温带阔叶林中氮的保留机制： “春坝”假设及研究实例

Matthew WARREN 邹晓明

(Institute for Tropical Ecosystem Studies , University of Puerto Rico , PO Box 23341-3341 , San Juan , PR 00931-3341 , USA)

摘 要 在过去的半个世纪中,森林生态系统物质能量流动模型的发展使得生态学者对矿物元素的来源、去处、转换速率及其干扰破坏的影响有了进一步的认识。其中“春坝”假设提出:在早春来临之际,林冠树木仍处于冬眠之时,林下地被植物先于林冠树木发芽开花,吸收土壤养分于植物体内,使得养分免于因雨水或雪水而造成的淋失而得以保留于森林生态系统中。本文对“春坝”假设的研究作一小结。现有的研究结果显示,早春地被植物对土壤氮的吸收量因不同生态系统而异,而土壤微生物对氮的吸收量远高于过去人们所认识的水平。早春地被物与土壤微生物都能在季节的变化中吸收土壤养分、共同起着“春坝”作用。两者所起作用大小因气候及生态系统的不同而有所改变。

关键词 早春植物 氮固定 养分保留 土壤微生物 春坝

SEASONAL NITROGEN RETENTION IN TEMPERATE HARDWOOD FORESTS : THE “ VERNAL DAM ” HYPOTHESIS AND CASE STUDIES

Matthew WARREN and Xiao-Ming ZOU

(Institute for Tropical Ecosystem Studies , University of Puerto Rico , PO Box 23341-3341 , San Juan , PR 00931-3341 , USA)

Abstract Over the past half century the development of ecosystem models which quantify material and energy flows through forest ecosystems have led ecologists to identify and characterize the various sources , sinks , and flux rates of mineral nutrients and how these are affected by disturbance. The “ Vernal Dam ” hypothesis suggests that during the early spring months when nutrient susceptibility to loss is highest , an ephemeral herbaceous community takes up nutrients in biomass as a mechanism to retain nutrients in the system. This paper evaluates evidence from several studies regarding the “ Vernal Dam ” hypothesis. The uptake of nutrients in plant biomass during the early spring months is highly variable across ecosystems , and microbial immobilization is a more important mechanism for retaining nutrients than traditionally thought. Suggestions are made for future research which considers the role of plants and microbes as a “ Vernal Dam ” , and how the roles of plants and microbes change under different climatic conditions and ecosystem types.

Key words Ephemeral plants , Nitrogen , Immobilization , Nutrient retention , Soil microbes , Vernal Dam

1 The “ Vernal Dam ” hypothesis

Toward the end of the 1960 's , the development of a valid ecosystem model and quantifying energy and material flows through forest ecosystems became the challenge and focus of forest ecologists (e. g. , Likens *et al.* , 1977). Identifying and quantifying the inputs , outputs , flux rates , sources , and sinks of nutrients and their various controls , was of obvious importance toward the advancement of understanding forest ecosystems. In northern temperate hardwood ecosystems , the potential for N losses through leaching or gaseous loss are high during the early spring months. During this period , overstory trees are

dormant , while physical and biological soil processes are active. Daytime temperatures increase , stimulating microbial activity in the soil and the mineralization of organic matter. The onset of decomposition before overstory plant uptake results in an ephemeral increase in soil nutrient pools. Melting snow and early spring precipitation cause increased infiltration and surface flow , which leach inorganic nutrients out of the ecosystem. Stream water chemistry for the Hubbard Brook forest ecosystem in New Hampshire (Fig. 1) indicates an increase and maximization of nitrate and base cation loss in streamwater during the months of March , April and May (Likens *et al.* , 1977). During this time , a dense , seasonal herbaceous

Fig. 1 Monthly nitrate flux from undisturbed Hubbard Brook forest watersheds (Modified from Likens *et al.* (1997))

