

Aboveground net primary production decline with stand age: potential causes

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It is well known to ecologists and forest managers that in mature forests aboveground biomass production declines as trees age. Forest age-sequence studies reveal that aboveground net primary production (ANPP) reaches a peak early in stand development and then gradually declines by as much as 76%, with a mean reduction of 34% (Table 1, Refs 1–13). The greatest declines occur in boreal and in cold temperate forests, and in a very infertile tropical forest in Amazonia. The rate and cause(s) of the decline are relevant to ecosystem ecology, forest management, and global carbon (C) budget issues. Changes in net primary production (NPP) affect C and nutrient cycling characteristics of forests. If the decline is sharp, forest managers will harvest forests on short rotations, increasing site disturbance and depletion of soil nutrients. The decline of ANPP in ageing forests is important to the global C budget because forests account for 90% of C contained in terrestrial ecosystems and 65% of terrestrial NPP

(Ref. 14). Stand-age distribution data have been incorporated in recent inventory-based estimates of global forest C storage¹⁵ but current simulation models of global terrestrial C production fail to incorporate the primary mechanisms for the age-related decline of forest ANPP (Refs 16–18). This omission is a concern because modeled global C budgets will be inaccurate unless models correctly represent the causes and magnitudes of forest decline.

Although the age-related decline of forest ANPP is a seemingly universal phenomenon, its ecophysiological cause(s) has not been examined rigorously until recently. Initially, the decline was attributed to an altered C balance (Hypothesis 1, H1) resulting from increasing respiratory costs and stable or decreasing C assimilation¹⁹. More recently, two other hypotheses have been proposed: nutrient limitation^{20–23} and stomatal constraint^{4,24,25}. Here, we review empirical data supporting each hypothesis and discuss a model-based synthesis²³ of causes for declining ANPP of mature stands in contrasting climates.

Hypotheses to explain ANPP decline with stand age

Before examining the three hypotheses, it is useful to review briefly several age-related changes in stand structure that have direct bearing on reduced ANPP in ageing stands. Most notable is the steady increase in woody biomass long after leaf area peaks (Fig. 1); however, it is less clear how the fraction of living woody biomass (i.e. sapwood)

Aboveground net primary production (ANPP) commonly reaches a maximum in young forest stands and decreases by 0–76% as stands mature. However, the mechanism(s) responsible for the decline are not well understood. Current hypotheses for declining ANPP with stand age include: (1) an altered balance between photosynthetic and respiring tissues, (2) decreasing soil nutrient availability, and (3) increasing stomatal limitation leading to reduced photosynthetic rates. Recent empirical and modeling studies reveal that mechanisms (2) and (3) are largely responsible for age-related decline in ANPP for forests in cold environments. Increasing respiratory costs appear to be relatively unimportant in explaining declining productivity in ageing stands.

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changes during stand development. This issue is critical to understanding why forest productivity decreases during stand development (see below). A second feature is that foliage mass declines in many forests as they mature²¹; it has been speculated that reduced nutrient availability is partly responsible^{20–22}.

Although hypotheses regarding changes in C flow during stand development were first published almost 30 years ago²⁶, few studies have tested these hypotheses, or examined the underlying causes. One reason for the lack of experimental tests is that it is difficult to measure each of the major components of the C budget [e.g. NPP, autotrophic respiration, and their sum gross primary production (GPP)] for a large-stature, mature forest, much less for several stands comprising a forest age-sequence. In most studies, the relationship between GPP and stand development is derived from forest ecosystem process models^{4,23}. These models predict that GPP is very low following a major disturbance

and increases in proportion to leaf area index (LAI) to a maximum at or soon after canopy closure, after which GPP either stabilizes or slowly declines, depending upon how LAI changes.

