Relative role of understory and overstory in carbon and nitrogen cycling in a southern Appalachian spruce–fir forest[1]

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Abstract: This study investigated aboveground pools and fluxes of biomass, carbon (C), and nitrogen (N) in the overstory and understory of a southern Appalachian red spruce (*Picea rubens* Sarg.) – Fraser fir (*Abies fraseri* (Pursh) Poir.) forest, following adelgid-induced fir mortality and spruce windthrow. Using fifty 20 m × 20 m plots, stratified by elevation (1700–1900 m), we estimated standing biomass and fluxes of all growth forms from periodic stand inventories (1998–2003), vegetation surveys, and existing or derived allometric equations. Total C and N pools and fluxes were calculated from plant- and tissue-specific C and N concentrations. Total aboveground biomass attained predisturbance values, ranging from 313 Mg·ha^{-1} at the lower elevations to 204 Mg·ha^{-1} at the upper elevations. Overstory biomass production (5650 kg·ha^{-1}·year^{-1}) and N uptake (11–15 kg·ha^{-1}·year^{-1}) exceeded earlier reported values, indicating forest recovery. Woody understory accounted for 3% of aboveground biomass, 10% of annual productivity, and 19% of total N uptake ($\sim$7 kg·ha^{-1}·year^{-1}). Herbaceous vegetation, which comprised only 1% of total biomass, took up 18–21 kg N·ha^{-1} annually, >50% of total ecosystem N uptake (37 kg·ha^{-1}·year^{-1}). This suggests that N-rich understory vegetation plays an important role in N cycling.

Résumé : Cette étude porte sur les réservoirs aériens et les flux de biomasse, de carbone (C) et d'azote (N) dans l'étage dominant et le sous-étage de la forêt Appalachienne méridionale d'épinette rouge (*Picea rubens* Sarg.) et de sapin de Fraser (*Abies fraseri* (Pursh) Poir.) à la suite de la mort du sapin causée par le puceron lanigère et du renversement de l'épinette par le vent. En utilisant 50 placettes-échantillons de 20 m × 20 m, stratifiées en fonction de l'altitude (1700–1900 m), nous avons estimé la biomasse sur pied et les flux de toutes les formes de vie à partir de relevés périodiques des peuplements (1998–2003), d'inventaires de la végétation et d'équations allométriques existantes ou dérivées. Les réservoirs de C et de N totaux et les flux ont été calculés à partir des concentrations de C et de N spécifiques aux plantes et aux tissus. La biomasse aérienne totale a atteint les valeurs antérieures à la perturbation, variant de 313 Mg·ha^{-1} à l'altitude la plus faible à 204 Mg·ha^{-1} à l'altitude la plus élevée. La production de biomasse de l'étage dominant (5650 kg·ha^{-1}·an^{-1}) et l'assimilation de N (11–15 kg·ha^{-1}·an^{-1}) dépassaient les valeurs déjà rapportées, ce qui est un indice du rétablissement de la forêt. Les plantes ligneuses en sous-étage représentaient 3 % de la biomasse aérienne, 10 % de la productivité annuelle et 19 % de l'assimilation totale de N (environ 7 kg·ha^{-1}·an^{-1}). La végétation herbacée, qui représentait seulement 1 % de la biomasse totale, prélevait 18–21 kg N·ha^{-1}·an^{-1}, soit plus de 50 % de l'assimilation totale de N dans l'écosystème (37 kg·ha^{-1}·an^{-1}). Cela indique que la végétation de sous-étage riche en N joue un rôle important dans le recyclage de N.

[Traduit par la Rédaction]

Introduction

Southern Appalachian red spruce (*Picea rubens* Sarg.) Fraser fir [*Abies fraseri* (Pursh) Poir] forests, 74% of which are located in Great Smoky Mountains National Park (GSMNP) in Tennessee and North Carolina, receive some of the highest amounts of atmospheric nitrogen (N) deposition ($\sim$30 kg·ha^{-1}·year^{-1}) and are considered N-saturated (Nodvin et al. 1995). The N retention capacity of these systems is limited and significant amounts ($\sim$15 kg·ha^{-1}·year^{-1}) of inorganic N leave the system via streamwater (Nodvin et al. 1995; Van Miegroet et al. 2001). In the Noland Divide Watershed (NDW) of GSMNP, Barker et al. (2002) found that the overstory of this system had an uptake rate of $\sim$8 kg·ha^{-1}·year^{-1}, though rates were spatially variable. Since that time, productivity in this forest has significantly recovered (Van Miegroet et al. 2007) and the uptake rate of the overstory may be considerably higher.

Increased N deposition in forested ecosystems can cause increased nitrate leaching and stream water export (Aber et al. 2003), decreased mycorrhizal community diversity (Egerton-Warburton and Allen 2000; Lilleskov et al. 2002), changes in lichen communities (Sigal and Nash 1983), and decreases in net primary productivity and foliar biomass (Aber et al. 1998). In the western United States, low background levels of atmospheric N deposition coupled with "hotspots" of elevated N deposition have caused significant impacts on ecosystem function (Fenn et al. 2003). In north-

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eastern forests, N deposition is altering N status, expressed by increased N in surface water, increased nitrification, and decreased C/N ratios in soil (Aber et al. 2003). The role of vegetation and soil in the uptake and storage of N has been the subject of some debate (Aber et al. 1989; Fenn et al. 1998). Nutrient uptake and sequestration by vegetation can retain large amounts of increased N deposition inputs within forest ecosystems (Aber et al. 1989, 1998; Fenn et al. 2003). However few, if any, studies have considered the role of understory in N uptake and retention.

Recent disturbances in high-elevation spruce–fir forests of the southern Appalachians have reduced the ability of this forest to take up N (Barker et al. 2002), such as the infestation of the balsam woolly adelgid (BWA, *Adelges piceae* (Ratzeburg) Nicholas et al. 1992), atmospheric pollution (Johnson et al. 1991), ice storms (Nicholas and Zedaker 1989), and gap dynamics (White et al. 1985; Busing and Clebsch 1987). The disturbance that has caused the most widespread and catastrophic damage to these forests is the infestation by the BWA. Prior to the onset of the BWA, these forests contained large amounts of biomass in the overstory (Whittaker 1966). After the BWA, which killed most mature fir, only 12% of fir stems remained alive, and these remaining individuals were exclusively in the smaller size categories (Smith and Nicholas 2000). In the years following the BWA-induced thinning of fir stands, many remaining dominant and codominant spruce were subject to windthrow events as a result of exposure to the more open canopy conditions (Hollingsworth and Hain 1991; Busing 2004). Since that time, the forest has shown signs of recovery, as indicated by increased standing live biomass, increased growth, and conifer regeneration (Van Miegroet et al. 2007).

