采伐和火烧对森林氮动态的影响

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摘要: 森林是重要的陆地生态系统类型, 它通过特有的养分循环机制维持其结构和功能。其中氮素对林木生长和发育十分重要, 而且常是森林生产力的限制因素。另一方面, 森林氮动态又常受到人类活动干扰的影响。根据国内外研究结果综述了采伐和火烧对森林氮动态的影响。结果表明采伐后环境因素的变化将影响森林 N 动态, 其中最为关注的是采伐后一系列因素引起的 N 损失, 如: N 淋溶增加、伴随生物量的 N 迁移以及因径流或侵蚀增加造成的枯枝落叶层和土壤层 N 流失。这些 N 损失又将影响更新林分的生长和生产力。此外, 采伐后 N 吸收速率一般下降, 但随着植被快速生长 N 吸收速率将不断增加。采伐后氨化和硝化过程增强, 但因短期内同化作用较弱, 生态系统中大部分 N 将发生损失。火烧对森林 N 动态的短期影响主要包括: 第一, 火烧时 N 直接挥发损失; 第二, 火烧后 N 有效性增加, 这主要由灰分沉积、根和微生物死亡及有机质 N 矿化增强等综合造成。随着时间延长, N 有效性逐渐降低, 这可能与火烧引起的有机质损失、植物 N 吸收增加、淋溶或侵蚀损失有关。然而, 目前关于火烧造成的长期生态影响, 如火烧后地上植被恢复与地下生物地球化学过程变化有何联系仍不太清楚。未来研究应着重于探讨氮素对森林采伐和火烧作出的短期响应将如何长期影响森林的结构和功能。此外, 建议在实施营林方案时需考虑采伐和火烧对生态系统氮的影响。

关键词: 森林; 采伐; 火烧; 氮动态
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Effects of harvesting and burning on forest N dynamics

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Abstract: Forests are important terrestrial ecosystems, with particular nutrient cycling mechanisms to maintain structure and functions. Nitrogen is essential for forest growth and development, and commonly limiting for the forest productivity. N dynamics in forest ecosystems are frequently disturbed by intensive human activities. Based on a variety of research results, some potentially important human disturbances such as harvesting and burning are discussed and their effects on forest N dynamics are reviewed.

It deserves more attention that the change of environment after harvesting will affect N dynamics in forest ecosystems. One of the major concerns with forest harvesting is loss of N due to increased N leaching, N removal in biomass, and loss of forest floor and soil N due to increased erosion and run-off. These N losses may lead to N limitations to the growth and

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productivity of regenerating forests. Also, nitrogen uptake rates generally decline after harvest, but rapid vegetation regrowth can lead to increases in nitrogen uptake rates. Ammonification and nitrification processes are stimulated after harvesting, by which N is becoming more moveable. Unfortunately in the situation of no assimilation after harvesting, much of N will be lost out of the ecosystems.

Fire affects N dynamics via multiple mechanisms. First, fire volatilizes N during combustion, leading to a net loss of N from the system. Second, a pulse of increased N availability is created by fire. This pulse could be the combined effect of ash residue, root and microbe death, and increased N mineralization from organic matter. As time passes, N availability drops, likely as a result of lost organic matter from combustion, increased plant uptake, leaching or erosion loss. However, long-term ecological effects of fire, including linkages between aboveground restoration and belowground biogeochemical processes, are still poorly understood. Future experimental work should be focused on understanding how the short-term responses of N to harvest and fire influence the structure and function of forest ecosystems in the long term. Also, the effects of harvest and fire on ecosystem N should be weighed for implementation of any forest management programs.

Key Words: forest ecosystem; harvesting; burning; N dynamics

Forests are important terrestrial ecosystems, covering about 1/3 of the land area on the Earth. A forest ecosystem maintains its structure and functions sustainablely by its particular nutrient cycling mechanisms. Nitrogen is an essential element for forest growth, and usually acts as a limiting nutrient for the productivity of forest ecosystem[1]. Mineralization of nitrogen from plant litter and soil organic matter is the main source of plant-available nitrogen in many forests[2]. Nitrification increases the potential for nitrogen leaching and denitrification, which represent losses of N from the ecosystem. These losses could limit the productivity of the regenerating forest, as well as result in environmental pollution. Plant uptake of available ammonium and nitrate immobilizes ecosystem nitrogen and prevents loss except under severe disturbance. In brief, disruptions in the biological cycling of nitrogen may have long-term impacts on ecosystem function and productivity.