Hypothesis 1: Photosynthesis–respiration imbalance

Kira and Shidei¹⁹ hypothesized that the decline in NPP with stand age was due to an altered balance between respiring and photosynthetic tissue. Biomass components that could be responsible for increased maintenance respiration include foliage, vascular cambium and/or sapwood. Of these tissues, foliage has the highest respiratory costs²⁷, but is unlikely to explain the decline in ANPP because foliage mass commonly remains stable or declines with stand age (Fig. 1). The maintenance respiration rate of phloem is high, but the amount of phloem is directly proportional to branch and stem surface areas, which stabilize or decline in older forests³. The assertion that increasing sapwood respiration is the cause for ANPP decline with stand age has been undermined by recent observations that it represents a small percentage (5 to 10%) of annual stand C budget^{4,28}, and that it increases little after canopy closure⁴. For example, in a lodgepole pine (*Pinus contorta*) age-sequence⁴, maintenance respiration for woody tissue increased by 18 g C m⁻² yr⁻¹ between 40-year-old and 245-year-old stands, whereas wood production and associated construction respiration decreased by 164 g C m⁻² yr⁻¹.

Hypothesis 2: Nutrient limitation

A second plausible explanation for the decline in ANPP is that nutrient limitation increases during stand development, particularly nitrogen (N) since it most commonly limits forest growth. In general, N mineralization and nitrification rates decrease during secondary succession²⁹. The decline is strongly controlled by litter decomposition which, in turn, is controlled by environmental conditions and chemical and physical characteristics of litter. One important stand-age effect is that the ratio of leaf:woody detritus input (with low and high C:N ratios, respectively) gradually decreases during stand development; this pattern has been observed for boreal needle-leaved evergreen, temperate needle-leaved evergreen, and temperate broad-leaved deciduous forests³⁰. A second stand-age effect is the accumulation of woody litter, which slows decomposition due to its low surface area:volume ratio compared with fine litter. The reductions in litter quality during stand development increase N immobilization during litter decomposition, which in turn decreases net N mineralization as stands age^{31,32}. A positive feedback between the vegetation and soil could exacerbate the decline of N availability during stand development. Both plant nutrient requirement and uptake peak near canopy closure, but uptake rates decline more rapidly than requirement, suggesting that retranslocation (the removal of nutrients from ageing tissue) increases in importance during stand development³⁰. Retranslocation of N from senescing foliage increases the C:N ratio of leaf detritus, lowering litter quality and further increasing N limitation³³.

Declining N availability during stand development adversely affects leaf photosynthesis and LAI, with the latter resulting in decreased light interception and GPP (Ref. 34). Increased N limitation also results in a relative shift in biomass allocation from aboveground tissues to fine root and mycorrhizal NPP (Refs 35,36). A major limitation of published forest age-sequence studies is that none includes estimates of fine root and mycorrhizal NPP, preventing the detection of shifts in biomass allocation. This mechanism should be addressed in future studies.

Hypothesis 3: Stomatal constraint

The newest hypothesis, thoroughly reviewed by Ryan and Yoder²⁵, is that as trees age, the stem height and length of their branches increases, leading to increased hydraulic resistance owing to a greater path length. Recent research by Sperry and colleagues³⁷ has demonstrated that trees decrease stomatal conductance to maintain a plant water status above a critical threshold that causes permanent cavitation of the water transport cells. A decrease in stomatal conductance caused by hydraulic constraints may decrease canopy photosynthesis because photosynthesis and stomatal conductance are tightly coupled³⁸. Ryan and

Waring⁴ used a forest ecosystem process model to simulate the C balance of young and old lodgepole pine stands, and obtained good agreement between modeled and measured ANPP when they assumed that maximum canopy photosynthetic rate declined by 18% for the old-growth stand. They hypothesized that the decline of ANPP is due to the reduced photosynthetic capacity of mature trees. Their hypothesis was corroborated by Yoder *et al.*²⁴, who found that photosynthetic rates were 14–30% lower and that stomata closed earlier in the day for mature rather than young lodgepole pine and ponderosa pine (*Pinus ponderosa*) trees. These findings were supported by measurements of stable C isotope ratio (¹³C/¹²C) for foliage and stem tissues; carboxylating enzymes involved in photosynthesis discriminate against the heavier C isotope (¹³C), with discrimination decreasing as the leaf mesophyll CO₂ concentration decreases. This situation commonly occurs when photosynthesis is limited more by stomatal conductance than by carboxylating enzyme activity.

