



Short communication

Tree biomass and net increment in an old aspen forest in New Mexico

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Abstract

Previous work indicated that net ecosystem production (NEP) was negative in a 90-year-old aspen (*Populus tremuloides* Michx.) forest in the Tesuque watershed of northern New Mexico. The loss of nitrogen (N) in streamwater was very low for this forest, which would be surprising if NEP were negative for a substantial period. We remeasured live tree biomass of this case-study forest after an additional 27 years of growth, as a long period with negative NEP would likely demonstrate declining live tree biomass. Contrary to expectation, live tree biomass increased substantially through this period (averaging $1.37 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). The net increment for this period was relatively high (within 10% of the mean annual increment) well into the second century of stand development in this high-elevation aspen forest. We conclude that the high retention of N was not anomalous given the later increase in live tree biomass, and we expect that NEP had not remained negative for a long period.

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Trends in biomass accumulation in old forests are interesting for at least three reasons. Forest stand development forms the foundation of our expectations of long-term changes in forest ecosystems; basic changes in demography, tree size, and growth comprise classic descriptors of change in managed and unmanaged forests. More recently, the role of forests as sinks and sources of carbon (C) leads to

important questions about rates of change in forests through stand development (Roy et al., 2001): do old forests gain or lose C? Trends in biomass accumulation in old forests are also important for understanding controls on ecosystem nutrient retention: would old forests with little or no accumulation of biomass retain nutrients effectively (Vitousek and Reiners, 1975)?

More than 20 years ago, Gosz (1980a) pointed out that the connection between net ecosystem aggradation of biomass and nutrient retention has been difficult to test critically, because most ecosystems show a positive net ecosystem production (NEP, the

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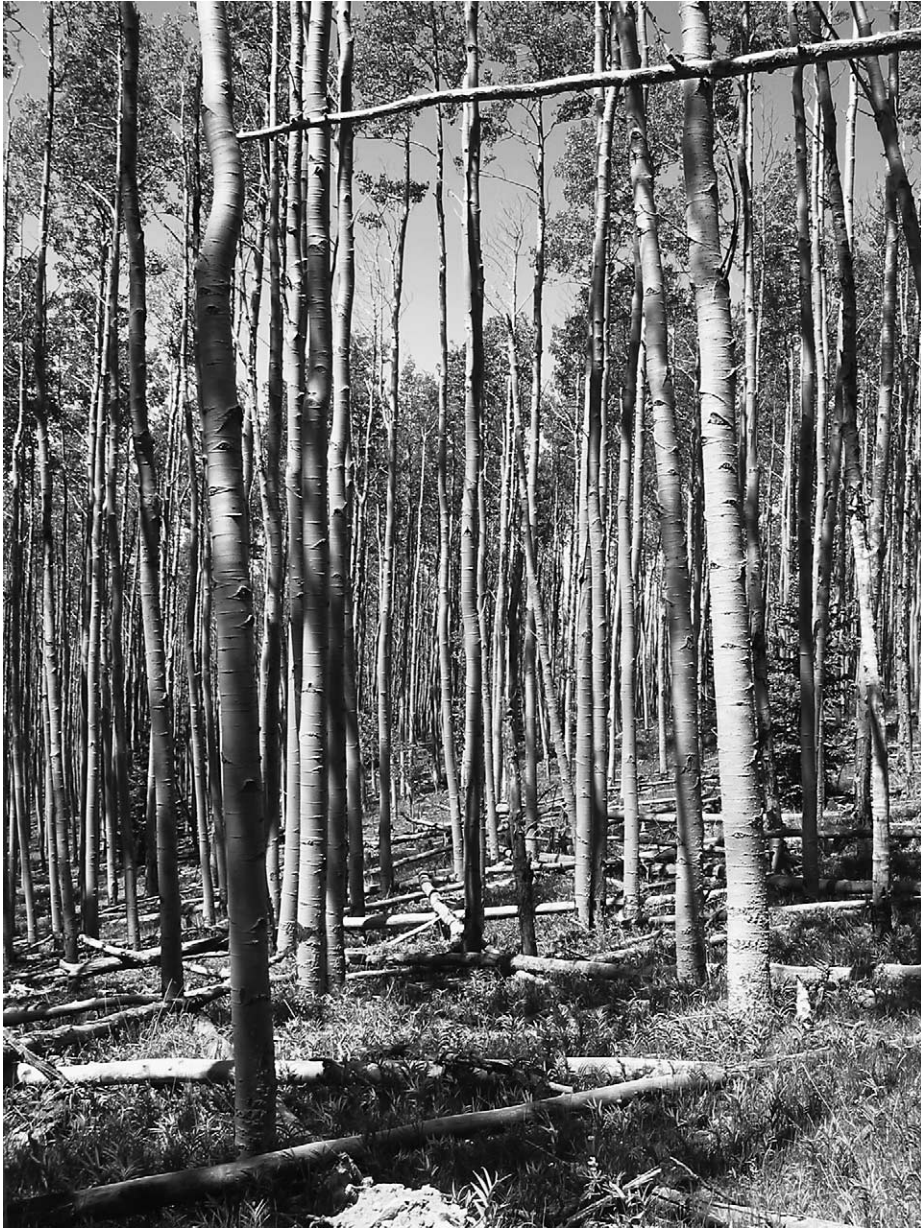


