

References and Notes

1. B. C. Pressman, *Fed. Proc.* **27**, 1283 (1968).
2. M. Pinkerton, L. K. Steinrauf, P. Dawkins, *Biochem. Biophys. Res. Commun.* **35**, 512 (1969).
3. M. Ohnishi and D. W. Urry, *Science* **168**, 1091 (1970).
4. V. T. Ivanov, I. A. Laine, N. D. Abdulaev, L. B. Senyavina, E. M. Popov, Y. A. Ovchinnikov, M. M. Shemyakin, *Biochem. Biophys. Res. Commun.* **34**, 803 (1969); V. T. Ivanov and Y. A. Ovchinnikov, in *Conformational Analysis*, G. Chiurdoglu, Ed. (Academic Press, New York, 1971), p. 117.
5. J. H. Young, G. A. Blondin, G. Vanderkooi, D. E. Green, *Proc. Nat. Acad. Sci. U.S.A.* **67**, 550 (1970).
6. W. K. Lutz, K. Winkler, J. D. Dunitz, *Helv. Chim. Acta* **54**, 1103 (1971).
7. A. Ahtarap, J. W. Chamberlin, M. Pinkerton, L. Steinrauf, *J. Amer. Chem. Soc.* **89**, 5737 (1967).
8. H. Hauptman and W. L. Duax, *Acta Crystallogr.*, in press.
9. H. Hauptman, J. Fisher, H. Hancock, D. A. Norton, *Acta Crystallogr. Sect. B* **25**, 811 (1969).
10. W. L. Duax and H. Hauptman, *J. Amer. Chem. Soc.*, in press.
11. J. Karle and I. L. Karle, *Acta Crystallogr.* **21**, 849 (1966); W. H. Zachariasen, *ibid.* **5**, 68 (1952).
12. G. Germain and M. M. Woolfson, *Acta Crystallogr. Sect. B* **24**, 91 (1968).
13. P. T. Beurskins, "The sign correlation procedure and some related topics," lecture notes from the NATO Meeting on Direct Methods held in York, England, 6 to 17 September 1971. Beurskins was one of the first workers to use a formula for cosine calculation; it was a precursor of the more accurate one employed here. While he recognized the importance of those cosines which were calculated to be negative, his applications were, for the most part, made to structures in the centrosymmetric space groups, in which the problem of enantiomorph selection does not arise.
14. In the procedure described here the introduction of the fourfold ambiguity represents an element of multiple solution. Symbolic addition shares this element of multiple solution in the case that the numeric values of the symbols are not uniquely determined and several possible combinations of values for each symbol must be assumed.
15. D. Sayre, *Acta Crystallogr.* **5**, 60 (1952); H. Hauptman and J. Karle, "Solution of the phase problem," *American Crystallographic Association Monograph 3* (Edwards, Ann Arbor, Mich., 1953), part 1.
16. J. Karle and H. Hauptman, *Acta Crystallogr.* **9**, 635 (1956).
17. C. Weeks and H. Hauptman, Abstract H4, American Crystallographic Association Meeting, Columbia, South Carolina, 1971.
18. We wish to thank Dr. C. Wenner of Roswell Park Memorial Institute for supplying the crystals of valinomycin and J. Fisher for writing some of the computer programs.

18 November 1971; revised 15 March 1972 ■

Revegetation following Forest Cutting: Mechanisms for Return to Steady-State Nutrient Cycling

Abstract. *Dense stands of a woody, successional species, Prunus pensylvanica L., develop rapidly, with early closure of canopy and rapid attainment of high values of net annual production and nutrient accumulation. Such rapid growth following disturbance tends to minimize losses of nutrients from the ecosystem, thus promoting a return to steady-state cycling characteristic of a mature forest.*

Because terrestrial plant communities have always been subjected to various forms of natural disturbances, such as wind storms, fires, and insect outbreaks, it is only reasonable to consider recovery from disturbance as a normal part of community maintenance and repair. Although the structural basis of recovery from disturbance has long been recognized, the functional basis is only now beginning to be understood, largely as a result of the whole ecosystem studies of nutrient cycling at the Hubbard Brook Experimental Forest in New Hampshire (1-3).

