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 examines 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, solifluction, 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*).

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3 May 1978; revised 11 December 1978

Fox (*1*) is correct in pointing out that I did not refer to the large amount of theoretical and empirical study on the importance of disturbance to the diversity of mid-latitude communities of plants and marine intertidal organisms. As stated (*2*, p. 1302) I intentionally restricted my attention to only two communities, tropical rain forests and coral reefs, and further limited it to the trees and corals themselves. I did not intend to give the impression that this subject has been neglected in theoretical or empirical studies at mid-latitudes; I have read and benefited from many of these studies, including Fox's present comment.

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## 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

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carbon annually accumulates in the atmosphere, the question arises, Where are the biotic releases going? Woodwell *et al.* question the validity of oceanic carbon sink models and stress the need for intensified research to resolve our understanding of the world carbon budget.

I question the correctness of their appraisal for several reasons. First, they assume that the current annual rate of forest removal is 1 percent. According to Food and Agriculture Organization (FAO) estimates (*2*), world forest removal for various uses including firewood was $2.43 \times 10^9$ $m^3$ in 1975. At 1.4 $m^3$/ton (*2*) and a carbon content of 0.45 (*1*), this amounts to $0.78 \times 10^{15}$ g of carbon per year from forest removal, not $7.4 \times 10^{15}$ g as estimated by Woodwell *et al.* The consequence of this correction, using the other assumptions the authors link with forest removal, brings the authors' midrange release estimate to a more manageable 0.4 to $0.8 \times 10^{15}$ g of carbon per year. Moreover, I also submit that the standing crop data (*3*) on which their total plant carbon masses are based represent potential productivity estimates, not actual biomass values, and that in some instances these assumed values (*4*) may be inflated by a factor of 2 or 3.

Furthermore, U.S. Forest Service national timber surveys (*5*) indicate that growth of all U.S. forests has exceeded all removals (including conversion to agriculture and urban uses) plus mortality for more than 25 years. In 1970, U.S. forests represented a sink for about $0.04 \times 10^9$ tons of atmospheric carbon (*6*). In addition, Forest Service projections of forest growth and product demands indicate that U.S. forests will continue as a carbon sink until about 1995 (*5*).

I conclude that Woodwell *et al.* (*1*) have managed to find a source of carbon input to the atmosphere that was not there to begin with. I hope that our oceanographers have not been fretting too much over their mixing ratios and that Train (*7*) will be less apprehensive about effects of forests on global $CO_2$ concentrations.

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8 August 1978; revised 6 December 1978

Ralston suggests that our appraisal of the release of carbon from the biota and humus is too high. We think he is wrong. His comments were answered in large part in the original article (*1*), but we treat his three points in sequence.

First, while the basis of our analysis was discussed in detail, we did not discuss our reasons for ignoring the FAO data, used in part by Bolin (*2*) as well as Ralston to derive a lower estimate of the biotic carbon release than ours. There are two sources of FAO data, the forest inventory that was last published in 1968 and the forest products data that Ralston has used. Persson (*3*) has attempted to improve the forest inventory. His appraisal is certainly one of the most useful and is now being used by some of us. The FAO forest products data refer to the removal of wood from forests; they do not include the quantity of carbon in branches, twigs, leaves, bark, and roots that are left to decay. They also do not include shrubs, herbs, and other plants, nor do they include the carbon in humus that is subject to decay. Finally, the conversion of forest land to other uses is not incorporated into the forest products data. Although the FAO data are potentially useful, they require considerable interpretation beyond what Ralston has supplied.

Second, Ralston questions our use of Whittaker and Likens' (*4*) analyses because they are based on "potential productivity estimates, not actual biomass values." The only reference given by Ralston to support this assertion is to a study where measured production in four North Carolina stands was less than expected on the basis of temperature and moisture (*5*). We are aware of recent global estimates that give biomass values (*6*) lower than those of Whittaker and Likens, but there are reviews that give higher totals as well (*7*). As far as we can judge, there is no basis for supplanting the Whittaker and Likens estimates.

Third, Ralston has cited U.S. Forest Service data showing an increase in the storage of carbon in forests in the United States. We addressed the question of regrowth of forests for New England and Maine, areas that have sustained some of the most extensive reforestation following the abandonment of agriculture, and showed that the probable magnitude of the storage in the temperate zone is less than $0.5 \times 10^{15}$ g annually (*1*, pp. 143-144). This is approximately the amount that Ralston would suggest is being stored if the U.S. data were applied to the temperate forests of the world. We considered this amount to be a maximum and judged the world flux to be in the other direction [table 2 in (*1*)].

Ralston's comments add little to the discussion and bring no change in our conclusion. Nevertheless, the questions he raises point to the uncertainties associated with these estimates, a major emphasis of the original article. There remains a clear need for new sets of data on the vegetation of the earth that are sufficiently comprehensive to offer a more satisfactory basis for such analyses.

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