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Forest carbon use efficiency: is respiration a constant fraction of gross primary production?

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Abstract

Carbon-use efficiency (CUE), the ratio of net primary production (NPP) to gross primary production (GPP), describes the capacity of forests to transfer carbon (C) from the atmosphere to terrestrial biomass. It is widely assumed in many landscape-scale carbon-cycling models that CUE for forests is a constant value of ~ 0.5 . To achieve a constant CUE, tree respiration must be a constant fraction of canopy photosynthesis. We conducted a literature survey to test the hypothesis that CUE is constant and universal among forest ecosystems. Of the 60 data points obtained from 26 papers published since 1975, more than half reported values of GPP that were not estimated independently from NPP; values of CUE calculated from independent estimates of GPP were greater than those calculated from estimates of GPP derived from NPP. The slope of the relationship between NPP and GPP for all forests was 0.53, but values of CUE varied from 0.23 to 0.83 for different forest types. CUE decreased with increasing age, and a substantial portion of the variation among forest types was caused by differences in stand age. When corrected for age the mean value of CUE was greatest for temperate deciduous forests and lowest for boreal forests. CUE also increased as the ratio of leaf mass-to-total mass increased. Contrary to the assumption of constancy, substantial variation in CUE has been reported in the literature. It may be inappropriate to assume that respiration is a constant fraction of GPP as adhering to this assumption may contribute to incorrect estimates of C cycles. A 20% error in current estimates of CUE used in landscape models (i.e. ranging from 0.4 to 0.6) could misrepresent an amount of C equal to total anthropogenic emissions of CO₂ when scaled to the terrestrial biosphere.

Keywords: age, biomass allocation, biome, carbon cycle, data synthesis, ecosystem, forest, gross primary production, net primary production, respiration

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Introduction

Plant respiration (R_a) exerts strong control over the retention of carbon (C) in ecosystems (Valentini *et al.*, 2000), yet the factors regulating R_a are not well understood and methods for calculating its contribution to the C budgets of individual ecosystems are poorly developed. Many models, such as CASA (Potter *et al.*, 1993) and FOREST-BGC (Running & Coughlan, 1988), circumvent uncertainties associated with quantifying R_a

by relying on a fixed value of carbon-use efficiency (CUE), defined as the ratio of net primary production (NPP) to gross primary production (GPP; Gifford, 2003). It has been argued that CUE is constant (Gifford, 1994, 1995, 2003; Dewar *et al.*, 1998), and Waring *et al.* (1998) suggested that a universal value of 0.47 is appropriate for most forests. However, methodological problems with its calculation may mask variation in CUE (Medlyn & Dewar, 1999).

Questions concerning the way CUE is calculated leave open the possibility that it may vary among forest types. The major elements of the C cycle contributing to CUE are GPP (annual photosynthesis), NPP (annual

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increment of reduced C), and R_a , where GPP is the sum of NPP and R_a . Of these three components, estimates of NPP for forest ecosystems are the most direct and robust as this component is comprised primarily of the annual increment of C in wood and foliage litter (Clark *et al.*, 2001; DeLucia *et al.*, 2005). Forest GPP is complex as it incorporates photosynthetic C gain by all the leaves in the overstory and understory and it is typically not measured directly. Gross primary production often is estimated indirectly by summing NPP and R_a , where R_a is scaled from tissue-specific measurements up to the ecosystem level (e.g. Waring *et al.*, 1998; Curtis *et al.*, 2005; Kerkhoff *et al.*, 2005). Furthermore, the portion of R_a associated with growth is calculated as a function of NPP. Herein lies the problem; in many studies, GPP is calculated in part from NPP and aspects of R_a similarly are derived from NPP. The lack of independence between estimates of NPP and GPP constrains the possible values of CUE to near 0.5, so the conclusion that CUE is constant among forests may be an artifact (Medlyn & Dewar, 1999).

We conducted a literature review to test the hypothesis that CUE is constant and universal among forest ecosystems. While the availability of publications reporting CUE or its components (NPP and GPP) is limited, values from ~ 0.2 to ~ 0.8 indicate that this ecosystem parameter is more variable than considered previously. The variation in CUE within ecosystems could reveal much needed information on biotic and abiotic factors regulating components of R_a . Similarly, quantifying variation in CUE among ecosystems could prove to be a useful tool when calculating large-scale C budgets.

Theoretical considerations

The different theories describing the behavior of plant respiration described below fuel uncertainty about the constancy of CUE. If R_a is proportional to GPP for forest stands that vary in species composition or age, or that are exposed to different climates or soil fertility, then CUE should be constant. Alternatively, if R_a is proportional to biomass then CUE should vary with differences in allocation.

At any moment in time R_a is regulated by the availability of sugars from photosynthesis and the demand for ATP by existing and developing tissues (Atkin & Tjoelker, 2003; Gonzalez-Meler *et al.*, 2004). Because R_a ultimately depends on sugars from photosynthesis, these two processes should remain in balance when integrated over long periods of time suggesting that R_a should be constrained by or be proportional to GPP (Dewar *et al.*, 1998). This theoretical argument and early observations with herbaceous plants that whole-plant

respiration was a fixed proportion of the photosynthetic rate (McCree & Troughton, 1966), paved the way for contemporary concepts regarding the constancy of CUE. The relationship between CUE and the ratio of plant respiration (R_a) to photosynthesis (GPP) is equivalent to $1 - \text{CUE}$ ($\text{CUE} = \text{NPP}/\text{GPP} = 1 - R_a/\text{GPP}$; Gifford, 1994; Amthor, 2000).

