References and Notes

1. M. J. Silver, W. Hoch, J. J. Kocsis, C. M. Ingerman, J. B. Smith, *Science* **183**, 1085 (1974).
2. A preliminary report was based on four of these cases [H. Pirkle and P. Carstens, *Circulation* **40**, Suppl. 3, abstr. 162 (1969)].
3. The general clinical histories in these cases had no features in common except the absence of noteworthy antecedent disease. The apparent predominance of women of childbearing age has raised the question of antiovulatory medication. This was excluded by history in two cases and by the postmortem histologic appearance of the endometrium in a third case. Antiovulatory medication was neither established nor excluded in the remaining cases.
4. Pulmonary aggregates and centrifugally isolated pellets of human platelets appeared the same when stained with hematoxylin and eosin, periodic acid–Schiff reagent, oil red O, Giesma stain, phosphotungstic acid–hematoxylin, and aldehyde fuchsin. The phosphotungstic acid–hematoxylin stain was used to look for fibrin. Arteries were distinguished from veins by the disposition of their elastin fibers as stained with the aldehyde fuchsin method [A. Samuelson, A. E. Becker, C. A. Wagenvoort, *Arch. Pathol.* **90**, 112 (1970)].
5. Other consistent pathologic findings in the lungs were focal edema, minute alveolar hemorrhages, and focal capillary hyperemia. All cases also had mild acute passive hyperemia of liver and spleen and cerebral edema.
6. We injected a rabbit intravenously with 1 mg of arachidonic acid per kilogram and found that the resulting pulmonary platelet aggregates exhibited the same morphologic characteristics observed in our human cases (Fig. 1).
7. J. E. French and J. C. F. Poole, *Proc. R. Soc. Lond. Ser. B* **157**, 170 (1963); J. C. Hoak, *Br. J. Exp. Pathol.* **45**, 44 (1964); A. Kjaerheim and T. Hovig, *Thromb. Diath. Haemorrh.* **7**, 1 (1962).
8. M. B. Zucker and J. Borrelli, *J. Appl. Physiol.* **7**, 432 (1955); K. Grette, *Acta Physiol. Scand.* **56**, Suppl. 195 (1962); T. H. Spaet and M. B. Zucker, *Am. J. Physiol.* **206**, 1267 (1964); R. B. Erichson and J. R. Cintron, *Thromb Diath. Haemorrh.* **18**, 80 (1967); N. F. Rodman and R. G. Mason, *Fed. Proc.* **26**, 95 (1967); M. J. Droller, *Lab. Invest.* **29**, 595 (1973).
9. G. H. Eeles and S. Sevitt, *J. Pathol. Bacteriol.* **93**, 275 (1967); M. Brozman, *Zentralbl. Allg. Pathol. Pathol. Anat.* **99**, 151 (1959).
10. E. P. Jenevein and D. L. Weiss, *Am. J. Pathol.* **45**, 313 (1964).
11. A. Nordöy and A. B. Chandler, *Scand. J. Haematol.* **1**, 16 (1964).
12. J. Kloeze, *Thromb. Diath. Haemorrh.* **23**, 286 (1970).
13. G. Bø and J. Hognestad, *Acta Physiol. Scand.* **85**, 523 (1972).
14. K. Rådegran, S. E. Bergentz, D. H. Lewis, U. Ljungqvist, P. Olsson, *Scand. J. Clin. Lab. Invest.* **28**, 423 (1971).
15. A. G. G. Turpie, M. A. Chernesky, R. P. B. Larke, M. A. Packham, J. F. Mustard, *Lab. Invest.* **28**, 575 (1973).
16. A. Hughes and R. S. Tonks, *J. Pathol. Bacteriol.* **84**, 379 (1962).
17. R. B. Davis, *Exp. Mol. Pathol.* **5**, 559 (1966).
18. H. C. Pirkle, J. G. Wallace, V. G. Allen, *Arch. Pathol.* **74**, 120 (1962).
19. S. Josephson, *Scand. J. Clin. Lab. Invest.* **26**, 113 (1970); L. Dexter, in *Pulmonary Embolic Disease*, A. A. Sasahara and M. Stein, Eds. (Grune & Stratton, New York, 1965), p. 101.
20. V. Gurewich, M. L. Cohen, D. P. Thomas, *Am. Heart J.* **76**, 784 (1968).
21. J. B. Smith, C. Ingerman, J. J. Kocsis, M. J. Silver, *J. Clin. Invest.* **52**, 965 (1973).
22. M. J. Silver, J. B. Smith, C. Ingerman, J. J. Kocsis, *Prostaglandins* **4**, 863 (1973); B. B. Vargaftig and P. Zirinis, *Nat. New Biol.* **244**, 114 (1973); A. L. Willis, *Prostaglandins* **5**, 1 (1974); M. Hamberg, J. Svensson, T. Wakabayashi, B. Samuelsson, *Proc. Natl. Acad. Sci. U.S.A.* **71**, 345 (1974).
23. We thank R. W. Wissler and J. C. F. Poole for helping in the identification of platelet aggregates in the first case. Supported by NIH grant H-4932.

