Implications of a predicted shift from upland oaks to red maple on forest hydrology and nutrient availability

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Abstract: Fire suppression has facilitated the spread of red maple (*Acer rubrum* L.), a fire-sensitive, yet highly adaptable species, in historically oak-dominated forests of the eastern United States. Here, we address whether a shift from upland oaks to red maple could influence forest hydrology and nutrient availability because of species-specific effects on precipitation distribution and inorganic nitrogen (N) cycling. In eastern Kentucky, we measured seasonal variations in red maple, chestnut oak (*Quercus montana* Willd.), and scarlet oak (*Quercus coccinea* Münchh.) throughfall and stemflow quantity and quality following discrete precipitation events, and we assessed net N mineralization rates in underlying soils over a 2-year period (2006–2008). Throughfall was 3%–9% lower underneath red maple than both oaks, but red maple generated 2–3× more stemflow. Consequently, NH_4^+ throughfall deposition was less under red maple than chestnut oak, whereas stemflow-derived nutrient inputs were substantially larger for red maple than both oaks. Soils underlying red maple had 5–13× greater winter net nitrification rates than soils under both oaks and 20%–30% greater rates of seasonal net ammonification than soils under chestnut oak. These findings suggest a spatial redistribution of water and nutrients via precipitation as red maple dominance increases and point to stemflow as an important mechanism that may foster red maple competitive success, further bolstering the mesophication process in the United States.

Résumé : La suppression des incendies a facilité la propagation de l'érable rouge (*Acer rubrum* L.), une espèce sensible au feu mais qui s'adapte très facilement dans les forêts jadis dominées par le chêne dans l'est des États-Unis. Dans cette étude, nous examinons si le remplacement du chêne en milieu sec par l'érable rouge pourrait influencer l'hydrologie forestière et la disponibilité des nutriments à cause d'effets propres à cette espèce sur la distribution des précipitations et le recyclage de l'azote (N) inorganique. Dans l'est du Kentucky, nous avons mesuré les variations saisonnières de la quantité et de la qualité de la précipitation au sol et de l'écoulement sur écorce chez l'érable rouge, le chêne de montagne (*Quercus montana* Willd.) et le chêne écarlate (*Quercus coccinea* Münchh.) lors d'épisodes discrets de précipitation et nous avons évalué les taux de minéralisation nette dans les sols sous-jacents sur une période de deux ans (2006–2008). La précipitation au sol était 3–9 % plus faible sous l'érable rouge comparativement aux deux autres espèces de chêne mais l'érable rouge générait 2–3 fois plus d'écoulement sur écorce. Par conséquent, les dépôts de NH_4^+ dans la précipitation au sol étaient plus faibles sous l'érable rouge que sous le chêne de montagne tandis que les apports de nutriments provenant de l'écoulement sur écorce étaient substantiellement plus importants que chez les deux espèces de chêne. Le taux de nitrification nette en hiver dans le sol sous l'érable rouge était 5–13 fois plus élevé que sous les deux espèces de chêne et le taux saisonnier d'ammonification nette était 20–30 % plus élevé que sous le chêne de montagne. Ces résultats montrent qu'il y a une redistribution spatiale de l'eau et des nutriments par le biais des précipitations à mesure que la dominance de l'érable rouge augmente et indiquent que l'écoulement sur écorce est un mécanisme important qui peut contribuer au succès compétitif de l'érable rouge, favorisant ainsi le processus de mésophication aux États-Unis.

[Traduit par la Rédaction]

Introduction

Individual tree species comprising forest communities can have important influences on soil properties and ecosystem processes (Boettcher and Kalisz 1990). Species-specific differences in leaf litter quantity and quality influence decomposition rates and nutrient availability (Cornwell et al. 2008). Interspecific variation in canopy architecture, leaf area, and bark texture influences precipitation interception and distribution, which in turn affects evaporation, water status, understory microclimate, nutrient inputs, and leaching (Levia and Frost 2003). Species impact carbon storage through variable growth rates, allocation, and longevity (Kirby and Potvin 2007) and can shape regional climate through differential albedo and evapotranspiration (Amiro et al. 2006). Differences in susceptibility to wind (Papaik and Canham 2006), flood (Kozlowski 1997), ice (Tremblay et al. 2005), or fire (Hengst and Dawson 1994) can lead to species-specific responses to disturbance and controls on disturbance intensity and magnitude. Discerning individual tree species' contributions to forest community and ecosystem dynamics is increasingly important as shifts in canopy

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composition unfold under changes in land use, the influence of invasive pests and pathogens (Lovett et al. 2006), climate change (Iverson et al. 2008), and altered disturbance regimes (Nowacki and Abrams 2008).

Over the last 80 years, the "super-generalist" red maple (*Acer rubrum* L.; Abrams 1998) has spread into historically oak-dominated forests of the eastern United States (US) (e.g., Fei and Steiner 2007). Red maple was once a minor forest constituent, limited to mesic coves, swamps, and riparian areas protected from fires (Abrams 1998). Dendrochronological analyses indicate substantial red maple recruitment into forest overstories following fire suppression, while upland oak recruitment has virtually ceased (Hutchinson et al. 2008). Moreover, disturbances to oak overstories, such as logging and wind, only accelerate the transition to red maple and other shade-tolerant species (Abrams and Nowacki 1992). Today, red maple can be found across sites of varying edaphic conditions (Abrams 1998), and studies indicate increased basal area (Lorimer 1984), density (Alderman et al. 2005), importance value and range expansion (Fei and Steiner 2007). While a native tree, red maple has many invasive characteristics that have contributed to its success, including high reproductive capacity, early maturity, flexible germination strategy (Hille Ris Lambers and Clark 2005), and ability to act as both an early and late successional tree species (Abrams 1998). Notably, Uva et al. (1997) classify red maple as weedy and (or) invasive in the northeast US.

On many sites, red maple's increase has coincided with a substantial decline in oak regeneration, presumably from decreased understory light and increased competition, since red maple and other shade-tolerant species proliferate without fire disturbances to suppress their growth and expansion (Lorimer et al. 1994). This trend has led many researchers to predict an inevitable transition from oaks to red maple or other fire-sensitive species (Abrams 2005; McEwan et al. 2005; Nowacki and Abrams 2008). While prescribed fires have been increasingly implemented in an attempt to curb red maple proliferation and promote oak regeneration, results thus far have been mixed (Brose et al. 2006) partly because of red maple's tenacity as an understory competitor (Alexander et al. 2008; Alexander and Arthur 2009).