At Hubbard Brook, experimental clear-cutting and subsequent herbicidal spraying of a 15.6-hectare watershed-ecosystem triggered a chain of events which led to pronounced changes in ecosystem function (3, 4). Significant increases in decomposition rates, nitrification, streamwater concentrations of dissolved inorganics (most notably nitrate-nitrogen), total hydrologic runoff, and erosion have been reported (2, 3, 5, 6). The combined effect of deforestation and suppression of vege-

tative regeneration with herbicides caused extreme open or loose cycling of nutrients (nutrient dumping), which were flushed from the forest soils into streams where they caused eutrophication.

The cutting and herbicide experiment raises important and fundamental questions about both the general impact of disturbance on the functioning of ecosystems and the means by which

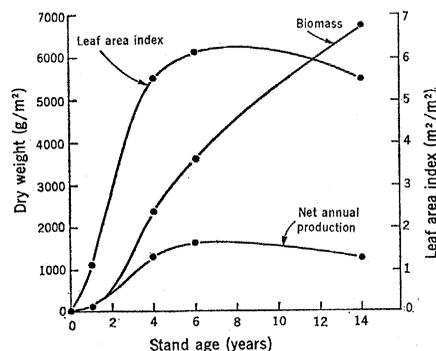


Fig. 1. Relationships of biomass, net annual production, and leaf area index to stand age.

such impact is attenuated by natural recovery processes. Because similar trends are produced by commercial clear-cutting practices in the Northeast (7), it is of considerable interest to understand these recovery processes, especially as they are related to nutrient circulation. We present data to show the importance of a fast-growing, short-lived, successional tree species, pin cherry (*Prunus pensylvanica* L.), in reducing the degradative nutrient losses found at Hubbard Brook, and discuss the implications for ecosystem stability and forestry practice. Disturbance is here defined as destruction of vegetation, or parts of vegetation, whether natural or man-induced.

Erosional and nutrient element losses from a forest ecosystem following disturbance are diminished by any form of vegetative regeneration, there being a roughly inverse relationship between the rate of regeneration and the amounts of erosional and nutrient losses (8). To measure the rate of recovery following cutting, we sampled naturally occurring stands of pin cherry in different stages of recovery (1, 4, 6, and 14 years after cutting). To minimize site differences between stands, we sampled stands which were all in north-central New Hampshire, all on the same geologic formation, all subjected to the same disturbance (clear-cutting), all broadly equivalent in drainage and elevation, and, most importantly, all densely stocked with, and dominated by, the same successional species—pin cherry.

We measured the rate of recovery of the ecosystem in terms of amount of biomass, rate of biomass accumulation (by measuring net annual primary production for each stand), rate of canopy closure as indicated by leaf area index (9), and rate of accumulation of nutrients (nitrogen, calcium, magnesium, potassium, and sodium) in plant tissues (10).

Our approach to biomass and production estimation (14) followed harvest techniques based on the allometric relations of individual sample trees (11, 12). Three to five replicate chemical analyses were made for each major tissue (leaves, current twigs, older branches, dead branches, roots, stem wood, and stem bark) from each of the three older stands (4, 6, and 14 years), and included macro-Kjeldahl nitrogen and cation analyses by atomic absorption spectrophotometry (13). For a particular stand, weights of the different plant parts were multiplied by the ap-

propriate nutrient concentrations to yield estimates of standing crop of each nutrient element per unit area of land surface (in grams per square meter).

Young, very dense stands of pin cherry develop rapidly (Fig. 1). Leaf area indexes equivalent to the upper end of the range for temperate deciduous forests (4.0 to 6.0) (14) were attained within 4 years. Reestablishment of a full canopy implies marked increases in transpiration compared to that in the disturbed condition and substantial moderation of soil temperatures during the growing season, the significance of which for nutrient loss is discussed below.

