surface tension is greater at the front surface of the spreading droplet (σ_{SL2}) than at the rear (σ_{SL1}). Marangoni flow pushes the drop forward, but this flow meets resistance. As the droplet moves, the advancing contact angle exceeds the receding contact angle, causing the profile of the drop to become asymmetric (see the second panel). The curvature of the advancing meniscus is less than that of the receding meniscus. This curvature difference of the expanding drop creates a pressure difference across the drop, producing a capillary flow that opposes the Marangoni flow. The drop moves only when the surface tension gradient overcomes the capillary effect.

Daniel *et al.* present an elegant solution. Not only do they overcome capillary flow, they harness it by creating a directional flow that enhances drop movement (see the third panel). They modified the solid surface so that the droplet grown on the hotter hydrophobic portion of the surface moves under both capillary flow and surface tension gradient to the cooler hydrophilic portion of the solid surface. The curvature of the advancing meniscus becomes greater than that of the receding meniscus, and capillary pressure moves the droplet further.

Daniel *et al.*'s observations show that the droplets form and grow through the condensation of nuclei. When the surface tension gradient becomes sufficiently large, the droplets begin to move along the solid surface toward the low-temperature region where the surface tension is higher. The droplet surface stretches, and the droplet assumes a semicylindrical shape. The surface stretch produces a larger surface tension gradient, which drives the flow and accelerates the droplet motion. The moving droplet coalesces with smaller droplets formed by the condensation of steam on the solid surface. Because these droplets are at a lower temperature and thus have a larger surface tension, droplet coalescence increases the surface tension gradient along the drop surface, moving the drop faster.

A simple model can be used to estimate the maximum lateral velocity at the drop surface (V_{max}) due to the surface tension gradient. The model ignores the gravitational and capillary force contributions. The spreading droplet rate is specified by the balance between the shear forces at the gas-liquid surface and the tractive forces due to the surface tension gradient (*5*, *6*):

$$V_{max} \approx (h/2\mu)\, d\sigma/dL$$

where h is the thickness of the spreading droplet, μ is the viscosity of the droplet liquid, and $d\sigma$ is the surface tension change along the drop length dL. Consider a water droplet with a diameter of 0.2 cm (corresponding to a droplet thickness of 0.1 cm) with a contact angle of 90°, viscosity of 10^{-2} g cm^{-1} s^{-1}, and surface tension gradient of $d\sigma/dL = 10$ dyne cm^{-2} (*7*). Using the equation above, we find that the droplet can move with a speed of 50 cm/s under the surface tension gradient alone. The additional capillary flow (which is proportional to σ/R, where R is the local drop curvature radius) can easily intensify the droplet movement so as to achieve speeds of more than a meter per second, as observed by Daniel *et al.*

The demonstration that capillary flow can aid the Marangoni flow to accelerate the wetting and spreading of liquids over surfaces is not only intriguing but holds great promise for practical applications. The underlying phenomena—droplet formation by nuclei condensation, growth by coalescing with other drops, and subsequent movement under the combined action of temperature and wettability gradients—are, however, quite complex. They must be better understood before the promise of this novel concept can be fully realized.

References

1. S. Daniel, M. K. Chaudhury, J. C. Chen, *Science* **291**, 633 (2001).
2. J. Thomson, *Philos. Mag. Ser. 4* **10**, 330 (1855) [summarized in J. C. Maxwell's article on "Capillary Action," *Encyclopedia Britannica* (Samuel L. Hall, New York, ed. 9, 1878)].
3. C. Marangoni, *Nuovo Cimento Ser. 2* **5/6**, 239 (1872).
4. D. A. Edwards, H. Brenner, D. T. Wasan, *Interfacial Transport Processes and Rheology* (Butterworth-Heinemann, Boston, MA, 1991), pp. 161–185.
5. B. Levich, V. Krylov, *Annu. Rev. Fluid Mech.* **1**, 239 (1969).
6. P. G. De Gennes, *Rev. Mod. Phys.* **57**, 827 (1985).
7. The value for the surface tension gradient is based on the surface tension difference of water between 20°C (σ =72.7 dyne/cm) and 80°C (σ = 62.6 dyne/cm).
8. T. Young, *Philos. Trans. R. Soc. London* **95**, 65 (1805).