Beyond the detriments to wildlife of losing an essential mast species such as oak (Rodewald and Abrams 2002), the ecological consequences of this shift have been largely untested. Anecdotally, red maple exhibits many traits that differ from co-occurring oak species, such as thinner leaves, denser canopies, and smoother bark. These species-specific differences between red maple and upland oaks could have important implications for forest hydrology, nutrient cycles, disturbance regimes, and successional trajectories.

In this study, we addressed whether a shift from upland oaks to red maple predicted under the current disturbance regime of limited fire could influence forest hydrology and nutrient cycling because of species-specific effects on precipitation distribution and inorganic nitrogen (N) cycling. We measured seasonal variations in red maple, chestnut oak (*Quercus montana* L.), and scarlet oak (*Quercus coccinea* Münchh.) throughfall and stemflow quantity and quality following discrete precipitation events, and we assessed net ammonification and nitrification rates in underlying soils. We hypothesized that red maple would have a denser canopy and generate less throughfall than oaks. Nutrient concentrations of red maple throughfall would be relatively higher because greater crown area would allow more nutrient collection and (or) leaching from foliar and branch surfaces; however, throughfall nutrient inputs would be lower because of less total volume. Additionally, we hypothesized that because of smoother bark red maple would have higher funneling capacity than either oak, leading to greater stemflow volume. Greater stemflow volume and higher nutrient inputs from red maple could then lead to higher net rates of inorganic N cycling due to greater soil moisture and carbon (C) and inorganic N inputs.

Methods

Study area

These studies were conducted on Klaber and Whittleton ridges in the Cumberland Ranger District of the Daniel Boone National Forest of eastern Kentucky, USA. These ridges are noncontiguous and separated by ~8.5 km. Soils are Latham-Shelocta silt loams of the Typic and Aquic Hapludults subgroups and are moderately deep, well-drained, and generally acidic (Hayes 1993). The climate is temperate, humid, and continental, with a mean annual temperature of 12 °C and annual precipitation (113 cm·year^{-1}) fairly well-distributed throughout the year (Foster and Conner 2001). The study areas along each ridge encompassed ~15 ha with similar slope (<20% grade) and elevation (~400 m). These areas have had minimum human influence since logging occurred in the early 1900s, and there has been no evidence of recent fires (>25 years; Blankenship and Arthur 2006).

Forest stands were second growth (60–80 years old; Washburn and Arthur 2003), and total overstory (≥10 cm diameter at breast height (DBH)) basal area and stem density were approximately 26.5 m^2·ha^{-1} and 532 trees·ha^{-1}, respectively (calculated from Blankenship and Arthur 2006). Oaks dominated overstory basal area (19.5 m^2·ha^{-1}) and stem density (242 trees·ha^{-1}) and included scarlet oak, chestnut oak, white oak (*Quercus alba* L.), and black oak (*Quercus velutina* Lam.). Red maple comprised a relatively small portion of overstory basal area (4.0 m^2·ha^{-1}), but its stem density (215 trees·ha^{-1}) was only 11% less than that of all oaks combined. Total midstory (stems 2–10 cm DBH) basal area and density were about 1.9 m^2·ha^{-1}and 808 trees·ha^{-1}, respectively. Red maple comprised substantially greater midstory basal area (1.1 m^2·ha^{-1}) and density (403 trees·ha^{-1}) than oaks (0.01 m^2·ha^{-1} and 2.5 trees·ha^{-1}, respectively). Oak seedlings were relatively abundant on the forest floor (9100 stems·ha^{-1}), but red maple seedling density was ~2.6× greater (23 400 stems·ha^{-1}; Green 2010).

Study design

From summer 2006 to spring 2008, we assessed throughfall and stemflow quantity and quality of red maple and two upland oak species (scarlet and chestnut oaks) seasonally (February, May, August, and November) during discrete precipitation events. Seasonal sampling was employed to capture changing canopy cover and weather patterns that could potentially alter any species-specific impacts. We

chose these two oak species because initial surveys of stand composition indicated that they were the most dominant representatives of the red (*Erythrobalanus*) and white (*Leucobalanus*) oak subgenera. We sampled a single canopy dominant or co-dominant tree (20–30 cm DBH) of each species within five blocks (~0.1 ha each) along each ridge (n = 10 trees per species), resulting in a randomized complete block design with block nested within ridge. Small midstory trees whose canopy overlapped with the target tree were manually removed prior to sampling to minimize influences caused by non-target species. Incident precipitation quantity and quality were simultaneously collected in adjacent open areas (~0.5 ha) near each ridge.

To determine whether the two upland oak species cycle inorganic N differently from red maple, we initiated seasonal sampling of in situ N mineralization rates within underlying mineral soils in May 2006. We focused on mineral soils because the organic horizon is often shallow (<0.5 cm depth) and most plant roots are found within the upper layer of the mineral soil (H.D. Alexander, personal observation). We used a similar study design as that detailed above using a different subset of trees to avoid disturbance effects stemming from throughfall and stemflow sampling. In August 2006, a "no-tree" area devoid of tree boles > 2 cm DBH within a 2 m radius was added to each block to allow assessment of N mineralization rates in the absence of large trees.

Tree characteristics

All sampled trees were assessed for several characteristics prior to initial sampling. Crown height and width were measured with a Vertex IV hypsometer (Haglof Inc., Madison, Missouri). Crown width was estimated in the four cardinal directions by walking out the estimated width of the crown, measuring distance back to the edge of the tree bole, and then adding in trunk radius. Crown area was calculated by using the average of these four widths to estimate the area of a circle. Crown volume was estimated only on throughfall and stemflow trees by assuming that the canopy occupied a cylindrical volume and by multiplying the crown depth by the crown area. Bark roughness was estimated as the mean depth of bark fissures measured ~1.5 m above ground in the four cardinal directions. Percent cover of bark epiphytes was visually estimated in the four cardinal directions within a 10 cm^2 area at ~1.5 m above ground using the following categories: 0 = <20%, 1 = 21%–40%, 2 = 41%–60%, 3 = 61%–80%, and 4 = 81%–100%.

Water collection

Throughfall was collected on opposite sides of each tree, ~0.5 m from the base of the bole and ~0.75 m above ground, using a 20 cm diameter (314 cm^2) polyethylene funnel attached to a 2 L amber polyethylene bottle. The neck of each funnel contained glass wool to prevent entry of debris. Collectors were cleaned with deionized water between precipitation events, and new glass wool filters were installed.

