Causes and Consequences of Monodominance in Tropical Lowland Forests

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ABSTRACT: Tropical canopy dominance in lowland, well-drained forests by one plant species is a long-standing conundrum in tropical biology. Research now shows that dominance is not the result of one trait or mechanism. We suggest that the striking dominance of *Gilbertiodendron dewevrei* in the Ituri Forest of northeastern Congo is the result of a number of traits in adult trees that significantly modify the understory environment, making it difficult for other species to regenerate there. Adults cast deep shade that reduces light levels in the understory of the *Gilbertiodendron* forest to levels significantly lower than in the mixed-species forest. Moreover, the monodominant forest has deep leaf litter that could inhibit the establishment of small-seeded species, and the leaf litter is slow to decompose, potentially causing the low availability of nitrogen. We expect that juveniles of *Gilbertiodendron* may have an advantage in this environment over other species. In general, it appears that all tropical monodominant species share a similar suite of traits.

Keywords: Gilbertiodendron, monodominance, Ituri Forest, Africa.

Understanding biological diversity is a primary goal in ecology, and nowhere is diversity greater than in the Tropics. A 1-ha plot, with 450 stems >10-cm diameter at breast height, can have >250 different tree species (Condit et al. 1996), compared to only 20–30 different species in a similar-sized temperate-zone plot. Mechanisms proposed to explain tropical diversity range from global factors, such as climate and latitude (e.g., Pianka 1966), to local processes, such as competition, herbivory, and predation (e.g., Janzen 1970; MacArthur 1970; Connell 1971). Understanding the origin and maintenance of tropical diversity remains a formidable challenge for ecologists (Schluter and Ricklefs 1993).

Although the Tropics are renowned for high species di-

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versity, they are not uniformly diverse across all habitats. In the past decade, ecologists have become increasingly interested in the existence of large expanses of tropical forests in which a single late successional tree species comprises >60% of the canopy trees (Connell and Lowman 1989; Hart 1990). These monodominant forests do not conform to the traditional image of tropical forests in which many species make up the canopy layer; hence, the existence of tropical monodominant forests is perplexing. Explanations of tropical diversity either ignore monodominant forests or predict that they should not exist (e.g., Janzen 1970; MacArthur 1970; Connell 1971).

Some monodominant forests, such as the Neotropical *Prioria copaifera* (Leguminosae: Caesalpinioideae) swamp forests in Panama and the *Mora excelsa* (Leguminosae: Caesalpinioideae) forests along the rivers in Guyana, may be due, in part, to seasonal flooding (ter Steege 1994). Nevertheless, flooding tolerance is not the sole explanation for their dominance, as other flood-tolerant species are rare in these stands (for *Prioria*, see Lopez and Kursar 1999). Other tropical monodominants have been explained as a sere in forest succession. These are early successional species that are not able to reproduce underneath their own canopy; hence, their dominance persists for only one generation (Connell and Lowman 1989; Hart 1990; Read et al. 1995). However, in some monodominant forests, canopy dominance is not restricted to one generation, but rather the dominant species successfully recruits and replaces itself under its own canopy. A number of particularly striking examples of such persistent monodominance occur in Africa, Central and South America, and Asia. Well-known persistent dominants in Asia are in the plant family Dipterocarpaceae, while those in the Neotropics and Africa tend to be in the family Leguminosae (subfamily Caesalpinioideae; Connell and Lowman 1989; Hart et al. 1989; Nascimento and Proctor 1997).

Here, we focus on the monodominance of *Gilbertiodendron dewevrei* in the Ituri Forest of Africa and explore a hypothesis that may help unravel the mystery of tropical monodominance. The Ituri Forest is characterized by large patches of monodominant *Gilbertiodendron* forests inter-

spersed with mixed-species forest. *Gilbertiodendron* regularly forms monodominant stands from southeastern Nigeria and Cameroon east across the entire Guineo-Congolian rain forest zone (Hart 1995). The monodominant forests vary in size, reaching hundreds of squared kilometers in which *Gilbertiodendron* comprises >90% of the canopy trees (Hart 1995).

Early attempts to explain monodominance on well-drained soils focused on single causes, for example, the role of ectomycorrhizae or poor-quality soils. However, in all cases of monodominance, levels of soil-bound nutrients in monodominant and adjacent mixed-species forests are not significantly different from one another (Rankin 1978; Hart et al. 1989; Conway 1992; Nascimento et al. 1997; Newbery et al. 1997). Moreover, not all monodominant species are ectomycorrhizal (Torti et al. 1997; Torti and Coley 1999). Our hypothesis states that *Gilbertiodendron* achieves dominance because it possesses a suite of traits that alter the understory environment in such a way that inhibits recruitment by other species. Specifically, we examine how adults might change the light and nutrient regimes in the understory. In addition to traits in the adult stage that create a particularly stressful understory environment, we identify a number of juvenile traits that could enable juveniles of *Gilbertiodendron* to cope with survival under conspecific adults.

Methods

Study Site

This study was conducted between 1995–1997 within the 13,000-km^2 Okapi Wildlife Reserve in the Ituri Forest of the Democratic Republic of the Congo, formerly Zaire. Areas of study were centered around the rural village of Epulu (1°25′N, 28°35′E), elevation 750 m. Annual rainfall (1987–1993) varied from 1,307–2,084 mm (1,700 average). The study site is a lowland tropical forest with a single well-marked dry season from January to March (Hart 1995). In addition to large stands of *Gilbertiodendron*, two other species attain some dominance. *Julbernardia seretii* (Leguminosae: Caesalpinioideae) can comprise as much as 60% of the canopy trees in a local patch (Hart 1995), and in the mixed-species forest, *Cynometra alexandri* (Leguminosae: Caesalpinioideae) is the most important species, although it never reaches the same level of dominance as *Gilbertiodendron*.