Sensitivity analysis using a forest ecosystem process model

Comparative and experimental studies for forests in different climates provide support for each of the hypotheses discussed. Is it possible that the importance of the three proposed mechanisms varies depending upon climate? It might be expected that the altered C balance mechanism (H1) is more likely to constrain NPP of old stands in warm climates²⁸ since for conditions in which trees normally occur, respiration increases exponentially with temperature, whereas photosynthesis increases linearly with temperature up to some optimum and then remains constant. Conversely, nutrient limitation (Hypothesis 2, H2) might be most prevalent for boreal forests due to the adverse effects of low soil temperature on decomposition. Because of the complexity of forest ecosystem processes, the only way to evaluate effectively the relative importance of these hypotheses is

Table 1. Aboveground net primary production (ANPP) for forest age-sequence studies in contrasting climates

Biome/Species	Location	Range of stand ages, in years (no. of stands shown in brackets)	ANPP (t dry mass ha ⁻¹ yr ⁻¹)			Refs
			Peak	Oldest	%Change*	
Boreal						
<i>Larix gmelinii</i>	Yakutsk, Siberia	50–380 (3)	4.9	2.4	-51	1
<i>Picea abies</i>	Russia	22–138 (10)	6.2	2.6	-58	2
Cold temperate						
<i>Abies balsamea</i>	New York, USA	0–60 (6)	3.2	1.1	-66	3
<i>Pinus contorta</i>	Colorado, USA	40–245 (3)	2.1	0.5	-76	4
<i>P. densiflora</i>	Mt Mino, Japan	18–390 (7)	16.1	7.4	-54	5
<i>Populus tremuloides</i>	Wisconsin, USA	8–63 (5)	11.1	10.7	-4	6
<i>P. grandidentata</i>	Michigan, USA	10–70 (6)	4.6	3.5	-24	7
<i>Pseudotsuga menziesii</i>	Washington, USA	22–73 (4)	9.3	5.1	-45	8
Warm temperate						
<i>Pinus elliottii</i>	Florida, USA	2–34 (6)	13.2	8.7	-34	9
<i>P. radiata</i>	Puruki, NZ (Tahi)	2–6 (5)	28.5	28.5	0	10
	(Rua)	2–7 (6)	29.2	23.5	-20	10
	(Toru)	2–8 (7)	31.1	31.1	0	10
Tropical						
<i>Pinus caribaea</i>	Afaka, Nigeria	5–15 (4)	19.2	18.5	-4	11
<i>P. kesiya</i>	Meghalaya, India	1–22 (9)	30.1	20.1	-33	12
Tropical rainforest	Amazonia	1–200 (8)	13.2	7.2	-45	13

*Minus sign denotes a decrease in ANPP.

^bContinuous measurements being taken.