The highest losses of nitrate occur during the early spring months of March, April, and May

layer develops, taking advantage of the full sun which reaches the forest floor through the open canopy and reduced competition for water and nutrients from overstory dominants (Fig. 2). Muller and Bormann (1976) observed that the N uptake by the spring herbaceous layer could potentially prevent the further loss of significant amounts of inorganic N, and serve as a short-term N sink. This observation led Muller and Bormann (1976) to propose a “ Vernal Dam ” hypothesis : “ The rapid spring growth of *Erythronium* (a spring herb) occurs when light intensity at the forest floor and soil nitrogen availability are high and coincides with the final stages of high spring runoff and nutrient loss. Senescence of *Erythronium* shoots occurs after canopy development, when stream discharge is low and nutrient losses from the ecosystem are correspondingly reduced. This temporal pattern suggests that *Erythronium* may act as a short-term sink, or “ Vernal Dam ” with nutrients incorporated in the accumulating biomass during the spring flushing period and released by shoot decomposition in the early summer. ” Muller and Bormann (1976) hypothesized that the herbaceous layer occurring in the early spring incorporated a significant amount of N into biomass, which would otherwise be lost from the ecosystem. The N sequestered in plant biomass was mineralized in later months and returned to the soil available pool, thus immobilizing N and creating a short-term N sink during the early spring months, which was later mineralized during the senescence of the herbaceous layer during the summer.

2 Case studies

In the early 1980 's, Blank *et al.* (1980) and Peterson and Rolfe (1982) found that spring N and K uptake by ephemeral plant communities was relatively high compared to other nutrient fluxes during the early spring months and could contribute to N retention in the ecosystems studied. Further work by Eickmeier and Schussler (1993) and Anderson and Eickmeier (1998) concentrated on the adaptations of the early spring plant community

to the light environment and nutrient status of the soil. Although these studies determined that N in spring ephemeral herb biomass was a significant pool, and that spring herbs were physiologically adapted to maximize N uptake under the ecological conditions of the early spring, the magnitude of the function of spring herbs as a “ Vernal Dam ” is still unclear. The amount of N uptake by spring ephemerals is highly variable. Rothstein (2000) reported spring ephemeral N uptake as $0.45 \text{ g} \cdot \text{m}^{-2}$ in a northern hardwood forest ecosystem in Michigan, whereas Anderson and Eickmeier (1998) reported a maximum value of $3.62 \text{ g} \cdot \text{m}^{-2}$ for a forest ecosystem in Tennessee. These substantial differences illustrate that the function of spring ephemerals as a “ Vernal Dam ” is likely to be highly variable among ecosystems. Three mechanisms may partly explain sources of variation of nutrient uptake by spring ephemeral herbs : light limitation, nutrient partitioning in belowground tissues, and freezing events.

The uptake of excess soil nutrients by a dominant spring herb *Claytonia virginica* L. is highly dependent on the amount of available light (Eickmeier & Schussler, 1993). The amount of nutrients sequestered by spring plants becomes light limited on cloudy and overcast days. Under light limited conditions, nutrient saturation occurs and spring herbs are unable to further take up excess nutrients, limiting the function of spring herbs as a “ Vernal Dam ” (Eickmeier & Schussler, 1993 ; Anderson & Eickmeier, 1998). Differences in the magnitude of N uptake by spring herbs between ecosystems in Northern Michigan ($44^{\circ}20' \text{ N}$) and Tennessee ($36^{\circ}03' \text{ N}$) could be due to differences in the intensity of photosynthetically active radiation (PAR) reaching the forest floor, caused by latitude and cloud cover during the early spring months.

Some spring herbs reallocate nutrients to belowground tissues, and uptake of excess soil N may be limited as plants utilize the resources stored in these tissues (Anderson & Eickmeier, 2000). The resorption of nutrients into belowground tissues also implies that a portion of the nutrients stored in above-ground biomass by the spring herbaceous communities does not enter the decomposition pathway to be mineralized and available later for plant uptake. The dominant spring herb *C. virginica* studied by Anderson and Eickmeier (2000) was found to have a N resorption efficiency of 80%, therefore the turnover of excess N available in the spring is probably much slower than previously thought.

