montane cloud forest (1850 m) of the Monte Verde Reserve in Costa Rica has revealed at least 22 species of trees with canopy roots. As in the temperate site, they sprout adventitiously from the boles and branches of host trees and run beneath the constantly moist bryoflora and accumulated organic matter. Canopy roots have recently been reported on two tree species in a Hawaiian cloud forest (*6*) (*Metrosideros collina* and *Cheirodendron trigynum*). Canopy-rooting species in the tropical environment are taxonomically diverse: for example, Lauraceae (*Ocotea* spp.), Flacourtiaceae (*Xylosma* sp.), Araliaceae (*Didymopanax pittieri*), and Cunoniaceae (*Weinmannia pinnata*). Thus, convergent evolution occurs (i) among geographically distant ecosystems and (ii) between some of the component woody taxa.

Discovery of this phenomenon forces a reconsideration of the nature of the relation between epiphyte and host tree, a subject of debate for many years. Although by definition epiphytes do not take nutrients directly from host trees (as parasites do), they have been implicated in host tree decline (*7*). Epiphytes have been termed "nutritional pirates," as they can intercept and tie up in their own biomass those nutrients borne in dust, precipitation, and canopy leachates, which would otherwise be available to host trees. However, in rainforest ecosystems where nutrients are readily leached from soil and canopy (and lost to all ecosystem members), tying up nutrients in epiphyte biomass does not "rob" or deny host trees of atmospheric nutrients. Rather, it immobilizes them within the system, and at worst delays their availability to host trees. Those trees with extensive networks of canopy roots gain access to the arboreal nutrient source generated and retained by epiphytes. In fact, epiphytes may substantially contribute to host tree nutrient status by trapping and retaining atmospheric nutrients.

The implications of canopy roots extend beyond the relations between epiphyte and host tree to the more general questions of ecosystem nutrient dynamics and their interrelations. Root distribution and morphology indicate that more direct nutrient transfer between canopy and forest floor vegetation is taking place than previously considered. Canopy roots provide an efficient mechanism for nutrient recycling with smaller amounts of nutrients lost to other ecosystem components or leached from the entire ecosystem. For vegetation growing on heavily leached soils, such a mechanism would contribute to the nutrient conservation and retention capacity upon which rainforests depend.

NALINI M. NADKARNI
College of Forest Resources, University of Washington, Seattle 98195

References and Notes

1. P. W. Richards, *Tropical Rain Forest* (Cambridge Univ. Press, 1952); C. Jordan, F. Golley, J. Hall, J. Hall, *Biotropica* **12**, 61 (1980); N. Stark and C. Jordan, *Ecology* **59**, 434 (1978).
2. P. Nye, *Plant Soil* **13**, 333 (1961).
3. R. Fonda, *Ecology* **55**, 927 (1974).
4. D. Perry, *Biotropica* **10**, 155 (1978).
5. A. Gill and P. Tomlinson, in *The Development and Function of Roots*, J. Torrey and D. Clarkson, Eds. (Academic Press, London, 1975), pp. 237–260; J. Jenik, *Preslia* **45**, 250 (1973); A. Gill, *J. Arnold Arbor. Harv. Univ.* **50**, 197 (1969).
6. P. Vitousek, personal communication, 1981.
7. D. Benzing and J. Seeman, *Selbyana* **2**, 148 (1978).
8. I thank C. Grier for support, D. Paulson for photography, W. Haber for tropical plant identification, D. Benzing for comments, A. M. Glyph, and the Monte Verde community. J. Agee and the National Park Service provided technical and financial assistance in the Olympics, and the Organization for Tropical Studies and the Tropical Science Center helped greatly in Costa Rica. This research was supported by a University of Washington graduate research fellowship, a U.S. Forest Service cooperative aid agreement, a Sigma Xi grant-in-aid, and a research grant from the U.S. Man and the Biosphere Secretariat.

