

The Big
one!LOW-DIVERSITY TROPICAL RAIN FORESTS:
SOME POSSIBLE MECHANISMS FOR THEIR EXISTENCE

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To most ecologists, the tropics are synonymous with diversity, and tropical rain forests are generally regarded as the epitome of complexity and variety. A 1-ha plot can include 250 or more species of trees over 10 cm in diameter (Whitmore 1984). Ecologists most often ask why there are so many species coexisting in one region. We would like to turn the question around and ask why low-diversity communities exist in a region renowned for its great wealth of species. In particular, what mechanisms produce and maintain low diversity among the canopy trees of some tropical rain forests?

In some tropical rain forests, 50% to 100% by number of the canopy trees are one species; we refer to these as single-dominant forests. (Measures of dominance other than numbers of canopy trees could be used, e.g., basal area, biomass, or canopy cover. Because most of the published data are numerical, we used this measure.) As we show, such forests have significantly less diversity in canopy tree species than where the canopy is not so dominated (fig. 1). Such low-diversity single-dominant forests are not rare; they occur commonly in each of the three major world regions of rain forest in Africa, the Americas, and Asia. For example, Richards (1952, p. 257) pointed out that in the huge northeastern basin of the Congo River, at least two-thirds of the area is occupied by rain forests dominated by single species. Richards also listed many examples of such forests in tropical America. Beard (1946) surveyed 40 ha in a Trinidadian rain forest in which 84% of the canopy trees were *Mora excelsa* (Leguminosae). For southeastern Asia, Anderson (1961) described a 527-km² rain forest in Sarawak in which more than three-fourths of the canopy trees were *Shorea albida* (Dipterocarpaceae). *Dryobalanops aromatica* (Dipterocarpaceae) dominates rain forests in patches over several thousand square kilometers in lowland eastern Malaysia (Whitmore 1984). In spite of their commonness, such single-dominant tropical rain forests have seldom been studied by ecologists.

We describe the occurrence and characteristics of these low-diversity forests, compare them with high-diversity ones, and then discuss some hypotheses about possible mechanisms for their existence. In particular, we suggest that maintaining a certain type of mycorrhizal association may enable a single tree species to

CANOPY TREES

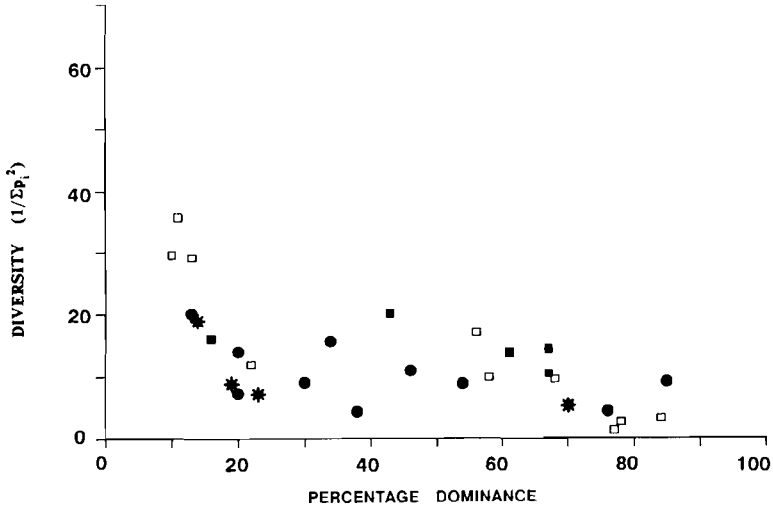


FIG. 1.—Diversity of canopy trees in relation to canopy dominance (the percentage of the most common species; see Appendix B). In calculating the index of diversity, data on the single most common species were omitted, for reasons given in the text). *Circles*, Uganda; *stars*, Nigeria; *solid squares*, Guyana; *open squares*, all other locations. Correlation coefficients: using y as $1/\Sigma p_i^2$, $r = -0.63$, $N = 29$, $P < 0.001$; using y as $e^{H'}$, $r = -0.70$, $N = 29$, $P < 0.001$.

achieve and hold dominance. Finally, we suggest some of the sorts of descriptive data and experiments needed to test the hypotheses.

METHODS

We summarize the results of all the published studies of single-dominant tropical rain forests that we have found to include estimates of the abundance of both canopy trees and seedlings or saplings of the dominant species. Such studies are uncommon; for example, the quantitative surveys by Holdridge et al. (1971) of rain-forest plots with dominant species in Costa Rica do not include data on such regeneration, which is essential for deciding whether the dominant species is persistent or not. We also include unpublished data from two plots in Queensland, Australia, and two in Costa Rica. We then compare the total canopy-tree diversity of these forests with that of other lowland tropical rain forests that are not dominated by a single species. Scientific names are those used in the source references. For each species, family names from O. Allen and Allen (1981) and Willis (1984) are given in the tables.

We have concentrated on forests that occur in places with large species pools, that is, in low-altitude tropical regions with high and relatively nonseasonal rainfall regimes and with soils that are not extreme (Gentry 1982). We did this because, despite the presence of a large species pool in the region, single species have sometimes achieved dominance in tropical rain forests. Single-species domi-

nance is of less interest in regions that have smaller species pools; thus, we have not considered tropical forests at high altitudes, on small islands, or with low or very seasonal rainfall and/or extreme soil conditions, for example, frequently flooded freshwater swamps or mangrove forests, all habitats with few species.

Therefore, all sites included in this paper are at latitudes of less than 18° and elevations below 1100 m (Appendix A). Higher-elevation montane regions have much smaller species pools than lowland ones and are often dominated by one species, for example, the Antarctic beech forests in Australia (Lowman 1986). All examples had at least 166 cm of annual rainfall, and we excluded sites with extreme seasonality, measured as the proportion of months with low rainfall. Thus, tropical seasonally dry forests (e.g., African miombo) are excluded. The seasonality measure we used is the ratio of the number of months with less than 60 mm of rainfall to the number of months with more than 100 mm of rainfall, following the method of Schmidt and Ferguson (1951) as used by Whitmore (1984, p. 54). In all of the 14 locations in Appendix A, this quotient is 0.43 or less. Thus, all examples fall into the three least-seasonal rainfall regimes discussed by Whitmore (1984). Rainfall data come either from the references cited in Appendix A or from Walter and Leith (1960) for the meteorological station nearest the site.

We are also interested in the effect of single-species dominance on the diversity of other organisms in tropical rain forests. Is the diversity reduced for the remainder of the canopy trees or in other components such as subcanopy trees, shrubs, herbs, lianas, epiphytes, animals, fungi, etc.? To answer these questions, we compared the diversity of single-dominant forests with other "mixed" forests with lesser degrees of dominance. The sites used in the comparison are described in Appendix A; data are given in Appendix B. They include all studies known to us in which the abundance of each species was published. At this point, we can compare only the diversity of canopy trees and of subcanopy trees between the two forest types; we have found no published data on other components in both types of forests.

Since we are interested in the effects of the presence of a dominant species on the *other* canopy species, we calculated diversity indexes using data only for the latter, excluding data from the single most common species. This means that, for the same total sample size, the number of canopy trees of species other than the dominant will be smaller in samples from single-dominant forests than in those from mixed forests. For subcanopy trees, we used the data for all species in calculating indexes.

To compare the two types of forests, it is necessary to use a diversity index that is not sensitive to sample size. One possibility is the reciprocal of Simpson's index, $1/\sum_{i=1}^S p_i^2$, where p_i is the proportion of the individuals in species i , and S is the number of species (Peet 1974). Using the data from Appendix B, we found no correlation between this index and sample size (excluding the most common species). For canopy trees, $r = 0.052$, $N = 29$, $P > 0.10$; for subcanopy trees, $r = 0.083$, $N = 30$, $P > 0.10$. Another commonly used index is the exponential form of the Shannon index, $e^{H'}$, where $H' = -\sum_{i=1}^S p_i \log p_i$. This index was significantly correlated with sample size for canopy trees ($r = 0.357$, $N = 29$, $P = 0.05$) but not

for subcanopy trees ($r = 0.017$, $N = 30$, $P > 0.10$). For these reasons, we used the reciprocal of Simpson's index.

