swift, 1983)

(Source: J. M. Anderson and M. J. Swift, Decomposition in tropical forests, in *Tropical Rain Forest: Ecology and Management*, Special Publication No. 2 of the British Ecological Society, eds S. L. Sutton, T. C. Whitmore and A. C. Chadwick; published in 1983 by Blackwell Scientific Publications.)

Tropical forests: nutrients are in live biomass, not litter

Table 2.12 A comparison of the quantities of mineral elements in the above-ground standing crop of vegetation with those returned annually in the litter in various tropical wet forests (after Edwards, 1982)

		Dry weight	2	Nutrient capital (kg ha ⁻¹)				
		(t ha ⁻¹)	N	P	к	Ca	Mg	
Lower montane forest	above-ground biomass (ABG)	301	683	37	664	1281	185	
(New Guinea)	total litter	7.6	91	5.1	28	95	19	
Lowland forest	above-ground biomass (ABG)	406	2430	59	435	423	201	
(Brazil)	litter	7.3	106	2.2	13	18	13	
Lowland forest	above-ground biomass (ABG)	233	1685	112	753	2370	320	
(Ghana)	litter	10.5	199	7.3	68	, 206	45	
(Source: P. J. Edwards Stur	ties of mineral cycling in a montane rain for	est in New Guinea: V.	Rates of cycl	ing in through	fall and litte	r fall, Journal	of Ecology	

(Source: P. J. Edwards, Studies of mineral cycling in a montane rain forest in New Guinea: V. Hates of cycling in throughtail and litter fail, Jour 1982, 70.)



Figure 6.10 Distribution of organic carbon in the abiotic portion (soil litter) and biomass (wood, leaves) of tropical ombrophilous forest and temperate coniferous forest (After Kira and Shidei, 1967; Longman and Jenik, 1974). Reproduced by permission of Longman Group Ltd Decomposition rate: -- maximum at medium rainfall -- increasing with temperature



Fig. 32.1. Depletion rates of herbaceous litter separated in temperature blocks. The maxima of the three "Nyquist" lines shift with increasing temperature range to higher values of precipitation.



Fig. 32.2. Influence of mean annual temperature (T) on depletion rates of fresh herbaceous litter $(D_{\rm H})$. The rates are in % of the reported litter pool per year. The regression curve is calculated from the running means of 5°C classes by Marquardt's least-squares method. Values higher than 100% indicate depletion times shorter than 1 year. Squares: tropical rain-forest data; triangles: tropical savanna data; circles: tropical mountain forest data; stars: data from other regions.



Decomposition rate:

synthesis of temperature and rainfall:

predicted by actual evapotranspiration

Fig. 31.2. Relationship between decomposition and actual evapotranspiration for seventeen sites (after Meentmeyer, 1985). Sites 10 to 17 are tropical forest. The rate of decomposition is expressed as the Litter Turnover Coefficient K where $K = L/X_{ss}$ (L = Annual Litter Fall and X_{ss} = mean annual accumulation of 01 and 02 litter): the independent variable is Actual Evapotranspiration (AET). The relationship between k (y) and AET (X) is given by $\log_{10} Y = 1.45 + 0.00$ (4X (r = 0.98, n = 17).

Tropical soils



Main soil constraints on plant productivity in the tropics

Low nutrient reserves >50% of area Aluminium toxicity >50% of area No major limitations <10% of area