The alternative view that R_a scales with biomass is rooted in the almost universal observation that whole-organism respiration varies with $\sim 3/4$ power of body size in animals (see Hedin, 2006). Reich *et al.* (2006) demonstrated whole-plant R_a scales with plant size and nitrogen content, but unlike animals the relationship is approximately linear. While Reich *et al.* (2006) base their conclusion on a vast data set; their observations were based on instantaneous measurements of specific rates of respiration from various parts of small herbaceous plants and tree saplings. It is unclear if seasonally integrated values of dynamic whole-plant respiration and photosynthesis for large trees follow this relationship. Woody tissues that provide support and conduction to large trees represent a substantial investment in live biomass and it is assumed that respiratory costs increase in proportion to this investment (Waring & Schlesinger, 1985). However, the decline in tissue specific rates of sapwood respiration (Carey *et al.*, 1997; Pruyn *et al.*, 2002) may produce a less than isometric scaling between R_a and dry mass.

Recognizing these contrasting views of how R_a is regulated, an increasing number of studies have taken the approach to divide R_a into maintenance and growth components; maintenance being proportional to plant size and growth being proportional to GPP (Amthor, 2000). While some modeling approaches have constrained growth and maintenance respiration to satisfy a fixed CUE value near 0.5 (e.g. Kerkhoff *et al.*, 2005), most approaches fit separate functions to growth and maintenance components resulting in CUE values that are different from 0.5 (e.g. Goetz *et al.*, 1999; Ito & Oikawa, 2002). The only empirical study relating growth and maintenance respiration and CUE showed that changes in growth and maintenance respiration related to plant age resulted in substantial variation in CUE values ranging from 0.2 to 0.7 (van Iersel, 2003).

It is axiomatic that following canopy closure the increase in R_a with stand age and tree size contributes to the decline in NPP, and that this decline would cause CUE to decline in old forests. Until recently, understanding of forest C cycling rested on the belief that GPP reached a maximum early in stand development as foliage occupied all available space, while R_a continue to increase as C increasingly was invested in woody tissues (Kira & Shidei, 1967; Odum, 1969; Waring & Schlesinger, 1985). This model is challenged by

observations that the increase in R_a with stand age is too small to explain the decline in NPP (Ryan & Waring, 1992). Recent observations that canopy photosynthesis becomes limited by the hydraulic properties of trees as they grow larger (Ryan *et al.*, 2006), have caused reconsideration of the importance of increasing R_a as the primary factor responsible for age-related decreases in NPP, and have instead embraced the importance in age-related decreases in GPP. If GPP and R_a decrease in proportion, CUE should remain constant as forests age.

The application of ecosystem models to the question of variation in CUE with stand age has yielded conflicting conclusions. A comparison of a young and an old stand of *Pinus contorta* revealed that the hydraulic limitations to photosynthesis, as well as reduced soil nutrient availability were the primary factors that contributed to the decline in NPP with age, while increasing sapwood respiration made only a small contribution to this decline (Murty *et al.*, 1996). In this case, simultaneous decreases in GPP and NPP would dampen the decline in CUE in aging stands. In contrast, Mäkelä and Valentine (2001) demonstrated that increasing sapwood respiration was responsible for the decrease in the ratio of NPP/GPP following canopy closure as stands of *Pinus sylvestris* aged. The tissue-specific rate of sapwood respiration declined with increasing tree height, but this decrease was insufficient to counter the large increases in sapwood volume. Methodological issues and contrasting theoretical results leave open the question of the constancy of forest CUE.

If CUE is variable among ecosystems or within an ecosystem with changes in resource availability, climate or age, what are the factors that control its variation? At scales from the individual leaf to the ecosystem, respiration and photosynthesis are closely coupled processes and it is not unreasonable to expect a predictable relationship between them. In addition to being coupled by availability of sugars, Dewar *et al.* (1998) asserted that the relationship between respiration and photosynthesis is regulated by leaf protein. Photosynthetic capacity is governed by the investment in leaf protein and because recycling of protein in leaves and elsewhere is energetically demanding, protein levels also govern respiration rates. While this coupling between R_a and GPP by sugars and protein levels should contribute to a relatively constant CUE for a given species or ecosystem, this set point may vary between ecosystems with different patterns of C allocation and with variation in resource availability. For example, if exposure to elevated CO_2 decreases leaf nitrogen content, and thus R_a , CUE may increase (Dewar *et al.*, 1998).

Having reported values as low as 0.12 for a moist tropical forest and as high as 0.63 for an ash plantation,

Amthor (2000) raised the question what is the 'allowable' range for CUE. Based on theoretical calculations of growth efficiency and the respiratory costs associated with maintenance, nutrient acquisition and transport, Amthor (2000) concluded that CUE should vary between 0.2 and 0.65 (see van Iersel, 2003 for experimental confirmation of this range in herbaceous species). This range is considerable, as a 25% increase in CUE is equivalent to a >37% increase in growth per unit of photosynthesis.

Compilation of data

To test the hypothesis that CUE is constant and universal among forest ecosystems, we conducted a search of the *Science Citation Index Expanded* database from *ISI Web of Knowledge*, *Web of Science* with 'forest' and 'production' as keywords, and with no restriction on date of publication. From this initial list, we identified articles that reported values of NPP (above and below-ground) and GPP for the same forest during the same time period. Additional articles were identified from the bibliography of these papers. While some papers relied on model estimates for some portion of the C budget for a specific forest, papers that relied solely on theoretical calculations were excluded. In total, 26 papers were identified and these articles reported 60 values of NPP and GPP that were then used to calculate CUE. Forests were assigned to one of six types according to Barbour and Billings (2000; Table 1).