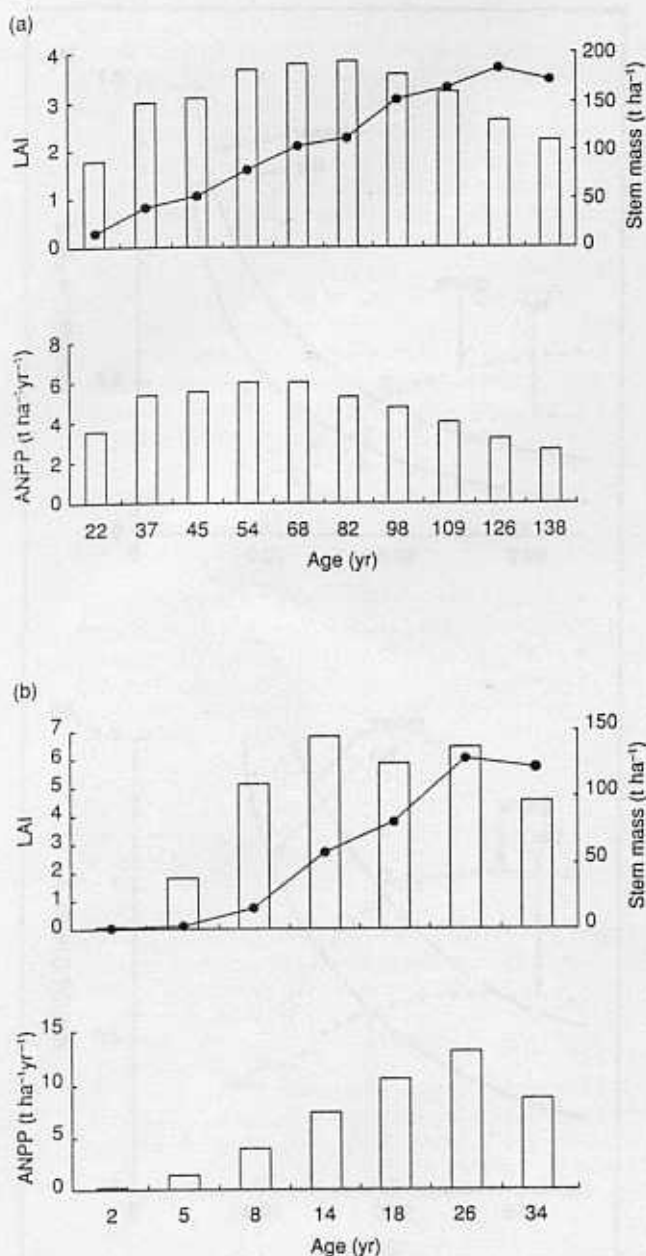


Fig. 1. Measured aboveground stem mass (filled circles), leaf area index (LAI) and aboveground net primary production (ANPP) for age-sequences of (a) boreal needle-leaf evergreen conifer (*Picea abies*)², and (b) a warm-temperate needle-leaf evergreen conifer (*Pinus elliottii*)⁹ age sequence.

through the use of ecosystem models integrating the key mechanisms.

This approach has recently been employed using the G'DAY model (see Box 1) to examine the relative contributions of altered C balance, N availability and stomatal constraint to the observed decline in NPP in ageing stands of lodgepole pine²³. The study adopted a graphical analysis involving the estimation of so-called photosynthetic and N-availability constraints to NPP (Box 1). The constraint curves are illustrated in Fig. 2a for a young (40 yr) and old (245 yr) subalpine lodgepole pine stand growing on infertile soil in Colorado, USA⁴. Both constraint curves change with age. The photosynthetic constraint curve is lower for the older

Box 1. The G'DAY model

G'DAY is a process-based, forest ecosystem model that simulates N cycling and the accumulation of tree biomass, litter and soil organic matter²⁴. G'DAY incorporates all three of the above ageing mechanisms²³. Hypothesis 1 is incorporated through equations that evaluate changes in maintenance respiration for foliage, fine roots and wood during stand development, including the effect of increased sapwood volume. The soil model in G'DAY simulates N availability using equations for the formation and decomposition of litter, and soil organic matter, including woody litter which accumulates during stand development (Hypothesis 2). The age effect on stomata is incorporated in equations for photosynthesis (Hypothesis 3).

When G'DAY simulates the growth of a newly established forest, some model compartments equilibrate rapidly (so-called 'fast variables', such as foliage, fine roots, leaf and root litter, and labile soil pools), while other pools change more gradually (such as recalcitrant soil organic matter, wood and woody litter). We learn a great deal about the model through an analysis of this 'fast variable' equilibrium. This analysis involves equating N and C fluxes into and out of the fast pools, which leads to two conservation equations: the so-called photosynthetic and N availability constraints to production^{26,29}. Constraint curves for young and old lodgepole pine stands (*Pinus contorta*) are displayed in Fig. 2a as graphs relating net primary production (NPP) to foliar N:C ratio²³. The photosynthetic constraint curve, representing the NPP achieved if C is conserved at the equilibrium, increases with foliar N:C ratio, for forests with sub-optimal leaf N concentrations. The N-cycling constraint, representing the NPP achieved if N is conserved, has a negative slope because soil N availability declines with increasing foliar N:C, owing to increased N immobilization in wood and soil²⁹. The NPP of the young and old stands is represented graphically by the intersections of the two constraint curves in Fig. 2a (i.e. the points where both C and N are conserved).

stand owing to its higher sapwood respiration rate and reduced photosynthetic rate (H1 and Hypothesis 3, H3). The N availability constraint is lower for the older stand because of its higher belowground allocation and because of increased N immobilization during decomposition of accumulated woody litter. NPP predicted by the model is obtained from the intersection of the photosynthetic and N availability constraint curves (intersections 1 and 2 for the old and young stands, respectively). Thus, in Fig. 2a, modeled NPP for the young and old stands are 0.45 and 0.30 kg C m⁻² yr⁻¹, respectively, representing a 35% decline in NPP with age; these results closely agree with measured values of 0.47 and 0.25 kg C m⁻² yr⁻¹.

