REVIEW

Carbon allocation in forest ecosystems

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Abstract

Carbon allocation plays a critical role in forest ecosystem carbon cycling. We reviewed existing literature and compiled annual carbon budgets for forest ecosystems to test a series of hypotheses addressing the patterns, plasticity, and limits of three components of allocation: *biomass*, the amount of material present; *flux*, the flow of carbon to a component per unit time; and *partitioning*, the fraction of gross primary productivity (GPP) used by a component. *Can annual carbon flux and partitioning be inferred from biomass?* Our survey revealed that biomass was poorly related to carbon flux and to partitioning of photosynthetically derived carbon, and should not be used to infer either. *Are component fluxes correlated?* Carbon fluxes to foliage, wood, and belowground production and respiration all increased linearly with increasing GPP (a rising tide lifts all boats). Autotrophic respiration was strongly linked to production for foliage, wood and roots, and aboveground net primary productivity and total belowground carbon flux (TBCF) were positively correlated across a broad productivity gradient. *How does carbon partitioning respond to variability in resources and environment?* Within sites, partitioning to aboveground wood production and TBCF responded to changes in stand age and resource availability, but not to competition (tree density). Increasing resource supply and stand age, with one exception, resulted in increased partitioning to aboveground wood production and decreased partitioning to TBCF. Partitioning to foliage production was much less sensitive to changes in resources and environment. Overall, changes in partitioning within a site in response to resource supply and age were small ($<15\%$ of GPP), but much greater than those inferred from global relationships. Across all sites, foliage production plus respiration, and total autotrophic respiration appear to use relatively constant fractions of GPP – partitioning to both was conservative across a broad range of GPP – but values did vary across sites. Partitioning to aboveground wood production and to TBCF were the most variable – conditions that favored high GPP increased partitioning to aboveground wood production and decreased partitioning to TBCF. *Do priorities exist for the products of photosynthesis?* The available data do not support the concept of priorities for the products of photosynthesis, because increasing GPP increased all fluxes. All facets of carbon allocation are important to understanding carbon cycling in forest ecosystems. Terrestrial ecosystem models require information on partitioning, yet we found few studies that measured all components of the carbon budget to allow estimation of partitioning coefficients. Future studies that measure complete annual carbon budgets contribute the most to understanding carbon allocation.

Nomenclature:

ANPP = aboveground net primary production; can refer to foliage ($\text{ANPP}_{\text{foliage}}$), wood ($\text{ANPP}_{\text{wood}}$), or total ($\text{ANPP}_{\text{total}} = \text{ANPP}_{\text{foliage}} + \text{ANPP}_{\text{wood}}$)

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$$BNPP_{root} = \text{belowground net primary production in roots}$$
$$F_a = \text{aboveground litterfall}$$
$$F_{soil} = \text{soil-surface } CO_2 \text{ efflux ('soil respiration')}$$
$$GPP = \text{gross primary production}$$
$$NPP = \text{net primary production } (ANPP_{total} + BNPP_{root})$$
$$R = \text{autotrophic respiration; can refer to foliage } (R_{foliage}), \text{ wood } (R_{wood}), \text{ roots}$$
$$(R_{root}), \text{ aboveground } (R_{above} = R_{foliage} + R_{wood}), \text{ or total } (R_{total} = R_{above} + R_{root})$$
$$TBCF = \text{total belowground carbon flux } (BNPP_{root} + R_{root} + C \text{ to root exudates and}$$
$$\text{mycorrhizae})$$

Introduction

Carbon allocation plays a critical role in forest ecosystem carbon cycling by shifting the products of photosynthesis between respiration and biomass production, ephemeral and long-lived tissues, and aboveground and belowground components. Changes in carbon allocation affect both the growth of individual plants (Cropper & Gholz, 1994), as well as terrestrial biogeochemistry *via* influences on litter quality and decomposition rates, carbon and nitrogen sequestration, and plant–atmosphere gas exchange (Friedlingstein *et al.*, 1999; Bird & Torn, 2006). An incomplete understanding of carbon allocation currently limits the capacity to model forest ecosystem metabolism and accurately predict the effects of global change on carbon cycling (Ryan *et al.*, 1997a; Friedlingstein *et al.*, 1999; Gower *et al.*, 1999; Landsberg, 2003).

While significant advances have been made in understanding terrestrial carbon cycling at local, regional, and global scales, large uncertainties remain about important and fundamental processes. Of total canopy photosynthesis, where does the carbon go? What is the magnitude of belowground carbon flux? What fraction of photosynthesis is used to produce plant tissues and what fraction is used for respiration? Do priorities exist for the products of photosynthesis? Do consistent carbon allocation patterns exist across forest ecosystems?

In this review, we first standardize definitions for the components of carbon allocation to facilitate comparison among past and future studies. We then synthesize annual carbon budget studies in forest ecosystems and test a series of hypotheses to determine: (i) patterns in carbon allocation, and (ii) the plasticity of and limits to carbon allocation in response to stand age, competition, and resource availability.

Prior studies and reviews have focused on: (i) interannual allocation of assimilates among functionally interdependent parts of trees at individual plant, tissue, and cellular levels (Cannell & Dewar, 1994; Friend *et al.*, 1994; Lacointe, 2000); (ii) a global scheme for dry matter production with changing resource availability (Friedlingstein *et al.*, 1999); and (iii) allocation to above- and belowground components of conifer-dominated forests (Gower *et al.*, 1994, 1995, 2001). Most research on carbon allocation has concentrated on evaluating patterns of biomass accumulation (e.g. root: shoot biomass; Tilman, 1988; Wilson, 1988; Jackson *et al.*, 1996; Cairns *et al.*, 1997) or net primary productivity (NPP) (e.g. Grier *et al.*, 1981; Runyon *et al.*, 1994; Gower *et al.*, 2001), and it is unknown if these surrogates are good approximations of the fraction of annual photosynthesis used by individual components. No work has examined all the components of allocation and their response to stand age, competition, and resource availability.

Carbon allocation terminology

Carbon allocation terminology employed in terrestrial ecosystem literature is inconsistent. The terms translocation, transport, distribution, allocation, partitioning, apportionment, and biomass allocation have all been used synonymously (Dickson & Isebrands, 1993; Gower *et al.*, 1995). The term carbon allocation has been used to mean everything from patterns in live biomass (e.g. Gower *et al.*, 1994; Enquist & Niklas, 2002; Litton *et al.*, 2003b), to the flux of carbon to a particular plant component (e.g. Dickson & Isebrands, 1993; Friend *et al.*, 1994; Haynes & Gower 1995; Keith *et al.*, 1997), to the distribution of flux as a fraction of gross photosynthesis (e.g. Ryan *et al.*, 1996a; Giardina *et al.*, 2003).

We propose these terms and definitions to standardize the vocabulary of carbon allocation for forest ecosystems: *biomass*, the amount of material present;

flux, the flow of carbon to a given component per unit time; and *partitioning*, the fraction of gross primary productivity (GPP) used by a given component.

Biomass is the mass of any or all organic components within an ecosystem (Odum, 1953). The focus of this review is on live biomass of vegetation in forest ecosystems (e.g. aboveground live biomass; $gC m^{-2}$), although aboveground live biomass estimates typically include biomass in nonliving heartwood tissue. The commonly used phrase 'biomass allocation' refers to the distribution of biomass in different components (e.g. root:shoot). However, the use of the term 'allocation' for such descriptors should be avoided, as it is ambiguous and misleading.

Flux is the rate at which carbon moves to or from a particular component of the forest ecosystem per unit ground area per unit time (e.g. NPP; $gC m^{-2} yr^{-1}$; Odum, 1953). Our emphasis in this review is on annual fluxes, although flux can be measured on daily (Dickson, 1987), monthly or even phenological (Cardon *et al.*, 2002) time scales.

Partitioning is the flux of carbon to a particular component as a fraction of total photosynthesis (GPP), expressed either as a percentage (%) or a proportion (0–1, no units). Partitioning coefficients are the information used by process-based terrestrial ecosystem models of forest carbon cycling to determine what proportion of photosynthesis a component receives.

In our scheme, the term carbon allocation is a general, overarching term that can refer to pattern (biomass) or process (flux and partitioning), or both. We propose that the term *carbon allocation* should not be used synonymously for any of the individual components listed above to avoid confusion.

Hypothesis testing

We investigated patterns, plasticity, and limits to the different facets of carbon allocation in response to stand age, competition, and resource availability by testing the following hypotheses:

(i) Annual carbon flux and partitioning can be inferred from biomass (as assumed in some terrestrial ecosystem models; e.g. Lüdeke *et al.*, 1994; Haxeltine & Prentice, 1996).
(ii) Component fluxes are correlated: (a) foliage production, foliage respiration, wood production, wood respiration, and total belowground carbon flux (TBCF) increase with increasing GPP, and (b) TBCF increases with aboveground production (Raich & Nadelhoffer, 1989; Nadelhoffer *et al.*, 1998).
(iii) (a) Autotrophic respiration is strongly related to production (Ryan *et al.*, 1997b; Waring *et al.*, 1998;

Gifford, 2003), and (b) this relationship does not vary for foliage, wood, and roots.
(iv) Partitioning to respiration is constant across a wide range of GPP in forest ecosystems (Ryan *et al.*, 1997b; Waring *et al.*, 1998; Gifford, 2003) and does not vary with resource availability, competition, or stand age (Ryan *et al.*, 2004).
(v) Partitioning to aboveground production increases and to TBCF decreases with increasing stand age (Davidson *et al.*, 2002; Ryan *et al.*, 2004), decreasing competition (Ryan *et al.*, 2004), and increasing resources (Thornley, 1972a, b; Cannell & Dewar, 1994; Friend *et al.*, 1994; McConnaughay & Coleman, 1999).
(vi) Priorities exist for the products of photosynthesis such that carbon is used first by higher priority tissues and only released to other tissues when those needs are satisfied (Waring & Pitman, 1985; Weinstein *et al.*, 1991).