Overstory vegetation characteristics and nutrient dynamics have been documented for spruce–fir (Johnson and Lindberg 1992; Nicholas et al. 1992; Busing 2004), with the most intensive determination of nutrient storage and uptake in southern Appalachians as part of the Integrated Forest Study (IFS) in the mid-1980s (Johnson et al. 1991; Johnson and Lindberg 1992). In that study, total standing live biomass of two post-adelgid red spruce plots was estimated between 273 and 314 Mg·ha⁻¹ for the Smokies Tower site (ST), located just outside of the NDW at 1740 m, and at 264 Mg·ha⁻¹ for the nearby Becking site (SS). Corresponding biomass production rates ranged from 1360 to 4530 kg·ha⁻¹·year⁻¹, and the uptake of N ranged from 7 to 13 kg·ha⁻¹·year⁻¹ (Johnson and Lindberg 1992). Pauley et al. (1996) provided an estimate of post-BWA biomass and N pools within the NDW of GSMNP. They found that spruce contained over 70% of overstory N, while fir contained less than 2%. Spruce needles accounted for over 35% of overstory N, but represented only 6% of overstory biomass, showing that biomass and nutrient dynamics are not necessarily congruent.

Compared with the overstory, the understory of this forest has received little attention and is not well understood (Barker et al. 2002). Several authors have characterized the pre-BWA understory of this forest (Oosting and Billings 1951; Crandall 1958; Ramseur 1960; Whittaker 1962), but this was done in a taxonomical or botanical manner and without much regard to nutrient cycling or ecosystem func-

tion. Smith and Nicholas (2000) analyzed regeneration of spruce and fir, but only focused on woody seedlings, saplings, and trees in the highest elevations. Johnson and Lindberg (1992) provided an estimate of understory pools but did not attempt to estimate understory C an N fluxes. Since the IFS analysis, the structure and function of the understory trees, shrubs, and herbs may have changed. With many young spruce and fir entering the stand since the BWA onset, and with those small trees containing a higher foliage to stem mass ratio (Waring and Schlesinger 1985), understory nutrient dynamics may have changed considerably.

We hypothesize that this disturbed forest may be recovering its ability to sequester and store excess N. The majority of research on this system so far has dealt with overstory response to these disturbances (Nicholas et al. 1992; Pauley et al. 1996; Smith and Nicholas 2000; Busing 2004) and not much is known about the importance of understory nutrient cycling. A complete understanding of how nutrients are cycled within the living components of this ecosystem requires the inclusion of the understory, especially when this ecosystem is in transition. We hypothesize that the understory is cycling a considerable portion of total ecosystem N. The objectives of this paper are to determine (*i*) the role of understory versus overstory in sequestering biomass and cycling N; (*ii*) whether overstory N and biomass dynamics have recently changed from prior measurements; and (*iii*) whether current biomass, and C and N dynamics show elevational patterns.

Methods

Study area

This research was conducted at the NDW (35°34′N, 83°29′W, 1700–1910 m), a 17.4 ha catchment within GSMNP. The broad elevation gradient, resulting variability in overstory species composition, similar parent material, and pre-existing plot infrastructure give us the ability to study watershed-level dynamics. Because of prior research at this site by others (Pauley et al. 1996; Barker et al. 2002), as well as access to data previously collected by collaborators (repeated 1993 and 1998 overstory measurements), we are able to evaluate changes in nutrient dynamics over time. While our analysis was done within only one watershed and thus has an somewhat limited inference space, the intensive sampling scheme and plot layout captured much of the variability existing at the larger landscape, and may thus reveal some general patterns and lead to conclusions that may also apply to spruce–fir forests within the GSMNP and the southern Appalachians.

Mean annual precipitation is >200 cm and is distributed evenly throughout the year (Johnson and Lindberg 1992). Ten percent of annual precipitation falls as snow and covers the ground for an average of 50 days/year (Johnson et al. 1991). Mean air temperatures range from –2 °C in February to 17 °C in August with a frost-free period from May to September (Shanks 1954; Johnson et al. 1991). The soils are mainly Inceptisols, occasionally with spodic characteristics (McCracken et al. 1962; Van Miegroet et al. 1993), and are underlain by Thunderhead Sandstone (King et al. 1968). They are generally shallow and have a silt loam to sandy loam texture, and are rich in N and C but low in exchange-

able bases (Johnson and Lindberg 1992). This catchment has not been impacted by logging or fire (Pyle and Schafale 1988), but has been severely impacted by the BWA beginning as early as 1977 (Pauley et al. 1996; Barker et al. 2002). A full description of current forest composition can be found in Van Miegroet et al. (2007).

In this study, we used a repeated overstory inventory of fifty 20 m × 20 m permanent plots, placed systematically within this high-elevation catchment, along nine elevation bands (1700, 1725, 1755, 1785, 1800, 1835, 1865, 1890, and 1910 m; Fig. 1). We determined watershed biomass and N dynamics of all vegetation strata, including overstory trees, understory woody trees and shrubs, herbs, and mosses. In analyzing the data for elevational patterns, the nine elevation bands of the NDW were split into three elevation ranges: low, the lowest three bands (1700, 1725, and 1755 m), totaling 19 plots; middle, the middle three elevation bands (1785, 1800, and 1835 m), totaling 19 plots; and high, the highest three elevation bands (1865, 1890, and 1910 m), totaling 12 plots. One-way analysis of variance (PROC ANOVA) was be used to determine significant differences in biomass, N pool, and uptake values across the three elevation ranges (SAS Institute Inc. 2002).

Overstory measurements

Barker et al. (2002) estimated overstory N uptake using repeated measurements (1993 and 1998) of individual tree diameter at 1.37 m above ground level (diameter at breast height, DBH) at each of the 50 permanent NDW plots. A similar methodology was used to determine overstory N uptake and production for the 1998–2003 period for each of the 50 NDW plots. DBH, species, and unique identification number of each live overstory (≥5 cm DBH) tree were recorded, using inventory protocol described in Zedaker and Nicholas (1990). As the NDW plots are part of a permanent plot system where individual trees are tagged and cataloged, and since an inventory had not been performed since 1998, new ingrowth was measured and tagged for future measurements.

