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

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Introduction

Primary production by terrestrial vegetation represents a globally important flux of carbon between the atmosphere and the biosphere, and is the basic process driving plant growth. In order to assess the efficiency of carbohydrate conversion into structural dry matter, a useful parameter is carbon use efficiency (CUE) (Amthor 2000, Cannell and Thornley 2000). The CUE, which is defined as the ratio of net primary production to gross primary production, can be used to assess not only the capacity of forests to transfer carbon from the atmosphere to the terrestrial biomass (DeLucia et al. 2007) but also to determine the impact of respiration on productivity in forests (Kira and Shidei 1967, Ryan et al. 1997).

Waring et al. (1998) performed a comparative analysis of temperate and subalpine forests, and calculated a conservative CUE value of 0.47 for all species. However, because species differences in CUE may exist (Ryan et al. 1997, Amthor 2000, Cannell and Thornley 2000, DeLucia et al. 2007), it is necessary to track the same woody species to determine whether or not CUE remains constant with stand development. In one of the early investigations on primary production in Japanese forests, Kira (1977) reported that CUE declines continuously with increasing biomass of the forests of *Abies veitchii* Lindl. on Mt. Fuji. However, the data on *A. veitchii* did not cover the whole period of stand development, which ranges from 4 to 60 years (Tadaki et al. 1970). Because the results of analyses of previously published data (Ryan et al. 1997, Waring et al. 1998, Mäkelä and Valentine 2001, DeLucia et al. 2007) also are biased toward relatively old stages of stand development, there is no information on CUE at early stages of stand development, such as the first four years. However, if data on early stand development were combined with existing data on changes in CUE, a more accurate estimate of CUE could be obtained in relation to forest development.

In this report, I describe the changes in CUE in relation to stand development of the Hinoki Cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) and have incorporated previously-published data on two early developmental stages , namely 1-year-old (Ogawa 1989, Ogawa et al. 1990) and 2-year-old (Ogawa *et al.* 1985, 1986) seedlings (Table 1). Because the reported models for CUE separate respiration into two components, growth and maintenance respiration (Waring et al. 1998, Medlyn and Dewar 1999, Mäkela and Valentine 2001), these models are complicated and are not easy to manipulate. Therefore, simple and practical models are needed for determining changes in CUE. In the present study, I present a simple mathematical model for determining changes in CUE, into which data on physiological variables and mass in woody species have been incorporated. Using this model, I then analyze the changes in CUE in relation to stand development.

Materials and methods
Data sources

The data sources for the present analysis of forests of Hinoki Cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) are listed in Table 1.

Table 1. Carbon use efficiency (CUE), annnual carbon budget and biomass of the aerial parts/components of the Hinoki Cypress (*Chamaecyparis obtusa* (Sieb. et Zucc.) Endl.) plantations in central Japan.

Locality	Age	GPP	NPP	R	CUE	a	r	r/a	y_L	y_T	y_L/y_T	References
	[yrs]	[Mg d.wt ha^{-1} yr^{-1}]				[yr^{-1}]			[Mg d.wt ha^{-1}]			
Minokamo, Gifu Prefecture	1	6.10	1.72	4.38	0.282	54.69	3.222	0.059	0.11	1.36	0.082	Ogawa 1989; Ogawa et al. 1990
Minokamo, Gifu Prefecture	2	22.79	8.91	13.88	0.391	57.60	2.762	0.048	0.40	5.03	0.079	Ogawa et al. 1985, 1986
Nagoya, Aichi Prefecture	10	25.40	14.80	10.60	0.583	2.10	0.373	0.178	12.12	28.44	0.426	Adu–Bredu and Hagihara 2003
Nagoya, Aichi Prefecture	11	29.80	16.88	12.92	0.566	2.36	0.346	0.147	12.63	37.34	0.338	Adu–Bredu and Hagihara 2003
Nagoya, Aichi Prefecture	12	31.08	16.90	14.18	0.544	2.68	0.301	0.112	11.59	47.14	0.246	Adu–Bredu and Hagihara 2003
Nagoya, Aichi Prefecture	13	31.28	16.58	14.70	0.530	2.81	0.257	0.091	11.13	57.22	0.195	Adu–Bredu and Hagihara 2003
Inabu, Aichi Prefecture	18	34.31	11.38	22.93	0.332	2.42	0.398	0.165	14.20	57.59	0.247	Hagihara and Hozumi 1983
Inabu, Aichi Prefecture	24	12.13	5.79	6.34	0.477	0.91	0.068	0.075	13.40	93.43	0.143	Ninomiya and Hozumi 1983; Miyaura and Hozumi 1985

GPP, gross primary production; NPP, net primary production; R, respiration; *a*, specific photosynthetic rate; *r*, specific respiration rate; y_L, leaf biomass; y_T, aboveground biomass