DESCRIPTIONS OF RAIN FORESTS WITH SINGLE-SPECIES DOMINANCE IN THE CANOPY

We classified single-dominant forests into two categories on the basis of whether or not the canopy dominant persists at the site beyond one generation in the absence of disturbances larger than individual tree falls. This classification is needed to distinguish forest stands in which it is likely that different mechanisms operate to produce single dominance. The criteria we used to classify each forest were (1) the abundance of juveniles (seedlings and small saplings) of the dominant species in undisturbed stands, (2) observations by the authors of the requirements for germination and survival of these juveniles, and/or (3) observations of the disturbance history of the site. If juveniles of the dominant were relatively common beneath the intact canopy or known to be tolerant of conditions near conspecific adults, or if there was no history of disturbance other than small tree falls, it was classified as type I. If the juveniles of the canopy dominant were absent in undisturbed stands but common in disturbed sites, if the authors observed that its seedlings require high light levels for germination and survival, and/or if the site had been disturbed and was undergoing colonization, we classified the stand as type II. Although these criteria are necessary, they are not sufficient to decide whether a species is persistent. Further observations of survival would be needed for an unequivocal judgment of persistence.

Type I: Rain Forests with a Persistent Dominant

In the first type of single-dominant rain forest (type I), the dominant species persists beyond one generation and continues to dominate. Its seedlings are tolerant of conditions beneath the canopy of conspecific adults and are thus likely to be common enough to enable the species to persist locally. The species may achieve dominance either by colonizing a large open patch as do type-II species but, in contrast, persisting beyond one generation or by gradually invading an existing forest via tree-by-tree replacement.

Davis and Richards (1934) were among the first to document in detail this type of single-dominant tropical rain forest. Three of their five plots in Guyana were in stands dominated by a single species that had abundant seedling and sapling regeneration, indicating that it would probably be persistent (table 1, sites 8, 9, 10). In Trinidad, one of these species, *Mora excelsa*, appears to be increasing in range, gradually invading the mixed, highly diverse forest (Marshall 1934; Beard 1946; Rankin 1978; see table 1, site 7). Because it has large, heavy seeds that are not dispersed far beyond the adult crown, its rate of spread is slow except when the seeds are moved by water in swamps or by floods. *Mora* forms a canopy at heights of 30–40 m, whereas the mixed-forest canopy is at 20–30 m. A similar invasion of mixed forest of *Gilbertiodendron dewevrei* (Leguminosae) is apparently occurring in Zaire (Hart et al. 1989).

Among the 12 study plots listed in table 1, the canopy dominant was also the most common species in the subcanopy layers at 5 of the sites and almost as

TABLE 1
TYPE-I RAIN FORESTS WITH PERSISTENT DOMINANT SPECIES

DOMINANT SPECIES*; LOCATION	SITE	NO. OF SPECIES (NO. OF INDIVIDUALS)		DOMINANT SPECIES			MOST-COMMON SUBCANOPY SPECIES (%)	SOURCE
		Canopy	Subcanopy	% of Canopy	% of Subcanopy	% of Seedlings		
<i>Gilbertiodendron dewevrei</i> (C); Bambesa, Uele R., Zaire	1	8 (244)	14 (274)	77	69	> 50	(dominant)	Gérard 1960, table VI
<i>Gilbertiodendron dewevrei</i> (C); Yangambi, Congo R., Zaire	2	1 (15)	37 (86)	100	9	> 50 of canopy spp.	<i>Isolona thon- neri</i> (16)	Louis 1947, figs. 5, 6
<i>Brachystegia laurentii</i> (C); Yangambi, Congo R., Zaire	3	6 (12)	10 (22)	58	18	abundant	<i>Garcinia punc- tata</i> (23)	Germaine & Evrard 1956, fig. 2
<i>Cynometra alexandri</i> (C); Budongo, Uganda	4	6 (109)	8 (484)	76	8	abundant	<i>Lasiodiscus mildbraedii</i> (62)	Eggeling 1947, plot 9
<i>Cynometra alexandri</i> (C); Budongo, Uganda	5	13 (97)	13 (252)	85	13	abundant	<i>Lepidoturus laxiflorus</i> (62)	Eggeling 1947, plot 10
<i>Tetraberlinia tubmaniana</i> (C); Bomi Hills, Liberia	6	13 + (43)	23 + (260)	56	40	abundant	(dominant)	Voorhoeve 1964, table 3

<i>Mora excelsa</i> (C); Mayaro, Trinidad	7	39 (3064)	82 (9488)	84	55	93% of ground cover	(dominant)	Beard 1946, table 1
<i>Mora excelsa</i> (C); Moraballi, Guyana	8	11 (67)	63 (395)	67	16	abundant	(dominant)	Davis & Richards 1934, plot I
<i>Mora gonggrijpii</i> (C); Moraballi, Guyana	9	21 (89)	65 (371)	61	18	abundant	(dominant)	Davis & Richards 1934, plot II
<i>Eperua falcata</i> (C); Moraballi, Guyana	10	15 (100)	70 (819)	67	16	abundant	<i>Catostemma fragrans</i> (17)	Davis & Richards 1934, plot V
<i>Pentaclethra macroloba</i> (M); La Selva, Costa Rica	11	43 (239)	171 (1443)	51	5	6†	—	D. & M. Lieberman, G. Hartshorn, & R. Peralta, unpubl. data, plot I
<i>Pentaclethra macroloba</i> (M); La Selva, Costa Rica	12	43 (210)	166 (1903)	59	7	5†	—	D. & M. Lieberman, G. Hartshorn, & R. Peralta, unpubl. data, plot III

NOTE.—We included all studies found that had estimates of the abundance of seedlings of the dominant species. The percentages are based on the number of trees in the designated layer.

* Subfamily of the Leguminosae: C, Caesalpinioideae; M, Mimosoideae.

† Percentages are based on 1921 seedlings at site 11, 1719 seedlings at site 12; no data from these sites on the most common subcanopy species.

TABLE 2

TYPE-II RAIN FORESTS WITH NONPERSISTENT DOMINANT SPECIES

DOMINANT SPECIES (FAMILY); LOCATION	SITE	NO. OF SPECIES (NO. OF INDIVIDUALS)		DOMINANT SPECIES			MOST-COMMON SUBCANOPY SPECIES (%)	SOURCE
		Canopy	Subcanopy	% of Canopy	% of Subcanopy	% of Seedlings		
<i>Bacchousia bancroftii</i> (Myrtaceae); Queens- land, Australia	13	12 (66)	42 (192)	68	21	few in forest; abundant at clear- cut sites	<i>Myristica in- sipida</i> (23)	this study
<i>Shorea albida</i> (Dipterocarpaceae); Baram, Sarawak	14	4 (45)	22 (104)	78	0	none	<i>Gonystylus bancanus</i> (12)	Anderson 1961, table I, plot 1
<i>Maesopsis eminii</i> (Rhamnaceae); Budongo, Uganda	15	12 (105)	37 (657)	70	2	none	<i>Maba abys- sinica</i> (22)	Eggeling 1947, plot 3
<i>Musanga cecropioides</i> (Urticaceae); Shasha, Nigeria	16	9 (77)	29 (274)	70	6	none	<i>Discogly- premna caloneura</i> (49)	Ross 1954, plot I
<i>Musanga cecropioides</i> (Urticaceae); Shasha, Nigeria	17	3 (18)	23 (255)	89	0.4	none	<i>Sarcocephalus diderichii</i> (21)	Ross 1954, plot II

NOTE.—We included all studies found that had estimates of the abundance of seedlings of the dominant species. The percentages are based on the number of trees in the designated layer.

abundant as the most common at site 3; species other than the canopy dominant were most common in the subcanopy at the remaining 6 sites. In every case in table 1, the degree of dominance was greater in the canopy than in the subcanopy layers. Anecdotal evidence indicates that seedlings of the canopy dominant were common at 10 sites. At sites 11 and 12, the seedlings are known to be shade-tolerant (Hartshorn 1972, 1975, 1978). Another point worth emphasizing is that although one species dominates the canopy, many other species are present, particularly in the subcanopy.