20 February 1981; revised 18 April 1981

Predation Through Geological Time: Evidence from Gastropod Shell Repair

Abstract. *Warm-water marine gastropods from soft-bottom habitats show an increase in the incidence of breakage-resistant shell characteristics over geological time. The hypothesis that breakage became a more important component of selection in the middle of the Mesozoic Era is supported by the finding that frequencies of breakage-induced shell repair increased from the Pennsylvanian and Triassic periods to the Cretaceous, Miocene, and Recent.*

Shell breakage by predators may be a more important agent of selection today than it may have been in the Paleozoic and early Mesozoic eras. This idea was presented as a hypothesis (*1*) to explain the Middle Mesozoic rise in the incidence of breakage-resistant shell characteristics and the concomitant decline of structurally weak features (*2*).

In order to test this hypothesis, we assessed the incidence of sublethal shell damage at various times in Earth history. Selection favoring the evolution of breakage-resistant shells can occur only if individuals in a population reproduce after they have suffered nonlethal shell-breaking attacks (*3*). If all breakage were lethal, there would be no selection between weak and strong shell variants, and no shells would show the scars that record nonlethal injury. High frequencies of sublethal damage imply that the shell, together with other defenses, is effective in protecting the gastropod against locally prevailing shell-breaking agents. The higher the frequency of sublethal shell damage, the greater is the likelihood that selection will maintain or enhance shell armor (*3*). Although it is impossible to measure the intensity of this selection, the hypothesis that shell breakage became a more important component of selection after the Triassic Period in the Mesozoic would be supported if the frequency of breakage-induced shell repair began to rise at that time (*3, 4*).

The exceptional preservation required to detect shell repair is rare, especially in Paleozoic and Mesozoic gastropods. Nevertheless, we obtained bulk samples of gastropods from two pre-Jurassic and three post-Jurassic time units (*5*). All species lived in sands and muds in warm shallow marine waters. A scar on the shell's exterior is the jagged trace of the outer lip where the latter was damaged and subsequently repaired by the mantle edge. For each species at each locality, the frequency of repair (defined as the number of scars per shell) was calculated for predetermined size classes as well as for the complete sample, which included all shells with one dimension greater than 5 mm. If a species was represented in a time unit by more than one sample, each sample was treated equally, and a mean frequency of repair was calculated. A single frequency of repair was used for each species in comparisons of repair between time units. Geographical and habitat variation of repair within and between species was evaluated in gastropods from the Pennsylvanian and Recent (*3, 4*). Although this variation is great (Table 1), it is less than the variation between time units.

Analysis of complete samples revealed an increase in the incidence of repair among gastropod species from the Pennsylvanian (late Paleozoic) and Triassic (early Mesozoic) to the Cretaceous (late Mesozoic), Miocene (late Cenozoic), and Recent (Table 1). This trend is statis-

0036-8075/81/1127-1024$01.00/0

tically significant both when all species are included in the analysis ($P < .002$) and when the comparison is restricted to high-spired species, which are relatively resistant to lethal breakage ($P < .00003$). The increase is also evident among species in the 10- to 19-mm and 20- to 29-mm size classes ($P < .007$ and .05, respectively) and among high-spired species in the 10- to 19-mm class ($P < .03$). No significant increase was found in the 5- to 9-mm size class or among trochiform species, which have relatively weak shells. [Jonckheere distribution-free test for ordered alternatives (*6*) was used.] Other temporal comparisons could not be made because some architectural types of gastropods (mechanically weak planispiral shells) were present only in the Pennsylvanian material, whereas others (sturdier shells with elongated apertures) appeared only in our samples from the Miocene and Recent.

Within the time span that we investigated, the increase in the frequency of repair took place between the Late Triassic and Late Cretaceous. For complete samples, each of the post-Jurassic time units showed higher frequencies of repair than did either of the two pre-Jurassic periods [distribution-free multiple-comparison test (*6*)]. Statistically significant differences in the 10- to 19-mm size class were found between the Triassic and Miocene assemblages and between the Triassic and Recent species. In the 20- to 29-mm class, for which no Triassic shells were available, significant differences appeared between the Pennsylvanian and Cretaceous and between the Pennsylvanian and Recent. No differences were found between the Pennsylvanian and Triassic assemblages, or among those from the Cretaceous, Miocene, and Recent.

