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Alphabetical order by author

1. Clark, David B. 1990. The role of disturbance in the regeneration of neotropical moist forests. In: Reproductive Ecology of Tropical Forest Plants. Man and Biosphere Series Vol. 7. K. S. Bawa, and M. Hadley, (eds.). UNESCO, Paris and Parthenon Publ. Group, Carnforth, UK. Pp.291-315
Document: S727
Abstract: Information on the incidence, extent and effects of different agents and types of disturbance in neotropical moist forests is reviewed. Disturbance in terrestrial systems is defined as a relatively discrete event causing changes in the physical structure of the environment. Disturbance affects forest by altering the structure of vegetation or exposing soil. An important descriptor of a forest's disturbance patterns is the mortality regime (modes of death) of the canopy trees. Different modes of death affect regeneration in quite different ways. Assessing the effects of disturbance other than outright mortality requires longitudinal studies of individual plants. Recent data on the physiological impacts of disturbance indicate that small changes in light levels can significantly affect regeneration. New technologies for measuring these small changes are discussed. Methodological problems in measuring and comparing disturbance regimes are evaluated, and some solutions are proposed. More research is needed to quantify different types of disturbances in tropical forests and to evaluate their ecophysiological effects. Disturbance regimes are important controllers of community structure and composition; they should be studied in order to understand how pristine communities function, and to facilitate management of altered systems.
2. Clark, David B. 1996. Abolishing virginity . Journal of Tropical Ecology 12: 735-39.
Document: NBINA-3938
3. Clark, David B, and Deborah A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. Biotropica 19, no. 3: 236-44.
Document: NBINA-2074
Abstract: We report data on population structure, growth, mortality, and distribution among microhabitats of *Dipteryx panamensis* (Papilionoideae), an emergent tree of tropical wet forest at the La Selva Biological Station, Costa Rica. We studied all seedlings (1980 cohort) on a 1-ha plot from 7 months to 5 yr post-germination. Population structure was determined by complete inventory of non-seedlings on a 4-ha plot. Growth, microsite distribution, and 2-yr survivorship were measured for individuals obtained by systematic searches of 150 ha of primary forest (= "extensive sample"). - At 7 mo. post-germination, 147 seedlings remained on the 1-ha plot; only two

were in gaps (*sensu* Brokaw 1982). The 4-ha population averaged two individuals/ha 300 mm in diameter, but included only one tree 100-300 mm in diameter. In the extensive sample, the 117 individuals 300 mm in diameter showed a continuous distribution of diameters. Seedling mortality was 97 percent from 7 mo to 5 yr post-germination. Rates of mortality decreased with increasing diameter; 104 of 105 individuals 100 mm in diameter survived 2 yr. Diameter growth of individuals 10 mm in diameter averaged 1 mm/yr, while individuals 100-700 mm, in diameter averaged 5-8 mm/yr. Diameter growth was positively correlated with crown position (Dawkins and Field 1978) for individuals 5-100 mm in diameter. Both diameter growth and height growth were higher in building-phase forest than under mature forest canopy.

4. Clark, David B, and Deborah A. Clark. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. *Oikos* 55, no. 2: 225-30.

Document: NBINA-6402

Abstract: Monthly censuses over 1 yr of 'artificial' seedlings made from plastic drinking straws 'planted' at 2 sites were used to evaluate community-level rates of physical damage in a Costa Rican rain forest. After 1 yr 82% of the artificial seedlings had been knocked over, flattened or uprooted. Litterfall and vertebrate activity contributed almost equally to the damage in cases where the agent was identified. The high rates of litterfall damage (approx. 19% p.a.) agreed with seedling mortality data for 3 species in the forest (*Pentaclethra macroleoba*, *Welfia georgii* and *Dipteryx panamensis*). Vertebrate digging damaged 15% of the seedling models, trampling flattened 3%, and 2% were uprooted or bitten into pieces by vertebrates. Higher rates of vertebrate damage in the first 2 months suggest a novelty response. Spatial variation in physical damage was indicated by significantly different rates at the 2 sites. Temporal variation in damage rates (litterfall and unknown causes) was related to rainfall.

5. Clark, David B., and Deborah A. Clark . 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6, no. 3: 321-31.

Document: NBINA-3903

Abstract: Occurrence and abundance of lianas and woody hemiepiphytes on canopy and emergent tree species in primary tropical wet forest at the La Selva Biological Station, Costa Rica were evaluated. Two pioneers, *Cecropia obtusifolia* and *C. insignis*, lacked both lianas and hemiepiphytes. Seven non-pioneer species (including *Simarouba amara* [*Quassia amara*]) differed significantly in their loads of lianas and hemiepiphytes. For non-pioneer species, two measures of liana and hemiepiphyte loads (percentage of crown occupied, and combined basal area of descending hemiepiphyte and liana roots and stems) increased significantly with tree diameter. In all non-pioneer species, most trees =70 cm diameter (50-97%) were colonized.