Light Measurements

We quantified the availability of photosynthetically active light in the understory of the *Gilbertiodendron* and mixed-species forests with light sensors (Licor, Lincoln, Nebr.) and a data logger (21X, Campbell Scientific, Logan, Utah). Light measurements were taken every second and averaged over the course of a day (0600–1800 hours). To estimate full sunlight, one light sensor was attached to a bamboo pole and secured above the canopy of an adult tree by a Mbuti Pygmy climber. Meanwhile, we leveled and placed two light sensors on the forest floor at positions that were roughly 2 m east and 2 m west of the data logger, under closed canopy, but free of small herbaceous plants directly shading the sensor. Light measurements were taken for 6-d periods, alternating between the *Gilbertiodendron* forest and the mixed-species forest. Five different, widely scattered sites were sampled in each forest type, for a total of 10 sites sampled.

We calculated the percentage of full sunlight reaching each understory sensor for each day by dividing the amount of sunlight recorded on an understory sensor by the amount recorded for the paired canopy sensor for the same period. Because the variance among sites was greater in the mixed-species forest than in the *Gilbertiodendron* forest (Levene's test, $P = .02$), we compared light reaching the understory of the two forests with a Kruskal-Wallis test. In addition, we further examined spatial heterogeneity of light in the two forests by comparing means among sites in each forest separately. Again, we used the Kruskal-Wallis test because variances in light levels between sites in the mixed-species forest were heterogeneous (Levene's test, $P < 0.001$). Finally, we created histograms of the distribution of light reaching the understory in the two forests to estimate the intensity of light reaching the floor as sun flecks.

Leaf Litter

We characterized leaf litter in the monodominant *Gilbertiodendron* and the mixed-species forest in three ways. First, we measured depth of litter by inserting a knife into the leaf litter to the soil surface, marking the place to which the knife was immersed and then measuring this depth with a caliper. Second, we measured the amount of litter mass per unit area by haphazardly placing a 20 × 33-cm box over the litter and then collecting, drying, and weighing the leaf litter under that box. These two measurements were taken in three separate monodominant and mixed-species forest stands with 15 replicates per forest type for litter depth and five replicates per forest type. Lastly, we measured the number of vertical layers of undecomposed leaves in the two forests by inserting the knife and then counting the number of leaves intercepted by the blade that did not show any evidence of decomposition (42 replicates/forest type).

We situated 15 litterfall traps in each forest type to discern whether the greater amount of leaf litter in the *Gilbertiodendron* forest is caused by high rates of litter fall or slow rates of decomposition. Traps were constructed of

plastic bags (60 cm × 80 cm) held above the forest floor with stakes with holes punctured for drainage (Proctor 1983). We collected, dried, and weighed litterfall every 2–3 wk for 10 wk. Field studies were interrupted by civil war, hence the short duration of data collection. Litterfall is the sum total of leaves, small branches and twigs (<2 cm diameter), flowers and fruits, and indiscernible matter.

Litter Decomposition Rates. There are a number of ways to estimate rates of decomposition (Schlesinger 1991). Assuming equilibrium conditions, one method is to weigh litterfall in traps and to divide this number by the standing litter mass on the forest floor (Schlesinger 1991). We employed this method and measured standing litter mass by collecting all leaf litter in an area equal to the size of a litter trap (60 cm × 80 cm), drying it, and then weighing it. This procedure was done during the wet season (August and September), three times at the beginning of the 10-wk period and then three times again at the end of the 10-wk period in each of the two forest types. These numbers were used to calculate an average standing litter mass for each forest type and then to estimate decomposition rate by dividing litterfall by standing biomass (Schlesinger 1991).

In addition to the above measurement of litter decomposition, we tested whether the rate of decomposition is a function of forest type or leaf litter type. We collected newly senescent leaves from *Gilbertiodendron* and various mixed-species forest trees and air dried them in the sun for 1 h. In 60 mesh bags, we put 11.1–11.2 g of *Gilbertiodendron* leaves, and in another 60 mesh bags, we put 10.8–10.9 g of mixed-species forest leaves. At six different locations in each forest type we placed five bags with mixed-forest litter and five bags with monodominant litter for a total of 30 bags per litter type per forest type. In addition, we calculated wet weight–dry weight ratios for five samples of the two litter types. One mesh bag from each of the six sites per forest type was to be collected every 10 wk over the course of a year, but because of the war, only the first 10-wk collection was possible.