Total net annual production, including estimates of below-ground production (10), for the young pin cherry stands is high (15) compared to that of other deciduous forests of natural origin, some of considerably older age, including the undisturbed forest at Hubbard Brook. Indeed, the value for the 6-year-old stand, 1650 g/m², exceeds the usual range for temperate climax forests (1200 to 1500 g/m²) (12, 15). Accretion of biomass is rapid in these young, dense, successional stands.

Incorporation of nutrient elements into the developing biomass of the three older stands is also rapid, especially for nitrogen and calcium (Fig. 2). We estimate, for example, annual uptake of nitrogen in the 4- and 6-year-old stands to be about 50 percent greater (10.0 compared with 6.5 g/m²) (5) than uptake in the mature, undisturbed ecosystem at Hubbard Brook. It is likely that the high rates of nutrient uptake and growth result from an adaptive capacity of this species to utilize the greater availability of water and nutrients on disturbed sites (10).

Our data indicate that, following severe disturbance such as clear-cutting, the growth and development of dense stands of successional species such as pin cherry may be extremely rapid. Such growth acts to minimize nutrient losses from the ecosystem. This regulation of nutrient cycling is achieved soon after disturbance by a complex interaction involving (i) channeling of water from runoff to evapotranspiration, thereby reducing erosion and nutrient loss; (ii) reduction in rates of decomposition through moderation of the microclimate during the growing season, so that the supply of soluble ions available for loss in drainage water is reduced; and (iii) simultaneous incorporation into the rapidly developing

biomass of nutrients that do become available and that otherwise might be lost from the system.

The extent of nutrient loss from a forest ecosystem following clear-cutting, while varying with local conditions, such as type of vegetation, the nature of the cutting, site characteristics (slope, drainage, and so forth), and degree of soil scarification, should nevertheless decrease according to the rate of revegetation. Dense stands of fast-growing, successional species will exhibit pronounced regulation of ecosystem function soon after disturbance, the net effect of which is to move the ecosystem rapidly back toward the steady-state, stable pattern of nutrient circulation that typifies the mature forest (5, 10, 16).

The implication of our data is that successional species, specially adapted to exploit disturbed conditions (10), ought to be considered integral components of the larger ecosystem, despite the fact that they are typically absent from the terminal, climax community. Successional species have evolved in relation to the pattern of disturbance in the climax community; indeed the design of the life cycle of pin cherry, particularly the storage in soil, longevity, and germination requirements of its seeds, assures that its occurrence is geared closely into the pattern of disturbance in the large system (10).

Silvicultural practice that ignores the function of successional, "weed," tree species like pin cherry because they are economically undesirable, may be eco-

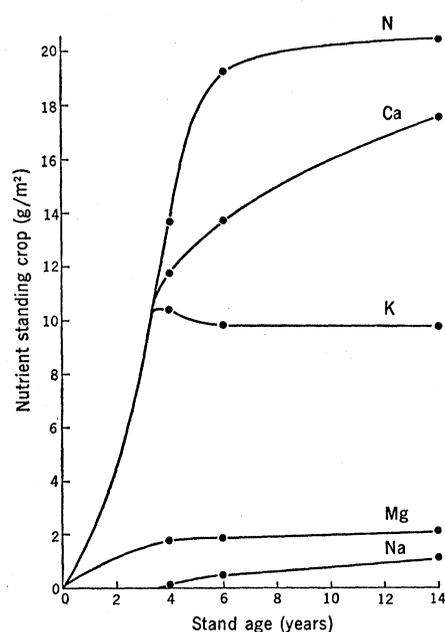


Fig. 2. Relationship of nutrient standing crop to stand age.

logically unsound. In the important issue of evaluating the effects of clear-cutting practices, the role of successional species in the recovery process is deserving of considerably more basic research.