Biomass of foliage, live branches, dead branches, bole bark, and bole wood were determined from DBH using the predictive equations of Nicholas (1992). Individual tree component masses were summed to equal total aboveground tree biomass. These equations were applied to red spruce, Fraser fir, and yellow birch (*Betula alleghaniensis* var. *alleghaniensis* Britt.) to estimate biomass of tree species within each plot. Aboveground biomass of other species was estimated similarly with the predictive equations of Weaver (1972). The C and N content of individual tree components was determined using the nutrient concentration values in Barker (2000). Current standing live biomass and N pools were determined using 2003 inventory data. Uptake fluxes were determined by mass difference of individual trees from the 1998 to the 2003 inventory (Clark et al. 2001). This allowed us to quantify how much N dynamics within those 5 years had changed relative to earlier studies (Johnson et al. 1991; Barker et al. 2002).

Nutrient uptake can vary considerably from one forest type to another and spatially within the same forest type and watershed (Barker et al. 2002). Also, various uptake calculation methods can produce dramatically different results

(Bockheim and Leide 1990; Barker et al. 2002). Because we were interested in change over time, and consistency in methodology is essential, the simpler of the eight N uptake determination methods (U_2, net aboveground increment) was used to compare our current uptake values with those of Barker et al. (2002). Belowground biomass and N content are not addressed in this study. Van Miegroet et al. (2007) provided an analysis of belowground biomass and C for this area.

Understory woody vegetation

Within each of the 50 permanent plots of the NDW, four 4 m × 4 m subplots were established as shown in Fig. 2 (gray boxes). In 2003, large understory woody vegetation (<5 cm but >2 cm DBH) was measured at 15 cm above ground level, and species-specific predictive equations of Nicholas (1992) and Weaver (1972) were used to calculate biomass of individual tree components based on this stem diameter as the independent variable. The C and N content of individual tree components of aboveground biomass were determined from values in Barker (2000). Production of other woody understory vegetation was determined using biomass accumulation ratios (BAR) of woody understory plants, i.e., empirical relationships between standing biomass and productivity (Whittaker 1962). They generally range from 1 to 3 in grasslands, from 2 to 10 in deserts, from 3 to 12 in shrublands, from 10 to 30 in woodlands, and from 20 to 50 in mature forests (Whittaker 1975). We used a conservative value of 10 based on Whittaker's reported findings from understory shrubs in the southern Appalachians (7.0; Whittaker 1966), general shrub communities (3–12; Whittaker 1975), and Alaback's values for forest understory of disturbed Sitka spruce (*Picea sitchensis* (Bong.) Carrière) sites in eastern Alaska (8; Alaback 1984).

Because of the lack of existing allometric equations for biomass and nutrient content of small understory woody vegetation (stems <2 cm DBH), a two-part, destructive–nondestructive double sampling approach was used to derive these equations. All destructive sampling was performed in the nearby Pisgah National Forest, North Carolina. Twelve individuals of each of four woody species [red spruce, Fraser fir, yellow birch, and hobblebush (*Viburnum lantanoides* Michx.)] were measured with a caliper at 15 cm above ground level, clipped at ground level, dried, and weighed. These four species were chosen because they were, by far, the most common understory woody vegetation. Allometric relationships between stem diameter and aboveground biomass were developed using the PROC REG procedure in SAS (SAS Institute Inc. 2002). Diameters of all small woody understory plants were measured in sixteen 1 m × 1 m subplots within each of the 50 permanent plots (Fig. 2; black boxes) and converted to biomass values using the calculated allometric equations. For species other than the four most common, the equation with the species most similar in growth form was applied. Seedling biomass increment was determined using a BAR of 10, similar to larger understory vegetation.

Herbaceous vegetation

Predictive biomass equations were produced for herbaceous vegetation in a manner similar to that used for understory woody vegetation, i.e., nondestructive survey within

Fig. 1. Map of the Noland Divide Watershed and the systematic network of 50 permanent plots.
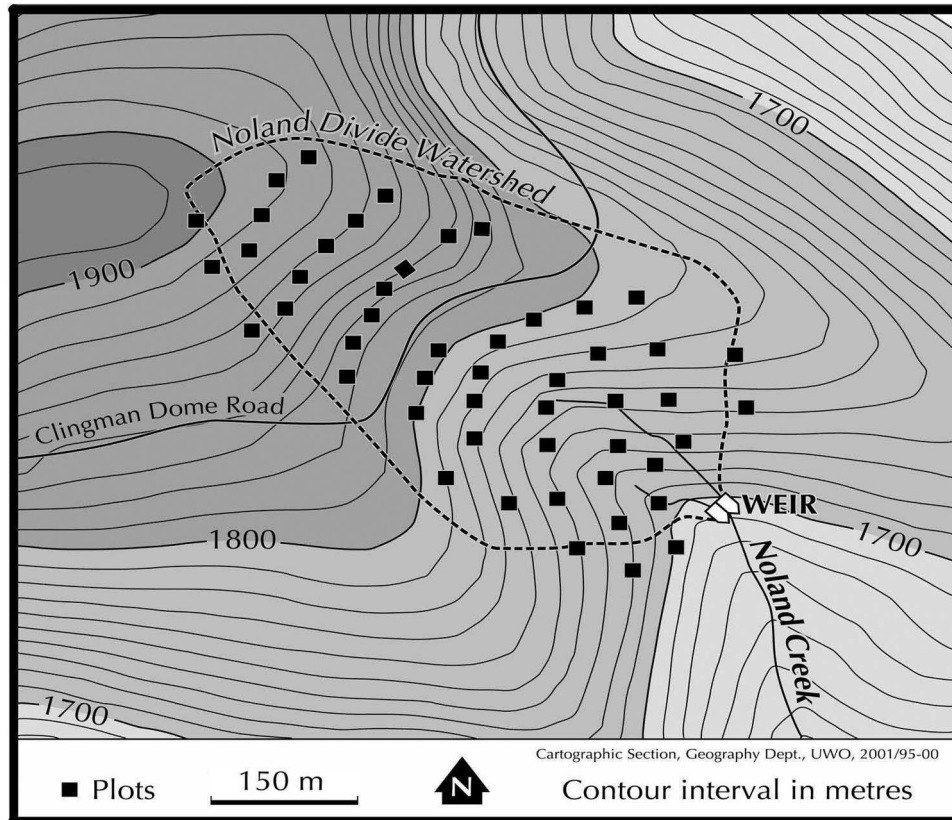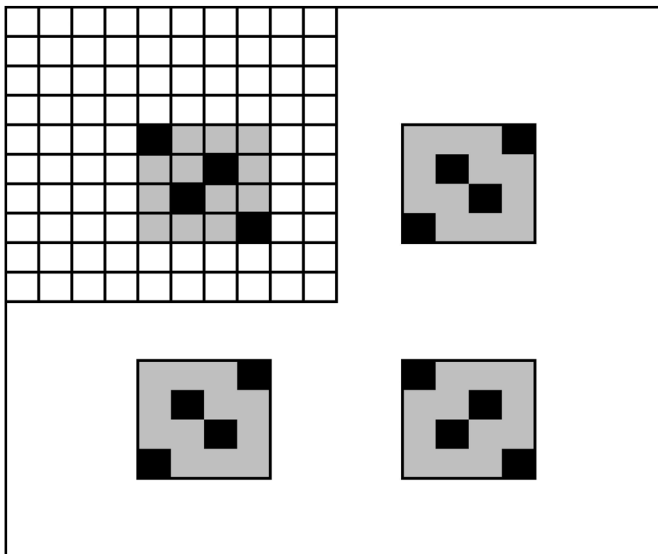