Many factors influence N dynamics in forests, and two contrasting types of disturbances (i. e., tree harvest and fire) have been identified as important influential factors[3]. Brais *et al.*[4] suggested that whole-tree harvesting could have significant effects on N dynamics in conifer forests of Canada. Comparisons of prescribed fire with unburned controls consistently show that prescribed fire results in a substantial short-term increase in N mineralization and the availability of inorganic N[5-7]. Kaye and Hart[8] also found that both thinning and prescribed burning increased N mineralization and inorganic N availability relative to the control in the southwestern US; whereas, DeLuca and Zouhar[9] found that only prescribed fire increased inorganic N pools in western Montana. To date little emphasis has been placed on quantifying long-term changes in N dynamics with increasing time since disturbance. With recognition of the role of harvest and fire in maintaining natural stand functions[10], there is growing need to better understand effects of these natural (or human) disturbances on nutrient availability, particularly N. The aim of this paper is to review the short- and long-term effects of harvesting and burning on N dynamics of forest ecosystems.

1 Effects of harvesting on N dynamics

1.1 Potential N losses

One of the major concerns with forest harvesting is loss of N due to increased N leaching, N removal in biomass, and loss of forest floor and soil N due to increased erosion and run-off. These N losses may lead to N limitations to the growth and productivity of regenerating forests. Special attention has been paid to the effects of whole-tree harvesting on N availability, because clear-cutting makes N loss more seriously, and a longer time will be required for the N level to recover.

Leaching losses of nutrients can be significant in the first 2 — 3 years following harvest. Whole-tree harvesting of northern hardwood forest stands in the Hubbard Brook experimental watershed led to significant leaching of N (140 kg hm^{-2} a^{-1})[11]. Thirty months after harvest in northern hardwood forests of Michigan, Mroz *et al.*[12] observed average soil N levels over a 1-meter depth had declined approximately 25 %. This decrease was assumed to be due to high leaching rates from soils coupled with high N export in the harvested plant biomass. Baeumler and Zech[13] found high levels of ammonium and nitrate export from a mountainous forest watershed with only 40% overstory removal. However, rapid post-vegetation growth slowed nutrient leaching after several years.

Removal of plant biomass is perhaps the most important effect of harvesting on total ecosystem N levels. Johnson and Todd[14] estimated that 315 kg N hm^{-2} were removed in harvested vegetation in a whole-tree harvested mature oak forest in the Central Hardwoods Region of the U. S. During clear-cutting, 307 kg hm^{-2}N in stemwood with bark and coarse branches (> 2 cm) were removed from a Chinese fir (*Cunninghamia lanceolata*) forest in Fujian Province[15]. Harvesting of woody biomass on tropical plantation sites every 10 years would lose around 200 kg N hm^{-2}[16].

Forest floor mass may also be affected by harvesting. Mroz *et al.*[12] measured forest floor N losses of 50 — 800 kg N hm^{-2} from low and high productivity forest sites, respectively, after harvest. Although the specific cause for these losses was not specified, it may be associated with forest floor removal and incorporation into the mineral soil. This mixing, however, may accelerate decomposition and N mineralization from forest floor litter[17].

1.2 Changes in N mineralization

Reduction in ecosystem N levels does not necessarily reduce soil available nitrogen. In fact, soil N content may actually increase following a harvest[18,19]. This increase is often attributed to increased decomposition and N mineralization of soil organic matter, forest floor litter, and fine roots. Blumfield and Xu[20] attributed higher N mineralization rate in a clear-cut hoop pine plantation to greater soil water content, higher soil temperature, and greater substrate availability, all favoring increased microbial activity. Polglase and Attiwill[21] found increases in litter decomposition and N mineralization rates in Australian *Eucalyptus* forests following harvest. Prescott[22] also found increases in forest floor N mineralization in clear-cut coastal montane forests of the Pacific Northwest. He suggested that a decline in litterfall associated with clear-cutting led to increases in microbial turnover and release of immobilized nitrogen. Very little work has been done on fine root turnover in harvested forest ecosystems, but results from Idol et al.[23] suggest a reduction in the longevity of fine roots in harvested forest stands, thus a potential for increased N returns from fine root turnover and decomposition.