Other examples of rain forests in which the dominant appears to persist beyond one generation have been described with anecdotal evidence. These forests are all described as having abundant seedlings and saplings or regenerating vegetative sprouts of the dominant species. Five examples are listed in Appendix C. In addition to these examples, many other rain forests dominated by single species have been described without sufficient evidence about regeneration to enable us to decide whether they were persistent or not. Examples are listed in Appendix C. Quantitative information on seedling and sapling abundance of the dominant species is clearly needed as a first step toward understanding the mechanisms underlying this phenomenon.

Type II: Rain Forests with a Nonpersistent Dominant

It is well known that colonizers of recently disturbed sites often have shade-intolerant seedlings that grow rapidly under full sunlight (Richards 1952). Because their seedlings cannot establish beneath a canopy, the dominant seldom if ever persists beyond one generation unless another relatively large disturbance occurs. An interesting example comes from a study of peat swamps in Sarawak (Anderson 1961, 1964). The dipterocarp *Shorea albida* forms long-lived single-dominant stands with a canopy 50–60 m in height, but without regeneration; in table 2, site 14 is an example from an undisturbed plot. In 1948, approximately 20% of the trees of the dominant species in a 527-km² forest were defoliated by a plague of unidentified "hairy caterpillars," probably tussock moths. Most of the damaged *S. albida* died over the next 10 yr. Since the subcanopy species were not damaged, the lower vegetation cover was left intact, and no seedling regeneration of *S. albida* occurred. In contrast, when a severe storm exposed a large patch (about ¼ ha) of ground surface, seedling regeneration of *S. albida* occurred (Anderson 1964).

Table 2 lists examples of this category taken from the few studies that we found having quantitative surveys of canopy and subcanopy trees along with estimates of the degree of seedling regeneration of the dominant species. Of the five sites in this table, the canopy dominant was rare in both the subcanopy and seedling layers at four sites and rare as a seedling at one. The subcanopy trees at the latter site may represent individuals in the initial cohort of colonists that became suppressed by other faster-growing members of the cohort that formed the canopy. Several other examples of forests that appear to fall into this category have been described, but without sufficient quantitative data; these are listed in Appendix C, type-II forests.

SUBCANOPY TREES

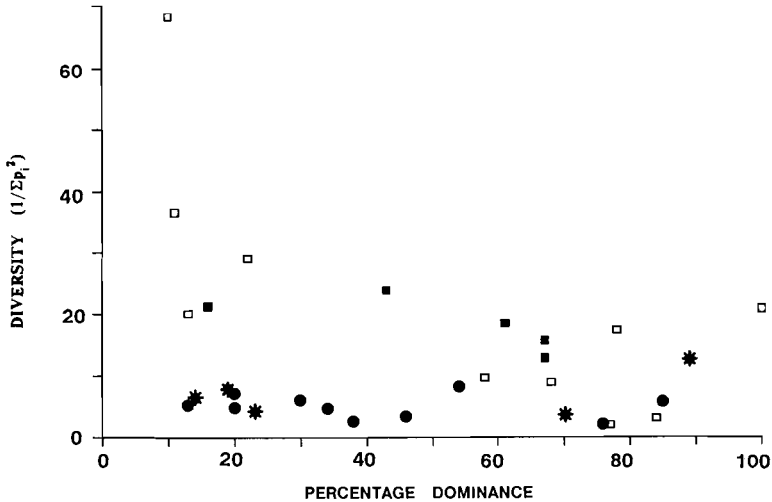


FIG. 2.—Diversity of subcanopy trees in relation to dominance in the canopy (as indicated by the percentage of the most common canopy species; see Appendix B). Symbols as in figure 1. Correlation coefficients: using y as $1/\Sigma p_i^2$, $r = -0.30$, $N = 30$, $P > 0.05$; using y as $e^{H'}$, $r = -0.33$, $N = 30$, $P > 0.05$.

*Effects of Single Dominance on the Diversity of
Other Canopy and Subcanopy Trees*

Figure 1 shows that the diversity of canopy trees (other than the most common species) decreases with increasing dominance by a single species. The pattern shown in figure 1 for $1/\Sigma p_i^2$ is very similar to that when $e^{H'}$ is used as an index; the regression equations for both indexes are given in figure 1, and the data are given in Appendix B. Figure 2 shows that the relationship between canopy dominance and the diversity of subcanopy trees is much weaker and more variable than it was for canopy trees; the correlation coefficient was not significant ($P > 0.05$). Thus, with a single species dominating the canopy, diversity of other canopy trees is significantly reduced, whereas subcanopy trees are not affected.

These relationships are not affected by the locations of the different studies. As shown in figures 1 and 2, the three locations with five or more study plots (Guyana, Uganda, and Nigeria) each show the same trend as that for all sites combined. Moreover, type-I and type-II forests do not differ significantly in the diversity of either the other canopy trees or subcanopy trees (Appendix B, note).

MECHANISMS THAT COULD PRODUCE SINGLE-SPECIES DOMINANCE
IN TROPICAL RAIN FORESTS

Most of the recent discussions of diversity in tropical rain forests concern the mechanisms that promote it (e.g., reviews in Connell 1978, 1979; Hubbell 1979, 1980; Hubbell and Foster 1986). However, some authors have proposed mecha-

TABLE 3

SOME MECHANISMS THAT COULD PRODUCE LOW DIVERSITY AMONG CANOPY TREES
IN TROPICAL AND SUBTROPICAL RAIN FORESTS

Type I: Dominant species persists beyond one generation

The juveniles of the dominant can establish and survive beneath unbroken canopy or in small tree-fall gaps. For several reasons, only a single species achieves dominance and persists.

A. Initial establishment of dominance

1. The dominant is the most common species first colonizing a large open patch.
2. The dominant gradually invades an existing rain forest by tree-by-tree replacement. It replaces existing species because it is superior to all other local species for one of the following reasons:
 - a. it is the most resistant to deleterious physical conditions or natural enemies (e.g., pathogens, parasites, herbivores); or
 - b. it is the superior competitor either in interference or in exploitation of resources.

B. Persistence beyond one generation

Once established, the dominant species persists for one or both of two reasons.

1. Its juveniles are so much more abundant than those of other canopy species that it has a higher probability of replacement, all other things being equal.
2. It is superior to all other local tree species for one or both of the reasons under A2.

Type II: Dominant species does not persist beyond one generation

Early invaders of a large patch soon after it is cleared by a disturbance often do not persist because their juveniles cannot establish and survive beneath unbroken canopy or in small tree-fall gaps. These colonists are often members of a single species for two reasons.

A. Only a short time is available for invasion before canopy closure.

B. Few species of trees are adapted to tolerate the conditions in a large, recently disturbed patch.

nisms that could lead to low diversity in rain-forest canopy trees (Richards 1952; Janzen 1974; Connell 1978, 1979; Malloch et al. 1980; Janos 1980a, 1983, 1985; Whitmore 1984; Alexander 1989). In this section, we review these suggestions, add others of our own, and propose a series of mechanisms that could produce single-species dominance in rain forests (listed in table 3).