P. L. MARKS

Section of Ecology and Systematics,
Cornell University,
Ithaca, New York 14850

F. H. BORMANN

School of Forestry,
Yale University,
New Haven, Connecticut 06511

References and Notes

1. G. E. Likens, F. H. Bormann, N. M. Johnson, R. S. Pierce, *Ecology* **48**, 772 (1967); N. M. Johnson, G. E. Likens, F. H. Bormann, R. S. Pierce, *Geochim. Cosmochim. Acta* **32**, 531 (1968); G. E. Likens and F. H. Bormann, in *Ecosystem Structure and Function*, J. A. Wiens, Ed. (Oregon State Univ. Press, Corvallis, 1971), p. 25; in *Interactions between Land and Water*, F. H. Whitehead, Ed. (International Association for Ecology, London, in press).
2. F. H. Bormann, G. E. Likens, D. Fisher, R. S. Pierce, *Science* **159**, 882 (1968); W. H. Smith, F. H. Bormann, G. E. Likens, *Soil Sci.* **106**, 471 (1968).
3. G. E. Likens, F. H. Bormann, N. M. Johnson, *Science* **163**, 1205 (1969); ———, D. Fisher, R. S. Pierce, *Ecol. Monogr.* **40**, 23 (1970).
4. F. H. Bormann and G. E. Likens, *Sci. Amer.* **223**, 92 (1970).
5. A. Dominski, thesis, Yale University (1971).
6. R. S. Pierce, J. W. Hornbeck, G. E. Likens, F. H. Bormann, in *Proceedings of the IASH-UNESCO Symposium on the Results of Research on Representative and Experimental Basins*, Wellington, New Zealand (1970), p. 311.
7. R. S. Pierce, C. W. Martin, C. C. Reeves, G. E. Likens, F. H. Bormann, unpublished data.
8. F. H. Bormann, G. E. Likens, J. S. Eaton, *BioScience* **19**, 600 (1969).
9. Leaf area index, the dimensionless ratio of the area of leaf surfaces (one side of blade only) above a particular area of ground surface to that area of ground surface, is a convenient measure of canopy closure.
10. P. L. Marks, thesis, Yale University (1971).
11. R. H. Whittaker, *Ecology* **42**, 177 (1961); *ibid.* **43**, 357 (1962); *ibid.* **46**, 365 (1965); G. L. Baskerville, *ibid.*, p. 867; *Forest Sci. Monogr.* **9** (1965); T. Kira and T. Shidei, *Jap. J. Ecol.* **17**, 70 (1967); T. Satoo, in *Analysis of Temperate Forest Ecosystems*, D. E. Reichle, Ed. (Springer-Verlag, New York, 1970), p. 55.
12. D. F. Westlake, *Biol. Rev. Cambridge Phil. Soc.* **38**, 385 (1963); R. H. Whittaker, *Ecology* **47**, 103 (1966); *Communities and Ecosystems* (Macmillan, London, 1970).
13. G. E. Likens and F. H. Bormann, *Yale Univ. Sch. For. Bull.* **79** (1970).
14. R. H. Whittaker and G. M. Woodwell, *Amer. J. Bot.* **54**, 931 (1967).
15. H. W. Art and P. L. Marks, in *Forest Biomass Studies*, H. E. Young, Ed. (Life Sciences and Agricultural Experiment Station, Univ. of Maine, Orono, 1971), p. 1.
16. F. H. Bormann, G. E. Likens, T. G. Siccamo, R. S. Pierce, in preparation.
17. Contribution No. 42 of the Hubbard Brook Ecosystem Study. Supported by NSF grants GB-6567, GB-6742, GB-14325, and GB-14289. Fieldwork was done through the cooperation of the Northeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture, Upper Darby, Pennsylvania. We thank F. T. Ledig, G. K. Voigt, T. G. Siccamo, R. S. Pierce, S. Filip, D. M. Smith, G. M. Furnival, T. Delevoryas, and H. J. Lutz for help and advice during the study, and J. S. Eaton, L. N. Miller, R. S. Pierce, T. G. Siccamo, and R. H. Whittaker for helpful comments on the manuscript.

13 March 1972