Tropical forest succession

Primary succession

Krakatau: before
… and after 1883

Coastal primary succession on Krakatau Islands:

Simplified: alternative paths all start with *I. pes-caprae* but then include

(i) *Casuarina* as the final stage

(ii) *Casuarina*/*Terminalia* transitory & *Ficus pubinervis* the final stage

(iii) *Terminalia* & *Barringtonia* as the final stage

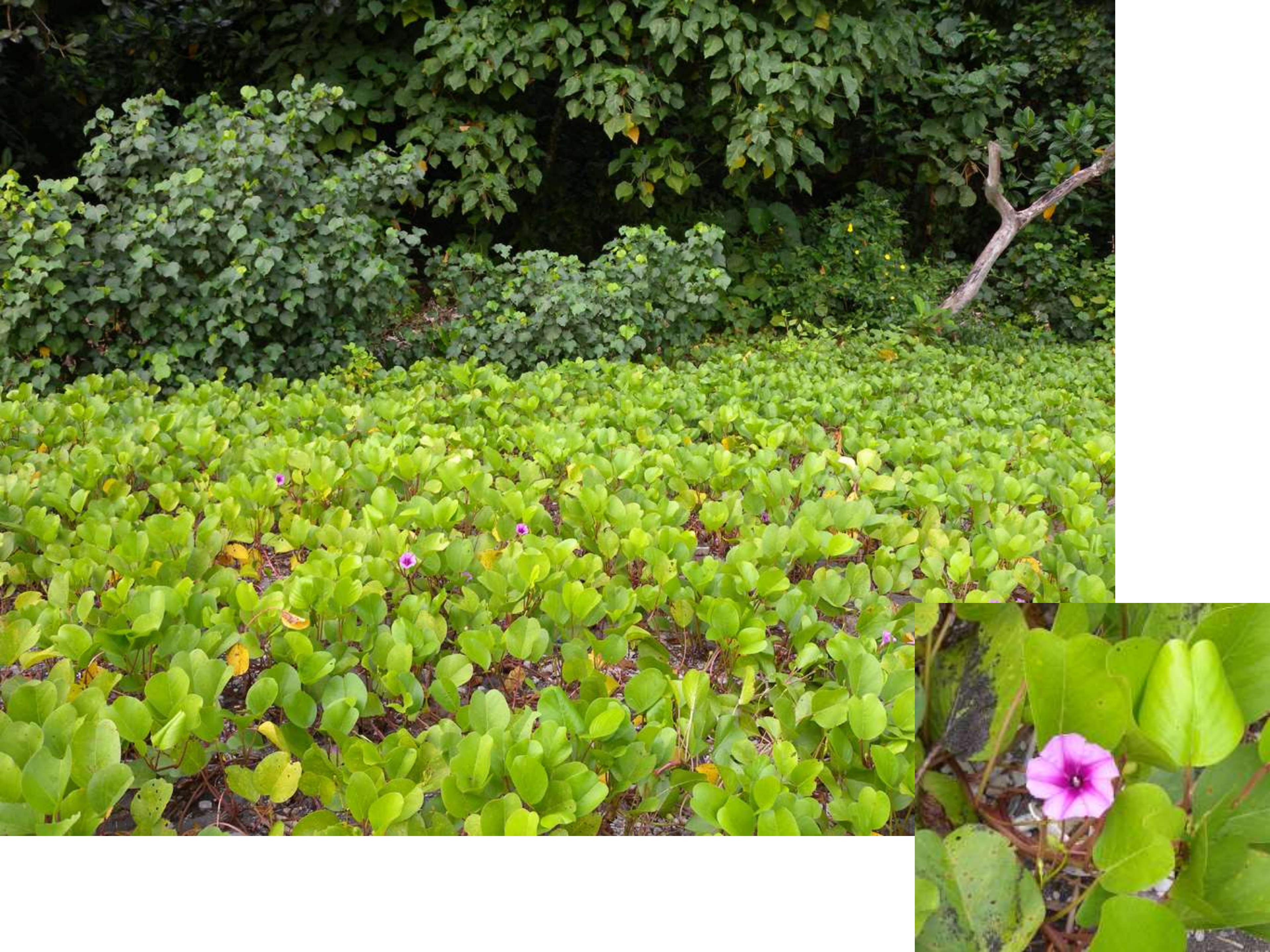
Terminalia

Casuarina

Ipomoea pes-caprae

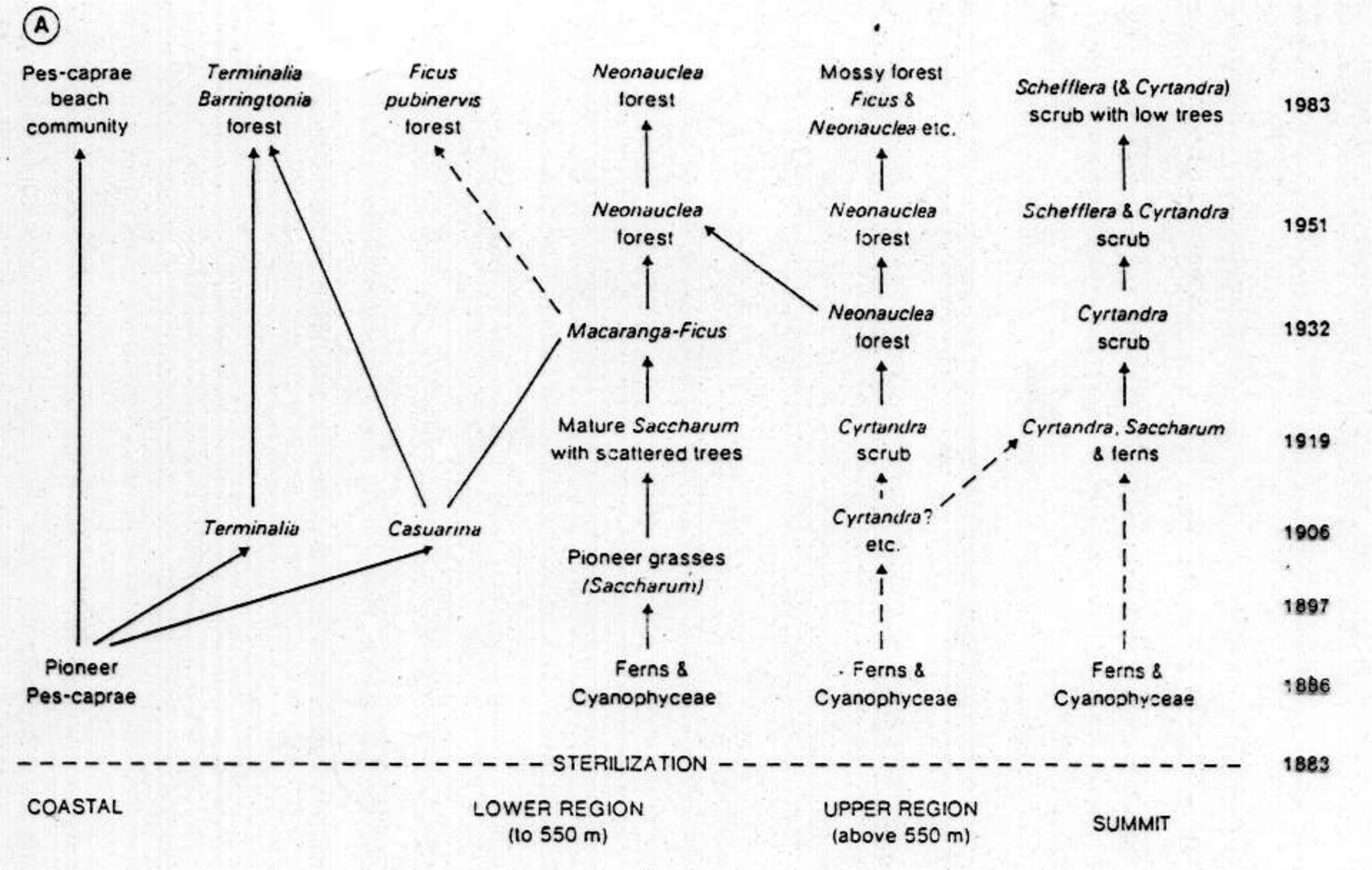
After Whittaker et al. 1989.

Note that the photos are illustrative of plant species, but are not from Krakatau Islands



After Whittaker et al. 1989.

Inland primary succession on Krakatau Islands:



Anak Krakatau island: succession is delayed

Casuarina coastal successional stage on Anak Krakatau




Hawaii Islands

Photo from 2000

Manam Island

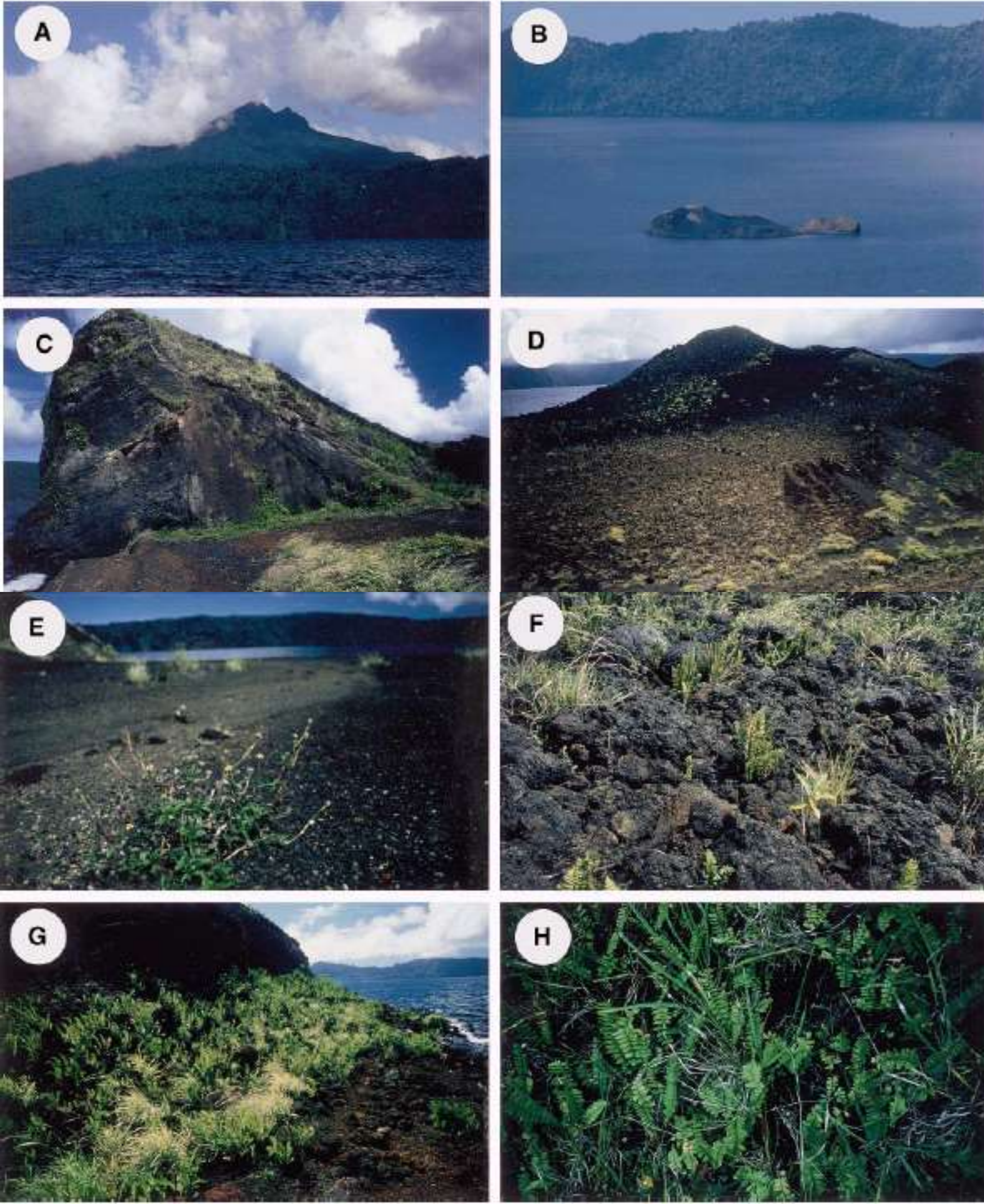
Manam island

Early primary succession on lava flows dominated by *Casuarina* and *Pandanus*

Long Island and Motmot: the case of nested islands

Around 1650s, the volcano caldera collapsed after a huge explosion (3-4 largest on Earth during past 2000 years), creating Lake Wisdom. In 1950s, a small volcanic Motmot island emerged from the lake. The succession was returned to the starting point during volcanic activity in 1968. Modern records of volcanic activity date from 1933, 1938, 1943, 1953, 1955, 1968, 1973, 1976 and 1993. Reports on the activity before 1930s survived only as folk legends, including a rather precise account of the 1650s explosion.

Primary succession Motmot Island



A: Cerisy Peak on Long Island

B: Motmot Island in the lake

C - H: The results of 50 years of primary succession: *Imperata cylindrica* grass (G), *Blechnum dentatum* fern (F, H), *Tridax procumbens* herb (E). *Cyperus polystachyos* (not shown) is also important early successional species on the island

From Thorton et al. 2001 J. Biogeogr .28:1311

(a) A rare view of Mt Cerisy as it emerges from cloud. (b): Motmot, as seen from the
ph is taken facing East, with Motmot's summit crater visible to the left and the south
the background. (c) Motmot's south ridge, looking South from the Eastern stepped
the top. (d) View looking northwards down the length of Motmot from the top of the
ca (L) Beauv. (Poaceae) can be seen amongst the scoria of the central hollow. (e) View
a [Fig. 2 (Habitat 2)], with Lake Wisdom and Long Island's caldera rim in the
ae). (f) Vegetation (conspicuous species include the grass, *Imperata cylindrica*; fern,
sapling, *Ficus wassa* Roxb.) established between large pieces of aa lava in the central

Karkar Island

30 yr old succession on a lava flow:
a closed forest rich in palms and vines

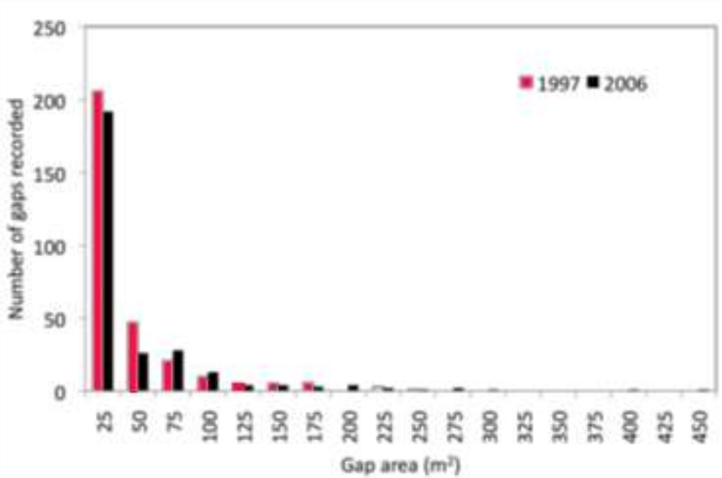
Secondary succession: forest regeneration in gaps

Dark understorey vs. enlightened canopy gap environment

Tropical forests are very dynamic:

gaps represent about 1% of the forest area which corresponds to 100 years of tree turnover

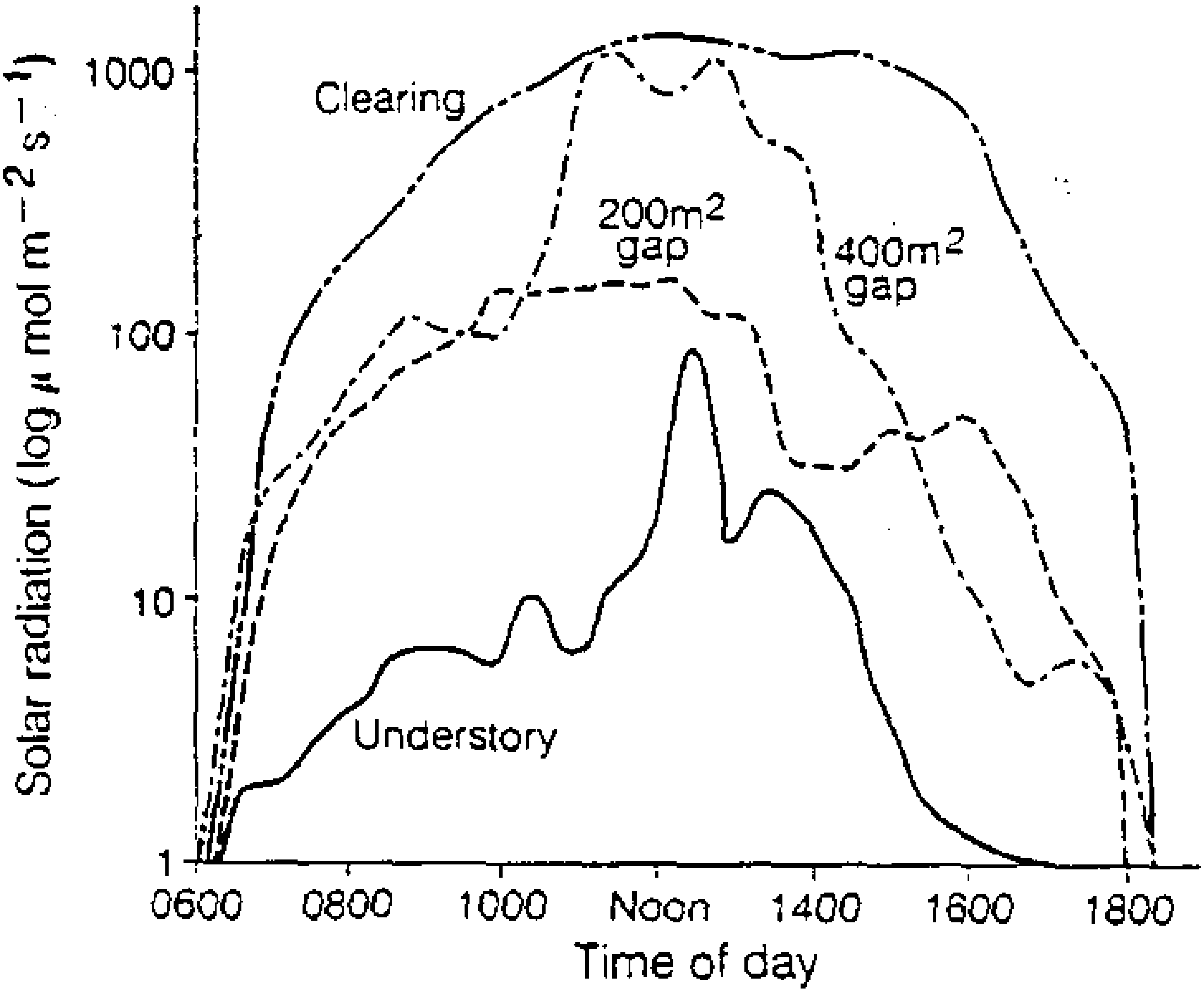
Site/country	Plot area (ha)	Time period (yrs)	Gap/yr (%)	Stand turnover (yrs)	Source
BCI, Panama					
young forest	14.6	3	0.63	159	Brokaw 1982a
young forest	1.5	10	0.73	137	Lang and Knight 1983
old forest	13.4	3	0.88	114	Brokaw 1982a
old forest	12.0	?	1.61	62	Foster and Brokaw 1982
La Selva, Costa Rica					
I (old terrace)	4.0	6	1.26	79	Hartshorn 1978
II (swamp)	2.0	5	0.84	119	Hartshorn 1978
II (upland)	2.0	5	0.73	137	Hartshorn 1978
III (hilly)	4.0	5	0.74	135	Hartshorn 1978
Palcazú, Peru	9.7	3	1.09	92	Hartshorn (unpubl. data)
San Carlos, Venezuela	1.0	5	0.96	104	Uhl and Murphy 1981



Gap sizes in 444 ha of lowland forest in La Selva

Size frequency distribution of canopy gaps in 444 hectares of old-growth forest at La Selva Biological Station. Gap sizes were determined by measuring canopy height at five-meter grid points using LiDAR imagery from 1997 and 2006. Source: Kellner et al. (2009).

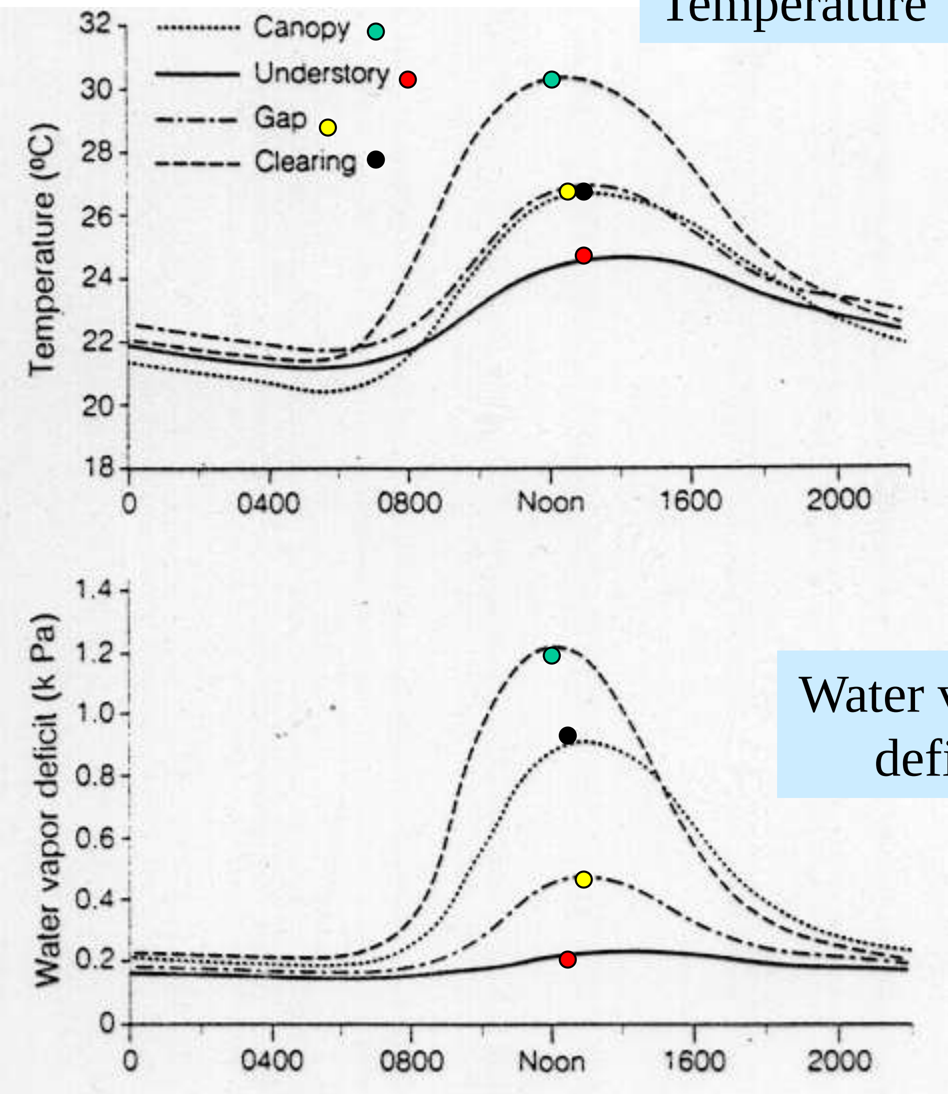
Solar radiation in the small and large canopy gap and the understorey



Abiotic conditions in canopy, canopy gap, and understorey

Temperature

Water vapour deficit



Light intensity

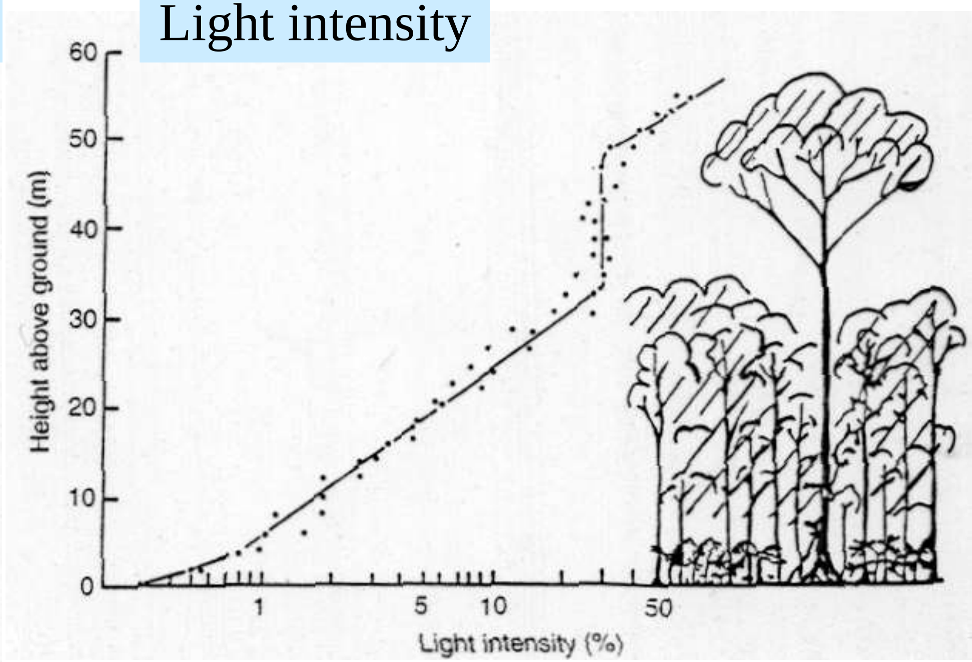
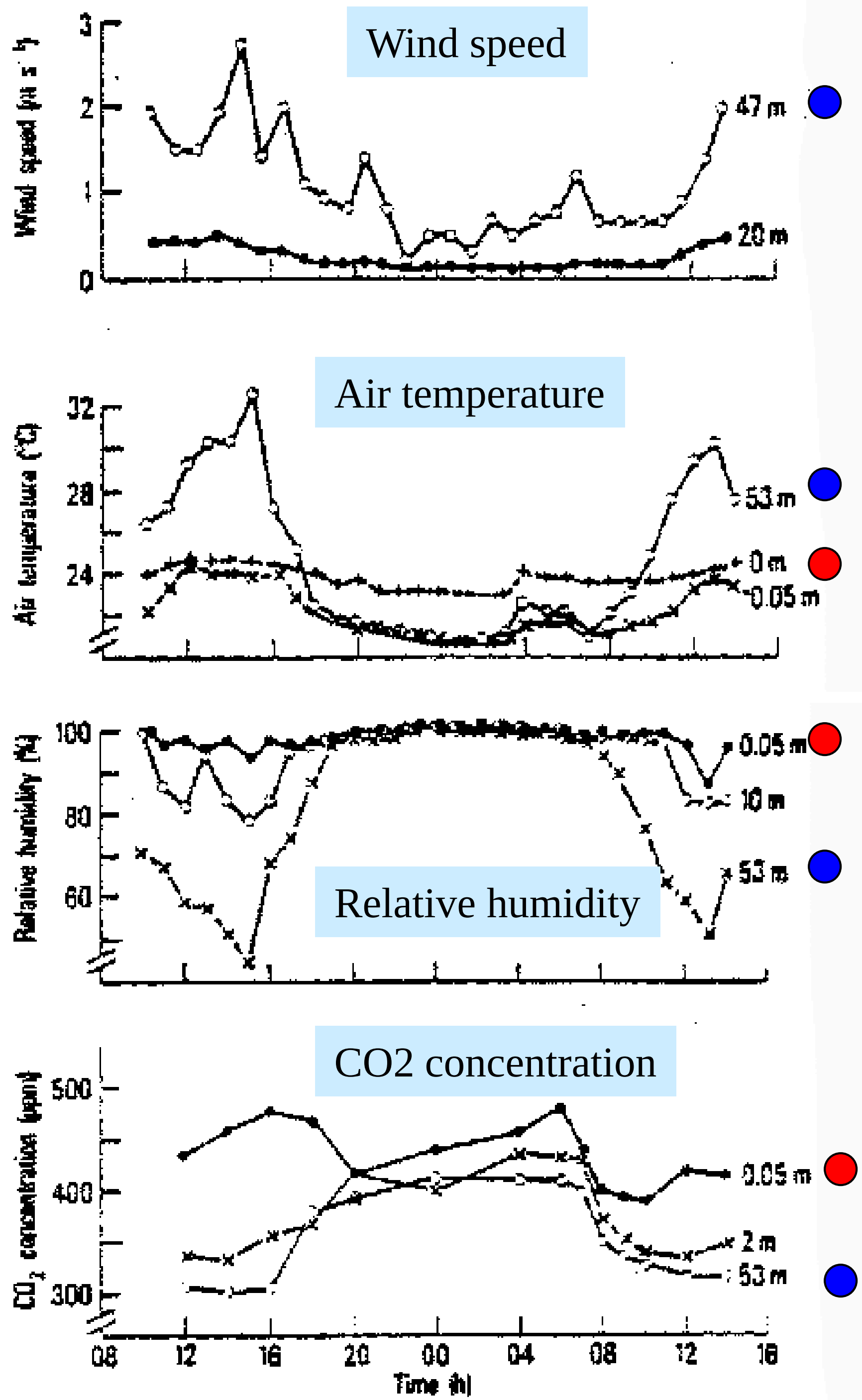


Figure 8.13 Intensity of light penetrating through the leaves of a tropical forest at various heights above the forest floor (after Kira 1978 with kind permission from Cambridge University Press).