Type I: Rain Forests with a Persistent Dominant

Seedlings of the species that dominate and persist in type-I forests must be able to establish and survive well beneath unbroken canopy or in small tree-fall gaps. A single species could initially achieve dominance in either of two ways: it could be the most common species quickly invading a large open patch, as in type-II forests, or it could gradually invade an existing rain forest by tree-by-tree replacement (table 3). In the first case, if the dominant produces abundant seeds that disperse into the large open patch during the short period available before initial canopy closure, these could grow to dominate the stand. Such a process has been observed twice for *Pentaclethra maculosa* (Leguminosae), a type-I dominant at La Selva, Costa Rica (Hartshorn, pers. comm.).

Alternatively, it could gradually invade an existing diverse rain forest by tree-by-tree replacement if it had some ecological advantages over all other species in these forests (table 3). First, the dominant might be the most resistant of all local species to deleterious physical conditions or to natural enemies (i.e., pathogens, parasites, or herbivores). For example, the dominant might tolerate unfavorable soils better than any other local species (Richards 1952, p. 262). Hartshorn (1972)

suggested that restrictive physical conditions, particularly poor soils, excluded many potentially competing species from his study site, and because *Pentaclethra macroloba* has excellent defenses against seed predation, it was able to reach dominance. The dominant also might have better protection than other species against herbivores through adaptations such as chemical toxins or mast fruiting at long intervals that might satiate seed predators (Janzen 1974). However, Boucher (1981) found that the latter applied only after the species had achieved dominance. When *Quercus oleoides* (Fagaceae) in Costa Rica was relatively rare, all its acorns were eaten; when it dominated the forest, some acorns survived to germinate. Thus, predator satiation enabled the species to maintain dominance but not to achieve it.

Second, the dominant might be superior to all other local species in interference competition. Such interference might operate indirectly, via soil microorganisms, as demonstrated by Kaminsky (1981) for allelopathy in temperate shrub species. Third, the dominant might be the most efficient in exploitative competition for resources such as light, water, or soil nutrients.

Once established, the single dominant species could persist beyond one generation for at least two reasons. First, its offspring are likely to be so much more abundant than those of the other uncommon canopy species that the dominant has a higher probability of replacing itself, all other things being equal. Whitmore (1984) suggested that such "reproductive pressure" might be responsible for the persistence of the dominant *Dryobalanops aromatica* in Malaya. Second, it would be more likely than other local species to replace itself if it were superior to them in resistance to deleterious physical conditions and natural enemies and/or in competition, as described above. A likely mechanism that could confer all these advantages on a single species is a particular type of mycorrhiza.

The Mycorrhiza Hypothesis for Type-I Forests

It has been suggested that plants of similar growth form living in the same type of habitat, such as trees in the canopy of rain forests in a local region, have quite similar requirements for resources (Connell 1978; Aarssen 1983; Goldberg and Werner 1983). Although species in different habitats (e.g., different vertical strata, slopes, aspects, etc.) exhibit important differences in requirements and tolerances for light, water, and mineral nutrients, it is difficult to conceive of mechanisms that could confer on a single species ecological advantages over many others within a single habitat, as the hypotheses in table 3 require. However, since most of the single dominant species in type-I forests belong to a few plant families and are often found on soils poor in available nutrients or water, one possible mechanism for conferring ecological advantages on a single tree species is the possession of one type of mycorrhizal association (Janos 1980a, 1983, 1985; Malloch et al. 1980; Alexander 1989). The significance of this fact derives from the differences between the two common types of mycorrhizae found on forest trees, the vesicular-arbuscular mycorrhizae (VAM) and the ectomycorrhizae (EM).

Janos (1983, 1985) has summarized the advantages that both types offer to the host plant. Both improve the performance of the host tree by increasing the uptake of mineral nutrients and water from the soil (Bowen 1980). However, EM

TABLE 4

CHARACTERISTICS OF ECTOMYCORRHIZAE (EM) AND VESICULAR-ARBUSCULAR MYCORRHIZAE (VAM)
RELEVANT TO SINGLE-SPECIES DOMINANCE IN TROPICAL RAIN FORESTS

Morphology

EM have more-massive structures external to root: sheath often covers root; hyphal strands longer, larger; internal structures may resemble roots. Thus, EM can exploit more efficiently a larger soil volume than VAM (Bowen 1980; Janos 1983, 1985). EM spores are more numerous, smaller, and wind-dispersed. VAM spores are larger, less widely dispersed.

Physiology

EM can take up organic nitrogen (Alexander 1983) and probably decompose organic litter directly (Trojanowski et al. 1984, in laboratory). VAM have never been cultured axenically and probably cannot decompose organic matter directly, although they have been grown in the laboratory with cut pieces of root (Warner and Mosse 1980). EM may reduce the rate at which saprophytic microorganisms decompose litter in low-nutrient soils (Gadgil and Gadgil 1971, 1975; Harmer and Alexander 1985). These two traits may enable EM to secure nutrients from litter *before* VAM can get them. A supporting example is a Brazilian white-sand forest dominated by EM trees; in this forest there were fewer saprophytic fungi and more litter accumulation than in a nearby forest in fertile soils, where EM were rare and VAM common (Singer and Araujo 1979).

Costs and benefits

EM probably cost the host more in energy than VAM because EM have relatively greater biomass and because enzymes that decompose litter may pose a greater hazard to host tissues (Malloch et al. 1980; Janos 1983, 1985; St. John and Coleman 1983). In low-nutrient soils, maintenance costs may exceed benefits (Slankis 1974). In high-nutrient soils, a host may reject the fungus for the same reason (Slankis 1974; Janos 1983).

Protection of host

EM offer the host excellent protection from natural enemies and stressful physical conditions (Marx 1972). In contrast, VAM may either increase or decrease the effect of natural enemies on hosts (Dehne 1982).

Host specificity

EM are relatively more host-specific than are VAM (Gerdemann 1968; Mosse 1973; Gerdemann and Trappe 1974; Trappe and Fogel 1977; Hall and Fish 1979; Janos 1980b; Redhead 1980). EM tree species have been found to also have VAM (Becker 1983; St. John and Coleman 1983; St. John and Uhl 1983).

Occurrence on tropical trees

Most tropical tree species surveyed in the Americas and Africa have VAM. EM are common in the tropics only in the plant families Dipterocarpaceae, Fagaceae, Myrtaceae, Leguminosae (Caesalpinioideae), and a few other families. Genera in table 1 and Appendix C from these families that have been found with EM are *Gilbertiodendron*, *Brachystegia*, *Eperua*, *Quercus*, and *Shorea* (Fassi and Fontana 1962; Trappe 1962; Fassi 1963; Singh 1966; Redhead 1968; Horak 1977; Malloch et al. 1980; Alexander 1989). *Mora* had VAM (Johnston 1949; EM were not recorded in his survey); Norris (1969) described *Mora* roots as resembling *Eperua*, which has EM. Seedlings of *Mora oleifera* from Golfito, Costa Rica, appeared to have EM (St. John, pers. comm.). *Cynometra* from nursery plots had VAM (Norani 1983).

have several characteristics that should give their hosts an advantage over those with VAM (these are summarized in table 4).

