

- Can. J. Fish. Aquat. Sci.* 37, 1540–1549
- 23 Lamarra, V.A., Jr (1975) *Verh. Int. Ver. Theor. Angew. Limnol.* 19, 2461–2468
- 24 Krokhin, E.M. (1975) in *Coupling of Land and Water Systems* (Hasler, A.D., ed.), pp. 153–156, Springer-Verlag
- 25 Threlkeld, S.T. (1988) *Limnol. Oceanogr.* 33, 1362–1375
- 26 Braband, Å., Faafeng, A. and Nilssen, J.P.M. (1990) *Can. J. Fish. Aquat. Sci.* 47, 364–372
- 27 Reinertsen, H., Jensen, A., Koksvick, J.I., Langeland, A. and Olsen, Y. (1990) *Can. J. Fish. Aquat. Sci.* 47, 166–173
- 28 Boers, P., van Ballegooijen, L. and Uunk, J. (1991) *Freshwater Biol.* 25, 9–20
- 29 Carpenter, S.R. *et al.* *Am. Nat.* (in press)
- 30 Bartell, S.M. (1981) *Hydrobiologia* 80, 139–146
- 31 Mazumder, A., McQueen, D.J., Taylor, W.D. and Lean, D.R.S. (1988) *Limnol. Oceanogr.* 33, 421–430
- 32 Vanni, M.J. and Findlay, D.L. (1991) *Ecology* 71, 921–937
- 33 Reinertsen, H., Jensen, A., Langeland, A. and Olsen, Y. (1986) *Can. J. Fish. Aquat. Sci.* 43, 1135–1141
- 34 Schindler, D.E. *Can. J. Fish. Aquat. Sci.* (in press)
- 35 Gliwicz, M.J. (1986) *Nature* 320, 746–748
- 36 Wright, D.L. and Shapiro, J. (1984) *Verh. Int. Ver. Theor. Angew. Limnol.* 22, 518–524
- 37 Clark, C.W. and Levy, D.A. (1988) *Am. Nat.* 131, 271–290
- 38 Holling, C.S. (1973) *Annu. Rev. Ecol. Syst.* 4, 1–23
- 39 DeAngelis, D.L., Bartell, S.M. and Brenkert, A.L. (1989) *Am. Nat.* 134, 778–805
- 40 De Angelis, D.L., Mulholland, P.J., Elwood, J.W., Palumbo, A.V. and Steinman, A.D. (1990) *Environ. Manage.* 14, 685–697
- 41 DeAngelis, D.L. (1992) *Dynamics of Nutrient Cycling and Food Webs*, Chapman & Hall
- 42 Pimm, S.L. and Lawton, J.H. (1977) *Nature* 268, 329–331
- 43 Jordan, C.F., Kline, J.R. and Sasscer, D.S. (1972) *Am. Nat.* 106, 237–253
- 44 Pomeroy, L.R. (1970) *Annu. Rev. Ecol. Syst.* 1, 171–190
- 45 Waide, J.B. (1988) in *Forest Hydrology and Ecology at Coweeta* (Swank, W.T. and Crossley, D.A., Jr, eds), pp. 383–405, Springer-Verlag
- 46 National Research Council (1992) *Restoration of Aquatic Ecosystems*, National Academy Press
- 47 Webster, J.R., Waide, J.B. and Patten, B.C. (1975) in *Mineral Cycling in Southeastern Ecosystems* (Howell, F.G., Gentry, J.B. and Smith, M.H., eds), pp. 1–27, Energy Research and Development Association
- 48 Pimm, S.L. (1984) *Nature* 307, 321–326

Effects of Plant Species on Nutrient Cycling

Sarah E. Hobbie

Plant species create positive feedbacks to patterns of nutrient cycling in natural ecosystems. For example, in nutrient-poor ecosystems, plants grow slowly, use nutrients efficiently and produce poor-quality litter that decomposes slowly and deters herbivores. In contrast, plant species from nutrient-rich ecosystems grow rapidly, produce readily degradable litter and sustain high rates of herbivory, further enhancing rates of nutrient cycling. Plants may also create positive feedbacks to nutrient cycling because of species' differences in carbon deposition and competition with microbes for nutrients in the rhizosphere. New research is showing that species' effects can be as or more important than abiotic factors, such as climate, in controlling ecosystem fertility.