Studies where GPP was estimated by summing the component parts of the C budget, including the major respiratory fluxes and NPP, were characterized as 'derived.' Waring *et al.* (1998) and Hamilton *et al.* (2002) exemplify this approach. Studies with derived values of GPP are vulnerable to errors associated with autocorrelation illustrated by Medlyn and Dewar (1999). 'Independent' estimates of GPP typically were obtained by micrometeorological methods, where gross ecosystem exchange was calculated as the sum of net ecosystem exchange and ecosystem respiration derived from eddy flux measurements (e.g. Granier *et al.*, 2000; Curtis *et al.*, 2005), by a locally calibrated model of canopy photosynthesis (e.g. Ryan *et al.*, 1996; Law *et al.*, 2000; Lai *et al.*, 2002; Gielen *et al.*, 2005), from direct measurements of canopy conductance (e.g. Schäfer *et al.*, 2003), or from a combination of these methods (e.g. Arneeth *et al.*, 1998; Malhi *et al.*, 1999; Turner *et al.*, 2003).

The major components of forest NPP are wood increment and litterfall, and virtually all studies used a biometric approach to calculate the increment of wood C, where the change in biomass C for whole trees were estimated from allometric equations applied to the annual change in diameter and measurements of

Table 1 Carbon use efficiency (CUE) of forest ecosystems

Forest type	Dominant species	Age (years)	Treatment	Method: NPP/GPP	GPP estimate	GPP	NPP	CUE	References
Boreal	<i>Picea mariana</i>	150	n/a	Biometric/scaling	Derived	1080	252	0.23	Ryan <i>et al.</i> (1997)
Boreal	<i>Pinus banksiana</i>	63	n/a	Biometric/scaling	Derived	880	229	0.26	Ryan <i>et al.</i> (1997)
Boreal	<i>Populus tremuloides</i>	53	n/a	Biometric/scaling	Derived	1160	416	0.36	Ryan <i>et al.</i> (1997)
Boreal	<i>Picea mariana</i>	115	n/a	Biometric/scaling	Derived	1090	307	0.28	Ryan <i>et al.</i> (1997)
Boreal	<i>Pinus banksiana</i>	63	n/a	Biometric/scaling	Derived	772	237	0.31	Ryan <i>et al.</i> (1997)
Boreal	<i>Populus tremuloides</i>	68	n/a	Biometric/scaling	Derived	1350	440	0.33	Ryan <i>et al.</i> (1997)
Boreal	<i>Picea mariana</i>	115	n/a	Micromet/model	Independent	963	517	0.54	Malhi <i>et al.</i> (1999)
Boreal	<i>Picea mariana</i>	120	n/a	Biometric, model/micromet, model	Independent	812	181	0.22	Turner <i>et al.</i> (2003)
West Coast Maritime	<i>Pseudotsuga menziesii</i>	500	n/a	Biometric/scaling	Derived	1906	597	0.31	Harmon <i>et al.</i> (2004)
West Coast Maritime	<i>Picea sitchensis</i> , <i>Tsuga heterophylla</i>	n/a	n/a	Biometric/scaling	Derived	1400	681	0.49	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Alnus rubra</i>	n/a	n/a	Biometric/scaling	Derived	1558	813	0.52	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Pseudotsuga menziesii</i>	n/a	n/a	Biometric/scaling	Derived	1665	770	0.46	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Tsuga heterophylla</i> , <i>Pseudotsuga menziesii</i>	n/a	n/a	Biometric/scaling	Derived	2404	1122.5	0.47	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Tsuga mertensiana</i>	n/a	n/a	Biometric/scaling	Derived	879	373	0.42	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Juniperus occidentalis</i>	n/a	n/a	Biometric/scaling	Derived	302	122	0.40	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Pinus ponderosa</i>	n/a	n/a	Biometric/scaling	Derived	364	159	0.44	Williams <i>et al.</i> (1997)
West Coast Maritime	<i>Pinus ponderosa</i>	45	n/a	Biometric/scaling	Derived	901	413	0.46	Law <i>et al.</i> (1999)
West Coast Maritime	<i>Pinus ponderosa</i>	15	n/a	Biometric/scaling	Derived	1192	357	0.30	Law <i>et al.</i> (2001)
West Coast Maritime	<i>Pinus ponderosa</i>	250	n/a	Biometric/scaling	Derived	1486	472	0.32	Law <i>et al.</i> (2001)
West Coast Maritime	<i>Pinus ponderosa</i>	250	n/a	Biometric/model	Independent	1235	406	0.33	Law <i>et al.</i> (2000)
Temperate Coniferous	<i>Pinus taeda</i>	15	Ambient CO ₂	Biometric/scaling	Derived	2371	705	0.30	Hamilton <i>et al.</i> (2002)
Temperate Coniferous	<i>Pinus taeda</i>	15	Elevated CO ₂	Biometric/scaling	Derived	2805	897	0.32	Hamilton <i>et al.</i> (2002)
Temperate Coniferous	<i>Pinus taeda</i>	12	Control	Biometric/scaling	Derived	1313	556	0.42	Maier <i>et al.</i> (2004)
Temperate Coniferous	<i>Pinus taeda</i>	12	Irrigated	Biometric/scaling	Derived	1584	680	0.43	Maier <i>et al.</i> (2004)
Temperate Coniferous	<i>Pinus taeda</i>	12	Fertilized	Biometric/scaling	Derived	2550	1032	0.40	Maier <i>et al.</i> (2004)
Temperate Coniferous	<i>Pinus taeda</i>	12	Irrigated, fertilized	Biometric/scaling	Derived	2664	1124	0.42	Maier <i>et al.</i> (2004)
Temperate Coniferous	<i>Pinus taeda</i>	16	n/a	Biometric/scaling	Derived	4124	2056	0.50	Kinerson <i>et al.</i> (1977)
Temperate Coniferous	<i>Pinus taeda</i>	8	Fertilized	Model/model	Derived	1795	1185	0.66	Lai <i>et al.</i> (2002)
Temperate Coniferous	<i>Pinus taeda</i>	8	Control	Model/model	Derived	1220	781	0.64	Lai <i>et al.</i> (2002)
Temperate Coniferous	<i>Pinus taeda</i>	15	Ambient CO ₂	Biometric/model	Independent	2140	899	0.42	Schafer <i>et al.</i> (2003)
Temperate Coniferous	<i>Pinus taeda</i>	15	Elevated CO ₂	Biometric/model	Independent	2899	1117	0.39	Schafer <i>et al.</i> (2003)
Temperate Coniferous	<i>Pinus taeda</i>	20	Control	Biometric/model	Independent	2950	904	0.31	Ryan <i>et al.</i> (1996)
Temperate Coniferous	<i>Pinus radiata</i>	20	Irrigated	Biometric/model	Independent	2690	1142	0.42	Ryan <i>et al.</i> (1996)