Methods

We divided the annual carbon budget into five major components, and estimated GPP as the sum of these five components (Fig. 1, Möller *et al.*, 1954; Ryan, 1991; Ryan *et al.*, 1996b, 2004). Components were: foliage aboveground NPP ($ANPP_{foliage}$), which includes
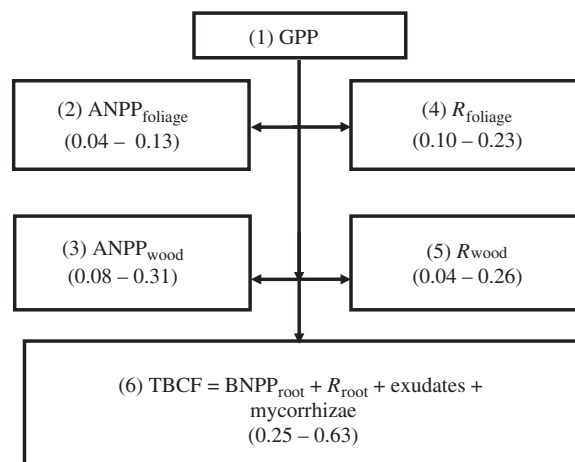
Fig. 1 Simplified diagram depicting the major components of the carbon budget in forest ecosystems, and the partitioning of (1) GPP into carbon fluxes to: (2) foliage ($ANPP_{foliage}$) and (3) wood ($ANPP_{wood}$) aboveground net primary productivity, (4) foliage ($R_{foliage}$), and (5) wood (R_{wood}) autotrophic respiration, and (6) total belowground carbon flux (TBCF). Values in parentheses are 10th and 90th percentiles of carbon partitioning for studies analyzed herein that provided information on all of the components of GPP ($n = 29$). Modified from Ryan *et al.* (2004). See Tables 1a and 1b and Nomenclature for term definitions.

reproductive tissues; wood aboveground NPP (ANPP$_{wood}$), which includes bark and branches; foliage respiration ($R_{foliage}$); wood respiration (R_{wood}); and TBCF, which includes root belowground NPP (BNPP$_{root}$), root respiration (R_{root}), root exudates, and carbon used by mycorrhizae.

Our calculation of GPP excludes foliage dark respiration during the light period, because of difficulties associated with estimation (Kirschbaum & Farquhar, 1984) and refixation (Loreto *et al.*, 1999, 2001). We do not address storage of photosynthates, reproduction, volatile organic compound emissions (VOCs), or herbivory. Carbon used for reproduction is included in ANPP$_{foliage}$ in most of the studies, and VOCs and herbivory are relatively minor sinks in forests (Clark *et al.*, 2001; Kesselmeier *et al.*, 2002; Pressley *et al.*, 2005). Understory data were included in stand-level estimates of biomass and flux where available. We assumed biomass was 50% carbon when originally given in units of organic matter.

We selected studies in this review from prior knowledge and literature review. Studies were required to measure at least TBCF and ANPP$_{total}$, or their individual components (Tables 1a and 1b). All but two studies estimated ANPP$_{foliage}$ and ANPP$_{wood}$ separately (Table 1a). ANPP$_{wood}$ was estimated as the annual production of live-tree wood biomass, generally calculated from tree diameter measurements and site- and species-specific allometric equations, using repeated sampling or tree-ring width from cores to estimate diameter change. ANPP$_{foliage}$ was estimated from change in foliage biomass, litterfall, or both, where foliage biomass was estimated with site- and species-specific allometric equations and litterfall with litter traps. See Clark *et al.* (2001) for a synthesis on estimating ANPP in forests.

Thirty four of 63 experiments directly estimated R_{above} ($R_{foliage} + R_{wood}$; Table 1a) based on: (i) gas exchange measurements and scaling techniques (e.g. see Ryan *et al.*, 1994, 1996a, 1997b; Sprugel *et al.*, 1995), or (ii) gas exchange measurements for maintenance respiration and growth respiration assuming a construction cost of 0.25 (Ryan, 1991).

TBCF was estimated in 51 of 63 experiments (Table 1b) using a conservation of mass, carbon balance technique originally known as TRCA or TBCA, total root or belowground carbon allocation (Raich & Nadelhoffer, 1989; Giardina & Ryan, 2002). We use TBCF instead of these terms for what is clearly a flux based on our terminology. TBCF was calculated as soil-surface CO_2 efflux (F_{soil}) minus aboveground litterfall (F_a) for studies that did not provide information on annual changes in soil carbon pools (Raich & Nadelhoffer, 1989). Where possible, however, TBCF was estimated

using a modification that does not assume a steady state in belowground carbon pools (TBCF = $F_{soil} - F_a$ + change in measured belowground carbon pools; Giardina & Ryan, 2002).

For the 12 experiments that did not directly measure F_{soil} (Table 1b), TBCF was estimated as the sum of independent measurements of BNPP$_{root}$ and R_{root}. For most of these studies, R_{root} was estimated with chamber measurements and scaling techniques. Three additional studies used for our analyses estimated R_{root} as: (i) coarse root respiration from biomass, temperature and stem respiration rates, and fine root respiration as a residual term of GPP (where GPP was estimated from annual gas-exchange rates and crown leaf area measurements; Benecke & Nordmeyer, 1982), (ii) maintenance respiration from tissue temperature and nitrogen content and growth respiration assuming a construction cost of 0.25 (Maier *et al.*, 2004), or (iii) F_{soil} differences between control and trenched (root-free) plots (Ewel *et al.*, 1987). These methods for estimating R_{root} and, thus, TBCF do not include carbon used for mycorrhizae and root exudates, a potentially large portion of flux to belowground (Fogel & Hunt, 1979; Sylvia, 1998).

For analyses of biomass, flux and partitioning across the entire gradient of GPP, we used only studies that measured all components included in the analysis (identified in Tables 1a and 1b). To assess patterns in partitioning within a given site in response to changes in resource availability, forest age, and competition we also included four studies that did not measure R_{above} (Keith *et al.*, 1997; Fornwalt, 1999; Stape, 2002; Litton *et al.*, 2004). For these four studies, where ANPP$_{total}$ and TBCF were measured but R_{above} was not, we calculated and summed $R_{foliage}$ and R_{wood} using relationships derived in this review. All of the above cases are clearly identified in Tables 1a and 1b and in corresponding analyses and figures.

Statistical analyses

Except where noted, all statistical analyses were performed in SPSS 10.0 (SPSS, 1999, Base 10.0 Application Guide, SPSS Inc., Chicago, IL). Data were tested for normal distributions and homogeneity of variance, and transformed where necessary. We used least-squares regression to test Hypotheses i–iv and vi. In all cases, we fit both linear and nonlinear regression models. Regression lines were forced through the origin whenever the equation constant was not significant at $\alpha = 0.05$. Goodness of fit and final model selection were determined by examining *P*-values, the sum of squares of the residuals, mean square of error, coefficient of determination (R^2), and by visual inspection of a plot of

Table 1a Studies used to examine patterns in carbon flux and partitioning across gradients of stand and environmental conditions

Species/ecosystem	Treatment*	ANPP_foliage	ANPP_wood	ANPP_total[†]	R_foliage	R_wood	R_above[‡]	TBCF[§]	GPP[¶]	Reference
‖**Eucalyptus saligna plantation; Pepeekeo, HI	2 yr C, 1 m × 1 m (n = 3)	316	1111	1427[a]	721	555	1276[a]	2353[a]	5057	Ryan et al. (2004)
	6 yr C, 1 m × 1 m (n = 3)	189	291	480[a]	537	168	705[a]	1185[a]	2369	
	2 yr C, 3 m × 3 m (n = 3)	385	1071	1456[a]	567	547	1114[a]	1843[a]	4413	
	6 yr C, 3 m × 3 m (n = 3)	266	562	828[a]	526	128	654[a]	1448[a]	2930	
	2 yr F, 1 m × 1 m (n = 3)	436	1805	2242[a]	644	775	1419[a]	1900[a]	5561	
	6 yr F, 1 m × 1 m (n = 3)	369	779	1148[a]	726	304	1030[a]	1740[a]	3919	
	2 yr F, 3 m × 3 m (n = 3)	449	1587	2036[a]	567	773	1340[a]	1580[a]	4955	
	6 yr F, 3 m × 3 m (n = 3)	270	816	1086[a]	644	314	958[a]	1442[a]	3486	
Eucalyptus grandis × urophylla clonal plantation; NE Bahia State, Brazil	4 yr (wet) C (n = 4)	168	1880	2048[a]				2235[a]		Stape (2002)
	4 yr (wet) I (n = 4)	203	2262	2465[a]				2460[a]		
	4 yr (wet) F (n = 4)	208	2075	2283[a]				2034[a]		
	4 yr (wet) IF (n = 4)	263	2397	2660[a]				2466[a]		
	5 yr (norm) C (n = 4)	129	800	929[a]				1161[a]		
	5 yr (norm) I (n = 4)	152	1948	2100[a]				1400[a]		
	5 yr (norm) F (n = 4)	149	823	972[a]				1041[a]		
	5 yr (norm) IF (n = 4)	154	1850	2004[a]				1340[a]		
Eucalyptus pauciflora; Brindabella, Australia	54 yr C (n = 3)	179	253	432[a]				510[a]		Keith et al. (1997)
	54 yr P F (n = 3)	169	330	499[a]				438[a]		
Eucalyptus globulus and Acacia mearnsii plantation; Victoria, Australia	11 yr 100% E. (n = 4)			341[a]				1460[a]		Forrester et al. (2006)
	11 yr 50:50 (n = 4)			411[a]				1631[a]		
	11 yr 100% A. (n = 3)			211[a]				1585[a]		
Pinus contorta; Yellowstone National Park, WY	13 yr low density (n = 4)	3	3	59[a]				68[a]		Litton et al. (2004)
	13 yr mod density (n = 4)	46	34	122[a]				237[a]		
	13 yr high den. (n = 4)	72	50	155[a]				306[a]		
	110 yr (n = 4)	56	126	219[a]				382[a]		
††‖**Pinus contorta; New Zealand	20 yr montane (n = 1)	350	1230	1580[b]	780	1740	2520[b]	1460[b]	5560	Benecke & Nordmeyer (1982)
	23 yr subalpine (n = 1)	320	580	900[b]	620	665	1285[b]	734[b]	2919	
††‖**Pinus radiata plantation; Canberra, Australia	20 yr C (n = 1)	84	515	599[c]	421	373	794[b]	1022[a]	2415	Ryan et al. (1996a)
	20 yr I (n = 1)	113	637	750[c]	295	450	745[b]	1036[a]	2531	
	20 yr IF (n = 1)	213	1078	1291[c]	681	727	1408[b]	739[a]	3438	
††‖**Pinus taeda plantation; Piedmont Region, NC	12 yr C (n = 4)	151	206	357[a]	279	195	474[a]	701[a]	1532	Maier et al. (2004)
	12 yr I (n = 4)	188	265	453[a]	346	227	573[a]	898[a]	1924	
	12 yr F (n = 4)	290	416	706[a]	520	470	990[a]	686[a]	2382	
	12 yr IF (n = 4)	358	482	840[a]	581	498	1079[a]	668[a]	2587	

(contd.)