Late season freezing events may also contribute to annual, seasonal, and spatial variation of N uptake by spring herbs. Freezing temperatures and frosts during the growing season of the herbaceous layer could potentially cause significant damage and mortality, resulting in a reduction of biomass. As a consequence of reduced photosynthetic tissue, nutrient uptake by the herbaceous layer

Fig.2 A northern hardwood forest during the spring , summer , and fall

Boxes represent the relative amount of soil microbial biomass. a) During the early spring months , nutrients are partitioned in an ephemeral community of spring herbs and soil microbial biomass , believed to function as a “ Vernal Dam ”. The canopy remains open before leaf flush , and overstory trees have not begun significant nutrient uptake. b) During the summer months , the canopy closes and overstory trees maximize nutrient uptake during growth of leaf and wood biomass. Nutrients are partitioned primarily in aboveground biomass of dominant overstory trees. Net mineralization occurs as microbial biomass is reduced and aboveground spring ephemeral tissues senesce. c) During the fall , overstory trees retranslocate nutrients and lose their leaves. Nutrients are partitioned into the detrital pool on the forest floor

could be limited as plants recover from freezing and frost damage to aboveground tissue. Late season freezing events are more frequent and severe in Northern Michigan than Tennessee , and may limit the functionality of spring ephemeral herbs as a mechanism of N retention during the early spring.

In 1979 , Vitousek and Melillo (1979) observed that nitrate losses from disturbed forests were highly variable , and identified several pathways which excess nitrogen could be retained or lost from forest ecosystems in the reduction or absence of plant uptake. These pathways included : nitrogen loss in streamwater or groundwater , losses to the atmosphere , immobilization by decomposers , clay fixation of ammonium , lags in nitrification , nitrate reduction to ammonium , nitrate adsorption on soil colloids , a lack of water for nitrogen transport , or the reestablishment of plant nitrogen uptake (Vitousek & Melillo , 1979). In 1984 , Vitousek and Matson demonstrated that for a pine plantation in North Carolina , immobilization of N by microbes was the most significant mechanism of N retention in the disturbed ecosystem (Vitousek & Matson , 1984). It became apparent that microbial immobilization of excess N could be an alternative to N uptake by the ephemeral herbaceous plant community during the spring and immobilize N during the period of peak N loss , buffering the system from further N losses. The “ Vernal Dam ” could be built by ephemeral plants , microbes , or both.

Zak *et al.* (1990) investigated the significance of N immobilization in the herbaceous layer and soil microbes

to test the relative importance of each mechanism of N retention in the early spring. By using a ^{15}N pool dilution technique , Zak *et al.* (1990) demonstrated that the size of the N pool in microbial biomass and ^{15}N uptake by microbes were much greater than that of the dominant spring herb *Allium triocum*. The N pool size of *A. triocum* was only about 11% of the microbial N pool , and the percent of added ^{15}N recovered in the microbial pool was about 20 times greater for ammonium and 10 times greater for nitrate than the plant pool (Zak *et al.* , 1990). Groffman *et al.* (1993) corroborated substantial microbial immobilization in the early spring by combining a short term ^{15}N pool dilution experiment with a longer-term 8 week study of soil N dynamics. In their study , pools of microbial biomass N increased by a factor of 10 over the eight week period from March to May , which corresponds with the period of peak N loss (Groffman *et al.* , 1993). The recovery of ^{15}N was again several orders of magnitude higher in microbial biomass than in plants (Groffman *et al.* , 1993). The results from these studies indicated that soil microbes might play a more significant role than spring ephemerals by acting as the “ Vernal Dam ”. Furthermore , the lack of response of the spring ephemeral community to excess N availability due to light limitation also led Anderson and Eickmeier (1998) to conclude that the role of *Claytonia virginica* and other spring ephemerals in the “ Vernal Dam ” is limited. However , a later study by Anderson and Eickmeier (2000) suggested that the nutrient use efficiency of spring ephemerals is decreased by excess available N , and less N in biomass is

resorbed in underground tissues. The amount of N stored in ephemeral plant biomass and returned to the soil in later months relative to other N pool sizes reemphasized the importance of spring ephemeral herbs in the "Vernal Dam" hypothesis (Anderson & Eickenmeier, 2000).