Temperate Coniferous	<i>Pinus radiata</i>	20	Irrigated, fertilized	Biometric/model	Independent	3690	1720	0.47	Ryan <i>et al.</i> (1996)
Temperate Coniferous	<i>Pinus radiata</i>	10	3-year-average	Biometric/model	Independent	1780	960	0.54	Armeth <i>et al.</i> (1998)
Temperate Coniferous	<i>Pinus radiata</i>	10	Dry year	Biometric/model	Independent	1690	880	0.52	Armeth <i>et al.</i> (1998)
Temperate Coniferous	<i>Pinus radiata</i>	10	Moist year	Biometric/model	Independent	1840	1060	0.58	Armeth <i>et al.</i> (1998)
Temperate Deciduous	<i>Liriodendron tulipifera</i>	48	n/a	Biometric/scaling	Derived	2170	730	0.34	Harris <i>et al.</i> (1975)
Temperate Deciduous	<i>Quercus rubra, Acer rubrum</i>	n/a	n/a	Biometric/scaling	Derived	1246	659	0.53	Waring <i>et al.</i> (1998)
Temperate Deciduous	<i>Nothofagus truncata</i>	n/a	n/a	Biometric/scaling	Derived	2470	1010	0.41	Waring <i>et al.</i> (1998)
Temperate Deciduous	<i>Liquidambar styraciflua</i>	12	Ambient CO ₂	Biometric/scaling	Derived	2002	1032	0.52	DeLucia <i>et al.</i> (2005), Norby <i>et al.</i> (2002)
Temperate Deciduous	<i>Liquidambar styraciflua</i>	12	Elevated CO ₂	Biometric/scaling	Derived	2438	1198	0.49	DeLucia <i>et al.</i> (2005), Norby <i>et al.</i> (2002)
Temperate Deciduous	<i>Betula ermanii, B. platyphylla, Quercus alba, Quercus pinus, Quercus mongolia</i>	40	n/a	Scaling/micromet	Derived	1146	817	0.71	Saigusa <i>et al.</i> (2002)
Temperate Deciduous	<i>Carya ovata</i>	57	n/a	Micromet/model	Independent	1725	944	0.55	Malhi <i>et al.</i> (1999)
Temperate Deciduous	<i>Populus alba</i>	5	Ambient CO ₂	Biometric/model	Independent	2585	1493	0.58	Gielen <i>et al.</i> (2005)
Temperate Deciduous	<i>Populus alba</i>	5	Elevated CO ₂	Biometric/model	Independent	2829	2029	0.72	Gielen <i>et al.</i> (2005)
Temperate Deciduous	<i>Populus nigra</i>	5	Ambient CO ₂	Biometric/model	Independent	2773	1983	0.72	Gielen <i>et al.</i> (2005)
Temperate Deciduous	<i>Populus nigra</i>	5	Elevated CO ₂	Biometric/model	Independent	2921	2413	0.83	Gielen <i>et al.</i> (2005)
Temperate Deciduous	<i>Populus x euramericana</i>	5	Ambient CO ₂	Biometric/model	Independent	2150	1532	0.71	Gielen <i>et al.</i> (2005)
Temperate Deciduous	<i>Populus x euramericana</i>	5	Elevated CO ₂	Biometric/model	Independent	2550	1853	0.73	Gielen <i>et al.</i> (2005)
Temperate Deciduous	<i>Fagus sylvatica</i>	40	n/a	Biometric/micromet	Independent	1298	522	0.40	Granier <i>et al.</i> (2000)
Temperate Mixed	<i>Pinus strobes, Acer rubrum</i>	76	n/a	Biometric/scaling	Derived	1585	661	0.42	Curtis <i>et al.</i> (2005)
Temperate Mixed	<i>Quercus alba, Quercus coccinea, Pinus rigida</i>	43	n/a	Biometric/scaling	Derived	1280	600	0.47	Harris <i>et al.</i> (1972)
Temperate Mixed	<i>Quercus alba, Quercus coccinea, Pinus rigida</i>	20	n/a	Biometric/scaling	Derived	1324	598	0.45	Whittaker & Woodwell (1969)
Temperate Mixed	<i>Pinus strobes, Acer rubrum</i>	76	n/a	Biometric/micromet	Independent	1221	661	0.54	Curtis <i>et al.</i> (2005)
Temperate Mixed	<i>Quercus rubra, Acer rubrum, Taxus canadensis</i>	100	n/a	Biometric, model/micromet, model	Independent	1639	637	0.39	Turner <i>et al.</i> (2003)
Tropical	<i>Eucalyptus saligna</i>	5	Control	Biometric/scaling	Derived	2950	1485	0.50	Giardina <i>et al.</i> (2003)
Tropical	<i>Eucalyptus saligna</i>	5	Fertilized	Biometric/scaling	Derived	3950	2100	0.53	Giardina <i>et al.</i> (2003)
Tropical	> 200 species/hectare	400	n/a	Biometric/scaling	Derived	3000	900	0.30	Chambers <i>et al.</i> (2000)
Tropical	> 200 species/hectare	500	n/a	Biometric/micromet	Independent	3040	1560	0.51	Malhi <i>et al.</i> (1999)

