When the blockage is total (*b*, *c* in the figure), the current is zero during a blockage just as it is when the channel is in one of its normal shut states, so it is not possible to say unambiguously whether a shut period is a blockage or not. In many cases, however, the blockages are identifiable as a characteristic component in the distribution of the durations of shut times, and from the dependence of their frequency on the free concentration of the blocking molecules. The work of Prod'hom *et al.* is unusual in that the simplest possible chemical agent, a single proton, produces ion-channel block, and that this block is incomplete; when the proton is bound the current is reduced to about one-third of its normal value, so blocked periods are unambiguously identifiable (unless they are very brief) by direct inspection of the record. Another unusual feature of the proton block is that it does not depend on membrane potential; the binding site for the proton must be outside the electric field of the membrane, on the extracellular surface of the channel. The mechanism seems to be quite different from that of most other blockers; rather than the blocker entering some way into the channel and plugging it, the authors suggest that the change of local surface potential produced by protonation reduces the cation concentration near the mouth of the channel and so reduces the flow of ions through the channel.

The pK of 7.4 for the protonation reaction corresponds to an equilibrium constant of about 40 nM for proton binding. This rather high affinity is similar to that found for block of nicotinic channels by tubocurarine molecules (at −100 mV). The association rate constant for tubocurarine binding to the blocking site has a conventional value, of the order of 10^7 M^{-1} s^{-1}, and the mean duration of the blockages (the reciprocal of the dissociation rate constant) is of the order of 2 s (Colquhoun, D. *et al. J. Physiol., Lond.* **293**, 247; 1979). Protons, however, are well known to be highly mobile, and the association rate constant for channel block by protons found by Prod'hom *et al.*, 4×10^{11} M^{-1} s^{-1}, is four orders of magnitude higher than for most other blockers. It is even slightly greater than that for association of H^+ and OH^- ions (see Eigen, M. & De Maeyer, L. *Proc. R. Soc.* **A247**, 505; 1958). This means that, despite the high equilibrium affinity for protons, they are bound for surprisingly short times, on average about 60 µs (and rather longer, about 150 µs, for deuterium ions). More generally, any proton-binding reaction with a pK value in the range 6–8 (equilibrium constant 1 µM–10 nM), for which effects might be obvious at physiological pH, is likely to produce brief bindings (2.5–250 µs) despite the rather high affinity. It will be interesting to see whether effects like this contribute to the extra noise that appears when many sorts of channel open, or to the appearance of subconductance levels. □

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Plant ecology

Moving in on the gaps

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NATURE abhors a vacuum, but the creation and refilling of vacancies in plant communities is important in the maintenance of species diversity in various habitats. Recent studies ranging from tropical forests[1], temperate woods[2], pine barrens[3] and assemblages of colonizing annuals[4] all confirm that the invasion of gaps in vegetation follows predictable patterns, depending on the requirements of the invasive species, and provides opportunities in both space and time for many early successional plants to maintain viable, if scattered, populations.

The idea of the 'regeneration niche' and its contribution to the richness of plant communities has been set out most clearly by Grubb[5]. The concept recognizes the dynamic nature of vegetation in which the death of mature individuals, particularly of large-bodied dominants such as trees in a forest, provides a new, if temporary, environment in which species with shorter life-spans and generation times take advantage of the more open conditions. The result is that many species associated with early stages in a succession can maintain themselves in a 'climax' system.

Canopy gaps undoubtedly contribute to the diversity of tropical forests, where gap turnover rates have been estimated at around 70–160 years (ref. 6). Studies such as those of Brokaw[1] on Barro Colorado Island in Panama confirm the existence and variety of regeneration niches in this setting. Invasive tree species following the creation of a gap vary in their time of appearance and in their gap-size requirements. *Trema micrantha* made its appearance within a year of gap formation, grew very rapidly (up to 7 metres per year), but failed to survive beyond the ninth year in any but the largest gaps. *Cecropia insignis* also arrived early, within the first three years, but grew slowly and occurred only in the larger gaps (more than 215 metres). In the same area, *Miconia argentea* could be recruited into the gap community up to the seventh year independent of gap size. Niche overlap is thus apparent, but the varied preferences of invasive species contribute to overall forest diversity.

Any contribution to the diversity of plant species will inevitably provide new opportunities for animals, for example, the production of succulent, edible fruits by many of the gap-regeneration species. This question has recently been reviewed by Leck[7], who finds that there are more bird-dispersed fruit trees in younger forests than in older ones, and that bird communities of these second-growth areas are indeed richer as a consequence. Of particular interest is the importance of such secondary growth in supporting migrant flocks of fruit-eating birds retreating from winter conditions in temperate North America.

It is not just in the tropical forests that migratory frugivores enrich the avifauna of the gaps. Skeate[8] has examined the relationships between birds and fruit in the so-called hammock communities of hardwood stands in the prairie, marsh and pine forests of Florida. Not only are gap species important in providing food for migrating birds, but their sequence of flowering is closely synchronized to the migratory pattern of their consumers. The gap relationships of the fruit-producing plants concerned, such as *Cornus florida* and *Aralia spinosa*, have been examined by Runkle and Yetter[2], who show that the former species is most dominant in larger gaps and the latter in older gaps. The regeneration patches in woodland provide a sequence of food-rich habitats for migrating birds along their entire routes to the tropics.

The importance of gaps and their regeneration as contributors to the animal and plant diversity of forests is thus evident from this type of work. What are the mechanisms of invasion and facilitation in the regenerative process? Are the bird-dispersed shrubs dependent on their avian vectors for dispersal into gaps? Or, like the pin cherry (*Prunus pensylvanica*), a gap species of the temperate woodlands, are they able to maintain seed banks over the 70 or more years between germination opportunities? Information is clearly needed about the respective roles of coevolution and of seed dormancy in the spatial and temporal complexity of the canopy gap. □

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