Ecologists have long recognized that vegetation can exert a strong influence over soil properties, and that individual plant species play an important role in determining soil fertility in natural ecosystems¹. Plant species create positive feedbacks to nutrient cycling, affecting nutrient cycling directly through uptake, use and loss of nutrients,

and indirectly by influencing microbial activity and herbivory.

Uptake and use

In general, differences among plant species in nutrient uptake and loss reinforce existing patterns of nutrient availability. In low-nutrient ecosystems such as tundra, boreal areas, desert and highly leached tropical systems, rates of nutrient mineralization from organic matter are slow, so nutrient supply and diffusion limit nutrient uptake^{2,3}. Plants from such low-nutrient environments have higher allocation to below-ground parts, including mycorrhizae, than plants from high-nutrient environments⁴ – at the expense of allocation to carbon (C) acquisition and growth⁵. Besides having traits that increase their ability to take up scarce nutrients, species from low-nutrient ecosystems have inherently low relative growth rates, and thus have a low demand for nutrients⁴.

In contrast, in high-nutrient ecosystems such as old-fields and some grasslands, the strength of the sink for nutrients controls plant nutrient uptake. Although roots are the immediate sink for soil nutri-

ents, the ultimate sink is whole-plant growth. Species from environments where soil nutrients are abundant allocate more to above-ground parts, have more rapid growth rates, and have higher rates of nutrient uptake per gram of root biomass than species from low-nutrient environments^{4,6}.

Once plants have taken up nutrients, further nutrient demand depends on the efficiency with which they use acquired nutrients⁷. In general, species from low-nutrient environments are more efficient than those from high-nutrient environments in their nutrient use^{7,8}, mainly because they have low productivity and long-lived tissues, minimizing losses due to abscission and maximizing cumulative photosynthesis per gram of nitrogen (N)⁴. Although the C:N ratio of plant leaves is high in N-poor habitats^{4,7}, such plants do not exhibit higher rates of C fixation per unit of N than plants with low leaf C:N⁹. Leaf retranslocation efficiencies vary inconsistently across gradients of nutrient availability, and leaching losses show no pattern with nutrient availability⁴.

In general, plant species reinforce patterns of nutrient availability in natural ecosystems through their uptake and use of nutrients^{4,7}. In low-nutrient ecosystems, plants grow slowly and use nutrients efficiently, minimizing

Sarah Hobbie is at the Dept of Integrative Biology, University of California, Berkeley, CA 94720, USA.

demand for and loss of nutrients – traits that result in slow cycling of nutrients. In contrast, plants from high-nutrient ecosystems grow rapidly and use nutrients inefficiently, promoting rapid cycling of nutrients.

Litter

Once nutrients are lost from the plant as litter, the quality of that litter (i.e. its C:N ratio and lignin content) influences how it decomposes. Because plants rely mainly on inorganic forms of nutrients, they depend on microbes to decompose litter and mineralize nutrients tied up in organic matter. Thus, although climate has a strong direct influence on litter decay, plant species also influence nutrient cycling through differences in litter quality. Species from low-nutrient environments produce poor-quality litter that decomposes slowly, further reducing nutrient availability, compared with species from high-nutrient environments^{2,4}.

In general, litter decay rate is inversely related to C:N and lignin:N ratios and positively related to N content^{2,10}. In temperate hardwood forests, for example, foliar litter decay rate is inversely related to the lignin:N ratio in litter¹⁰ and annual net N mineralization rates are well correlated with native foliar litter decay rates^{8,11}. Thus, canopy lignin content is a good predictor of annual net N mineralization rate – a potentially powerful relationship that has recently allowed remote sensing of N mineralization rates using the spectral signal of canopy lignin content¹².

Unfortunately, correlative evidence alone cannot distinguish cause from effect. The strong correlation between litter quality and N mineralization rates may indicate that litter quality determines litter decay rate and thus N mineralization rate. Alternatively, abiotic factors such as temperature and moisture may control N mineralization rates, and plant species with particular foliar chemistries may establish on soils with particular nutrient regimes¹³. For example, species that produce high concentrations of C-based secondary metabolites, such as lignin and tan-

nin, tend to establish on poor-quality soils¹⁴.