CUE is defined as the ratio of net primary production (NPP, gC m⁻² yr⁻¹) to gross primary production (GPP, gC m⁻² yr⁻¹). The methods used to estimate these parameters are shown as the column titled 'method: NPP/GPP', which indicates the method used to estimate NPP and GPP, respectively. The methods were: Biometric, the summation of tissue-specific increment; Scaling, chamber-based measurement of respiratory fluxes scaled to a yearly estimate using a temperature response function; Micromet, micrometeorological measurement of carbon flux by eddy-covariance; Model, the use of mathematical models to estimate carbon fluxes, generally a site-specific model of canopy photosynthesis. "GPP estimate" indicates if this value was estimated independently from NPP or if it was derived in part from NPP.

biomass C accumulated in litter traps. CUE was calculated as the simple ratio, NPP/GPP.

Data analysis

Data were analyzed with mixed linear models and regression analyses after the residuals were checked for homoscedasticity and normality (Proc Mixed, Proc Reg, SAS 9.1). Log transformations were performed when needed to satisfy analysis assumptions. ANCOVA analyses were checked for interactions between the covariate and fixed effects. If an interaction was not detected, it was assumed that the levels of the fixed effect did not differ in their relationship to the covariate. Restricted maximum likelihood (REML) was used to compute mean squares, as this method is preferred over ANOVA for unbalanced data (Spilke *et al.*, 2005). Variation in forest NPP caused by the fixed effect of the GPP estimation method (two levels, independent, and derived) was investigated using ANCOVA with GPP as a covariate. A separate ANCOVA was used to evaluate the possible interactive effects of GPP estimation method and forest age on CUE. GPP estimation method was included as a fixed effect with forest age as a covariate. Variation in CUE caused by the fixed effect of forest type (six levels) was estimated using ANCOVA with forest age included as a covariate. Linear contrasts using the *t*-statistic were used to test for significant differences between forest types. The experiment-wise error rate was controlled at $\alpha = 0.05$ using the Tukey adjustment.

Results and discussion

The data available in the literature are limited and biased toward temperate North American ecosystems that either were plantations or were strongly dominated by a single species. Of the 60 published values that met our selection criteria, 36 were from temperate conifer or deciduous forests, or temperate mixed forests (Table 1). Tropical forests represent approximately 40–50% of land area in forests worldwide and approximately 30% of forest productivity (Whittaker, 1975; Dixon *et al.*, 1994), but only two studies were conducted in native tropical forests. Plantations or monocultures represented 49 of the published studies and eight studies presented data from boreal forests. Experimental manipulations were rare. Four studies included exposure of large plots to Free Air CO₂ Enrichment (FACE), and another four experiments manipulated water or nutrient availability. No studies explicitly included stand age as a variable, but three studies independently quantified the major components of the C cycle for *Pinus ponderosa* forests that varied in age from 15 to 250 years. Because of the restricted scope of

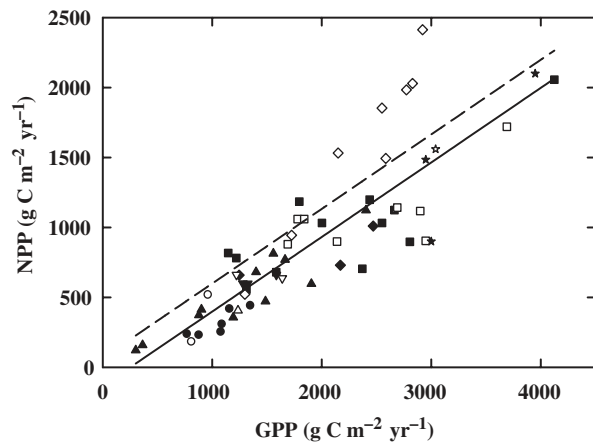


Fig. 1 The relationship between net primary production (NPP) and gross primary production (GPP) for different forest types. Closed symbols represent values of GPP that were derived from estimates of NPP and R_a ; open symbols represent values of GPP that were estimated independently from NPP. Symbols for the different forest types are: boreal (circles), West Coast Maritime (triangles), temperate conifer (squares), temperate deciduous (diamonds), temperate mixed (inverted triangles), and Tropical (stars). The intercept of the relationship between NPP and derived estimates of GPP (solid line) was significantly lower than the intercept for the relationship between NPP and independent estimates of GPP (dashed line; see results).

studies published to date it may not be advisable to extrapolate a single value of CUE to forests worldwide.