Lianas occupied more trees and had a smaller mean host diameter than did hemiepiphytes; however, basal area of descending roots or stems was equivalent for the two life forms in occupied trees. The relationship between annual tree diameter growth and loads of hemiepiphytes and lianas for six non-pioneer species was tested. Five of the 6 species showed a significant negative correlation between loads and diameter growth (*Dipteryx panamensis*, *Hyeronima oblonga*, *Lecythis ampla*, *Miconia guianensis*, *Pithecellobium elegans*, but not *Hymenolobium mesoamericanum*). Existing published data are tabulated and compared with these results, and show that high incidence of lianas and hemiepiphytes at La Selva is paralleled in most other Neotropical wet forests.

6. Clark, David B, and Deborah A. Clark. 1991. The impact of physical damage on canopy tree regeneration in tropical rain forest. *Journal of Ecology* 79, no. 2: 447-57.

Document: NBINA-2075

Abstract: Data are presented on frequency, rates of occurrence and consequences of physical damage (from falling trees, branches and litter) to individuals of 9 canopy tree species in primary tropical rain forest in Costa Rica. The species were *Dipteryx panamensis*, *Hyeronima alchorneoides*, *Hymenolobium mesoamericanum*, *Lecythis ampla*, *Pithecellobium elegans*, *Miconia guianensis*, *Simarouba amara* [*Quassia simarouba*], *Cecropia insignis* and *C. obtusifolia*.

7. Clark, David B, and Deborah A. Clark. 1996. Abundance, growth and mortality of very large trees in neotropical lowland rain forest. *Forest Ecology and Management* 80, no. 1-3: 235-44.

Document: NBINA-2085

Abstract: Very large trees, arbitrarily defined as those over 70 cm diameter above buttresses, account for a major portion of the above-ground biomass in neotropical rain forests. Owing to the scarcity of individuals of a given species and the difficulty of accurate measurement, there are few species-level data on the growth, mortality, and abundance of species that regularly reach emergent status. We report such data for very large individuals from old-growth tropical wet forest at the La Selva Biological Station in the Atlantic lowlands of the Republic of Costa Rica. The landscape-scale abundance of all species reaching over 70 cm diameter was assessed using 515 0.01-ha quadrats located at grid points in a 500 ha area of old-growth forest. In the total sample of 2301 stems 10 cm or more in diameter, very large individuals accounted for 2% of the stems, 23% of the basal area, and 27% of the estimated above-ground biomass. Growth and survival for five species that regularly attain emergent status were measured in a 150 ha area within the 500 ha plot. Survival of 282 very large individuals of the five species was measured over 6 years. The mean annual mortality rate of the total sample was only 0.6% year⁻¹. Mean annual diameter growth increments varied from 1.9 to 5.2 mm year⁻¹.

among species, and were negatively correlated with diameter in four of the five species. For a sample of 193 individuals measured over 7 years, growth almost exactly equalled losses in basal area and biomass due to mortality. Because all of these species are regularly recruiting new trees into the over 70 cm diameter class, the amount of biomass in the large-individual size class is increasing over the 150 ha old-growth study area. Historic disturbance and/or current climatic change are hypothesized to account for the increase. We identify lack of standard diameter measurement criteria, and small and potentially unrepresentative plot locations as two problems in assessing the role of very large trees in other neotropical forests. Future studies should sample larger areas; this will increase the generality of the conclusions and will make possible a species-level comparison of the ecology of very large tropical trees.

8. Clark, David B, and Deborah A. Clark. 2000. Tree growth, mortality, physical condition, and microsite in old-growth lowland tropical rain forest. *Ecology* 81, no. 1: 294.

Document: NBINA-3663

Abstract: The goal of this long-term research has been to assess the relationship between annually measured tree performance and microsite conditions for nine canopy and emergent tree species in old-growth lowland tropical rain forest. The study site, the La Selva Biological Station in northeast Costa Rica, is tropical wet forest (annual mean precipitation 4 in; annual mean temperature 26 °C). We used unbiased selection criteria to assemble a sample of 2000 individuals of these species in all size classes except small seedlings. We annually assessed diameter and height growth as well as stem condition and indices of crown lighting and forest structure. These data cover the period 1983-1993, and the study is ongoing as of 1999. To our knowledge the data represent the longest-running and most highly quality-controlled measurements that combine annual tree growth and mortality with associated microsite conditions in tropical forests. The data provide the most detailed insight currently available into how environmental conditions interact with past performance and ontogenetic potential in tropical rain forest trees. The focus on an annual time step allows resolution of important aspects of regeneration that are obscured or not measurable with longer inter-census intervals. The data have been used to study the nature and diversity of and survival; the effects of physical damage on regeneration; ecophysiology of saplings; the ecological role of very large trees in old-growth forest; and interannual variations in tree growth.

9. Clark, David B, and Deborah A. Clark. 2006. Tree growth, mortality, physical condition, and microsite in old-growth lowland tropical rain forest . *Ecology* 87, no. 8: 2132.