Fig. 2. Layout of one of the fifty 20 m × 20 m plots of the Noland Divide Watershed showing the four 4 m × 4 m plots (grey boxes) and the sixteen 1 m × 1 m plots (black boxes).

the NDW plots was coupled with destructive sampling outside the permanent plots to protect plot integrity (Forman 1969). In the nondestructive herbaceous survey of the permanent plot system, the sixteen 1 m × 1 m subplots used for the small woody vegetation survey were used. Percent cover of all herbaceous plant species present within each subplot was estimated via ocular estimation to the nearest

percent. Herbaceous vegetation was defined as all nonwoody herbs, grasses, and mosses. Concurrent with the nondestructive sampling in the permanent plots was a destructive sampling of herbaceous plants in temporary 1 m × 1 m plots established in the fall of 2003 outside the permanent NDW plots but still within the NDW. Each of these temporary plots was centered 10 m west of the northwest corner of the permanent NDW plots to capture the entire watershed yet not interfere with the permanent plot system. Percent cover by species was assessed by ocular estimation to the nearest percent. Then each species was clipped at ground level and placed in a uniquely numbered plastic bag until adequate samples ($n = 12$) of each species present in our surveys were measured and collected. If additional samples were needed, they were selectively sampled randomly from populations throughout the watershed to obtain adequate observations and ranges of all species.

Once removed from the field in individually labeled and sealed Ziploc® bags, plant specimens were individually oven-dried at 65 °C for 24 h and weighed. Dry weights were then used to develop species-specific predictive equations to estimate dry plant biomass from percent cover estimates using the PROC REG procedure in SAS (SAS Institute Inc. 2002). Dried plant specimens were then ground through a 40 mesh screen in a Wiley mill and analyzed for C and N using a LECO CHN analyzer (LECO Corp. St. Joseph, Missouri).

Because of the relatively short growing season (May–September) only one sampling period was necessary during the year (Yarie 1980). Therefore, aboveground herbaceous biomass was assumed to be the peak standing biomass at

the end of the growing season. It was assumed that herbaceous biomass and N are cycled annually; therefore, pool estimates were used as N uptake values as well, with two exceptions: *Rubus* and moss species. Since the aboveground portion of *Rubus* is semelparous and each stem usually survives for two seasons, flux of biomass and N into the herbaceous pool was estimated to be one-half of the live biomass pool. Although mosses contribute little in terms of ecosystem biomass, their high turnover rates and high nutrient content make them important in biogeochemical cycling (Tamm 1953; Binkley and Graham 1981). Mosses were destructively and nondestructively surveyed similar to forbs and estimated by percent cover. Production was estimated as one-third of the estimated biomass following Tamm (1953).

Results

Distribution of biomass, carbon, and nitrogen in vegetation

These forests contained large amounts of biomass in the live aboveground vegetation components (Table 1). Biomass values averaged from 313 Mg·ha^{-1} in the lower watershed to 204 Mg·ha^{-1} in the upper watershed. The vast majority (96%–97%) of aboveground live biomass was in trees > 5 cm DBH. Woody vegetation <5 cm DBH contained 7.8 Mg·ha^{-1}, a considerably smaller proportion of aboveground biomass (2.7%–3.9%), with smaller understory woody vegetation (<2 cm DBH) concentrated in the lower watershed and larger understory woody vegetation (2–5 cm DBH) concentrated in the upper watershed. Understory herbaceous vegetation, on average 1.7 Mg·ha^{-1}, represented only a small proportion (0.6%–1.0%) of total aboveground live biomass.

Allometric equations for the relationship between herbaceous plant percent cover and standing herbaceous biomass are shown in Table 2, with nomenclature following Radford et al. (1968). Linear relationships were most effective in describing this relationship, with R^2 ranging from 0.76 to 0.98. Allometric equations for understory woody vegetation <2 cm DBH are shown in Table 3 and required a correction factor for logarithmic bias (Sprugel 1983). Log-linear relationships were most effective in describing this relationship, with R^2 ranging from 0.78 to 0.93. Aboveground C pools were on average 48.2% of biomass values, and the distribution of C in the ecosystem was very similar to that of biomass. Therefore, for the remainder of this paper, biomass and C dynamics will be discussed simultaneously.

Aboveground N pools were on average 0.22% of biomass values, but the N distribution did not follow that of biomass and C. Overstory trees contained on average 489 kg N·ha^{-1}, a smaller proportion of aboveground N (78%–84%) when compared with biomass and C; however, the overstory still contained the majority of N in this system. Understory woody vegetation contained a considerably smaller amount (70 kg·ha^{-1}) and proportion of aboveground N (10.8%–14.4%), but this was four times higher than the small woody vegetation proportion of biomass and C pools. Herbaceous vegetation represented the smallest absolute (34 kg·ha^{-1}) and relative N pool (4.7%–7.7%) of any of the vegetation strata. However, total live aboveground N in the herbaceous layer was disproportionately higher (eight times) than biomass and C pools.

