predictions of the time-evolution and duration of flares and their correlation with spectral index and pre-flare X-ray compactness, suitable for direct comparison with observations.

Other complications need to be addressed to refine the flare model. The most successful theory of the quiescent phases of active galactic X-ray activity is focused on steady-state electromagnetic pair cascades[3,4], where photons and pairs interact through Compton scattering (electron–photon collisions), and pair-producing photon–photon collisions. Such cascades efficiently generate X-rays and rapidly cool pairs and protons, and could significantly hamper both the pre-flare accumulation of protons (and consequently affect the triggering of the instability), and also alter the evolution of the flare. The inclusion of photons below ultraviolet energies to model radio-loud sources could also be very influential.

The extension of Kirk and Mastichiadis's model to include time dependence is already in progress, as is the development of more complete time-dependent models including pair cascades[5,6] that will yield more powerful diagnostic information from comparisons between theory and observation. Interesting by-products of these models include neutrons and neutrinos that are spawned by pions created in photon–proton interactions[1,6]. Modelling X-ray variability with these developments promises exciting times ahead for astrophysicists who are probing the interior regions of active galactic nuclei. □

Matthew G. Baring is in the Department of Physics, North Carolina State University, Raleigh, North Carolina 27695, USA.

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ECOLOGY

A leaf for all seasons

Peter D. Moore

THE form and physiology of leaves vary according to the environment within which they develop — leaves used to sun or shade, together with humid or arid conditions, display a whole range of morphological and biochemical adaptations to different light intensities and moisture regimes. In environments where there is strong seasonal variation in these conditions the type of leaf formed may vary with the season, especially as a response to drought. One habitat where one might not expect such adaptation to occur is the humid understorey of tropical forest in Central America, but it seems that it does. Mulkey and colleagues, writing in *Proceedings of the National Academy of Sciences*[1], describe their observations on the shrub *Psychotria marginata* (Rubiaceae), and their finding that it produces drought-resistant leaves in anticipation of the annual dry season.

Leaves are extremely plastic organs. Even within a single plant they can often vary in their structure according to their position, especially on large, long-lived perennials such as trees. The complexity of architectural structure in a tree leads to the generation of its own heterogeneous microclimate and the conditions experienced by leaves in the lower layers of branches differ in many respects from those of the upper canopy. Light intensity is lower, humidity is generally higher and less variable, temperatures are lower and more uniform, wind speeds are lower, and so on.

Trees often respond to these variations in microclimate by producing leaves with different morphological and biochemical properties at different positions in their canopies. Those leaves that originate in the shade tend to be less thick, and have a thinner epidermis, fewer stomata and a lower density of hairs, all characters associated with the enhancement of light trapping and a low emphasis on water conservation. Owing to the high degree of structural complexity, these features of leaf variation within individual trees are particularly apparent in tropical rain forests[2]. Such intra-plant variation in leaf form may relate to the genetic mosaics[3] known to exist among many perennial plants, but work in this area is still in its infancy.

Drought resistance in leaves can also vary within a single plant temporally as well as spatially. In regions with strong seasonal climate contrasts, such as areas with Mediterranean climates — hot dry summers and cool moist winters — a range of leaf strategies is available, including the deciduous and evergreen options[4]. The production of different types of leaves with morphological and physiological features appropriate for the contrasting seasons has been recorded from such habitats[5].

Harper[6] has pointed out that the leaves of trees can be considered as populations and has shown that leaves are produced in cohorts that subsequently age and die together, a feature that is only too obvious in deciduous trees, but is less clearly evident in evergreens. Phases of leaf birth need not be an annual event but may be more frequent, as Mulkey and colleagues[1] have now observed in the tropical evergreen shrub *P. marginata*. Their work was carried out in Panama, and it turns out that in the *P. marginata* understorey leaves are produced in two waves, the first in May/June and the second in December/January (at the beginning and the end of the wet season respectively). From January through to April, the shrub experiences a degree of lower water availability during the 'dry' season; precipitation for the 13-week dry season is about 88 mm, compared with an annual total of 2,600 mm, but humidity is always in excess of 65 per cent. Demographic studies of these two cohorts of leaves show that they survive for at least two years. Photosynthetic assimilation rates are the same in both sets of leaves, but those leaves produced immediately before the dry season have lower transpiration rates and higher water-use efficiencies while maintaining their photosynthetic production. This differential is maintained even in plants that are irrigated throughout the dry season.

There are obvious advantages for a tropical forest plant in producing a cohort of leaves capable of conserving water during such a dry spell, especially in years of the Southern Oscillation when the dry season may be extended. The maturation of fruits also corresponds with the beginning of the dry period, and extra water is then required for the production of these fleshy organs. 'Wet season' leaves are generally produced in greater quantities (up to 70 per cent of total leaf production), but there are evident benefits in maintaining the two leaf types as a hedge against excessive drought. The advantages of retaining wet-season leaves are more subtle and may be related to the higher stomatal conductance of this leaf type during periods of high water availability, leading to higher carbon dioxide concentrations in the mesophyll.

The production of 'dry season' leaves does not seem to be related to the onset

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of drought, for it precedes this event and is maintained even under irrigated conditions (though prolonged irrigation for several years does interfere with the synchrony of leaf production[7]). There appears, therefore, to be an endogenous rhythm associated with the generation of the two types of leaf. The occurrence of this heterophylly in a rain forest plant that is subject to only very mild seasonal drought is in itself intriguing, but it also raises questions about palaeoclimate. How long, for instance, has this region been subject to a dry season? That in turn begs the question of how long it takes for such heterophylly to evolve. □

Peter D. Moore is in the Division of Life Sciences, King's College, Campden Hill Road, London W8 7AH, UK.