Stemflow was collected using polyurethane foam collars adhered to the bole of each tree ~120 cm above ground and angled slightly downward to facilitate collection. Each collar was attached to an 80 L collection vessel using 1.25 cm diameter silicone tubing. Prior to each event, collection bins were tightly covered, lined with chemically inert polypropylene bags, and tested for leaks using deionized water. Points along the collar with leakage were resealed with silicone sealant.

Incident precipitation, throughfall, and stemflow were collected within 48 h of each precipitation event, which was the time required to access both ridges. Total volume, pH, and electrical conductivity (EC) were measured in the field; pH and EC were acquired with a portable meter (Hanna Instruments, Model HI 98129, Woonsocket, Rhode Island, USA) calibrated prior to each sampling. One 500 mL stemflow and one 500 mL throughfall subsample (pooled from the two collectors per tree) were obtained from each tree. When volumes were sufficient, random duplicate throughfall and (or) stemflow samples were collected from individual trees and analyzed to test for variation within the experimental unit (i.e., tree). The funneling ratio (Herwitz 1986), which provides an estimate of the branch-funneling effect and the aboveground woody surface area contacted by stemflow drainage, was computed for each tree and event as $F = S/PB$, where F is the funneling ratio, S is the stemflow volume for the given tree (mL), P is the rainfall depth (cm), and B is the tree basal area (cm^2). A funneling ratio of 1.0 indicates that measured stemflow volume would be equal to the measured volume from a hypothetical rain gauge with a collecting area the size of the basal area of the tree. A ratio greater than 1.0 indicates that branches contributed to funneling water to the stem, increasing the total volume of water captured by the tree.

The stemflow collecting apparatus occasionally malfunctioned for various reasons (e.g., extreme weather pulling the collection tube from the vessel or debris falling on the device) resulting in some variation in the number of experimental units on several sampling dates. Precipitation collectors for Whittleton Ridge were tampered with during the February 2007 sampling, rendering these data unavailable, and a black bear destroyed equipment at Whittleton Ridge in fall 2007, limiting sampling to Klaber Ridge. Devices were reinstalled in February 2008.

Water samples were stored on ice and returned to the laboratory where a subsample was immediately filtered through a 0.45 $\mu mol \cdot L^{-1}$ membrane filter for future analysis of cations, anions, and dissolved organic carbon (DOC). All samples were kept in the dark at 4 °C until analysis. Within 24 h, inorganic N (NH_4^+-N and NO_3^- + NO_2^--N) was analyzed colorimetrically with an automated continuous-flow analyzer (Bran-Luebbe Autoanalyzer 3, Bran+Luebbe, Chicago, Illinois, USA), and within 1 week, water samples were digested with potassium persulfate and analyzed colorimetrically to obtain total N concentration. Within 72 h, base cations (Ca^{2+}, Mg^{2+}, Na^+, and K^+) were measured using an atomic absorption spectrometer (Avanta AAS, GBC Scientific Equipment, Hampshire, Illinois, USA), and anions (SO_4^-, PO_4^{3-}, and Cl^-) were assessed via ion chromatography (ICS-2000, Dionex Corporation, Sunnyvale, California, USA). Inorganic phosphate concentrations were below detection limits (0.03 $mg \cdot L^{-1}$) on most sampling dates, so are not reported here. Total carbon, total organic carbon (TOC), and DOC were analyzed within 72 h with a TOC analyzer (TOC 5000-A, Shimadzu Scientific Instruments, Columbia, Maryland, USA). Total carbon was obtained on unfiltered

samples; TOC was analyzed on unfiltered, acidified samples; and DOC was analyzed on filtered and acidified samples. During October 2006, we noticed a few samples with TOC concentrations less than DOC concentrations and determined this discrepancy to be due to a faulty filtering system. These DOC data were eliminated from further analyses. Ten percent of all samples were analyzed as replicates. Mean concentrations are volume-weighted, and deposition estimates were calculated as content (concentration × volume) divided by the collecting area, which was either the area of the funnel(s) or basal area of the tree.

Soil moisture

To determine if differences in throughfall and stemflow inputs impacted moisture content of underlying upper mineral soils, we determined gravimetric soil moisture beneath trees of each species after each rainfall event. The trees sampled were of similar size and within 10 m of those equipped with stemflow collars. Mineral soils (A horizon) were sampled to a depth of 5 cm at a distance 0.5 m from the edge of each tree bole and in the center of each no-tree area using a 2.5 cm diameter metal soil corer. This distance from each tree was chosen to incorporate the effects of both stemflow and throughfall. The O horizon was removed prior to collection. Soils were stored in the laboratory at 4 °C until processed within 1 day of collection. Each sample was weighed, dried to constant mass at 105 °C, and reweighed. Values are reported on a soil dry mass basis: soil moisture (%) = (wet mass – dry mass)/dry mass.

Net N mineralization

To assess species-specific variation in net rates of seasonal (February, May, August, and November) inorganic N cycling, we collected two replicate soil samples 0.5 m from the bole of each tree and near the center of each no-tree area using a 4 cm diameter PVC corer. As stated above, this distance would presumably incorporate the effects of both throughfall and stemflow. Organic horizons were removed in the field, and upper mineral soils (0–5 cm) were placed in separate polyethylene bags and returned to the laboratory on ice for analysis of initial inorganic N concentrations (NH_4^+-N and NO_3^--N in μg N·(g soil)$^{-1}$). In situ net N mineralization was determined using two PVC soil incubation tubes driven ~10 cm into the soil, which were loosely covered with duct tape and left in place for 28 days, when the upper mineral soils (0–5 cm) were removed and analyzed in the same manner as initial samples. Upon return to the laboratory, soil samples were stored at 4 °C and processed within 1 day of collection. Mineral soils were sieved through a 2 mm mesh sieve to homogenize the sample and remove large rocks, debris, and root material. A 10 g subsample was placed in extraction cups with 50 mL of 1 mol·L^{-1} KCl and shaken for 1 h. The solution was filtered on No. 40 Whatman paper, and the supernatant analyzed colorimetrically for available inorganic N (NH_4^+-N and NO_3^--N) with a Bran-Luebbe Autoanalyzer 3. Net ammonification and nitrification were calculated as the total NH_4^+-N and NO_3^--N (μg N·(g soil)$^{-1}$·day^{-1}), respectively, accumulated over the 28-day incubation period.