1.3 Changes in N uptake

In contrast to net N mineralization, harvesting may lead to a significant decline in total stand N uptake. In a Pacific Northwest forest, Gholz *et al.*[24] found a 92% decline in N uptake after harvest but increased to 50% of pre-harvest levels after three years. Studies in a 70-year-old maple-oak forest in northern Michigan have shown that rapid vegetation growth following whole-tree harvesting can lead to N uptake rates that exceed pre-harvest levels in as few as 4 — 5 years[25]. The explanation for the result is straightforward. Harvesting removes most of the plant biomass from the forest. Thus, plant demands for N on an area basis should decline. With vegetation regrowth several years after harvest, plant demands for N should increase rapidly, perhaps up to or exceeding preharvest levels. This rapid transfer of soil N into regrowing plant biomass helps reduce N leaching or denitrification.

1.4 Changes in N nitrification

Nitrification increases the potential for nitrogen leaching and denitrification, which represent losses of N from the ecosystem. The effects of harvesting on net nitrification rates are variable. In general, soil ammonium: nitrate ratio declines after harvest[26]. This may be due to increases in nitrification rates or an altered balance of N mineralization (i. e., ammonification), nitrification, and uptake. Neill *et al.*[27] found increases in nitrification rates during the first year after clearing of lowland Amazon forest. Increased net nitrification during a three-year period following clear-cutting had been noted by Piirainen *et al.* for Finnish spruce forests[28]. Walley *et al.*[29] also found that nitrification rates in clear-cut forests increased despite decreases in N mineralization potentials. Moreover, potential NO_3^- accumulation was found in 3 — 6-year-old harvest-regenerated jack pine (*Pinus banksiana*) stands in northern Lower Michigan, USA[30]. However, Jerabkova and Prescott[31] found no change in nitrification rates after clear-cutting in aspen- and spruce-dominated boreal forests. Because nitrification rates are generally controlled by soil ammonium availability[32], the competition for mineralized N between plants and nitrifiers may in large part determine nitrification rates. Soon after a harvest, declines in the amount of N taken up by plants may allow nitrifying bacteria greater access to the available pool of ammonium. Thus, nitrification may be expected to increase soon after harvest. After 5 — 10 years of regeneration, N uptake may increase to levels above preharvest conditions. Competition for soil N between nitrifying bacteria and plants would be intense. Thus, nitrification rates may be decline with time.

Other factors, including forest floor tannin content, low soil pH (< 5.0) and low soil water availability can also influence nitrification rates[33]. Donaldson and Henderson[34] found tannins leached from the forest floor may inhibit autotrophic nitrification. Ste-Marie and Paré[35] suggested that changes in soil pH were more important in controlling the activity of autotrophic nitrifiers. After harvest, soil pH increases, and the activity of autotrophic nitrifiers increases. Stark and Firestone did see increases in nitrification rates with increasing soil water availability[33]. Further study is needed to understand the variability in space and time of post-harvest nitrification.

1.5 Summary of N dynamics initiated by harvesting

Studies on the effects of forest harvesting on nitrogen dynamics have yielded mixed results due to the varied interactions of environmental conditions and composition of substrate. Generally, nitrogen uptake rates decline drastically after harvest[24], but rapid vegetation regrowth can result in nitrogen uptake rates that exceed pre-harvest levels within 5 years[25]. Many studies have shown that harvesting leads to an increase in both net nitrogen mineralization and nitrification[22,29]. Increases in N-mineralization and nitrification rates after a harvest have been attributed to two factors: (1) altered soil temperature and soil water availability as a result of increased direct solar radiation to the forest floor, and (2) increased availability of labile organic matter in the soil in the form of slash and roots of the cut trees. Several other factors such as the quality of soil organic matter and slash, the extent of physical disturbance of soils, and rates of denitrification can affect leaching losses of available N after harvesting[36].

Although there is great variability in these responses among forest ecosystems, it also has been learned that response of the biota (recovering vegetation) is largely responsible for regulating N change as the forest recovers from the disturbance of the harvest regime. The type of vegetation that persists or colonizes after harvest affects N inputs through biological N fixation, N uptake, and the quantity of labile substrates for mineralization.