Fig. 1. Image of 123-year-old aspen forest, showing substantial woody debris as a result of high mortality over previous 3 decades.

net change in organic matter in the forest) except in times of major disturbances such as fires. Gosz (1980a) hypothesized that a 95-year-old aspen forest (*Populus tremuloides* Michx.) in the Tesuque watershed of New Mexico may have had rates of tree mortality and heterotrophic respiration that exceeded the slow growth rate of surviving trees,

giving a negative rate of NEP. Over a 5-year period, the estimated rate of NEP by Gosz was on the order of $-2.0 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ($-1.0 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$), at a time when the total stem biomass was on the order of 115 Mg ha^{-1} (60 Mg C ha^{-1}). Despite apparently negative rates of NEP, the watershed showed remarkably low rates of nitrogen (N) loss in stream

water and trace gas flux, amounting to less than $0.15 \text{ g N m}^{-2} \text{ yr}^{-1}$ compared with atmospheric deposition of $0.35\text{--}0.65 \text{ g N m}^{-2} \text{ yr}^{-1}$ (Gosz, 1980a,b; Stark et al., 2002).

As a first step in a project to examine the mechanisms of strong retention of N despite negative NEP, we remeasured the live tree biomass in this aspen-dominated watershed 27 years after Gosz's (1980a) characterization. We expected that live tree biomass would have declined over time, and if this were true, then it would be worthwhile to verify that NEP was also negative, and to examine controls on nutrient retention in an old, non-aggrading ecosystem. If live tree biomass had increased, then we expected NEP would be more likely to be near 0 or positive, and the strong retention of N would not be unexpected.

1. Site description and methods

The 3.4 ha watershed is the Tesuque watershed of the Sangre de Cristo Mountains in the Santa Fe National Forest in northern New Mexico (Gosz, 1980a, 1980b; Vitousek et al., 1982; Stark and Hart, 1997; Stark et al., 2002). This forest was used as a reference watershed for manipulations in adjacent watersheds (such as cutting 25% of the trees in a dispersed or block design). Precipitation ranges from 500 to 750 mm yr^{-1} , with 100–250 mm of stream runoff. The soil is a Medio cobbly loam series of typic Cryocrepts developed from the Embudo granite formation. The watershed ranges from 3110 to 3230 m in elevation, and was within the perimeter of a large, stand replacing fire in 1880 (E. Margolis and T. Swetnam, personal communication). Establishment of other trees has been limited to fewer than 25 spruces (*Picea engelmannii* Parry ex. Engelm.) per hectare.