Table 1a. (Contd.)

Species/ecosystem	Treatment*	ANPP$_{foliage}$	ANPP$_{wood}$	ANPP$_{total}$[†]	R$_{foliage}$	R$_{wood}$	R$_{above}$[‡]	TBCF[§]	GPP[¶]	Reference
††∥*Pinus ponderosa*; Central OR	21 yr (n = 1)	23	33	76[c]	60	3	127[b]	614[a]	817	Law et al. (2001)
	50/250 yr (n = 1)	76	81	173[c]	131	63	199[b]	671[a]	1043	
††∥**Pinus elliottii* plantation; Bradford, FL	7–9 yr (n = 1)	59	115	199[b]			430[b]	778[a]	1407	Gholz & Fisher (1982), Gholz et al. (1986), Ewel et al. (1987)
Pseudotsuga menziesii; Cascades, WA	26–29 yr (n = 1)	179	482	686[b]				1136[a]	2482	Long & Turner (1975), Turner & Long (1975)
	42 yr (n = 1)	112	353	496[a]			660[b]	361[a]		
Abies amabilis; Cascades, WA	180 yr (n = 1)	46	111	157[a]				583[a]		Vogt et al. (1980), Grier et al. (1981)
††∥**Picea mariana*, N-BOREAS	150 yr (n = 1)	50	73	132[a]	121	103	229[b]	502[b]	863	Gower et al. (1997), Ryan et al. (1997b)
††∥**Pinus banksiana*, N-BOREAS	63 yr (n = 1)	39	65	115[a]	106	22	134[b]	428[b]	677	
††∥**Populus tremuloides* N-BOREAS	53 yr (n = 1)	98	214	342[a]	75	77	171[b]	390[b]	903	
††∥***P. mariana*, S-BOREAS	115 yr (n = 1)	53	80	142[a]	195	87	291[b]	352[b]	785	
††∥***P. banksiana*, S-BOREAS	63 yr (n = 1)	56	59	122[a]	129	30	161[b]	273[b]	556	
††∥***P. tremuloides* S-BOREAS	68 yr (n = 1)	119	176	361[a]	105	123	290[b]	393[b]	1044	
P. tremuloides; WY	19 yr (n = 3)	59	54	159[a]				394[a]		Fornwalt (1999)
	62 yr (n = 3)	117	124	280[a]				500[b]		
∥**Oak-Hickory; Oak Ridge, TN	55 yr (n = 1)			510[a]	191	196	387[b]	432[a]	1329	Malhi et al. (1999)
∥Tropical forest; Manaus, Brazil	Old growth (n = 1)			870[a]	410	390	800[b]	950[a]	2620	Malhi et al. (1999)
∥Tropical forest; Manaus, Brazil	Old growth *terra firme* (n = 2)	330	320	650[a]	980	420	1400[b]	810[a]	2860	Chambers et al. (2001, 2004)
Ash Forest; HI	Old growth (n = 1)	307	234	541[a]				583[a]		Raich (1998), Raich et al. (2000)
Edge Forest; HI	Old growth (n = 1)	287	99	385[a]				490[a]		
Interior forest; HI	Old growth (n = 1)	188	45	292[a]				443[a]		
Temperate deciduous; Walker Branch, TN	50–120 yr (n = 1)	226	220	539[a]				724[a]		Curtis et al. (2002)
Temperate deciduous; Morgan Monroe, IN	80 yr (n = 1)	213	292	529[a]				994[a]		
Temperate deciduous; Harvard Forest, MA	60 yr (n = 1)	130	130	320[a]				670[a]		
Temperate deciduous; UMBS, MI	90 yr (n = 1)	133	185	338[a]				999[a]		
Temperate deciduous; WI	66 yr (n = 1)	135	155	300[a]				675[a]		
††∥**Nothofagus solandri*; New Zealand	52 yr montane (n = 1)	470	930	1400[b]	500	970	1470[b]	840[b]	3710	Benecke & Nordmeyer (1982)
	52 yr subalpine (n = 1)	260	390	650[b]	290	241	531[b]	389[b]	1570	

††‖**Liriodendron; Oak Ridge, TN	~50 yr (n = 1)	141		166	352^a	396	660	1066^b	744^b	2162	Harris et al. (1975)
††‖Second-growth, Brookhaven, NY	~45 yr (oaks + pines) (n = 1)	181		200	381^a			487^b	338^b	1206	Whittaker & Woodwell (1969)

*C, Control; I, Irrigated; F, Fertilized; IF, Irrigated + Fertilized; yr, year.

†Total aboveground net primary production ($ANPP_{total} = ANPP_{foliage} + ANPP_{wood}$) was estimated as (a) Δ in biomass (wood and foliage; estimated with allometric equations) + litterfall (foliage and branch); (b) difference in harvest biomass at T_1 and T_2; (c) Δ in biomass from allometric equations (wood) and LAI and leaf area per unit mass values (foliage).

‡Aboveground autotrophic respiration ($R_{above} = R_{foliage} + R_{wood}$) was estimated as: (a) maintenance respiration from direct measurements and growth respiration assuming a construction cost of 0.25, or (b) chamber measurements and scaling techniques.

§Total belowground carbon flux (TBCF; see Table 1b).

¶Gross primary production (GPP) was estimated as: $ANPP_{foliage} + ANPP_{wood} + R_{foliage} + R_{wood} + TBCF$.

‖Studies that directly estimated $ANPP_{total}$ and R_{above}, and were used in the analysis in Fig. 6a–c.

**Studies used to examine the relationship between biomass and carbon flux and partitioning (Figs 2 and 3).

††Studies that directly estimated $BNPP_{root}$ and R_{root} (see Table 1b), and were used in the analysis in Fig. 6d.

All numbers are g C m^{-2} yr^{-1}. For those studies with $n > 1$, values represent treatment means. Numbers in italics refer to values not published in the original manuscript. See footnotes and 'Methods' for a description of how values were estimated.

Table 1b Studies used to examine total belowground carbon flux (TBCF)

Species/ecosystem	Treatment*	$BNPP_{root}$†	R_{root}‡	F_{soil}	F_a	Δ Coarse roots	Δ SOM	Δ Litter	Δ Dead roots	TBCF§	Reference
Eucalyptus saligna plantation; Pepeekeo, HI	2 yr C, 1 m × 1 m (n = 3)			2460	415	216	19	73		2353^a	Ryan et al. (2004)
	6 yr C, 1 m × 1 m (n = 3)			1404	418	56	76	66		1185^a	
	2 yr C, 3 m × 3 m (n = 3)			2036	380	208	−55	34		1843^a	
	6 yr C, 3 m × 3 m (n = 3)			1439	413	109	237	76		1448^a	
	2 yr F, 1 m × 1 m (n = 3)			1854	518	350	100	114		1900^a	
	6 yr F, 1 m × 1 m (n = 3)			2240	646	151	−71	65		1740^a	
	2 yr F, 3 m × 3 m (n = 3)			1753	433	308	−88	39		1580^a	
	6 yr F 3 m × 3 m (n = 3)			1845	530	158	−121	90		1442^a	
Eucalyptus grandis × urophylla clonal plantation; NE Bahia State, Brazil	4 yr (wet) C (n = 4)			2087	229	455	−110	68	−36	2235^a	Stape (2002)
	4 yr (wet) I (n = 4)			2337	246	546	−173	31	−35	2460^a	
	4 yr (wet) F (n = 4)			1832	278	506	−30	38	−34	2034^a	
	4 yr (wet) IF (n = 4)			2276	304	581	−80	30	−37	2466^a	
	5 yr (norm) C (n = 4)			1333	215	176	−110	7	−30	1161^a	
	5 yr (norm) I (n = 4)			1482	253	425	−173	−52	−29	1400^a	
	5 yr (norm) F (n = 4)			1184	231	179	−30	−33	−28	1041^a	
	5 yr (norm) IF (n = 4)			1340	263	408	−80	−34	−31	1340^a	

(contd.)

Table 1b. (Contd.)