NPP was linearly related to GPP among forest ecosystems that varied in GPP from 302 $\text{g C m}^{-2} \text{yr}^{-1}$ for a mixed juniper–oak forest to 4124 $\text{g C m}^{-2} \text{yr}^{-1}$ for a young loblolly pine plantation (Fig. 1). The slope of this relationship ($\text{NPP} = 0.53 \times \text{GPP} - 110.1$, $\text{g C m}^{-2} \text{yr}^{-1}$, $r^2 = 0.72$, $P < 0.01$) represents a global estimate of CUE and was similar to the value of 0.47 from Waring *et al.* (1998); however, individual estimates of CUE varied considerably and systematically from the putative global value (Fig. 2). Moreover, values of CUE that relied on ‘independent’ estimates of GPP were significantly greater from those that relied on ‘derived’ estimates. While there was no difference in the slope of GPP vs. NPP between methods (ANCOVA, $P > 0.1$), the intercept was higher for studies where GPP was estimated independently from other components of the C budget ($\text{NPP} = 0.53 \times \text{GPP} + 66.05$) compared with those with ‘derived’ estimates ($\text{NPP} = 0.53 \times \text{GPP} - 134.51$; ANCOVA, $P < 0.001$). The average CUE value for data with a derived estimate of GPP was 0.42 ($n = 38$) vs. 0.52 ($n = 22$) for data with an independent estimate of GPP.

Analysis of published values revealed significant variation in CUE among forest ecosystems, even after an adjustment for differences in stand age was applied

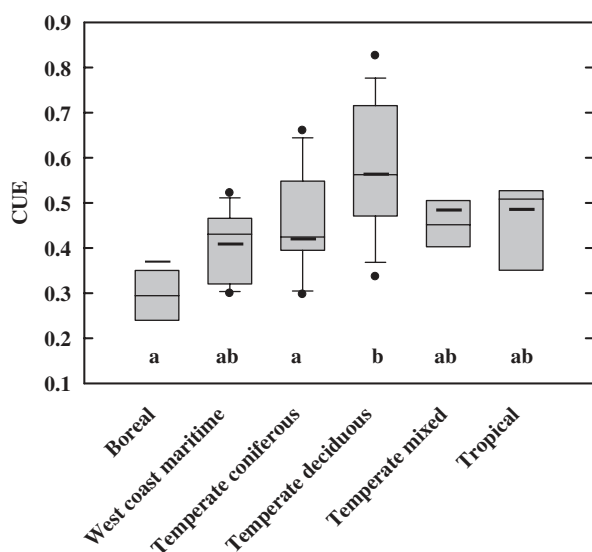


Fig. 2 Carbon use efficiencies (CUE) of major forest types. From left to right: boreal, $n = 8$; West Coast Maritime, $n = 12$; temperate conifer, $n = 17$; temperate deciduous, $n = 14$; temperate mixed, $n = 5$; tropical, $n = 4$. The thin solid lines in the box plots indicate the median of the raw data and the bold lines indicate the mean after the forest type was adjusted to the mean age of all forests (67.8 years). The top and bottom of the boxes indicate the 25th and the 75th percentiles, the whiskers above and below the boxes indicate the 90th and 10th percentiles, and closed circles indicate probable outliers. Categories that do not share the same letter are significantly different at $P < 0.05$ after a Tukey adjustment was applied to control the experiment-wise error rate and after correcting for differences in stand age (ANCOVA, PROC MIXED, SAS 9.1). Age was not known for seven of the West Coast Maritime forest stands, so when stand age was included as a statistical covariate these data were dropped from the analysis. As a result of the reduction in degrees of freedom, CUE for West Coast Maritime was not different from temperate deciduous forest for the age adjusted means (bold lines), but temperate coniferous forest was significantly different from temperate deciduous forest ($P < 0.05$).

(ANCOVA, $P < 0.01$; Fig. 2). Stand age was included as a covariate in the statistical analysis as it also affects CUE. The lowest value of CUE (0.22) was for a 115-year-old stand of *Picea mariana* and the highest value (0.83) was for a 5-year-old stand of *Populus nigra* exposed to elevated atmospheric CO_2 (Table 1). The average value of CUE for old boreal forests (0.32) was the lowest among different forest types and the average value (0.59) was highest for temperate deciduous forests. CUE for temperate deciduous forest was approximately 26% greater than the universal value of 0.47 reported by Waring *et al.* (1998), while the value for the few tropical forests in this study (0.46) was similar to this universal value.

In addition to generally low productivity, the low values of CUE for boreal forests may be associated with high rates of C loss during the dormant season (Goulden *et al.*, 1997; Ryan *et al.*, 1997). Maintaining a disproportionately large quantity of biomass in foliage enhances nutrient retention by black spruce but also results in substantial C losses from foliage during the dormant season. High respiratory losses by foliage are reflected in the GPP/leaf mass ratio. The average value of the ratio of GPP to leaf C for forests in this study was 6.5 ± 4.0 SD ($n = 41$); this value was below 2 for boreal spruce forests and ~ 8 for temperate deciduous and conifer forests. Of the two values representing native tropical forests, one value for a moist forest in the Amazon was as low as the CUE values for boreal spruce forests (0.32; Chambers *et al.*, 2004). This low value may be associated with high respiratory costs associated with warm conditions and a long growing season. Alternatively, if nutrient deficiencies limit growth, C would be in excess and may be returned to the atmosphere by futile respiratory cycles (Chambers *et al.*, 2004).