Document: NBINA-4664

Abstract: Tree species richness in tropical rain forest typically exceeds

several hundred species over mesoscale landscapes. There is no generally accepted ecological theory that accounts for the coexistence of so many species with the same general morphologies and the same basic requirements of light, nutrients, water, and physical space. In part, this lack of theory rests on the lack of understanding of the post-establishment ecology for the vast majority of tropical tree species. Of even more immediate concern is the lack of data on tree performance in relation to climate; such data are critical to project effects of global climate change on tropical forests. Here we present data from a project designed to examine the post-establishment ecology of 10 species of tropical wet forest trees selected to span a range of predicted life history patterns. The study site was terra firme old-growth tropical wet forest at the La Selva Biological Station in Costa Rica. Particular emphasis has been placed on evaluating the precision of measurements, metadata development, and annual measurements of all individuals. Because the climates of all forest environments show significant interannual variation, the annual time interval is a powerful scale at which to study the relation of tree performance to climate variation. It is also a temporal interval that captures the scale of microhabitat variations and the responses of trees to this variation in tropical rain forest. We present data on survivorship, growth, and microhabitat for 3381 individuals from 50 cm tall to canopy-level individuals measured annually between 1983 and 2000 (the study is ongoing and complete through 2005), thus adding seven years' data and the dominant canopy species at La Selva to the data set we published in 2000. The data set is unique in its scope (number of years of continuous annual measurements, number of monitored individuals) as well as in the degree of metadata documentation and unrestricted access to the raw data. The data have been used to study life history patterns, relations with microhabitats including edaphic factors and crown light environments, relations among ecophysiology, morphology, and performance, and the relation of tree performance to climate variation both at local and global scales. The data have also been used in a diversity of remote sensing studies.

10. Clark, David B, Deborah A Clark, and J. M. Read. 1998. Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *The Journal of Ecology* 86, no. 1: 101-12.

Document: NBINA-4339

Abstract: 1) Do local edaphic factors over short environmental gradients affect the distribution and abundance of tree species in tropical rain forests? We addressed this question by examining the responses of tree species to soil type, topographic position and slope angle in an upland old-growth tropical rain forest landscape in Costa Rica, Central America. 2) The study area covered 216 ha of non-swamp old growth and included replicated landscape units such as ridgetop to swale catenas, small watersheds, and alluvial terraces. An existing soils map was refined using additional sampling along a regularly spaced grid. Three soil units were defined:

residual soils derived from in-place weathering of basaltic parent material; old alluvial terrace soils formed by precontemporary flooding; and soils of stream valleys. A Geographic Information System was used to assign soil type to 2190 post-establishment individuals of nine tree species in a long-term demographic study. Topographic position and slope angle were measured in the field. 3) Data from 433 regularly spaced sample points were used to generate an expected distribution of edaphic variables, which was compared with the number of individuals of each species in each edaphic category. 4) Non-random distributions among soil types were found for seven of the nine species, with topographic positions for six species, and with slope angle classes for four species. 5) The issue of what constitutes an independent sample of establishment was analysed by considering the old-growth character of the landscape and evidence for frequent dispersal among edaphic units. A re-analysis of species' distributions using only individuals 4 cm diameter showed that results from the original analyses were robust. 6) Soil type (residual vs. old alluvial) was not significantly related to diameter growth. Three species showed significant differences in size class distributions between soil types with increasing diameter. 7) Tree species in tropical rain forests are frequently non-randomly distributed along relatively short edaphic gradients on upland soils. Future studies should increase the number of species and spatial scale analysed, incorporate better analyses of edaphic variables, and include experiments to identify the ecological processes that generate these non-random distributions.

11. Clark, David B., Deborah A. Clark, and P. M. Rich. 1993. Comparative analysis of microhabitat utilization by saplings of nine tree species in Neotropical rain forest. *Biotropica* 25, no. 4: 397-407.

Document: NBINA-2077

Abstract: Static and dynamic analyses were used to evaluate crown light environments and forest structure around 424 saplings (0.5-5 m tall) of 2 pioneer species (*Cecropia insignis* and *C. obtusifolia*) and 7 non-pioneer species (*Dipteryx panamensis*, *Hyeronima alchorneoides*, *Hymenolobium mesoamericanum*, *Lecythis ampla*, *Pithecellobium elegans*, *Minquartia guianensis* and *Simarouba amara* [*Quassia simarouba*]) in old growth tropical wet forest at the La Selva Biological Station, Costa Rica. Saplings of all species were found in relatively dark sites. The 2 pioneer species were found in microsites with higher light than the other species and were also significantly different from each other; forest structure around saplings was similar for both *Cecropia* spp. The percentage of photosynthetically active radiation (PAR) reaching a site was not significantly different between non-pioneer species; forest structure around saplings varied significantly among these species. For 6 of the 9 species, short term height and diameter increment were correlated with PAR, or its direct or diffuse components, reaching a site. Over time, all species had progressively reduced crown illumination and fewer individuals in gap/building sites than at the initial encounter 2-8 yr earlier.

12. Clark, David B., Deborah A. Clark, P. M. Rich, S. Weiss, and Steven F. Oberbauer. 1996. Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forestry Research* 26, no. 5: 747-57.