Species/ecosystem	Treatment*	BNPP$_{root}$†	R$_{root}$‡	F$_{soil}$	F$_a$	Δ Coarse roots	Δ SOM	Δ Litter	Δ Dead roots	TBCF§	Reference
Eucalyptus pauciflora; Brindabella, Australia	54 yr C (n = 3)			711	246	45				510[a]	Keith et al. (1997)
	54 yr P F (n = 3)			655	277	60				438[a]	
Eucalyptus globulus and *Acacia mearnsii* plantation; Victoria, Australia	11 yr 100% E. (n = 4)			1523	115	52				1460[a]	Forrester et al. (2006)
	11 yr 50:50 (n = 4)			1758	173	46				1631[a]	
	11 yr 100% A. (n = 3)			1730	152	6				1585[a]	
Pinus contorta; Yellowstone National Park, WY	13 yr low den. (n = 4)			156	59	1	−18	3	−15	68[a]	Litton et al. (2004)
	13 yr mod den. (n = 4)			303	69	10	−5	13	−15	237[a]	
	13 yr high den. (n = 4)			351	72	17	1	24	−14	306[a]	
	110 yr (n = 4)			460	106	22		6		382[a]	
P. contorta; New Zealand	20 yr mont. (n = 1)	480[a]	980[a]							1460[b]	Benecke & Nordmeyer (1982)
	23 yr subalp. (n = 1)	360[a]	374[a]							734[b]	
Pinus radiata plantation; Canberra, Australia	20 yr C (n = 1)	304[b]	274[b]	987	84	119				1022[a]	Ryan et al. (1996a)
	20 yr I (n = 1)	391[b]	309[b]	991	111	156				1036[a]	
	20 yr IF (n = 1)	429[b]	373[b]	625	182	296				739[a]	
Pinus taeda plantation; Piedmont Region, NC	12 yr C (n = 4)	199[b]	283[b]	811	110					701[a]	Maier et al. (2004)
	12 yr I (n = 4)	227[b]	331[b]	1038	140					898[a]	
	12 yr F (n = 4)	326[b]	528[b]	926	240					686[a]	
	12 yr IF (n = 4)	284[b]	461[b]	938	270					668[a]	
Pinus ponderosa; Central OR	21 yr (n = 1)	281[c]	333[b]	654	50	10				614[a]	Law et al. (2001)
	50/250 yr (n = 1)	299[c]	372[b]	780	132	23				671[a]	
Pinus elliottii plantation; Bradford, FL	7–9 yr (n = 1)	245[a]	430[c]	850	179	46		61		778[a]	Gholz & Fisher (1982), Gholz et al. (1986), Ewel et al. (1987)
	26–29 yr (n = 1)	308[a]	810[c]	1300	250	25		61		1136[a]	
Pseudotsuga menziesi; Cascades, WA	42 yr (n = 1)			490	129					361[a]	Long & Turner (1975), Turner & Long (1975)
Abies amabilis; Cascades,WA	180 yr (n = 1)			681	98					583[a]	Vogt et al. (1980), Grier et al. (1981)
Picea mariana	150 yr (n = 1)	120[d]	382[b]							502[b]	Gower et al. (1997), Ryan et al. (1997b)
Pinus banksiana	63 yr (n = 1)	114[d]	314[b]							428[b]	
Populus tremuloides	53 yr (n = 1)	74[d]	316[b]							390[b]	
P. mariana	115 yr (n = 1)	160[d]	192[b]							352[b]	
P. banksiana	63 yr (n = 1)	122[d]	151[b]							273[b]	
P. tremuloides	68 yr (n = 1)	79[d]	314[b]							393[b]	
P. tremuloides; WY	19 yr (n = 3)			502	109					394[a]	Fornwalt (1999)
	62 yr (n = 3)			664	164					500[a]	

Location	Age (n)	BNPP$_{root}$	R$_{root}$				TBCF	Reference
Oak-Hickory; Oak Ridge, TN	55 yr (n = 1)			753	360	39	*432*[a]	Malhi et al. (1999)
Evergreen broadleaf forest; Brazil	Old growth (n = 1)			1650	700		*950*[a]	Chambers et al. (2001, 2004), Raich (1998),
Evergreen broadleaf forest; Brazil	Old growth *terra firme* (n = 2)			1210	400		*810*[a]	Raich et al. (2000)
Ash forest; HI	Old growth (n = 1)			890	307		*583*[a]	
Edge forest; HI	Old growth (n = 1)			776	287		*490*[a]	
Interior forest; HI	Old growth (n = 1)			653	211		*443*[a]	
Temperate deciduous; Walker Branch, TN	50–120 yr (n = 1)	188[d]		950	226		*724*[a]	Curtis et al. (2002)
Temperate deciduous; Morgan Monroe, IN	80 yr (n = 1)	520[d]		1207	213		*994*[a]	
Temperate deciduous; Harvard Forest, MA	60 yr (n = 1)	245[d]		800	130		*670*[a]	
Temperate deciduous; UMBS, MI	90 yr (n = 1)	301[d]		1132	133		*999*[a]	
Temperate deciduous; Chequamegon, WI	66 yr (n = 1)	211[d]		810	135		*675*[a]	
Nothofagus solandri; New Zealand	52 yr montane (n = 1)	280[a]	560[a]				840[b]	Benecke & Nordmeyer (1982)
	52 yr subalpine (n = 1)	250[a]	139[a]				389[b]	
Temperate deciduous; *Liriodendron*; TN	~50 yr (n = 1)	374[a]	370[b]	1040	229	25	744[b]	Harris et al. (1975)
Second-growth; Brookhaven, NY	~45 yr (oaks + pines) (n = 1)	150[b]	188[b]	464	150	22	338[b]	Whittaker & Woodwell (1969)

*C = Control; I = Irrigated; F = Fertilized; IF = Irrigated + Fertilized; yr, year.

†Belowground net primary production in roots (BNPP$_{root}$) was estimated as: (a) difference in harvest biomass at T_1 and T_2; (b) Δ in biomass (coarse roots; estimated with allometric equations) and with soil cores (fine roots); (c) TBCF − R_{root}; (d) allometric equations (coarse roots) and minirhizotrons and/or soil coring (fine roots).

‡Belowground autotrophic respiration (R_{root}; sum of growth and maintenance respiration for coarse and fine roots) was estimated as: (a) coarse root respiration from biomass, temperature and stem respiration rates and fine root respiration as a residual term of GPP; (b) chamber measurements and scaling techniques; (c) soil-surface CO_2 efflux differences between control and trenched (root-free) plots.

§Total belowground carbon flux (TBCF) was estimated as (a) Soil-surface CO_2 efflux (F_{soil}) – Aboveground litterfall (F_a Δ Soil C pools; (b) BNPP$_{root}$ + R_{root}.

All numbers are g C m^{-2} yr^{-1}. For those studies with $n > 1$, numbers represent treatment means. Numbers in italics refer to values not published in the original manuscript.
See footnotes and *Methods* for a description of how values were estimated.

residuals vs. the independent variable. We estimated R^2 as $1 - $ (SSR/corrected SST) where SSR is the sum of squares of the residuals and corrected SST is the total sum of squares of deviations from the overall mean. To test for differences in slopes between production and respiration among components (Hypothesis iiib), we used analysis of covariance and linear contrasts (PROC MIXED; SAS, 1997, SAS System for Windows, Ver. 8.02, SAS Institute, Cary, NC, USA).

No formal statistical analysis was used to test Hypothesis v about partitioning in response to stand age, resource availability and competition. We examined overall patterns in partitioning for the few studies available. We used one-way analysis of variance to test if partitioning to respiration varied within a site with changes in stand age ($n = 4$) or resource availability ($n = 7$).

For several of the regression analyses, the potential for autocorrelation exists because the dependent variable is part of the independent variable. For example, when analyzing $NPP_{foliage}$ vs. GPP, $NPP_{foliage}$ is the dependent variable and is also part of the independent variable because GPP was calculated as the sum of individual components (Fig. 1). In these cases, it is possible that significant relationships are the result of autocorrelation and are not biologically meaningful. We assessed the potential effect of autocorrelation in each instance by removing the autocorrelated variable from the independent variable and rerunning the analysis. For example, we compared the original regression of $NPP_{foliage}$ vs. GPP to that of a regression of $NPP_{foliage}$ vs. GPP minus $NPP_{foliage}$. In all cases, removing the autocorrelated variable only slightly changed the R^2 and slope of the relationship and did not change the significance ($P < 0.01$ for all significant models with and without autocorrelated variables). Thus, autocorrelation of variables had minor impact on our analyses, and did not influence the biological interpretations or conclusions drawn.

Results and discussion

Biomass vs. carbon flux and partitioning

Hypothesis (i): *Annual carbon flux and partitioning can be inferred from biomass*

Biomass patterns have led to much of the current understanding of carbon allocation (e.g. Tilman, 1988; Wilson, 1988; Jackson *et al.*, 1996; Cairns *et al.*, 1997), and it may be reasonable in annual plants to infer flux and partitioning from biomass. However, because trees accumulate biomass in both long-lived woody structures and short-lived foliage and fine roots, forest biomass reflects both flux and retention and may not be related

to flux or partitioning of current-year assimilates. For example, root biomass is probably a poor proxy for TBCF because roots serve as support and storage structures in addition to acquiring resources (Tilman, 1988).