Given the superiority of EM over VAM as described in table 4, how might possession of the EM association allow a single tree species to achieve dominance and then persist at a site? Several authors have suggested possible mechanisms. The first was Baylis, who stated that an EM tree might achieve dominance by having "an exclusive fungus partner in the soil" (1975, p. 384). Malloch et al. (1980, p. 2115) suggested that there could be niche differentiation among the

TABLE 5

QUANTITATIVE SURVEYS OF MYCORRHIZAE THAT LOOKED FOR BOTH VESICULAR-ARBUSCULAR MYCORRHIZAE (VAM) AND ECTOMYCORRHIZAE (EM) IN TROPICAL AND SUBTROPICAL RAIN FORESTS

LOCATION	NO. OF SPECIES EXAMINED	SPECIES (%)			SOURCE
		VAM	EM	No Mycorrhizae	
Nigeria	51	86	6	8	Redhead 1968
Sri Lanka	63	86	8	6	Alwis & Abeynayake 1980
Brazil	86	67	3	29	St. John 1980
Venezuela*					
Terra Firme	8	87	25	0	St. John & Uhl
Caatinga	4	100	50	0	1983

* Species having both VAM and EM (one in the Terra Firme forest, two in the Caatinga) were included in both categories.

different species of EM fungi and that adjacent conspecifics could avoid competition for soil nutrients by using different fungal partners. They surmised that EM species would be inferior competitors to VAM (p. 2116). Janos (1983, 1985), summarizing a large literature, suggested several reasons why the EM association could have a competitive advantage over the VAM association on soils with low or variable nutrients (see table 4). Alexander (1989) suggested that EM legumes would have a competitive advantage over VAM trees in soils with low or variable nutrients and that once an EM tree species achieved dominance, only individuals capable of forming ectomycorrhizae could be incorporated into the existing mycelial network. Presumably, this is true because VAM fungal spores or mycelia would be rare or absent in such stands.

At this point, we propose a hypothetical sequence by which a single species of tropical EM tree could achieve dominance and then persist beyond one generation. The sequence involves three steps: invasion of a site by a single species of EM tree, its increase accompanied by the decrease of the other tree species, and its persistence beyond one generation.

Gradual invasion of EM into a VAM forest.—It is likely that only a single species of EM tree with its EM fungus will gradually invade a diverse tropical rain-forest site and achieve dominance for several reasons. These involve the rarity and greater host specificity of EM over VAM associations in the tropics. EM associations are rare in the tropics except where members of the Dipterocarpaceae dominate forests in the region of the central Sunda shelf of southeastern Asia (Whitmore 1984). All dipterocarps that have been examined have the EM association (Singh 1966; Horak 1977). Elsewhere in southeastern Asia, where dipterocarps are a lower proportion of the canopy species (Alwis and Abeynayake 1980), and in Africa and South and Central America, the majority of the tree species that have been examined in tropical rain forests have VAM; only a small sample from one of the Venezuelan sites had a high proportion of EM (table 5). These findings should be regarded as tentative at this time. As shown in table 5, we have found only four surveys of the incidence of mycorrhizae in which both

VAM and EM were recorded. Other surveys looked for only one type, either VAM (Janse 1896; Johnston 1949) or EM (Singh 1966; Horak 1977; Singer and Araujo 1979). Moreover, only two studies (St. John 1980; St. John and Uhl 1983) took into account the relative abundance of the different tree species, which would indicate the actual abundance of the different types of mycorrhizae. Finally, apparently no surveys of mycorrhizae in a number of species in single-dominant stands have yet been made.

If we accept the findings in table 5 that most species in diverse Neotropical and African rain forests have VAM, there would probably be few species of EM fungal spores or mycelia present in the soil. Given the relatively greater host specificity of EM fungi compared with VAM fungi, few of the invading tree species capable of forming an EM association would be able to do so with the particular EM fungal species present. Even though EM tree invaders may form an association with VAM (since VAM fungi are not host-specific and EM trees have been found also to have VAM, as described earlier), if they cannot also form an association with the EM fungal species already present, they will probably be at a competitive disadvantage compared with those that can do so. With all these constraints, we suggest that an EM invasion of a VAM forest will frequently involve only a single species.

Replacement of VAM trees by EM trees.—If a tree species with an EM association were invading gradually, it would tend to replace the resident tree species with the VAM association. As pointed out in table 4, the EM association is apparently more resistant to deleterious physical conditions (e.g., water stress) or to natural enemies (e.g., pathogens) than is the VAM association. In addition, EM fungi may interfere directly with VAM fungi by producing toxins. Such interference by EM fungi against decomposer organisms has been suggested (Gadgil and Gadgil 1971, 1975). Finally, EM fungi may give their hosts a greater competitive advantage in exploiting soil nutrients than do VAM fungi, for the reasons shown in table 4.

Persistence of a single dominant EM species.—Once a tree species with an EM association occupies much of a stand, either as the first colonizer of a disturbed site or after gradual tree-by-tree replacement, it may continue to persist for several reasons. First, a high proportion of the fungal mycelia and spore populations in the soil should belong to the particular EM fungi associated with the dominant tree species. This increases the chances both of inoculating new seedlings of the dominant species and of maintaining the population of the fungus (Janos 1980a, 1983). Any arriving spores of other EM fungal species that happen to be suitable for association with the dominant tree should be able to establish and persist, whereas spores of unsuitable species will eventually perish for lack of a host. Kovacic et al. (1984) found that in a forest dominated by ponderosa pine (an EM species) in Colorado, the understory plants were mainly non-mycorrhizal and there were few VAM spores in the soil. In single-dominant forests that also have VAM tree species, newly arriving species are probably able to form an association with the VAM fungi present. However, if they cannot associate with the EM fungal species present, they are at a competitive disadvantage, for the reasons given above. If the seedlings of the dominant can tolerate the other

physical and biotic conditions associated with conspecific adults, the species tends to persist for more than one generation.

Persistence of the dominant may be aided by a characteristic of such forests that may reduce disturbance rates. Rankin (1978) observed many tree falls after a hurricane in a diverse forest in Trinidad, but none in the adjacent forest on the same terrain dominated by *Mora excelsa*. She suggested that the more even canopy characteristic of single-dominant forests reduces wind damage. Given the positive feedbacks of this mutualistic system, the single dominant species should gradually increase in abundance and spread in area as well, as is apparently happening with *M. excelsa* in Trinidad (Marshall 1934; Beard 1946; Rankin 1978). Again, this contrasts with diverse VAM forests, where, because all trees share similar fungi, the VAM association should not confer a competitive advantage on a single species.

Seven of the eight species in table 1 are members of the subfamily Caesalpinioideae of the Leguminosae. Because legumes often have nitrogen-fixing bacteria in root nodules, the question arises whether their advantage could lie in this symbiosis. O. Allen and Allen (1981) found that only 28% of the species of Caesalpinioideae were nodulated, whereas over 90% were nodulated in the Mimosoideae and Papilionoideae. In the one mimosoid genus in table 1, *Pentaclethra*, one species has been tested and was nodulated. Five of the six caesalpinoid genera in table 1 have been tested for nodulation: two were negative, one was positive, two had some species positive and some negative. Thus, single-species dominance seems not to be strongly associated with a nitrogen-fixer symbiosis. At this point it is impossible to be more definite, since we have not found a case in which the same species has been examined for both nodulation and mycorrhizal type.

These points can be summarized in the following "mycorrhiza hypothesis." A single tree species could either quickly invade a large disturbed patch or gradually replace other species and persist in some tropical rain forests as a result of a particular EM association not shared by other local tree species. Only a single species of tree with an EM association invades either because it is the first colonizer of disturbed patches and/or because the EM fungus is relatively rare and host-specific to that species. If it invades gradually, the species should increase and replace tree species with only a VAM association because of its greater ability to secure organic and mineral nutrients both before and after they become available to VAM trees or non-mycorrhizal species and/or because of its greater protection against deleterious physical conditions and natural enemies. It should also continue to persist because of these advantages over VAM trees and because few other tree species can invade and form an association with the particular species of EM fungus on the dominant.

The studies in table 4 indicate that the EM association should be more advantageous to the host than the VAM association. Therefore, one might expect most tropical forests to be dominated by trees having an EM association. This may not occur for several reasons. First, VAM may be superior to EM in some soils since the costs to the host are probably lower for VAM (table 4). Second, although EM are superior to VAM in procuring nitrogen from organic sources, VAM may be

superior to EM in garnering other soil nutrients, for example, phosphorus. To our knowledge there is no published evidence of such a superiority of VAM, probably because there are few studies that compare directly any physiological or ecological properties of EM and VAM. Third, EM trees invade and supplant VAM trees only if this process of competitive elimination is not counteracted by other factors such as disturbance, niche diversification, competitive equivalence, environmental variation, and compensatory mechanisms acting on recruitment, growth, or mortality (Connell 1978, 1987; Connell et al. 1984; Chesson and Case 1986). The operation of such factors may in part account for the rarity of EM species in many tropical rain forests.