A recent experiment by Wedin and Tilman¹⁵ supports the interpretation that species' characteristics can determine nutrient availability independent of climate. They have shown that when old-field grass species differing in litter quality and growth phenology are planted on similar soils, these soils diverge in their rates and timing of annual net N mineralization. Differences in N mineralization rates are best explained by interspecific differences in below-ground litter quality. The species that create the lowest rates of N mineralization, *Andropogon gerardi* and *Schizachyrium scoparium*, are also superior competitors in low-N sites, while the species that create the highest rates of N mineralization, *Poa pratensis* and *Agropyron repens*, are superior competitors on high-N soils. Thus, these grass species create positive feedbacks to nutrient availability in the habitats in which they naturally occur.

Most likely, distributions of plant species are both a cause and an effect of patterns of nutrient cycling in natural ecosystems. As with nutrient uptake and use, species reinforce patterns of nutrient availability because those that grow on nutrient-poor soils produce recalcitrant litter that decomposes slowly, whereas those that occur on fertile soils produce easily-degraded litter. The key to understanding the controls over nutrient cycling in any ecosystem is to tease apart the relative importance of substrate and abiotic effects on decomposition; this can be done using either controlled laboratory incubations or field experiments in which substrate (vegetation) is varied while other factors such as climate are held constant¹⁶. Such experiments have revealed that, in some cases, substrate effects are more significant than abiotic effects in controlling soil processes^{2,17}.

Rhizosphere effects

One of the most important but least understood ways in which plants may affect nutrient cycling is by fixing C that is then rapidly made available to microbes in the roots and rhizosphere. Microbes that take advantage of such readily

available C range from symbiotic N-fixing bacteria and mycorrhizae to free-living heterotrophic soil microbes.

Plant species that host the N-fixing bacteria *Rhizobium* or *Frankia* may add N to ecosystems through litter input or, potentially, by having low demand for soil N, thereby increasing its availability to other species. An example of the effects of an N-fixer on nutrient cycling can be seen in the invasion of *Myrica faya*, an N-fixing tree, in Hawaii¹⁸. Soils associated with *Myrica faya* have larger soil N pools, higher potential rates of N mineralization and support greater growth of seedlings of the native tree, *Metrosideros polymorpha*, than do soils associated with *M. polymorpha* alone.

A more subtle way in which plant species may affect rates of nutrient cycling is through their association with mycorrhizal fungi. As mentioned above, mycorrhizae greatly enhance the ability of plants to acquire nutrients, especially when C is abundant relative to soil nutrients. Mycorrhizae may also influence nutrient cycling by providing a pathway along which labile C travels to soil microbes. Norton *et al.*¹⁹ have recently demonstrated that the highest concentrations of new photosynthate occur in young roots and mycorrhizal root tips of *Pinus ponderosa* seedlings, and that mycorrhizal root tips have higher rates of C deposition to the rhizosphere than other root classes. Furthermore, a large percentage of recent photosynthate ends up in the bulk soil, presumably because of C transported through mycorrhizal hyphae from the roots. Thus, C that flows from plants to microbes *via* mycorrhizae may be an important energy source for free-living heterotrophic microbes, as well as for the mycorrhizal fungi.

Due to root turnover, sloughed cells, exudates and secretions, the rhizosphere strongly influences heterotrophic microbes that depend on C as an energy source. Indeed, the rhizosphere tends to support higher microbial biomass, a more active population of microbes and a higher ratio of bacteria:fungi than the bulk soil^{20–22}. Such enhanced C availability in the rhizosphere has been suggested to increase N

immobilization by heterotrophic soil microbes²², attract microbial grazers that in turn increase N mineralization rates^{23,24}, or be unavailable to soil microbes, if microbes are limited by N rather than C availability²¹. However, few data exist to support any of these suggestions; thus, how rhizodeposition affects microbial processes deserves increased and careful study.