Leaf litter

Because net N mineralization rates are often correlated with leaf litter quality (Scott and Binkley 1997), we estimated leaf litter contribution beneath each target tree and no-tree area. Before leaf fall in 2006, we installed a 1 m^2 mesh screen ~0.5 m from the bole of each tree and in the center of each no-tree area. We collected litter weekly throughout leaf fall; litter was then air-dried, sorted by species, dried at 60 °C, and weighed to determine mass and species composition. This estimation method assumes that litter displaced from the collecting screen between sampling dates because of wind or other mechanisms was similarly replaced.

Statistics

Differences in water and soil variables were analyzed in a factorial treatment arrangement (season and species as fixed effects) within a repeated measures (tree = repeated unit), randomized complete block design, with ridge and block nested within ridge, as random factors using PROC MIXED of SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA). Tree and leaf litter characteristics were assessed similarly but without the seasonal component. The initial models consistently revealed statistically significant differences between throughfall and stemflow; thus, these variables were analyzed and presented separately. Because our primary objective was to assess differences among species, we were only interested in seasonal effects when they interacted with species, which occurred rarely. Thus, we present the overall results for species effects only but the species data by season is provided as supplementary data[3]. All variables were tested for normality and homogeneity of variance prior to analyses and were transformed using logarithmic and square-root transformations when they did not meet these underlying assumptions. F values were computed based on Type III sums of square, and degrees of freedom were estimated using Satterthwaite's approximation. For all significant factors and interactions ($P < 0.05$), least squares means were compared via a post-hoc Fisher's least significant difference test to determine differences among means at $\alpha = 0.05$. All P values reported are those generated from transformed data, but means and standard errors are presented for untransformed data.

Results

Tree characteristics of red maple often differed from both oak species (Table 1). On average, red maple were smaller in diameter, lower in basal area, and shorter in height than chestnut and scarlet oak ($P < 0.01$ for all comparisons). Average crown width was ~0.4 and 0.6 m greater than chestnut ($P = 0.05$) and scarlet oak ($P < 0.01$) and encompassed ~10 ($P = 0.04$) and 13 m^2 ($P = 0.01$) more area, respectively. Red maple mean crown depth was 0.8 and 2.3 m less than scarlet and chestnut oak, respectively, and while these differences were not significant ($P = 0.12$), red maple's smaller crown depth resulted in similar crown volume among species ($P = 0.54$). Red maple's bark was 2× smoother than scarlet oak and 5× smoother than chestnut oak ($P < 0.001$ for both), and scarlet oak was twice as

[3] Supplementary data for this article are available on the journal Web site (http://cjfr.nrc.ca).

Table 1. Tree characteristics of red maple, chestnut oak, and scarlet oak at study initiation along two ridges in the Daniel Boone National Forest of eastern Kentucky.

Tree characteristic	Red maple	Chestnut oak	Scarlet oak
DBH (cm)	22.2±0.6a	26.1±0.6b	27.7±0.5b
Basal area ($cm^2 \cdot tree^{-1}$)	393.3±22.7a	541.1±23.1b	604.8±21.7b
Height (m)	16.2±0.4a	18.2±0.5b	18.5±0.4b
Crown width (m)	4.2±0.1a	3.8±0.1b	3.6±0.2b
Crown area (m^2)	59.0±6.7a	49.2±4.4b	45.8±6.5b
Crown depth (m)	11.8±0.9	14.1±1.0	12.6±0.7
Crown volume (m^3)	645.5±75.7	660.4±66.6	575.9±83.3
Bark roughness (mm)	2.6±0.4a	12.1±0.5b	5.3±0.4c
Bark epiphyte index	1.7±0.3a	2.1±0.2a	1.0±0.2b

Note: Values are mean ± SE. Different lowercase letters indicate significant differences ($P < 0.05$).

smooth as chestnut oak ($P < 0.001$). Epiphyte cover was similar between red maple and chestnut oak ($P = 0.24$), which was approximately twice as high as scarlet oak ($P = 0.04$ and <0.01, respectively).

The amount of precipitation distributed into throughfall and stemflow varied between red maple and both oak species. Red maple produced significantly lower throughfall volume than chestnut oak ($P = 0.003$) and scarlet oak ($P = 0.05$; Fig. 1A), resulting in a lower percentage of precipitation falling as throughfall (69% compared with 78% and 72% for chestnut and scarlet oak, respectively). Stemflow production was ~2.5× greater from red maple than either oak ($P < 0.001$ for all comparisons; Fig. 1B), largely due to funneling from leaves and (or) branches, as indicated by a funneling ratio (21.5) that was 3× greater than chestnut oak (7.6) and twice as high as scarlet oak (9.5; $P < 0.001$ for both comparisons; Fig. 1B).

Throughfall N and C exhibited some species differences. There was no species effect on throughfall NH_4^+ concentrations ($P = 0.49$; Fig. 2A), but red maple throughfall deposition of NH_4^+ was lower than that from chestnut oak ($P = 0.01$; Fig. 2B). Throughfall NO_3^- concentration was similar among species ($P = 0.06$; Fig. 2C), as was NO_3^- deposition ($P = 0.34$; Fig. 2D). There was no species effect on total organic nitrogen (TON) or DOC concentration or deposition via throughfall ($P > 0.05$ for all comparisons; Figs. 2E–2H).

Species effects on stemflow N and C concentrations were minimal, but red maple's high stemflow volume often led to greater deposition. Stemflow NH_4^+ concentrations were independent of species ($P = 0.92$; Fig. 2I), but red maple NH_4^+ deposition via stemflow was consistently 2–3× greater than either oak ($P < 0.01$ for both; Fig. 2J). NO_3^- concentrations within red maple stemflow were significantly higher than chestnut oak ($P = 0.004$; Fig. 2K) but not scarlet oak ($P = 0.60$). Overall, red maple deposition of NO_3^- via stemflow was higher than both chestnut oak ($P < 0.001$) and scarlet oak ($P = 0.02$; Fig. 2L), but this effect interacted with season (species × season; $P = 0.009$) because deposition was similar among species in summer (see supplementary data[3]), and red maple and scarlet oak deposition were similar in spring ($P = 0.21$). Stemflow TON concentrations were similar among species ($P = 0.92$; Fig. 2M), but red maple TON deposition was ~2× greater than either oak ($P < 0.01$ for both; Fig. 2N). DOC concentrations within red maple stemflow were ~2–3× lower than those of chestnut and scarlet oak ($P < 0.01$ for both comparisons; Fig. 2O), but red maple's higher stemflow volume led to

Fig. 1. Volume and percentage of precipitation passing through the canopy as throughfall (A) and stemflow volume and funneling ratio (within each bar) (B) for red maple (RM), chestnut oak (CO), and scarlet oak (SO). Means ± SE are based on seasonal data collected from 2006–2008. Throughfall and stemflow volume were calculated based on the area of the collecting funnel and basal area of the tree, respectively. Note different scales for throughfall and stemflow volume. Different lowercase letters indicate significant differences ($P < 0.05$).