Figure 2.41 Diurnal patterns of temperature and vapour pressure deficit in different environments within lowland tropical rain forest in Costa Rica. (After Fetcher *et al.*, 1985.) (Reproduced with permission from N. Fetcher, S. F. Oberbauer and B. R. Strain, Vegetation effects on microclimate in lowland tropical forest in Costa Rica, *International Journal of Biometeorology*, 1985, **29**, 147, 148.)

Diurnal variation in microclimate in forest gaps and canopy



canopy

understorey

Fig. 7.1. The microclimate above the forest canopy strongly differs from that at ground level as is shown here by the daily march of wind speed, air temperature, relative humidity, and CO_2 concentration at various canopy-levels in lowland rain forest at Pasoh, Malaya, 21–22 November 1973. Night time shaded. (After Aoki *et al.* 1978, in Whitmore 1984*a*, fig. 4.7.)

Gaps provide optimum environment for plant growth [high light levels, no competition from existing plants]

Plants have to maximise their growth to occupy gaps before anybody else does!

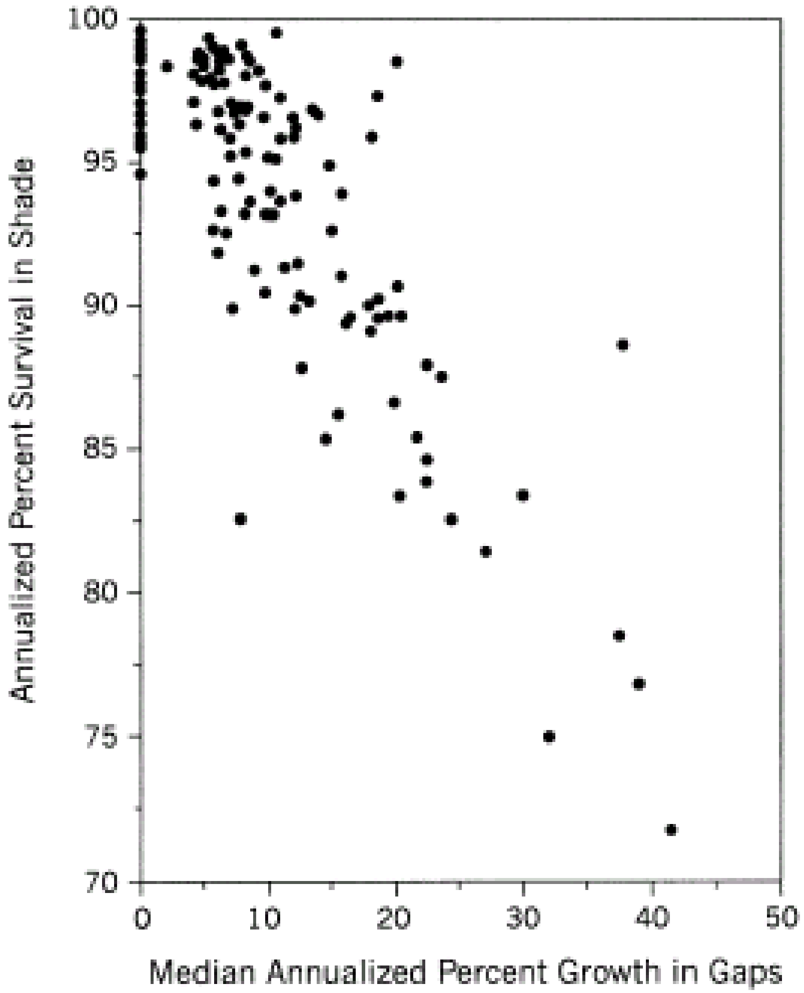


Fig. 3 The tradeoff between survivorship and growth for trees from BCI, Panama. The annual survival rate (*vertical axis*) is for saplings in the shaded understory. The annual growth rate (*horizontal axis*) is for saplings in tree fall gaps. Sapling d.b.h. was initially between 1 cm and 4 cm. Many slowly growing species have median growth rates of zero because d.b.h. was measured to the nearest 5 mm and slow growth was undetectable. Drawn from data in Welden et al. (1991) following Hubbell and Foster (1992)

Trade-off between:
growth in gaps
and
survival in shade

This means there have to be
disturbance-specialists
and
species avoiding disturbance

Trade-off between maximum growth rate and lifespan

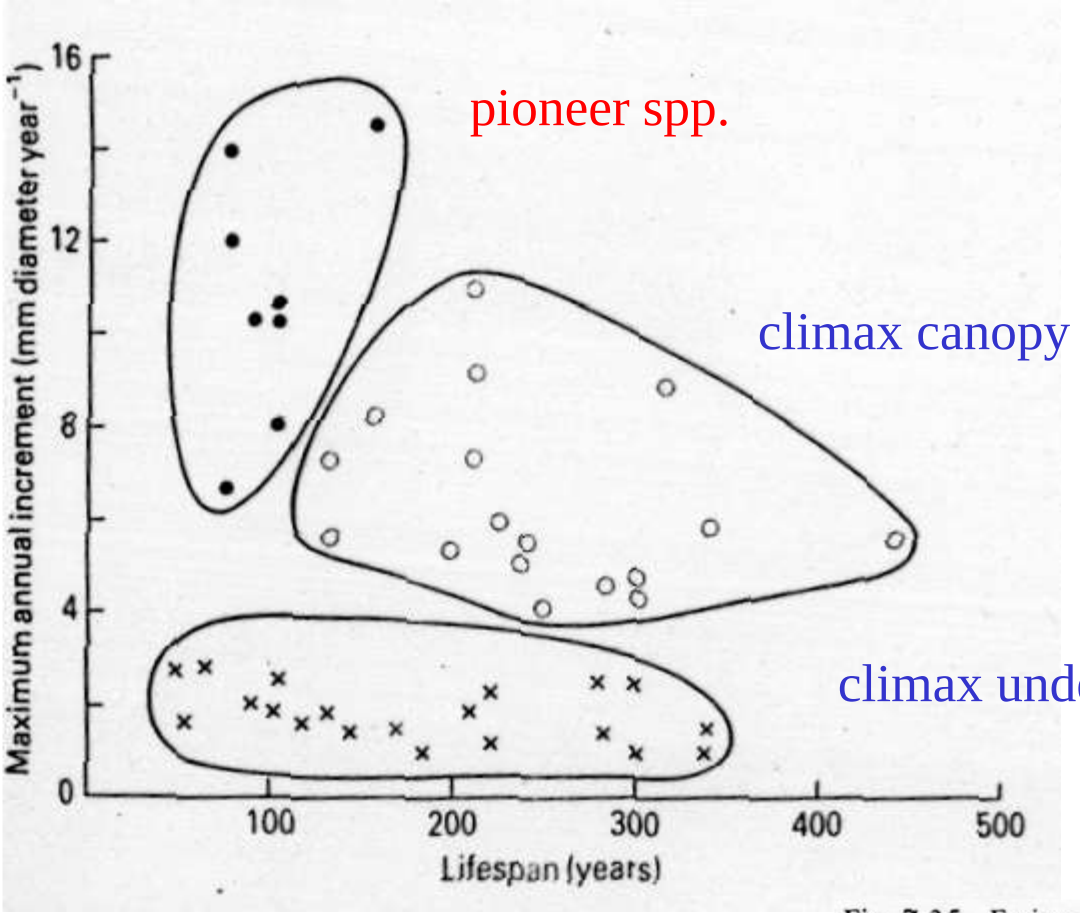
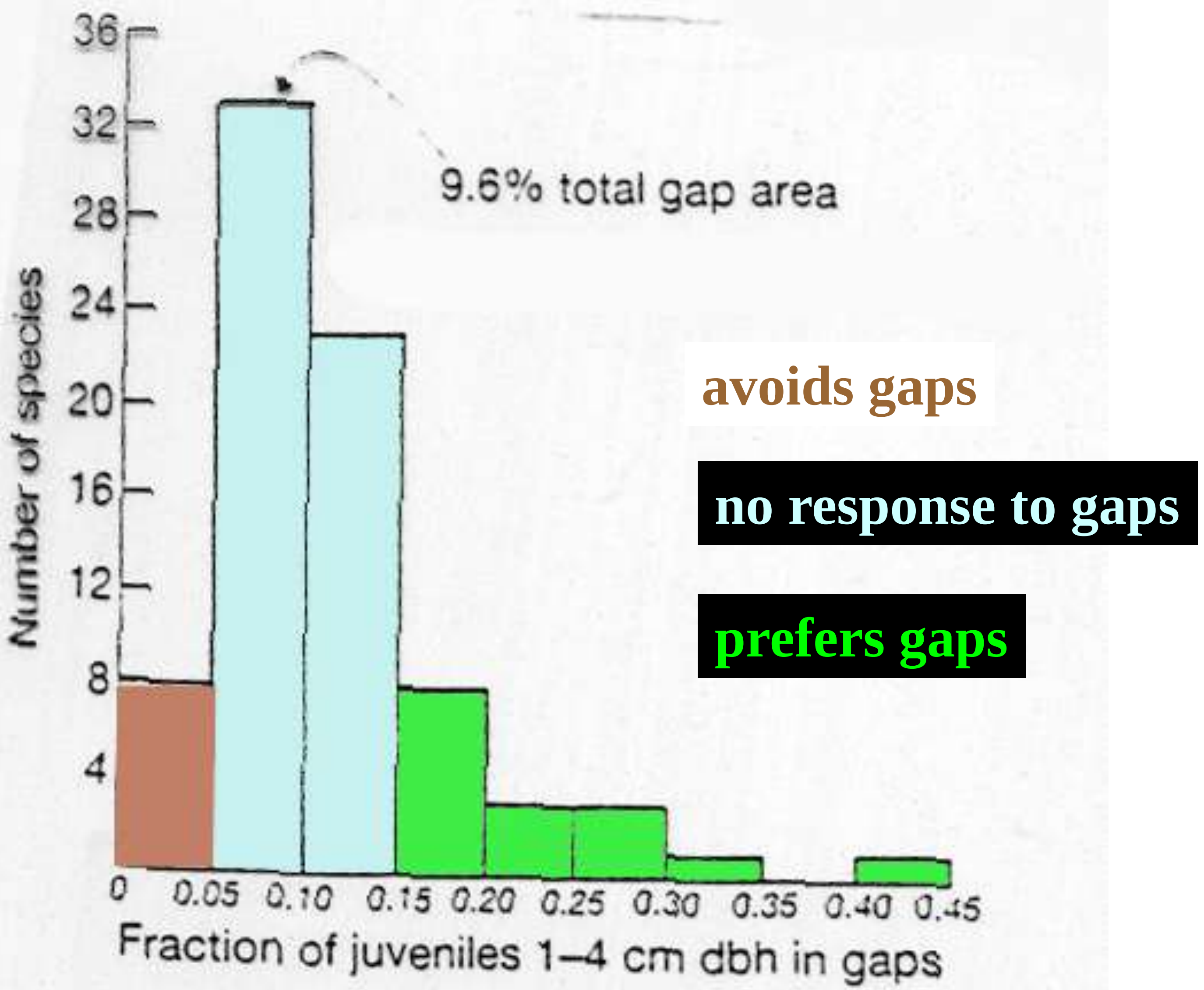


Fig. 7.35. Estimated life span and growth rate of the 46 common tree species at La Selva, Costa Rica. (Data of Lieberman *et al.* 1985.) X, Climax species with slow maximum growth rate, none reach the canopy top. ○, Climax species with medium to fast growth rate. Growth is stimulated by a canopy gap. Most reach the canopy top.
• Pioneer species, growth rate fast to very fast. All except the slowest-growing reach the canopy top.



Proportion of seedlings found in gaps for 81 canopy trees at BCI
The forest has 9.6% area in gaps, trees with similar proportion of seedlings in gaps thus show no response to gaps/understorey

Classification of forest trees by regeneration mode

Germination & establishment can take place:

<u>A. under closed canopy: climax, shade-tolerant, primary tree species</u>

Aa. Species able to grow long periods as juveniles under closed canopy [slow and consistent growth in shade, weak response to high light levels]

Ab. Species waiting in the understorey for a canopy opening [lack of growth and limited survival in shade, strong response to high light]

<u>B. only in high light: pioneer, large-gap, secondary tree species</u>

Ba. Species of small stature and short life span

Bb. Long-lived, large (often emergent) species

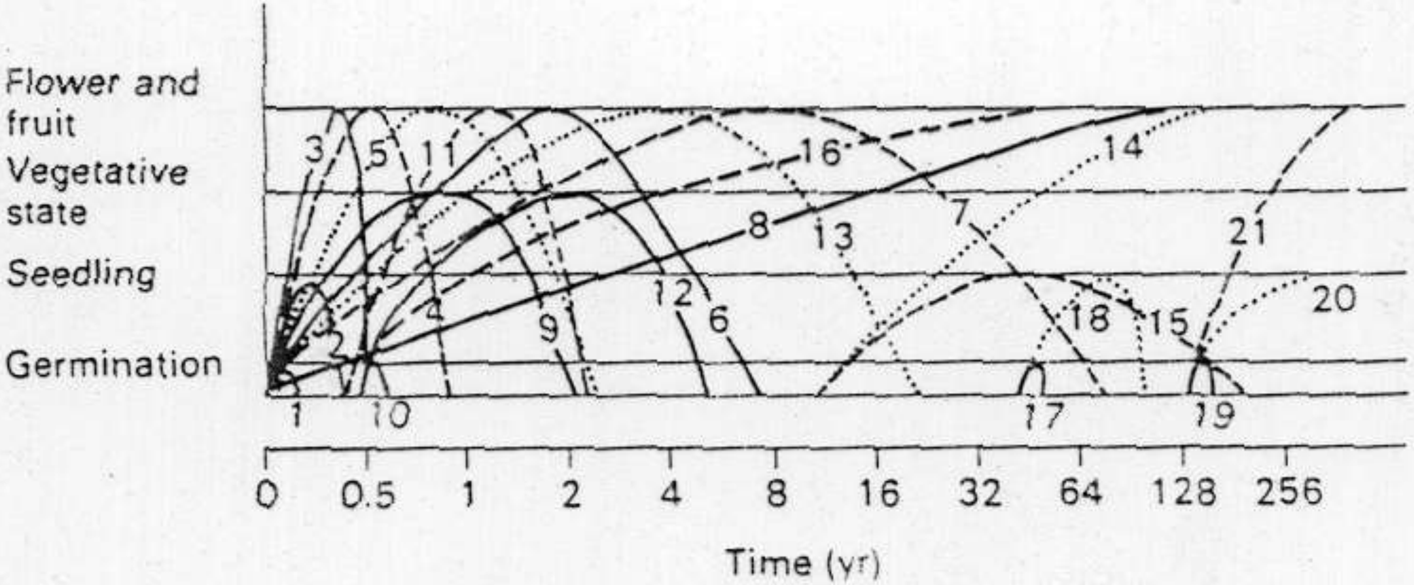


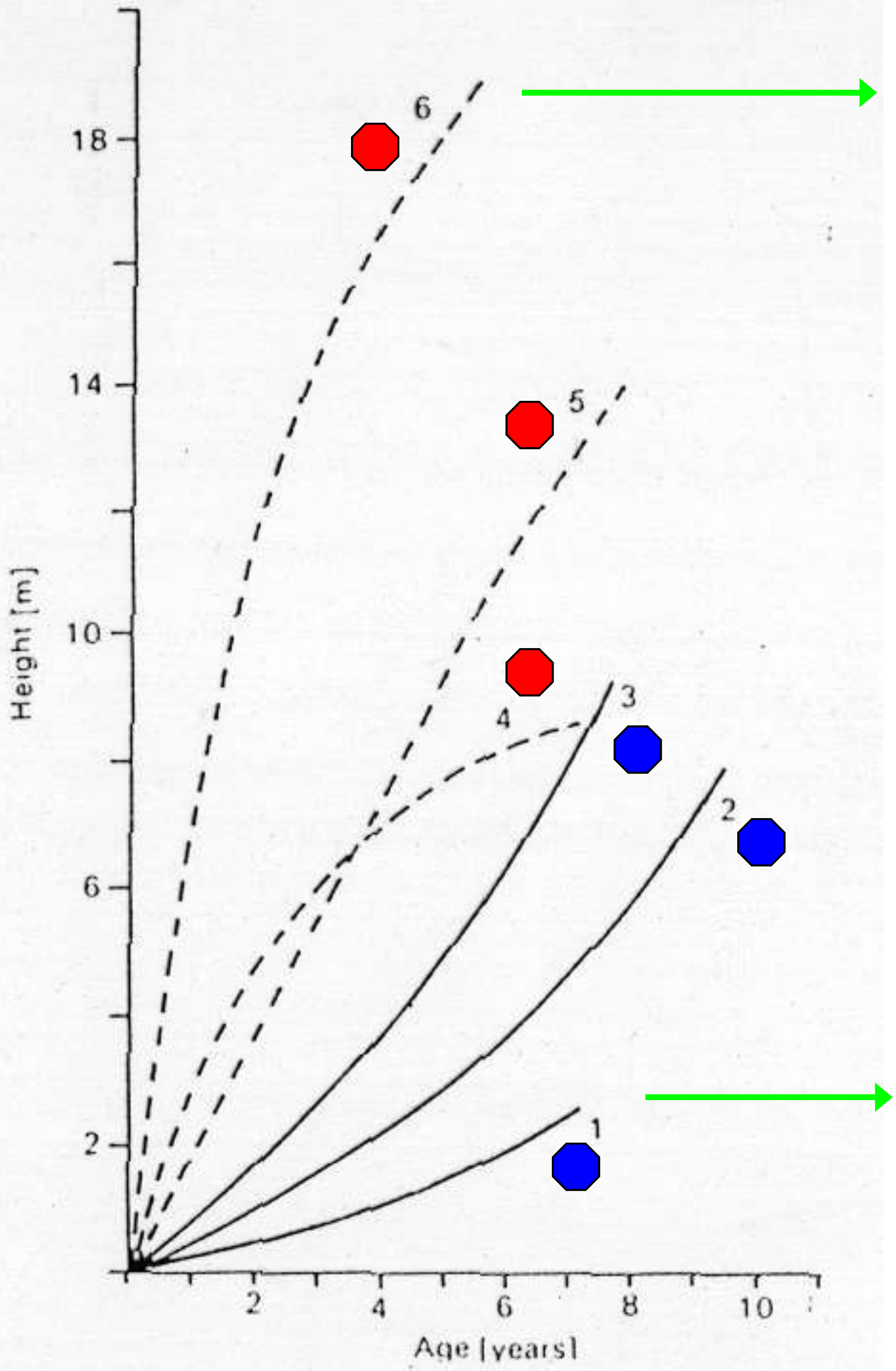
Fig. 6.15 Model showing differing patterns of *life-cycles* in tropical forests. 1 – germinate and die; 2 – germinate, form a few leaves, and die; 3 – finish life-span in months; 4 – *annuals*; 5 – biennials; 6 – life-span less than 10 yr; 7 – secondary, canopy; 8 – primary, canopy, prompt germination; *9 – vegetative only; 10 –* delayed germination and die; 11 – delayed germination, annual; 12 – delayed germination, vegetative *only; 13 – life-span less* than 30 yr; 14 – prolonged dormancy, long life-span; 15 – *prolonged dormancy, medium life-span; 16 – primary, canopy,* delayed germination; 17 – prolonged dormancy, germinate and *die; 18 – prolonged dormancy, remain as small plants; 19 – late* stage prompt germination and die; 20 – late stage prompt *germination, suppressed growth; 21 – late stage prompt ger*mination in gaps, primary, canopy. (After Gómez-Pompa *et al.* 1976.)

Life cycles
of tropical trees

Pioneer trees grow VERY fast

Homalantus novoguineensis
4 years after having been planted as a 1.5 m sapling (New Guinea)

Forest regeneration 8.5 years after cyclone "Agnes" in Queensland. Photo Len Webb



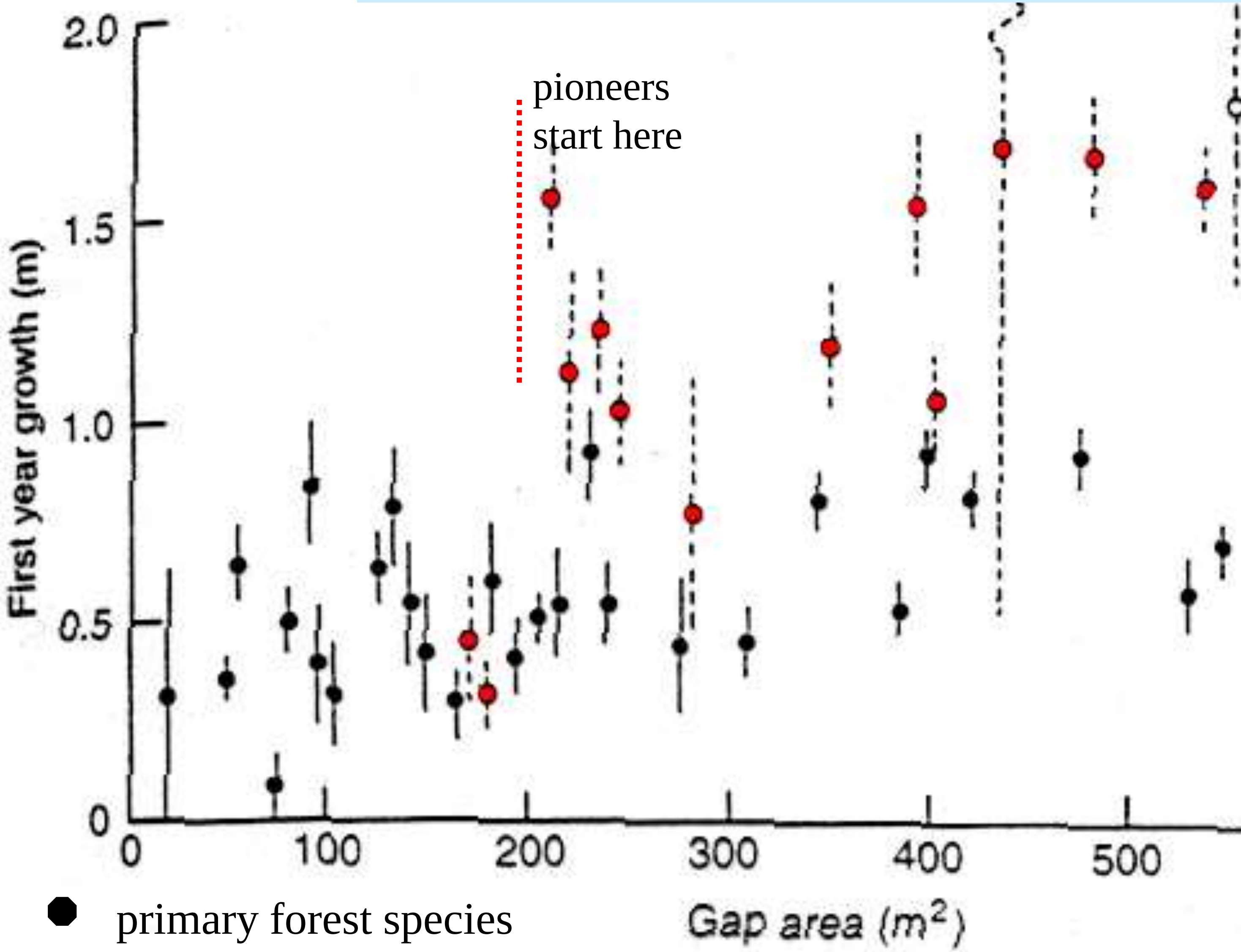
Height growth of young trees (Zaire)

primary forest spp.

pioneer spp.

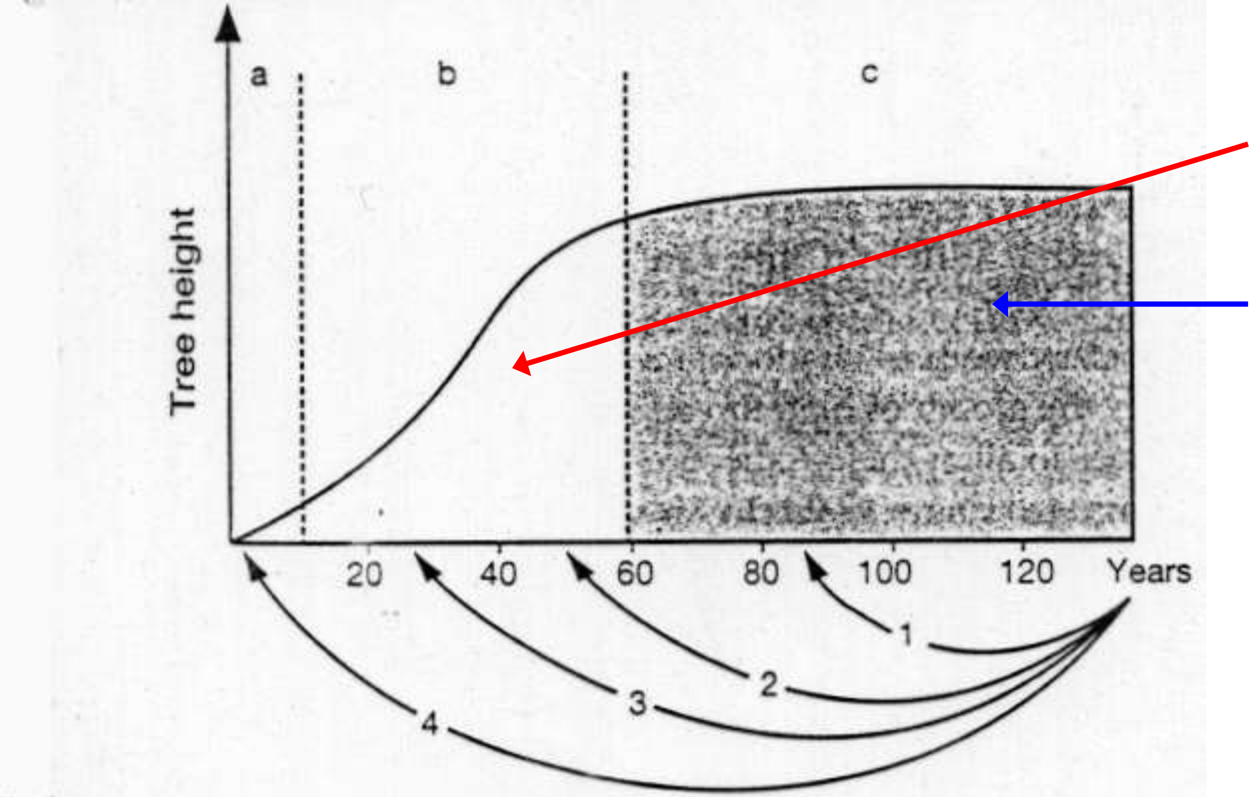
Fig. 18.10 Height growth under natural conditions of young trees in Zaïre. After Lebrun & Gilbert (1954). Continuous lines, primary forest species: 1 *Scorodophloeus zenkeri*, 2 *Oxystigma oxyphyllum*, 3 *Gilbertiodendron dewevrei*. Broken lines, seral (pioneer) species: 4 *Caloncoba welwitschii*, 5 *Terminalia superba*, 6 *Musanga cecropioides*.