Whether the quantity or quality of C that ends up in the rhizosphere differs among plants species also has yet to be determined. However, studies of individual plants from low-nutrient environments suggest that they allocate more C below ground than plants from high-nutrient environments⁴. The importance of mycorrhizae for nutrient acquisition suggests that much of the below-ground C allocation in low-nutrient environments supports mycorrhizae. Thus, species from low-nutrient environments potentially deposit proportionally more C to the rhizosphere than species from high-nutrient environments, because of root turnover, exudation and mycorrhizae (but see Ref. 25 for a discussion of patterns of below-ground productivity among ecosystems). Whether high allocation to below-ground C reduces²⁶ or enhances²³ nutrient availability deserves further attention, as does the role of competition between microbes and plants for nutrients in determining partitioning of nutrients between plants and microbes²¹.

Herbivore-mediated effects

Plant species interact with herbivores to influence nutrient cycling through differences in palatability and in physiological response to herbivory. Plants from low-nutrient environments invest heavily in C-based secondary metabolites such as terpenes and polyphenols that are effective defenses against herbivores¹⁴. Because many of the compounds that deter herbivores are also antimicrobial agents²⁷, litter containing such compounds decomposes slowly. Furthermore, in relatively low-nutrient ecosystems where browsers feed preferentially on palatable species with high-quality litter, they may promote the establishment and growth of species with more recalcitrant

litter that slows rates of nutrient cycling, especially if fast-growing species cannot sustain heavy browsing due to low N availability. These more heavily defended species may create a nutrient regime that is no longer suitable for less well-defended, palatable species^{27,28}. For example, moose (*Alces alces*) on Isle Royale, Lake Superior (USA), preferentially browse early-successional species like paper birch (*Betula papyrifera*) and aspen (*Populus tremuloides*), allowing establishment of white spruce (*Picea glauca*), whose lignin-rich litter decomposes slowly, decreasing N availability²⁸.

In grasslands such as the Serengeti, Tanzania, and perhaps in more nutrient-rich ecosystems in general, herbivores enhance, rather than decrease, nutrient availability^{27,29-31}. Where grazing limits production more than does nutrient availability, grazers may increase nutrient cycling rates because plant regrowth contains higher N concentrations, because of deposition of feces and urine, or because grazing causes shifts in plant allocation that lead to lower rates of N immobilization^{4,26,27,30,31}. In the saltwater marshes of the Hudson Bay region in Canada, sedge species, but not dicotyledonous species, are able to regrow and increase their relative abundance in response to grazing by lesser snow geese (*Chen caerulescens caerulescens*)³⁰. Because sedges are the preferred food of lesser snow geese, the geese continue to graze in these sedge-dominated areas, increasing rates of nutrient cycling both by depositing feces that are rich in soluble N, and by opening up sites that are then colonized by N-fixing algae^{30,31}. Increased rates of nutrient cycling further favor the sedge species, creating a positive feedback to grazing³⁰. New empirical and simulation model studies of prairie dog (*Cynomys ludovicianus*) colonies in the Wyoming prairie, USA, reveal that grazing-adapted populations of grasses that increase shoot biomass when grazed, while reducing root biomass, may decrease available C for microbes, promoting lower rates of N immobilization and potentially greater N loss from the system through denitrification and leaching²⁶. Conceivably, inter-

specific differences in allocation patterns, such as rootiness in low-nutrient environments and shootiness in high-nutrient environments, could create positive feedbacks to nutrient immobilization rates through a similar mechanism.

Overall, species characteristics in low- and high-nutrient ecosystems create positive feedbacks, mediated through herbivory, that decrease and enhance nutrient availability, respectively⁴. In nutrient-poor ecosystems such as the boreal forest, herbivores select for plants with well-defended, poor-quality litter, over both short and evolutionary time scales, that further reduces nutrient availability. In contrast, herbivory in more nutrient-rich systems like the Serengeti increases nutrient availability, either by speeding up rates of nutrient return to soils or by decreasing nutrient immobilization by microbes. Low rates of microbial and plant uptake caused by herbivory could result in the accumulation of large inorganic nutrient pools, promoting nutrient losses through ammonium volatilization, nitrate leaching and trace gas production²⁶. Extreme nutrient losses due to herbivory could convert a high-nutrient ecosystem to a low-nutrient ecosystem, which is consistent with the occurrence of *Artemisia frigida* (a shrub that produces low-quality litter) on older prairie dog colonies in the Wyoming study²⁶ and with the conversion of many grasslands to shrublands in response to intense grazing³².