The increase in the frequency of repair through time would be more dramatic if we excluded species whose adult shells have a thick or expanded outer lip since these species are less susceptible to lip damage and are less likely to require repair than are thin-lipped ones. Frequencies of repair among complete samples from the Recent are significantly lower in thick-lipped species than in those with thin lips ($P < .02$). This is also the case for Miocene species in the 20- to 29-mm and 30- to 39-mm size classes ($P < .05$ and .02 respectively; Mann-Whitney U test). Thick-lipped species are common only in the Cenozoic and are not well represented in the Pennsylvanian and Triassic assemblages that we studied (*2*).

A more detailed analysis of the post-Jurassic increase in repair frequencies suggests that early shell-breaking predators were weaker than their later counterparts. Powerful predators can demolish small shells and sublethally damage large ones, whereas weak predators primarily attack only small shells. Accordingly, the presence of strong predators should result in a greater frequency of repair as shell length increases, partly because more time has been available for a larger (older) shell to be attacked, and partly because smaller shells are likely to be broken lethally when attacked. This expectation has been confirmed for Cretaceous, Miocene, and Recent shells but not for the pre-Jurassic assemblages (Fig. 1).

In the older assemblages, the size-specific frequency of repair (number of scars divided by total number of shells of all species in a given size class) remains roughly the same as shell length increases. Analyses of individual samples revealed that the frequency of repair increases in the larger size classes in 6 out of 11 samples from the Pennsylvanian (56 percent), 3 out of 7 from the Triassic (43 percent), 14 out of 21 from the Miocene (67 percent), and 8 out of 10 from the Recent (80 percent). Pre-Jurassic agents of breakage were apparently less likely to concentrate attacks on larger shells than were post-Jurassic predators.

Our limited data support the hypothe-

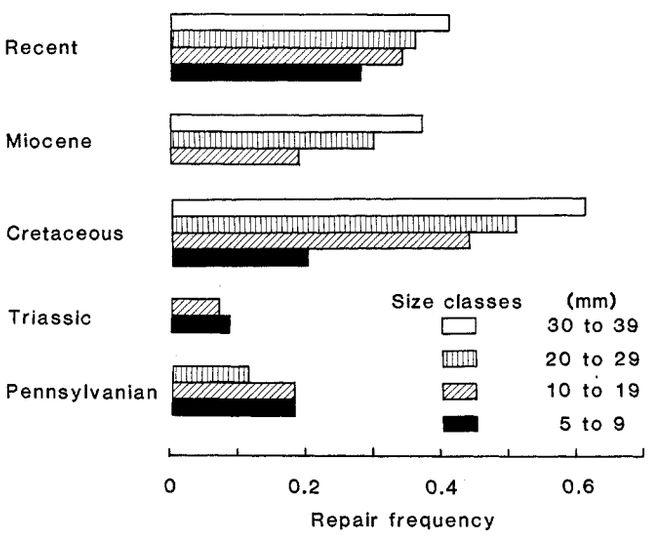

Fig. 1. Size-specific frequency of repair (number of scars divided by total number of shells of all species in a size class) through geological time.

Table 1. Median frequencies of shell repair in gastropods through time. N is the number of species and F is the frequency of repair.

Assemblage	Shell repair in 5- to 9-mm class		10- to 19-mm class		20- to 29-mm class		Complete sample	
	N	F	N	F	N	F	N	F
Recent, all species	3	.40	26	.27	15	.33	53	.28
Venado Beach, Panama			8	.37	7	.44	18	.37
Wom, Papua New Guinea			6	.12			13	.08
Pujada Bay, Mindanao			6	.31			12	.25
Dodinga Bay, Halmahera			5	.38			7	.44
Tumon Bay, Guam					4	.27	9	.29
Miocene, all species			16	.20	14	.34	19	.40
Gatun 1			5	.14	10	.33	17	.33
Gatun 2			7	.18	10	.33	12	.36
Gatun 3							9	.19
Cretaceous, Ripley (14 sites)	7	.20	7	.41	3	.50	24	.35
Triassic, St. Cassian Group	10	.08	7	.06			11	.08
Pennsylvanian, all species	8	.15	15	.11	4	.08	16	.13
Grindstone Creek	5	.21	7	.05			12	.17
Wolf Mountain			5	.14			5	.11
Colony Creek 1							5	.09
Colony Creek 2	5	.11					8	.09
Finis 1			6	.07			7	.06
Finis 2			5	0			7	.04
Wayland			6	.32			7	.31