Growth of pioneer and primary trees in gaps: pioneer trees need LARGE gaps



● primary forest species
● pioneer species

Figure 8.18 Height growth of pioneer (o) and primary species (•) versus gap area at 30 sites on Barro Colorado Island, Panama. The data represent the mean ± one standard error of the first year's recorded growth in height (after Brokaw 1985

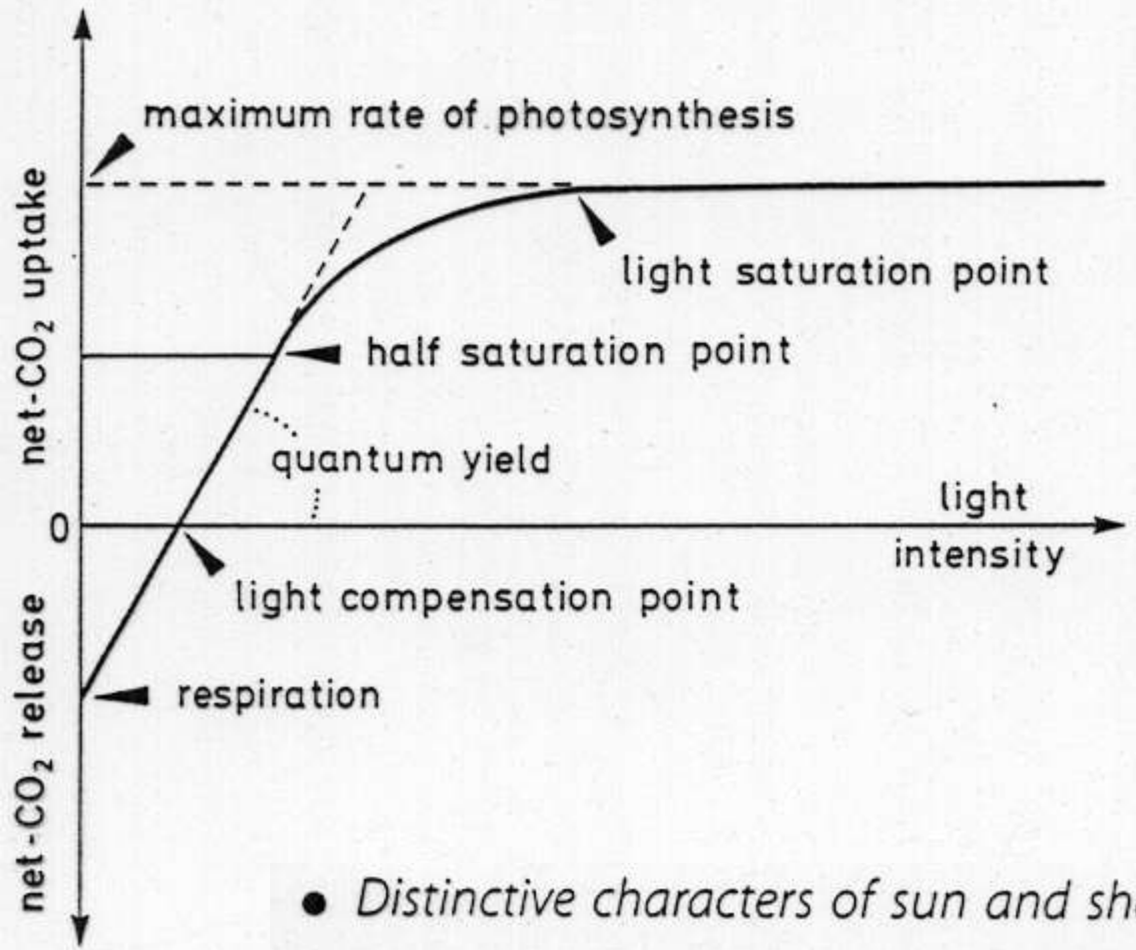


Small gap - regeneration of mature forest species
Large gap - invasion of pioneer species

Figure 4.10. The forest growth cycle is influenced by the size of gaps in the canopy. 1, 2 and 3 are short cycles due to the replacement of dead trees by young trees growing up to fill the gap. Large gaps allow the full forest growth cycle to occur as in the long cycle 4. **a** = pioneer species invade large gap, **b** = building phase, **c** = mature phase forest. (After Huc and Rosalina 1981.)

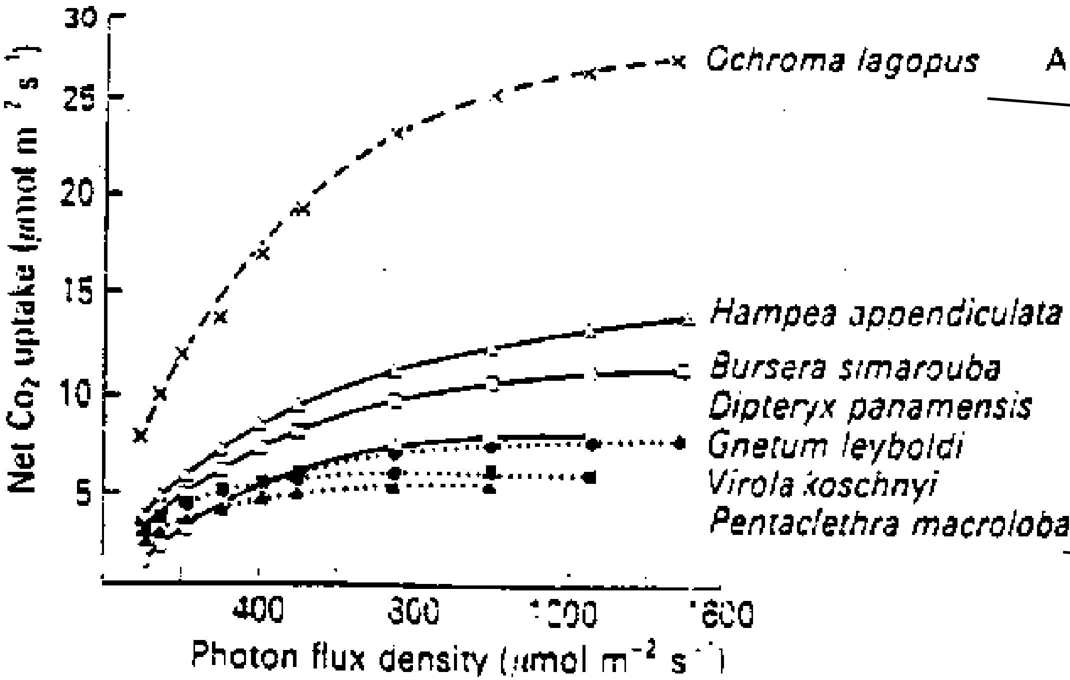
Succession and photosynthesis

- *Light-response curves and their cardinal points*



- *Distinctive characters of sun and shade plants*

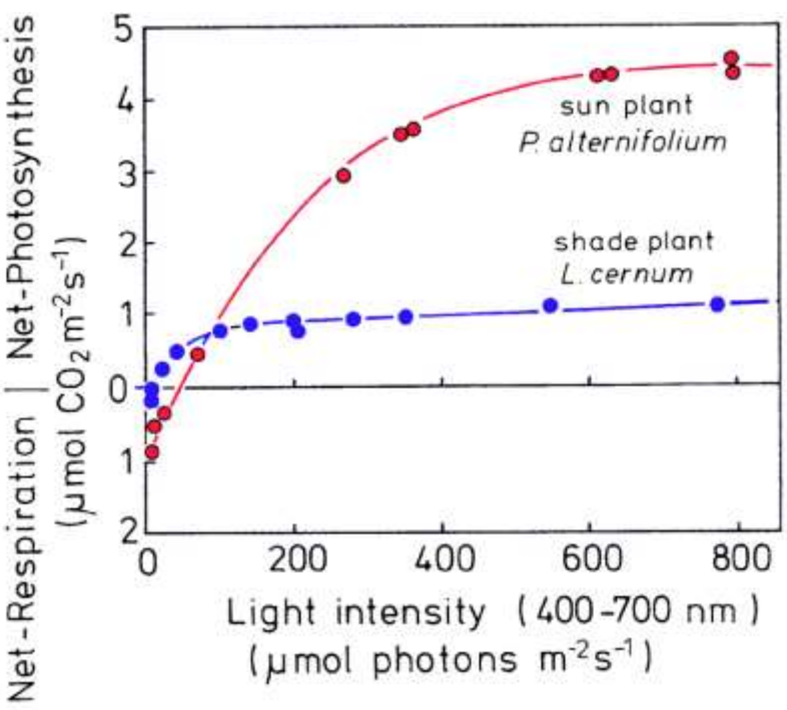
	shade plants	*sun plants*
respiration	low	high
light compensation point	low	high
half saturation point	low	high
light saturation point	low	high
maximum rate of photosynthesis	low	high



pioneer species

gap-dependent

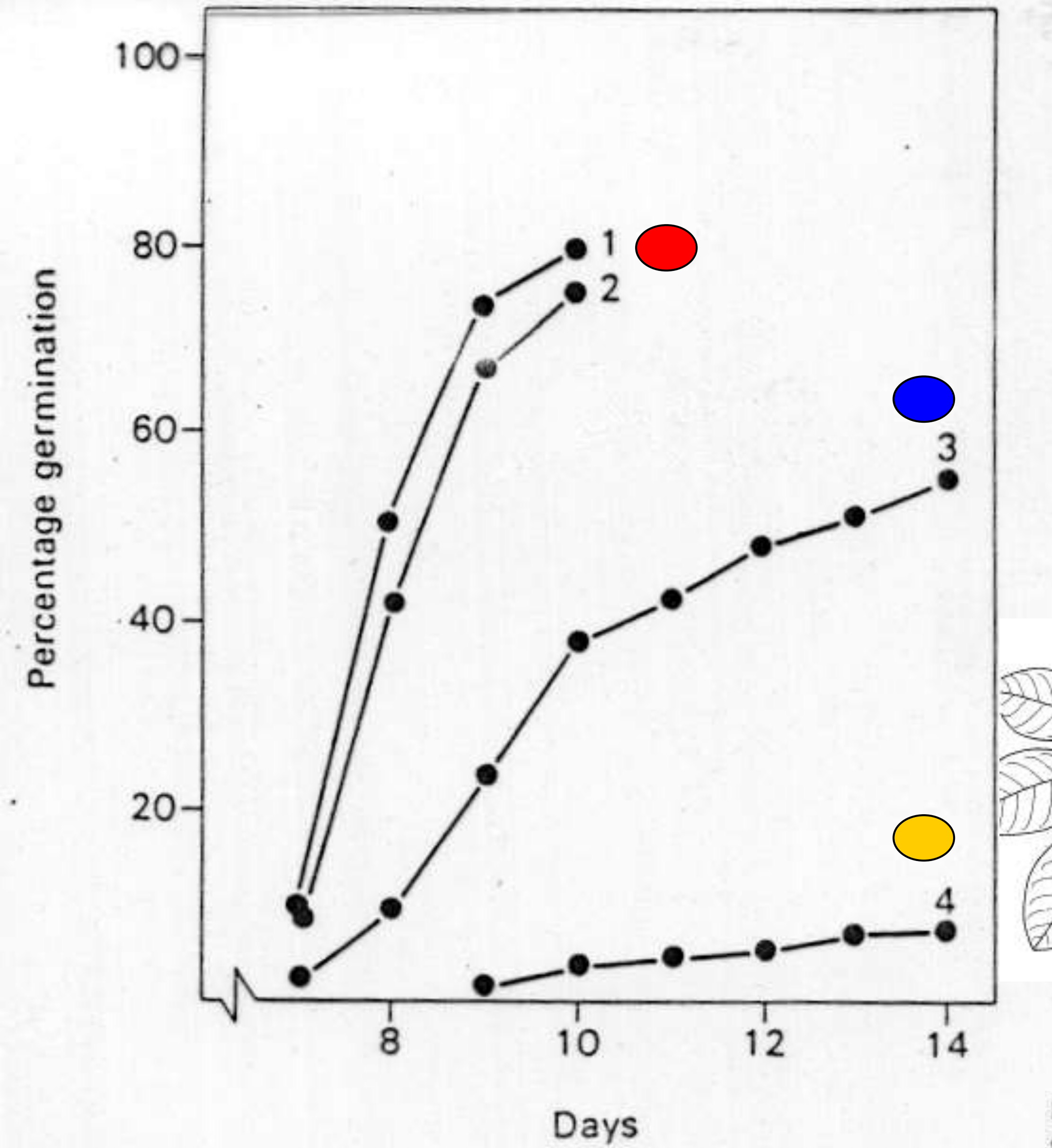
shade-tolerant



Photosynthesis saturation curves

Fig. 7.17. Photosynthesis rate of seven tree species at La Selva, Costa Rica. A, pioneer; B, gap-dependent; C, shade-tolerant canopy species. (After Oberbauer and Strain 1984, fig. 1.)

Rate of photosynthesis (measured as net CO_2 uptake) increases to an asymptote with increasing light. The maximum decreases with increasing species shade tolerance.



Cecropia obtusifolia germination in

centre of a canopy gap

close to the gap edge

edge of the gap

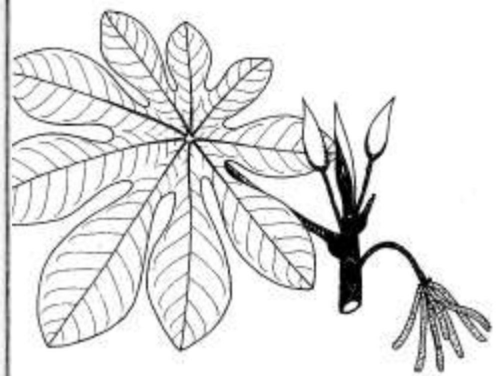


Fig. 3.4 Differential germination of light-sensitive *Cecropia obtusifolia* seeds placed in petri-dishes across a crown gap in a Mexican rain forest, caused by the fall of a 30 m *Spondias mombin* tree. Positions 1 and 2 near the centre of the gap; 3 and 4 progressively closer to the edge; 5–8 at the edge and inside the forest, where the low R/FR ratios kept all seeds dormant for the month's duration of the experiment. Total distance covered – 20 m. (After Vázquez-Yanes and Smith 1982.)

Solar radiation and pioneer tree germination in gap/understorey

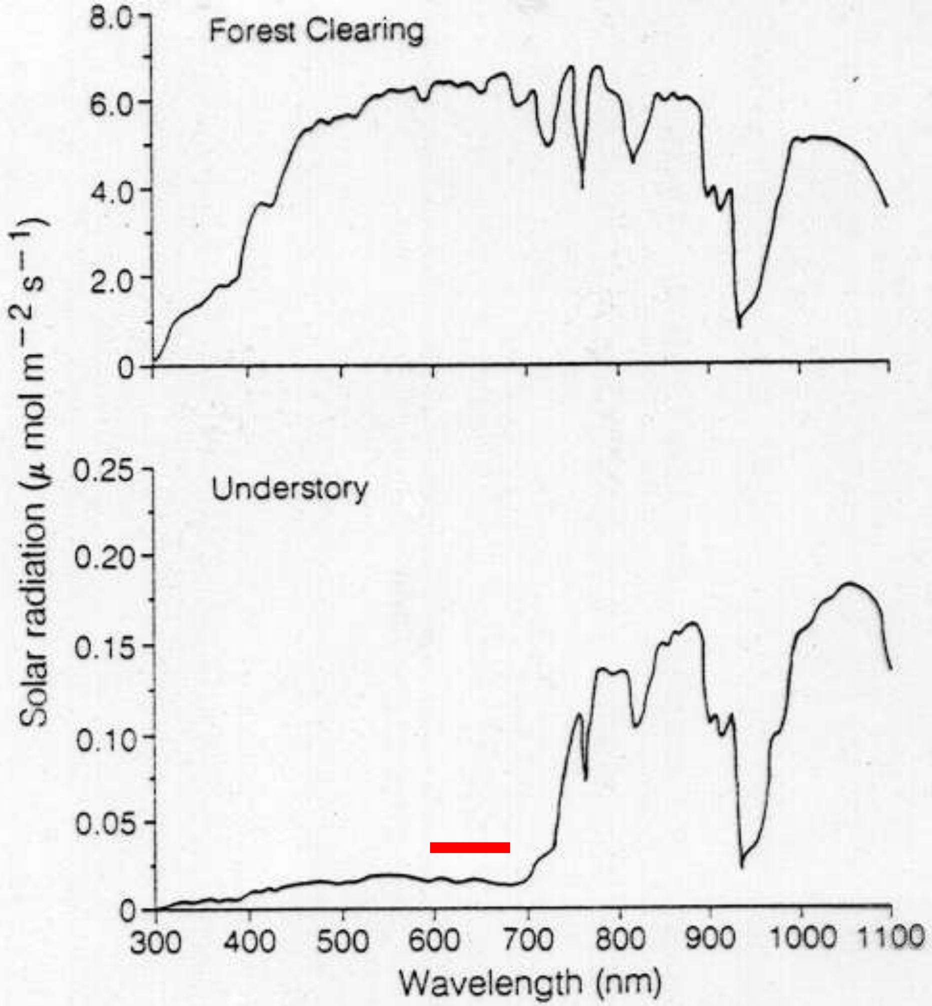


Figure 2.42 Spectral distribution of radiation in full sun, and beneath the rain forest canopy at Barro Colorado Island, Panama. (After Lee, 1987.) (Reproduced with permission from D. W. Lee, The spectral distribution of radiation in two neotropical rainforests, *Biotropica*, 1987, **19**(2), 163.)

Cecropis obtusifolia *Piper auritum*

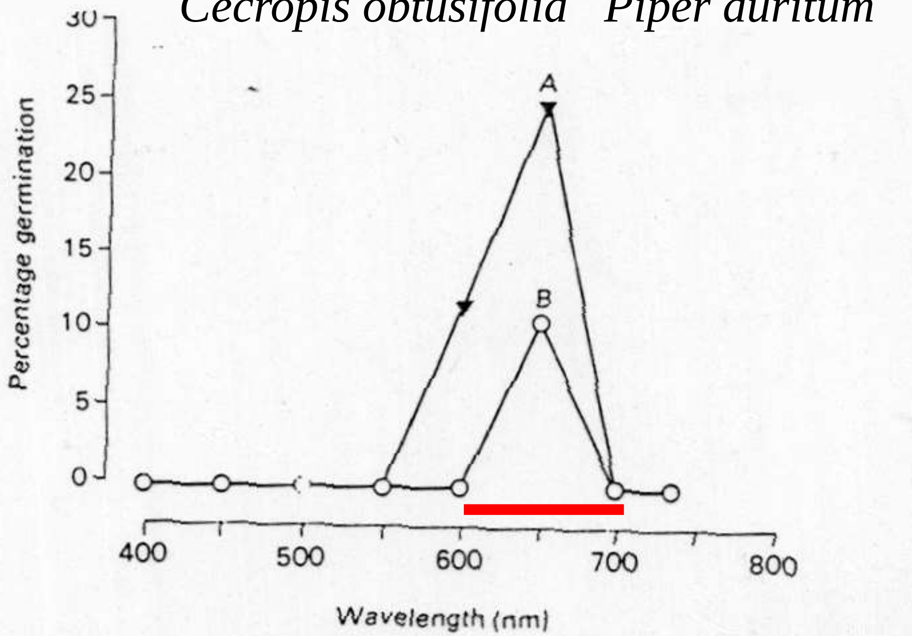
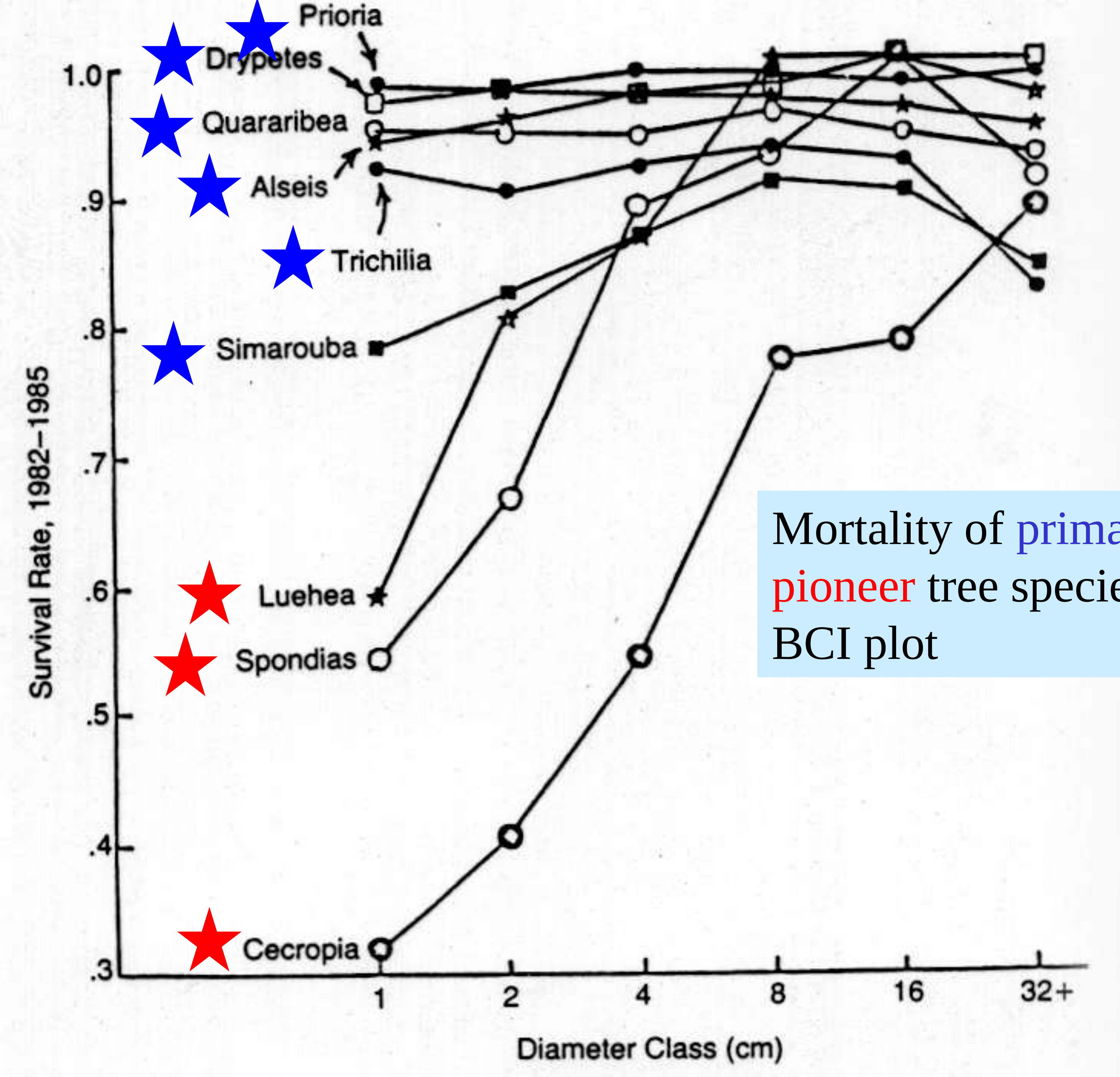
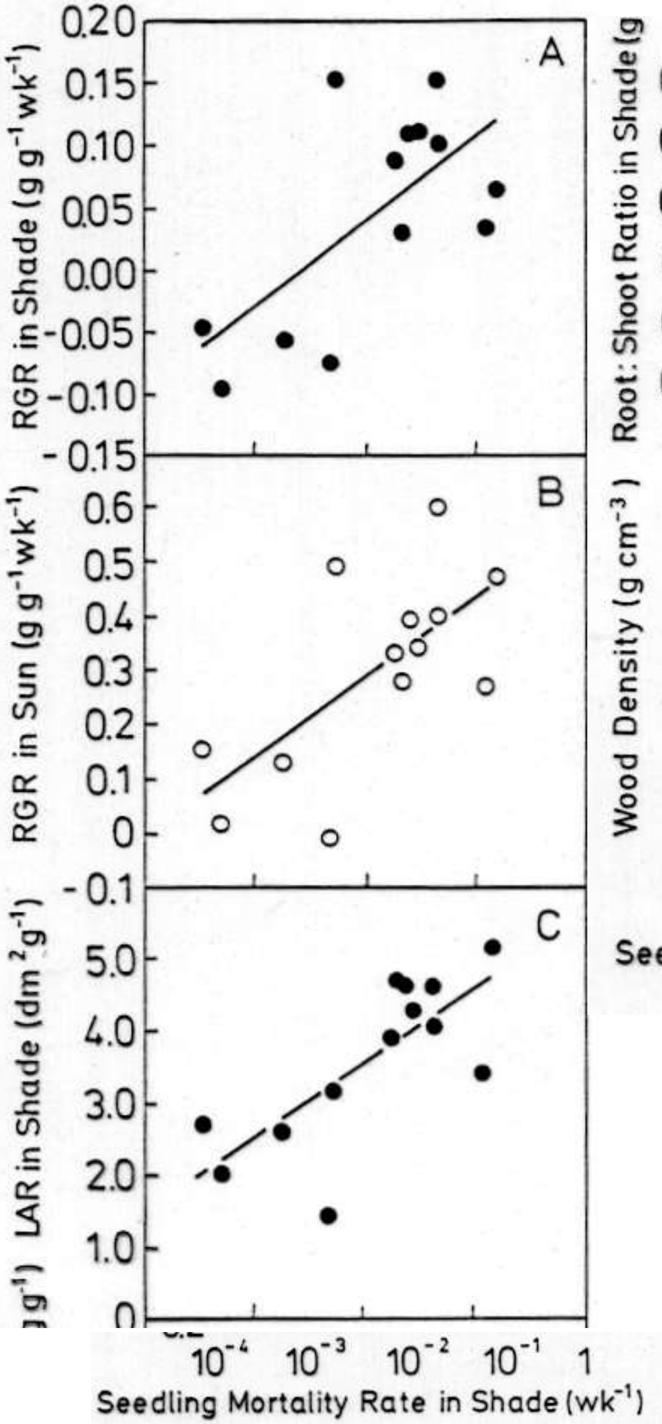


Fig. 5.33 Wavelength dependence of the breaking of seed dormancy by light, in (A) *Cecropia obtusifolia*; and (B) *Piper auritum*. Seeds were kept in the dark, except for 6 h irradiation at different wavelengths, and the final germination percentages were recorded after 1 month. (From Vázquez-Yanes and Smith 1982.)