PERSPECTIVES: ECOLOGY

Tropical Forest Diversity— The Plot Thickens

David F. R. P. Burslem, Nancy C. Garwood, Sean C. Thomas

The tropical forests of the world support a huge number of tree species—more tree species are found in 0.5 km^2 of some tropical forests than in all of North America or Europe. Although tropical ecologists have put forward a number of hypotheses to explain this species diversity, testing these hypotheses has been hampered by the lack of field studies with sufficiently large long-term data sets.

Enhanced online at www.sciencemag.org/cgi/content/full/291/5504/606

To fill this void, the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute has formed a network of permanent forest sites in the tropics—the forest dynamics plot (FDP) network—that are between 15 and 52 ha in size (see the figure, next page) (*1*). By counting, identifying, and measuring all trees greater than 1 cm in diameter in the FDP sites at 5-year intervals—with a standardized protocol (*2*) to facilitate comparisons between sites—CTFS has obtained a unique and comprehensive data set. This data set provides valuable insight into the distribution, abundance, and dynamics of tropical tree species. The physical, demographic, and taxonomic information accumulated for each site has also catalyzed research on, for example, the dynamics of soil seed banks (*3*), photosynthesis (*4*), the economics of nontimber forest products (*5*), and molecular analyses of gene flow within tree populations (*6*).

Two decades' worth of results from the 16 FDP sites were discussed at a workshop on tropical forest diversity in Singapore (*7*). One goal of the workshop was to determine from the FDP data sets the factors that are most crucial for maintaining species diversity in tropical forests. Factors that are thought to be important for species coexistence include: habitat disturbance (different regeneration requirements); natural enemies (different susceptibilities to pests, predators, and pathogens); limitations on seed dispersal; variation in nutrient availability; niche differentiation (different requirements for limiting resources); competitive equivalence (inability of a species to outcompete similar species); and fluctuating recruitment (which, together with juvenile persistence, may result in a species "storage effect"). Hubbell (USA) (*8*) concluded that evidence from the FDP sites supports the contribution of at least four factors—niche differentiation, natural enemies, seed dispersal limitation, and competitive equivalence—to the maintenance of tropical forest diversity. Data did not show, however, that habitat disturbance or fluctuating recruitment were important factors.

Although debate continues, the FDP data suggest that no single factor is likely to be sufficient to account for tropical tree diversity. The historical polarization of this debate into camps favoring different

---

D. F. R. P. Burslem is in the Department of Plant and Soil Science, University of Aberdeen, Aberdeen AB24 3UU, UK. E-mail: d.burslem@abdn.ac.uk. N. C. Garwood is in the Department of Botany, Natural History Museum, London SW7 5BD, UK. E-mail: ncg@nhm.ac.uk. S. C. Thomas is in the Faculty of Forestry, University of Toronto, Toronto M5S 3B3, Canada. E-mail: sc.thomas@utoronto.ca

theories of how species coexist may be an artifact of the limited data available to earlier workers, and the tendency for individual researchers to work on a narrow range of tropical forest sites. The network approach advocated by CTFS erodes these constraints, as illustrated by the emerging trend to compare FDP data sets from two or more tropical forest sites (*9*).

There are two strategies for comparing FDP sites. The first is to examine the effects of the biophysical environment on ecological processes at FDP sites that differ in climate, soils, or topography. The second is to investigate the stability of ecological processes in sites that are far apart and that have different floras (and faunas) but similar environmental characteristics, such as rainfall and soils. An example of the first approach was provided by Debski (UK), who compared the lowland dipterocarp forests of a hilly site straddling two major soil types in Sarawak, Borneo, with a more uniform site in the Malay Peninsula. He found that soil type was consistently more important than topographic position in dictating the distribution of tree species. Garwood (UK) described the effect of climate on the phenology of seed germination and dispersal in a seasonally dry site in Panama compared with a permanently wet site in Ecuador. Thomas and Makana (Canada) presented the workshop's only intercontinental comparison, an examination of commercial timber trees in FDP sites in Malaysia and the Democratic Republic of the Congo. They found differences in the distribution of stem sizes and in the biomechanical properties of wood between the two sites, which may reflect variations in disturbance due to climatic factors such as wind.

