importance of disturbance to mid-latitude plant species diversity gives the impression that this subject has been neglected. To the contrary, the relation between species diversity and disturbance is currently the subject of much theoretical and empirical study (4-9). I will not discuss similar work on mid-latitude marine intertidal communities (10). Grime (7) presented much direct evidence that plant species richness in British pastures is greatest at intermediate levels of either disturbance or physiological stress. The intermediate-disturbance hypothesis illustrated in Connell’s figure 1 was also inferred by Grime and is illustrated in his figure 4, a transect from undisturbed pasture to a heavily trampled path. Grubb’s (8) recent account of the regeneration niche in relation to plant species diversity is an important synthesis for both mid-latitudes and tropics, complementing Connell’s paper. Connell deals more with levels of species richness and frequency of disturbance, while Grubb emphasizes the variety and ubiquity of plant species’ adaptations for occupying different Niches appearing during the process of regeneration which follows disturbance. Both conclude that diversification in the regeneration niche accounts for a large part of plant species diversity.

Horn (4) deduced the intermediate-disturbance hypothesis from a Markov-chain model of forest succession, finding that diversity is greatest at an intermediate level of the ratio of disturbance to dynamic stability. That is, the effect of disturbance upon diversity is relative to the rate of compositional recovery [see also (5)]. Horn’s result lends insight into observations that species diversity is often greatest midway along gradients in physiological stress instead of where there is least stress (7). A gradient in physiological stress is ipso facto a gradient in dynamic stability (that is, rate of plant growth, plant replacement, and compositional change). If there were an approximately constant level of disturbance across the gradient (11), then we might observe the same effect as along a gradient in disturbance, because it is the ratio of disturbance to recovery that is important.

Both Connell and Grime compare the intermediate-disturbance hypothesis to the paradigm that competition limits diversity. Disturbance is seen as a way of continually forestalling competitive elimination of a great many species. This explanation represents only one aspect of a broader theoretical synthesis which has recently emerged. Temporally variable events that are uncorrelated in space, like tree blowdowns, desert rainstorms, badger disturbances, or fires, create spatial heterogeneity that can serve as a basis for niche diversification (5, 8, 9). This particular sort of spatio-temporal heterogeneity (“disturbance” in a broad sense) and dispersal among patches are keys to the maintenance of species diversity by disturbance (5). Many of what Connell calls nonequilibrium hypotheses are now understood in the context of macroscopic equilibrium (5).

There are geographical and evolutionary corollaries to the intermediate-disturbance hypothesis. Latitudinal gradients in forest tree species diversity may be owed in part to the increase in thunderstorm frequency (and by inference the frequency of windthrow) from the poles to the equator (12). Horn’s (4) result on the ratio of disturbance to dynamic stability provides an attractive partial explanation for the evolution of plant species diversity in a wide range of vegetation types. This ratio is probably characteristic of a vegetation type, inasmuch as the factors determining it (climate, soils, physiographic processes, and variability caused by fire, wind, landslide, solifluxion, ice action, herbivory, and variable rainfall) have probably been associated with a vegetation type over evolutionary time, during large fluctuations in its areal extent, degree of geographical isolation, and geographical location. A characteristic level of disturbance or spatio-temporal heterogeneity may thus have been more constantly associated with a flora or a vegetation type through evolutionary time than have area or geographical subdivision, two factors invoked as alternative explanations for the evolution of plant species diversity (13).

JOHN F. FOX
Institute of Arctic Biology,
University of Alaska, Fairbanks 99701

References and Notes
3. The measure of diversity is 1 - \sum P_i, applied to the 17 species of table 2.4 in (2); sample areas were 0.56 ha, west coast, and 2.83 ha, north coast.

Where Has All the Carbon Gone?

Woodwell et al. (1), in discussing biota and the world carbon budget, conclude that terrestrial vegetation, mainly forest, is a major source of release of carbon to the atmosphere. They find that “the most probable range for the total world release from the biota annually is 4 to 8 \times 10^{15} g of carbon.” They also mention that if these appraisals are correct, carbon released from the biota approximately equals that released from burning fossil fuels. Since only 2.3 \times 10^{15} g of
Intermediate-Disturbance Hypothesis
J. H. CONNELL

Science 204 (4399), 1345.
DOI: 10.1126/science.204.4399.1345