The contribution of each hypothesized mechanism to the overall NPP decline can be quantified by evaluating the constraint curves with only that mechanism (e.g. H1, H2 or H3) incorporated into G'DAY. Table 2 lists responses to all three hypotheses: increased sapwood respiration, reduced N availability, and stomatal limitation. Under the assumption that maximum photosynthetic rate and respiratory costs are identical in the young and old stands, but that they differ in accumulated woody litter and belowground allocation, modeled NPP is 23% lower for the old stand. This percentage represents the decline due to H2 alone, and can be further divided into percentages associated with woody litter accumulation (13%) and altered allocation (11%). The NPP decline associated with increased stomatal constraint (H3) is 14%, while only a 3% decline is attributed to increased sapwood respiration (H1). Table 2 indicates that no single hypothesis can completely explain the NPP decline, but it is largely due to reduced N availability (23%) and lower maximum photosynthetic rate (14%).

The approach can also be used to examine the effects of climate on the relative importance of the three hypotheses for NPP decline with age. Figure 2b shows results for a warm site with mean annual temperature of 27°C and a growing

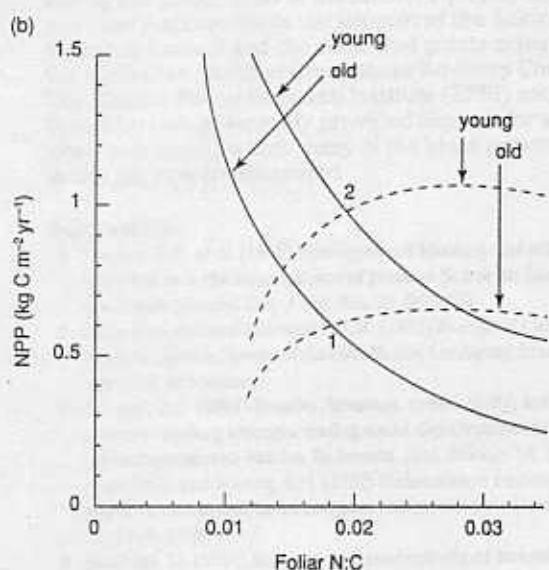
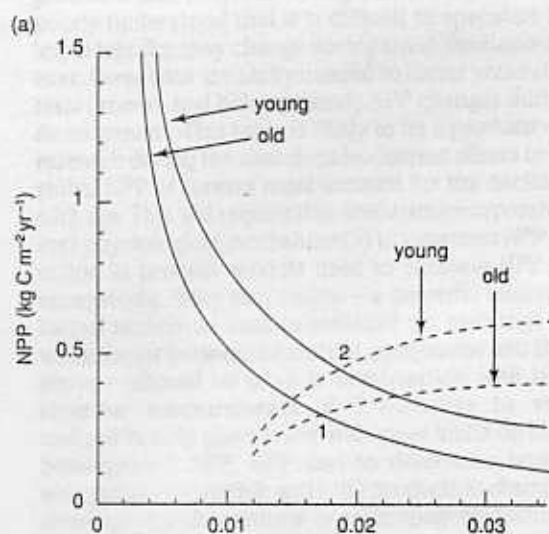


Fig. 2. Graphical analysis of the photosynthetic constraints (dashed lines) and N availability constraints (solid lines) on net primary production (NPP) for stands in (a) cool and (b) warm environments with mean annual air temperatures of 3.8 and 27°C, respectively, soil temperatures of 4.0 and 22°C, and growing season incident PAR (photosynthetically active radiation) of 1.2 and 4.0 GJ m⁻² yr⁻¹, respectively. Constraint curves shown in (a) were derived by parameterizing G'DAY (see Box 1) for 40- and 245-year-old stands of lodgepole pine (*Pinus contorta*). Parameters differing between the young and old stands are sapwood volume (43% higher for the old stand), photosynthetic rate (16% lower for the old stand), woody litter (zero for the young stand), and C partitioning coefficients (i.e. foliage:wood:fine roots = 0.16:0.42:0.42 and 0.19:0.23:0.58, for the young and old stands, respectively).