The amount of biomass and nutrients contained in the forest differed among elevations bands. Total live ecosystem biomass and C, and N content were highest at lower elevations compared to mid and high elevations. Overstory biomass and C and N pools also tended to be higher at the lower elevations but the differences were statistically significant for N pools only. Elevation patterns, however, varied by overstory species. There was significantly more overstory fir biomass and C and N in higher elevations while biomass, C, and N of pools in birch were significantly greater at lower elevations than at higher elevations. There were no distinct patterns for spruce overstory; however, more biomass, C, and N was stored in small understory spruce at lower elevations. No other differences could be detected, possibly because of the high degree of variability that is common in these forests. Coefficients of variation (CV) for the pool size of individual forest components across species were often high (37%–95%) and by species even higher (routinely >100%).

Carbon and nitrogen fluxes

Over the last 5 years this system has produced large amounts of new biomass, ∼7370 kg biomass·ha^{-1}·year^{-1}, with the highest levels of net production, 7730 kg·ha^{-1}·year^{-1} in the lower elevation range (Table 4). Most biomass production occurred in the overstory, 5650 kg·ha^{-1}·year^{-1}, accounting for 75%–78% of the total. Woody vegetation <5 cm DBH produced 824 kg·ha^{-1} biomass annually, 11% of aboveground live production, with small woody understory vegetation (<2 cm DBH) production concentrated in the lower elevations and larger woody understory vegetation (2–5 cm DBH) production, mostly fir, concentrated in the higher elevations. Herbaceous vegetation produced 933 kg·ha^{-1}·year^{-1} live aboveground biomass, 11%–14% of the total, concentrated in the upper elevations.

Total aboveground N uptake was 37 kg·ha^{-1}·year^{-1} across the watershed with the highest uptake values, 43 kg·ha^{-1}·year^{-1}, in the higher elevations. The distribution of N uptake across forest components did not follow biomass and C increment patterns. Overstory took up 11–15 kg·ha^{-1}·year^{-1} or about 31% of total aboveground N uptake. Understory woody vegetation took up an additional 7 kg·ha^{-1}·year^{-1} or about 19% of total N uptake, with generally higher N uptake values for smaller understory woody vegetation (<2 cm DBH) in the lower watershed and larger understory woody vegetation (2–5 cm DBH) in the upper watershed. Herbaceous vegetation, despite the modest biomass pools and fluxes, took up 18–21 kg N·ha^{-1}·year^{-1}, exceeding that of the overstory. The herbaceous vegetation was responsible for 51% of total aboveground N uptake by vegetation annually, disproportionately high for its relative pool size. There were some patterns in N uptake with elevation, although many were not statistically significant. Total ecosystem N and overstory N uptake rates were highest in the high elevation band. Patterns by overstory species were consistent with those of biomass and C increments: highest for fir at highest elevations and for birch at the lower elevations, with no discernible pattern for spruce. For the other overstory components, N uptake also generally followed spatial patterns in biomass increment.

Table 1. Aboveground live pools of biomass (Mg·ha^{-1}), carbon (Mg·ha^{-1}), and nitrogen (kg·ha^{-1}) for different forest components at three different elevation ranges within the Noland Divide Watershed of Great Smoky Mountains National Park (±SD).

Elevation range	Species	Biomass (Mg·ha^{-1})			Carbon (Mg·ha^{-1})			Nitrogen (kg·ha^{-1})		
		Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Overstory	*Abies*	4.63±6.46b*	7.80±6.24b	33.3±26.0a	2.27±3.17b	3.83±3.06b	16.3±12.7a	18±25b	30±24b	127±100a
Vegetation	*Betula*	105±111a	50.6±56.1ab	7.26±14.9b	51.6±54.3a	24.8±27.5ab	3.54±7.28b	240±246a	118±128ab	18±36b
>5 cm DBH	*Picea*	191±90.6†	198±111	152±91.4	91.3±43.3	94.9±53.2	72.6±43.7	307±132	317±166	243±138
	Other	1.88±2.15	1.70±2.79	2.20±3.02	0.901±1.03	0.815±1.34	1.05±1.45	5±5.6	4.6±7.4	5.8±8
Overstory total		303±103a	259±102ab	195±84.5b	146±50.2a	124±48.8ab	93.5±40.3b	570±206a	469±160ab	394±128b
Understory	*Abies*	1.73±1.40	2.08±2.93	3.35±4.95	0.868±0.702	1.05±1.47	1.68±2.49	17±14	21±29	33±49
Vegetation	*Betula*	0.106±0.463	0.294±0.491	0.201±0.431	0.055±0.238	0.151±0.253	0.103±0.221	1±4.3	2.8±4.6	1.9±4
2–5 cm DBH	*Picea*	1.01±1.16	1.24±2.28	1.07±1.28	0.517±0.593	0.637±1.170	0.550±0.654	8.4±10	10.3±19	8.9±11
	Other	0.928±1.16	0.930±1.89	0.481±0.613	0.463±0.578	0.465±0.940	0.242±0.312	7.6±9.4	7.7±15	4.1±5.5
	Total	3.77±1.53	4.55±4.45	5.10±5.71	1.90±0.78	2.30±2.25	2.58±2.88	34±14	41±41	48±56
Understory	*Abies*	0.479±0.779	0.795±1.05	1.05±1.41	0.241±0.392	0.400±0.527	0.525±0.711	4.8±7.7	7.9±10	10±14
Vegetation	*Betula*	0.031±0.063	0.013±0.040	0.013±0.039	0.016±0.032	0.0068±0.021	0.0067±0.020	0.3±0.6	0.1±0.4	0.1±0.4
<2 cm DBH	*Picea*	1.71±2.09a	0.752±1.10ab	0.196±0.139b	0.875±1.07a	0.386±0.563ab	0.100±0.071b	14±17a	6.2±9.1ab	1.6±1.2b
	Other	2.46±3.21	1.06±1.18	1.57±2.67	1.23±1.61	0.527±0.586	0.779±1.32	20±27	8.6±10	12±21
	Total	4.68±4.44	2.62±1.73	2.83±3.96	2.36±2.24	1.32±0.873	1.41±1.97	39±37	23±15	25±34
Herbaceous		1.64±0.518	1.74±1.04	1.98±0.897	0.745±0.239	0.815±0.503	0.946±0.438	32±10	34±20	39±17
Understory total		10.0±4.90	8.91±4.95	9.90±6.84	5.00±2.49	4.43±2.50	4.94±3.44	105±41	99±48	112±64
Ecosystem total		313±102a	267±101ab	204±83.3b	151±49.7a	129±48.5ab	98.4±39.8b	675±198a	567±153ab	506±128b

Note: DBH, diameter at breast height.
*Different letters indicate statistical differences ($p < 0.05$) among elevation bands for each species or forest component.
†When there were no statistical differences, no letters were used.