Soil constraint	Tropical America		Tropical Africa		Tropical Asia		Humid tropics	
	10%ha	(**)	10°ha	(%)	10°ha	(%)	10"ha	(%)
Low nutrient reserves	543	(66)	285	(67)	101	(45)	929	(64)
Aluminum toxicity	490	(61)	226	(53)	92	(41)	808	(56)
High P fixation	379	(47)	84	(20)	74	(33)	517	(37)
Acid, not Al toxic	88	(11)	92	(22)	. 74	(33)	255	(18)
Slopes steeper than 30%	145	(18)	22	(5)	73	(33)	241	(17)
Poor drainage	90	. (11)	59	(14)	42	(19)	101	(13)
Shallow depth	54	(7)	17	(4)	77	(12)	98	(7)
No major limitations	28	(3)	7	(2)		(2)	40	(7)
Acid sulfate soils	2	(-)1	5	(1)	6	(3)	13	(3)
Gravel	2	(-)	6	(1)	1	(5)	10	(1)
Salinity	3	(-)	1	(-)	4	(2)	8	(-)

Area distribution of soil constraints in humid tropical regions. Calculated according to Sanchez et al. (1982a)

Soil quality limits to cultivation



Red soils of humid tropics (oxisols, ultisols):

- high acidity
- aluminium toxicity deficiency of P, K, Ca, Mg
- low cation exchange capacity = high leaching
- high organic content

General distribution of main kinds of soils in the humid tropics (calculated from Table 4.1)

General soil grouping	Humid tropical America (%)	Humid tropical Africa (%)	Humid tropical Asia and Pacific (%))	World's humid tropics (%)
Acid. low native fertility soils (Ferralsols.	81	56	38	63
Moderately fertile, well-drained soils (Luvisols, Vertisols, Charmonic and the Control of Control o	7	12	33	15
Poorly drained soils (Glevsols)	6	12	6	8
Very infertile sandy soils (Arenosols, Podzols)	2	16	6	7
Shallow soils (Lithosols)	3	3	10	5
Organic soils (Histosols)	1	1	6	2
Total	100	100	100	100





K, Ca in biomass, N, P in soil



Figure 2.46 Nutrient stocks in living biomass and litter and in soils of tropical forests. The locations of the lowland forest sites are (1) and (7) Venezuela; (2) and (3) Brazil; (4) Ivory Coast; (5) Thailand; (6) Ghana. The montane forest sites are located in (8) Costa Rica; (9) Colombia; (10) New Guinea; (11) Venezuela. (After Jordan, 1985.) (Redrawn with permission from C. F. Jordan, Nutrient Cycling in Tropical Forest Ecosystems; published by John Wiley and Sons, 1985.)



Figure 2.48 Concentrations of NO₃-nitrogen and potassium in soil water collected at 40 cm depth over a five-year period in forest and cut-and-burn plots in lowland rain forest in Venezuela. (After Uhl and Jordan, 1984.) (Reprinted with permission from C. Uhl and C. F. Jordan, Succession and nutrient dynamics following forest cutting and burning in Amazonia, *Ecology*, 1984. **65**, 1485.)

Slash-and-burn agriculture: the effect on soil nutrients

Concentration of nitrates and potassium leached in soil water



Main features of tropical forests



Structural features of lowland rainforests estimated for trees with DBH > 10 cm

	Barro Colorado, Plateau	La Selva, Costa Rica	Luquillos. Puerto Rico	Rosario, Cuba	S Carlos, Venezuela. terra firme	Pasoh. Malaysia	Mangroves, Malaysia
Standing crop (tons/ha)	270	221	379	257	234-261	426	470
Basal area (m ² /ha)	29	25	36	30	28	31	33
No. of trees/ha	414	446	710	1183	786	596	500
Annual mortality (%)	1.98	2.03	1.22		1.12	1.19	2.26
No. of deaths counted	2069	1386	167		88	944	33
LAI			6-7	8.5	6.4-7.5	7-8	50
Leaf fall (g dry wt/m ²)	610	660	494	620	500-757	703	576
Total litter fall (g dry wt/m ²)	1152	1090	861	820	625-1025	1110	763

Table 6.3 Structure, dynamics, and above-ground biomass in selected forests

Standing biomass	221 - 470 t/ha
Basal area	25 - 36 m2/ha
No. of trees	414 - 1183 per ha
Annual mortality	1.1 - 2.3%
LAI	6 - 8.5
Leaf fall	4.94 - 7.6 t/ha
Total litter fall 6.3 -	11.5 t/ha