Nutrient Availability. We estimated the relative availability of nitrogen in the two forest types by using mixed-bed resins (INOAC NM-60 H^+/OH^- Form Type I Beads, Baker). We put 8.9 g of resin into 64 nylon bags and then distributed these along two transects, one in a *Gilbertiodendron* forest and one in the mixed-species forest. At every 5 m along a transect (16 sample points per transect), we placed one resin bag in the leaf litter and one 2–3 cm into the mineral soil. The bags were collected after 30 d and replaced with 64 new bags for another 30-d period. After collection, the bags were dried using silica gel and then analyzed at Oregon State University, Corvallis. Air-dried beads were extracted with 90 mL of 1 M KCl, shaken

for 1 h, and allowed to equilibrate for 18 h, then filtered. Extracts were analyzed for ammonium and nitrate with an Alpkem Rapid Flow Analyzer 300 (Alpkem, Clackamas, Oreg.; Binkley and Matson 1983). Differences in nitrogen between soils and leaf litter in the two forest types were analyzed by a repeated-measures ANOVA. In this design, total variance was partitioned into between and within sample point effects, each of which had a separate error term. Between sample point effects were the two forest types (*Gilbertiodendron* vs. mixed) and its error term. Within sample point effects were bag placement (soil vs. litter), trial (trial 1 vs. trial 2), all relevant interaction effects, and the appropriate error terms.

Leaf Litter Invertebrates

Because micro- and macrofauna are known to be important to the decomposition process (Schlesinger 1991; Lavelle et al. 1995), we surveyed leaf litter arthropods to determine whether they differed in abundance between forest types. Using Winkler funnels, we collected leaf litter equal to 1 m^2 of ground area every 5 m along four 100-m transects, two in the *Gilbertiodendron* forest and two in the mixed-species forest (Fisher 1999). The litter was hung in the funnels for 12 h, after which time it was remixed and rehung for another 12 h. This procedure was continued for a total of 48 h, or until all the litter had been processed. We collected the invertebrates from the funnels in 95% ethanol and sorted them by counting the number of individuals per order and then estimating the number of morphospecies per order for each of the four transects.

Results

Light Measurements

The understory of the *Gilbertiodendron* forest is considerably shadier than that of the mixed-species forest. The total daily photosynthetic photon flux density (PPFD; mol m^{-2}) measured by the canopy sensors above the two forests did not differ significantly, whereas the total daily PPFD reaching the understory was significantly different (table 1). On average, PPFD levels in the understory of *Gilbertiodendron* forest were only 0.57% full sunlight, whereas those in the mixed-species understory were 1.15% full sunlight. In addition, understory light levels among the five *Gilbertiodendron* sites tested were not significantly different, whereas those among the five mixed-forest sites were significantly different suggesting that the light regime is more homogeneous in the *Gilbertiodendron* forest (table 1). The *Gilbertiodendron* forest experiences weak sun flecks (30–60 μmol $m^{-2} s^{-1}$), whereas the mixed-species forest experiences

both weak and more intense sun flecks (70–120 μmol m^{-2} s^{-1}; fig. 1).

Leaf Litter

All three characterizations of leaf litter in the two forests showed essentially the same result: leaf litter is greater in the *Gilbertiodendron* forest than in the mixed-species forest (fig. 2). Both the mean litter depth and the mean litter mass in the *Gilbertiodendron* forest were almost three times that in the mixed-species forest (ANOVA, $F = 158.1$, df $= 1,88$, $P < .00001$ and $F = 62.0$, df $= 1,28$, $P < .0001$, respectively; fig. 2A, 2B). Likewise, the number of undecomposed leaves also differed significantly between the two forests, with an average of 2.0 $\pm$ 0.2 leaves in the *Gilbertiodendron* forest and 0.6 $\pm$ 0.1 leaves in the mixed-species forest ($t = 6.5$, df $= 83$, $P < .00001$; fig. 2C).

In contrast, total litterfall in the two forests over the 10-wk period did not differ significantly (fig. 2D). Because litterfall data could not be collected for an entire year, we do not know if there are differences in litterfall between the two forests at other times of the year, especially during the dry season when some trees in the mixed-species forest are deciduous.

Litter Decomposition Rates. Both measures of decomposition rate showed dramatically slower decomposition in the *Gilbertiodendron* forest compared to the mixed-species forest. The value of k obtained from litterfall/standing litter biomass indicates much slower decomposition rates in the *Gilbertiodendron* forest than in the mixed-species forest. The $1/k$, or mean turnover time for litter in the mixed-species forest, was 3.2 mo, whereas the turnover time for litter in the *Gilbertiodendron* forest was more than double that, 7.1 mo. Similarly, decomposition, as measured by weight loss from mesh bags, showed a significant difference between the two forest types (two-way ANOVA, $F = 5.4$, df $= 1,20$, $P = .03$; fig. 2E). *Gilbertiodendron* and mixed-forest litter decomposed two to three times faster in the mixed-species forest than in the monodominant forest (fig. 2E).
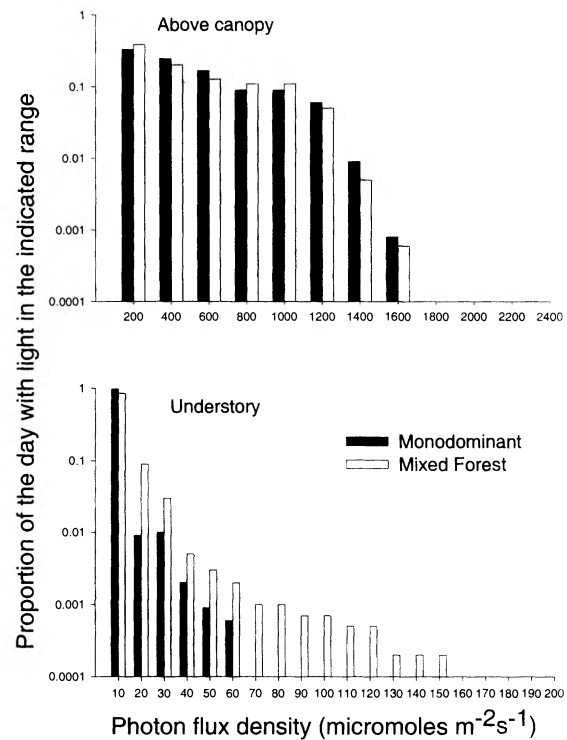

Figure 1: Distribution of light intensity (photosynthetic photon flux density) above the canopy and in the understory of the monodominant *Gilbertiodendron* and the mixed-species forests during the day.