Table 2. Predictive biomass equation for herbaceous vegetation in the form $y = ax$ where y is the species biomass (g), a is a coefficient, and x is the estimated percent cover.

Species	No. of observations	a	r^2	Standard error of estimate (g)
Aconitum uncinatum L.	7	1.293	0.980	0.076
Arisaema triphyllum (L.) Schott	12	0.504	0.760	0.085
Aster sp.	15	0.919	0.907	0.079
Chelone lyoni Pursh	13	1.439	0.794	0.211
Clintonia borealis (Ait.) Raf.	15	0.699	0.950	0.043
Cimicifuga americana Michx.	12	0.590	0.932	0.048
Dryopteris campyloptera Clarkson	16	1.257	0.883	0.118
Ageratina altissima var. *altissima* (L.) King & H.E. Robins	14	1.294	0.856	0.148
Galium triflorum Michx.	12	0.583	0.912	0.055
Grass	16	2.012	0.891	0.182
Houstonia serpyllifolia Michx.	12	1.246	0.973	0.063
Impatiens pallida Nutt.	13	0.865	0.872	0.096
Laportea canadensis (L.) Weddell	12	0.723	0.865	0.086
Lycopodium sp.	12	4.793	0.946	0.346
Monarda didyma L.	12	1.466	0.941	0.111
Moss	16	4.636	0.942	0.298
Oxalis montana Raf.	14	0.309	0.968	0.016
Prunella vulgaris L.	13	0.910	0.886	0.094
Rubus canadensis L.	15	9.108	0.900	0.811
Rudbeckia laciniata L.	12	2.395	0.965	0.138
Solidago glomerata Michx.	13	0.939	0.833	0.121
Sambucus racemosa var. *racemosa* L.	12	1.410	0.863	0.169
Rugelia nudicaulis Shuttlw. ex Chapman	21	0.979	0.960	0.045
Tiarella cordifolia L.	11	0.666	0.930	0.058
Trillium sp.	8	0.634	0.927	0.067
Viola sp.	12	0.403	0.972	0.021

Discussion

Distribution of biomass, carbon, and nitrogen in vegetation

The majority of biomass and C was contained in the overstory of this system. Biomass values in the lower elevations attained pre-BWA levels (>300 Mg·ha^{-1}), but aboveground biomass and C pools decreased sharply with increasing elevation where the BWA had a greater effect (Smith and Nicholas 1999). Recent forest recovery is also indicated by the higher overstory biomass than those reported around 20 years ago for nearby lower elevation (ST, 252–261 Mg·ha^{-1}) and middle elevation (SS, 223 Mg·ha^{-1}) (Johnson and Lindberg 1992).

Higher elevation spruce–fir stands contained less biomass than the lower elevations, even before the onset of the BWA, but present biomass levels at upper elevations are still at the very lowest of pre-BWA historic observations (200–310 Mg·ha^{-1}; Oosting and Billings 1951; Whittaker 1966). This elevational pattern is likely a result of the initial wave of fir mortality, heaviest at the higher elevations, and one would expect the loss of overstory biomass and C with elevation to be a response to the greater amounts of disturbance at higher elevations as well as the naturally lower historic levels of aboveground biomass and C in the higher elevations. Prevalence of fir increased with elevation while prevalence of birch decreased with elevation, a trend that is typical of southern Appalachian spruce–fir forests (Whittaker 1966).

In general, understory spruce biomass was concentrated in the lower elevations and fir seedlings and saplings in the higher elevations, reflecting pre-adelgid composition. However, the biomass of fir trees 2–5 cm DBH was greater than that of spruce even at the lower elevations. Balsam fir (*Abies balsamea* (L.)) is a prolific sprouter and responds well to release under a spruce midstory. It is possible that fir was able to claim understory positions before understory spruce was able to respond to the recent canopy openings, especially at the higher elevations where disturbances were most severe. These stands are currently well stocked with small fir trees, i.e., advanced regeneration is present, ensuring that fir will be an important component of future spruce–fir forests, at least until the next wave of BWA-induced mortality.

The shifts in composition and distribution of the small woody understory (<2 cm DBH) with elevation closely resemble the pre-BWA overstory distribution of spruce and fir, where spruce is more abundant at lower elevations, while fir dominates higher elevations (Oosting and Billings 1951; Whittaker 1956). This supports the hypothesis that this forest may be returning to pre-BWA conditions, at least in the immediate future, in absence of further BWA-induced mortality. The large amount of "other" species in the small woody understory size-class represents the abundance of shrubs and other small diameter woody plants across elevations.

The herbaceous biomass in NDW was substantially higher than values reported for various conifer systems (30–200 kg·ha^{-1}), and among the ecosystems cited by Muller

Table 3. Predictive biomass equation information for small woody understory vegetation in the form $y = \ln(a + bx)$, where y is the biomass, a is the intercept, b is the coefficient, and x is the stem caliper at 15 cm above ground level.

Species	No. of observations	a	b	r^2	Standard error of estimate (g)	Correction factor
Abies fraseri	10	3.199	1.144	0.780	0.215	1.02
Betula alleghaniensis var. *alleghaniensis*	8	1.148	2.435	0.879	0.368	1.07
Picea rubens	10	2.269	1.755	0.876	0.234	1.03
Viburnum lantanoides	10	1.512	2.143	0.930	0.207	1.02

(2003), only woody understory biomass in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) forests in Oregon (8700 kg·ha^{-1}) approximates our values. Though the herbaceous vegetation represented a rather insignificant amount of biomass, this stratum contained a far greater proportion of N-rich foliage and green stems, similar to an observation made by Welch et al. (2007) for the herbaceous layers in eastern deciduous forests. As a result, the herbaceous layer in this system contained a disproportionately high amount of N (4.7%–7.7% of the total N pool) and served a larger role in the storage of N than biomass.