Document: S2722

Abstract: Light is a key resource controlling tree regeneration in the understory of closed-canopy old-growth forests. To evaluate the distribution of understory light environments at a landscape scale, we used stratified random sampling in a 500-ha stand of Costa Rican tropical rain forest. Fifteen 100 m long transects were placed using random coordinates within two soil-geomorphology units (flat alluvial terraces and dissected ridge-slope-swale terrain). At 2.5-m intervals we measured canopy height and slope angle, classified topographic position, and took canopy photographs with a fish-eye lens at 1 and 3 m above the ground (and at 0.6 and 5 m height at five stations per transect). Photographs were analyzed for global site factor (GSF), which is analogous to the percentage of full sun radiation reaching a point. Canopy height and GSF at 1 and 3 m above the ground were significantly autocorrelated (Moran's I) at 2.5-m intervals. The autocorrelation rapidly declined at greater intervals, reaching nonsignificance at ca. 20 m. Both canopy height and GSF at 3 m height had a weak tendency for negative autocorrelations at intervals of 25-50 m. Median canopy height (615 stations) was 23 m (range 0-37). Caps (canopy height less than or equal to 2 m, Brokaw 1982) were only 1.5% of sample points. Caps were more frequent on steep slopes than on terraces, ridgetops, swales, and gentle slopes. Canopy height varied significantly across this topographic gradient. At all four heights (0.6, 1, 3, and 5 m) median GSF was less than or equal to 2.4%. GSF values 8% accounted for only 3% of the total sample ($N = 1380$). GSF was only weakly negatively correlated with canopy height and the relation was not monotonic. Under canopies 13-19 m tall, nearly all GSF values were less than or equal to 5%. Higher GSFs were more frequent under both shorter and taller canopies. Given the observed variance in GSF and canopy height, 100-200 points separated by intervals of greater than or equal to 20 m are necessary to measure the forest-wide means of these variables to $\pm 10\%$. We discuss implications of these results for current approaches to modeling understory light based on canopy characteristics. We compared the random background of light environments from 1-3 m above the ground at La Selva with those occupied by saplings of pioneer and nonpioneer tree species. The two pioneers (*Cecropia* spp.) occurred in microsites significantly brighter than random sites, while sapling microsites of all five nonpioneer species were significantly darker than random. Comparing the landscape-scale distribution of key resources with species' actual distributions at similar scales offers a quantitative method for assessing plant life histories within and among forests.

13. Clark, David B, M. W Palmer, and Deborah A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80, no. 2: 2662-75.

Document: NBINA-4293

Abstract: Tropical rain forests have the highest tree diversity on earth. Nonrandom spatial distributions of these species in relation to edaphic factors could be one mechanism responsible for maintaining this diversity. We examined the prevalence of nonrandom distributions of trees and palms in relation to soil type and topographic position ("edaphic biases") over a mesoscale (573 ha) old-growth tropical rain forest (TRF) landscape at the La Selva Biological Station, Costa Rica. All trees and palms greater than or equal to 10 cm diameter were measured and identified in 1170 circular 0.01-ha plots centered on an existing 50 x 100 m grid. Topographic position was classified for each plot, and slope and aspect were measured. Soil type data were taken from a previous study (Clark et al. 1998). A total of 5127 trees and palms were identified in 267 species. Detrended Correspondence Analysis and Canonical Correspondence Analysis showed that highly significant edaphic gradients were present, with swamp or highly fertile soils separated from the less fertile, well-drained upland soils. Species composition remained significantly related to topographic position when soil type was controlled for. The main floristic gradients were still significant when flooded sites were excluded from the analyses. Randomization tests on a weighted preference index were used to examine the relations of individual species to soil types arid, within the dominant soil type, to topographic position. Of the 132 species with N greater than or equal to 5 individuals, 33 showed significant associations with soil type. Within the dominant soil type, 13 of 110 analyzable species were nonrandomly associated with one or more topographic positions. For a variety of seasons, including issues relating to sample size and adequate edaphic characterization of landscapes, we suggest that the similar to 30% of species shown to be edaphically biased in this study is an underestimate of the true degree of edaphically related distributional biases. To evaluate this hypothesis will require mesoscale vegetation sampling combined with quantitative soil analyses at the same scale in a range of tropical rain forests. If edaphic distributional biases are shown to be common, this suggests that edaphically linked processes leading to differential recruitment are similarly common.

14. Clark, David B., C. Soto-Castro, Luis Diego Alfaro-Alvarado, and J. M. Read. 2004. Quantifying mortality of tropical rain forest trees using high-spatial-resolution satellite data. *Ecology Letters* 7: 52-59.