Leaf area index (by remote sensing)

Buermann et al. 2008, J. Biogeography 35, 1160-1176

Measuring forest structure



Emergent trees



Drip apex of the leaves



Epiphylls



buttresses

support roots

stilt roots Pandanus

aerial roots





climbers

Trunk epiphyte Epipremnum. Queensland. Len Webb photo

epiphytes

SE Asia: Asplenium ferns

The second second second second

Neotropics: bromelias [Vriesea Aechmea,, Bilbergia, Guzmania]

icha,

ens

Forest seasonality, epiphytic bromeliad diversity and % of CAM species in Trinidad





Smith 1989

epiphytes





epiphytic moss carpets





Fragmented forest Converted forest

Inland water No data

copyright mongabay.com

Seasonally flooded grasslands

Agricultural mosiacs Subdesertic vegetation



Amazon river system drawn over Europe





Seasonal fluctuation of water level in Amazon and Rhine rivers



Annual fluctuation of water level in Amazon river



Low inclination of Amazon river + water level fluctuation + flat landscape

large inundated areas of varzea forests



Figure 1. Watertable for the main body of the Amazon river. The low inclination reflects the low altitudes of the Amazon basin (After Soares, 1959).



Varzea: periodically inundated forests of white water Amazon

High water: 6-8 months




Varzea - floating and truly aquatic macrophytes are species rich. 'Floating meadows' are often 10-100s ha in extent, dominated by *Paspalum repens* and *Echinochloa polystachya*. Free-floating aquatic plants form floating mats of *Eichhornia*, *Pistia, Limnobium, Salvinia, Azolla, Lemna* etc.



Varzea - everything floats, even cattle



White and black waters



The confluence of white water Amazon and black water Rio Negro

White-water sediments originate in the Andes and carry heavy sediment loads (pH=7)

Black-water rivers receive drainage from bleached sands of the central lowlands – low nutrients and stained black (pH=4)





Fig. 14.5 Profile diagram of igapó on Rio Negro near Manaus. After Takeuchi (1962). Key: 1 Eugenia inundata, 2 Campsiandra latifolia, 3 Symmeria paniculata, 4 Coccoloba sp.

Igapo - periodically inundated forests in black water river systems (Rio Negro)

Black waters are stained by humic acids and tannins, low in nutrients. Forest dominated by palms and legumes.







Terra firme forest: non-inundated lowlands

Cerrado: shrubland in dry areas







Cerrado



Caatinga:

dry forest/shrubland on sandy soils

Brasil:



caatinga



Cerrado zonation on a moisture gradient



Fig. 5. The influence of topography and drainage on the forms of cerrado. The heights refer to the vegetation and not to the schematic relief (after Furley, 1996).

Three (Neotropical) rainfall gradients





Gallery forest surrounded by cerrado in Brasil

SE Asia gallery forest

ll a	Swampy Gallery forest (evergreen)	Cerradão	
11	Valley forest (mainly evergreen)	Cerrado	
	"Dry forest" (evergreen seasonal)	Grassland	
1.19	Carrasco (low evergreen forest on white sand)	Approximate position of Base Camp 12*49'S 51*46'W	
7772	Deciduous seasonal forest (trees mostly		



Monodominant forests: on extremely nutrient-poor white sands (e.g., Guyana)

Mora excelsa, the forest dominant:





Present Potential Vegetation





Fig. 7.2. Physiognomy of savannas with examples from all over the world. Transects of Vareschi (1980, with kind permission of R. Ulmer)

Typical savanna trees:

Africa: Adansonia, Terminalia, Acacia America: Vochysia, Caesalpinia Australia: Acacia, Melaleuca, Terminalia

C4 plants: higher photosynthetic rate, more efficient water use, but higher optimum temperature than C3 plants