EARTHQUAKES

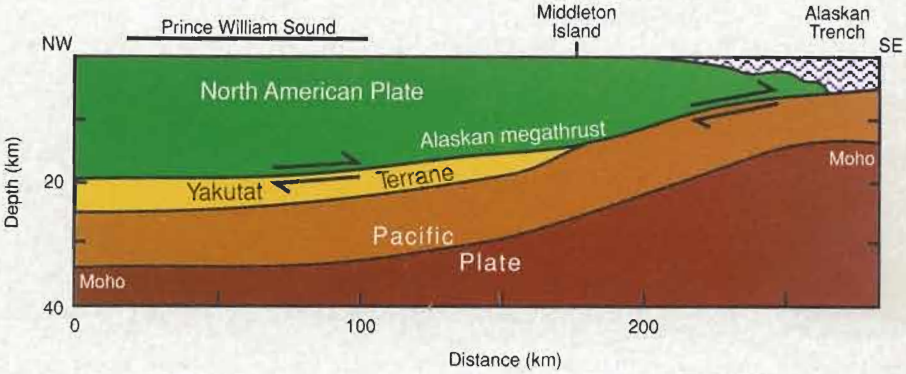
The exception is the rule

Heidi Houston

GREAT earthquakes on subduction zones, such as those along the Pacific rim, can cause death and damage not only through the direct shaking but also by the tsunami waves they can generate. Accurate forecasts could reduce such losses, but seismological crystal balls are clouded by two problems explored at a recent conference*: how can the locked and dangerous segments of a subduction zone be distinguished from those slipping smoothly and safely; and how can accurate forecasts be made when these locked segments may rupture differently from cycle to cycle? Efforts to address these problems show greatest promise at subduction zones for which modern seismicity can be compared with other data such as slip distributions in past earthquakes, plate-boundary structure, prehistoric seismicity and modern strain accumulation.

A decade of advances in determining details of the rupture of great earthquakes (those whose magnitude exceeds 8.0) has resulted in an increased appreciation of the complexity of this process. In the few places where the historical record spans several cycles of great earthquakes, the variability in the mode of rupture is striking. Several factors, in addition to the inter-event time, can vary from cycle to cycle, including whether a region ruptures in one event or more, the direction and velocity of rupture, the distribution of slip, and whether the shallow part of the subduction zone slips (H. Kanamori, California Institute of Technology; S. Beck, University of Arizona). These factors can significantly affect seismic and tsunami hazards.

For example, in 1906 a 500-km segment of the Ecuador–Colombia subduction zone ruptured in a magnitude 8.8 earthquake. The same segment slipped in a sequence of events in 1942 (magnitude 7.6), 1958 (7.7) and 1979 (8.2), for which the seismic moment released totalled only about one-fifth of the 1906 event (Beck; ref. 1). Because the earlier earthquake ruptured a longer region at once, it was also able to rupture over a greater width downdip and with a greater displacement. Along the Nankai trough in southwest Japan, historical data spanning 1,300 years with 11 great and several large earthquakes reveal two occasions on which the entire 500-km segment ruptured at once, and four occasions where the segment broke in two events separated by anything from 32 hours to three years[2]. Generally, an earthquake along the eastern part of the trough triggered one to the west. Despite wide variations in the intervals between events, this history had been considered an example of characteristic (regular) earthquake behaviour. But important features of these events differ. For example, the 1605 event produced extensive tsunami damage, but no reports of damage by shaking as occurred at many of the other events (Kanamori).



Inferred crustal structure in the Prince William Sound region of the Alaskan subduction zone from TACT seismic sounding. A continuous, gently-dipping reflector near the depth of the 1964 Alaska earthquake epicentre is interpreted as the megathrust (major interplate boundary and slip plane of the 1964 earthquake) separating the North American plate from the subducted Yakutat terrane, a microplate that has become entrained between the North American and Pacific plates and appears sutured to the Pacific plate in this region[4]. Currently seismicity is concentrated in the subducting package and exhibits downdip tension; the megathrust itself is seismically quiet, accumulating strain. (Courtesy R. A. Page.)

Along the Nicaraguan trench, a very recent underthrusting earthquake (2 September 1992) produced an anomalously large and damaging tsunami for its surface-wave magnitude, but was barely felt by people living on the coast, in contrast to other events of a similar size along the Mid-American trench. The weak shaking is attributed to smooth slow rupture propagation, which may be related to slip extending through low-velocity material all the way to the sea floor. Shallow slip is an efficient generator of tsunamis. However, some of the largest tsunamis are believed to be related to slumping of soft sediments near the trench. As the Nicaraguan trench has little sediment, the tsunami there illustrates that even zones without soft sediments can produce large tsunamis if the faulting extends to the sea floor (Kanamori).

This variability poses a problem for the recently contested seismic-gap hypothesis (see Seth Stein's News and Views article[3]), which states that sites for future earthquakes are likely to be found in regions, termed seismic gaps, along a major plate boundary that have not recently ruptured in major earthquakes (S. P. Nishenko, US Geological Survey, Golden, Colorado). However, recent earthquakes have not occurred preferentially in the gaps, but have tended to cluster in both space and time (D. D. Jackson, University of California, Los Angeles). This behaviour may be partly due to clustering and partly due to aseismic slip along some plate boundaries, rendering them incapable of a large earthquake.

An example of the difficulty with the seismic-gap hypothesis can be seen in the Shumagin Gap, a section of the Aleutian subduction zone. Most of the Aleutian arc east and west of the Shumagin Island section has ruptured in great earthquakes this century (T. M. Boyd, Colorado School of Mines). From this history, the Shumagin section was designated a seismic gap and monitored intensely. However, a decade of geodetic surveill-

*Wadati Conference on Great Subduction Zone Earthquakes, Fairbanks, Alaska, 16–19 September 1992.