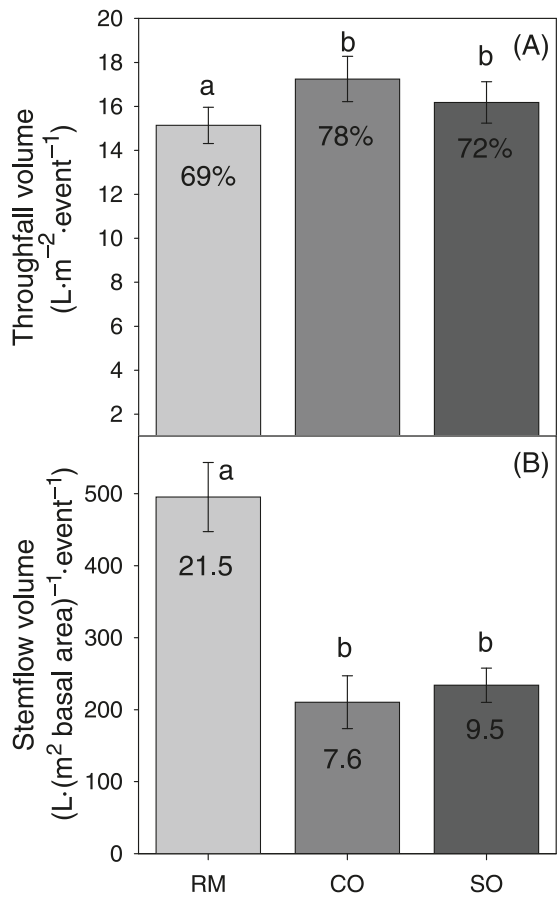
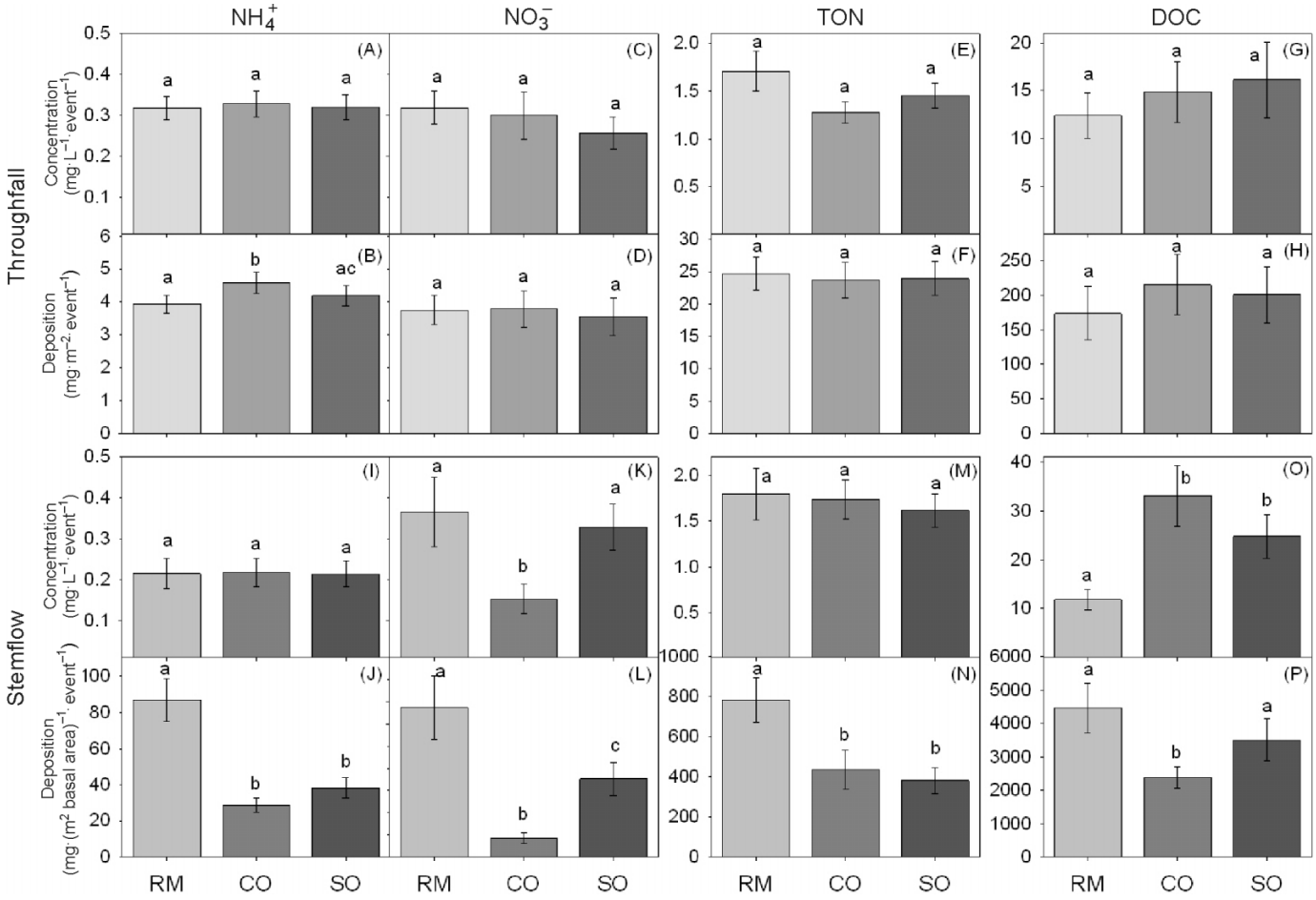


Fig. 2. Throughfall and stemflow NH_4^+, NO_3^-, total organic nitrogen (TON), and dissolved organic carbon (DOC) volume-weighted concentrations and deposition for red maple (RM), chestnut oak (CO), and scarlet oak (SO). Means ± SE are based on data collected seasonally from 2006–2008. Different lowercase letters indicate significant differences ($P < 0.05$).