Mortality of primary forest and pioneer tree species in the 50 ha BCI plot

Trade-offs between seedling mortality in shade and other life-history traits



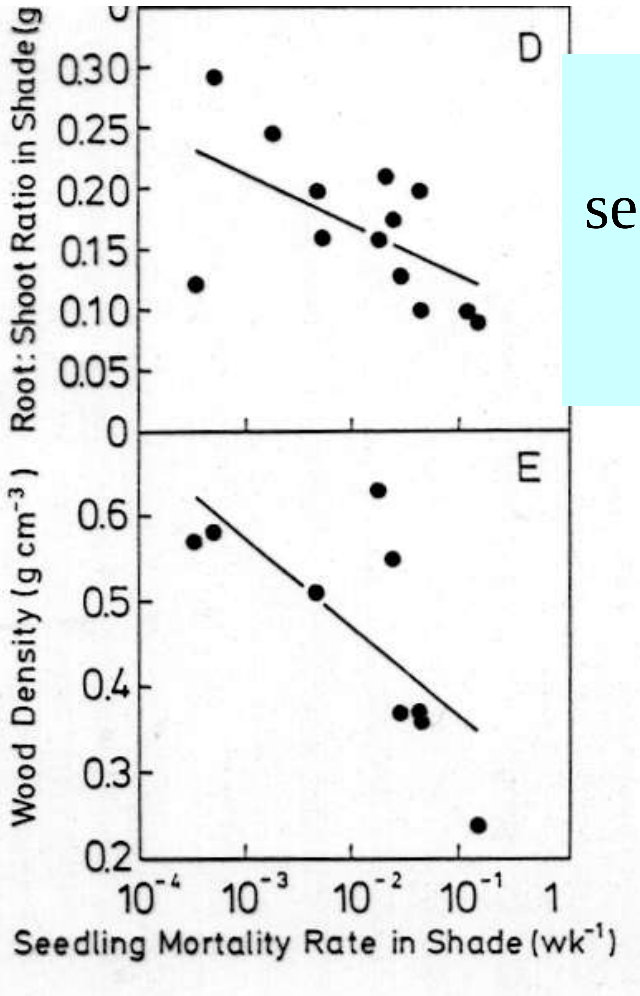


Fig. 3.30A-E.
Seedling mortality rate during the first year in the shade of 13 tropical tree species related to relative growth rate (RGR) in shade and sun (A, B), leaf area ratio (LAR) (C), root:shoot ratio (D) and wood density (E). (After Kitajima 1994)

Longevity of saplings in forest understorey (Barro Colorado)

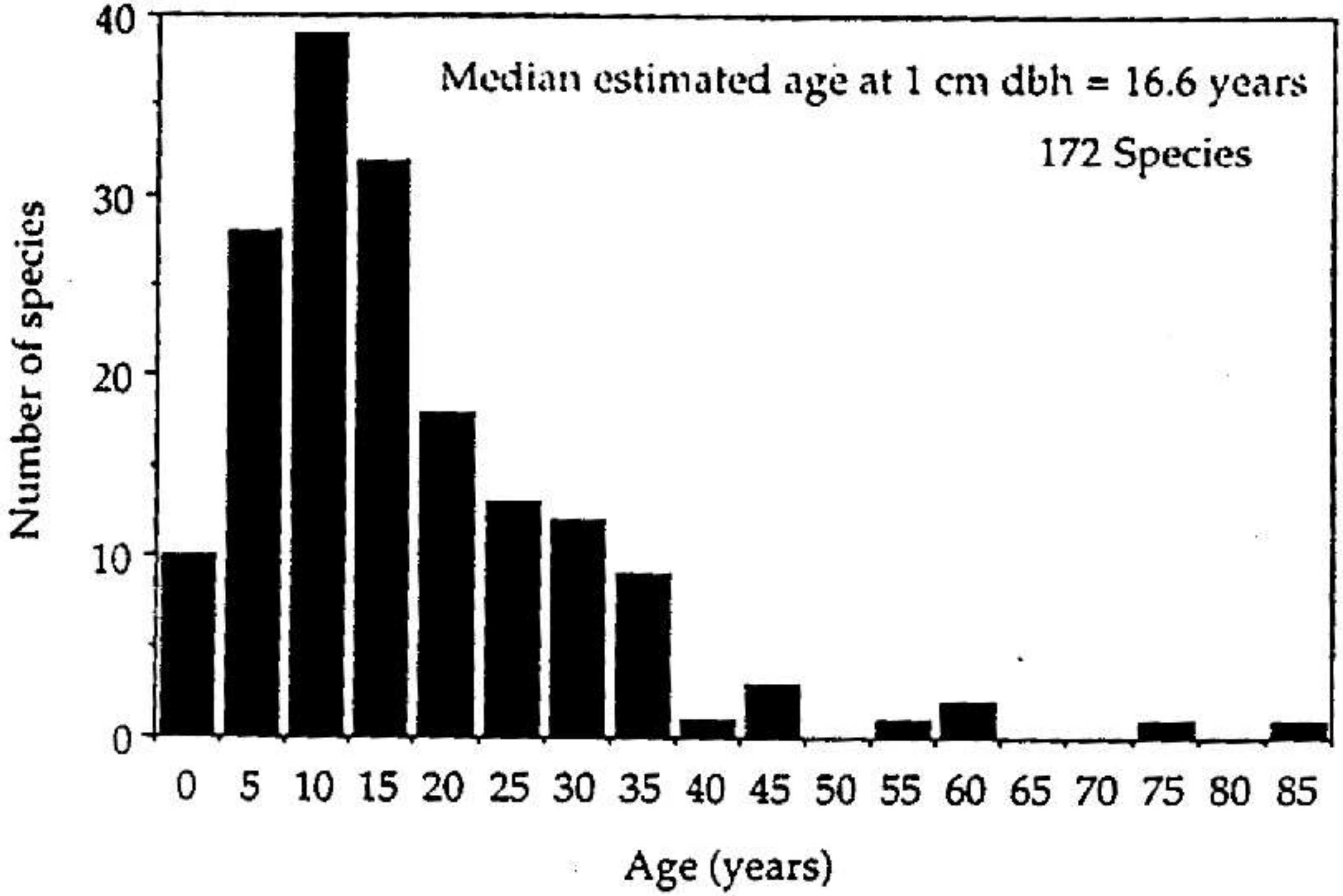


Figure 2.6 Distribution of estimated ages of saplings upon reaching 1 cm dbh for 172 BCI canopy trees, understory trees, treelets, and shrubs. (Ages are probably underestimated (see text)

Table 7.4 Some common rain forest pioneer tree species*

Stature	Neotropics	Africa†	Eastern tropics
Small, 2–7.9 m tall	*Cordia nitida* *Ocotea atirrensis* some *Piper* *Vernonia patens* *Vismia baccifera*	*Ficus capensis* *Leea guineensis* *Phyllanthus muellerianus* *Rauvolfia vomitoria*	*Commersonia bartramia* *Glochidion* spp. *Macaranga* >> 100 spp. some *Mallotus* spp. some *Melastoma* spp. *Phyllanthus* spp. *Pipturus* spp. *Trichospermum*, 8 spp.
Medium, 8–29 m tall	*Trema* *Alchornea triplinervia* *Cecropia*, c. 100 spp. *Cordia* spp. *Jacaranda copaia* *Muntingia calabura* *Ochroma lagopus* *Schefflera (Didymopanax) morototoni*	*Trema* *Anthocleista nobilis* *Psydrax arnoldiana* *Cleistopholis patens* *Macaranga* *Maesopsis eminii* *Musanga cecropioides* *Spathodea campanulata* *Vernonia conferta* *Vismia guineensis*	*Trema* *Acacia aulacocarpa* *Acacia mangium* *Adinandra dumosa* *Alphitonia petrei* *Anthocephalus*, 2 spp. few *Macaranga* spp. *Ploiarium alternifolium*
Large, > 30 m tall	*Ceiba pentandra* *Cedrelinga catenaeformis* *Goupia glabra* *Laetia procera*	*Aucoumea klaineana* *Ceiba pentandra* *Lophira alata* *Milicia excelsa* *Milicia regia* *Nauclea diderrichii* *Ricinodendron heudelotii* *Terminalia ivorensis* *Terminalia superba*	*Eucalyptus deglupta* *Octomeles Sumatrana* *Paraserianthes (Albizia) falcataria*

Trema orientalis, Ulmaceae, Africa, Asia

Ochroma pyramidale (balsa), Bombacaceae, America

Cecropia spp., Cecropiaceae, America

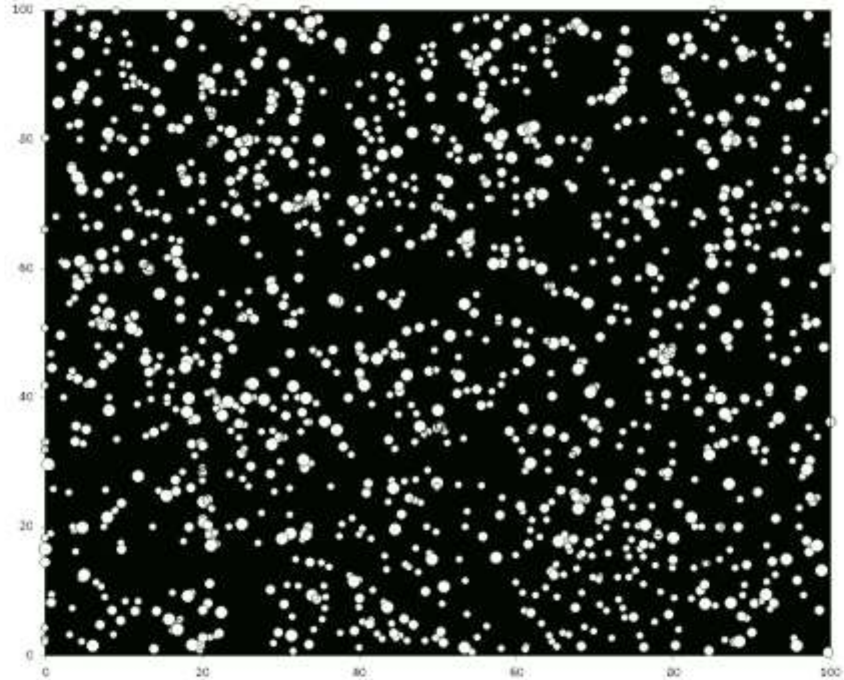
Macaranga spp., Euphorbiaceae, Asia, Australia (Africa)

Secondary forest regrowth
lowland New Guinea forest

Primary forest cleared in March 2006

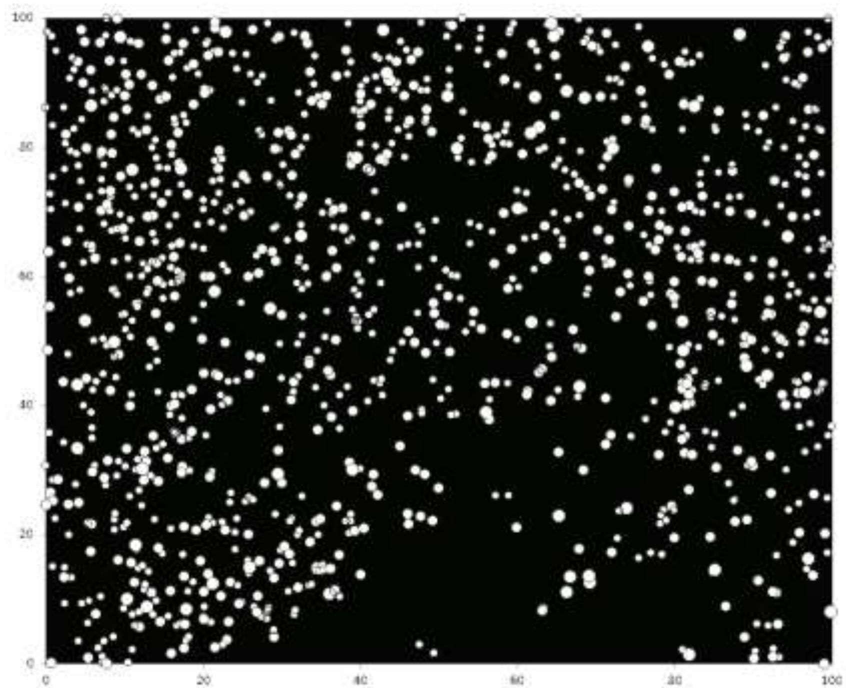
Secondary succession Aug 2008
[2 years 5 months old]

Secondary succession Aug 2011
[5 years 5 months old]



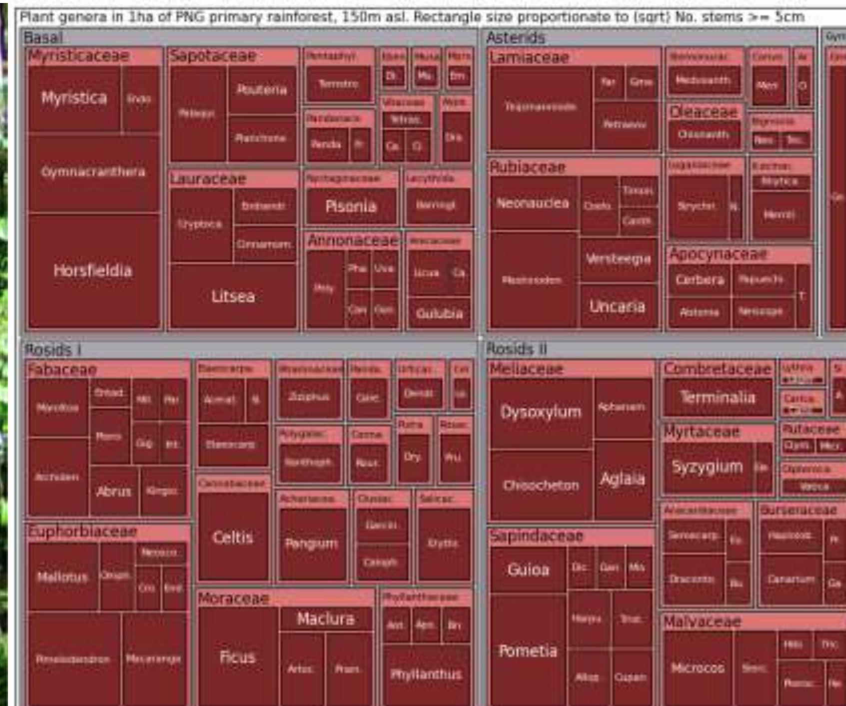
1 ha plots

primary



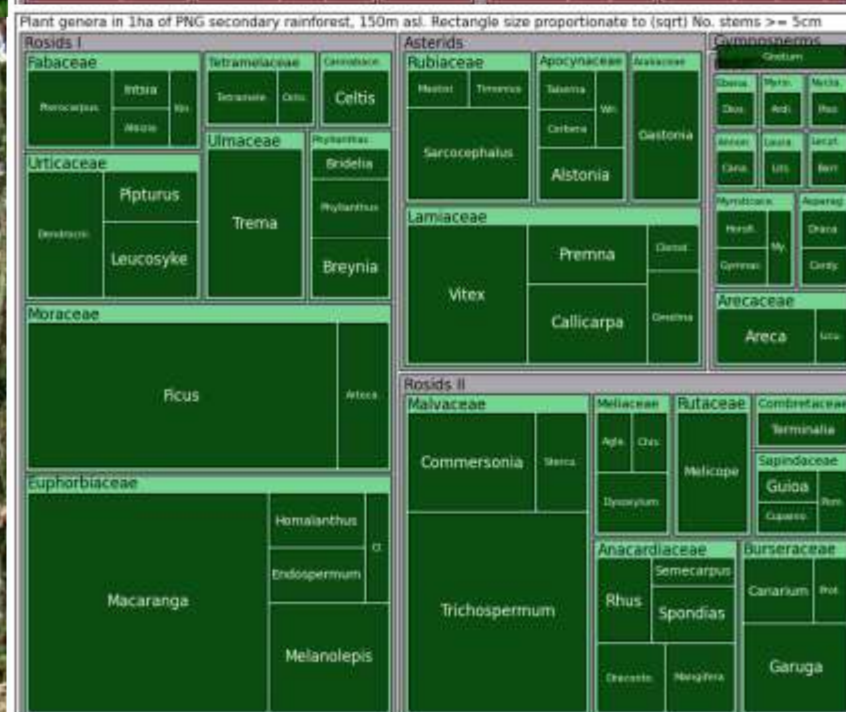
secondary

DBH
5-10
11-20
>20



1 ha plots

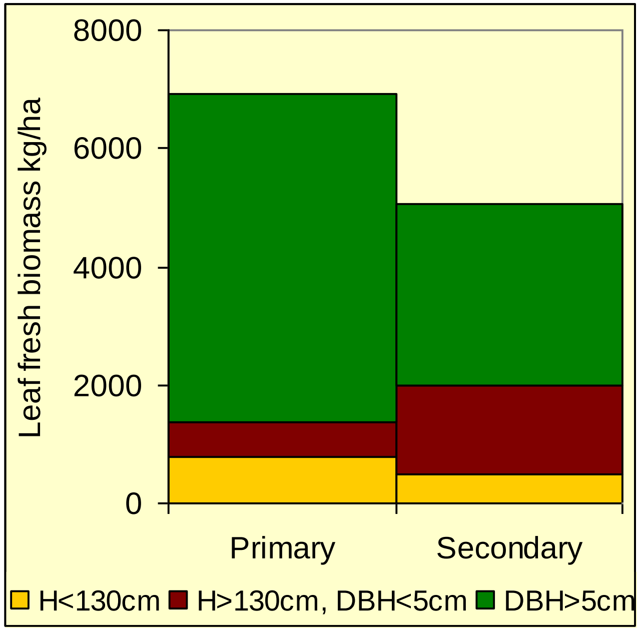
primary



secondary

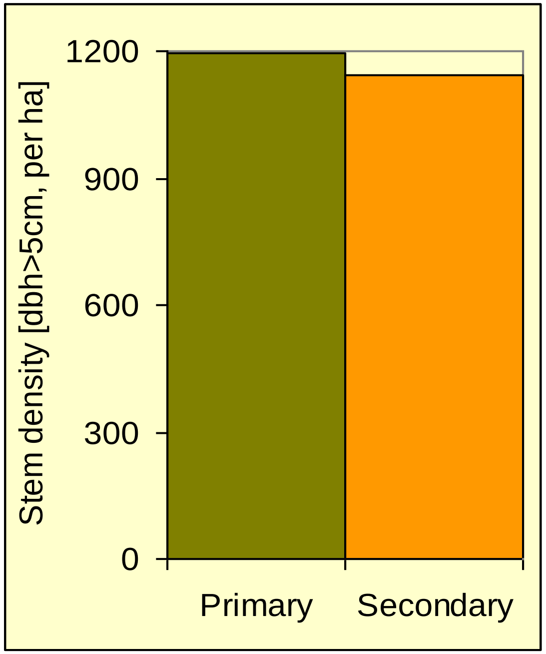
Secondary vs. primary forest structure

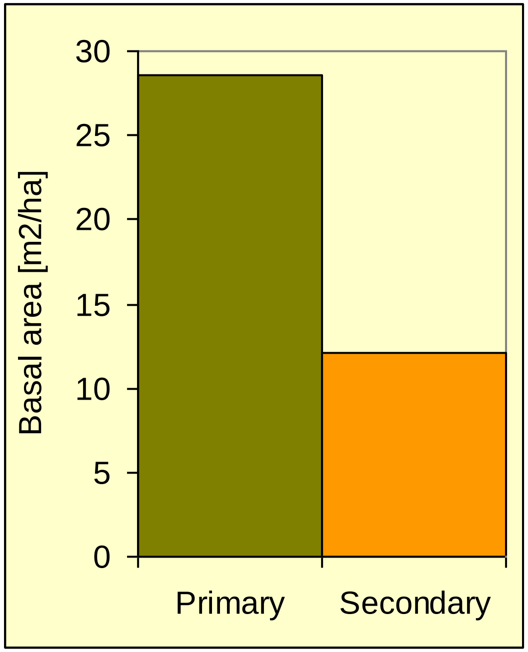
R. Montgomery et al.

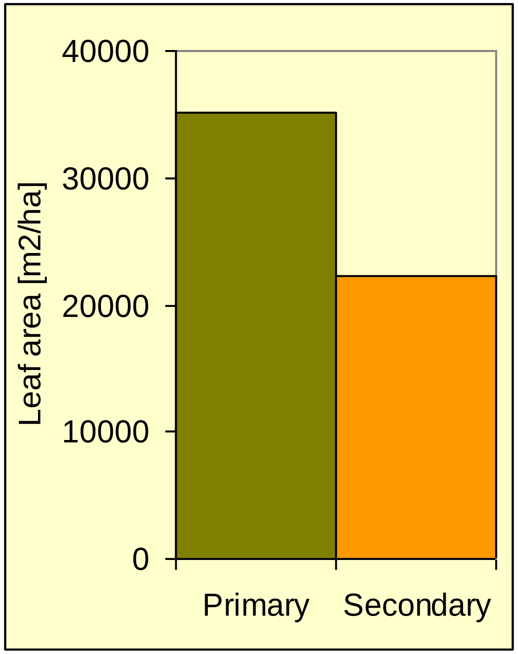


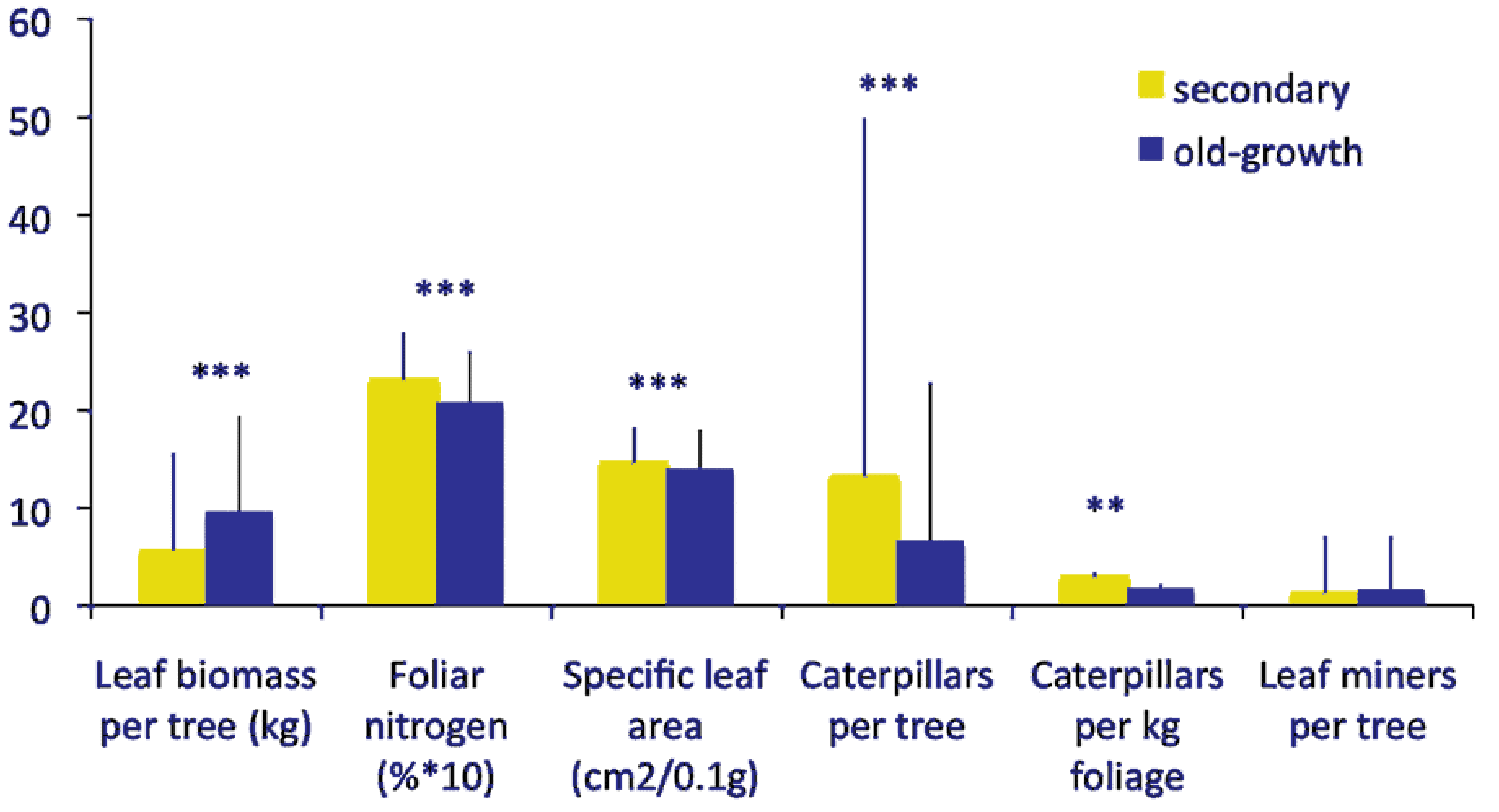
Secondary forest has
- 73% of primary forest leaf area