Biomass does not appear to be a good predictor of carbon flux in forests. The ratio of TBCF: $ANPP_{total} + R_{above}$ was not dependent on root:shoot biomass (Fig. 2a), TBCF was not related to total belowground biomass ($R^2 = 0.00$; $n = 43$; $P = 0.80$), and there was no relationship between $ANPP_{total} + R_{above}$ and aboveground biomass ($R^2 = 0.04$; $n = 34$; $P = 0.24$). If we omit the structural component of biomass and focus on the
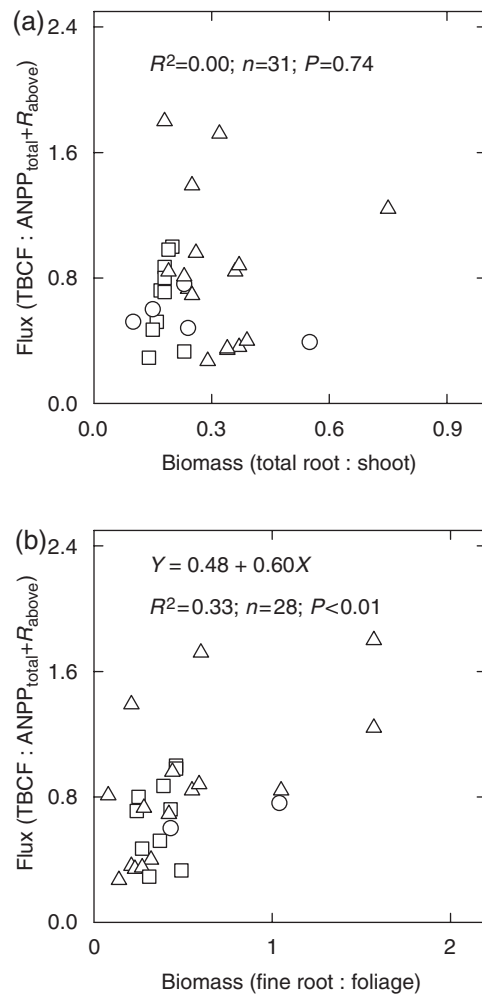
Fig. 2 Carbon flux is poorly related to biomass in forest ecosystems. Biomass ratios and flux (TBCF: $ANPP_{total} + R_{above}$, an ecosystem carbon flux analog to root:shoot biomass) were not related for (a) total root:shoot across diverse forest ecosystems that represent gradients in resource availability, stand age and competition. A somewhat better relationship existed between (b) flux and fine root:foliage biomass. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. TBCF, total belowground carbon flux.

metabolically active components (foliage and fine roots), the relationship between flux and biomass improves (Fig. 2b) but biomass is still only able to explain 33% of the variability in flux and is not likely to be useful for prediction.

The data also do not support the hypothesis that carbon partitioning in forests can be inferred from biomass. Biomass ratios are often used as proxies for partitioning, but we found no relationship between partitioning to $ANPP_{total} + R_{above}$ and the ratio of aboveground: total biomass (Fig. 3a). Likewise, no relationship existed between partitioning to individual aboveground components and biomass ($R^2 \leq 0.10$; $n = 28$; $P \geq 0.11$). The same was true for belowground, where the ratio of belowground: total biomass only explained 3% of the variation in partitioning to TBCF across studies (Fig. 3b). Moreover, no relationship existed between partitioning to TBCF and root:shoot biomass ($R^2 = 0.05$; $n = 32$; $P = 0.22$).

(a)

$R^2=0.03$; $n=32$; $P=0.31$

Partitioning to aboveground ($ANPP_{total}+R_{above}$ / GPP)

Aboveground : total biomass

(b)

$R^2=0.03$; $n=32$; $P=0.31$

Partitioning to belowground (TBCF / GPP)

Belowground : total biomass
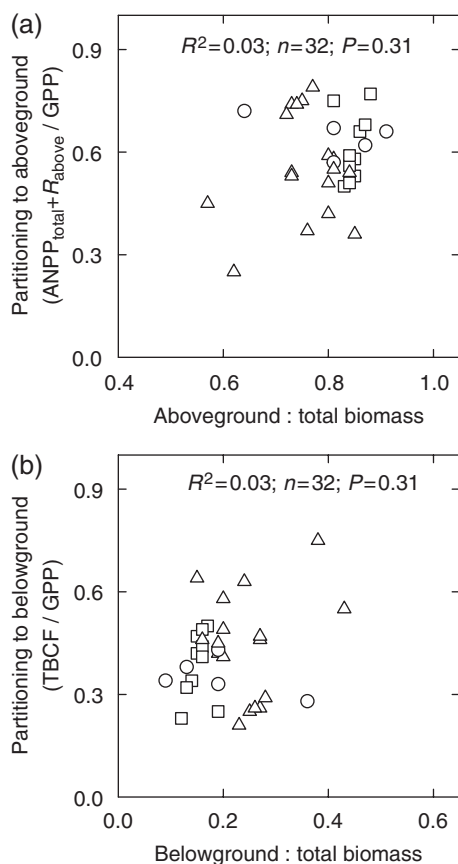
Fig. 3 Carbon partitioning is poorly related to biomass for both (a) aboveground and (b) belowground across diverse forest ecosystems that represent gradients in resource availability, stand age and competition (Table 1a). Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests.
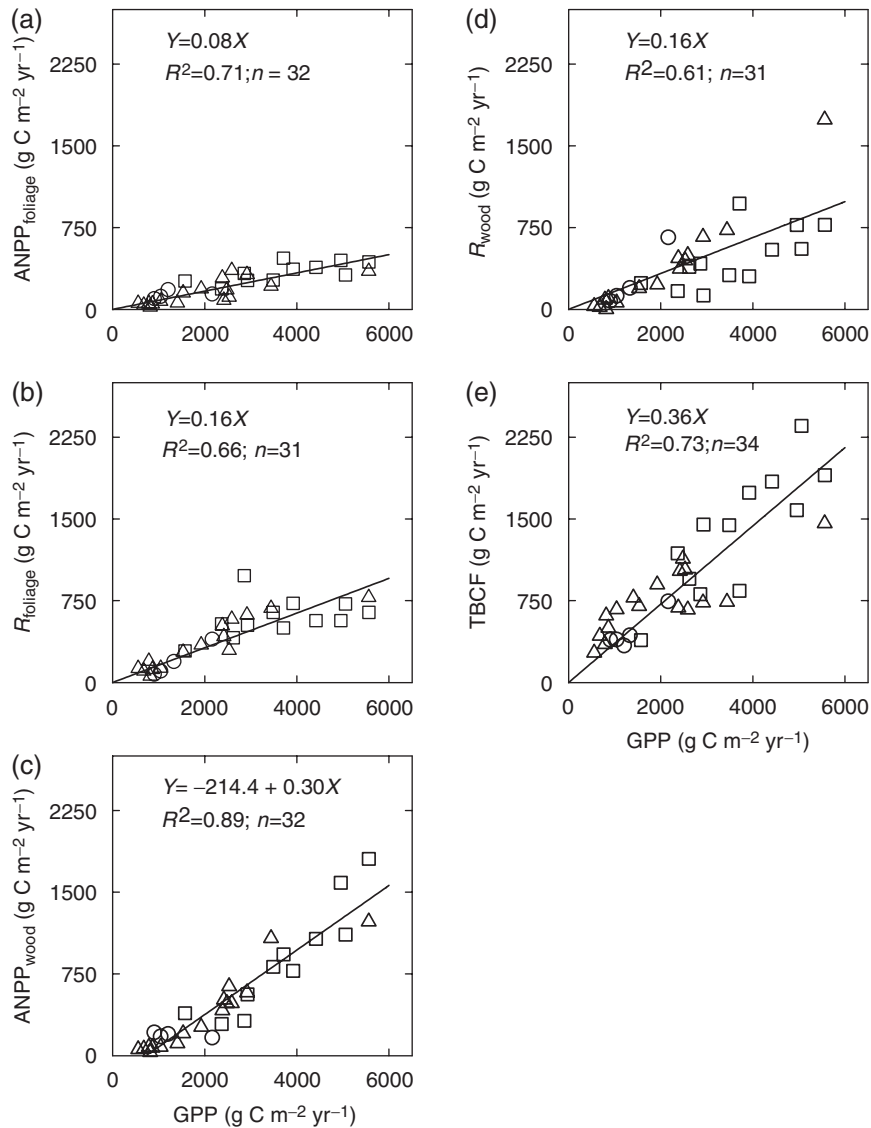
Flux

Hypothesis (ii): *Component fluxes are correlated: (a) foliage production, foliage respiration, wood production, wood respiration, and total belowground carbon flux increase with increasing GPP, and (b) total belowground carbon flux increases with aboveground production*

Across forests, $ANPP_{foliage}$, $R_{foliage}$, $ANPP_{wood}$, R_{wood}, and TBCF were all linearly and positively related to GPP (Fig. 4a–e; $P < 0.01$, $R^2 = 0.61$–0.89) which supports part (a) of our hypothesis. Slopes appear to differ by component, indicating that increasing GPP does not increase all component fluxes proportionately. $ANPP_{foliage}$, in particular, increased less per unit increase in GPP than did other components (Fig. 4a). The relationship between $ANPP_{foliage}$ and GPP across forests is robust ($R^2 = 0.71$) and may provide an independent method for estimating GPP, as $ANPP_{foliage}$ is commonly measured in forest ecosystem studies.

TBCF and $ANPP_{total}$ ($ANPP_{foliage} + ANPP_{wood}$) were tightly related across a wide range of environmental gradients and forest types (Fig. 5), as hypothesized, because all component fluxes increased with GPP. TBCF was also tightly linked to $ANPP_{total}$ across large gradients in tree density and stand age in *Pinus contorta* forests (Litton *et al.*, 2004). Soil-surface CO_2 efflux (F_{soil}) is the largest flux within the mass balance equation for estimating TBCF (Giardina & Ryan, 2002; Litton *et al.*, 2003a), and there is an increasing appreciation of a tight link between carbon fixed in the forest canopy and the flux of carbon from soils as CO_2 (Högberg *et al.*, 2001; Irvine *et al.*, 2005). However, other studies have shown a lack of correlation between F_{soil} or TBCF and ANPP across diverse forested landscapes (Campbell *et al.*, 2004). Our results also differ from those of Palmroth *et al.* (2006), where TBCF declined as productivity (estimated from leaf area index) increased following disturbance. The global relationship between TBCF and $ANPP_{total}$ shown here may not be accurate for estimating TBCF for a specific site (Gower *et al.*, 1996; Nadelhoffer *et al.*, 1998; Davidson *et al.*, 2002).