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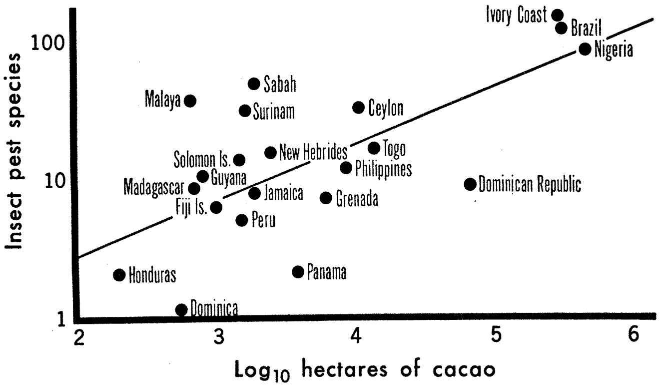
Rapid Asymptotic Species Accumulation in Phytophagous Insect Communities: The Pests of Cacao

Abstract. *The number of cacao insect pests is described by a species-area curve. Either annual cacao productivity or area in cultivation of the crop predicts the number of associated insect pest species, when the world's cacao-producing regions are compared. Analysis of covariance does not discriminate different species-area regressions for native as opposed to nonnative cacao-producing regions; the numbers of insect pest species per unit area of cacao in regions of long-standing cultivation do not exceed the numbers in regions of recent introduction. This demonstrates that the number of cacao insect pest species rises rapidly to an asymptote set by the area in cultivation in each region.*

Species interactions are the focus of community biology. Considerations of matter and energy circulation, productivity, and stability depend on the shape and time course of the species accrual curve. Communities accrue species by colonization, speciation, and extinction; the net number of species at any time is the difference between cumulative addition and extinction. There is a spectrum of possible time courses for species accumulation. At one extreme, communities could grow nonasymptotically; the net number of species in the community could increase at a significant rate through evolutionary or geologic periods. The other extreme is asymptotic growth in ecological time. Theories based on nonasymptotic assumptions explain species richness differences as a result of age differences among communities (*1*). Asymptotic theories hold variation in species richness to result from differences in the relatively age-independent structural properties of the environment (*2, 3*). Evidence that nonasymptotic species accumulation actually occurs is poor (*4*) whereas there is no question that species richness in some communities equilibrates rapidly (*4, 5*).

But communities may accumulate species in different fashions. For example, bird species interact differently than plant or insect species. This led Whittaker (*6*) to predict that insect and plant communities do not become saturated with species, even though bird communities do (*3, 7*). Independent reasoning has led Janzen (*8*) to predict species saturation of phytophagous insect communities, but only after periods of evolutionary time. The problem, then, is to discover how rapidly species assemblages actually equilibrate and whether there is a great variation in time to equilibration (that is, do some communities become saturated rapidly while others require long evolutionary or geologic periods?).

Species saturation is usually verified with reference to the geographic area supporting the species assemblage; I show it here for phytophagous insects with reference to the geographic range of the host plant species. Cacao, *Theobroma cacao*, is a sterculiaceous understory tree native to central and tropical South America (*9*). It has been introduced throughout the tropics during the last 300 years, and cocoa is made from the fruit. Using data from Entwistle (*10*), I have determined the number of insect pest species reported from each region of cacao cultivation. These pests are strikingly autochthonous. Fewer than 15 percent of the 1905 presently reported species are known from more than one cocoa-producing area, and fewer than 1.5 percent are reported as "widespread," "very widespread," or "general." This means that insect pests have been rapidly and independently recruited from the the fauna of each cacao introduction region. Saturation has followed this rapid accumulation of pest species, as shown by a species-area relation (Fig. 1). The species-area relation is $S = kA^z$, where S is the number of species, A the area of the region considered, k a constant for the biota in question, and z the ratio of log species change to log area change (*11*). In this case, the relation shows that an upper limit is set on the number of associated insect species by the area of cacao cultivation in each region. Annual cocoa productivity is highly correlated with area in cacao cultivation [data from (*12*)] on a per region basis (*13*). If cocoa productivity is used as an index of area, ten more regions can be considered; these regions list no data on area in cacao cultivation but do list cocoa productivity. Figure 2 demonstrates that the statistical significance of the species-area relation is preserved when all regions are considered for which there is even indirect information on cacao area and insect species.