DOC inputs greater than chestnut oak only (P = 0.02; Fig. 2P).

Throughfall pH and EC did not vary by species (P = 0.74 and 0.97, respectively), but chestnut oak stemflow had lower pH and higher EC than both red maple and scarlet oak (P < 0.01 for all), while red maple had lower stemflow pH (P < 0.001) than scarlet oak (Table 2). Cation and anion concentrations in throughfall never varied among tree species (P > 0.05 for all; Table 2), but deposition of Mg^{2+} and K^+ via chestnut oak throughfall was ~20% higher than scarlet oak or red maple (P < 0.05 for all; Table 2). Stemflow cation and anion concentrations were generally highest for chestnut oak and lowest for red maple (Table 2), but red maple deposition was often greater than that of both oaks because of greater stemflow volume (P > 0.05 for all comparisons; Table 2).

Upper mineral soil moisture did not exhibit an overall species effect (P = 0.12; Fig. 3), but net rates of ammonification and nitrification varied significantly among species (P = 0.02 and 0.003, respectively; Figs. 4A and 4B). Red maple had significantly greater ammonification rates than chestnut oak (P = 0.005) and marginally higher rates than scarlet oak (P = 0.07) but did not differ from no-tree areas (P = 0.95). Red maple also had significantly greater nitrification rates than both chestnut oak (P = 0.02) and scarlet oak (P = 0.008), but this effect depended on season (season×species: P = 0.002; see supplementary data[3]). Winter nitrification rates underneath red maple were ~5×

Fig. 3. Gravimetric soil moisture of upper mineral soils (0–5 cm) underneath red maple (RM), chestnut oak (CO), scarlet oak (SO), and no-tree areas. Means ± SE are based on data collected seasonally from 2006–2008.

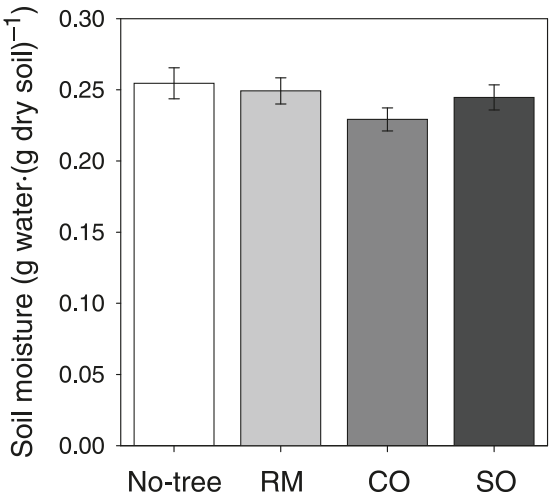


Table 2. pH, electrical conductivity (EC), volume-weighted cation and anion concentrations, and deposition for red maple, chestnut oak, and scarlet oak throughfall and stemflow.

		Throughfall			Stemflow		
	Incident precipitation	Red maple	Chestnut oak	Scarlet oak	Red maple	Chestnut oak	Scarlet oak
pH	5.7±0.1	5.1±0.1	5.2±0.1	5.2±0.1	4.4±0.1a	4.2±0.1b	4.6±0.1c
EC (μS)	10.7±1.2	26.1±1.7	26.0±1.7	25.9±1.6	62.5±4.5a	94.3±5.7b	73.6±4.5a
Concentration (mg·L^{-1})							
Ca^{2+}	0.27±0.04	0.91±0.08	0.83±0.06	0.88±0.09	1.72±0.27a	3.50±0.39b	2.85±0.26b
Mg^{2+}	0.09±0.01	0.30±0.02	0.32±0.02	0.30±0.02	0.35±0.08a	1.07±0.13b	0.44±0.04c
Na^{+}	0.80±0.09	1.10±0.08	1.00±0.08	1.00±0.08	0.61±0.09	0.86±0.10	0.72±0.07
K^{+}	0.26±0.05	2.34±0.21	2.62±0.25	2.46±0.25	6.11±0.67a	10.26±0.96b	10.34±0.65b
SO_4^{-}	1.88±0.17	3.96±0.35	3.75±0.30	4.02±0.35	8.44±0.90a	15.51±1.59b	11.33±0.98ab
Cl^{-}	0.99±0.14	1.17±0.09	1.25±0.10	1.22±0.09	1.92±0.23	3.42±0.48	2.41±0.23
Deposition (mg·m^{-2})							
Ca^{2+}	4.3±0.6	11.2±0.7	12.0±0.8	11.6±0.9	662.5±86.7	487.7±63.3	483.4±42.3
Mg^{2+}	1.6±0.2	3.8±0.2a	4.5±0.2b	3.9±0.2a	158.1±25.9	117.9±15.3	84.9±9.6
Na^{+}	13.3±1.3	12.7±0.6	13.6±0.8	12.4±0.6	276.4±35.6a	167.7±31.2b	164.1±19.3b
K^{+}	4.6±0.9	32.0±3.0a	39.6±3.5b	34.8±3.1ab	2754.5±239.3a	1655.2±200.3b	2146.0±176.1a
SO_4^{-}	30.8±2.7	50.9±3.8	56.7±4.5	54.1±3.9	3744.3±481.0a	2107.6±227.6b	2038.3±163.2b
Cl^{-}	17.9±3.1	14.5±1.2a	18.1±1.7b	17.0±1.8b	825.8±87.5a	430.9±53.2b	440.1±45.8b

Note: Means ± SE are based on seasonal data collected from 2006–2008. Different lowercase letters indicate significant differences ($P < 0.05$). Throughfall and stemflow differences among species were analyzed separately.

Fig. 4. In situ net rates of ammonification and nitrification within underlying upper mineral soils (0–5 cm) of red maple (RM), chestnut oak (CO), scarlet oak (SO), and no-tree areas. Means ± SE are based on seasonal data collected from 2006–2008. Different lowercase letters indicate significant differences ($P < 0.05$).