Decomposition was not significantly different for the two litter types when placed in the same forest type (fig. 2E).

Nutrient Availability. Relative nitrogen availability, as determined with resin bags, differed in the two forest types, with one-third the nitrogen (ammonium and nitrate combined) available in the *Gilbertiodendron* forest (4.0‰ $\pm$ 0.8‰) than that available in the mixed-species forest (12.4‰ $\pm$ 0.8‰; $F = 54.1$, df $= 1,30$, $P < .0001$). In addition to a forest effect, there was also a strong soil horizon effect for nitrogen availability, depending on whether the resin bags were placed in the soil (10.6‰ $\pm$ 0.7‰) or in

Table 1: Values of total daily photosynthetic photon flux density (mol m^{-2} d^{-1}) measured above the canopy and in the understory of the monodominant *Gilbertiodendron* forest and the mixed-species forest (± 1 SE)

	Gilbertiodendron forest	Mixed-species forest	Difference between forest types[a]
Above canopy average	17.56 $\pm$ .80	17.39 $\pm$ 1.09	$P > .7$
Understory average	.10 $\pm$ .0009	.20 $\pm$ .03	$P = .02$
Variability among understory sites[b]	$P = .11$	$P = .003$	...

[a] Kruskal-Wallis tests; df $= 1$.
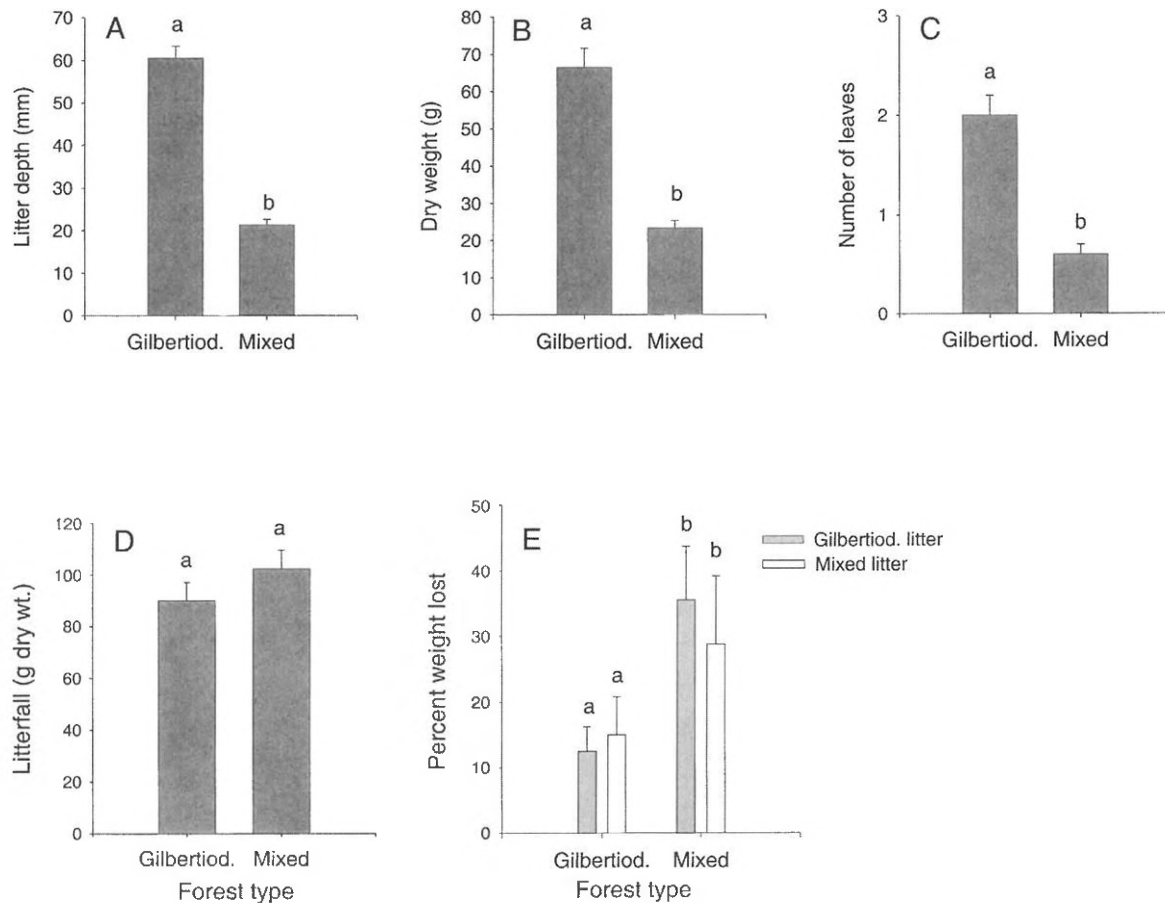
[b] Kruskal-Wallis tests; df $= 4$.