Document: NBINA-1106

Abstract: Assessment of forest responses to climate change is severely hampered by the limited information on tree death on short temporal and broad spatial scales, particularly in tropical forests. We used 1-m resolution panchromatic IKONOS and 0.7-m resolution QuickBird satellite data,

acquired in 2000 and 2002, respectively, to evaluate tree death rates at the La Selva Biological Station in old-growth Tropical Wet Forest in Costa Rica, Central America. Using a calibration factor derived from ground inspection of tree deaths predicted from the images, we calculated a landscape-scale annual exponential death rate of 2.8%. This corresponds closely to data for all canopy-level trees in 18 forest inventory plots, each of 0.5 ha, for a mostly-overlapping 2-year period (2.8% per year). This study shows that high-spatial-resolution satellite data can now be used to measure old-growth tropical rain forest tree death rates, suggesting many new avenues for tropical forest ecology and global change research.

15. Clark, Deborah A., and David B. Clark. 1987. Análisis de la regeneración de árboles del dosel en bosque muy húmedo tropical: aspectos teóricos y prácticos. *Revista de Biología Tropical* 35, no. Supl 1: 41-54.

Document: R

Abstract: A central concept in current models of tropical tree regeneration is that many species require a gap in order to regenerate. An operational approach to the analysis of regeneration is proposed here, focusing on effects of specific environmental factors, such as light availability, and evaluating processes in all juvenile stages for each species. Preliminary data are reported on the juvenile stages of 6 canopy tree species (*Lecythis ampla*, *Minquartia guianensis*, *Pithecellobium pedicellare*, *Hymenolobium pulcherrimum*, *Hyeronima oblonga*, *Dipteryx panamensis*) at the La Selva Biological Station, Costa Rica. The number of crowns above individuals decreased with increasing stem diameter. The 6 species did not differ in the number of crowns above juveniles 10 cm in diameter; however, marked interspecific differences existed in the 10-20 cm diameter class. For most juveniles of 10 cm diameter the incident light was lateral, and not from canopy openings directly above. Species did not differ in crown position for juveniles up to 10 cm diameter, but significant differences existed in the 10-20 cm class. Annual diameter increment was correlated with crown position for many species/size combinations. The differences in mortality rates of juveniles 1 cm diameter did not follow preliminary tolerance classifications. All juveniles 2-30 cm in diameter (N = 173) survived 2 years. A simple classification based on dependency on gaps will not adequately categorize the regeneration process for these species.

16. Clark, Deborah A., and David B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* 62: 315-44.

Document: NBINA-2076

Abstract: Survival, growth and microsite conditions were evaluated annually during 1983-89 for 6 non-pioneer tree species in primary tropical wet forest at La Selva Biological Station, Costa Rica. The species were *Lecythis ampla*, *Hymenolobium mesoamericanum*, *Dipteryx panamensis*, *Pithecellobium elegans*, *Hyeronima alchorneoides* (all emergents), and

Miconia guianensis (a canopy species). Microsites were evaluated in terms of number of overtopping crowns, forest phase (gap, building, mature), and crown illumination index. For comparison, microsites were also evaluated for 2 pioneers (*Cecropia insignis*, *C. obtusifolia*) and a high-light demander (*Simarouba amara* [*Quassia simarouba*]). Results showed that, for non-pioneer tropical trees, life history classification based on generalized concepts such as gap dependence and shade tolerance is inadequate to describe the complex size-dependent patterns of life history differences and similarities between species.

17. Clark, Deborah A., and David B. Clark. 1994. Climate-induced variation in canopy tree growth in a Costa Rican tropical rain forest. *Journal of Ecology* 82, no. 4: 865-72.

Document: NBINA-2083

Abstract: Data are presented and discussed on annual growth (diameter) over 8 yr (1984-92) for saplings and adults of nonpioneer tree species in a lowland neotropical rain forest at La Selva Biological Station, Costa Rica. The species included 5 emergents (*Lecythis ampla*, *Hymenolobium mesoamericanum*, *Dipteryx panamensis*, *Pithecellobium elegans*, *Hieronima alchorneoides*) and one canopy species (*Miconia guianensis*).

18. Clark, Deborah A., and David B. Clark. 1999. Assessing the growth of tropical rain forest trees: Issues for forest modeling and management. *Ecological Applications* 9, no. 3: 981-97.

Document: NBINA-2082

Abstract: Growth performance was assessed for a diverse suite of canopy and emergent tree species in a lowland neotropical rain forest (the La Selva Biological Station, northeastern Costa Rica). Species were evaluated based on annual diameter measurements of large samples of individuals in all post-seedling size classes, over a 12-yr period. The study species were seven non-pioneers (*Miconia guianensis*, *Lecythis ampla*, *Hymenolobium mesoamericanum*, *Simarouba amara*, *Dipteryx panamensis*, *Pithecellobium elegans*, and *Hieronima alchorneoides*) and two pioneers (*Cecropia obtusifolia* and *C. insignis*). For each species, inherent growth capacity through ontogeny was estimated as the mean of the five largest annual increments (from different individuals) in each juvenile and adult size class. At all tree sizes, species differed highly significantly in this measure. In the small sapling sizes (less than or equal to 4-cm diameter), the two pioneers showed markedly higher maximum growth than all the non-pioneers, in line with current understanding. This growth advantage, however, was quickly lost with increasing tree size. For eight of the nine species, the ontogenetic patterns of maximal growth closely corresponded to species groupings previously based on juvenile microsites (forest stage, light levels). Average growth rates, however, which are the combined result of environmental and biotic factors, did not show this correspondence. The groups based on microsite occupancy and growth potential provide a starting point for