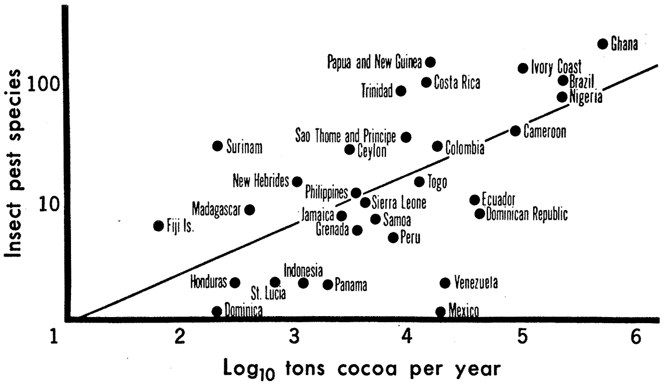


Fig. 1 (left). Number of cacao-associated insect pest species as a function of area in cacao cultivation. Only regions which have at least one reported cacao pest and with geographically congruent pest (*10*) and cacao area (*12*) data are considered. The equation $Y = 0.897X - 0.315$ describes the line ($r = .658$, $.001 < P < .01$). Fig. 2 (right). Number of cacao-associated insect species as a function of the modern maximum of annual cocoa productivity. Productivity is a good index to area of cultivation for a region (*13*). Only regions with at least one reported cacao pest and with geographically congruent pest (*10*) and cacao production (*12*) data are considered. The equation $Y = 0.430X - 0.024$ describes the line ($r = .597$, $P < .001$).

Figures 1 and 2 show that area sets an upper limit on the number of insect species associated with cacao, but there is a possibility that this upper limit changes with time, either in slope (z) or intercept (k). Cacao is native to the New World mainland tropics; it has been spread to other tropical regions only within the last 300 years. If insect/host species switching rates are so low that the system has not equilibrated secondarily, the species-area line for native areas of cacao would lie above that for nonnative areas. However, this is not so. Analysis of covariance does not discriminate different slopes or intercepts for mainland New World regions (including Trinidad) compared to Asian, African, and Oceanian regions, for either Fig. 1 [test of identity of slopes: F (1/17) < 1, not significant; test of identity of intercepts: F (1/17) < 1, not significant] or Fig. 2 [test of identity of slopes: F (1/27) = 1.87, not significant; test of identity of intercepts: F (1/27) < 1, not significant].

The limited data on regional histories of cocoa productivity reinforce the conclusion that a large proportion of the saturation number of pest species is added rapidly. For example, between 1880 and 1939 Brazil increased productivity from 8,000 to 124,000 tons, and between 1938 and 1962 Australian New Guinea increased productivity from 100 to 14,200 tons (*12*). Both of these increases are of the order of half the modern logarithmic range of global cocoa productivity. This means that within 60 years Brazil and within 30 years Australian New Guinea moved their abscissal location approximately halfway across Fig. 2 without associated insect richness lagging behind; points for both regions are above the species-area regression line (Fig. 2). Unfortunately, complementary data on the time rate of pest appearance are not also available.

The few available specific dates of regional cacao introduction also indicate very rapid approach to the insect richness asymptote. The crop was introduced into Madagascar in 1898 and into Nigeria in 1890. Both these regions are now above the species-area line (Figs. 1 and 2); the insect pests of cacao in these areas have been recruited within 72 and 80 years, respectively. Most dramatically, Sabah had less than 30 hectares of cacao before 1956, and there are now 52 cacao insect pest species on this island for approximately 1980 hectares of the crop. That this rapid increase is asymptotic is shown by insect species richnesses of regions where cacao has been cultivated for longer periods. Based on the earliest reports, the crop has been farmed on Trinidad since 1727 (*10*), on São Thomé since 1822, and on Hispaniola since 1730 (*14*). If the high rates of increase in number of insect pests had continued undiminished through these long periods of cultivation, there would be no species-area relation.

It might be argued, since native population and species densities of *Theobroma* are greatest in the upper Amazon and on the northwestern side of the Andes, that only these two regions should be considered as "native" for the pests of the crop. Since little cacao is commercially grown in the upper Amazon this area must be ignored, however much is grown on the western side of the northern Andes, in Colombia, Ecuador, and Peru (*9*). If insect adaptation to new host species were so slow that 300 years is insufficient to allow the recruitment of a saturated pest community, Colombia, Ecuador, and Peru would tend to be above the regression line. However only one of the other three is above the line, and the other two are well below it (Fig. 2).