Type II: Rain Forests with a Nonpersistent Dominant

Type-II forests are created when a relatively large open patch is invaded by shade-intolerant trees. The patch may be an area of grassland or shrubland being invaded by the forest (Eggeling 1947) or a large patch recently opened by an intense disturbance. The disturbed patch must be large enough that the group of trees colonizing it will constitute a recognizable forest stand. For the purposes of definition, let us assume that a grove of 100 canopy trees represents such a stand. In the examples of type-II forests in table 2, the average population density of canopy trees of at least 20 cm in diameter at breast height (dbh) was 93 per ha. On this basis, we suggest that a disturbed patch of about 1 ha, which would contain about 100 canopy trees, represents the minimum size of disturbed patch required to create a type-II forest stand.

This size is much larger than most canopy gaps formed by tree falls. In lowland rain forests in Costa Rica, Hartshorn (1978) measured gaps ranging up to 376 m², and Sanford et al. (1986) found them ranging up to 780 m². On Barro Colorado Island, Panama, Brokaw (1985) studied gaps ranging up to 705 m². These workers pointed out that larger gaps occur less frequently than smaller ones. However, all regions experience occasional strong windstorms or floods, landslides, hurricanes with intense rain, and droughts, which can be followed by fires, all of which can produce very large gaps. Some tropical regions are subject to these intense disturbances more frequently than others. For example, Salo et al. (1986) found that about 12% of the forest in the upper Amazon basin was in successional stages on newly deposited soils caused by channel changes of the meandering rivers. Early-colonizing type-II forests dominated by single species occupied some lesser proportion of such areas. Anderson (1964) described large gaps ranging up to 100 ha in peat-swamp forests in Sarawak, caused by windstorms and lightning. Johns (1986) documented extensive disturbances in tropical rain forests in New Guinea caused by landslides, volcanic activity, drought and fires, lightning strikes, hurricanes, and river meanders. The seedlings in such invasions are of necessity tolerant of the high light levels and desiccation characteristic of such open sites, and intolerant of the shade and associated physical and biotic conditions beneath unbroken canopy or in small tree-fall gaps.

For at least two reasons, such type-II forests are composed mainly of a single species. First, the time available for invasion of large gaps is short. In tropical rain forests the first invaders quickly form a closed canopy (Richards 1952; Ross 1954).

Once this occurs, the growth of later invaders beneath the closed canopy is suppressed during the lifetime of the canopy trees. Therefore, the species that happens to have seeds available for colonization at the appropriate time is likely to come to dominate the canopy.

Second, in large openings created by intense disturbances, the physical and biotic conditions are much harsher than those in small tree-fall gaps or beneath the intact canopy. Light levels are higher, desiccation is greater, and the spores or mycelia of mycorrhizal fungi may be absent (Janos 1980a). Because the conditions in large openings (and also in some created by less intense disturbances) are extreme, specialized adaptations for initial establishment and survival of such "ruderals" are required (Grime 1977). Janos (1980a) has suggested that the colonists of such sites might be plants that do not require mycorrhizae or those that have the EM association, both of which are relatively rare in the tropics. Since the spores of EM fungi are wind-dispersed, they may be more likely to invade bare patches before those of VAM, which have larger spores with lower dispersal capabilities (Janos 1980a).

However, large openings, in which most organisms (including buried seeds and fungi) have been killed, occur rarely in rain forests under natural conditions (since very intense disturbances are much rarer than minor ones). There has thus probably been little selective pressure for species to evolve the specialized adaptations needed for invading the gaps. Therefore, as Denslow (1980) suggested, the size of the pool of species with adaptations for early invasion of large gaps should be much smaller than that of species able to become established beneath an intact canopy or in the small tree-fall gaps that occur much more commonly.

Existing evidence supports some of these suggested mechanisms. Although large natural disturbances are relatively rare in the tropics, man-made ones have recently become common as a result of large-scale forest clearing. A few tree genera are characteristic invaders of abandoned farms and clear-cut areas over large regions: *Cecropia*, *Musanga*, *Ochroma*, *Trema*, *Macaranga*, *Mallotus*, *Acacia*, *Dendrocnide*, *Eucalyptus*, *Anisoptera*, *Shorea* (Richards 1952; Whitmore 1984). None of the species in the type-II forests listed in table 2 and Appendix C have, to our knowledge, been examined for mycorrhizae. However, other species in the same genus or family have been found to have the EM association (e.g., *Shorea*, *Anisoptera*, Singh 1966; *Eucalyptus*, Horak 1977; the families Dipterocarpaceae, Rhamnaceae, Myrtaceae, and Euphorbiaceae and the subfamily Caesalpinioideae of the Leguminosae, Malloch et al. 1980).

Although these observations tend to support Janos' (1980a) hypothesis, inferences about the occurrence of mycorrhizae in a particular species based on records of other members of the genus or family must be regarded with caution, since few tree species have been examined for mycorrhizae in tropical and subtropical forests. Moreover, intense disturbances may not completely remove mycorrhizal fungi from the soil. Parke et al. (1984) found that pine and fir seedlings germinated in soils from clear-cut and burned areas in Oregon had only 40% less EM colonization than those in soils from nearby undisturbed sites. Clearly, direct observations of these single dominant species are needed to test these hypotheses.

In summary, several constraints could reduce the number of species available

to colonize a large open patch (≥ 1 ha), which should result in single-species dominance. First, the period available for invasion before canopy closure is short, owing to the rapid growth of these early-colonizing ruderals. Second, it is probable that few species have evolved the adaptations necessary to become established in the extreme environmental conditions of large openings, especially because these occur relatively rarely under natural conditions.

Family Dominance at High Diversity

Richards (1952) pointed out that not only are some rain-forest canopies dominated by a single species, but others are dominated by several species in the same family. The best-known example of such "family dominance" is among species of the Dipterocarpaceae in southeastern Asia. This is interesting in relation to the mycorrhizal hypothesis, since, as described earlier, all members of the Dipterocarpaceae that have been examined have had the EM association. Moreover, the same EM fungus has been found on more than one species of Dipterocarpaceae (Horak 1977; Becker 1983).

We looked for evidence of family dominance in the single-dominant forests in tables 1 and 2. (For this analysis, we treated the three subfamilies of the Leguminosae as separate families.) Of the 12 type-I persistent forests in table 1, 8 had other species in the same family as the dominant. At sites 4, 9, 10, 11, and 12, these accounted for 1% to 3% of the canopy trees; at site 8, 9%; and at site 6, 10%. Site 1 showed a high degree of family dominance; the first and second most common species, both in the Caesalpinioideae, accounted for 76% and 22% of the canopy trees, respectively. Thus, there is evidence that the most common species in a few type-I forests shares its dominance with other members of the same family; at 5 of the 8 sites, these were in the Caesalpinioideae. Among the canopy trees in the 5 type-II forests in table 2, only one had other species in the same family as the dominant. At site 13, the dominant accounted for 68% of the canopy trees; two other species in the same family had 1% each. Thus, type-II nonpersistent forests showed little family dominance.

These findings lead us to suggest the following hypothetical sequence. Once one EM tree species becomes dominant, it becomes easier for other EM tree species of the same family to invade, since they may be more able to form a symbiosis with the EM fungi associated with the dominant than would tree species from a different family. Thus, over time, single-species dominance by one EM species could progress toward shared family dominance.