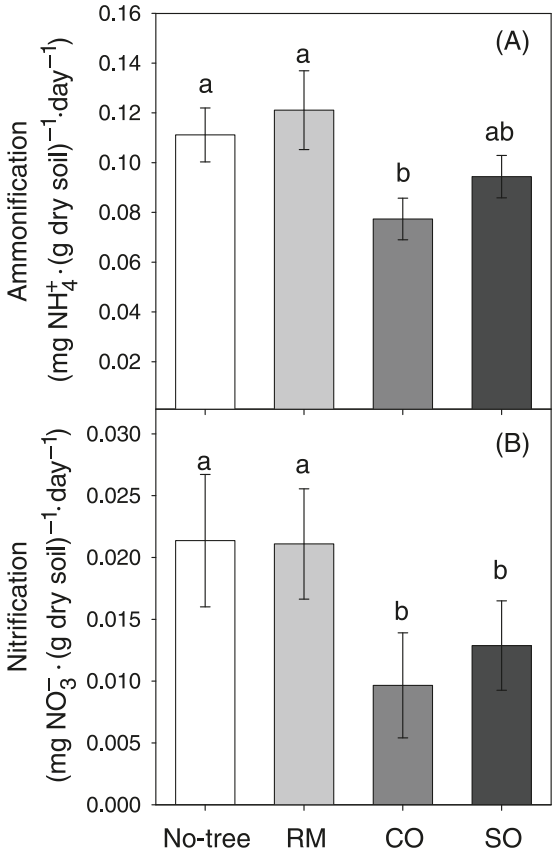
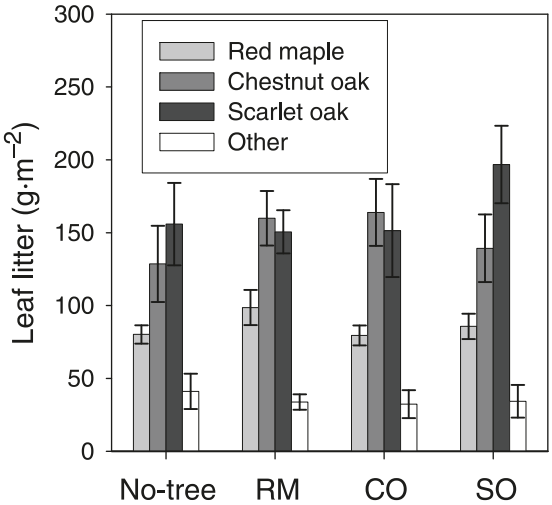


Fig. 5. Leaf litter mass underneath red maple (RM), chestnut oak (CO), scarlet oak (SO), and no-tree areas measured throughout the litterfall period in fall 2006.



greater (0.04 μg N·(g dry soil)$^{-1}$·day^{-1}) than chestnut oak (–0.01 μg N·(g dry soil)$^{-1}$·day^{-1}; $P < 0.001$) and 13× greater than scarlet oak (0.003 μg N·(g dry soil)$^{-1}$·day^{-1}; $P = 0.003$). Leaf litter species composition and mass did not vary significantly among species or no-tree locations ($P > 0.05$ for all comparisons; Fig. 5), suggesting leaf litter quality (which is known to vary among species; e.g., Carreiro et al. 2000) and quantity were not responsible for the observed differences in mineralization rates. Notably, the mass of red maple leaf litter was consistently lower than that of each oak regardless of treatment.

Discussion

Much of the research evaluating red maple's increased dominance has focused on fire suppression as the causal factor and on red maple physiological traits allowing its expansion (Abrams 1998), but attempts to link this canopy shift to forest ecosystem dynamics have been scarce. Only recently have Nowacki and Abrams (2008) presented a conceptual model linking fire disturbances (or lack thereof) to shifts in species composition. They suggested that fire suppression has initiated a new path of forest succession in many stands and that this successional path becomes increasingly entrenched in the continued absence of fire. They argue that without fire, shade-tolerant, fire-intolerant species like red maple create cool damp conditions in their understory through their thick dark canopies and easily decomposable leaf litter. This "mesophication" process creates a positive feedback loop that favors fire-intolerant species and renders forests less conducive to future fire disturbances. Our current findings build upon this supposition by providing evidence that increased red maple dominance would likely lead to important changes in forest hydrology and nutrient cycling and that these changes could act as additional mechanisms by which red maple contributes to this mesophication process by creating conditions that potentially foster the proliferation of this species.

As hypothesized, red maples captured and directed more precipitation down their stems compared with both oaks, leading to lower throughfall volume and greater stemflow yields. Based on average throughfall generation per event and average growing season (1 April – 31 August) precipitation during 2006–2008, soils underlying a red maple crown would receive roughly 26–52 $L \cdot m^{-2}$ less throughfall and 7–16 $mg \cdot m^{-2}$ less NH_4^+ during the growing season than those underlying chestnut oak and scarlet oak. In contrast, red maple would generate 5000–7000 L more $stemflow \cdot m^{-2}$ of basal area than either oak and would deposit via stemflow 3–4 $g \cdot m^{-2}$ more total inorganic nitrogen, 8–10 $g \cdot m^{-2}$ of TON, and 24–51 $g \cdot m^{-2}$ of DOC. Our analyses of upper mineral soil (0–5 cm) moisture did not capture these large species differences in stemflow, which may reflect the tendency of stemflow to be deposited directly at the base of the tree and (or) move along "preferential flow paths" (Johnson and Lehmann 2006), i.e., paths with low resistance often created by root growth through the soil. This could lead to estimates of bulk soil moisture that underestimate the true magnitude of water flow. Our sites also have relatively well-drained soils, and estimates in the upper soil layers may not be indicative of water movement and content throughout the soil profile.

Differences in stemflow generation among species likely reflect differences in bark roughness and crown area. Red maple bark was 2× and 4× smoother than that of scarlet oak and chestnut oak, respectively. Smooth bark has low water storage capacity (Herwitz 1985), low resistance to flow (Voigt 1960), and few obstacles to generate canopy drip (Carlyle-Moses and Price 2006). Red maple also had greater crown area than either oak, and larger crowns have greater surface area to capture and funnel rain water (Aboal et al. 1999).