treating the great numbers of species of tropical rain forest trees as many fewer functional types, a sine qua non for modeling these complex forests. The exceptional growth capacity of one of our focal non-pioneer species (*Simarouba*) suggests that it represents a hitherto unrecognized functional type among tropical rain forest trees. The data from this long-term study indicate that several assumptions of current forest-dynamics models are not applicable to trees of this biome. For most species (1) diameter growth during regeneration was not correlated with tree size; (2) adult sizes were not characterized by a constant maximal basal-area increment; and (3) growth capacity did not decline toward zero as trees approached maximum size. Evaluation of overall increment distributions revealed a broad adult size range of exclusively high growth in the emergent *Hymenolobium*; for two additional species, sectors of the adult size range showed an absence of very low or negative growth. At most sizes, however, all nine species displayed the full range of growth increments, from slightly negative to observed maxima. Describing the performance of tropical rain forest canopy trees will require similar analysis of growth data obtained from many individuals and intervals, and stratified across juvenile and adult life stages. More realistic forest-dynamics models will depend on such evaluations of many tree species, in diverse tropical rain forests. Such models are greatly needed, both for designing management for this biome and for predicting its responses to changing climate and atmospheric conditions.

19. Clark, Deborah A., David B. Clark, M. R Sandoval, and Marco Vinicio Castro-Campos. 1995. Edaphic and human effects on landscape-scale distribution of tropical rain forest palms. *Ecology* 76, no. 8: 2581-94.
Document: NBINA-2084

Abstract: Landscape-level spatial variation in distribution and abundance of 7 species of canopy and subcanopy palms within 568 ha of nonswamp old-growth lowland forest at the La Selva Biological Station, Costa Rica. Plant community structure was related to marked within-forest variability in both soil and topography, and total stem density of palms varied with both factors. Steep sites had twice as many large palms (10 m tall) per hectare than those on gentler topography or at lower slope positions. The combined density of subcanopy and canopy palms also varied significantly among soil types in the smallest size class (1-5 m tall), but not for larger individuals. Local (point) species richness of the subcanopy and canopy palms varied among soil types. Of the 7 species, 2 (*Astrocaryum alatum* and *A. confertum*) were rare. All others showed significant edaphic variation in their distribution and/or estimated density. Two closely related species had strong and opposite edaphic associations. *Euterpe macropadix* was biased toward steep topography and less fertile sites. *Prestoea decurrens* was nearly omnipresent on soil types with gentle topography while absent from half the points on steep slopes. Two other closely related species, *Iriartea deltoidea* and *Socratea exorrhiza*, while virtually omnipresent across soil types and topographic positions, showed marked reciprocal variation in

density between related soils. The spatial distribution of *I. deltoidea* also indicated local removal of this species from one sector of the old-growth forest by human harvesting (with subsequent apparent release of *S. exorrhiza* in this site). The most abundant species, *Welfia georgii*, while present at all sample points, showed significant among-soil variation in density. This substructuring of the arborescent palm guild results from the interplay of edaphic variation and past human activity. The results suggest that marked spatial heterogeneity in community structure, at small to large scale (0.5 to 103 ha), may be general among tropical wet forests.

20. Fichtler, E, Deborah A Clark, and M. Worbes. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ¹⁴C. *Biotropica* 35, no. 3: 306-17.

Document: NBINA-2073

Abstract: In an old-growth tropical wet forest at La Selva, Costa Rica, we combined radiocarbon (¹⁴C) dating and tree-ring analysis to estimate the ages of large trees of canopy and emergent species spanning a broad range of wood densities and growth rates. We collected samples from the trunks of 29 fallen, dead individuals. We found that all eight sampled species formed visible growth rings, which varied considerably in distinctiveness. For five of the six species for which we combined wood anatomical studies with ¹⁴C-dates (ring ages), the analyses demonstrated that growth rings were of annual formation. The oldest tree we found by direct ring counting was a *Hymenolobium mesoamericanum* Lima (Papilionaceae) specimen, with an age of ca. 530 years at the time of death. All other sampled individuals, including very large trees of slow-growing species, had died at ages between 200 and 300 years. These results show that, even in an everwet tropical rain forest, tree growth of many species can be rhythmic, with an annual periodicity. This study thus raises the possibility of extending tree-ring analyses throughout the tropical forest types lacking a strong dry season or annual flooding. Our findings and similar measurements from other tropical forests indicate that the maximum ages of tropical emergent trees are unlikely to be much greater than 600 years, and that these trees often die earlier from various natural causes.

21. Keller, Michael, David B Clark, Deborah A Clark, A. M Weitz, and Edzo Veldkamp. 1996. If a tree falls in the forest. *Science* 273: 201.

Document: S2710

22. Oberbauer, Steven F., David B. Clark , Deborah A. Clark, and M. Quesada. 1988. Crown light environments of saplings of two species of rain forest emergent trees . *Oecologia* 75: 207-12.