Forest dynamics and FDP plots. The forest dynamics plot (FDP) network has grown from the original 50-ha site established in 1980 in Panama to include more than 16 sites in 13 countries. In each FDP site, all trees greater than 1 cm in diameter are individually marked, mapped, identified, and measured at 5-year intervals. This global data set includes over 3 million trees comprising 6500 different species (about 10% of the total tropical tree flora). Two or more censuses have been completed in 8 of the 16 plots; a second census will start soon in two more plots.

Although early workers commonly assumed that the greater tree diversity of tropical forests was accompanied by an even spatial distribution of species, recent studies (*10*) indicate that tropical trees nearly always show a marked degree of clumping. Such clumping could be caused either by limited dispersal of seeds or by the association of species with habitat variables such as canopy openings or soil type. Distinguishing between these two alternatives is akin to the problem of deciding whether habitat differentiation or dispersal limitation is the more important factor in maintaining species diversity. Investigators have examined clumping in FDP sites in several different ways—by analyzing tree spatial distribution data with randomization methods (Valencia, Ecuador; John, India; Gunatilleke, Sri Lanka; Kenfack, Cameroon; Ahmad, UK); by directly measuring seed dispersal and combining these data with simulations of microsite occupancy (Dalling, Panama; Seidler, USA); and by reciprocal transfer of tree seedlings between habitats (Palmiotto, USA; Kuo, Taiwan). Taken together, these studies emphasize that both habitat specificity and dispersal limitation contribute to clumping of tree species, with their relative importance being determined by dispersal mode, site history, and habitat complexity.

Workshop presentations—ranging from discussion of the species composition and biogeographical relationships of flora in recently established FDP sites (Hara, Japan) to long-term tree mortality in well-established FDP sites (Sukumar, India)—illustrated how FDP research has evolved during the last two decades. Early FDP studies were usually descriptions of species composition, diversity, and distribution. It is only with the accumulation of more census data that the emphasis has switched to seeking the underlying causes of these patterns.

The FDP sites are becoming focal points for local networks of smaller plots. Dattaraja (India) reported on the relationship between species diversity and local rainfall and soil type derived from data from small plots surrounding the Mudumalai FDP site in India; Ohkubo (Japan) discussed the effects of forest fragmentation on the area surrounding the Lambir FDP site in Sarawak, Borneo.

The flood of new information from the expanding network of FDP sites has resulted in a rapid evolution in how ecologists think about the forces that shape tropical tree diversity. One area for future research is to expand theoretical models so that they incorporate more than one factor important for maintaining tree diversity. A second pressing concern is to apply what we have learned about the maintenance of diversity in relatively pristine tropical forests to a more accurate prediction of how tropical forests respond to the impact of humans through logging and forest fragmentation. Existing tropical FDP sites will surely provide a platform for future advances in both the theory and practice of tropical forest management and conservation.

References

1. www.ctfs.si.edu/bib/bib_page.htm
2. R. Condit, *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots* (Springer-Verlag, New York, 1998).
3. J. W. Dalling *et al.*, *Ecology* **79**, 564 (1998).
4. S. J. Davies, *Ecology* **79**, 2292 (1998); S. C. Thomas, F. A. Bazzaz, *Ecology* **80**, 1607 (1999).
5. R. Godoy *et al.*, *Econ. Bot.* **47**, 220 (1993); I. A. U. N. Gunatilleke *et al.*, *Econ. Bot.* **47**, 282 (1993); P. Hall, K. S. Bawa, *Econ. Bot.* **47**, 234 (1993).
6. J. D. Nason *et al.*, *Nature* **391**, 685 (1998); E. A. Stacy *et al.*, *Am. Nat.* **148**, 275 (1996).
7. "Exploring Forest Diversity and Change: Science and Policy Results from the Network of Forest Dynamics Plots," 31 May to 3 June 2000, National Institute of Education, Nanyang Technological University, Republic of Singapore.
8. The authors named here are not necessarily the sole authors of their presentations at the workshop.
9. R. Condit *et al.*, *J. Ecol.* **84**, 549 (1996).
10. R. Condit *et al.*, *Science* **288**, 1414 (2000).