For forests represented in this survey, CUE was positively correlated with the fraction of total C (above- and belowground) in foliage (Fig. 3). Because respiration and growth depend on substrates made available by photosynthesis, it is reasonable to expect these processes to be coordinated (Thornley & Cannell,

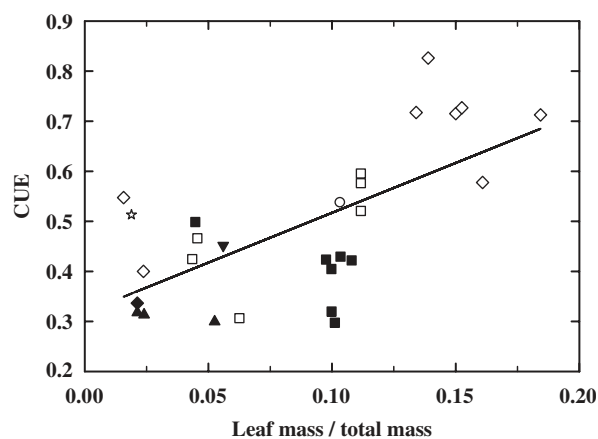


Fig. 3 Relationship between forest carbon-use efficiency (CUE) and the mass of foliage carbon (C) as a fraction of total forest C. Closed symbols represent values where gross primary production (GPP) was derived from estimates of net primary production (NPP) and R_a and open symbols represent values with independent estimates of GPP (boreal, circles, $n = 1$; West Coast Maritime, triangles, $n = 3$; temperate conifer, squares, $n = 13$; temperate deciduous, diamonds, $n = 9$; temperate mixed, inverted triangles, $n = 1$; Tropical, stars, $n = 1$; CUE = $0.318 + 1.991 \times \text{leaf mass/total mass}$, $r^2 = 0.429$, $P < 0.01$). Values for foliage mass were only available for a subset of data in Table 1.

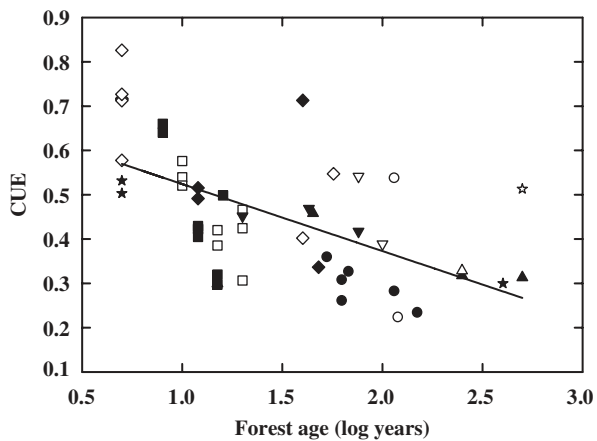


Fig. 4 The relationship between forest carbon-use efficiency (CUE) and stand age. Closed symbols denote points where gross primary production (GPP) was derived from estimates of net primary production (NPP) and R_a , and open symbols denote points with an independent estimate of GPP. Boreal, circles, $n = 8$; West Coast Maritime, triangle, $n = 5$; temperate conifer, squares, $n = 17$; temperate deciduous, diamonds, $n = 12$; temperate mixed, inverted triangles, $n = 5$; tropical, stars, $n = 4$. $CUE = 0.679 - 0.153 \times \text{stand age}$; $r^2 = 0.356$; $P < 0.01$.

2000), at least over relatively long time periods. Storage reserves in trees may uncouple these processes over short-time intervals (Kozłowski, 1992; Körner, 2003), and Arneth *et al.* (1998) demonstrate that CUE varies widely with the changing seasons within a year. The correlation between CUE and the fractional investment of C in foliage suggests that the level at which the rate of carbohydrate supply and its rate of utilization are coordinated varies with C allocation patterns (Trumbore, 2006). The conversion efficiency of new photosynthate into biomass declines as trees invest proportionately more C in roots and support structures and less in foliage.

When data from different forest types were combined, there was a strong decrease in CUE with stand age (Fig. 4). The decreases in GPP ($\log GPP = \log AGE \times -0.14 + 3.5$; $r = -0.41$, $P < 0.01$) and NPP ($\log NPP = \log AGE \times -0.29 + 3.3$; $r = -0.60$, $P < 0.01$) with forest age were weak but statistically significant and NPP decreased more strongly with age than GPP (Wilks' Lambda m test, $P < 0.01$). The proportionately stronger decrease in NPP than GPP suggests that R_a increased with stand age and presumably with the accumulation of woody mass in older forests. This is supported by the decrease in the fractional investment in foliage by older forests (leaf mass/total mass = $-0.03168 + 0.1305/\log(\text{age})$, $r^2 = 0.787$, $P < 0.01$). The increase in R_a with age and allocation to woody tissues supports the traditional theory that R_a scales with biomass. In addition, the increase in the proportion of support and conduct-

ing tissues and the associated respiratory costs contribute to the decline in NPP and CUE as forests age (Mäkelä & Valentine, 2001). This conclusion is at best tentative as it is based on the trend derived from a compilation of data where age is confounded with forest type. Whereas the ratio of growth-to-canopy photosynthesis for individual Scots pine trees decreased from 0.65 at 13 years old to 0.45 for trees over 200 years old (Vanninen & Mäkelä, 2005), no trend in CUE with age was discernable when different aged stand of *Pinus ponderosa* are compared (CUE for 15- and 250-year-old stands were 0.30 and 0.32, respectively; Table 1).