Figure 2: Comparison of mean litter depth (*A*), dry weight (*B*), and number of undecomposed leaves (*C*) in the two forest types. *D*, Comparison of litterfall in the two forest types. *E*, Comparison of decomposition as measured by weight loss of *Gilbertiodendron* litter and mixed-forest litter in both forest types.

the leaf litter (5.8‰ ± 0.7‰; $F = 25.6$, df $= 1, 30$, $P < .0001$). There was significant interaction between forest type and placement ($F = 4.69$, df $= 1, 30$, $P = .04$); however, the mean for soil was higher in both forest types.

Analyzed separately, there was less availability of both nitrate (NO_3^-) and ammonium (NH_4^+) in the monodominant forest than in the mixed-species forest (NO_3^- $F = 51.2$, df $= 1, 30$, $P < .0001$; NH_4^+ $F = 7.7$, df $= 1, 30$, $P = .009$). Moreover, in both forest types, about four times more nitrate was measured in the soil than in the leaf litter (soil $= 8.5‰ ± 0.6‰$; litter $= 2.2‰ ± 0.6‰$, $F = 60.2$, df $= 1, 30$, $P < .0001$). In contrast, more ammonium was available in the leaf litter (3.6‰ ± 0.3‰) than in the soil (2.1‰ ± 0.3‰; $F = 15.1$, df $= 1, 30$, $P = .0005$). Although significant interaction effects did exist for NO_3^- ($F = 19.5$, df $= 1, 30$, $P = .0001$), nitrate was always higher in the soil than in the litter. Significant interactions between placement and forest type also occurred for am-

monium ($F = 16.3$, df $= 1, 30$, $P = .0003$). In *Gilbertiodendron* forest, the availability of NH_4^+ was higher in the soil than in the litter, but in the mixed forest, the opposite pattern was found: the availability of NH_4^+ was higher in the litter than in the soil. There were no significant effects of trial or any interaction involving trial.

Leaf Litter Invertebrates

There was a notable paucity in numbers of leaf litter arthropods in the *Gilbertiodendron* forest (table 2). A total of 2,440 arthropods was collected in the two monodominant forest surveys and almost five times that (11,492) in the mixed-species forest surveys. Winkler funnels are especially effective in ant and mite surveys and, hence, the difference in sheer numbers in the two forest types is most remarkable for these two groups (table 2). Contrary to number counts, the forests differed little in their repre-

Table 2: Overall counts and numbers of morphospecies per invertebrate category for two surveys in each the monodominant, *Gilbertiodendron* forest and the mixed-species forest

| | Monodominant | | | | Mixed-species | | | |
| | Forest 1 | | Forest 2 | | Forest 1 | | Forest 2 | |
Group	Total	Spp	Total	Spp	Total	Spp	Total	Spp
Hymenoptera	661	52	630	73	4,669	106	2,510	101
Coleoptera	217	45	186	65	630	91	227	64
Snails	21	7	67	14	80	11	31	11
Spiders	5	5	17	13	36	22	27	19
Isopods	5	3	3	3	22	7	1	1
Acari	178	21	420	17	1,241	23	1,912	41
Diplopoda	1	1	5	2	2	2	3	3
Diptera	6	4	6	8	9	8	22	22
Hemiptera	1	1	3	2	12	8	1	1
Homoptera	0	0	3	4	1	1	2	0
Dermaptera	0	0	2	0	4	3	0	0
Isoptera	0	0	1	1	2	2	40	3
Blattoidae	0	0	0	0	1	1	2	2
Pseudoscorpiones	0	0	1	1	3	3	0	0
Orthoptera	0	0	1	1	0	0	2	2
Total	1,095	139	1,345	204	6,712	288	4,780	270

Note: Total = gross number count. Spp = number of morphospecies.

sentations of orders. The two surveys in the *Gilbertio-dendron* forest had nine and 14 orders, whereas the two surveys in the mixed-species forest had 12 and 13 orders. Moreover, there was considerable overlap among the orders represented (table 2).

Discussion

We propose that *Gilbertiodendron* significantly alters the understory environment in ways that make it difficult for other tree species to establish themselves and to survive there. In addition, we suspect that saplings of *Gilbertiodendron* can regenerate in the understory of adult *Gilbertiodendron* trees because they are stress tolerators. First, we discuss the mechanisms by which adults alter the understory and then the potential adaptations of *Gilbertiodendron* juveniles to this stressful environment.

Adult Traits

The understory of a *Gilbertiodendron* forest is extremely shaded compared with that of the mixed-species forest. The *Gilbertiodendron* forest understory is not only low in light when compared with the adjacent mixed-species forest but also shadier than most forests. Estimates in the literature of the percentage of full sunlight in the understory of temperate and tropical forests range from 1.0%–3.8% (Pearcy 1983; Chazdon and Fetcher 1984; Raich 1989; Canham et

al. 1990; Smith et al. 1992). These reported values are consistent with our measurements in the mixed-species forest but are considerably higher than those in the *Gilbertio-dendron* forest. The lack of light penetration to the understory of a *Gilbertiodendron* forest results from a high leaf area index created by the dense upper canopy (Vierling and Wessman 2000). Moreover, because *Gilbertiodendron* trees have a deep canopy with many lower branches, light to the understory is further hindered. Our finding of 0.57% full sunlight for sensors placed on the forest floor is slightly lower than that recorded by Vierling and Wessman (2000) at 3-m above ground (1.2%) in a *Gilbertiodendron* forest in the Republic of Congo. This discrepancy could be due to the difference in sensor height in the two studies or due to the fact that the *Gilbertiodendron* forest in the Republic of Congo lacks an understory tree, such as *Scaphopetalum*, which dominates the understory of the *Gilbertiodendron* forest at Ituri (L. Vierling, personal communication).