2 Effects of burning on N dynamics

A comprehensive evaluation of the effects of fire on ecosystem nitrogen (N) is urgently needed for directing future fire management. Many previous studies have addressed the impact of fire on ecosystem N using comparisons of burned and unburned sites[37-39]. Wan *et al.*[40] used a meta-analysis method to search for the general patterns in the effects of fire on ecosystem N dynamics from highly variable results of individual fire research projects reported in the literature.

2.1 Immediate responses

Nitrogen is readily volatilized by heating during a fire. Jensen *et al.* [41] observed volatilization of nitrogen at about 200℃. At a temperature of 500℃, nearly half of the N in organic matter may be volatilized[3]. DeBano *et al.* [42] found that a dry intense fire (812℃) resulted in a 67% loss of N through combustion in a California chaparral forest. Mendham *et al.* [43] measured up to 350 and 200 kg hm^{-2} of N volatilized from the Red Earth and Grey Sand sites in south-western Australia, respectively.

Despite a significant loss of N during combustion, the available forms of nitrogen (NH_4^+-N and NO_3^--N) are commonly higher on burned than unburned sites. This condition could be the combined effect of ash residue, root and microbe death, and increased N mineralization from soil organic matter. Christensen[44] reported that fire in California chaparral left an ash residue that was extremely high in NH_4^+ and organic N. Similarly, Matson *et al.* [45] attributed increases in N availability to microbial death following slash and burn on volcanic soils in Costa Rica.

Numerous other studies have identified an immediate increase in soil NH_4^+ and NO_3^- following fire. For example, Covington and Sackett[5] reported a 20-fold increase in inorganic N immediately after prescribed burning in a ponderosa pine forest in southwestern Arizona, and inorganic N was almost entirely in the form of NH_4^+. DeLuca and Zouhar[9] found an immediate 10-fold increase in NH_4^+ after prescribed fire in a ponderosa pine ecosystem, in western Montana. Prieto-Fernández *et al.* [46] found that a prescribed burn in *Pinus pinaster* forest in Spain resulted in a 13-fold increase of inorganic N following fire, which was almost entirely due to a 19-fold increase in NH_4^+. In Venezuela, Montagnini and Buschbacher[47] observed 2- to 5-fold increases in soil NO_3^--N concentrations following slash burning and attributed this pulse to enhanced nitrification rates. Knoepp and Swank[48] suggested that the increase in soil available nitrogen after fire results from two processes: (1) volatilization of organic N from the soil surface and its condensation after downward movement into cooler soil layer and (2) increases in N mineralization and nitrification caused by altered soil temperature, pH value, and microbial activities. However, no study has clearly separated the relative contribution of these processes to this postfire inorganic N pulse.

2.2 Long-term effects

Despite a pulse of increased N availability produced by fire, this increase is short-lived. Processes such as plant uptake, nitrification and leaching of NO_3^-, denitrification, and erosion loss act to reduce this pulse to pre-fire levels[3,9,49]. For example, Leitch *et al.* [50] estimated that 82 kg hm^{-2} of N was removed in overland flow from a single thunderstorm following severe wildfire in a eucalypt forest. Once the pulse of elevated inorganic N diminishes, decomposition processes again limit N availability. Fire, therefore, may influence this long-term mineralization potential by decreasing the quality and size of the remaining organic N pool[51].

Forest fire has been shown to exert long-lasting effects on N dynamics, although the magnitude varies widely between different investigations. MacKenzie *et al.* [52] found that high-severity burned plots had a significantly lower net N mineralization rate five years following fire. This is likely a result of net organic matter loss during combustion. Monleon *et al.* [6] observed a 31% — 60% decrease in N mineralization rates 2 and 5 years following prescribed burning compared to the control. Wright and Hart[53] measured mineralization rates through an anaerobic incubation of soil receiving prescribed burns every two years for 20 years. Mineralization rates of these soils were 25% less than control plots, suggesting repeated fire may reduce N availability in the long run. Similarly, White *et al.* [54] reported that in hardwood dominated forests of the Roanoke River Basin, North Carolina, N mineralization decreases for 20 years after fire and then begins to increase. DeLuca and Zouhar[9] also found lower potentially mineralizable N in burned plots than no-burn control plots 2, 3, 11 and 12 years after a fire. These studies demonstrate that fire appear to lower N availability on the scale of several years to decades following fire. The mechanisms responsible for such long-term effects include changes to the physical characteristics of the soil, organic matter content, and microbial activity or populations[3].