Implications

Plant species can potentially affect nutrient cycling in a variety of ways, from differences in uptake, loss, litter quality, and associations with microbes, to differences in effects on herbivory. In general, plant species characteristics create positive feedbacks to patterns of nutrient cycling, further reducing nutrient availability in low-nutrient habitats, but enhancing nutrient availability in high-nutrient habitats. Such feedbacks are created because species that occur in low-nutrient habitats grow slowly, use nutrients conservatively, and produce litter high in secondary metabolites that deters herbivores and decomposes and releases

nutrients slowly. In contrast, species from high-nutrient environments grow quickly, take up and lose nutrients rapidly, produce high-quality litter and sustain high rates of herbivory, all factors that result in rapid rates of nutrient cycling. Critical to our understanding of how plant species affect nutrient cycling is better knowledge of the controls over plant C inputs from roots to soil, how these inputs affect microbial nutrient utilization and partitioning of nutrients between plants and microbes, and how C inputs to soil are affected by increased atmospheric CO₂.

Ecosystem perturbations such as climate warming and land use change will undoubtedly increase future rates of extinction and invasion. In order to predict whether a particular species' loss from or addition to a system will significantly alter nutrient cycling in that system, we must understand the relative importance of all factors that influence nutrient cycling, including species' traits. Furthermore, we must understand the rates at which species-mediated feedbacks to nutrient cycling occur compared with predicted rates of vegetation change, especially since vegetation will undoubtedly change more rapidly in the future than it has in the past. Thus, models that make predictions about the effects of climate warming, for example, on nutrient cycling must incorporate changes in vegetation if they are to be accurate.

To date, existing models that have examined the response of nutrient cycling through ecosystems to climate change have treated species' effects on nutrient cycling both implicitly and explicitly. The CENTURY model, which simulates grassland biogeochemistry, contains no species *per se*, but instead includes plant lignin as a variable³³. The model of Pastor and Post³⁴ predicts individual species' responses to climate warming in North American temperate forests and exhibits important feedbacks of vegetation to nutrient cycling. In their simulations, the effect of vegetation change on decomposition and thus nutrient cycling is sometimes great enough to offset the direct effects of climate change on N availability. Furthermore, in

this model, vegetation change creates positive feedbacks to nutrient cycling because soils with low water-holding capacity favor species with poor-quality litter that further reduces N availability, while soils with high water-holding capacity favor species with high-quality litter that enhances N availability. These simulations reveal complex interactions between the factors that constrain species in their response to climate change and the feedbacks to nutrient cycling created by species' traits such as litter quality, emphasizing the importance of understanding species' effects on nutrient cycling through natural ecosystems.

Acknowledgements

The writing of this review was supported by a National Science Foundation predoctoral fellowship. I thank F.S. Chapin, D. Kellogg, J. Pastor, M. Weiss and two anonymous reviewers for their comments on the manuscript.