The "Vernal Dam" hypothesis involves two critical assumptions: that N taken up by spring ephemeral plants would otherwise be lost from the system, and that N mineralized in the decomposing tissues of ephemeral herbs increases the amount of N available for plant uptake (Rothstein, 2000). These assumptions were tested directly by excluding ephemeral plants from experimental plots and measuring N pools, nitrate leaching out of the rooting zone, and N mineralization in a northern Michigan ecosystem. Rothstein (2000) observed that N fluxes through the spring ephemeral herb community were very small relative to other N fluxes through the ecosystem. Furthermore, the exclusion of ephemeral herbs had no detectable effects on nitrate leaching. These results led Rothstein (2000) to conclude that spring N dynamics are governed by overstory trees, soil microbes, and processes in soil detrital pools. This conclusion was based on the overall magnitude of N fluxes and storage in those pools.

3 Summary and future perspectives

Several important conclusions have become apparent based on the results of the studies which have considered the "Vernal Dam" hypothesis. The studies by Blank *et al.* (1980), Peterson and Rolfe (1982), Eickmeier and Schussler (1993), Anderson and Eickmeier (1998; 2000), and Rothstein (2000) have illustrated that spring herbs can retain a small portion of ephemeral pools of available nutrients during the early spring months. Furthermore, the amount of N retained by plants is comparable with N leaching losses during the same period. However, the magnitude of N retention compared to other N pools and fluxes and the function of spring ephemerals as a "Vernal Dam" is questionable. That is, of the excess nutrients in soil solution during the spring months which are susceptible to loss, the amount of nutrients taken up by the spring ephemeral community is highly variable across ecosystems. The function of spring ephemeral herbs as a "Vernal Dam" can be limited by light availability, freezing events, and the resorption of nutrients into below-ground plant tissues. Rothstein (2000) has pointed out that although spring ephemerals take up approximately $0.3 \text{ g} \cdot \text{m}^{-2}$ of N during the early spring, this quantity is very small compared to the $213 \text{ g} \cdot \text{N} \cdot \text{m}^{-2}$ contained in soil organic matter in the top 10 cm of northern Michigan soils, and the $3.3 \text{ g} \cdot \text{N} \cdot \text{m}^{-2}$ returned to the forest floor from overstory litterfall. In the forest ecosystem studied by Anderson and Eickmeier (1998), where the dominant ephemeral herb was shown to take up about $1.4 \text{ g} \cdot \text{N} \cdot \text{m}^{-2}$, after accounting for nutrient resorption under ambient conditions, the amount of N uptake is less than one

third of the $4.62 \text{ g} \cdot \text{N} \cdot \text{m}^{-2}$ returned to the forest floor in overstory litterfall. Other than uptake by the spring herbaceous plants, several other mechanisms of nutrient retention exist in forest ecosystems, and can play a significant role in the creation of a "Vernal Dam". Zak *et al.* (1990), Groffman *et al.* (1993) and Rothstein (2000) have clearly demonstrated the importance of microbial N immobilization functioning as a "Vernal Dam". Rothstein (2000) reported that $3.2\text{--}3.7 \text{ g} \cdot \text{N} \cdot \text{m}^{-2}$ are immobilized by soil microbes during the early spring, which fully accounts for the $3.3 \text{ g} \cdot \text{N} \cdot \text{m}^{-2}$ added to the forest floor from overstory litterfall. Nitrogen uptake by plants is over three times less in northern Michigan compared to Tennessee, and soil microbes compensate for the lack of plant N uptake at the northern Michigan site.