If this happens, we conjecture that tropical rain forests could go through gradual shifts in tree diversity, from a highly diverse forest with most species sharing a few species of VAM fungi, to a less diverse forest dominated by a single EM species, and on to a highly diverse forest dominated by many tree species from a few families that associate with EM, perhaps exemplified by the dipterocarp forests of southeastern Asia. The latter assemblages would probably tend to maintain their diversity because different EM tree species in the same family should be nearly equivalent in competitive ability. This is the same reasoning that has been applied to diverse forests with the VAM association (Janos 1983; Hubbell and Foster 1986).

TESTING THE PREDICTIONS OF THE VARIOUS HYPOTHESES CONCERNING
SINGLE-DOMINANT RAIN FORESTS

In testing the hypotheses listed in table 3, the first thing to be decided is whether the species dominating the canopy is persistent (type I) or not (type II), since the mechanisms are quite different in each case. In this paper, we make the distinction from the presence of seedling regeneration of the dominant species. However, this information is seldom gathered in a quantitative manner; it has been done for only one of the species in tables 1 and 2.

If the dominant is not persistent (type II), the hypotheses in table 3 could be tested in various ways. The first hypothesis is that one species dominates because it was the most abundant invader during the short time available between disturbance and canopy closure soon thereafter. One possible test would be to compare the relative abundance of species in seeds dispersing into the disturbed patch and already in the seed bank with that of trees in the canopy of the first forest occupying the patch. This is feasible, since in warm, wet climates, canopy closure in disturbed patches happens within a few years. We have not found any study in which the species composition of seeds immigrating into disturbed sites has been compared with that of the initial forest stand that subsequently occupied the site.

The results of such a comparison would also provide a test of the second hypothesis, that the initial conditions in a disturbed patch are unfavorable to all but a few species. If seeds of many species invaded but only one came to dominate, the local environment must have selected against most species. Field experiments that ameliorated the deleterious physical or biotic conditions would be necessary to determine which of these conditions led to the dominance of the successful species.

If the dominant is persistent (type I), various experiments might distinguish between the different hypotheses listed in table 3. The hypothesis that the dominant is the most resistant to deleterious physical and biotic conditions could be tested by removing or reducing natural enemies or by ameliorating deleterious physical conditions in laboratory or field experiments. The next set of hypotheses suggests that the dominant is the superior competitor. Again, laboratory and field experiments could test some of these (of the sort described in Connell 1983). Because both competition and natural enemies could act together, manipulation of both in the same experiments to test for interactions is desirable (Connell 1983, 1989; Quinn and Dunham 1983; Sih et al. 1985).

Of particular interest in this regard is the mycorrhiza hypothesis. It predicts that, except in soils of high nutrient content, a single EM tree species invading together with its EM fungal associate should increase as the VAM or non-mycorrhizal species decrease. Several tests of these predictions seem appropriate. First, the existence and extent of each of the mycorrhizal types in single-dominant rain forests need to be directly sampled and compared with such surveys in diverse forests (see, e.g., table 5). To our knowledge, this has not yet been done.

Alexander (1989) emphasized that few tropical legumes have been shown to have EM. However, no evidence was given about which, if any, of the samples

Such single-dominant forests are of two types: the dominant either persists at the site beyond one generation or it does not.

In forests with a persistent dominant species (type I), one species may achieve dominance either by colonizing most of a large open patch and persisting thereafter or by gradually replacing the existing residents. The latter could take place either because the dominant is the species most resistant to deleterious physical or biotic conditions or because it is superior in competition to all others. One possible mechanism enabling one species to replace and exclude many others is the possession of an ectomycorrhizal (EM) association. Most tropical tree species sampled in the Neotropics and Africa have a different type, the vesicular-arbuscular mycorrhizal (VAM) association. Various characteristics of the EM association, such as its greater host specificity, the greater protection it gives its host from natural enemies and deleterious physical factors, and its ability to secure nutrients in both organic and inorganic form before they are available to a VAM association, may confer an advantage on its host tree species that allows it to replace itself and to displace or exclude VAM host trees. This "mycorrhiza hypothesis" needs to be tested; various types of surveys and experiments are suggested as appropriate tests. In forests where the VAM type is more common, most tree species are associated with the same set of fungal species and thus may be nearly equivalent in competitive ability for securing resources. Such equivalence promotes diversity, as suggested by earlier work. Examples of nonpersistent dominants (type II) are those that first colonize large open patches (>1 ha). Dominance probably results when few species are available for colonization during the short period open to invasion after a disturbance and few are adapted to the conditions in recently disturbed large patches.

We suggest that after a single EM tree species achieves dominance in a type-I forest, other species in the same family are more likely to invade than are those of a different family. Thus, a many-species VAM rain forest might gradually shift to one with a single EM species dominant, leading to a forest of higher diversity dominated by several species from a few families that associate with EM fungi (e.g., as found in dipterocarp forests in southeastern Asia). The latter forests should tend to maintain their diversity because, like VAM forests, EM species in the same family may be nearly equivalent in competitive ability.

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APPENDIX A

CHARACTERISTICS OF THE STUDY AREAS FROM WHICH DATA WERE ANALYZED

LOCATION; ELEVATION; SOURCE	SITE	LATITUDE, LONGITUDE	RAINFALL		SAMPLE- PLOT SIZE, m ²	CANOPY TREE, LOWER SIZE LIMIT*
			Annual, cm	No. of Mo., < 6 cm/ > 10 cm		
Bambesa, Uele R., Zaire; 621 m; Gérard 1960	1	3°N, 26°E	180	2/9	12 relevees, area unknown	32 cm in dbh
Yangambi, Congo R., Zaire; 487 m; Louis 1947	2	1°N, 24°E	196	1/9	1000 (trees), 5 (seedlings)	20 m in ht.
Yangambi, Congo R., Zaire; 487 m; Germaine & Evrard 1956	3	1°N, 24°E	196	1/9	800	20 m in ht.
Budongo forest, Uganda; 1100 m; Eggeling 1947	4, 5, 15, 26-32	2°N, 31°E	184	1/8	1.42 × 10 ⁴	40 cm in dbh
Bomi Hills, Liberia; ~190 m; Voorhoeve 1964	6	7°N, 11°W	243	2/9	5500	30 cm in dbh
Mayaro District, Trinidad; <100 m; Beard 1946	7, 25	10°N, 61°W	> 200	0/11	40 × 10 ⁴	39 cm in dbh
Moraballi Ck., Guyana; <100 m; Davis & Richards 1934	8, 9, 10, 18, 19	6°N, 58°W	267	0/12	1.49 × 10 ⁴	40 cm in dbh

La Selva, Costa Rica; 50 m; D. & M. Lieberman, G. Hartshorn, R. Peralta, unpubl. data	11, 12	10°N, 84°W	365	0/12	4.0×10^4	40 cm in dbh
Woopan Ck., CSIRO plot 31, Queensland, Australia; 80 m; this paper	13	18°S, 146°E	375	0/10	1×10^4	30 cm in dbh
Baram R., Sarawak; <20 m; Anderson 1961	14	4°N, 114°E	319	0/12	2024	29 cm in dbh
Shasha Forest Reserve, Nigeria; <100 m; Richards 1939; Ross 1954	16, 17, 22, 23, 24	7°N, 4°E	208	3/7	1860	16, 10 cm; 17, 20 cm; 22,23,24, 30 cm in dbh
Tinjar R., Sarawak; ≈400 m; Richards 1936	20	3°N, 114°E	≈450	0/12	1.42×10^4	40 cm in dbh
Massa Mé, Ivory Coast; 50 m; Aubreville 1938	21	6°N, 4°W	166	3/8	≈ 1.4×10^4	30 cm in dbh
Davies Ck., Queensland, Australia; 850 m; Connell et al. 1984, unpubl. data	33	17°S, 146°E	230	2/6	1.68×10^4	30 cm in dbh

NOTE.—Seedling upper height limits: site 2, 400 cm; sites 11, 12, 100 cm. Rainfall data come from sites named except as follows: site 13, Babinda, Queensland; site 14, Miri, Sarawak; sites 16, 17, 22, 23, 24, Akilla, Nigeria; site 6, Daru, Sierra Leone; sites 7, 25, Rio Claro, Trinidad; sites 8, 9, 10, 18, 19, H. M. Penal Settlement, Mazaruni R., Guyana; sites 11, 12, Holdridge et al. 1971; site 21, Le Mé, Ivory Coast (Aubreville 1932, p. 218); site 33, CSIRO study site on Mt. Haig, Queensland. Sites 26, 27 are plots 1, 2; and sites 28–32 are plots 4–8 in Eggeling 1947; sites 22–24 are plots 1–3 in Richards 1939; site 25 is the *Carapa* forest plot in Beard 1946; sites 18, 19 are plots III, IV in Davis and Richards 1934; site 20 is plot 1, mixed forest, in Richards 1936.