In addition to overall shade, the *Gilbertiodendron* forest also differs from the mixed-species forest in that light levels are less variable. The uniformity of light levels in the *Gilbertiodendron* forest is probably due to the fact that the *Gilbertiodendron* forest has fewer and smaller gaps than the mixed-species forest (Hart et al. 1989; S. Torti, personal observation). A homogeneously low-light understory clearly has implications for the population dynamics of other species in the plant community. The lack of light gaps undoubtedly hinders the recruitment of pioneer spe-

cies in the *Gilbertiodendron* forest. Moreover, shade-tolerant species that can establish in the understory, but need a canopy gap at some stage of their ontogeny, would also be at a disadvantage (Clark and Clark 1992).

All three measures of leaf litter on the forest floor show that there is more leaf litter in the *Gilbertiodendron* forest than in the mixed-species forest. Moreover, the litterfall data suggest that the accumulation of leaf litter in the *Gilbertiodendron* forest may not be a result of greater production of litter from the canopy. A slower rate of decomposition is likely responsible for the leaf litter buildup in the *Gilbertiodendron* forest. We predict that litter accumulation is caused by differences in both litter quality and decomposition processes among forest types.

The deep leaf litter in the *Gilbertiodendron* forest may physically hinder the germination and establishment of competitors. Both temperate and tropical studies have shown that deep leaf litter can prevent seed germination and survival by absorbing light (Sydes and Grime 1981; Facelli and Pickett 1991; Molofsky and Augspurger 1992; Facelli and Facelli 1993). Additionally, deep leaf litter could pose a mechanical barrier to seedling establishment if seeds on the top of the leaf litter must penetrate through the leaves to the soil to take root (Carson and Peterson 1990; Facelli and Pickett 1991; Fassi and Moser 1991; Metcalfe and Grubb 1997). Small-seeded species, which have relatively few reserves, may experience a greater negative effect from deep leaf litter than do large-seeded species. The species that coexist with *Gilbertiodendron* in the monodominant forest tend to have large seeds, and a preliminary study suggests that one small-seeded species, *Uapaca guanensis*, has low establishment success in *Gilbertiodendron* litter (S. Torti, unpublished data).

Concomitant with litter accumulation is a lower availability of ammonium and nitrate in the *Gilbertiodendron* forest than in the mixed-species forest. Although estimating nitrogen supply rates with resin beads may not reflect true supply rates, the technique is appropriate and informative for comparing rates of nutrient supply between two forest types (Binkley and Matson 1983). Low nitrogen availability in the *Gilbertiodendron* forest could result from slow decomposition and the low nitrogen content of *Gilbertiodendron* leaves (Gross et al. 2000). A slow rate of nutrient turnover could negatively affect the survival of some tree species in the understory of the *Gilbertiodendron* forest.

Finally, *Gilbertiodendron* trees have poor seed dispersal, and there are no known animal seed dispersers. Seeds are dispersed ballistically and the maximum dispersal distance measured beyond the edge of the crown is 3.25 ± 2.5 m (Hart 1985). A steep seed shadow created by poor dispersal would contribute to the gregarious habit of *Gilbertiodendron* trees (Hart 1985; Leigh 1994).

Juvenile Traits

One often-cited hypothesis for tropical monodominance is that ectomycorrhizae (EM) are critical; hence, plants that form EM might have a competitive advantage over species with vesicular-arbuscular mycorrhizae (VAM; Janos 1985; Connell and Lowman 1989). Virtually all plants form mycorrhizae, but most tropical trees form VAM, whereas many north temperate trees form EM (Janos 1985). Ectomycorrhizae are predicted to be superior to VAM for a number of reasons, and hence, a plant forming them might have a competitive edge over other plant species with VAM (for extensive reviews, see Janos 1985; Connell and Lowman 1989). This could be especially true in the understory of a *Gilbertiodendron* forest where both light and nutrient resources are limiting. However, recent tests of this hypothesis have shown that EM are not critical for monodominance. *Mora excelsa*, which forms large monodominant forests in Trinidad, forms VAM but not EM (Torti et al. 1997). Moreover, in the Ituri Forest, two of the three dominant species (*Gilbertiodendron* and *Julbernardia*) form EM, whereas the third, *Cynometra alexandri*, does not (Peyronel and Fassi 1957; Fassi 1960; Fassi and Fontana 1961; Torti and Coley 1999). Furthermore, *Manilkara* sp., which never attains any level of notable dominance in the Ituri Forest, also forms EM (Torti and Coley 1999). Based on these observations, we conclude that the presence of EM is neither necessary nor sufficient to explain dominance. Even if EM are important, additional factors must be present for a species to attain monodominance.

There are a number of *Gilbertiodendron* traits, in addition to EM, that could allow *Gilbertiodendron* juveniles to recruit more successfully in the understory of conspecifics than other species. *Gilbertiodendron* has the largest seed (18.2 g dry weight; Hart 1985) of the shade-tolerant species from the Ituri studied thus far, which may result in enhanced establishment success. Moreover, *Gilbertiodendron* saplings had significantly higher survival rates than *Julbernardia* saplings over a 10-yr period (Hart 1995), suggesting they might better tolerate the extreme shade cast by adult trees than other species.