In order to fully understand N dynamics during the early spring months of northern temperate hardwood ecosystems, future studies are needed that simultaneously quantify the various N pools and fluxes. Although several studies have quantified N leaching losses using watershed-ecosystem techniques (e.g. Muller & Bormann, 1976), or lysimeters (Rothstein, 2000), information on N gaseous loss during the early spring months is lacking. The amount of N retained in forest ecosystems during the early spring by soil microbes or plants may be overestimated relative to total N losses from the system. Furthermore, Johnson *et al.* (2000) illustrated that abiotic N immobilization was an important mechanism of N retention in several forest soils, and no studies to date have investigated the importance of abiotic N retention as a buffer against N losses during the early spring. The spring ephemeral plant community and soil microbes have been emphasized as mechanisms which retain N during the early spring, however empirical data which consider both pools are only available for one ecosystem type in northern Michigan (Rothstein, 2000). There may be a trade-off between soil microbes and ephemeral plants in their respective roles as a functioning "Vernal Dam". Moreover, the trade-off between microbial immobilization versus plant uptake may be a consequence of plant-microbe competition for nutrients available in the soil. As ephemeral plants become physiologically limited by environmental conditions or disturbance, soil microbes may compensate for the lack of plant uptake and reduce N losses. This hypothesis has yet to be tested as there are no data available which consider both plant and microbial N pools during the early spring across environmental gradients. Cross-site comparisons are needed which quantify the roles of major N sinks as mechanisms of N retention during the early spring months, and how these sinks relate to N availability and flux rates across changing environmental conditions and contrasting forest ecosystems.

References

Anderson, W. B. & W. G. Eickmeier. 1998. Physiological and

- morphological responses to shade and nutrient additions of *Claytonia virginica* (Portulacaceae): implications for the “Vernal Dam” hypothesis. Canadian Journal of Botany, **76**: 1340 ~ 1349.
- Anderson, W. B. & W. G. Eickmeier. 2000. Nutrient resorption in *Claytonia virginica* L.: implications for deciduous forest nutrient cycling. Canadian Journal of Botany, **78**: 832 ~ 839.
- Blank, J. L., R. K. Olsen & P. M. Vitousek. 1980. Nutrient uptake by a diverse spring ephemeral community. Oecologia, **47**: 96 ~ 98.
- Eickmeier, W. G. & E. E. Schussler. 1993. Responses of the spring ephemeral *Claytonia virginica* L. to light and nutrient manipulations and implications for the “Vernal Dam” hypothesis. Bulletin of Torrey Botanical Club, **120**: 157 ~ 165.
- Groffman, P. M., D. R. Zak, S. Christensen, A. Mosier & J. M. Tiedje. 1993. Early spring nitrogen dynamics in a temperate forest landscape. Ecology, **74**: 1579 ~ 1585.
- Johnson, D. W., W. Cheng & I. C. Burke. 2000. Biotic and abiotic nitrogen retention in a variety of forest soils. Soil Society of the America Journal, **64**: 1503 ~ 1514.
- Likens, G. E., F. H. Bormann, R. S. Pierce, J. S. Eaton & N. M. Johnson. 1977. Biogeochemistry of a forested ecosystem. New York: Springer-Verlag.
- Muller, R. N. & F. H. Bormann. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics in the northern hardwood forest. Science, **193**: 1126 ~ 1128.
- Peterson, D. L. & G. L. Rolfe. 1982. Nutrient dynamics of herbaceous vegetation in upland and floodplain forest communities. American Midland Naturalist, **107**: 325 ~ 339.
- Rothstein, D. E. 2000. Spring ephemeral herbs and nitrogen cycling in a northern hardwood forest: an experimental test of the “Vernal Dam” hypothesis. Oecologia, **124**: 446 ~ 453.
- Vitousek, P. M. & J. M. Melillo. 1979. Nitrate losses from disturbed forests: patterns and mechanisms. Forest Science, **25**: 605 ~ 619.
- Vitousek, P. M. & P. A. Matson. 1984. Mechanisms of nitrogen retention in forest ecosystems: a field experiment. Science, **225**: 51 ~ 52.
- Zak, D. R., P. M. Groffman, K. S. Pregitzer, S. Christensen & J. M. Tiedje. 1990. The “Vernal Dam”: Plant-microbe competition for nitrogen in northern hardwood forests. Ecology, **71**: 651 ~ 656.

责任编辑 : 黄建辉 责任编辑 : 周玉荣