	C ₄ plants	C3 plants
Type of plant	Herbaceous, mostly grasses and sedges	Herbs, shrubs or trees
Marphology	14- 11 (11) (11) (11) (11) (11)	
Leaf characters	Vascular bundle sheath present with cells packed with agranal chloroplasts	No vascular bundle sheath
Physiology		
Photosynthetic rate	40–80 mg $CO_2 dm^{-2} h^{-1}$ in full sunlight; no light saturation	10–35 mg CO ₂ dm ⁻² h ⁻¹ in full sunlight; light saturation at 10–25% full sunlight
Response to temperature	Growth and photosynthesis optimal at 30-45 °C	Growth and photosynthesis optimal at 10–25 °C
CO ₂ compensation point	0-10 ppm CO,	. 3070 ppm CO.
Sugar transport out of the leaves	Rapid and efficient	Slower and less efficient
Water requirements (g water needed to produce 1 g dry matter)	260-350	400-900
Biochemistry		
Carbon fixation	C ₄ (Hatch–Slack) and C ₃ (Calvin) cycles	C ₃ pathway only
Photorespiration	Not detected	Present





20 origins of C4 photosynthesis and one reversal to C3 photosynthesis in grasses Edwards E J, and Smith S A PNAS 2010;107:2532-2537



mean annual temperature (MAT), using values generated from 1,146,612 geo-referenced herbarium specimens.

Edwards E J , and Smith S A PNAS 2010;107:2532-2537



Composition of savanna vegetation in Guinea

Species



Grassland primary production: limited by rainfall



Figure 2.11 Plant biomass (above-ground, dry weight, in kilograms per hectare) in grasslands in Namibia in relation to the annual precipitation (mm) (after Walter 1973 with kind



Anthropic grasslands C4 grasses (*Imperata*...)

maintained by fire

productive, but biological desert



Savanna vegetation is shaped by fires



Removal of plant primary production in savanna: fire, grazing ungulates and detritivore

Table 3.12 Annual production and removal of grasses in the Serengeti region of Tanzania (after Sinclair, 1975)

	Long grassland	Short grassland	Kopjes
	kg ha ⁻¹ yr ⁻¹ (%)	kg ha ⁻¹ yr ⁻¹ (%)	kg ha ⁻¹ yr ⁻¹ (%)
grass production	5978	4703	5978
ungulate consumption	1122 (18.8)	1597 (34.0)	122 (2.0)
small mammal consumption	69 (1.2)	4 (0.1)	259 (4.3)
grasshopper consumption	456 (7.6)	194 (4.1)	484 (8.1)
total animal consumption	1647 (27.6)	1795 (38.2)	865 (14.4)
removed by burning	3185 (53.3)	586 (12.5)	3430 (57.4)
removed by detritivores	1146 (19.2)	2322 (49.5)	1683 (28.2)

(Source: A. R. E. Sinclair, The resource limitation of trophic levels in tropical grassland ecosystems, Journal of Animal Ecology, 1975, 44, 516.)

Nitrogen in savanna: input through rain and bacterial fixation, loss through fire

Table 7.8. Nitrogen balances in two humid tropical savannas in South America, Central Venezuela (Trachypogon savanna) and in Africa, Ivory Coast. (Medina 1987, 1993)

	Venezuela (kg N ha ⁻¹ a	Ivory Coast a ⁻¹)
Input through rain Biological fixation	19 (inorganic 4.5)	2.6
Blue-green algae Rhizosphere association	1.4 - 2.5 9 - 12	0.7
Losses through fire	17 - 23	8.5
Balance	+4.9 to + 6.8	+1.0
	14.2 to 1 0.0	+1.0

Forests of South-East Asia and Australia



Lowland forests

. . Fig. 19.2 Remaining lowland propical forest in Malesia in the early 1980s. Based on Whitmore (1984b). The forest area shown is

mostly evergreen rain forest, but a small part consists of seasonal forest. In the first half of the nineteenth century the greater nart of the Malay Peninsula, Sumatera and Borneo, as well as New Guinea, was covered with tropical rain forest.