To the extent that variation in resource availability redirects C among different biomass pools that have different growth and respiratory costs, fertilization, irrigation, and exposure to elevated CO_2 should change the value of CUE unless compensatory cost mechanisms are in effect. Only 10 studies in this survey imposed experimental manipulations of resource availability or made observations in moist and dry years; there are too few observations to draw firm conclusions about the effect of variation in resources, though it appears that exposure to elevated CO_2 may not influence CUE while fertilization or irrigation may cause this ratio to increase (Table 1).

Theoretical considerations lead to contrasting predictions of how growth under elevated levels of CO_2 should affect CUE. Amthor (2000) raised the possibility that by stimulating translocation, growth and the accumulation of nonstructural carbohydrates, elevated CO_2 may increase whole-plant respiration causing CUE to decline. Alternatively, reduction of leaf nitrogen and protein in plants exposed to elevated CO_2 may contribute to lower maintenance respiration thereby increasing CUE (Dewar *et al.*, 1998). No effect on CUE was detected in two independent studies conducted at the Duke Free Air CO_2 Enrichment (FACE) experiment, where plots within an intact loblolly pine plantation were exposed to plus $200 \mu L L^{-1} CO_2$ (Hamilton *et al.*, 2002; Schäfer *et al.*, 2003). While elevated CO_2 stimulated GPP and NPP it did not appear to alter C allocation (DeLucia *et al.*, 2002) and its effect on R_a was small (Schäfer *et al.*, 2003). In a similar experiment, exposure of sweetgum trees to elevated CO_2 caused a redirection of new C to fine root production (Norby *et al.*, 2002) and 28% stimulation in R_a (DeLucia *et al.*, 2005). However, this increase in R_a contributed to only a small decrease in CUE from 0.52 for forest plots exposed to ambient CO_2 to 0.49 for those exposed to elevated CO_2 (Table 1).

The potential for elevated CO_2 to affect CUE may depend on tree age or genotype. In contrast to the studies discussed above, exposure to elevated CO_2 of a very young, high-density *Populus* stand on fertile soils

consistently increased CUE (Table 1). After 3 years, elevated CO₂ caused proportionately greater increases in NPP (21–36%) than GPP (5–19%) among three different *Populus* genotypes, and though it was not measured, this larger stimulation in NPP suggests that R_a became a lower percentage of GPP under elevated CO₂ (Gielen *et al.*, 2005). Unlike loblolly pine and sweetgum, exposure to elevated CO₂ caused a significant reduction in leaf nitrogen in *Populus* (Gielen *et al.*, 2003) and lower leaf nitrogen levels may have reduced R_a and increased CUE, as suggested by Dewar *et al.* (1998).

The few studies that explicitly examined the effect of fertilization or irrigation revealed that for some species CUE might increase with the addition of these limiting resources (Table 1). Irrigation and fertilization of a 20-year-old *Pinus radiata* plantation increased GPP from 2950 to 3690 g C m⁻² yr⁻¹ (Ryan *et al.*, 1996). However, a reduction in fine root production and fine root respiration contributed to a less than proportionate increase in R_a , and CUE increased with combined fertilization and irrigation from 0.31 to 0.47. Similarly, fertilization of *Eucalyptus saligna* decreased the fraction of GPP allocated to below ground processes causing a slight increase in CUE (Giardina *et al.*, 2003; Table 1). However, either independently or in combination with irrigation, fertilization caused GPP and R_a to increase proportionately for young loblolly pine stands and, thus, had no effect on CUE (Lai *et al.*, 2002; Maier *et al.*, 2004). While CUE calculated over short periods changed dramatically at different times of the year, inter-annual variation in precipitation had no effect on CUE for *P. radiata* (Arneth *et al.*, 1998). Giardina *et al.* (2003) concluded that variation in climate, forest type, or edaphic factors might exert a greater effect on CUE than fertilization. By affecting the ratio of photosynthesis to respiration, changes in temperature may influence CUE. None of the experiments in our survey examined the temperature dependence of CUE, however, in a mesocosm experiment with *Populus deltoids*, Hartley *et al.* (2006) found that changes in growth temperature altered the relationship between canopy photosynthesis and ecosystem respiration, presumably causing a decrease in CUE.

Conclusion

While the number of published values is small and biased toward temperate plantations, systematic variation among forest types is sufficiently large to reject the hypothesis that CUE is constant among forests. Theoretical considerations would lead us to believe that respiration should be a fixed proportion of photosynthesis (e.g. constant CUE); this expectation does not seem to hold for estimates made over either very short or

long time periods. Over a short period, within a single year, carbohydrate storage and dynamic patterns of C allocation contributed to widely varying values of CUE (Arneth *et al.*, 1998). At the other extreme, as forests age over decades, changes in C allocation captured by a decreasing ratio of leaf-to-total mass contribute to declining CUE. In theory, CUE is a robust integrator of factors affecting GPP, R_a and NPP and current methods could resolve variations in CUE greater than ± 0.1 units (Curtis *et al.*, 2005). Detecting potential variation in CUE will help resolve uncertainties about the regulation of R_a among forests of different ages and between different types of forests. However, until additional studies that rely on independent estimates of GPP from NPP to calculate CUE are conducted, it may not be prudent to assume that R_a is either a constant fraction of canopy photosynthesis or proportional to biomass.

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