but only
- 42% of primary forest basal area



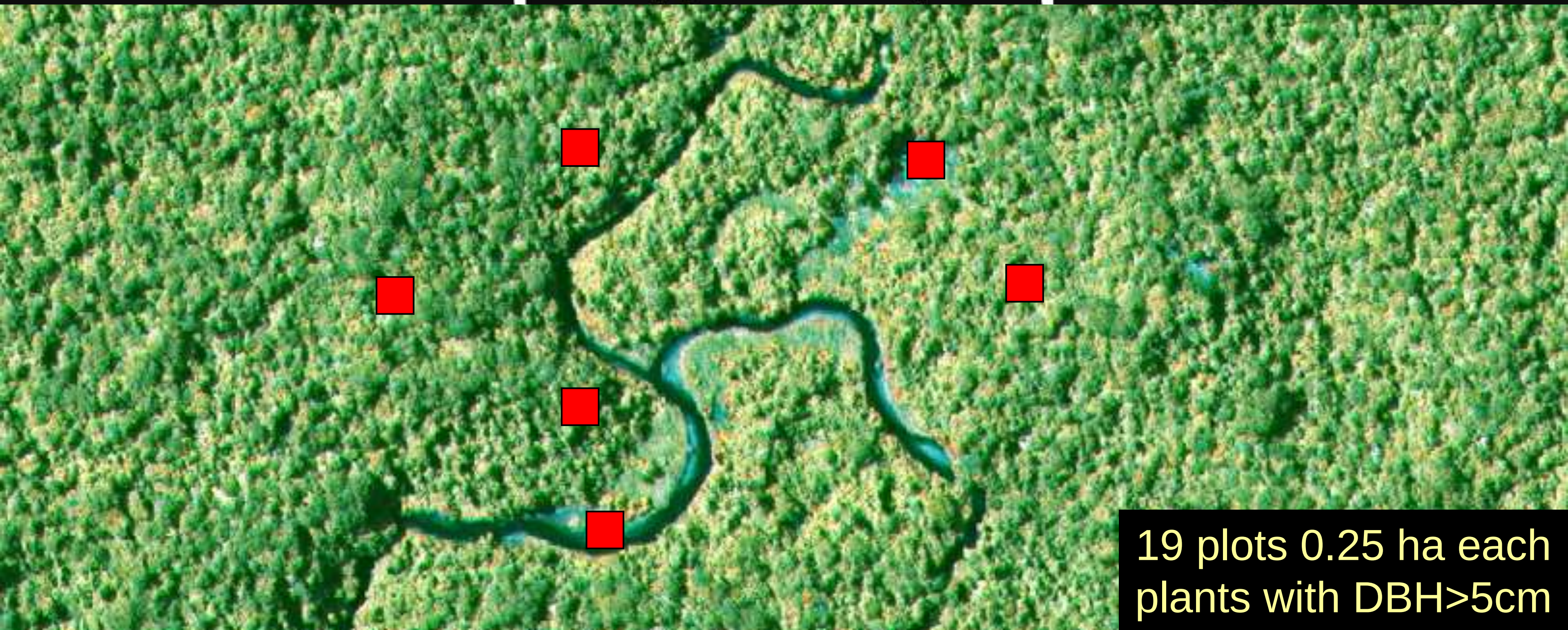




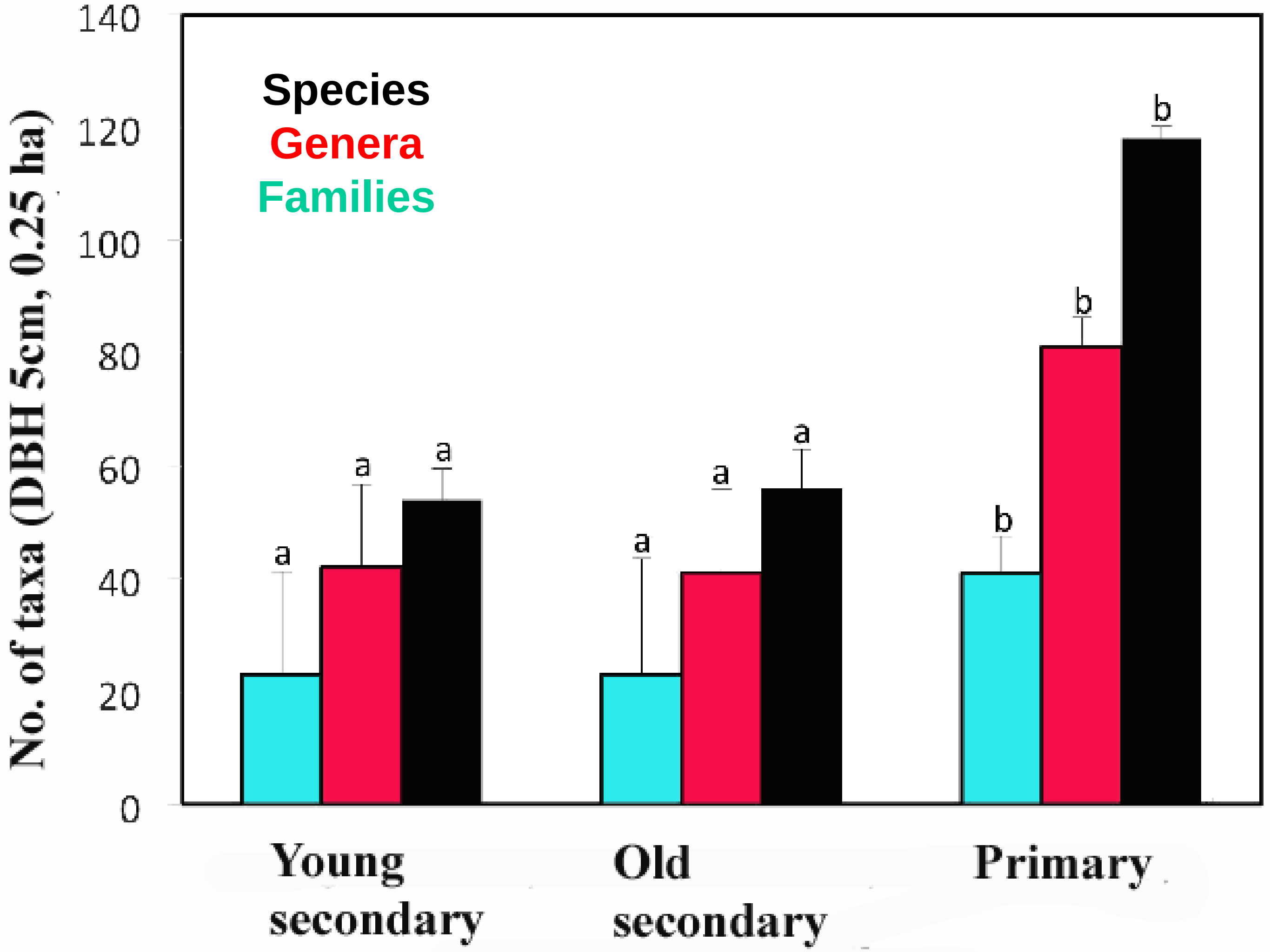


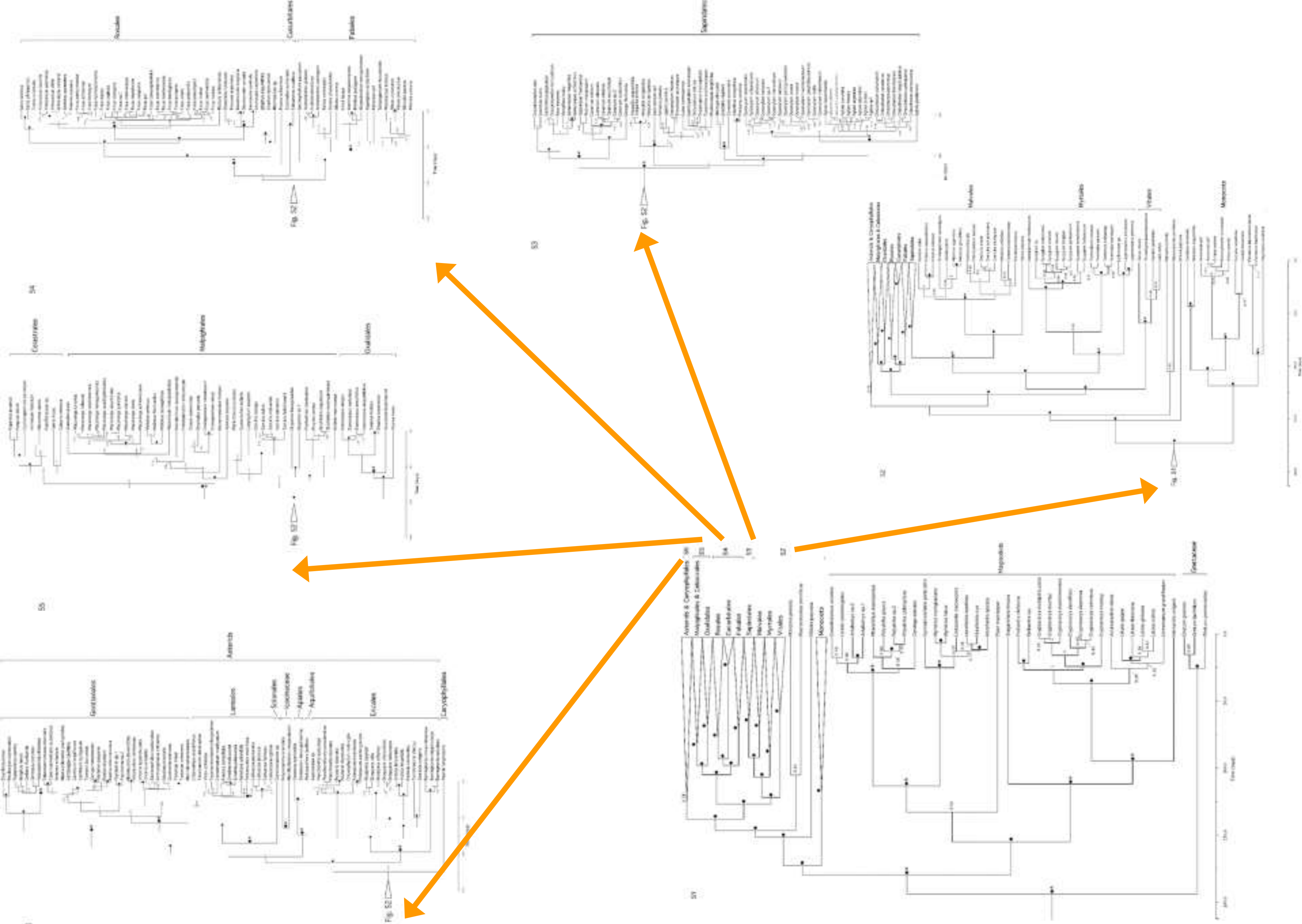
Whitfeld et al. Ecology 2012

primary forest secondary forest 2.5 yrs 5.5 yrs

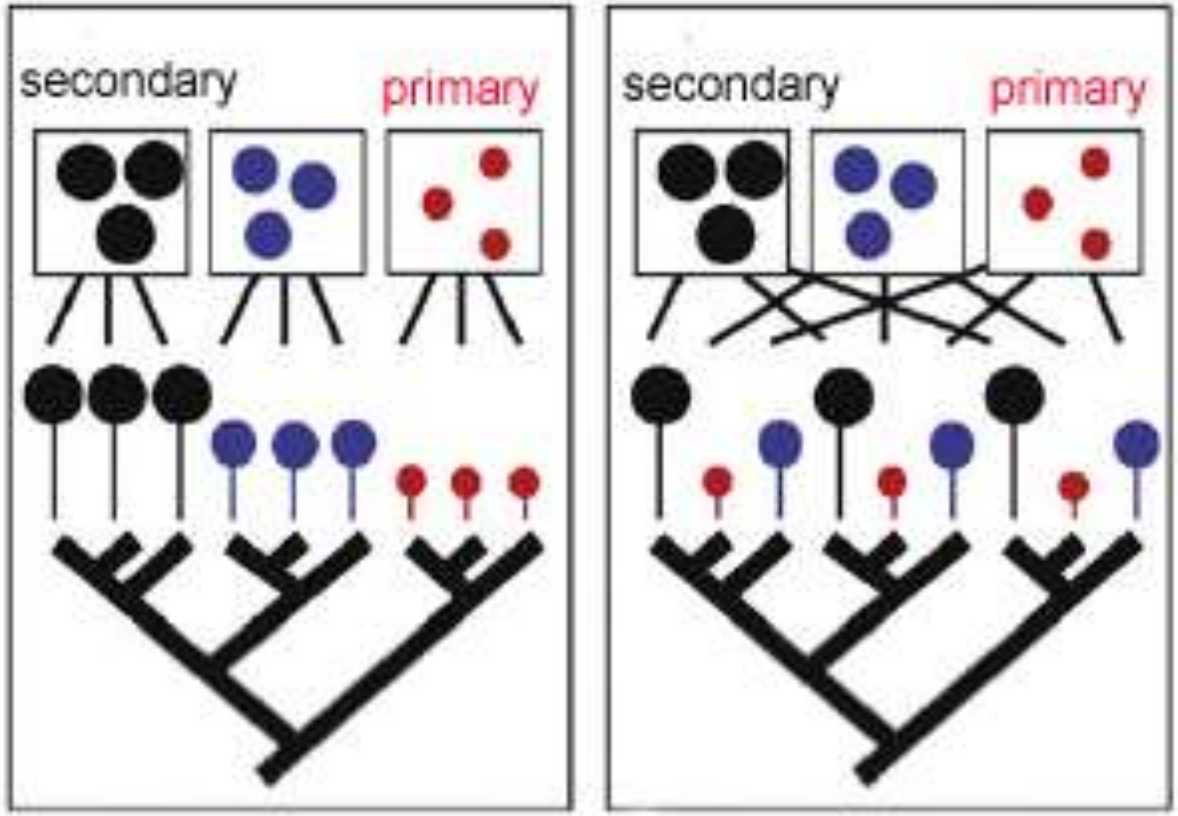


Plant phylogenetic diversity during rainforest succession





Phylogeny of 349 plant species ≥5 cm dbh from New Guinea lowland rain forest



communities

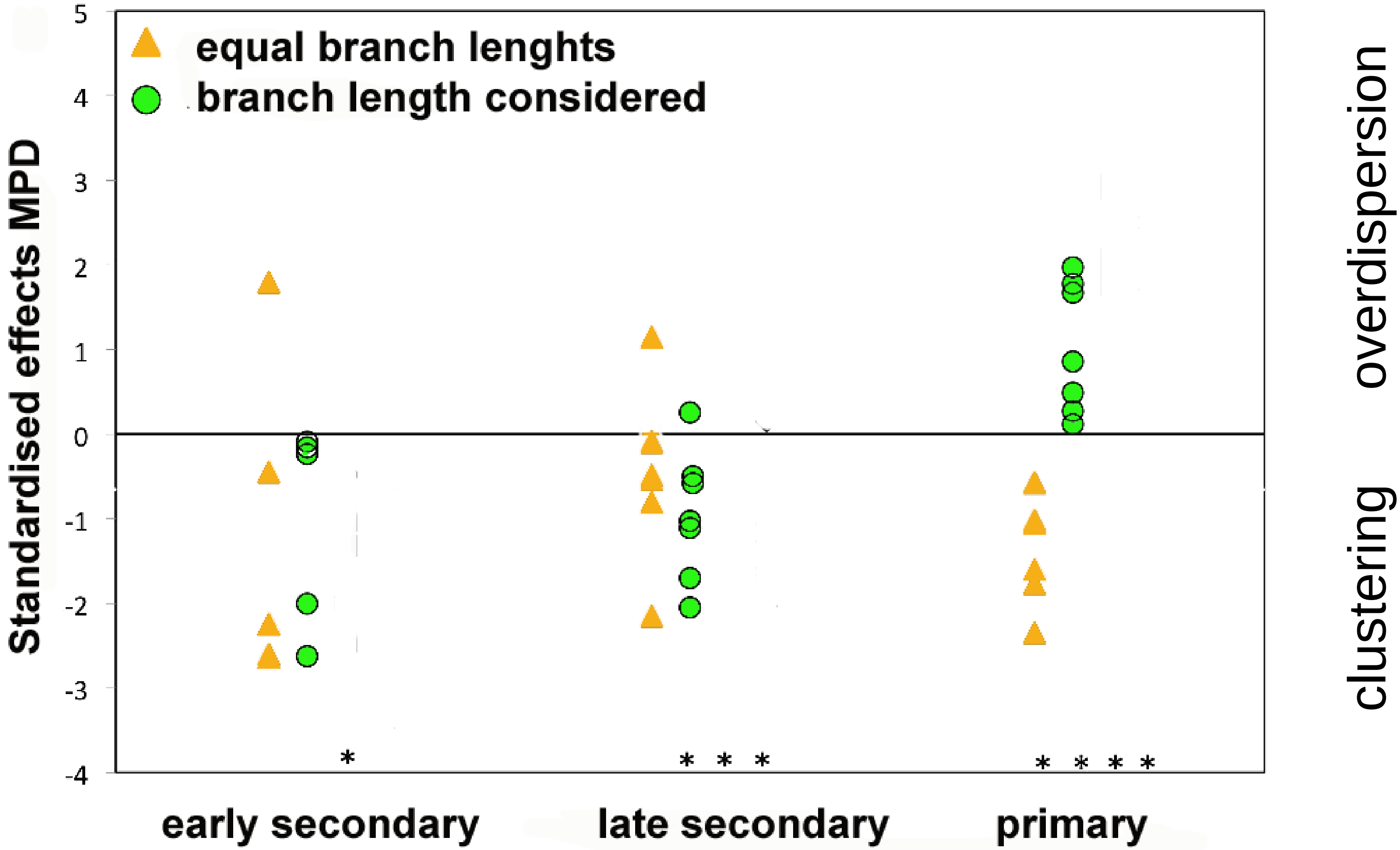
species pool

phylogenetic clustering phylogenetic overdispersion

Net Relatedness Index (NRI) is a metric of phylogenetic clustering, based on the mean pairwise distance between taxa in an observed sample compared to random draws from the species pool. Positive NRI indicates phylogenetic clustering, while negative NRI indicates overdispersion.

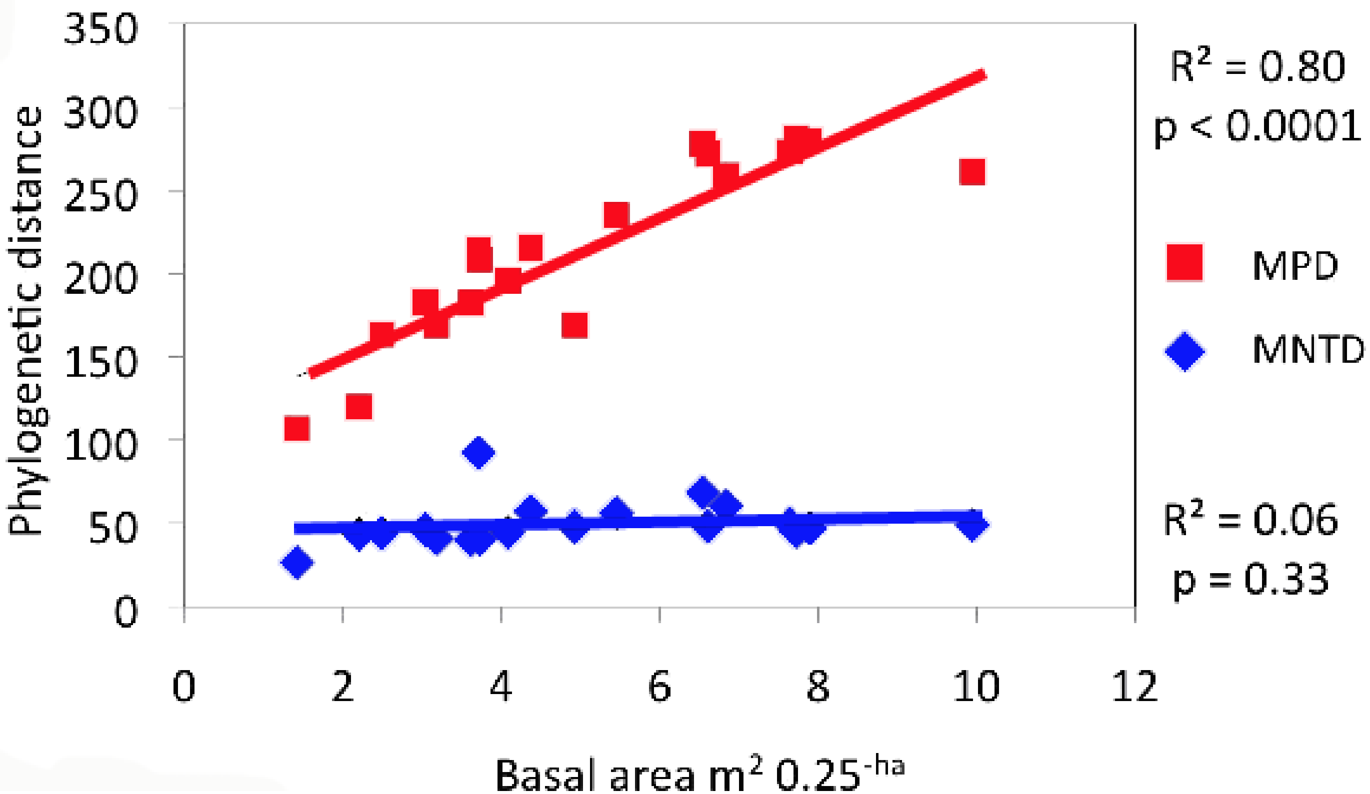
Emerson & Gillespie 2008, TREE 23:619

Distribution of phylogenetic distance between plant species in rainforest plots compared to random selection from species pool (mean pair-wise distance MPD)



Whitfeld et al. Ecography 2011

Fylogenetic diversity of trees with increasing successional age of the forest



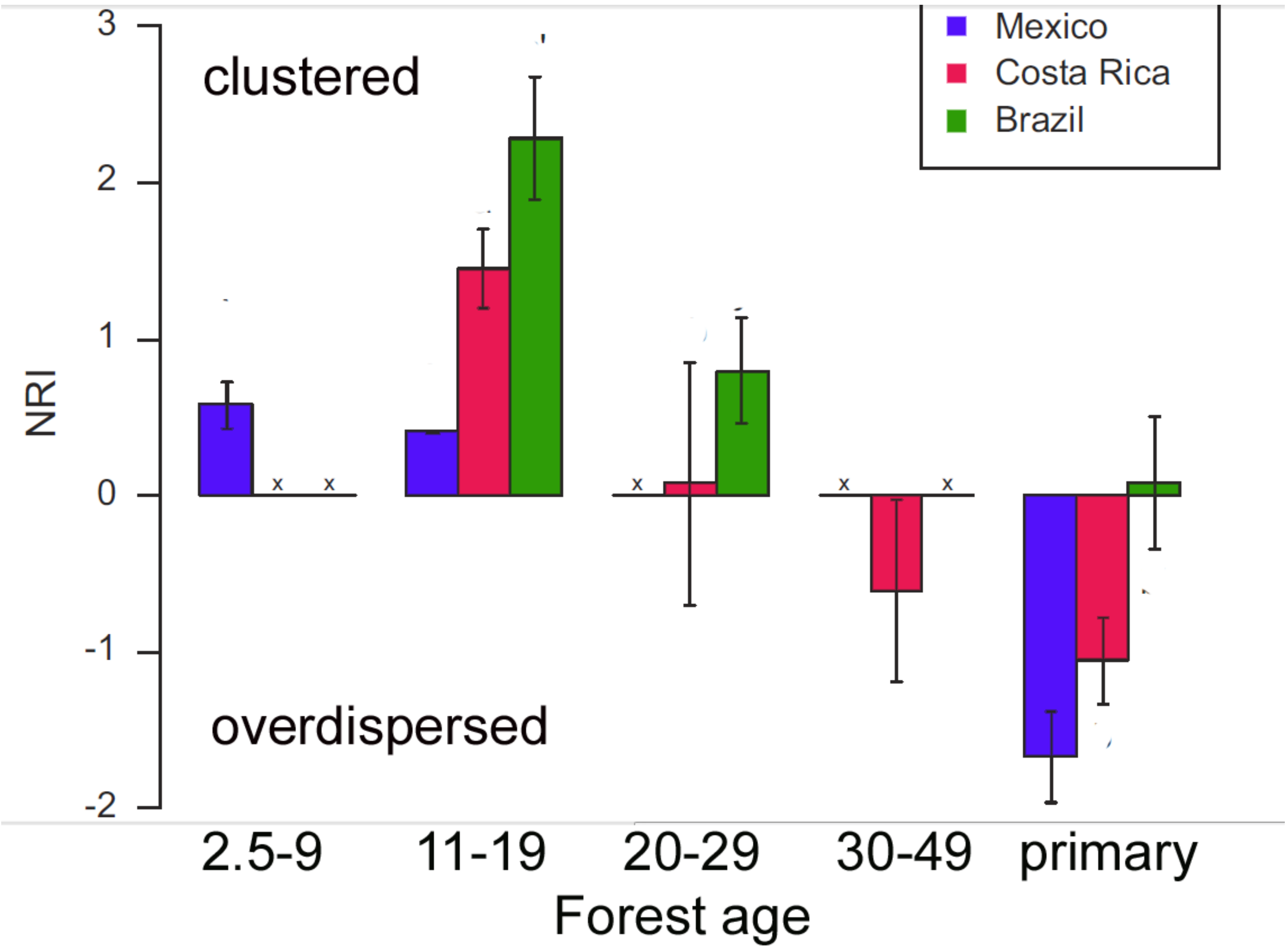
(trees with dbh>5cm, in 0.25 ha plots, succession age approximated by basal area)

MPD = mean pair-wise distance
[measures phylogenetic distance to all other trees in the plot]

MNTD = mean nearest taxon distance
[measures phylogenetic distance to the nearest relative of each tree in the plot]

Whitfeld et al. Ecography 2011

Phylogenetic structure of rainforest vegetation during succession



Letcher et al., Perspectives in Plant Ecology, Evolution and Systematics 14 (2012) 79– 87

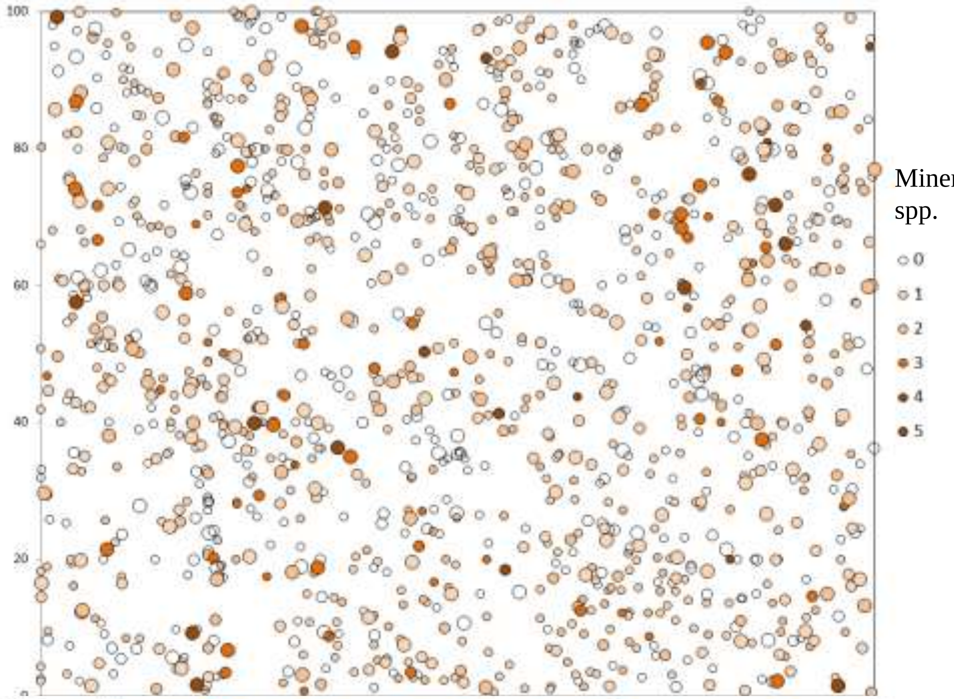
Pioneer plants have large, thin leaves designed to produce a large photosynthetic area as fast as possible. The leaves are short lived and palatable to herbivores, thus suffering large damage.

Examples are all *Macaranga* spp. from New Guinea

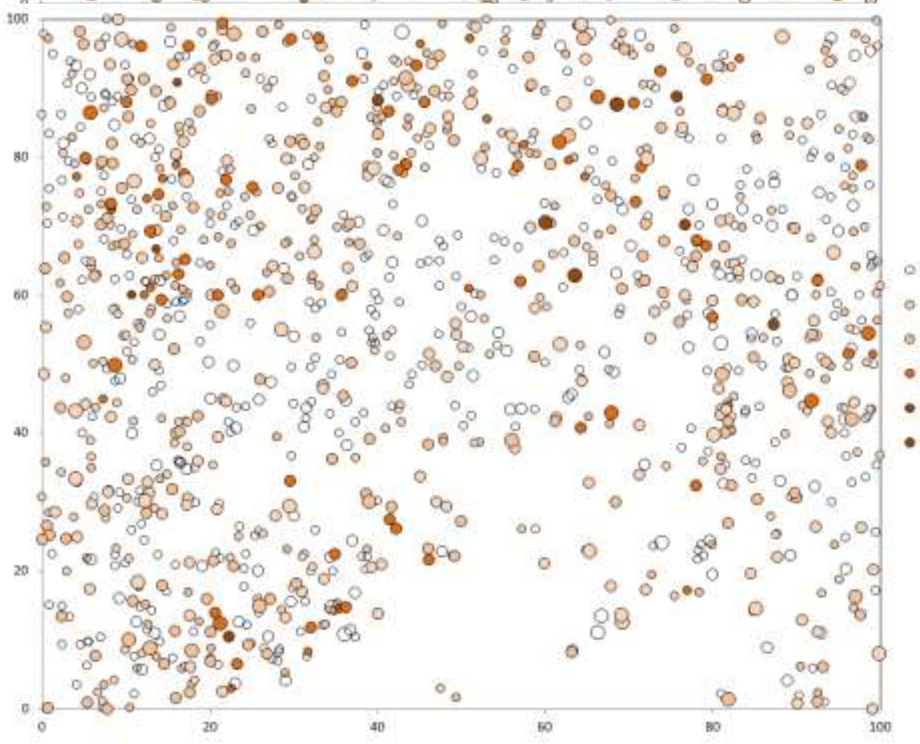
Cecropia plants - *Azteca* ants, America; plants produce glykogen rich muellerian bodies

Endospermum plants - *Camponotus* ants, New Guinea

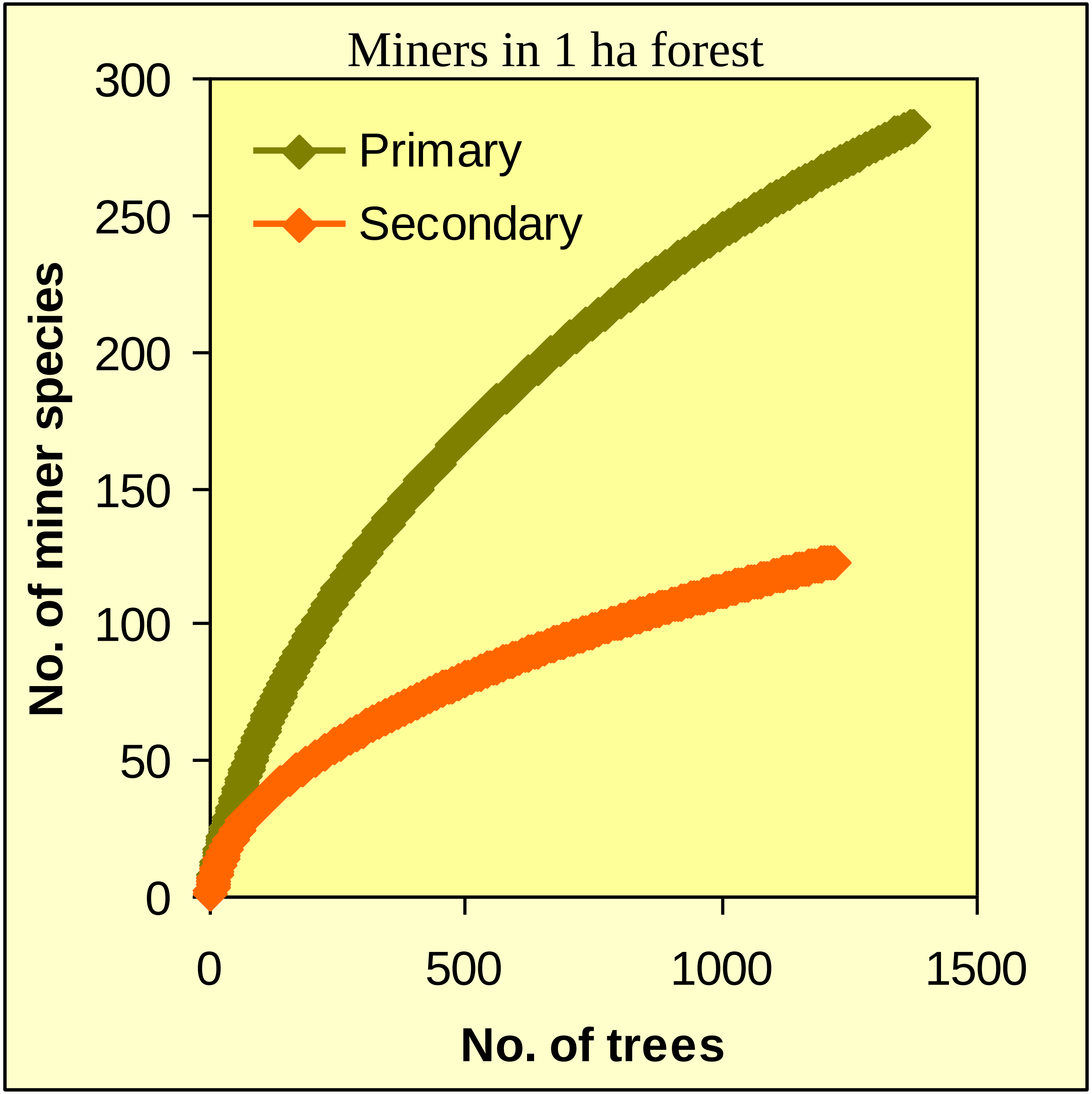
Macaranga plants - *Crematogaster* ants, South East Asia