Montane forests



Forests on limestone outcrops



Fig. 10.16. Limestone outcrops which still carry their distinctive forest formation: in many places this has been altered by fire (often started by mineral prospectors). Rain-forest and monsoon-forest limestone are distinguished by the latter being enclosed by dotted lines. (Based on Whitmore, 1984b.)

Peat swamp forests (A) and freshwater swamp forests (B)



Fig. 10.18. (a) Peat swamp forest. The western stands, in Sumatra, Malaya and Borneo, have long been known but the full extent of those in west New Guinea was only discovered in 1982/83. Shallow peat lands are being developed for agriculture. Deep peat is likely to remain under forest, it is a valuable timber producing resource and has been heavily exploited in west Malesia, especially in Sarawak.

(b) Freshwater swamp forest and seasonal swamp forest formations. The extent in Sumatra, Kalimantan and west New Guinea has recently been accurately surveyed for the first time. Very substantial areas in the west have been converted to agricultural lands, especially wetland rice. Similar changes are planged for New Guinea.



Borneo: forest types



ieath	forest
190.0441	101.001



Montane forest

Lowiand dipterocarp



Forest on ultrabasic



Freshwater swamp forest



Peat swamp forest



Mangrove

Forest on limestone



Dipterocarp lowland forests - a SE Asian speciality





Fig. 77. Shorea falciferoides Foxw. a. Habit, b. leaf of seedling 1.2 m high, c. fruit, d. nut, all × § (a SAN 37512, \$ 5718, c-d \$ 2125).

37512, Fig. 41. Vatica umbonata (HOOK. f.) BURCK. a. Habit, x], b-c. young fruits, x], d. ripe fruit, lateral view, e. ditto, apical view, both nat. size (a SAN 68373, flowers from SAN 15367, b A 4743, c FRI 12496, d-e BRUN 933).



Dipterocarpus applanatus

Dipterocarpoideae - limited to SE Asia and New Guinea



Fig. 2. Range of the Dipterocarpaceae: Dipterocarpoideae (line and 2 fossil sites in E. Africa), Monotoideae (2 genera, Afro-Madagascan, interrupted line, dots Monotes, squares Marquesia), Pakaraimoideae (monotypic genus in northern South America).

Borneo - the center of species richness and endemism of dipterocarps



Fig. 3. Density map of Dipterocarpaceae in Malesia, total number of species in each island.

Fig. 4. Density map of *Dipterocarpaceae* in Malesia, segregated into endemics (above the hyphen) and non-endemics (below the hyphen).



Fig. 2.24. Profile showing mature (ends) and building phases of the lowland evergreen dipterocarp rain forest at Belalong, Brunei. Plot area 60×7.5 m, all trees over 4.5 m tall shown. (Ashton 1964 in Whitmore 1984a, Fig. 2.1; see latter for species names.)

Dipterocarps shown hatched; note how these still have tall, narrow, youthful monopodial crowns in the building phase, which change to sympodial, broader than deep, and with several large limbs in the mature phase.

Dipterocarps: the dominant component of lowland forests

Predominance of dipterocarps among the big trees in Sabah lowland rainforest. Source: Burgess 1961
New Guinea lowland forests [no dipterocarps, lower stature]



Lowland forest New Guinea:

canopy gap

understorey (with a BF JU student for scale)



Peat forests of Borneo

Peat and heath forests share many species (Borneo 25-70%, including *Shorea albida*, *Casuarina nobilis* etc.) and also conifers (*Agathis, Dacrydium, Podocarpus*); also supplementary means of obtaining nutrients (myrmecophily: *Hydnophytum*, insectivory: *Nepenthes, Drosera*) are common





Zones of the peat swamp forest in Borneo



Figure 33. Fair aware foreix is the deta of the Barlen River, waiting Barleo. Five segetation zones can be distinguished, each with its own farest type. The pooneit hype 64, found on the high central parts of raised bogs, occurs latter intent, Miter Whitnese 1984a.)