Our understory biomass and N pools exceeded values recorded during IFS in the spruce–fir forest (5.8–8.7 Mg·ha^{-1} for biomass and 48–85 kg·ha^{-1} for the aboveground N pool) (Johnson and Lindberg 1992), indicating a denser understory and possibly signaling dynamic changes in ecosystem structure over the last two decades. Huber (2005) observed a similar temporal trend in understory biomass and N accumulation in the wake of massive Norway spruce [*Picea abies* (L.) Karst.] dieback caused by bark beetle attacks in Bavaria, Germany. As in this study, understory N pools in the German chronosquence study were substantially higher 15–20 years after the disturbance (100–126 kg N·ha^{-1}), compared with intact (65 kg N·ha^{-1}) or more recently disturbed spruce stands (44–66 kg N·ha^{-1}) (Huber 2005).

Despite large variations among individual ecosystem components, overall biomass and C and N content were remarkably similar among elevation bands. The coefficient of variation (CV) for overall biomass, 37%, was lower than the CV of individual forest components: overstory, 38%; small woody understory, 74%; large woody understory, 95%; herbaceous vegetation, 46%; and total understory, 56%. The CVs for N pools were lower, 27% for total N pools, and followed a trend similar to that of biomass.

Carbon and nitrogen fluxes

Net biomass production rates of this system (7.3–8.0 Mg·ha^{-1}·year^{-1}) were considerably higher than post-adelgid measurements at the Tower site (1.4–4.5 Mg·ha^{-1}·year^{-1}; Johnson and Lindberg 1992), and reached the high end of pre-BWA measurements (4.5–8.5 Mg·ha^{-1}·year^{-1}; Whittaker 1962, 1966). This would indicate that the overstory in this forest has recovered its productivity since the mid-1980s.

Though the overstory contained the vast majority (97%) of ecosystem biomass and C, it was responsible for only 77% of the ecosystem productivity, the majority as nonphotosynthetic tissues (bole, bark, and branches) with relatively long turnover time (i.e., C sequestration). Overstory uptake of N also increased since the Barker et al. (2002) estimates (from 7.8 kg·ha^{-1} in 1998 to 11.5 kg·ha^{-1} in 2003). Produc-

tivity increases in aggrading forests or after disturbance owing to the rapid expansion of foliage to capture critical light resources (Waring and Schlesinger 1985). The increased ability to take up N, an increase of 47% in 5 years, was another important sign that this system is recovering not only standing biomass and N but also ecosystem processes.

Understory played an important role in N cycling, accounting for two-thirds of annual aboveground N uptake, especially by the herbaceous layer. There is only limited published understory N uptake data against which to compare our estimates, but the 18–21 kg N·ha^{-1}·year^{-1} for the herbaceous uptake and 25–30 kg N·ha^{-1}·year^{-1} for total annual understory N uptake were within the range of values (8–106 kg N·ha^{-1}·year^{-1}) reported for eastern deciduous forests (Muller 2003). Compared with mature trees, the woody understory had a higher proportion of their mass as photosynthetic needles and leaves and were therefore more important to the N pools and fluxes in this system than to biomass. Herbaceous vegetation contained only a small proportion of total aboveground biomass (0.7%) and N (5.8%), but accounted for a disproportionately large amount of N uptake (51%) and was actually responsible for much of the annual N cycling in this forest. This was due to the fact that herbaceous vegetation must produce new aboveground tissue each year and this tissue contains a higher proportion of N-rich foliage compared with the other forest components. Through this seasonal biomass accumulation and turnover pulses, understory may stimulate internal N cycling (Welch et al. 2007) and curtail N leaching losses (Muller 2003). In Bavarian spruce forests subject to similar stressors and disturbances as the high-elevation spruce–fir in the Appalachians (high atmospheric N inputs and insect-induced dieback), Huber (2005) had similarly noted that while the net N uptake by understory vegetation was generally limited, this stratum nevertheless had a significant role in curtailing NO$_3$-N leaching losses. Lower NO$_3$ leaching in beech gaps at the Solling site in Germany was similarly associated with more abundant ground vegetation (Bauhus and Bartsch 1995). On the other hand, small amounts of biomass in the understory makes this vegetation stratum less important in terms of long-term sequestration of C or retention of N.

It appears that different elevation bands cycled biomass and nutrients differently. Similar to the pools, fir was more important to the sequestration of biomass and N at higher elevations, while birch showed the opposite trend. Overall, the overstory and the total live ecosystem uptake of N was significantly higher at the higher elevations, while biomass and C increments showed no trend with elevation.

The CV for ecosystem biomass production, 24%, is considerably lower than the CV of individual forest components: overstory, 35%; small woody understory, 95%; large

Table 4. Aboveground production of biomass and carbon and uptake of nitrogen (kg·ha^{-1}·year^{-1}) for different forest components at three different elevation ranges within the Noland Divide Watershed of Great Smoky Mountains National Park (±SD).