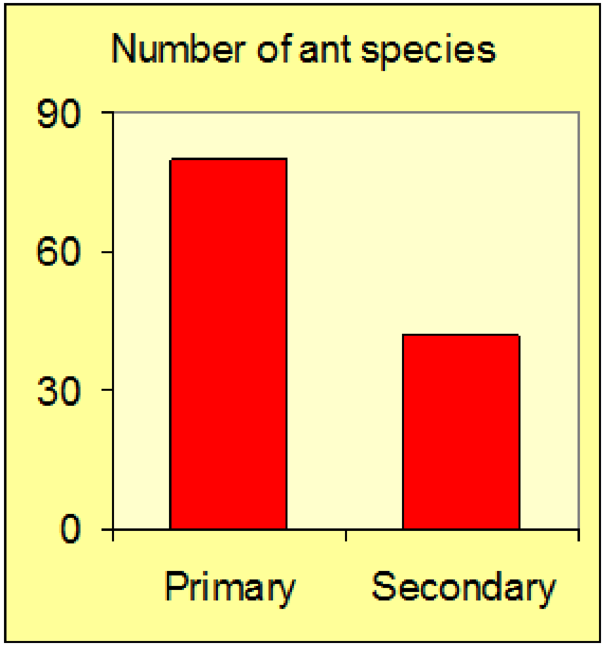
primary



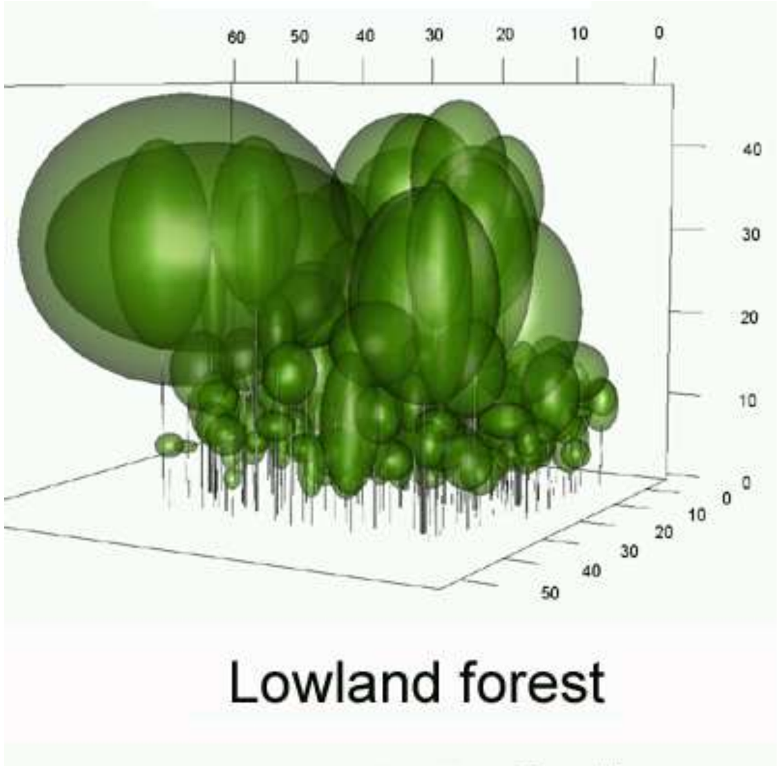
secondary

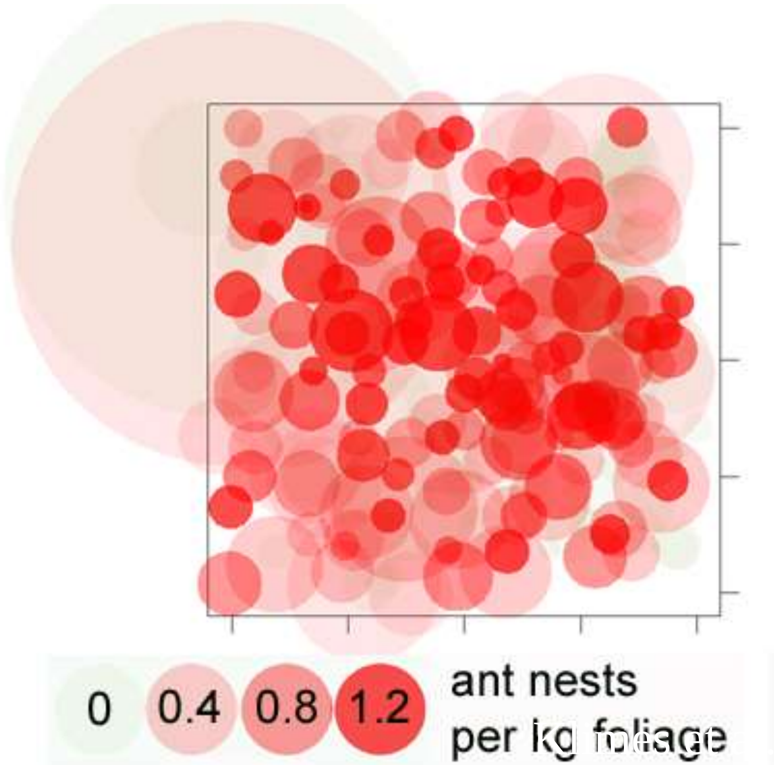


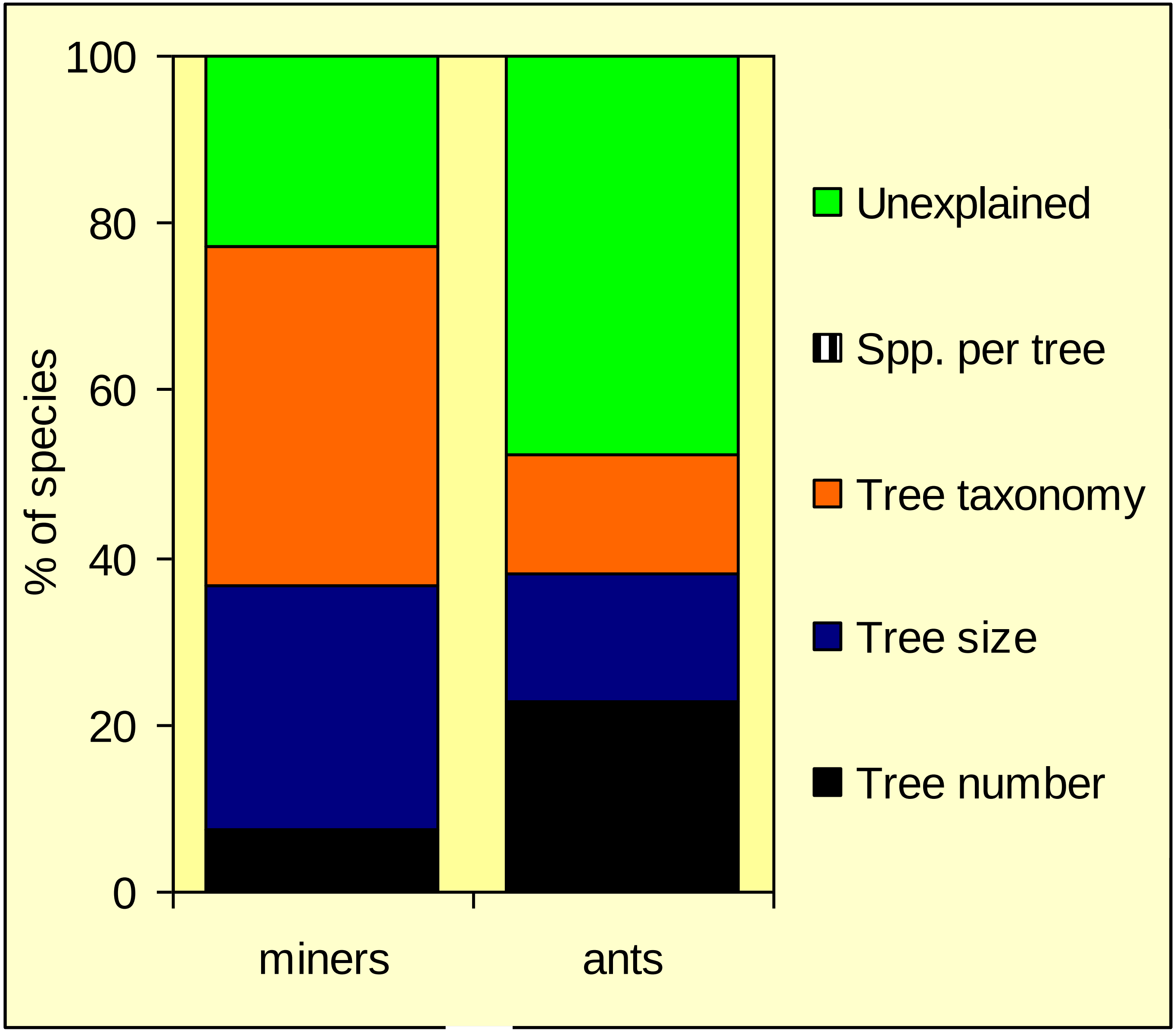
Miners in 1 ha forest
Primary
Secondary
No. of miner species
No. of trees
300
250
200
150
100
50
0
0
500
1000
1500



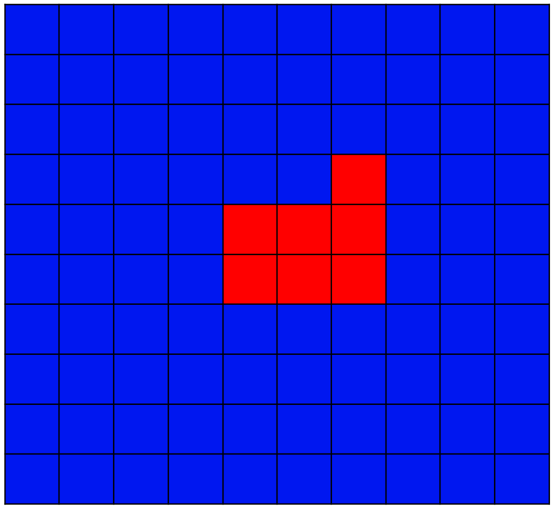
Arboreal ant species per 1 ha of forest

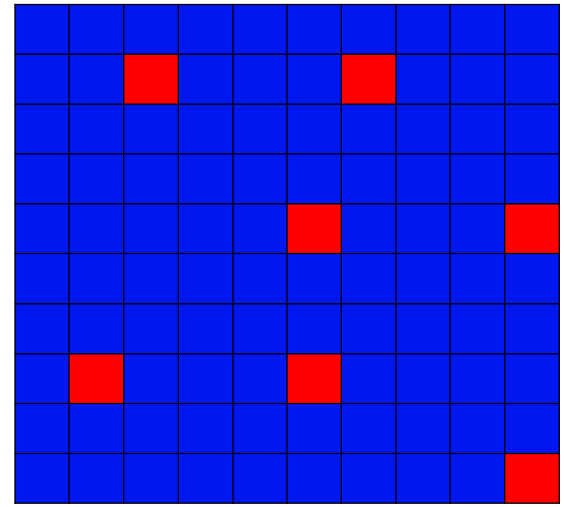





100
80
60
40
20
0
% of species
miners
ants
Unexplained
Spp. per tree
Tree taxonomy
Tree size
Tree number

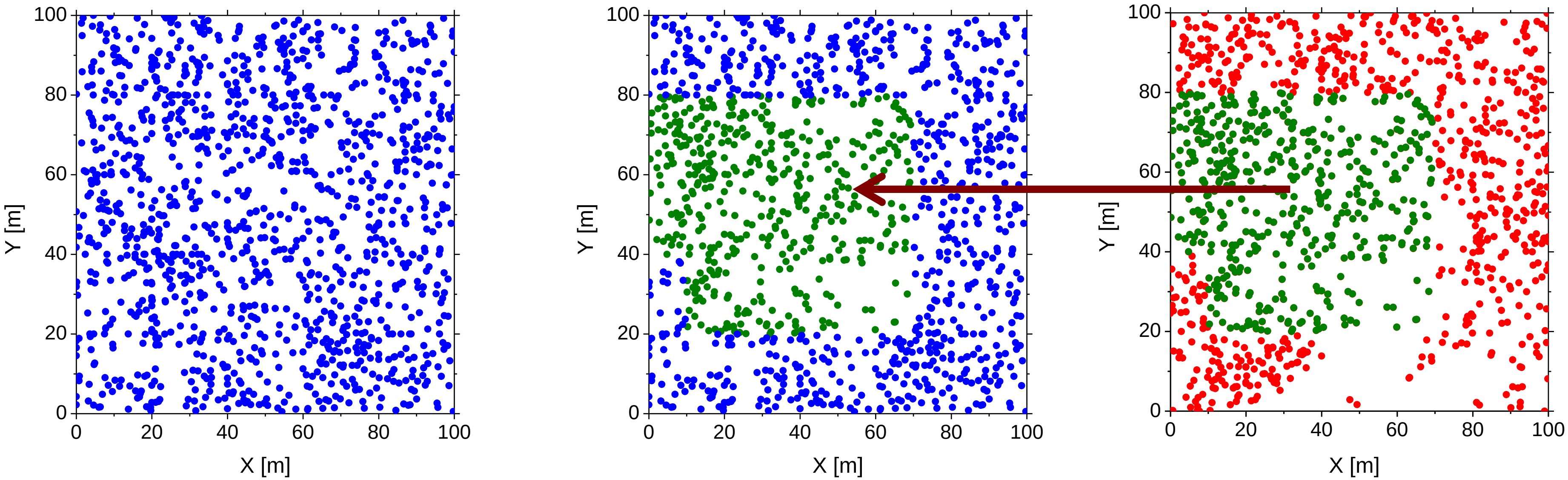
Intermediate disturbance hypothesis: converting primary forests to secondary forests





O.Kaman

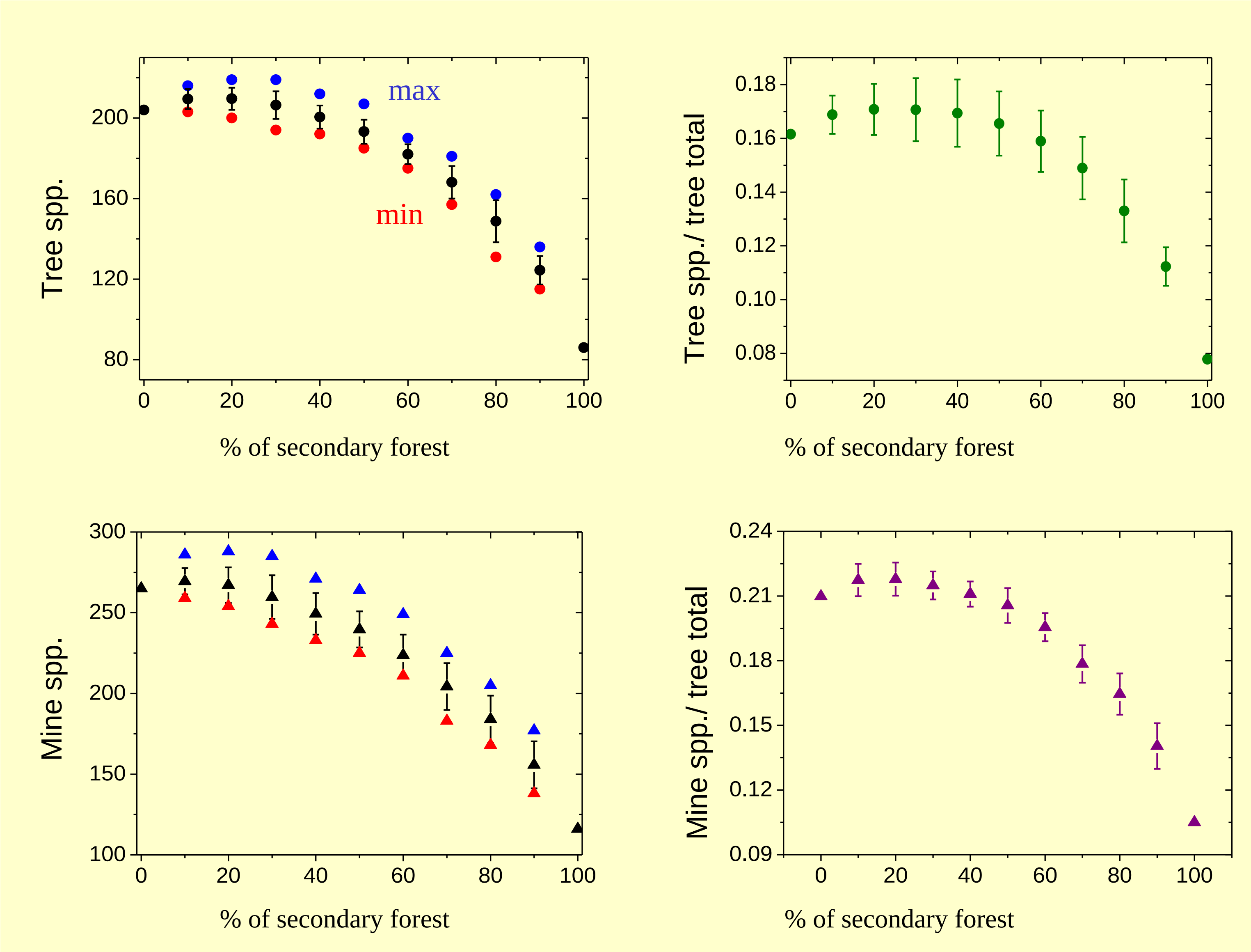
1 ha primary forest **60% primary + 40% secondary** **1 ha secondary forest**



Species richness of trees and leaf miners in virtual forests

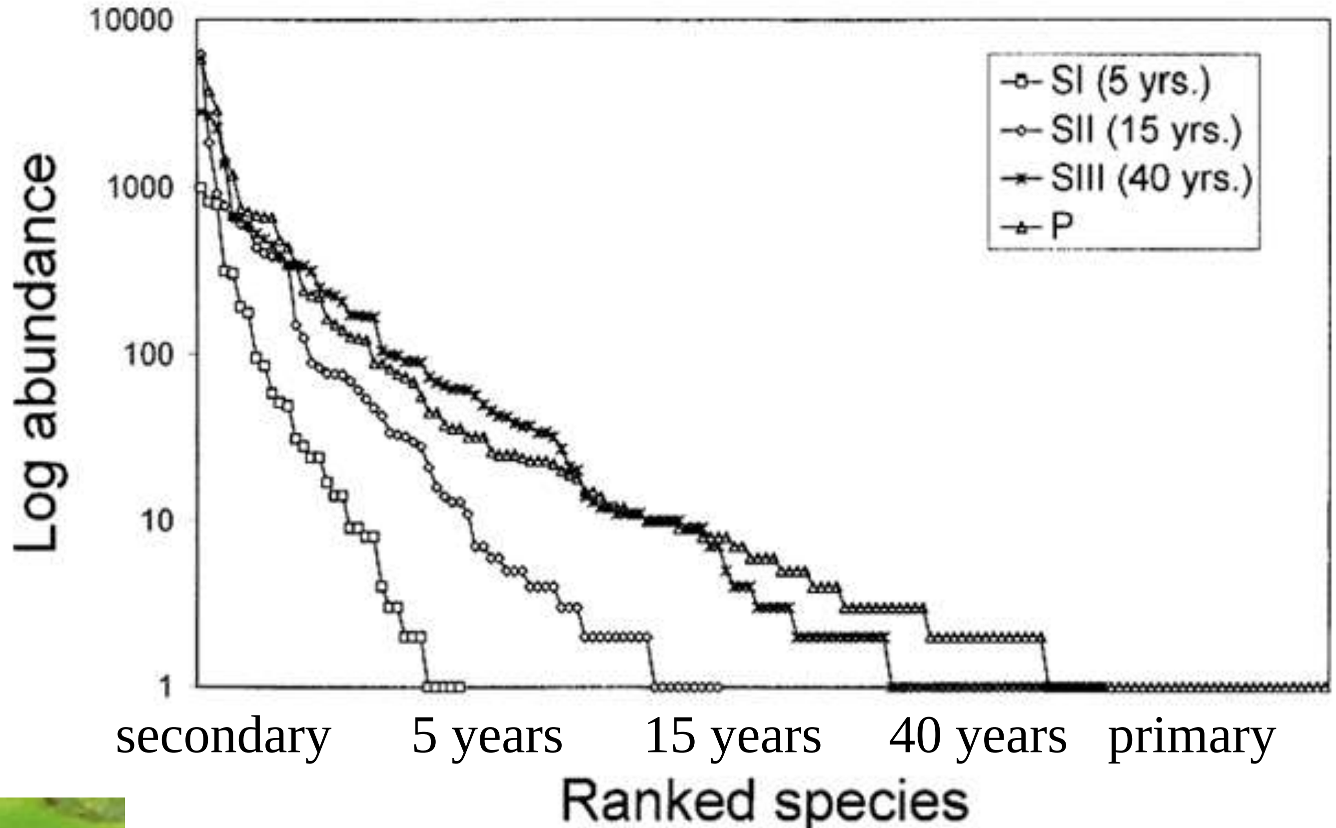
1 ha primary forest: 1263 trees, 204 tree spp., 265 mine sp

1 ha secondary forest: 1105 trees, 86 spp., 116 mine spp.



O. Kaman in prep.

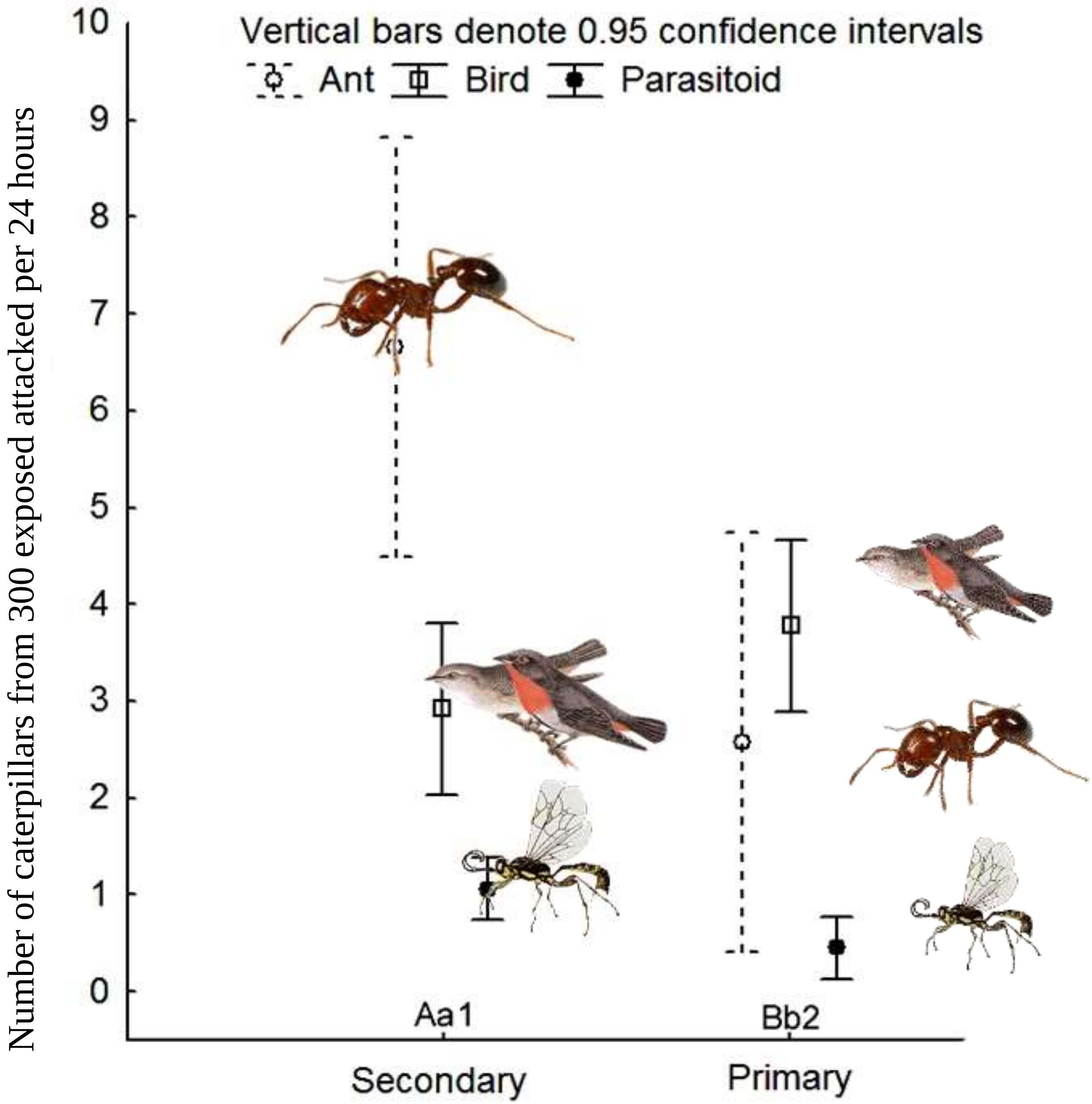
Ant community structure



Secondary forest 5 years old – 15 years – 40 years – primary forest

Rank-abundance plots for all ants in three ages of regenerating forest (5, 15, and 40 years old) and mature forest (P). Source: Floren and Linsenmair (2001, fig. 4).

How dangerous are secondary forests for herbivorous insects?



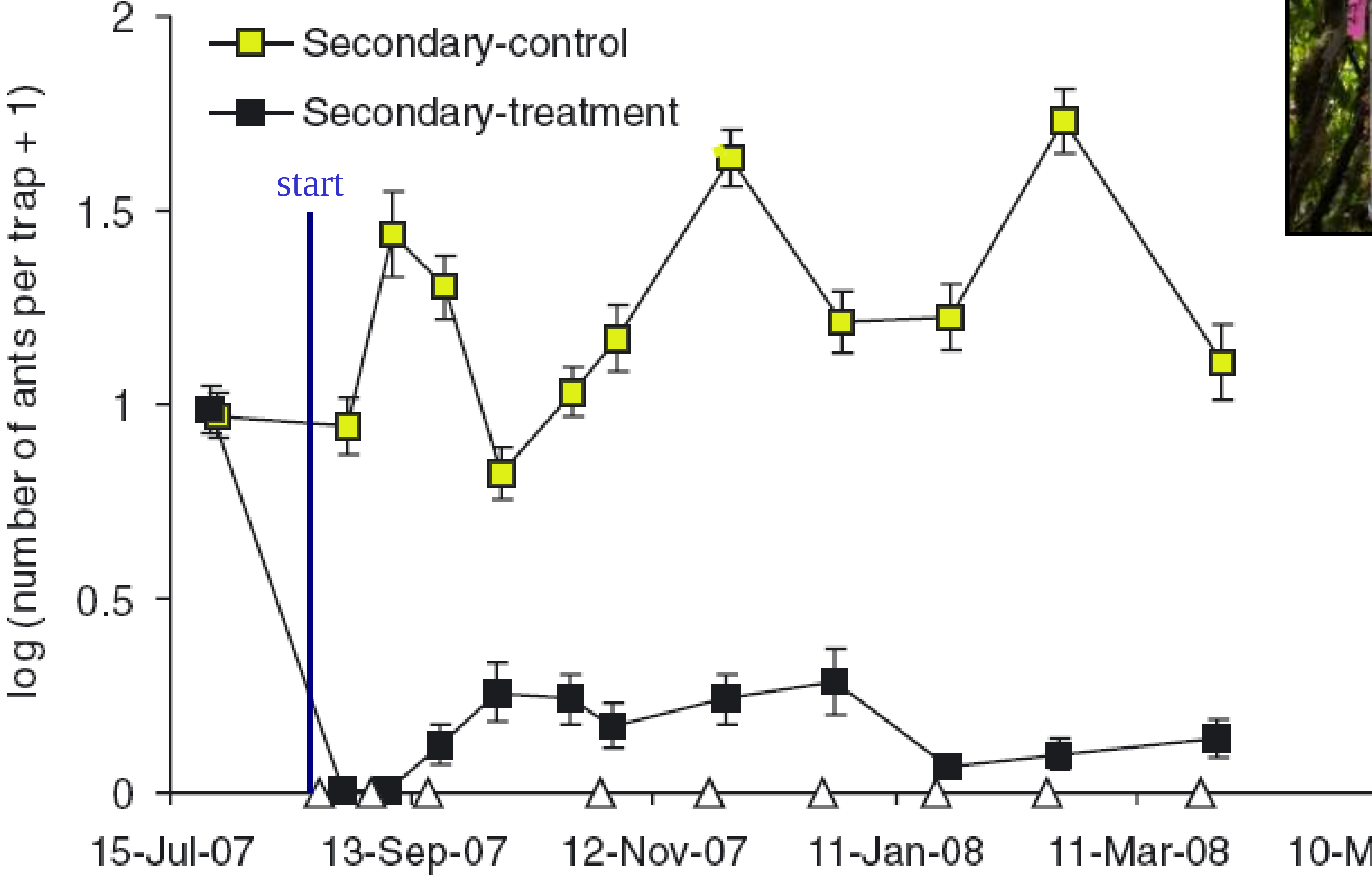
K. Sam

Sam & Novotny, 2012, J. Trop. Ecol.

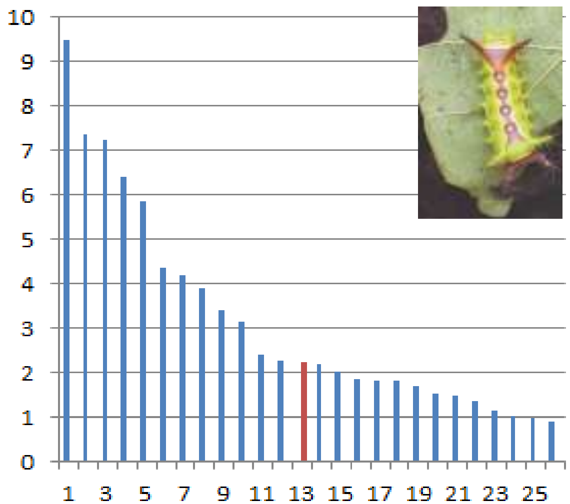
How will a secondary rainforest look without ants?