sis that shell-breaking predators became more important as agents of selection among gastropods in the middle Mesozoic. The fossil record further shows that shell-breaking fish and crustaceans appeared in the Devonian but did not diversify on a large scale until the Jurassic (*1, 2, 7*). These trends through time were accompanied by other important changes in shallow-water marine communities, including increased disturbance of soft sediments by burrowing animals (*8*) and increased destruction of rocks by boring and grazing organisms (*9*). The biological component of selection has evidently undergone substantial change over the course of Earth history.

GEERAT J. VERMEIJ
Department of Zoology, University of Maryland, College Park 20742
DAVID E. SCHINDEL
Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06520
EDITH ZIPSER
Department of Zoology, University of Maryland

References and Notes

1. A. Papp, H. Zapfe, F. Bachmayer, A. F. Tauber, *K. Akad. Wiss. Wien Math. Naturwiss. Klasse Sitzberichte* **155**, 281 (1947).
2. G. J. Vermeij, *Nature (London)* **254**, 419 (1975); *Paleobiology* **3**, 245 (1977).
3. ———, E. Zipser, E. C. Dudley, *Paleobiology* **6**, 352 (1980); G. J. Vermeij, *Malacologia*, in press.
4. G. J. Vermeij and E. C. Dudley, *Cret. Res.*, in press; G. J. Vermeij, E. Zipser, R. Zardini, *J. Paleontol.*, in press; D. E. Schindel and G. J. Vermeij, *ibid.*, in press.
5. Material was obtained from several localities in seven stratigraphic intervals in Middle and Upper Pennsylvanian strata of north-central Texas (Strawn Group: Grindstone Creek, East Mountain, and Palo Pinto shales; Canyon Group: Wolf Mountain and Colony Creek shales; Cisco Group: Finis and Wayland shales; collections in Yale Peabody Museum), from the St. Cassian Group of the Upper Triassic of northern Italy (Museo de Cortina d'Ampezzo), from the Ripley Formation in the Upper Cretaceous of the southeastern United States (U.S. National Museum of Natural History), from the Lower Gatun Formation in the Upper Miocene of Panama (U.S. National Museum of Natural History and Vermeij collections), and from the Recent (ten localities in the tropical Western and Eastern Pacific; Vermeij collection). All measured samples contained at least ten well-preserved shells. Median frequencies of repair (Table 1) illustrate the observed trend but were not used in the statistical treatment of the data. Further details of the method are given in (*3, 4*).
6. M. Hollander and D. A. Wolfe, *Nonparametric Statistical Methods* (Wiley, New York, 1973), p. 503.
7. J. A. Moy-Thomas and R. S. Miles, *Palaeozoic Fishes* (Chapman & Hall, London, 1971), p. 259; F. R. Schram, *San Diego Soc. Nat. Hist. Trans.* **19**, 57 (1979).
8. C. W. Thayer, *Science* **203**, 458 (1979).
9. R. G. Bromley, *Palaeontology* **18**, 725 (1975); J. G. Carter, *Peabody Mus. Nat. Hist. Yale Univ. Bull.* **41**, 1 (1979).
10. We thank N. F. Sohl, W. P. Woodring, and R. Zardini for the use of collections under their care; M. Greene for cleaning the Pennsylvanian shells; and E. Russek for advice on statistics. The work was supported by a grant from the NSF Program of Biological Oceanography to G.J.V.