Hypothesis (iii): *Autotrophic respiration is strongly related to production, and (b) this relationship does not vary for foliage, wood, and roots*

Autotrophic respiration was strongly linked to production for all components (Fig. 6), which supports part (a) of our hypothesis. However, the relationship differed by component ($P < 0.02$), refuting part (b) of our hypothesis. The slope of the relationship between respiration

Fig. 4 (a) Foliage production (ANPP$_{foliage}$), (b) foliage respiration ($R_{foliage}$), (c) wood production (ANPP$_{wood}$), (d) wood respiration (R_{wood}), and (e) total belowground carbon flux (TBCF) all exhibited strong linear relationships with GPP across diverse forest ecosystems ($P < 0.01$). Zero-intercept regressions were used where the constant was not significant at $\alpha = 0.05$. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. GPP, gross primary productivity.

and production was lower for wood (Fig. 6b) than for foliage (Fig. 6a) or roots (Fig. 6d), indicating that respiration per unit production is lower for wood, likely as a result of its lower metabolic activity. These relationships correspond to mean (± 1 SE) carbon use efficiencies [CUE = NPP/(NPP + Respiration)] of 0.36 (± 0.02), 0.60 (± 0.03), 0.51 (± 0.02), 0.41 (± 0.03), and 0.43 (± 0.02) for foliage, wood, aboveground, roots, and total, respectively.

Autotrophic respiration can be partitioned into components based on its function, and one of the most common distinctions is between respiration used for biomass production (growth respiration) and that used

to support existing biomass (maintenance respiration). The strong relationships between autotrophic respiration and production (Fig. 6) support an important link between total respiration and growth, even though respiration required for growth is only a portion of total respiration (<10% for foliage and ~50% for wood; Ryan *et al.*, 1996a). This further suggests that maintenance processes are also linked with the metabolic processes that promote growth, or that growth respiration reflects the energetic cost of constructing the compounds in tissues (Penning de Vries *et al.*, 1974; Williams *et al.*, 1989). These relationships provide a method of generating estimates of respiration that are sensitive to flux
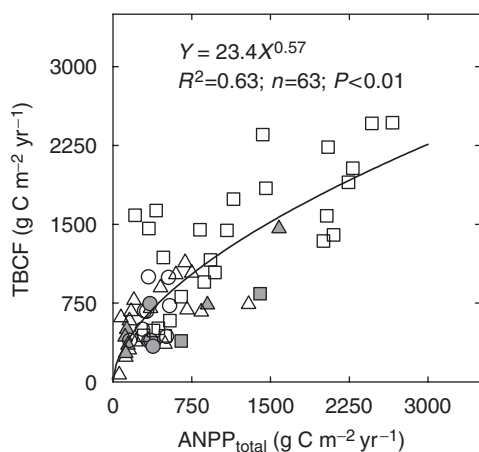
Fig. 5 Across forests, carbon flux to belowground (TBCF) increased with total aboveground net primary production ($ANPP_{total}$). TBCF was estimated as soil-surface CO_2 efflux minus aboveground litterfall plus any measured changes in soil carbon pools for all studies except those indicated with gray fill, where TBCF was estimated as $BNPP_{root} + R_{root}$. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests. TBCF, total belowground carbon flux.

used by different components, and may yield more realistic estimates than assuming a whole plant carbon use efficiency suggested by Waring *et al.* (1998) or Gifford (2003). We, therefore, recommend that when necessary, forest autotrophic respiration be estimated by component ($R_{foliage}$, R_{wood}, and R_{root}) because components differ in their relationship between respiration and production.

Partitioning to respiration

Hypothesis (iv): *Partitioning to respiration is constant across a wide range of GPP in forest ecosystems and does not vary with resource availability, competition, or stand age*

Despite numerous studies on forest production, little information is available on stand-level autotrophic respiration (R_{total}), a key component of annual carbon budgets (Sprugel *et al.*, 1995; Ryan *et al.*, 1996a; Waring *et al.*, 1998). Previous studies have suggested that R_{total} can consume 30–90% of GPP in forests (Ryan *et al.*, 1997b; Waring *et al.*, 1998; Amthor & Baldocchi, 2001; Gifford, 2003), yet measurements are sparse and techniques laborious.

Based on data for sites where measurements exist for all components, R_{total} used an average of 57% of GPP (Fig. 7), and the relationship had low variability among

sites ($R^2 = 0.95$; SE = 2.3%), which supports our hypothesis. Our estimate of partitioning to respiration (57%) agrees well with a 5-year average for a northern hardwood forest (58%, Curtis *et al.*, 2005) and is similar to, but higher than average values compiled in other studies (53%, Waring *et al.*, 1998; 53%, Gifford, 2003). Our results, however, differ from those of DeLucia *et al.* (2007), where partitioning to respiration averaged 0.47 across a range of sites, possibly because GPP was estimated independently with models for many of the studies.

Partitioning to R_{total} did vary across sites – the range for studies analyzed was 42–71%. Three ecosystems used in this synthesis exhibited substantially higher partitioning to R_{total} than the average (57%), for unknown reasons: 71% for boreal spruce (Ryan *et al.*, 1997b); 66% for boreal pine (Ryan *et al.*, 1997b); and 68% for a primary tropical forest (Chambers *et al.*, 2004). DeLucia *et al.* (2007) also report a range of values for partitioning to respiration (17–77%).

Partitioning to R_{total} did not vary within a site with changes in stand age ($P = 0.60$; $n = 4$) or resource availability ($P = 0.77$; $n = 7$), which supports the second part of our hypothesis. Other studies, some of them included in our compilation, have also shown that partitioning to R_{total} did not vary with stand age (Law *et al.*, 1999; Ryan *et al.*, 2004), resource availability (Ryan *et al.*, 1996a, 2004; Keith *et al.*, 1997; Waring *et al.*, 1998; McDowell *et al.*, 2001; Giardina *et al.*, 2004), aboveground biomass (Ryan *et al.*, 1997b), or competition (Ryan *et al.*, 2004).

Partitioning in response to stand age, competition, and resource availability

Hypothesis (v): *Partitioning to aboveground production increases and to total belowground flux decreases with increasing stand age, decreasing competition, and increasing resources*

Stand age and tree density. Changes in partitioning with stand age generally supported our hypothesis. For most studies, partitioning to $ANPP_{foliage}$ and $ANPP_{wood}$ increased with stand age (Fig. 8a and b), together with a decrease to TBCF (Fig. 8c). One exception was lodgepole pine stands in Wyoming, where partitioning to $ANPP_{foliage}$ decreased in older stands (Litton *et al.*, 2003a, 2004). Another exception were the *Eucalyptus saligna* stands in Hawaii, where partitioning to $ANPP_{wood}$ decreased and to TBCF increased with age (Ryan *et al.*, 2004).

Intraspecific competition (tree density) had no large or consistent effect on partitioning (Fig. 8d–f), which
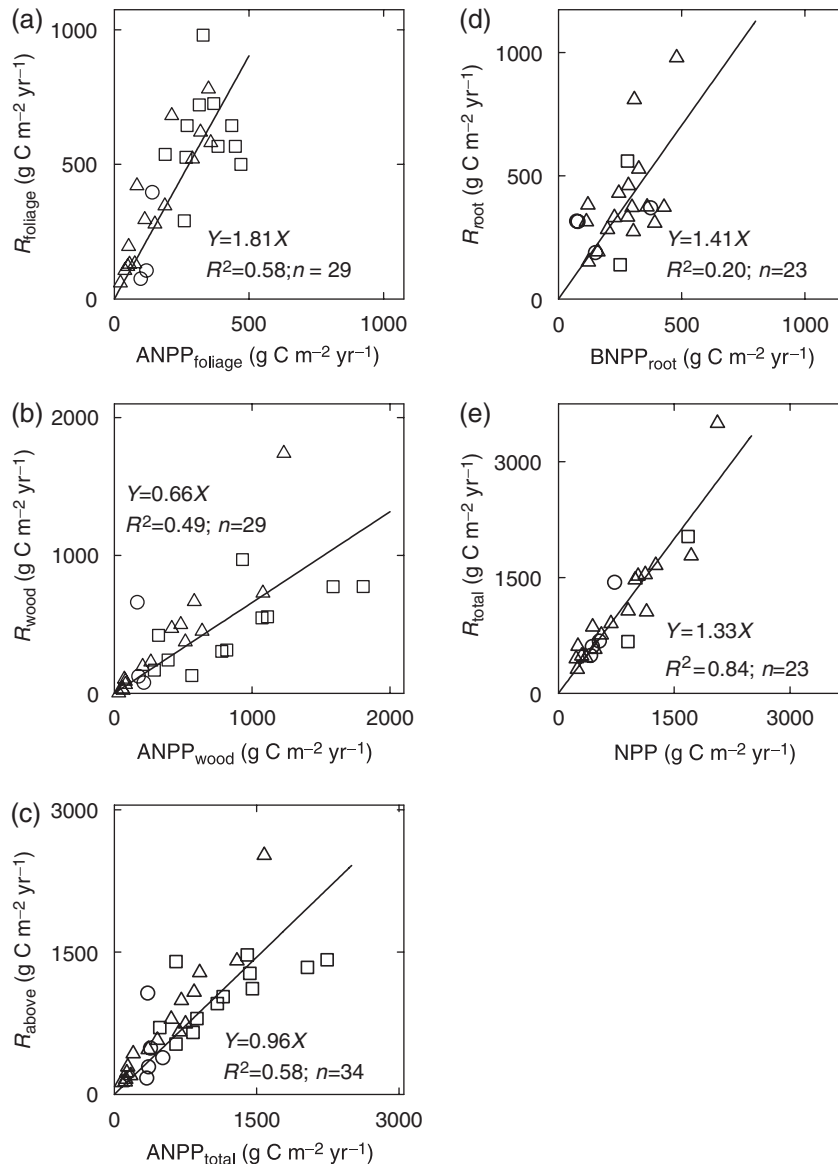
Fig. 6 Autotrophic respiration (R) was strongly linked ($P < 0.01$) to net primary productivity (NPP) for (a) foliage, (b) wood, (c) total aboveground (foliage + wood), (d) roots, and (e) total ecosystem (aboveground + belowground). These relationships correspond to carbon use efficiencies [CUE = NPP/(NPP + Respiration)] of 0.36, 0.60, 0.51, 0.41, and 0.43, respectively. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests.

does not support our hypothesis. Shifts in partitioning to ANPP$_{foliage}$ and ANPP$_{wood}$ were site specific, showing both small increases and decreases, while partitioning to TBCF varied minimally with competition.