Document: NBINA-6301

Abstract: The crown light environments of saplings of two Costa Rican rain forest tree species were simultaneously compared. The species, *Dipteryx*

panamensis (Pitt.) Record & Mell., a relatively shade-intolerant species, and *Lecythis ampla* Miers, a shade-tolerant species, have contrasting growth and branching patterns. Quantum sensors were placed throughout the crowns of saplings up to 2.5 m tall and quantum fluxes were recorded with microloggers for seven-day periods. The shade-intolerant species had total quantum flux densities 35% larger than those of the shade tolerant species, but totals for both species were less than 2% of full sun. More than 90% of the quantum flux densities measured within the crowns of both species were less than $25 \mu\text{mol m}^{-2} \text{s}^{-1}$. Lateral light was an important component of daily quantum flux totals for saplings of both species, the half-hour with the maximum average irradiance for the day frequently occurred in mid-morning or mid afternoon. Despite dissimilar crown and leaf display, there was no difference in the overall variability of irradiance within the crowns of the two species. However, quantum fluxes received within the crowns differed substantially in both species. Within-crown locations differed significantly from day to day because of variation in weather conditions. Daily total quantum flux densities and totals expressed as a percent of full sun were significantly correlated with height growth over the previous 12 months.

23. Oberbauer, Steven F., David B. Clark, Deborah A. Clark, P. M. Rich, and G. Vega Chavarría. 1993. Light environment, gas exchange, and annual growth of saplings of three species of rain forest trees in Costa Rica. *Journal of Tropical Ecology* 9, no. 4: 511-23.

Document: NBINA-3934

Abstract: Light environment, leaf physiological characteristics, and growth were compared for forest-grown saplings of three species of tropical trees with known life histories. Light environment was assessed both by hemispherical canopy photography and a quantitative visual index of crown illumination. Leaf gas exchange characteristics were measured by infrared gas analysis. The species tested included *Lecythis ampla*, a species tolerant of understory conditions, *Pithecellobium elegans*, a species found in relatively bright sites, and *Simarouba amara*, a fast-growing, light-demanding species. Annual height and diameter growth did not significantly differ between the three species, but highest average rates were found for *Simarouba*. Likewise, saplings of the three species were found in similar low light environments although *Simarouba* saplings were found in slightly brighter sites and *Lecythis* saplings were found in the lowest light environments. Despite similar light regimes, the species differed markedly in leaf area and gas exchange. Leaf areas of *Lecythis* saplings were five and ten-fold greater than *Simarouba* and *Pithecellobium* saplings, respectively. Light-saturated leaf photosynthesis and leaf dark respiration rates of *Lecythis* were about half those of *Simarouba*; rates of *Pithecellobium* were intermediate. *Lecythis* had the highest leaf photosynthesis at understory diffuse light levels.

Measures of annual growth were positively correlated with estimates of both direct and diffuse light with the strongest correlations between sapling performance and diffuse light.

24. Oberbauer, Steven F, Deborah A Clark , David B Clark, and M. Quesada. 1989. Comparative analysis of photosynthetic light environments within the crowns of juvenile rain forest trees. *Tree Physiology* 5, no. 1: 13-23.

Document: NBINA-6401

Abstract: Irradiances within the crowns of saplings of two tropical tree species were simultaneously compared in primary rain forest at La Selva Biological Station, Costa Rica. The species examined, *Minuartia guianensis*, a relatively slow-growing canopy species, and *Pithecellobium pedicellare*, a less-tolerant emergent species, have different crown and leaf display patterns. Crown light environments were assessed by placing arrays of quantum sensors among leaves, and recording at 5-s intervals for seven days with microloggers. Median total daily quantum flux densities for saplings of both species were less than 2% of full sun and did not differ significantly. More than 90% of the measurements within the crowns of these saplings were less than 25 $\mu\text{mol}/\text{m}^2$ per second. Spatial variability of photon flux densities within sapling crowns was similar for the 2 species despite differences in leaf display patterns. In saplings of both species, photon flux densities varied significantly over the relatively short distances within crowns and from day to day. Height growth of both species was significantly correlated with total daily photon flux densities and with percentage of full sun. However, only the tolerant species, *Minuartia*, showed a significant correlation between diam. growth and crown light environment.

25. Poorter, Lourens, Steven F. Oberbauer, and David B. Clark. 1995. Leaf optical properties along a vertical gradient in tropical rain forest canopy in Costa Rica. *American Journal of Botany* 82, no. 10: 1257-63.