Another suggested mechanism for monodominance is that dominant species possess well-defended leaves and seeds that allow them to escape predation (Janzen 1974). Well-defended seeds produced in mass quantities on a supra-annual basis could swamp seed predators and provide the dominant species with an establishment edge over other, nonmasting species (Janzen 1974). Results of studies testing this hypothesis are contradictory. Hart (1995) found that *Gilbertiodendron* seeds suffered heavy predation and did not experience an establishment advantage over other species during one masting event. In contrast, two monodominant mast-fruiters in the Neotropics, (*M. ex-*

Table 3: Proposed suite of traits necessary for a plant to be a tropical monodominant

Trait	Proposed mechanism
Adult traits:	
Deep canopy	Deep canopy with high leaf area index casts shade creating an environment too light limiting for other species.
Uniform canopy/dies standing	A uniform canopy may decrease the destructive effects of windstorms, resulting in fewer canopy gaps. Trees that tend to die standing would also decrease the number of large gaps.
Deep leaf litter	Poor-quality leaf litter accumulates and creates a physical barrier to the establishment of other species.
Low nutrient turnover	Leaf litter is slow to decompose, thereby slowing the turnover of nutrients.
Mast fruiting	Mast fruiting may swamp seed predators and increase survivorship of offspring.
Poor dispersal	Promotes gregarious habit, as seeds germinate close to parent tree.
Juvenile traits:	
Ectomycorrhizae (EM)	EM are better scavengers for nutrients, can decompose leaf litter, protect roots from herbivores and pathogens, etc.
Shade-tolerant saplings	Saplings can survive long enough to capitalize on gaps when they form.
Large seeds	Ample reserves for germination, establishment in deep leaf litter and survival in the light limiting understory.
Low seed predation	Masting and satiation of seed predators, or other mechanisms, increases average survival of seeds.
Long-lived leaves	Long-lived leaves and high-efficiency use of carbon and nitrogen lead to high survivorship.
Low leaf damage	Seedlings and saplings survive or grow better than other species because they suffer lower leaf damage.

Note: Plants do not have to possess all traits, but the possession of just a few does not result in monodominance.

celsa in Trinidad and *Peltogyne gracilipes* in Brazil), are relatively free from seed predators (Rankin 1978; Nascimento and Proctor 1997). In addition, satiation of predators appears to be important to the maintenance of a Central American monodominant species, *Quercus oleoides* (Fagaceae; Boucher 1981), as well as to the family-level dominance of some Dipterocarpaceae forests in southeast Asia (Janzen 1974; Ashton 1988; Ashton et al. 1988; Curran et al. 1999). Therefore, escape from seed predation resulting from mast fruiting may be a factor leading to dominance for some species, but it does not alone explain the existence of all monodominant forests, as many species that are mast fruiters do not form monodominant stands.

Finally, a corollary to the Janzen (1974) hypothesis is that mast-fruiting gregarious species should have well-defended leaves, which would provide dominants with an additional competitive advantage over other species in the community. In general, mature leaves tend to be long lived and tough and, therefore, suffer little damage (Coley 1983). On the other hand, young leaves tend to experience high rates of damage, but damage rates to young leaves are known to vary considerably across species (Coley 1983). Escape from herbivory, especially when leaves are expanding, could be an important factor leading to enhanced survival of seedlings of the dominant species. This hypothesis has only been tested for one monodominant species, *Gilbertiodendron*, and the results show that young leaves of *Gilbertiodendron* do not escape herbivore and pathogen damage but, in fact, suffer more intense damage than any other species surveyed in the community (Gross et al. 2000).

Monodominance Results from a Suite of Traits

In summary, our research, in addition to work by Hart et al. (1989), suggests that there is no one ecological mechanism responsible for the monodominance of *Gilbertiodendron*. *Gilbertiodendron* possesses a suite of traits that change conditions in the understory, and these traits are self reinforcing (table 3). The *Gilbertiodendron* system appears to be another example of species-specific effects, whereby various traits of a dominant competitor interact with one another to reinforce the species dominance in the community (for others, see Wedin and Tilman 1990; Hobbie 1992; Canham et al. 1994; Newbery et al. 1997). This study has elucidated the importance of canopy structure, deep leaf litter, and low nitrogen turnover as agents that create an understory environment that differs markedly from that of the adjacent mixed-species forest. The conditions created by adults, in turn, may have profound implications for interactions among seedlings and saplings in the understory, and ultimately, their regeneration.

We predict that future studies will show that *Gilbertiodendron* saplings are able to regenerate in the understory of the *Gilbertiodendron* forest because they are able to tolerate the stressful conditions of a resource-limited environment. Research on plant functional types shows that species vary tremendously in their growth rates and other morphological and physiological parameters, but one strategy that appears repeatedly is that of stress tolerance (Reich et al. 1997). Species that are stress tolerators share a suite of physiological traits, such as slow growth, shade tolerance, tough, fibrous leaves, and long-lived roots and leaves (Grime

Table 4: Overview of all tropical monodominant species (>60% dominance) in lowland, moist rain forest on well-drained soils