Upper mineral soils near red maple trees had higher rates of inorganic N cycling compared with both oaks, and we hypothesized that greater inputs of stemflow-derived nutrients and water would contribute to these findings. Net ammonification rates were significantly higher than chestnut oak and marginally higher than scarlet oak ($P = 0.07$), and rates of net winter nitrification were higher compared with both oaks. Higher net ammonification rates reflected relatively higher stemflow TON deposition, and higher winter net nitrification beneath red maple corresponded with relatively higher stemflow inputs of TON, NH_4^+ (the precursor to nitrate), and slightly (but not significantly) higher soil moisture. Because ammonification and nitrification rates underneath red maple were similar to no-tree areas, which received no stemflow, there may be characteristics of oak stemflow or soils that limit these processes. Oak stemflow had a higher C/N ratio (32–39; data not shown) compared with that of red maple (17); thus, microbes in soils adjacent to oak boles may be N limited. The secondary carbon compounds within oak stemflow may also inhibit soil microbes. For instance, some oak bark is high in tannins (Parker 1977), and tannins have been shown to reduce N mineralization not only by providing a labile C source but also by lowering N availability by binding with proteins (Kraus et al. 2004).

The idea that stemflow affects N mineralization has been suggested in previous studies, although species-specific effects were not explicitly addressed. Boerner and Koslowsky (1989) measured a zone of high N mineralization near the trunks of sugar maple (*Acer saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), and white ash (*Fraxinus americana* L.) and suggested stemflow nutrients as causal factors. Chang and Matzner (2000) measured increased nitrification rates in areas proximal to European beech (*Fagus sylvatica* L.) stems and linked this to high soil moisture because of high stemflow volume.

In some other studies, differences in N mineralization rates between red maple and oaks were attributed to differences in leaf litter. For instance, Finzi et al. (1998) measured higher N mineralization rates underneath red maple in Connecticut compared with northern red oak (*Q. rubra* L.) and American beech, which was presumed to be due to the relatively lower C/N ratio of red maple leaf litter and consequent effects on underlying soils. Notably, measurements were taken beyond the zone of stemflow influence (2 m from the bole). In contrast, Washburn and Arthur (2003), working on Whittleton Ridge and nearby Koomer Ridge, Kentucky, measured lower summer net N mineralization rates underneath red maple compared with chestnut oak. The authors suggested possible differences in microbial communities between species. This finding was only relevant to the organic horizon and may reflect differences in litter chemistry because the forest floor underneath red maple (0.5 m from tree bole) contained more red maple litter than chestnut oak litter, and red maple leaf litter on our sites in Kentucky has a high C/N ratio (H.D. Alexander, unpublished data), which may promote microbial immobilization of N and relatively slower N mineralization rates in organic horizons. In the current study, leaf litter could not be the primary factor controlling species differences in N mineralization rates because differences in leaf litter quantity and composition underlying red maple and oaks were not evi-

dent. The differences between our study and the other two suggest that the relative effects of leaf litter and stemflow on N cycling within underlying soils may depend on (1) sampling distance from tree bole, (2) degree of leaf litter mixing, (3) leaf litter chemistry, which can vary geographically even within one tree species, and (or) (4) whether N mineralization rates were measured in the organic horizon as opposed to the mineral soil.

Implications

Water and nutrient inputs via rainfall will likely undergo a spatial redistribution as red maple dominance increases across deciduous forests of the eastern US. Less of these resources will be distributed across the forest floor and more will be concentrated within a narrow zone immediately surrounding red maple boles. These resources could foster red maple growth and survival, thereby favoring this species' proliferation and further promoting the mesophication process. For instance, red maple's greater ability to channel precipitation as stemflow could decrease its susceptibility to water shortages. While stemflow is generally restricted to an area ~0.5–1 m from the tree bole (Chang and Matzner 2000), this is an area where changes in resource availability or microclimate could have meaningful consequences for an individual tree. Stemflow can be an important mechanism of groundwater recharge to deep soils (Taniguchi et al. 1996), and trees and shrubs in semiarid and arid regions have been shown to uncouple from short-term drought conditions by storing stemflow-derived water at their bases (Martinez-Meza and Whitford 1996). An ability to funnel even small precipitation volumes could be an effective strategy in temperate regions if trees grow on xeric sandy soils, such as those sampled here because summer droughts are common across the eastern US, and fluctuations in climatic extremes are predicted to increase with global warming (Watson et al. 1998). Notably, Abrams and Mostoller (1995) found that of six tree species in central Pennsylvania, red maple saplings had the largest percentage decrease in photosynthesis during drought, and Abrams and Kubiske (1990) found red maple seedlings had limited ability to adjust osmotically during drought. Both findings suggest a high sensitivity of physiological processes to low water availability in seedling and sapling stages that could be partially overcome with tree maturity and increased stemflow, with the tree preferentially funneling more water to the center of its own root system.

Furthermore, large inputs of stemflow-derived nutrients could favor red maple growth, since this species has previously been shown to be particularly responsive to elevated N levels. Recently, Bedison and McNeil (2009) found a positive correlation between atmospheric N deposition and basal area growth among red maples of all size classes, although those ranging in size from 2.0 to 9.9 cm DBH exhibited the most pronounced response. Red maple seedling growth has exhibited increased growth when fertilized with N (Zaccherio and Finzi 2007), and red maple sapling growth has been positively correlated with net rates of N mineralization (Finzi and Canham 2000). Kobe (2006) utilized a modeling approach to test for changes in red maple sapling growth in response to soil resources across a landscape gradient in Michigan and found increased growth with increased availability of soil water and N (Kobe 2006).

Conclusions

The results presented here highlight how a shift in forest canopy dominance from upland oaks to red maple could impact forest dynamics. In this study, red maple altered forest hydrology by capturing and funneling more precipitation along its stem, thus generating greater stemflow volume. High stemflow and consequently greater yields of water and nutrients could promote conditions that favor red maple by preferentially delivering resources near red maple's bole where its roots are most highly concentrated. This could be especially beneficial in certain situations, such as during droughts and (or) on soils with low nutrient availability. Binkley and Giardina (1998) suggested that individual tree impacts on underlying soils may directly or indirectly improve their status or decrease that of their competitors. These results hint at how red maple's unique characteristics, such as smooth bark and wide canopy, and its potential impacts on surrounding soils could do just that and may help explain red maple's ability to establish and grow on a variety of sites in the absence of fire. Importantly, any factor that promotes red maple dominance will have a negative feedback to fire occurrences. Red maple's leaf litter has been suggested to have faster decomposition and lower flammability than that of upland oaks (Nowacki and Abrams 2008), but potentially, the delivery of large volumes of stemflow could further create fuel discontinuity by promoting cool damp conditions near the bole of red maple trees. These findings ultimately suggest that an increase in red maple dominance could have various effects on several ecosystem properties and processes, including forest hydrology, nutrient cycling, and disturbance regimes.

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