Elevation range	Species	Biomass (kg·ha^{-1}·year^{-1})			Carbon (kg·ha^{-1}·year^{-1})			Nitrogen (kg·ha^{-1}·year^{-1})		
		Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Overstory	*Abies*	280±800b*	550±754b	2480±2410a	137±393b	270±370b	1220±1180a	1.1±3b	2.1±2.9b	9.7±9.3a
Vegetation	*Betula*	1810±1870a	656±774b	220±395b	889±922a	321±380b	108±193b	4.1±4.1a	1.5±1.8b	0.5±0.9b
>5 cm DBH	*Picea*	3840±1610†	4050±2440	2840±1640	1830±769	1930±1160	1360±785	5.9±2.2	6±3	4.3±2.3
	Other	80±114	71±152	57±106	38±54	34±73	28±51	0.2±0.3	0.2±0.4	0.2±0.3
Overstory total		6010±1530	5320±2660	5600±1670	2900±748	2560±1280	2710±820	11.2±3.5b	9.8±4.6b	14.6±7.5a
Understory	*Abies*	173±140	208±293	335±495	87±70	105±147	168±249	1.7±1.4	2.1±2.9	3.3±4.9
Vegetation	*Betula*	11±46	29±49	20±43	5±24	15±25	10±22	0.1±0.4	0.3±0.5	0.2±0.4
2–5 cm DBH	*Picea*	101±116	124±228	107±128	52±59	64±117	55±65	0.8±1	1±1.9	0.9±1.1
	Other	93±116	93±189	48±61	46±58	47±94	24±31	0.8±0.9	0.8±1.5	0.4±0.6
	Total	377±153	455±445	510±571	190±78	230±225	258±288	3.4±1.4	4.1±4.1	4.8±5.6
Understory	*Abies*	48±78	79±105	104±141	24±39	40±53	53±71	0.5±0.8	0.8±1	1±1.4
Vegetation	*Betula*	3.1±6	1.3±4	1.3±4	1.6±3	0.7±2	0.7±2	0±0.1	0±0	0±0
<2 cm DBH	*Picea*	171±209a	75±110ab	20±14b	88±107a	39±56ab	10±7b	1.4±1.7a	0.6±0.9ab	0.2±0.1b
	Other	246±321	106±118	157±266	123±161	53±59	78±132	2±2.7	0.9±1	1.2±2.1
	Total	468±444	262±173	283±396	236±224	132±87	141±197	3.9±3.7	2.3±1.5	2.5±3.4
Herbaceous		880±303	925±538	1030±479	396±134	436±258	491±232	17.7±6.3‡	18.7±10.4‡	20.9±9.5‡
Understory total		1730±496	1640±706	1830±778	823±245	798±346	890±388	25.0±6.2	25.1±11.2	28.2±10.4
Ecosystem total		7730±1310	6970±2500	7430±1070	3720±638	3360±1210	3600±522	36.2±5.8b	34.9±10.4b	42.8±7.6a

*Different letters indicate statistical differences ($p < 0.05$) among elevation bands for each species or forest component.

†When there were no statistical differences, no letters were used.

‡Values include potential resorption.

woody understory, 79%; herbaceous vegetation, 46%; and total understory, 37%. Thus, the overall plot productivity appeared spatially more uniform than the productivities of the individual forest components or the distribution of standing biomass.

Estimates of productivity required several assumptions in the calculations. Error in overstory productivity (>5 cm DBH) is likely relatively small because we had discrete measurements at two time periods. The mass difference approach of determining production and uptake (Clark et al. 2001) was previously used in this watershed by Barker et al. (2002) in their analysis of variability in N pools and fluxes within the NDW, and it was necessary to use the same approach to compare our results with prior research. Production values for understory woody plants (<5 cm DBH) were determined using a BAR of 10, i.e., production was calculated as 10% of current biomass. This value was a conservative estimate based on the BAR of woody forest understory plants (Whittaker 1966, 1975; Alaback 1984). Actual production may have been somewhat higher depending on light and nutrient resources because of openings in the canopy. When estimating understory production, we assumed moss production to be one-third of live biomass following Tamm (1953). We further assumed that because *Rubus* is semelparous, it generally produces total plant biomass over the course of two seasons; annual production was one-half of the total standing biomass. Realistically, individual *Rubus* stems may sprout, flower, set seed, and die within 1 year or it may take 3–5 years depending on the individual. Hence, assuming that the value of production as 50% of standing stock may be an underestimate, but it seems to be the best available data.

Another source of potential error in our N uptake estimates is the resorption of nutrients between the aboveground and belowground portion of perennial herbaceous plants. Understory N uptake values may be overestimated because uptake rates calculated here are actually estimates of N requirement and assume that N requirement is met entirely by N uptake. In reality, N requirement could have been met by N stored in their root systems as well as N assimilation from the soil and atmosphere. We need to account for N resorption to more accurately assess uptake by perennial forbs. Resorption rates of N during drought periods have reached 31%–41% for grasses in a tallgrass prairie (Heckathorn and DeLucia 1994) and 58% for foliage of dry tropical tree species (Lal et al. 2001). Aerts (1996) performed a metalanalysis of nutrient resorption in forbs ($n = 33$) and determined an N resorption efficiency of 41%. Based on these studies, as well as the fact that not all understory species in the southern Appalachian spruce–fir forests are perennials, a broad assumption of 50% N resorption across all herbaceous species (annual and perennial) is probably a conservative estimate, as it is unlikely that herbaceous resorption would exceed that value. Even these conservative estimates of herbaceous N uptake (9.3 kg·ha^{-1}·year^{-1} at 50% resorption) still approach our estimates of overstory N uptake (11.5 kg·ha^{-1}·year^{-1}), and when other woody understory components are included, understory N uptake (16.3 kg·ha^{-1}·year^{-1}) exceeds the overstory estimates. Though the ability of the understory component of this system to permanently sequester N may be limited, its ability to take up and recycle large amounts of N may keep these nutrients on site and represents a dynamic mechanism of N retention. What is not known at this time is to what extent the high N deposition regime may alter the composition and the biogeochemical functioning of the understory in the future (see Gilliam 2006).

Conclusions

Nutrient cycling in this forest has changed, with 2003 overstory N uptake rates considerably higher than the 1998 rates reported by Barker et al. (2002). It appears that neither the BWA nor other disturbances have significantly suppressed productivity of this site; production values are as high as or higher than pre-adelgid values. The lower elevations of these forests appear to have completely recovered from the catastrophic effects of the BWA in terms of biomass and productivity. Upper elevation stands still have much recovery ahead of them, but the destructive effects of the BWA as well as subsequent windthrow mortality of exposed overstory spruce stems have passed for now. It is hypothesized that the overstory will not decline below present biomass and C levels in the near future, and that this stratum has indeed begun to rapidly sequester more biomass and C.

Though conducted in a small catchment, this research provides important insight into the C and nutrient dynamics of post-BWA southern Appalachian spruce–fir forests. The understory of this system, especially the herbaceous layer, is very important to the overall productivity of this system. It serves a vital role in cycling nutrients as well as keeping nutrients on site. Though this understory offers little long-term storage of C, biomass, and nutrients, the continual uptake and cycling of N are preventing additional N from being leached to stream water. As this forest recovers its overstory stand dynamics, the relationships between overstory and understory communities may shift. Future work should address the relationships between overstory, understory, and site variables to determine how nutrient cycling in this forest may change in the future.

Acknowledgements

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