Document: NBINA-3596

Abstract: Leaf optical properties (400-1.100 nm) were compared for four species of rain forest trees with crowns in understory, mid-canopy, and canopy positions to test whether optical properties change with light environment. The species tested represent a spectrum of regeneration patterns ranging from shade tolerant to light demanding. Overall, leaf optical properties of the four species were similar. Differences in absorptance were small, but statistically significant among the species and positions along the canopy gradient. Species absorptance differences corresponded somewhat to shade tolerance; two of the shade species showed higher absorptance in lower light environments, while the sun species showed the reverse pattern. Specific leaf mass (leaf weight per unit area) and chlorophyll content per unit leaf weight also changed along the canopy gradient. Specific leaf mass

was positively correlated and chlorophyll per unit leaf weight was negatively correlated with increasing light environment. Consequently, the efficiency of absorption, as represented by the absorptance per unit leaf weight, increased as light level decreased. largely due to changes in specific leaf mass. In contrast, efficiency of absorption per unit leaf chlorophyll was relatively constant with light environment for the two species measured for chlorophyll.

26. Rhoades, C. C., Robert L. Sanford, and David B. Clark. 1994. Gender dependent influences on soil phosphorus by the dioecious lowland tropical tree *Simarouba amara*. *Biotropica* 26, no. 4: 362-68.

Document: NBINA-3550

Abstract: Soil phosphorus contents below canopies of the lowland tropical rainforest tree species *Simarouba amara* [*Quassia simarouba*] were compared with soil sampled beyond the edge of *Q. simarouba* canopies at La Selva Biological Station, Costa Rica. The data showed that trees affect soil phosphorus concentrations and that differences below individual trees are related to gender for this dioecious species. Soil sampled adjacent to female trees had significantly higher soil phosphorus levels for several indices of phosphorus availability than soil sampled beyond tree crowns. Male trees did not significantly modify soil phosphorus levels. Analysis of total mineral phosphorus below and beyond the canopies of male and female of *Q. simarouba* found no differences in the total amount of phosphorus combined within bound and labile soil fractions. A small increase in soil organic matter was found under tree canopies, but there was no gender-related difference. The results indicate that increased phosphorus availability beneath female *Q. simarouba* arises from a gender-related modification in phosphorus cycling rather than from higher recruitment of females on sites rich in phosphorus or organic matter. It is suggested that gender-dependent controls on soil phosphorus may include below-canopy enrichment of available phosphorus through fruit and litter cycling or increases in phosphorus transformation from bound to labile

27. Rich, P. M., David B. Clark, Deborah A. Clark, and Steven F. Oberbauer. 1993. Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. *Agricultural and Forest Meteorology* 65, no. 1/2: 107-27.

Document: S3354

Abstract: Daily photosynthetic photon flux density (PPFD) was monitored for 1 year in the understory of a tropical wet forest along a transect extending from a treefall gap to the closed canopy at La Selva Biological Station, Costa Rica. Quantum sensors attached to data loggers were operated continuously. Hemispherical photographs were taken monthly above the sensors. An additional quantum sensor was used to monitor PPFD outside the canopy. Sensor measurements show large differences between gap and closed-canopy locations and high daily and seasonal

variability at each sensor location, with notable increases in solar radiation in gap stations during September and April. The photographs demonstrate that seasonal variation in PPFd results primarily from shifts in the solar angle relative to canopy openings and secondarily from variation in PPFd levels outside the canopy (cloudiness). Photographs also demonstrate an overall decrease in PPFd with time, for the gap stations, owing to vegetation regrowth. Analyses reveal excellent agreement between sensor PPFd measurements and estimates from hemispherical photographs. Long-term monitoring of PPFd enables calibration of hemispherical photography to permit estimation of PPFd with a high degree of reliability.

28. Sterck, F. J., David B Clark, Deborah A Clark, and F. Bongers. 1999. Light fluctuations, crown traits, and response delays for tree saplings in a Costa Rican lowland rain forest. *Journal of Tropical Ecology* 15, no. 1: 83-95.

Document: NBINA-3934

Abstract: Light environment, leaf physiological characteristics, and growth were compared for forest-grown saplings of three species of tropical trees with known life histories. Light environment was assessed both by hemispherical canopy photography and a quantitative visual index of crown illumination. Leaf gas exchange characteristics were measured by infrared gas analysis. The species tested included *Lecythis ampla*, a species tolerant of understory conditions, *Pithecellobium elegans*, a species found in relatively bright sites, and *Simarouba amara*, a fast-growing, light-demanding species. Annual height and diameter growth did not significantly differ between the three species, but highest average rates were found for *Simarouba*. Likewise, saplings of the three species were found in similar low light environments although *Simarouba* saplings were found in slightly brighter sites and *Lecythis* saplings were found in the lowest light environments. Despite similar light regimes, the species differed markedly in leaf area and gas exchange. Leaf areas of *Lecythis* saplings were and *Lecythis* saplings were found in the lowest light environments. Despite similar light regimes, the species differed markedly in leaf area and gas exchange. Leaf areas of *Lecythis* saplings were five and ten-fold greater than *Simarouba* and *Pithecellobium* saplings, respectively. Light-saturated leaf photosynthesis and leaf dark respiration rates of *Lecythis* were about half those of *Simarouba*; rates of *Pithecellobium* were intermediate. *Lecythis* had the highest leaf photosynthesis at understory diffuse light levels. Measures of annual growth were positively correlated with estimates of both direct and diffuse light with the strongest correlations between sapling performance and diffuse light.

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