season incident PAR (photosynthetically active radiation) of 4.0 GJ m⁻² (cf., 3.8°C and 1.2 GJ m⁻², respectively, for the lodgepole pine stand). The temperature increase affects simulated maintenance respiration and decomposition rates, while the higher radiation affects GPP; the net effect is that both the photosynthetic and N availability constraint curves are higher for the warm site (Fig. 2b) than their counter-

Table 2. Modeled percentage NPP decline between young and old forest stands in cool and warm climates resulting from the three major hypotheses for declining NPP: increasing sapwood respiration (H1), reduced nitrogen (N) availability (H2), and increased stomatal constraint (H3)

Hypothesis included in model	Cool site		Warm site	
	Sapwood C content of old stand			
	low ^a	high ^b	low ^a	high ^b
	Percentage decrease in NPP between young and old stands			
Cumulative effects (H1 + H2 + H3)	35	38	38	42
Sapwood respiration (H1)	3	9	4	14
N availability (H2)	23	22	22	* ^c
Woody litter accumulation ^d	13	11	9	*
Shift in C allocation ^d	11	9	14	*
Stomatal constraint (H3)	14	14	17	19

^aSapwood C content for young and old stands (4.1 and 5.9 kg C m⁻², respectively).

^bSapwood C content for young and old stands (4.1 and 9.6 kg C m⁻², respectively).

^cThe percentage is not given because constraint curves do not intersect for the young stand.

^dThe decline due to reduced N availability (H2) is separated into percentages associated with woody litter accumulation and altered allocation. Results are presented with sapwood carbon (C) content as measured at the 245-year-old lodgepole pine stand, and for a hypothetical stand with higher sapwood C content.

parts at the cold site (Fig. 2a). The predicted NPP for the young and old stands in the warm environment are 0.98 and 0.62 kg C m⁻² yr⁻¹, respectively (Fig. 2b). Of the 38% decline in NPP, the reductions due to respiration, N availability and maximum photosynthetic rate are 4%, 22% and 17%, respectively, compared with 3%, 23% and 14% for the cold site. Expressed on a relative basis, the old and young stands show similar NPP differences in the two environments and similar contributions from the three mechanisms. However, there is a tendency for N availability to be more important at the cool site and for sapwood respiration and stomatal constraint to be more important at the warm site. One notable difference between the sites is that N immobilization in woody litter is more important at the cool site (13% NPP decline compared to 9% at the warm site), whereas increased belowground allocation is more important at the warm site (Table 2).

The results above suggest that nutrient availability is marginally more important at the cool sites and that woody respiration contributes little to the decline of NPP at either site. But those results are based on a single parameterization of G'DAY for infertile lodgepole pine stands whose sapwood biomass increases relatively little after canopy closure (sapwood C of 4.1 and 5.9 kg C m⁻² at ages 40 and 245 years, respectively). If we assume instead that sapwood biomass is much higher in the old stand (9.6 kg C m⁻²), woody respiration accounts for a higher proportion of the decline of NPP [9% and 14% in the cold and warm environments, respectively (Table 2)].

Conclusion

There is still an incomplete understanding of the factor(s) controlling C exchange between forest ecosystems and the atmosphere. Evidence from recent empirical and modeling studies suggests that decreased nutrient availability and enhanced stomatal limitation are the major causes for the aboveground NPP decline as stands age. Sapwood respiration costs are important only if sapwood biomass

continues to accumulate as stands mature. Changes in below-ground C and N cycles during stand development are so poorly understood that it is difficult to speculate how this important flux may change during stand development; however, these data are badly needed to better understand how total (above- and belowground) NPP changes during stand development. This topic is likely to be a productive area of research during the next decade. Current efforts to estimate global NPP of forests must account for the decline in NPP with age. This will require that scientists incorporate the correct physiological mechanism(s) to constrain NPP and allocation in process models used to simulate NPP of forest ecosystems. Eddy correlation – a powerful micrometeorological technique used to measure net exchange of C and water vapor between terrestrial ecosystems and the atmosphere – should be used in combination with traditional chamber measurements of C exchange by vegetation and soil to help place lower and upper limits on above- and belowground NPP, GPP and to determine how the net ecosystem (vegetation and soil) production changes during development after natural or anthropogenic disturbances.

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