Nutrient and water availability. Increased nutrient availability increased partitioning to ANPP and decreased partitioning to TBCF for all studies (Fig. 9a–c), strongly supporting our hypothesis. Fertilization increased partitioning to both ANPP$_{foliage}$ (Fig. 9a) and ANPP$_{wood}$ (Fig. 9b) in all cases except one, where phosphorous

fertilization resulted in a decrease in partitioning to ANPP$_{foliage}$. Partitioning to TBCF decreased with fertilization for all studies (Fig. 9c).

Water availability also changed partitioning (Fig. 9d–f), in support of our hypothesis, but results were not as consistent as for nutrient availability. Partitioning to ANPP$_{wood}$ increased with irrigation for all studies (Fig. 9e), while partitioning to ANPP$_{foliage}$ increased in two studies and decreased in two (Fig. 9d). Partitioning to TBCF decreased with irrigation for all but one study (Fig. 9f). Further support for the effect of water
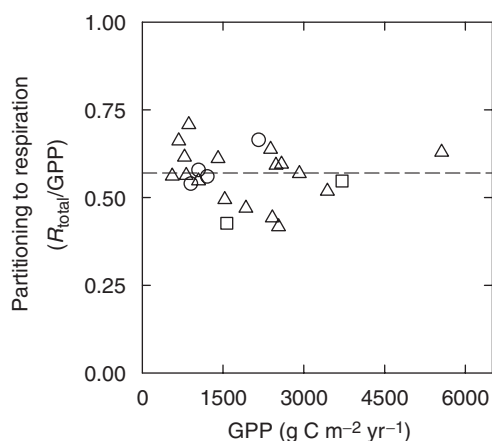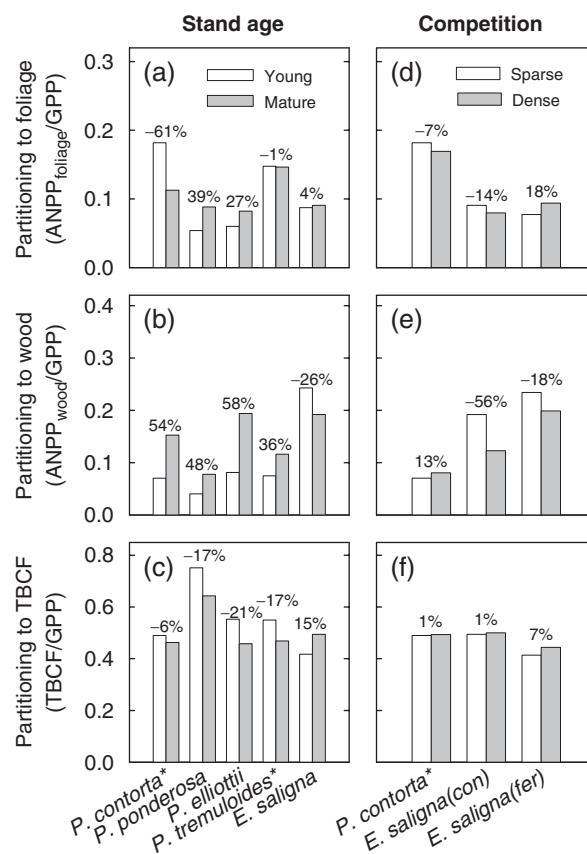
Fig. 7 There was a strong central tendency in partitioning to respiration (R_{total}) across diverse forest ecosystems that represent gradients in resource availability, stand age and competition [0.57 ± 0.02 (Mean ± 1 SE)]. The dashed line is the slope of the relationship between GPP and R_{total} (R_{total} = 0.57 × GPP; R^2 = 0.95; n = 23; $P < 0.01$). However, partitioning to R_{total} did vary across sites – the range for studies analyzed was 42–71%. Triangles are needleleaf evergreen forests, circles are temperate deciduous forests, and squares are broadleaf evergreen forests.

Fig. 8 Carbon partitioning varied with stand age (a–c), but not competition (i.e. tree density; d–f). Variation with age was a result of increased partitioning to (a) $ANPP_{foliage}$ and (b) $ANPP_{wood}$, (c) and decreased partitioning to TBCF in mature stands for all sites but *Eucalyptus saligna*. Data are from Litton *et al.* (2004) for *Pinus contorta*, Law *et al.* (2001) for *Pinus ponderosa*, Ewel *et al.* (1987) and Gholz & Fisher (1982) for *Pinus elliottii*, Fornwalt (1999) for *Populus tremuloides*, and Ryan *et al.* (2004) for *E. saligna*. For studies denoted with an *, $R_{foliage}$ and R_{wood} were estimated using relationships with $ANPP_{foliage}$ and $ANPP_{wood}$ (Fig. 6a and b). TBCF, total belowground carbon flux.

availability on partitioning is evident in *Eucalyptus grandis*, where the effect of irrigation was greater in a drier year (Stape, 2002).

The use of a 2 × 2 factorial design that manipulated both nutrient and water availability in the *E. grandis* (Stape, 2002), *Pinus radiata* (Ryan *et al.*, 1996a), and *Pinus taeda* (Maier *et al.*, 2004) studies allowed us to examine the combined effect of increased nutrient and water supply on partitioning (Fig. 9g–i). Results supported our hypothesis and were similar to the two separate analyses where increased resource supply resulted in greater partitioning to $ANPP_{foliage}$ and $ANPP_{wood}$ (Fig. 9g and h; one exception being partitioning to $ANPP_{foliage}$ for *E. grandis* in a normal precipitation year) and decreased partitioning to TBCF (Fig. 9i). The effect of fertilization plus irrigation on partitioning in the *E. grandis* stands was greater in a drier year.
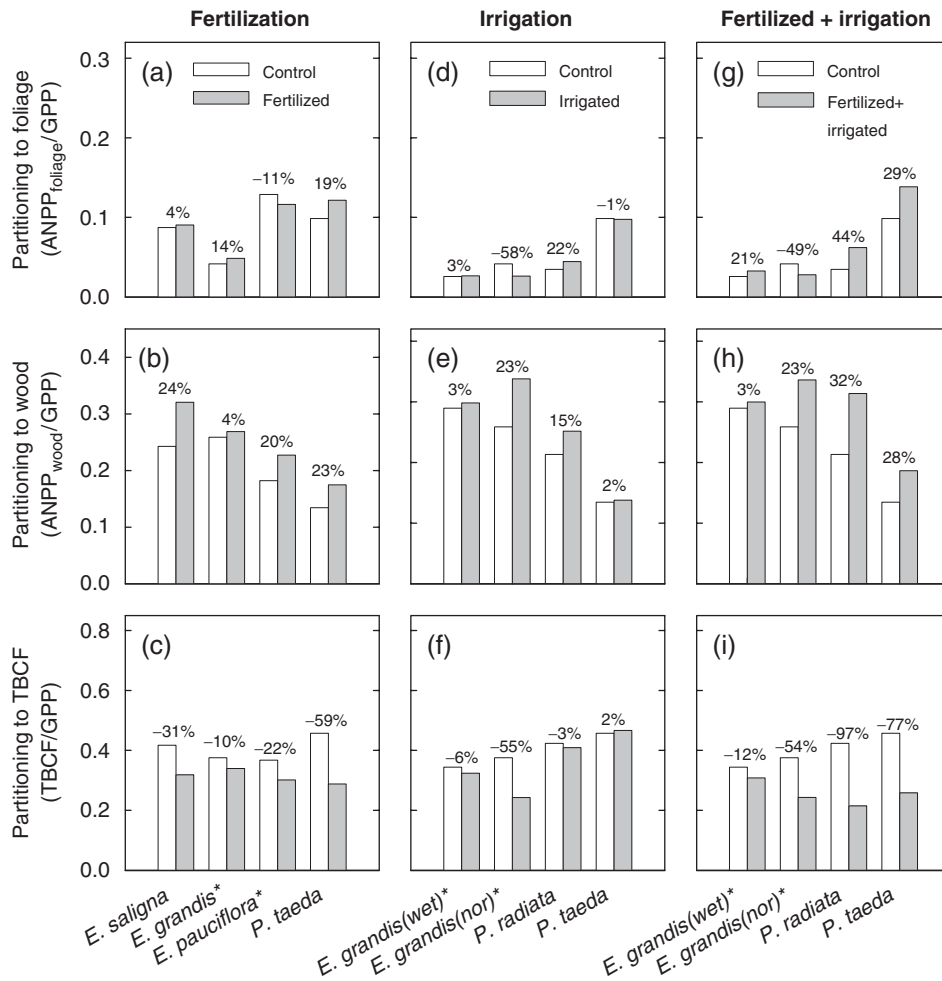
Partitioning to $ANPP_{wood}$ and TBCF varied widely across a broad productivity gradient, with partitioning to $ANPP_{wood}$ increasing and partitioning to TBCF decreasing (Fig. 10b and c). Partitioning to $ANPP_{foliage}$ was remarkably conservative across the gradient (0.26 ± 0.03; Fig. 10a). Shifts in partitioning occurred whether as a result of changes in resources within a site (Fig. 9) or changes in resources across sites (Fig. 10b and c). However, partitioning trends within a site prompted by changing resources or stand age did not correspond in magnitude with changes across the entire productivity gradient. The range in partitioning

seen across studies (Fig. 1) far exceeded changes in partitioning observed within a given site (Fig. 10d–f). For example, TBCF varied from 21% to 75% of GPP across all studies, but within a site change never exceeded 15% of GPP. Still, within-site changes in partitioning in response to resource supply were much greater than expected from the global relationship between GPP and partitioning (Fig. 10c and d).