Klimes et al. 2011
Ecol. Entomol **36**:94

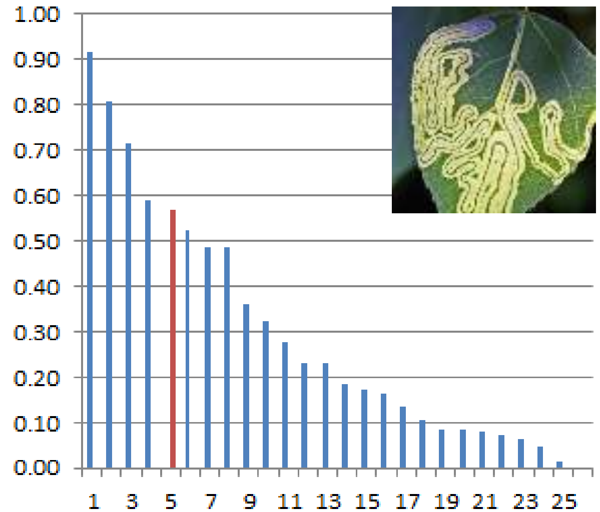
Ant activity decreased by 90% in the secondary forest canopy



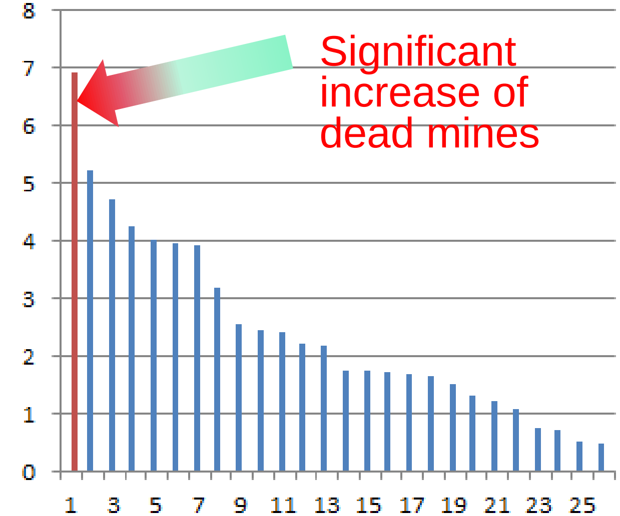
Ants do not suppress herbivores and herbivory as much as expected



No caterpillars / kg of leaves

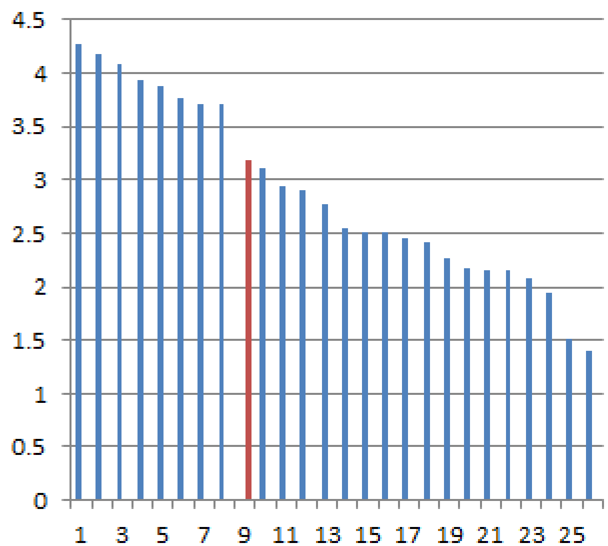


No live mines / kg of leaves

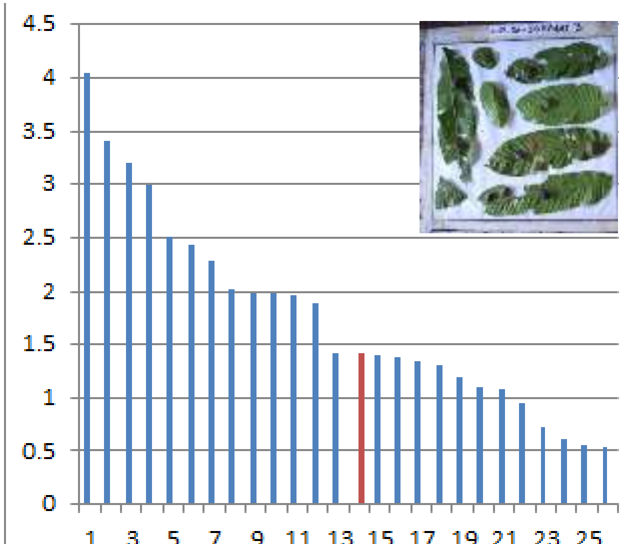


No dead mines / kg of leaves

treatment
[no ants]
x
control



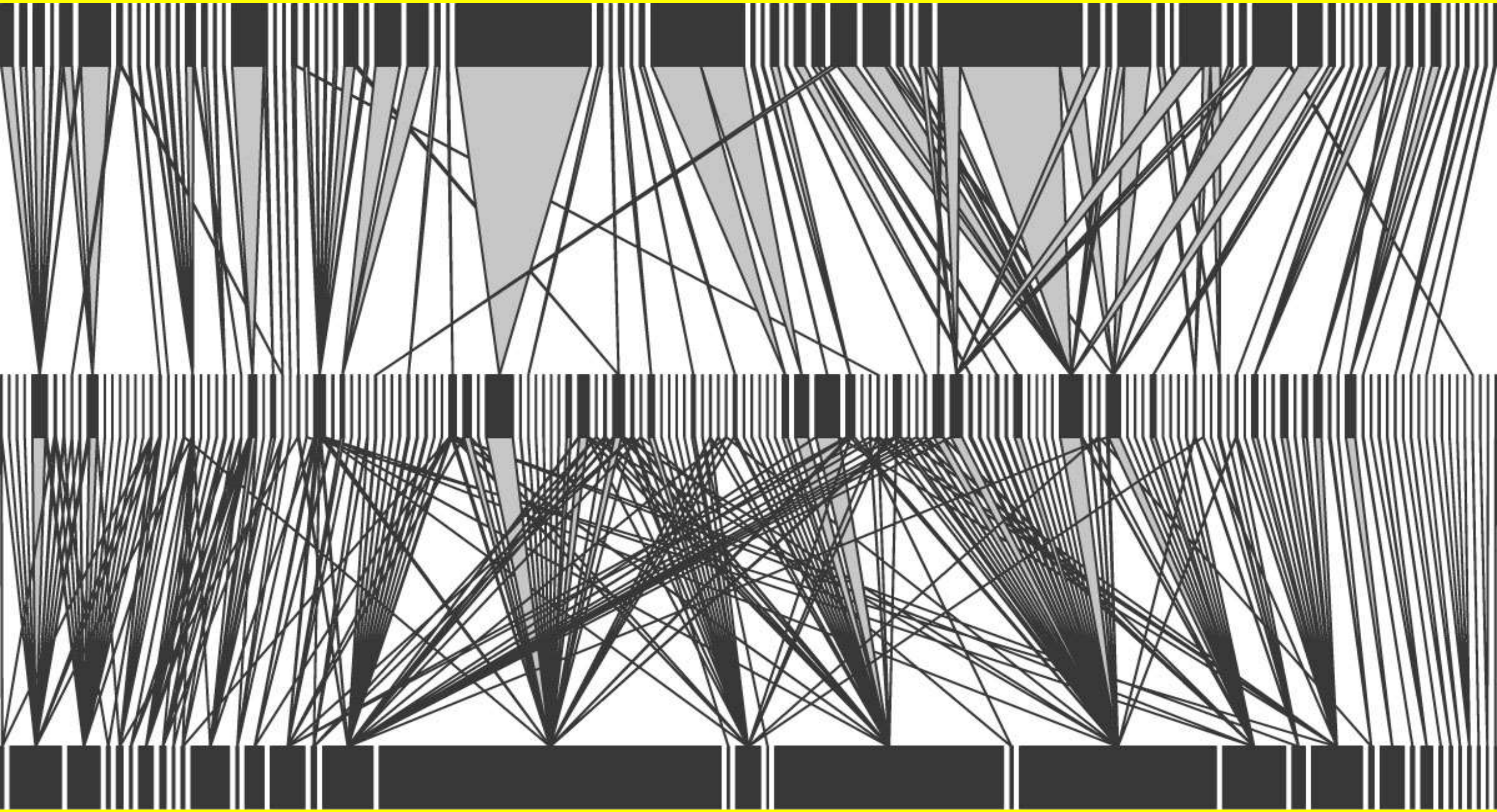
% mature leaves consumed



% young leaves consumed

Not all secondary forest food webs are simple

1,523 Hymenoptera and Diptera parasitoids from 166 species



38 tree species - 11,621 caterpillars from 267 species

Jan Hrcek et al. 2013 *Oecologia* **173**: 521

Parasitoids:

Braconidae

Ichneumonidae

Tachinidae

Chalcidoidea

Bethylidae

Attribute	Pioneer	Shade-tolerant
Specific wood gravity	Low	High
Radial gradients in specific wood gravity	Present	Absent
Light-saturated photosynthetic rate (area and mass based)	High	Low
Leaf nitrogen content (area and mass based)	High	Low
LMA (leaf mass per unit area)	Low	High
SLA (leaf area per mass)	High	Low
Leaf density	Low	High
Leaf toughness	Low	High
Photosynthetic nitrogen use efficiency	High	Low
Photosynthetic phosphorus use efficiency	High	Low
Leaf life span	Short	Long
Transpiration rate	High	Low
Maximum stomatal conductance	High	Low
Maximum growth rate	High	Low
Vulnerability to cavitation	High	Low
Leaf-specific hydraulic conductance	High	Low
Stem hydraulic conductance	High	Low
Height growth	Rapid	Slow
Herbivore resistance	Low	High

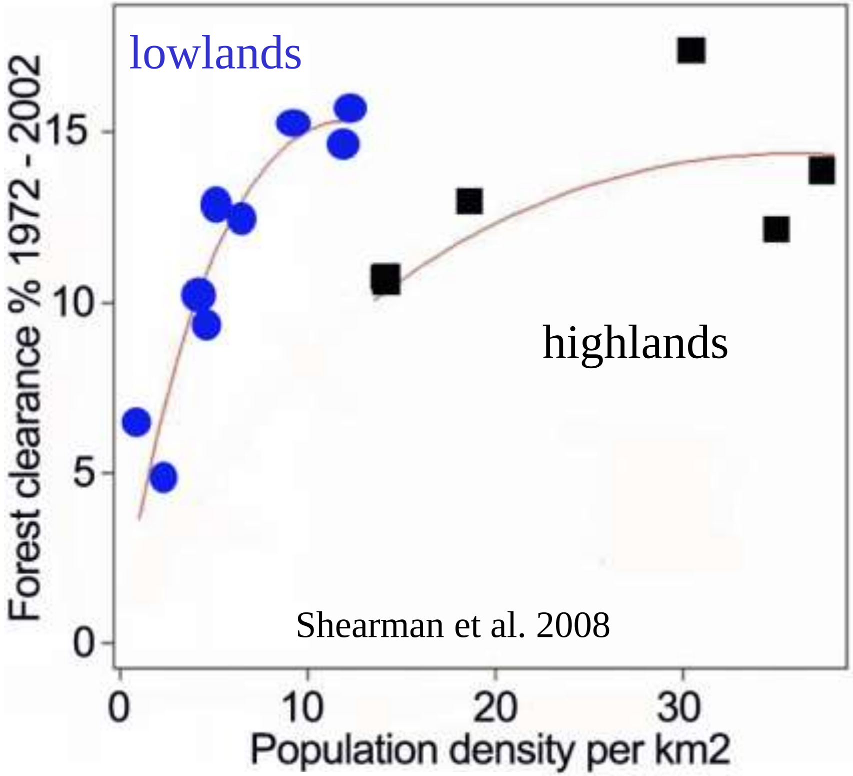
Life history traits of pioneer and climax trees

	Pioneer	Climax
Germination	Only in canopy gaps open to the sky which receive some full sunlight	Usually below canopy
Seedlings	Cannot survive below canopy in shade, never found there	Can survive below canopy, forming a 'seedling bank'
Seeds	Usually small, produced copiously and more or less continuously, and from early in life	Often large, not copious, often produced annually or less frequently and only on trees that have (almost) reached full height
Soil seed bank	Many species	Few species
Dispersal	By wind or animals, often for a considerable distance	By diverse means, including gravity, sometimes only a short distance
Dormancy	Capable of dormancy ('orthodox') commonly abundant in forest soil as a seed bank	Often with no capacity for dormancy ('recalcitrant'), seldom found in soil seed bank
Growth rate	Carbon fixation rate, unit leaf rate, and relative growth rates high	These rates lower
Compensation point	High	Low
Height growth	Fast	Often slow
Leaf life*	Short, one generation present, viz. high turn-over rate	Long, sometimes several generations present so slow turn-over rate
Herbivory	Leaves susceptible, soft, little chemical defence	Leaves sometimes less susceptible due to mechanical toughness or toxic chemicals
Wood	Usually pale, low density, not siliceous	Variable, pale to very dark, low to high density, sometimes siliceous
Ecological range	Wide	Sometimes narrow
Longevity	Often short	Sometimes very long

Ecological traits of different stages in tropical forest succession

	Pioneer	Early secondary	Late secondary	Climax
Community age	1–3 years	5–15 years	20–50 years	>100 years
Canopy height	5–8 m	12–20 m	20–30 m	30–60 m
Number of strata	1, very dense	2, well-differentiated	3, increasingly difficult to discern with age	4–5, difficult to discern
Lower stratum	Dense, tangled	Dense, large herbaceous species frequent	Relatively scarce	Scarce
Growth	Very fast	Very fast	Dominants fast, others slow	Slow or very slow
Lifespan of dominants	Very short, less than 10 years	Short, 10–25 years	Usually 40–100 years, some more	Very long, 100–1000 years or more
Shade tolerance of dominants	Very intolerant	Very intolerant	Tolerant as juveniles, later intolerant	Tolerant, except in adult stage
Regeneration of dominants	Very scarce	Practically absent	Absent or abundant, large mortality in	Abundant
Seed viability	Long, latent in soil	Long, latent in soil	Short to medium	Short
Epiphytes	Absent	Few	Many, but few species	Many species
Vines, lianas	Abundant, herbaceous but few species	Abundant, herbaceous, few species	Abundant, but few of them large	Abundant, with some very large, woody species
Shrubs	Many, but few species	Relatively abundant but few species	Few	Few, but many species
Grasses	Abundant	Scarce to abundant	Scarce	Scarce

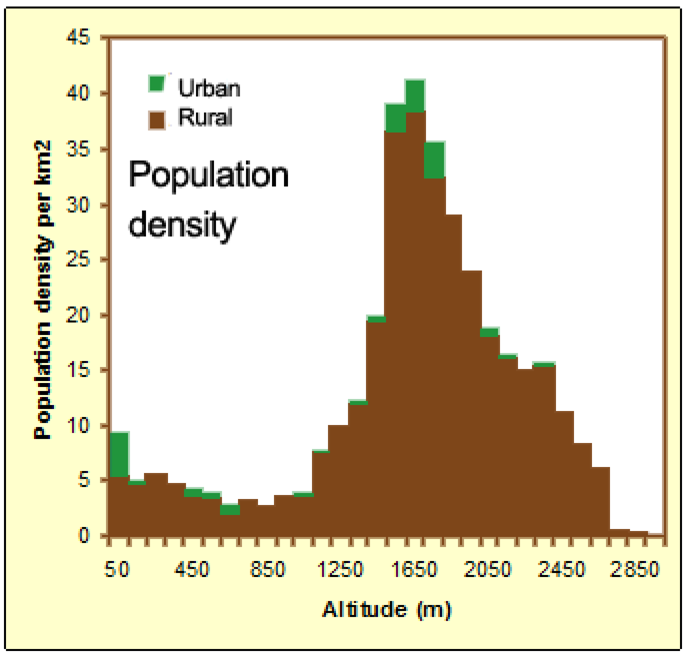
Slash
&
burn
[swidden]
agriculture

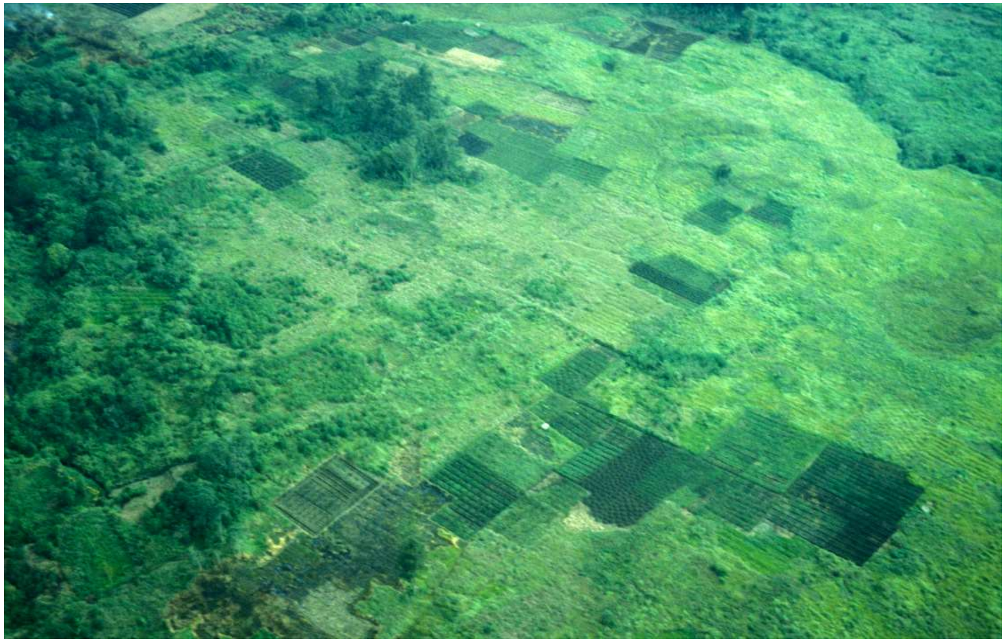


New Guinea Highlands:

- low per capita deforestation
- higher population densities
- more productive agriculture

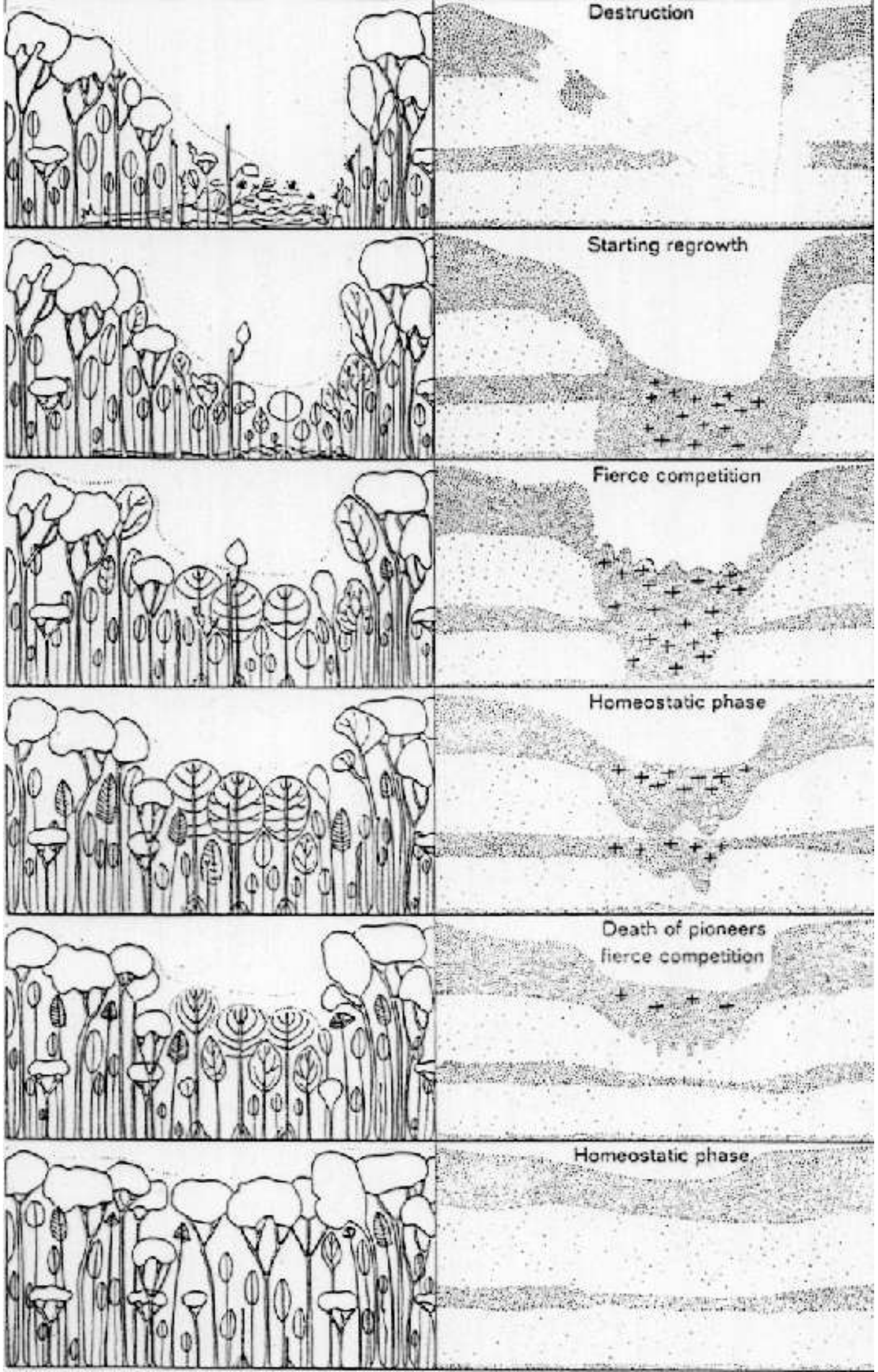
Do we need more pesticides to protect rainforests?





Intensive agriculture in New Guinea highlands (sweet potato)

First contact with outside world in 1932



Succession time series in a forest gap

densely shaded areas - maximum growth
crosses - maximum competition

Fig. 8.3 How a chablis fills up on a place where the undergrowth is destructed, in six stages. The *densely shaded* parts indicate the zones where most of the growth takes place; the *crosses* the places where competition is strongest (Hallé et al. 1978)

Initial grassland stages of rainforest succession

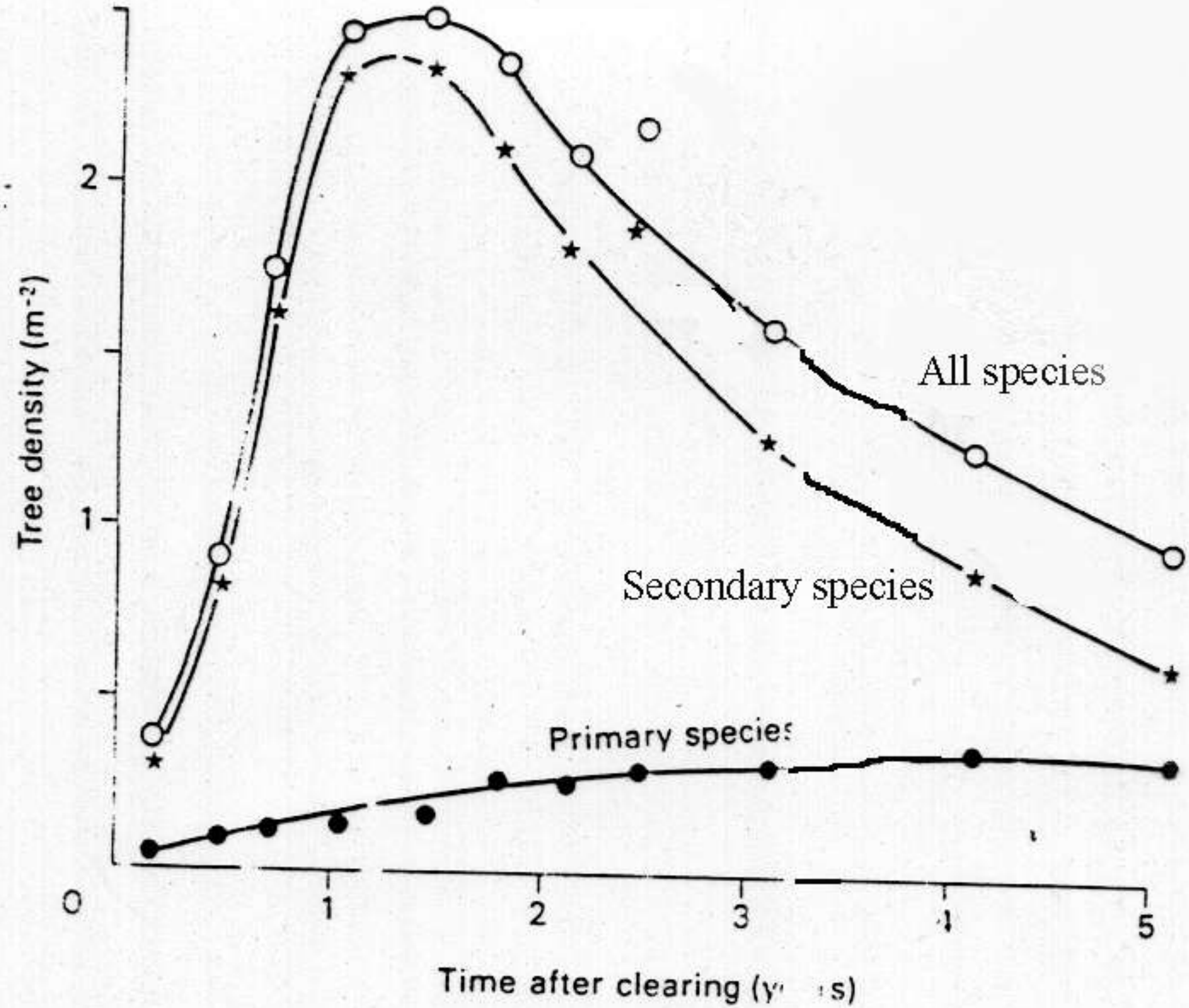
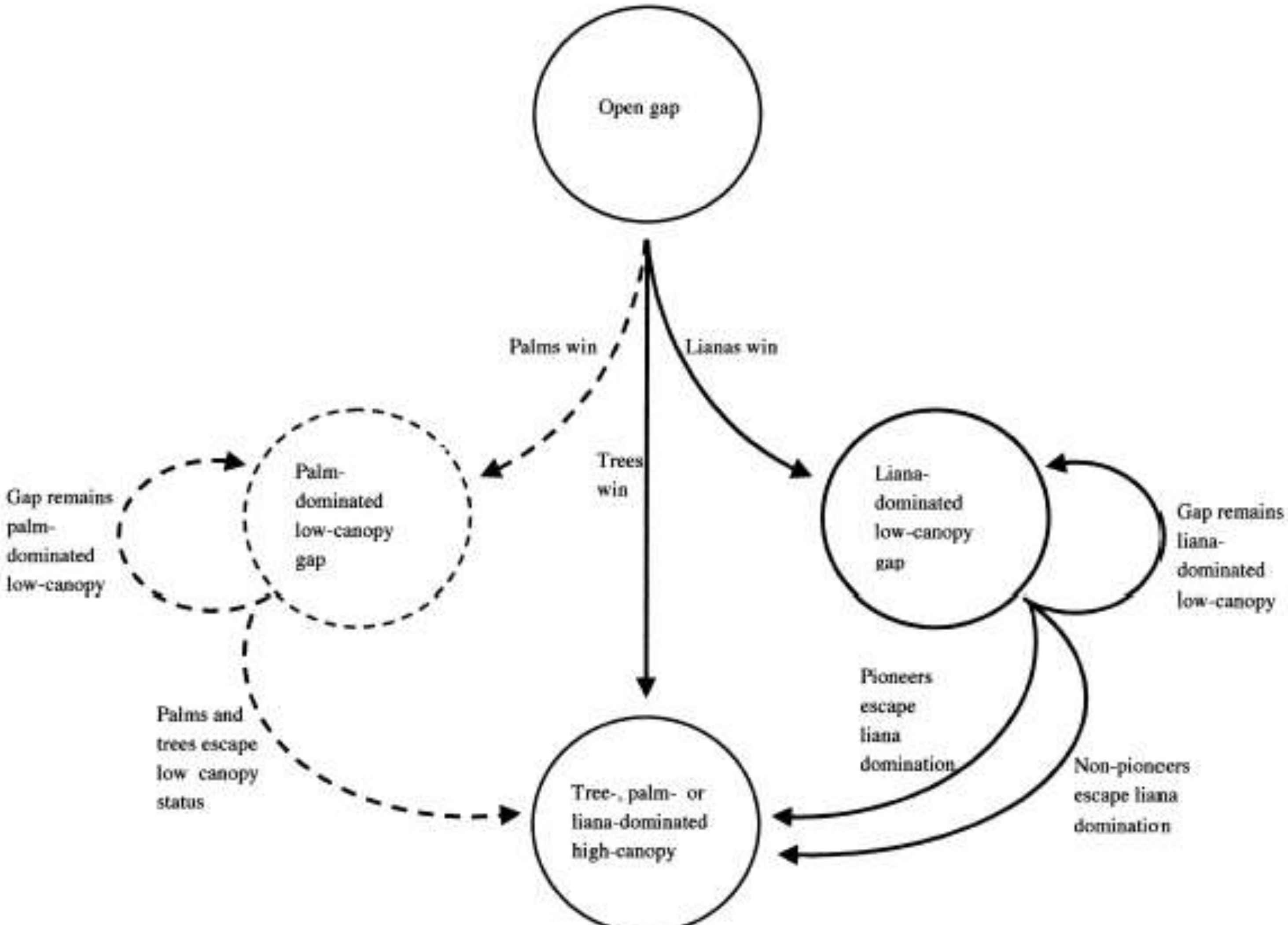


Fig. 6.14 Density of trees in a clearing in Ghana during the first 5 years of succession. (After Swaine and Hall 1983.)