It might be argued that regions growing more cacao would have invested more in entomologic research and hence would have discovered more local pests of the crop. But given the general importance of the species-area phenomenon (*11*), larger areas have more species than smaller ones. Hence, if an "entomologist-area" relation exists, the greater number of entomologists in larger areas would tend to help find the greater number of species there, rather than produce a spurious correlation. Since cacao-associated insects are recorded (*10*) from many areas without local research institutions (*12*) and work on the systematic entomology of the crop has been worldwide, the pest data can be interpreted as a first approximation of global patterns.

This report is consistent with that of Opler (*15*), which shows a species-area relation for the microlepidoptera of California oak species, and with my earlier results (*4, 16*), which show that the asymptote of insect species accumulation on British trees is reached within 300 years.

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References and Notes

1. A. Belt, *A Naturalist in Nicaragua* (Murray, London, 1874); A. R. Wallace, *Tropical Nature and Other Essays* (Macmillan, London, 1898); M. A. Buzas and T. G. Gibson, *Science* **163**, 72 (1969); P. J. Darlington, *Zoogeography* (Wiley, New York, 1960); M. J. Dunbar, *Am. Nat.* **94**, 129 (1960); D. M. Raup and S. M. Stanley, *Principles of Paleontology* (Freeman, San Francisco, 1971); G. H. Schwabe, in *Biogeography and Ecology in South America*, E. G. Fittkau, J. Illies, H. Klinge, G. H. Schwabe, H. Sioloi, Eds. (Junk, The Hague, 1969); L. A. Zenkevitch, in *Oceanography*, M. Sears, Ed. (AAAS, Washington, D.C., 1961).
2. E. O. Wilson, *Brookhaven Symp. Biol. No. 22* (1969), p. 38.
3. R. H. MacArthur, *Biol. Rev.* **40**, 510 (1965).
4. D. R. Strong, *Proc. Natl. Acad. Sci. U.S.A.*, in press.
5. D. S. Simberloff and E. O. Wilson, *Ecology* **50**, 278 (1969).
6. R. H. Whittaker, *Brookhaven Symp. Biol. No. 22* (1969), p. 178.
7. R. H. MacArthur, in *Speciation in Tropical Environments*, R. H. Lowe-McConnel, Ed. (Academic Press, London, 1969); J. M. Diamond, *Science* **179**, 759 (1973).
8. D. H. Janzen, *Am. Nat.* **107**, 786 (1973).
9. F. Hardy, *Cacao Manual* (Inter-American Institute of Agricultural Sciences, Costa Rica, 1960).
10. P. F. Entwistle, *Pests of Cocoa* (Longmans, London, 1972).
11. D. S. Simberloff, in *Models in Paleobiology*, T. J. M. Schopf, Ed. (Freeman, San Francisco, 1972).
12. C. A. Krug and E. Quatrey-Papafio, *FAO (Food Agric. Organ. U.N.) Agric. Stud. No. 63* (1964).
13. Area of cacao productivity (*12*) is a function of the modern (1950 to present) maximum annual productivity of cocoa. The correlation coefficient $r = .8598$, $P < .001$, leaving only 26 percent of the variance in cultivation area of cacao unexplained by the modern maximum of annual cocoa productivity. This justifies the indirect species-area curve of Fig. 2, which includes more points than Fig. 1. The equation $Y = 0.735X + 2.093$ describes the regression of "area in cacao" upon "annual cacao productivity."
14. C. J. J. Van Hall, *Cacao* (Macmillan, New York, ed. 2, 1932).
15. P. A. Opler, *Am. Sci.* **62**, 67 (1974).
17. I thank L. Abele, K. Heck, D. H. Janzen, E. McCoy, P. Opler, T. Ray, and M. Wang for discussion of this work and M. Lasley for technical help. Supported by NSF grant GB-42575.

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Rhizoplane Fibrils in Wheat: Demonstration and Derivation

Abstract. *Aggregates of fine, curved fibrils extend from the rhizoplane of soil-grown wheat roots into the rhizosphere. The fibril diameter is usually between 3 and 10 nanometers. The fibrils arise as extracellular products of the root, and some aggregates are intimately associated with microbial cells and soil particles.*

The roots of plants play a vital role in the activities of the biosphere. Epstein (*1*) stated that "the root is the interface between terrestrial life and the mineral substrate supplying all other essential elements." The interface between root and soil can be a region of high metabolic activity as a result of plant-microflora associations (*2–4*). Many noninvading microorganisms are concentrated at the root surface or rhizoplane (*5*) and in the immediate soil zone or rhizosphere. This microflora influences the mineral nutrition of the root (*2, 6*) and is in turn subject to influences from the soil environment. Some attempts have been made by agricultural scientists to describe the structure of the rhizoplane and rhizosphere in terms of the three-dimensional disposition of plant and microbial cells (*7, 8*). These attempts have been revealing but can and should be pursued further.