Hypothesis (vi): *Priorities exist for the products of photosynthesis such that carbon is used first by higher priority tissues and only released to other tissues when those needs are satisfied*

Fig. 9 Carbon partitioning varied with resource availability with an increase in aboveground partitioning to both ANPP$_{foliage}$ (a–c) and ANPP$_{wood}$ (d–f), and a decrease in partitioning to TBCF (g–i) in fertilized and irrigated stands compared to control stands. Note that the effect of increased water availability on partitioning was diminished in a wetter than normal year (wet) for *Eucalyptus grandis*. Data are from Ryan *et al.* (2004) for *Eucalyptus saligna*, Stape (2002) for *E. grandis*, Keith *et al.* (1997) for *Eucalyptus pauciflora*, Maier *et al.* (2004) for *Pinus taeda*, and Ryan *et al.* (1996a) for *Pinus radiata*. For studies denoted with an *, R$_{foliage}$ and R$_{wood}$ were estimated using relationships with ANPP$_{foliage}$ and ANPP$_{wood}$ (Fig. 6a and b).

Our review showed no support for the concept of priorities for the products of photosynthesis in the sense of a 'tipping bucket' model, where the highest-priority pool fills first, followed by the next priority, etc. As GPP increased across sites, all component fluxes increased (Fig. 4). This suggests that all components are likely to first receive some proportion of GPP to satisfy base needs. Partitioning to foliage (ANPP$_{foliage}$ + R$_{foliage}$), however, is conservative and partitioning to ANPP$_{wood}$ and TBCF is primarily determined by resource availability (Fig. 10).

In place of priorities, we suggest that the following points should be considered when conceptualizing how carbon is partitioned in forest ecosystems. First, foliage (ANPP$_{foliage}$ + R$_{foliage}$) and R$_{total}$ use relatively constant fractions of GPP and change little with forest age,

competition, and resource availability. Partitioning to both was conservative across all forests (Figs 7 and 10a). Second, partitioning to ANPP$_{wood}$ and TBCF are the most sensitive to resources and environment. Partitioning to ANPP$_{wood}$ is low and to TBCF high at low resource availability, and increasing GPP shifts partitioning between these components (Fig. 10b and c).

How do data, theory, and models compare?

The general postulate behind existing carbon allocation theory is that plants maximize growth rate by partitioning carbon to various plant organs to optimize the capture of limiting resources (Thornley, 1972a, b; Cannell & Dewar, 1994; Friend *et al.*, 1994; McConnaughay & Coleman, 1999). The observed responses
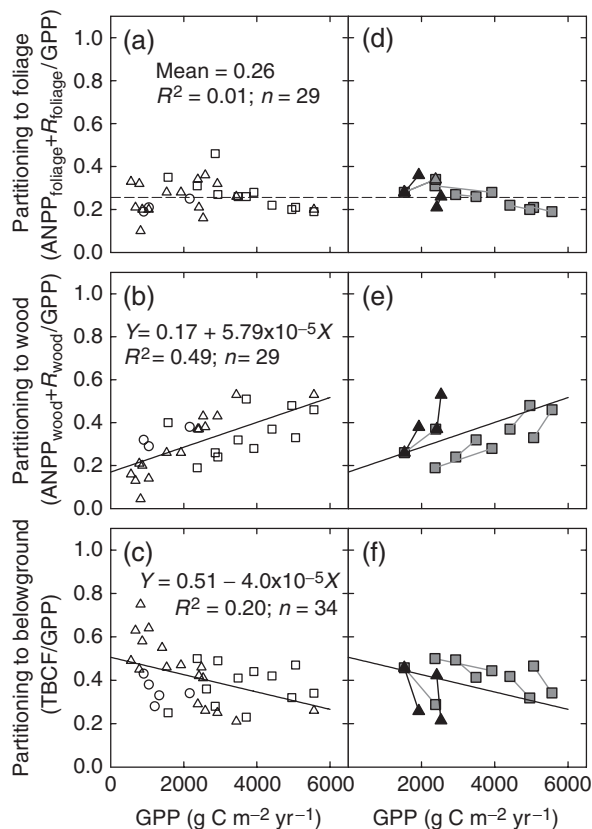
Fig. 10 Carbon partitioning to (a) foliage ($ANPP_{foliage} + R_{foliage}$) was conservative [slope $= -0.3 \times 10^{-6}$; $P = 0.70$; dotted line is a mean value for all forests (0.26 ± 0.03)], while partitioning to (b) wood ($ANPP_{wood} + R_{wood}$) increased and to (c) belowground (TBCF) decreased with increasing GPP across diverse forest ecosystems. Change in resource availability within a site led to minimal change in carbon partitioning to (d) foliage ($ANPP_{foliage} + R_{foliage}$), but a much greater response in partitioning to (e) wood ($ANPP_{wood} + R_{wood}$), and (f) belowground (TBCF) than would be predicted from global relationships (gray fill and lines represent changes in nutrient availability, and black fill and lines changes in nutrient + water availability). Triangles are needleleaf evergreen, circles are temperate deciduous, and squares are broadleaf evergreen forests.

to resource availability in our survey support this prediction. Our survey also supports the idea that resource supply increases GPP while simultaneously decreasing partitioning to TBCF (Giardina et al., 2003).

Understanding the current and future role of forest ecosystems in global carbon cycling is primarily accomplished with the use of terrestrial ecosystem models, and our hypotheses were largely based on how carbon allocation is treated in models (see Cramer et al., 2001). Models differ widely on the relative importance of partitioning to individual components, limits to partitioning, shape of the response function, and response to resource availability. In general, models have either a static or dynamic carbon allocation scheme. Static

models use either fixed partitioning coefficients or observed patterns in biomass or flux to estimate coefficients. Dynamic models use partitioning indices referenced to physiological processes so that partitioning can vary with ontogeny, environment and resource availability. Often, dynamic partitioning schemes have fixed limits for some or all components and use simple linear responses to change partitioning. A thorough comparison of our results with current terrestrial ecosystem and dynamic global vegetation models would be a useful and important exercise to determine if models can accurately predict changes in flux and partitioning with variability in stand age and resource availability. While this exercise was outside of the scope of this work, there are several important generalizations that can made about models and carbon allocation based on our results.

The use of constant partitioning coefficients in static models is unlikely to provide a realistic picture of forest carbon cycling. Friedlingstein et al. (1999) showed that a dynamic carbon allocation scheme in the CASA model, where partitioning varied based on resource supply, changed the relative proportion of biomass in foliage, wood and roots and decreased total global biomass by 10% compared with the original static allocation scheme. Here, our survey indicates that biomass is a poor predictor of flux and partitioning. In addition, resource availability always caused shifts in partitioning, especially to TBCF and $ANPP_{wood}$. Finally, partitioning changed with stand age, although the pattern differed by species.

Should a fixed partitioning coefficient be used to estimate R_{total}? Our analysis and prior analyses (using some of the same studies; Gifford, 1994, 2003; Waring et al., 1998) show that there is a strong central tendency in partitioning to R_{total} and that this does not change within a site in response to forest age and resource supply. Models that do estimate R_{total}, therefore, should show the same lack of response in partitioning. Fixed partitioning to R_{total} also does not support the assumption that respiration is a 'tax' that must be supplied first.

Some dynamic partitioning schemes use the hypothesis that partitioning to different tissues follows a priority, where lower priority tissues only receive carbon after the needs of higher priority tissues are satisfied (Waring & Pitman, 1985; Weinstein et al., 1991). Our data do not support the concept of 'priorities' for the products of photosynthesis (see Hypothesis vi), because increasing GPP resulted in a linear increase in all component fluxes.

Conclusions: carbon allocation patterns and constraints

Our review has shown that carbon allocation in forests is best understood by examining all facets of allocation

(biomass, flux, and partitioning). While data on some components remain sparse, especially belowground flux and autotrophic respiration, this survey and the testing of our hypotheses support several important generalizations:

  (i) Biomass should not be used to infer either flux or partitioning in forests because trees accumulate biomass in both long- and short-lived tissues, and flux and partitioning are not proportional to retention (Figs 2 and 3).

  (ii) Component carbon fluxes are strongly linked. Flux of carbon to all components increases with increasing GPP (a rising tide lifts all boats), regardless of forest type, gradients in resource supply, tree density, or stand age (Fig. 4).

  (iii) Autotrophic respiration is linearly related to production for individual components and for all components combined (Fig. 6). However, respiration should be estimated by component (foliage, wood, and roots), because components differ in the respiration vs. production relationship, and such estimates would reflect differences among stands in flux for individual components.

  (iv) Partitioning to R_{total} is conservative across a wide range of GPP (57%; Fig. 7) and does not change with resources, stand age or competition within an individual site. However, sites do differ for unknown reasons.

  (v) Partitioning to TBCF and $ANPP_{wood}$: (a) is sensitive to changes in water and nutrient availability within a site (Fig. 9), (b) varies with age (Fig. 8), but the pattern is not consistent across all studies, and (c) does not vary with intraspecific competition (tree density; Fig. 8).

  (vi) Partitioning to foliage ($ANPP_{foliage} + R_{foliage}$) is conservative across a wide range of forests (0.26 ± 0.03; Fig. 10).

  (vii) Partitioning to wood ($ANPP_{wood} + R_{wood}$) is low and to TBCF is high at low resource availability, but these patterns shift with increasing GPP (i.e. resource availability), whether as a result of changes in resources within a site or from changes across sites (Fig. 10).

  (viii) Available data do not support the concept of priorities for the products of photosynthesis.

  (ix) Carbon fluxes vary more among forests than does partitioning. Partitioning is critical to understanding carbon allocation, and should be an area of focus for future work and models.

We identified patterns in and responses to carbon allocation, but several areas require further study. Changes in flux and partitioning with forest development, particularly to belowground, remain poorly understood. The cause of differences in partitioning to autotrophic respiration among sites is not known. The response of partitioning to changes in stand age and resource availability is relatively consistent among studies, but none have examined the shape or duration of the response. Finally, other factors such as intraspecific genotypic diversity (Crutsinger *et al.*, 2006), atmospheric CO_2 concentrations (Schäfer *et al.*, 2003; Palmroth *et al.*, 2006) and temperature (Raich *et al.*, 2006) may influence carbon allocation but data are limited.

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