Barro Colorado Island:
approximately 8% of canopy gaps become quickly dominated by palms or lianas that block canopy development for many years



regenerate via one of three pathways.
high canopy. This was the most abun-
ıd older. Alternatively, gaps could be
ted the majority of these low-canopy
w-canopy gaps are characterized by a
ees. We depicted the palm-dominated
ıon (only 2.3% of all gaps followed a
nated gaps, however, is likely to be a
ıay be important in the many tropical

Schnitzer et al. 2000, J. Ecol. 88: 655

Tree gaps blocked by lianas

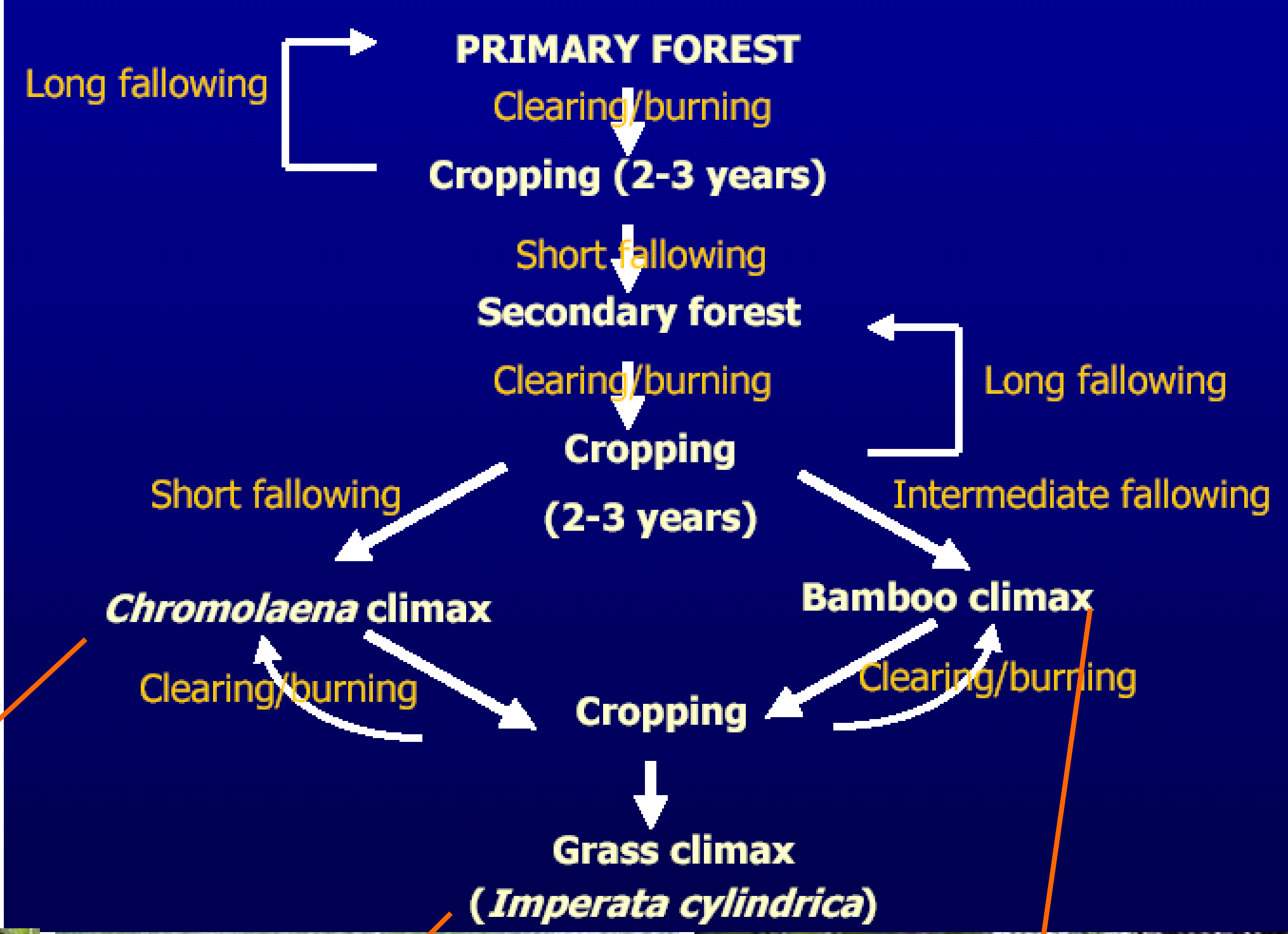
Peru

Panama

Photo S. Schnitzer

Succession after slash-and-burn agriculture

Thailand



[*Paspalum* is alien in Malaysia]

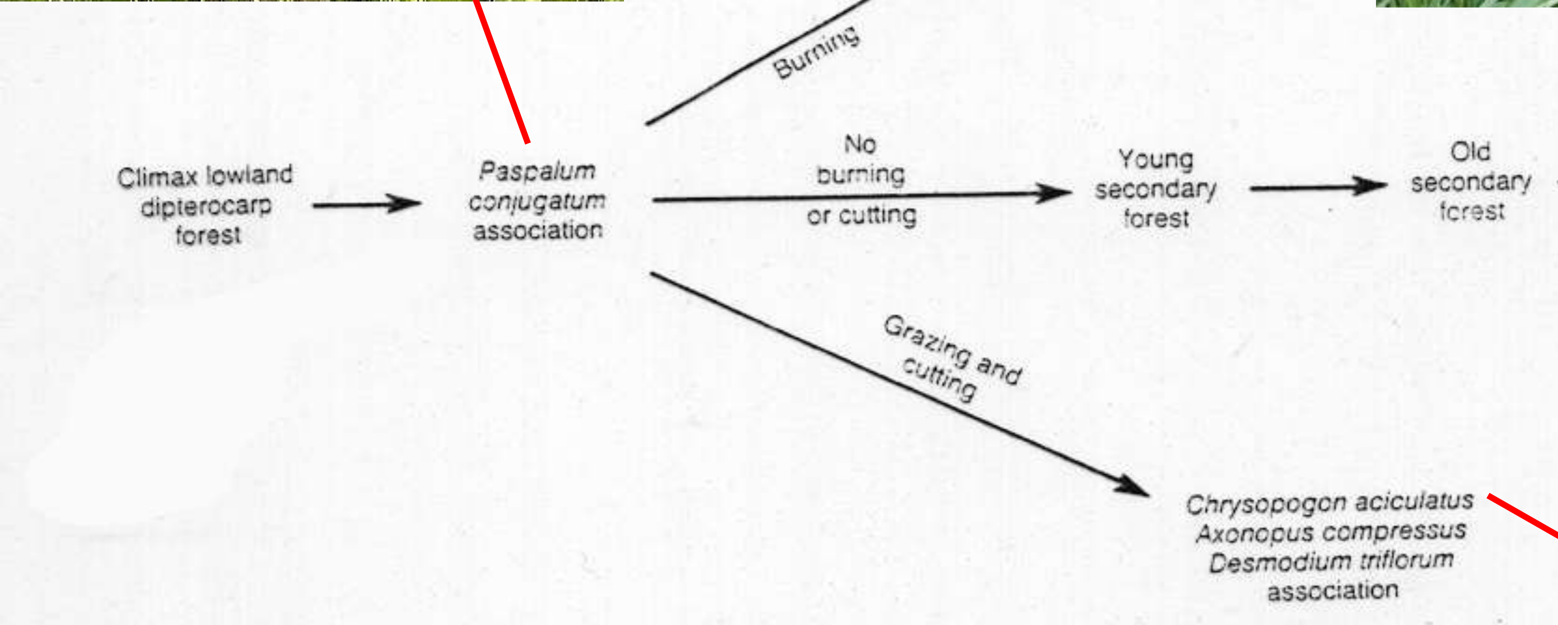
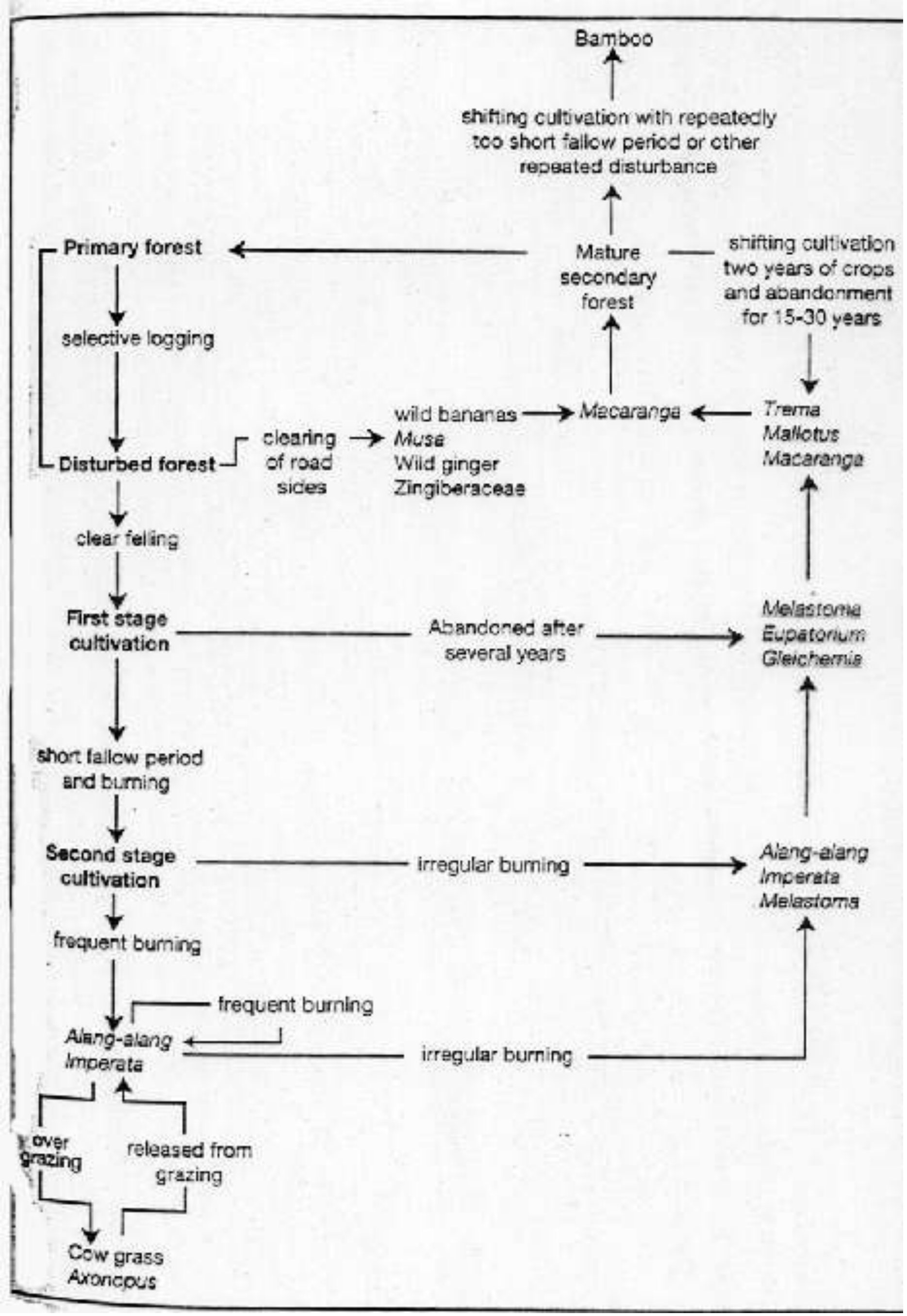


Fig. 18.18 Secondary successions leading to four main grassland communities in tropical rain forest. Paha
Verboom (1968), modified.

Another example of variable succession paths (Malaysia)



Successional paths leading to
(i) primary forest,
(ii) bamboo thickets
(iii) *Imperata* grasslands,
(iv) *Axonotus* grasslands
depending on disturbance regime

Different disturbance events lead to different succession pathways:

Mesquita et al. 2001, J. Ecol. 89:528

Amazonia:

- clear-cut forest sited dominated after 10 years by *Cecropia* spp.
- abandoned pastures by *Vismia* spp.

Vismia guianensis (Clusiaceae)

Cecropia sp. (Cecropiaceae)

Early successional vegetation types

Climbers are particularly abundant in some pioneer vegetation (e.g. riverine)

Some canopy gaps are closed by climbing bamboo thickets (montane forest, Vietnam)

Imperata and other grasslands:

forest succession blocked by fires

Succession on riverine alluvium deposits in Amazonia

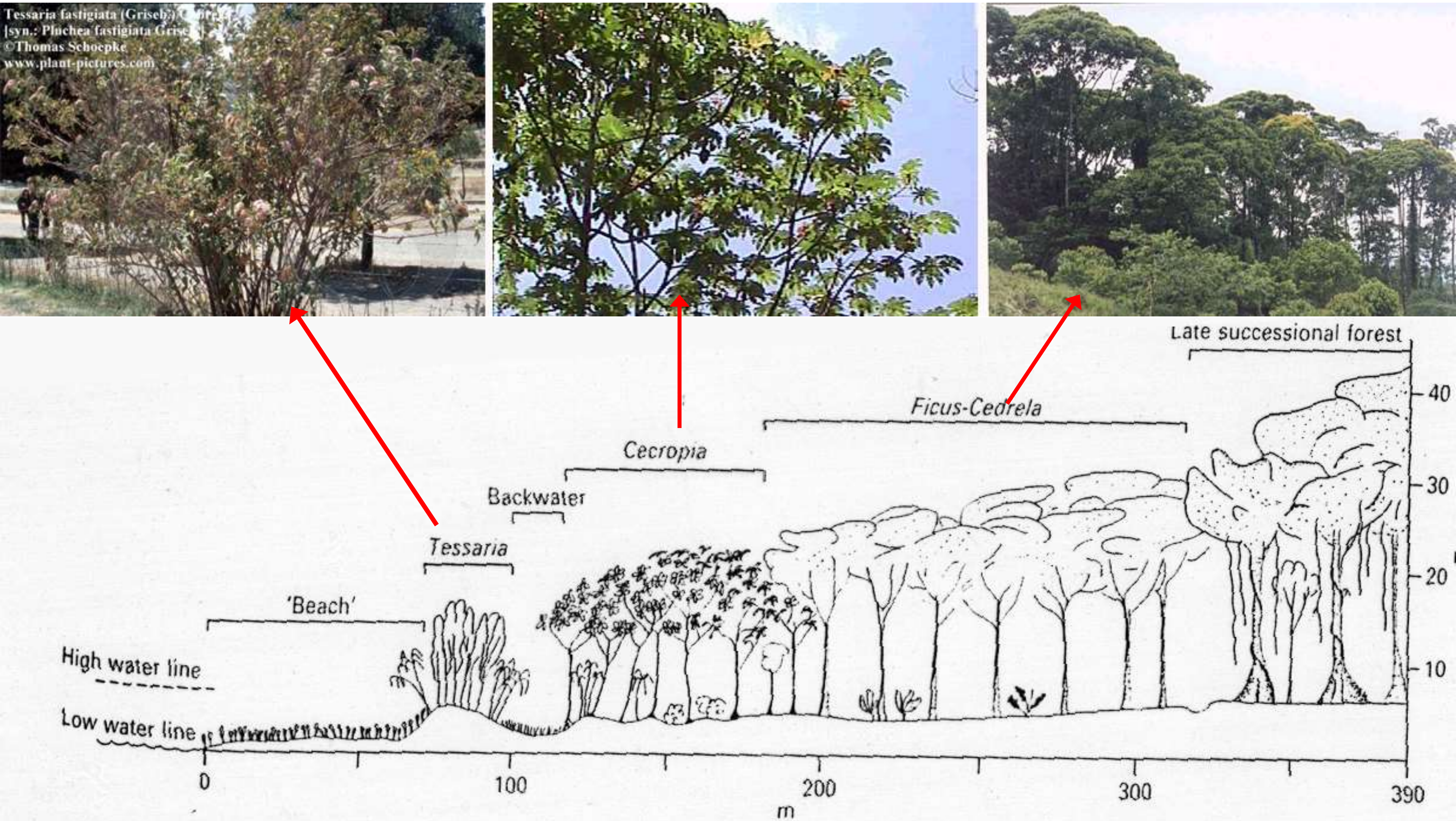
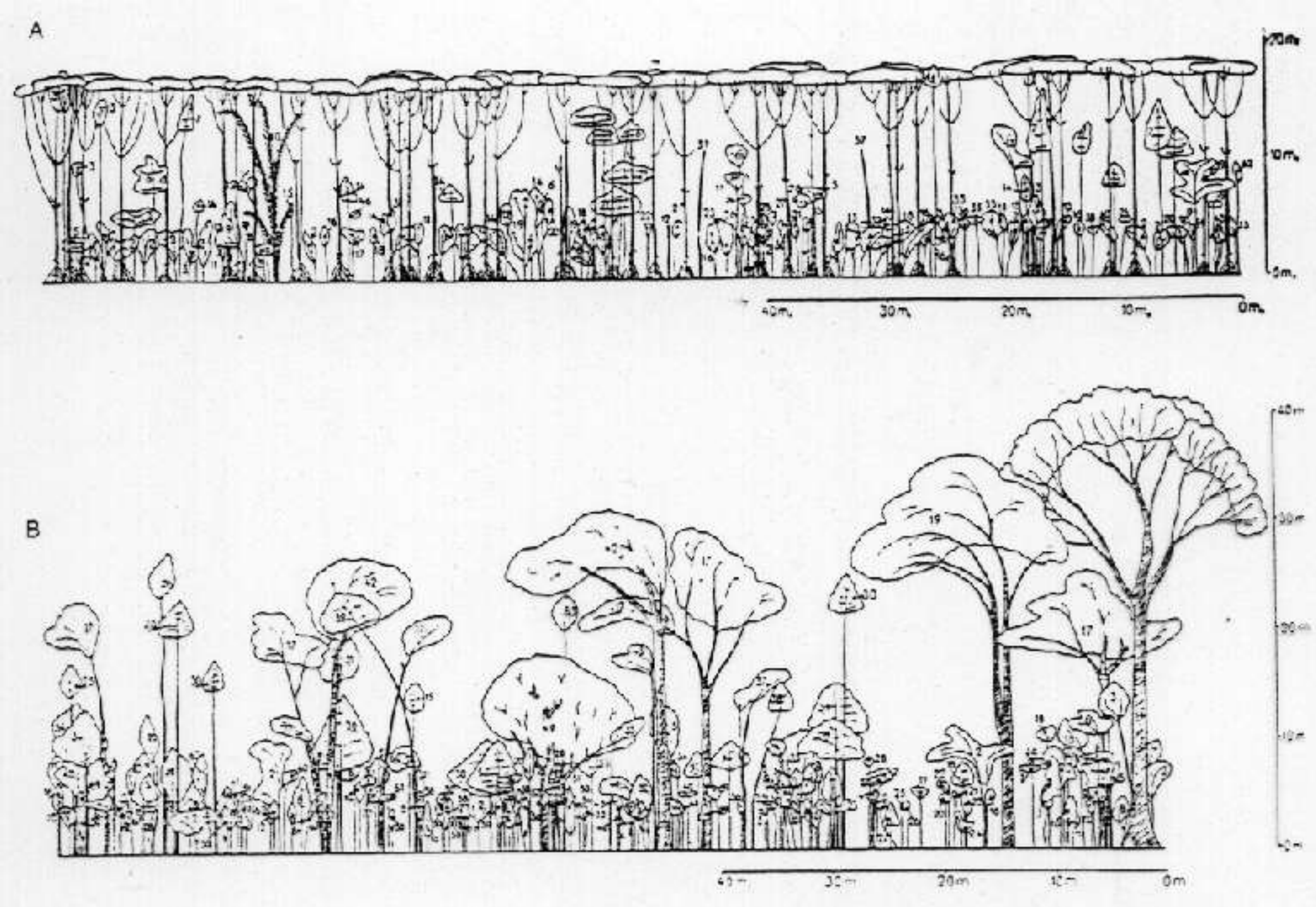


Fig. 7.38. Primary succession on newly deposited riverine alluvium, at Cocha Cashu on the Rio Manu in Peruvian Amazonia. (Salo *et al.* 1986, fig. 3.)



Musanga cecropioides

Louis (1947b). The upper
f which the most abundant
mary or old secondary)
ee is *Scorodophloeus*
0 m wide. Lianes and

Succession from a secondary *Musanga cecropioides* forest to primary forest in Zaire

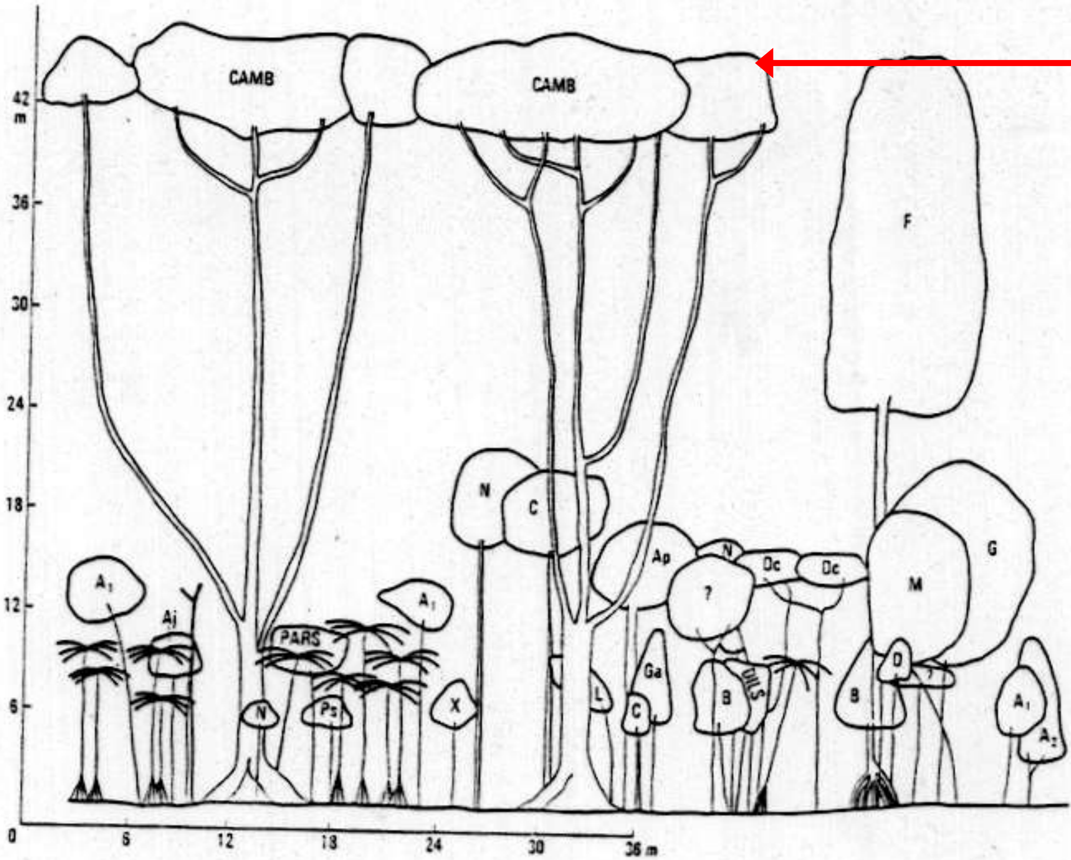


Fig. 2.22. Forest on the north coast of Kolombangara, Solomon Islands, dominated by overmature trees of the light-demanding climax species *Campnosperma brevipetiolatum* (CAMB) which is not regenerating itself (See Whitmore 1974, fig. 2.3 for full species names.)

This forest resulted from massive disturbance, and unless that is repeated it will change in composition to resemble that of Fig. 2.23, whose species are already present in the lower part of the canopy.

Campnospermum brevipetiolatum

The ghost of past disturbance event - *Campnospermum* canopy formed as a result of past massive disturbance but the tree does not regenerate itself so unless there is another disturbance the forest will change Solomon Islands.

Invasive plants in secondary succession:
two species form 30% biomass in a lowland secondary rainforest in Madang, New Guinea

Spathodea campanulata, Bignoniaceae, Africa
Piper aduncum, Piperaceae, tropical America

Some tropical plants from ‘100 worst invasive species’ list aliens are typically limited to secondary forests

Monospecific *Miconia* stand in Tahiti

Miconia calvescens, tropical America

Lantana camara, tropical America

Invasive plants in secondary succession:

two species represent 30% biomass in a lowland secondary rainforest in New Guinea

Spathodea campanulata, Bignoniaceae, Africa
Piper aduncum, Piperaceae, tropical America

Experimental removal of invasive *Piper aduncum* during secondary succession

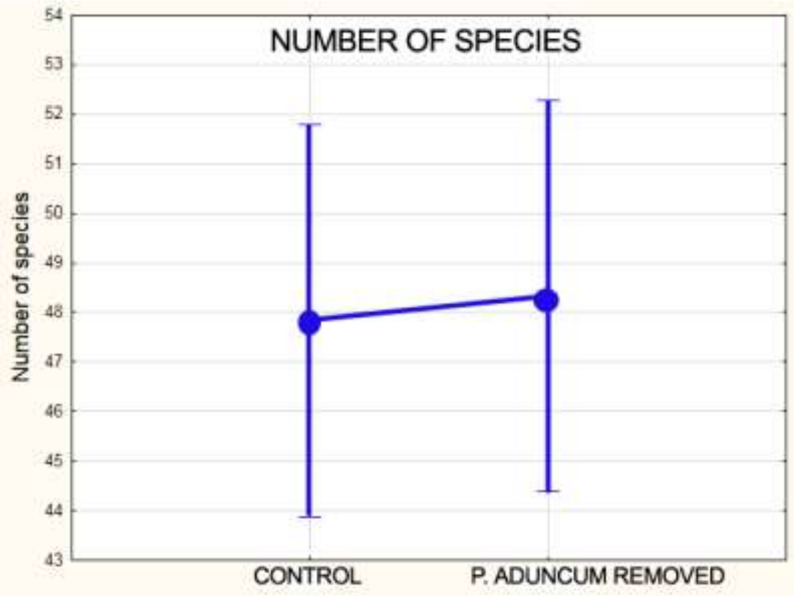
Control

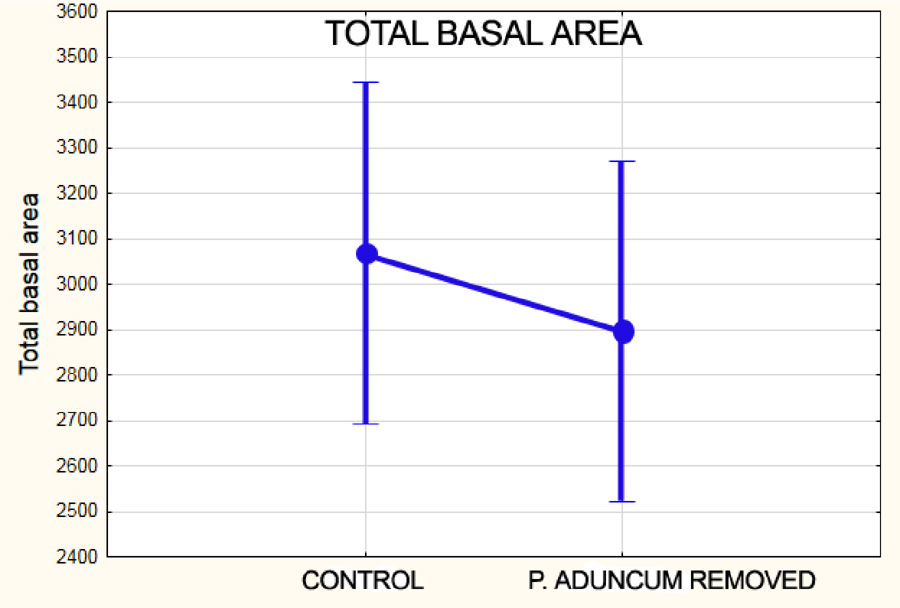
Removal

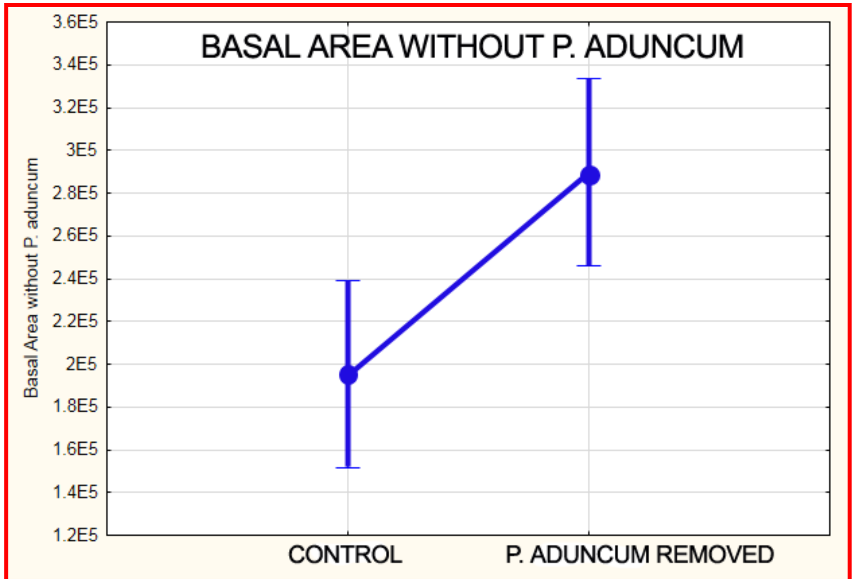
J. Leps

Old gardens (15 x 15 m), 5 pairs of control and experimental plots for 5 years

Piper aduncum removal: no effect on total species diversity and biomass, but increased the biomass of native plant species







Secondary forests:
- phylogenetically clustered vegetation
- open to invasive plants
- herbivore food webs with high connectivity
- top-down and bottom-up control of food webs still not well understood