References

- Zinke, P.J. (1962) *Ecology* 43, 130–133
- Flanagan, P.W. and Van Cleve, K. (1983) *Can. J. For. Res.* 13, 795–817
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. and Linkins, A.E. (1992) in *Arctic Ecosystems in a Changing Climate* (Chapin, F.S., III, Jefferies, R.L., Reynolds, J.F., Shaver, G.R. and Svoboda, J., eds), pp. 281–300, Academic Press
- Chapin, F.S., III (1991) in *Response of Plants to Multiple Stresses* (Mooney, H.A., Winner, W.E. and Pell, E.J., eds), pp. 67–88, Academic Press
- Bloom, A.J., Chapin, F.S., III and Mooney, H.A. (1985) *Annu. Rev. Ecol. Syst.* 16, 363–392
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*, Princeton University Press
- Vitousek, P.M. (1982) *Am. Nat.* 119, 553–572
- Pastor, J., Aber, J.D., McLaugherty, C.A. and Melillo, J.M. (1984) *Ecology* 65, 256–268
- Field, C.B. and Mooney, H.A. (1986) in *On the Economy of Plant Form and Function* (Givnish, T.J., ed.), pp. 25–55, Cambridge University Press
- Melillo, J.M., Aber, J.D. and Muratore, J.F. (1982) *Ecology* 63, 621–626
- McLaugherty, C.A., Pastor, J., Aber, J.D. and Melillo, J.M. (1985) *Ecology* 66, 266–275
- Wessman, C.A., Aber, J.D., Peterson, D.L. and Melillo, J.M. (1988) *Nature* 335, 154–156
- Aber, J.D., Wessman, C.A., Peterson, D.L., Melillo, J.M. and Fownes, J.H. (1990) in *Remote Sensing of Biosphere Functioning* (Hobbs, R. and Mooney, H.A., eds), pp. 87–101, Springer-Verlag
- Coley, P.D., Bryant, J.P. and Chapin, F.S., III (1985) *Science* 230, 895–899
- Wedin, D.A. and Tilman, D. (1990) *Oecologia* 84, 433–441
- Van Cleve, K., Chapin, F.S., III, Dyrness, C.T. and Viereck, L.A. (1991) *BioScience* 41, 78–88
- Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R. and Laundre, J.A. (1991) *Ecology* 72, 242–253
- Vitousek, P.M. and Walker, L.R. (1989) *Ecol. Monogr.* 59, 247–265
- Norton, J.M., Smith, J.L. and Firestone, M.K. (1990) *Soil Biol. Biochem.* 22, 449–455
- Norton, J.M. and Firestone, M.K. (1991) *Appl. Environ. Microbiol.* 57, 1161–1167
- Van Veen, J.A., Merckx, R. and van de Geijn, S.C. (1989) *Plant and Soil* 115, 179–188
- Smith, J.L. and Paul, E.A. (1990) in *Soil Biochemistry 6* (Bollag, J.M. and Stotzky, G., eds), pp. 357–396, Marcel Dekker
- Clarholm, M. (1985) in *Ecological Interactions in Soil* (Fitter, A.H., Atkinson, D., Read, D.J. and Usher, M.B., eds), pp. 355–365, Blackwell Scientific Publications
- Ingham, R.E., Trofymow, J.A., Ingham, E.R. and Coleman, D.C. (1985) *Ecol. Monogr.* 55, 119–140
- Raich, J.W. and Nadelhoffer, K.J. (1989) *Ecology* 70, 1346–1354
- Holland, E.A., Parton, W.J., Detling, J.K. and Coppock, D.L. *Am. Nat.* (in press)
- Bryant, J.P. *et al.* (1991) *Annu. Rev. Ecol. Syst.* 22, 431–446
- Pastor, J., Naiman, R.J., Dewey, B. and McInnes, P. (1988) *BioScience* 38, 770–777
- McNaughton, S.J., Ruess, R.W. and Seagle, S.W. (1988) *BioScience* 38, 794–800
- Jefferies, R.L. (1989) in *Plant Form and Vegetation Structure: Adaptation, Plasticity and Relation to Herbivory* (Werger, M.J.A., ed.), pp. 1–20, SPB Academic
- Ruess, R.W., Hik, D.S. and Jefferies, R.L. (1989) *Oecologia* 79, 23–29
- Schlesinger, W.H. *et al.* (1990) *Science* 247, 1043–1048
- Shimel, D.S., Parton, W.J., Kittel, T.G.F., Ojima, D.S. and Cole, C.V. (1990) *Climatic Change* 17, 13–25
- Pastor, J. and Post, W.M. (1988) *Nature* 334, 55–58

Letters to the Editor

TREE welcomes correspondence. Letters to the Editor may address issues raised in the pages of *TREE*, or other matters of general interest to ecologists and evolutionary biologists. Letters should be no more than 300 words long, and should be sent to The Editor, *TREE*, Elsevier Trends Journals, 68 Hills Road, Cambridge, UK CB2 1LA. The decision to publish rests with the Editor, and the author(s) of any *TREE* article criticized in a Letter will normally be invited to reply.