* dbh, Diameter at breast height.

APPENDIX B
DIVERSITY INDEXES FROM STUDIES OF TROPICAL RAIN FORESTS

LOCATION	SITE	DOMINANCE, %	CANOPY TREES				SUBCANOPY TREES			
			No. of Trees	No. of Species	$1/\sum p_i^2$	$e^{H'}$	No. of Trees	No. of Species	$1/\sum p_i^2$	$e^{H'}$
SOUTH AMERICA										
Guyana	8	67	22	11	10.5	8.4	395	63	15.6	25.6
	10	67	33	15	14.3	11.7	819	70	12.7	24.1
	9	61	35	21	13.8	14.5	371	65	18.4	32.2
	19	43	73	33	20.1	22.4	644	84	23.8	38.2
	18	16	77	30	16.0	19.6	554	83	21.2	35.4
Trinidad	7	84	490	39	3.3	7.7	9488	82	3.1	7.5
	25	22	1345	72	11.9	25.5	11321	101	29.0	29.0
AFRICA										
Uganda	5	85	15	13	9.2	10.7	252	13	5.8	7.7
	4	76	26	6	4.5	4.8	484	8	2.2	3.2
	15	54	69	22	8.9	12.7	613	35	8.2	13.0
	32	46	72	23	10.9	13.5	414	19	3.4	5.3
	27	38	89	13	4.5	6.2	413	32	2.7	6.3
	31	34	61	25	15.6	16.9	607	41	4.9	9.0
	28	30	111	28	8.9	13.2	619	47	6.2	11.8

	30	20	114	26	14.0	16.6	474	43	4.9	11.8
	26	20	91	18	7.3	8.8	359	30	7.1	12.2
	29	13	132	34	20.0	23.1	600	48	5.3	11.1
Zaire	2	100	0	1	—	—	86	36	20.8	25.9
	1	77	56	8	1.4	1.9	274	14	2.0	3.0
	3	58	5	6	10.0	3.8	22	10	9.6	7.7
Nigeria	17	89	2	3	—	—	255	23	12.5	21.5
	16	70	23	9	5.4	5.9	274	29	3.7	7.6
	22	23	98	17	7.2	9.5	479	30	4.4	8.5
	23	19	117	24	8.9	12.3	636	39	7.9	11.9
	24	14	120	40	18.8	24.9	443	57	6.5	16.3
Ivory Coast	21	13	91	35	29.2	26.9	637	68	20.0	33.9
Liberia	6	56	19	13	17.1	10.6	260	23+	—	—
SOUTHEASTERN ASIA AND AUSTRALIA										
Sarawak	14	78	10	4	2.8	2.6	104	22	17.3	19.0
	20	10	56	32	29.6	24.7	199	88	68.2	67.3
Australia	13	68	21	12	9.6	8.6	192	42	8.9	16.7
	33	11	338	73	35.7	47.3	989	113	36.5	54.1

NOTE.—See Appendix A for details of each study site. The number of canopy trees does not include those of the single most common species; subcanopy trees include all species. Empty cells indicate that the sample size was too small (≤ 2) or that several species were combined (site 6). The diversity indexes ($1/\sum p_i^2$) of type-I forests (sites 1–10) versus type-II forests (sites 13–17) were compared using the Mann-Whitney U -test. For canopy tree species (type I, $N = 9$; type II, $N = 4$), $U = 11$, $P > 0.10$. For subcanopy tree species (type I, $N = 9$; type II, $N = 5$), $U = 22$, $P > 0.10$. (Data were not sufficient to calculate diversity indexes for canopy trees at sites 2, 11, 12, and 17 and for subcanopy trees at sites 6, 11, and 12.)

APPENDIX C

EXAMPLES, BASED ON NONQUANTITATIVE EVIDENCE, OF SINGLE-DOMINANT TROPICAL AND SUBTROPICAL RAIN FORESTS

Family	Species	Location	Source
1. TYPE-I FORESTS			
Leguminosae			
Caesalpinioideae	<i>Mora oleifera</i>	Costa Rica	Holdridge et al. 1971, p. 242
Fagaceae	<i>Quercus oleoides</i>	Costa Rica	Boucher 1983, p. 319
Dipterocarpaceae	<i>Shorea curtisii</i>	Malaysia	Burgess 1975, p. 77
	<i>Dryobalanops aromatica</i>	Malaysia	Whitmore 1984, p. 80
Lauraceae	<i>Eusideroxylon zwageri</i>	Indonesia	Richards 1952, p. 259
2. TYPE-II FORESTS			
Leguminosae			
Caesalpinioideae	<i>Peltogyne</i> sp.	Guyana	Myers 1936, p. 180
Dipterocarpaceae	<i>Shorea parvifolia</i>	Malaysia	Whitmore 1984, p. 221
	<i>Anisoptera thurifera</i>	New Guinea	Whitmore 1984, p. 219
	<i>Anisoptera polyandra</i>	New Guinea	Pajmans 1976, p. 69
Casuarinaceae	<i>Casuarina</i> aff. <i>cunninghamiana</i>	New Guinea	Whitmore 1984, p. 195
	<i>Casuarina papuana</i>	New Guinea	Pajmans 1976, p. 69
Myrtaceae	<i>Eucalyptus deglupta</i>	New Britain	Richards 1952, p. 255
Tetrameleaceae	<i>Octomeles sumatranus</i>	New Guinea	Richards 1952, p. 255

Moraceae	<i>Cecropia mexicana</i> , <i>C. longipes</i>	Panama	Richards 1952, p. 397
Ulmaceae	<i>Trema</i> spp.	Panama, Malaysia, Africa	Richards 1952, pp. 255, 393, 397
Bombacaceae	<i>Ochroma</i> spp.	Panama, West Africa	Richards 1952, pp. 397, 398
Euphorbiaceae	<i>Macaranga</i> spp.	West Africa, Malaysia	Richards 1952, pp. 381, 383
Sapindaceae	<i>Mallotus</i> spp.	southeastern Asia	Richards 1952, p. 383
	<i>Allophylus edulis</i>	South America	Singer & Morello 1960, p. 550
3. SINGLE-DOMINANT FORESTS NOT CLASSIFIED BY TYPE*			
Apocynaceae	<i>Aspidosperma excelsum</i>	Guyana	Richards 1952, p. 256
Leguminosae Caesalpinioideae	<i>Dicymbe corymbosa</i>	Guyana	Richards 1952, p. 255
	<i>Dimorphandra conjugata</i>	Guyana	Richards 1952, p. 256
	<i>Intsia bijuga</i>	New Guinea	Richards 1952, p. 260
Chrysobalanaceae	<i>Parinari excelsa</i>	Uganda	Richards 1952, p. 258
Dipterocarpaceae	<i>Parashorea malaanonan</i>	Sabah	Whitmore 1984, p. 222
Altingaceae	<i>Altingia excelsa</i>	Indonesia	Richards 1952, p. 38
Fagaceae	<i>Castanopsis acuminatissima</i>	New Guinea	Pajmans 1976, p. 89

* These forests cannot be classified because of a lack of information.

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