In addition, long-term effects of fire on N depend on specific ecosystem processes determined by interactions between soil, climate and vegetation[55]. Nitrogen dynamics will change with time and recovering vegetation after fire. The plant abundance and composition affects N availability by modifying ecosystem N inputs, mineralization rates, and plant N uptake. During the first years following fire, slow microbial biomass recovery creates an opportunity for fire-surviving plants and pioneer species to take advantage of a less competitive environment and intercept the large pool of inorganic N. As time progresses, grasses may be replaced by shrubs and trees. This changes quantity and quality of plant residue and causes N cycling to progress at a rate much slower than soon after the fire[5]. In this scenario, net nitrification is very low, suggesting a stagnant N cycle and general lack of mineralization and nitrification (e. g., MacKenzie *et al.* [52]). Interestingly, a few chronosequence studies have shown the opposite pattern, whereby N availability either increases, or does not decline, from young to mature forests[54, 56, 57]. For example, MacKenzie *et al.* [57] found that forest-floor N mineralization potentials increased with time since stand-replacing fire in ponderosa pine (*Pinus ponderosa*)/Douglas fir (*Pseudotsuga menziesii*) forests of western Montana. This is partially attributed to the accumulation of organic matter pools through stand development. However, Paré *et al.* partially attribute the maintenance of N availability in their boreal forest chronosequence to the persistence of some deciduous species in late successional stages[56]. Hence, the postfire dynamics of N and its relationship to vegetation establishment need further research.

Several other studies focused on N cycling suggest that important belowground differences exist following prescribed fire and regeneration of forest stands. For example, biotic changes may occur; heterotrophic microbes are generally found to decrease, whereas autotrophic microbes tend to increase following moderate to severe fires[3]. Subsequent changes in the microbial community biomass and composition will increasingly reflect changes in quantity/quality of soil organic matter and vegetation recovery (species and biomass). On the other hand, root biomass is the primary determinant of successional changes in N uptake by vegetation after fire. The changes in root biomass that occur through postfire succession are much larger than the successional changes in uptake capacity and in N availability[58]. Overall, the effects of fire on belowground systems and the resulting processes that feedback to aboveground systems are complex and highly variable. However, long-term ecological effects of fire, including linkages between aboveground restoration and belowground biogeochemical processes, are still poorly understood[8].

2.3 Summary of N dynamics initiated by fire

Fire affects N dynamics via multiple mechanisms. First, fire volatilizes N during combustion, leading to a net loss of N from the system. Second, during combustion, ash residue is formed that is greatly enriched in N, primarily in the form of NH_4^+ and organic N. Other contribution to this immediate N pulse include microbe mediated mineralization of organic matter, and root and microbe death resulting from soil heating. As time passes, N mineralization diminishes, leading to levels of N availability near or below pre-fire conditions. This is likely associated with lost organic matter from combustion, increased plant uptake, leaching or erosion loss. The net effect of these mechanisms may affect ecosystem productivity, thus emphasizing the importance of fire to ecosystem function.

3 Harvesting and fire research and management

Nitrogen dynamics is of particular concern in studies of forest management. Rapid and substantial losses of N through harvesting and fuel combustion may presumably alter the long-term N dynamics. However, few studies have been done on how the short-term responses of N to harvesting and fire influence the structure and function of forest ecosystems in the long term. To improve our understanding on these issues, properly designed and long-term experimental studies are needed. Such studies should use consistent methods to facilitate comparison and integration of results across various forest ecosystems. The chronosequence approach had been utilized in several studies because of its efficiency in generating meaningful results on long-term trends[2, 59-61]. Also, research methodologies and analyses can be kept relatively constant in chronosequence studies. Recently, the use of ^{15}N isotope tracer techniques can provide important insights into N dynamics with time since harvest or fire[62]. In the absence of long-term field trials, a process-based ecosystem model (such as CENTURY 4.0) may provide an alternative means of examining the long-term effects of disturbances on N dynamics of forest ecosystems. In addition, vegetation-specific responses of ecosystems to harvest and fire necessitate appropriate forest management programs for different ecosystems. The positive vs. negative, short-term vs. long-term effects of harvest and fire on ecosystem N should be weighed for implementation of any forest management programs.

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