A tropical peatbog (Kauai, Hawaii Islands)

Heath forest (keranga) in Brunei



Fig. 15.9 Profile diagram of kerangas forest in Brunei, Borneo. The width is 18 m, the trees reach up to 20 m height (After Brünig in Whitmore 1975, p. 127; also includes a list of species)





Limestone forest

New Guinea

Borneo





Above-ground biomass t/ha

Species richness of different forest types

Dipterocarp	650
Heat	470
Limestone	380
Alluvial	250



Montane forests



Forest altitudinal zonation in Malesia

New Guinea, montane forest at 2,200 m asl





Mt. Wilhem, New Guinea

timber line at 3,600 m asl





Nypa fruticosa swamp



Monospecific sago swamps





Metroxylon sago - the sago palm





Sago production

today on Sepik river, New Guinea

in 1860 on Ceram Island

(Alfred Russel Wallace, The Malay Archipelago)



Sago: bon apetite!



Photo G. Weiblen



Sago proteins: in the form of cerambycid larvae





It is an extraordinary sight to witness a whole tree-trunk converted into food with so little labour and preparation. A good-sized tree will supply a man with food for a whole year. The labour to produce this is very moderate; <u>in ten days a man may produce food for the whole</u> <u>year</u>. The effect of this cheapness of food is decidedly prejudicial, for the inhabitants of the sago countries are never so well off as those where rice is cultivated.

The Malay Archipelago (1869) by Alfred Russell Wallace



Sago & fish subsistence:

a present-day hunter-gatherer societies

Mangrove forests



Mangrove (New Guinea) in low and high tide





Mangrove species: distinct zonation on the salinity gradient Australia



Figure 1.8. Schematic and generalized profile of a tidal flat in northeastern Australia (Queensland) to contrast zonation in a region of high rainfall with the region shown in Figure 1.7. The seaward zone is usually *Avicennia*. The salt flat in Figure 1.7 corresponds to the *Ceriops* zone in Figure 1.8. It is assumed that rainfall is the controlling factor, but site (like distance up river), latitude, tidal range, and substrate affect the zonation. Profiles similar to Figure 1.7 therefore can occur in eastern Australia in drier areas. (Courtesy of N. C. Duke)

Mangrove species: distinct zonation on the salinity gradient Malaysia



Figure 2.19 Longitudinal distribution of vegetation belts along the Sungei Sedili Besar, southern Peninsular Malaysia. Density of shading indicates frequency of occurrence, highest density suggests continuous occurrence. Transect length 35 km. (Modified from Corner, 1978). Reproduced by permission of Gardens Bulletin Singapore, published by Singapore Botanic Gardens.







Ceriops



Mangrove trees: leaves of uniform morphology

Figure 4.11. Mangrove leaf shape outlines to show uniform size and shape.

(D) Sonneratia: left, S. caseolaris; right, S. alba; (E) above, Xylocarpus mekongensis (one leaflet), Excoecaria agallocha; below, Lumnitzera racemosa, Laguncularia racemosa.

Mangrove trees: aerial roots of great morphological diversity







Avicennia breathing roots





Bruguiera "knee" roots



Rhizophora stilt roots

Lyn Webb photo, Queensland

Species richness of mangroves - the SE Asia peak







Niche occupation patterns in mangrove forests on two continents Figure 20.2 Distribution of mangrove taxa among categories of intertidal zone height (L, low; M, mid; H, high) and position within an estuary (D, downstream; I, intermediate; U, upstream) in the ACEP and IWP regions. Numbers of taxa per cell (1–6) are indicated by the sizes of the dots. Generalized taxa distributed in more than one category within each ecological axis are indicated by hatching. (Data from Duke 1993.)