	Leguminosae: Caesalpinioideae							Dipterocarpaceae	
	Gilbertio-dendron dewevrei[a]	*Julbernardia seretii*[a]	*Cynometra alexandri*[a]	*Mora excelsa*[b]	*Mora gonggrijpii*[c]	*Eperua falcata*[d]	*Peltogyne gracilipes*[e]	*Dryanobalanops aromatica*[f]	*Shorea curtisii*[g]
Deep canopy	Yes	No	No	Yes	Yes	No	?	No	?
Uniform canopy/dies standing	Yes	No	No	Yes	?	No	Yes	Yes	?
Deep leaf litter	Yes	No	No	Yes	Yes	Yes	?	Yes	Yes
Low nutrient turnover	Yes	No	No	?	?	?	?	?	?
Poor dispersal	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Mast fruiting	Yes	Yes	?	Yes	?	?	Yes	Yes	Yes
Ectomycorrhizae	Yes	Yes	No	No	?	Yes	?	Yes	Yes
Shade tolerant	Yes	No	No	Yes	Yes	Yes	Yes	Yes	Yes
Large seeds	Yes	No	No	Yes	Yes	Yes	?	No	Yes
Escape seed predation	No	No	No	Yes	Yes	No	Yes	No	No
Escape herbivory on young leaves	No	No	No	?	?	No	Yes	?	?

[a] Fassi and Fontana 1961; Hart et al. 1989; Hart 1995; Torti and Coley 1999.
[b] Beard 1946; Rankin 1978; Steege 1994; Torti et al. 1997.
[c] Steege 1994.
[d] Davis and Richards 1933; Forget 1989.
[e] Nacimento and Proctor 1997.
[f] Anderson et al. 1983; Putz and Appanah 1987; Ithoh 1995.
[g] Grubb et al. 1994.

1977; Chapin 1980; Chapin et al. 1993; Cornelissen et al. 1996; Grime et al. 1997). These traits reduce the annual nutrient requirements of plants and are advantageous in a resource-limited environment (Chapin 1980).

In many ways, the *Gilbertiodendron* forest is comparable to a late successional forest in temperate regions. The canopy trees modify the understory environment such that their own seedlings and saplings are the most competitive. The dominant species appears stable and is able to regenerate under itself. Similar suites of traits and an analogous process seem likely for the monodominant patches of sugar maple and hemlock in North American temperate forests (Frelich et al. 1993; Pacala et al. 1996).

A Comparison of Tropical Monodominant Forests in an Ecological and Historical Context

Although the hypothesis that a particular suite of traits is critical to monodominance seems well founded in the case of *Gilbertiodendron*, does it have broad applicability? In addition, do historical factors play a major role in monodominance, and do these factors differ among tropical regions? Below, we argue that the suite of traits required for monodominance seems to be shared among all monodominants; however, the specific historical factor allowing for dominance may have differed in the three tropical regions.

In a literature survey, we qualitatively assessed whether the suite of traits described in the *Gilbertiodendron* system

(table 3) could be generalized to all monodominant species. In general, we found that monodominant species do share similar traits, although not all monodominants have every trait identified as potentially important (table 4). In addition, when one compares dominant species to shade-tolerant nondominants, one finds that nondominants tend to lack many of these traits. A more sophisticated analysis, whereby each of the traits was quantified for dominant and nondominant species in each community and then subjected to a discriminant function analysis, would be ideal. Such data are necessary for a definitive answer as to whether there are actually qualitative differences between dominant and nondominant species or as to whether the main differences are quantitative. That is, are dominant species simply at the extreme of the continuum for stress tolerance, for example, degree of shade tolerance? Such a result would be consistent with many temperate studies (Canham 1988, 1989; Poulsen and Platt 1989; Canham et al. 1994), which show that species vary in their shade tolerance and that the ability to tolerate extreme shade for extended periods of time leads to dominance.

Tropical monodominance is not distributed uniformly across the three tropical regions. Whereas much of the Congo Basin is scattered with monodominant forests, the Amazon is relatively devoid of dominance, except for *Peltogyne gracilipes* in Brazil (Nascimento et al. 1997). Moreover, in Asia, although there are several species that form monodominant stands, dominance is generally at the family level. A number of factors could account for these patterns.

First, differential disturbance rates at a regional scale could limit the establishment of monodominant forests if young patches are eliminated every few hundred years. Second, regional diversity probably influences dominance. It may be easier for a potentially dominant species to attain dominance if the pool of competitors is reduced, such as on islands, as this could increase the rate of competitive exclusion (Huston 1994). Overall, the African Tropics are less diverse than the Neotropics (Barthlott et al. 1996); hence, it may be relatively easier for a species to become dominant in Africa.

Finally, a comprehensive understanding of tropical monodominance includes a knowledge of factors that ultimately limit the distribution, success, and life span of monodominant forests. Charcoal samples from the Ituri Forest, dated at approximately 2,000 before present, a time during which there were no marked climatic changes in Central Africa, reveal no records of *Gilbertiodendron*, but they do show evidence of *Julbernardia* and *Cynometra* (Hart et al. 1996). These data and the astounding dominance of *Gilbertiodendron* today suggest that monodominance can be historically transient and that monodominant forests may arise and disappear regularly.

Conclusion

Since the publication of the two most influential papers on tropical monodominance (Connell and Lowman 1989; Hart et al. 1989), research has resulted in a more detailed understanding of the phenomenon. We now know that no single mechanism is responsible but that suites of traits in both the adult and juvenile stages appear to be important. Here, we have identified a number of adult traits that change the understory environment in ways that could make it difficult for other species to regenerate. Juveniles of the dominant species may have traits that enable them to tolerate the stressful conditions created by adults. Thus, it seems that a positive feedback is established that favors regeneration of the monodominant species. Moreover, monodominants worldwide share a suite of similar traits.

Acknowledgments

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