The original sampling design was based on a systematic grid with plot centers at a spacing of 25 m \times 25 m, giving 55 cells across the watershed. The biomass of each grid cell was estimated in 1971 (age 91 years) and 1976 (96 years) based on the diameters of trees within a square 0.01 ha plot in the center of each cell, and biomass regression equations determined from trees in an adjacent watershed (Gosz, 1980a). Some aspen suckers have developed periodically within the watershed, but few survived the

browsing by elk over the past few decades. The resampling in 2003 (Fig. 1, age 123 years) used 27 plots (circular 0.01 m²) arrayed across the watershed, and the same regression equations. We note that some of the live aspen trees had rotted heartwood, but the use of the same regression equation at all points in time would provide valid biomass estimates as long as the incidence of heartrot (within diameter classes) had not changed over time. If the incidence of heart rot had increased (within each diameter class), then the net increment of wood would be overestimated. The hypothesis of a net reduction in live tree biomass was tested with a 1-tailed *t*-test of the 2003 values versus the mean from the 1976 sampling.

2. Results and discussion

The forest had 3070 trees ha^{-1} , with a total aboveground mass of 148 Mg ha^{-1} in 1971 (Fig. 2). Density declined by 26% (to 2270 trees ha^{-1}) by 1976, but the gross increment matched the mortality, leaving total live tree mass at 149 Mg ha^{-1} . Over the next 27 years, density declined to just 900 trees ha^{-1} , while live tree mass increased to 186 Mg ha^{-1} . The spatial variation among 100-m² plots increased over time, with coefficients of variation of about 35% in the 1970s to 50% in 2003. The live tree mass in 2003 was significantly greater than in 1976 ($P = 0.02$), refuting the hypothesis that live tree mass declined. We did not measure the mass of dead wood in the forest, but it was apparent from more than 30 years of familiarity with this stand that dead wood mass likely increased substantially by 2003 (see Fig. 1).

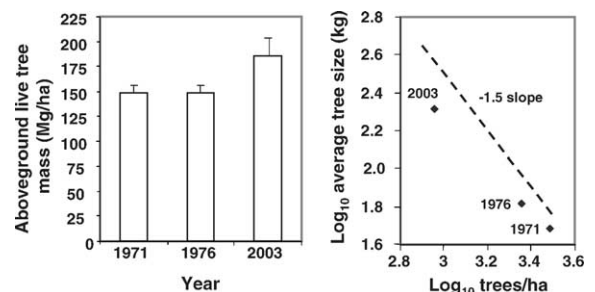


Fig. 2. Aboveground live tree mass at three ages (left; with standard error bars), and the self-thinning pattern (right, solid line is -1.5 slope for reference).

The annual net increment of live tree mass was about $1.37 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ from age 96 to age 123 years, which is within 10% of the mean annual increment (MAI) of $1.51 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. The MAI of aspen stands in the southwestern United States typically show a long plateau; Site Class 2 stands (such as this Tesuque forest) are expected to have an MAI within 10% of the rotation maximum from about age 60–130 years (Jones et al., 1985). Old aspen forests continue to accrue live stem mass well into their second century, despite declining current annual increments.

The high rates of mortality may appear to indicate the stand had become “decadent” early in its second century of stand development, but the mortality was concentrated in the smaller size classes. The slope of the “self-thinning” curve of the logarithm of the average tree size as a function of the logarithm of tree density was relatively steep (-1.2 , $r^2 = 0.99$, $P = 0.02$), indicating that mortality was not restricted to the larger size classes. Contrary to expectations from three decades earlier, the aspen stand appeared to be developing normally with long-term gross increment continuing to exceed mortality.

The future development of this forest is difficult to predict. If the majority of the overstory aspen died over the next few decades, the near absence of a coniferous understory would lead to a very low-density forest. Alternatively, episodic sprouting of new shoots from existing aspen root systems could lead to a second generation of aspen if the browsing pressure by elk were reduced.

Given a positive net increment of live tree mass, we expect that the overall NEP was likely positive as well. A positive NEP may be expected to provide a strong capacity for retaining limiting nutrients (Vitousek and Reiners, 1975), so the high net retention of N in this aspen forest was not anomalous. If the NEP was truly negative 3 decades ago, we expect this was a transient condition (given the return to positive NEP), and any period of negative NEP was too short to impair the N retention capacity in this forest.

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