In recent years, considerable attention has been focused on extracellular plant materials (*9*). One class of these, fibrillar polygalacturonic acid (*10, 11*), can form extensive weblike structures of great surface area which project from cells into the external milieu. These extracellular structures (made up of distinctive curved fibrils which have diameters between 20 nm and the resolution limit for sectioned material) are known to exist on the surface of some roots grown in laboratory culture (*12*). Their function has not been studied, but these fibril aggregates with their acidic character could take part in the uptake of minerals (including heavy metals) and act as anchor sites for both microbes and extracellular enzymes. Their small but significant protein component (*13, 14*) indicates that they may have some enzymatic activity of their own (*10*), a suggestion reinforced by some findings of Halperin (*15*). It is of interest to know if these or similar fibrils exist at the rhizoplane (or in the rhizosphere). This report documents the existence of electron-opaque fibrils on soil-grown roots of common wheat and demonstrates that these fibrils are plant-derived.

Wheat, *Triticum aestivum* L. emend Thell., was grown under controlled environmental conditions in a growth chamber in pots containing Lethbridge soil (Canada Agriculture Research Station, Lethbridge, Alberta) for 19 days, at which time soil samples containing well-developed roots were taken. Root tips plus adhering soil were placed for 90 minutes at room temperature in a large volume of chemical fixative (7 percent glutaraldehyde in $0.05M$ phosphate buffer at *p*H 6.8). Each sample was washed with buffer so as to minimize displacement of adhering soil. A cold postfixation in ruthenium-osmium (*16*) was given according to the method of Leppard *et al.* (*13*). Final washes were in distilled water at room temperature, and the sample was dehydrated slowly by using an ethanol series followed by propylene oxide. Embedding was in Spurr's low-viscosity medium (*17*). Sections were cut with glass knives on a Porter-Blum MT-2B ultramicrotome, as described previously for embedded material containing mineral

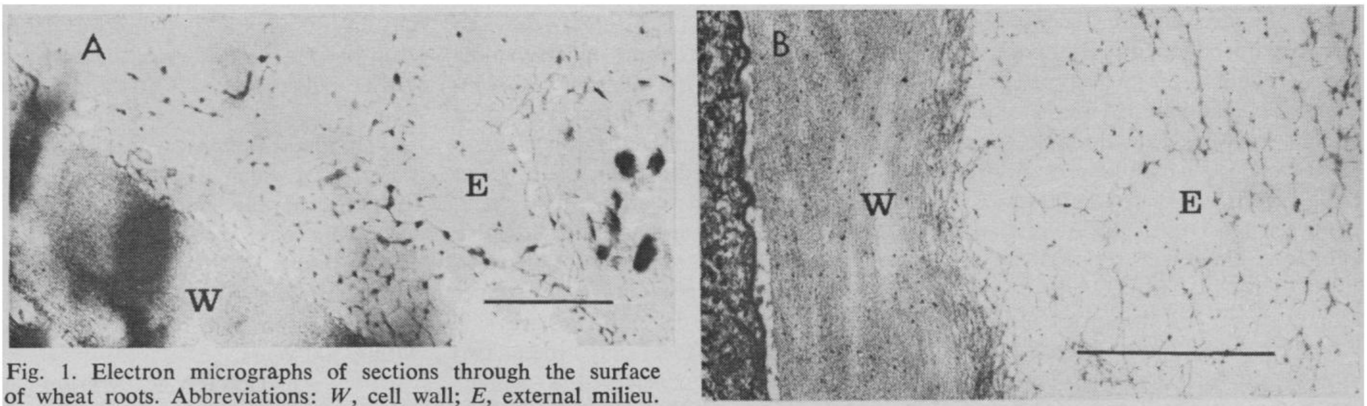

Fig. 1. Electron micrographs of sections through the surface of wheat roots. Abbreviations: *W*, cell wall; *E*, external milieu. The scale bar indicates 500 nm. (A) Electron-opaque fibrils extending from the cell wall into the rhizosphere of a soil-grown root. Many of these fibrils are coarse. (B) Electron-opaque fibrils extending from the cell wall of an axenically grown root. Many of these fibrils are delicate. It is not known whether the ratio of coarse to delicate fibrils is diagnostic of the growth conditions.