29 January 1981; revised 12 August 1981

Intrathecal Interferon Reduces Exacerbations of Multiple Sclerosis

Abstract. *Ten patients with multiple sclerosis who were treated with human fibroblast interferon (IFN-B) for 6 months showed a significant reduction in their exacerbation rates compared with their rates before treatment ($P < .01$). The IFN-B was administered intrathecally by serial lumbar punctures. There was no significant change in the exacerbation rates of ten multiple sclerosis control patients before and during the period of observation. The IFN-B recipients have now been on the study a mean of 1.5 years, the controls, 1.2 years. The clinical condition of five of the IFN-B recipients and one of the control patients has improved, whereas the condition of five of the controls and one of the IFN-B recipients has deteriorated ($P < .036$). These findings warrant cautious optimism about the efficacy of intrathecal IFN-B in altering the course of multiple sclerosis and support concepts of a viral or dysimmune etiology of the disease.*

There is evidence that multiple sclerosis (MS) is caused (at least partially) by a viral infection of the central nervous system (CNS) that acts as a "trigger" for repeated exacerbations of neurologic symptoms characteristic of the disease (*1, 2*). Interferon (IFN) is a naturally occurring biologic product with potent antiviral activities (*3*). It does not cross the blood-brain barrier in significant quantity when administered systemically, but can be safely administered intrathecally (*4*). For these reasons we conducted a randomized controlled study of the effects of intrathecally administered human fibroblast interferon (IFN-B) in a series of MS patients.

We included in this study 20 patients (15 women and 5 men aged 15 to 40 years, mean age 30.7 years) who fulfilled clinical and laboratory criteria (*5, 6*) for making the diagnosis of MS with certainty (Table 1). We obtained the informed consent of each patient. The patients were randomly assigned to a group of ten IFN-B recipients or ten controls. The study was not blinded; serial lumbar punctures to inject placebo in the controls were not justified. There were seven women and three men (aged 20 to 40 years, mean age 30.2 years) in the recipient group and eight women and two men (aged 15 to 39 years, mean age 31.1 years) in the control group. Duration of disease prior to entering the study was 1.0 to 19.4 years (mean 8.0 years) in the recipient group and 2.8 to 20.5 years (mean 8.5 years) in the controls. The types of diseases were: exacerbating-remitting with residua (ER-R) in two IFN-B recipients and two controls; exacerbating-remitting, progressive (ER-P) in three IFN-B recipients and one control; and stable with residua (S-R) in five IFN-B recipients and seven controls. The basis for this classification has been described elsewhere (*6, 7*).

All IFN-B recipients had received adrenocorticotropin (ACTH) intravenously or intramuscularly or oral steroids during exacerbations prior to the study; they agreed that they would not receive these therapies should they exacerbate for at least the first year of the study. Should they desire such treatments for relapses after the first year, then ACTH or oral prednisone could be administered without withdrawing them from the study. Controls received these steroids for exacerbations as required during the study. Two controls (see Table 1, controls 1 and 9) also took oral prednisone (10 to 30 mg) on alternate days during the study (as they had done for the previous 1 to 2 years). Initially there were 12 patients in each group. One recipient and two controls withdrew shortly after entering the study; one recipient died during the first month of the study but his death was not related to IFN-B administration.

Each patient underwent a complete neurologic examination at the beginning of the study and at least monthly after entering the study. The recipients were also assessed semiweekly for the first month of the study (when they were receiving IFN-B twice per week). The severity of the patients' symptoms and signs were scored by disability status according to the method described by Kurtzke (*8*). On the basis of the severity of the signs, an overall assessment of the patients' clinical condition (improved, unchanged, worsened) was made at the time of each reevaluation.

An exacerbation was defined as a separate episode or period of development of new symptoms or a group of symptoms when the clinical course had been stationary or improving during the previous month (*6, 9*). The bout had to last longer than 24 hours and there had to be objective neurologic changes confirming the deterioration on examination. If symptoms progressed after a stationary

0036-8075/81/1127-1026$01.00/0