Modeling

Net primary production (NPP) over any time interval is defined as

$$NPP = GPP - R \qquad (1)$$

where GPP and R represent gross primary production and respiration (sum of stand growth and maintenance respiration), respectively (Ogawa 1977; Waring et al. 1998). By dividing both sides by GPP, CUE (Amthor 2000; Gifford 2003; Delucia et al. 2007) is given by

$$CUE = \frac{NPP}{GPP} = 1 - \frac{R}{GPP} \qquad (2)$$

Because R and GPP can be expressed by the products of specific respiration rate r and aboveground biomass y_T, and of specific gross photosynthetic rate a and leaf biomass y_L, Equation 2 can be rewritten as

$$CUE = 1 - \frac{r y_T}{a y_L} = 1 - \frac{r}{a} \frac{1}{y_L/y_T} \qquad (3)$$

Equation 3 suggests that CUE is determined by two ratios, r/a and $1/(y_L/y_T)$, which are related to the physiological state and mass of the trees, respectively. Because y_L and y_T can be expressed as the products of mean leaf mass w_L and aboveground mass w_T and stand density ρ, the ratio y_L/y_T corresponds to the leaf mass ratio (LMR) in the aboveground parts and can be expressed as follows:

$$\frac{y_L}{y_T} = \frac{w_L \rho}{w_T \rho} = \frac{w_L}{w_T} = LMR \qquad (4)$$

In the present analysis, CUE and the two ratios, r/a and y_L/y_T, are given in relation not to the stand age, but to the aboveground biomass of the stand, because stand biomass, instead of age, can be considered as a measure of time. Furthermore, Equation 3 was generalized into the following form in order to determine the relationship between CUE and LMR:

$$CUE = A - \frac{B}{y_L/y_T} \qquad (5)$$

where if A=1 and B=r/a, then Equation 5 reduces to Equation 3.
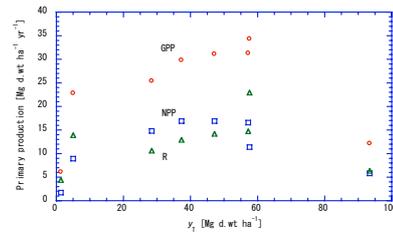
Results and Discussion

Fig. 1. Trends in primary production with the aboveground biomass of the stand, y_T. Circles, gross primary production (GPP); squares, net primary production (NPP); triangles, respiration (R).
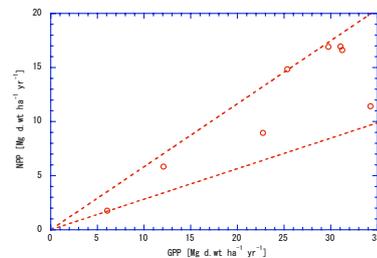

Fig. 2. Relationship between net primary production (NPP) and gross primary production (GPP). Upper broken line, carbon use efficiency (CUE)=0.583 (maximum); lower broken line, CUE=0.282 (minimum).
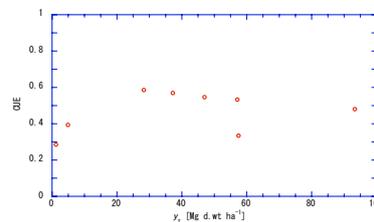

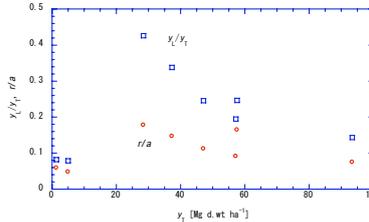Fig. 3. Changes in carbon use efficiency (CUE) with the aboveground biomass of the stand, y_T.

Fig. 4. Changes in the leaf mass ratio (y_L/y_T) and ratios of specific respiration rate to specific gross photosynthetic rate (r/a) with the aboveground biomass of the stand y_T. Specific respiration rate *r* and specific gross photosynthetic rate *a* are defined as R/y_T and GPP/y_L, respectively (cf. Equations 2 and 3).
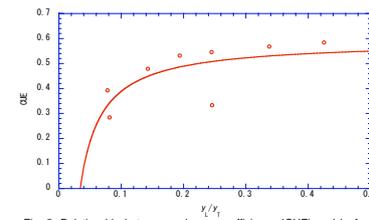

Fig. 5. Relationship between carbon use efficiency (CUE) and leaf mass ratio (y_L/y_T). The smooth curve depicts the regression of a hyperbolic model given by Equation 5, where the coefficient of determination is 0.505.

Conclusions

The GPP and respiration (R) tended to increase with increasing aboveground biomass, reached their maximum values at a biomass of approximately 60 Mg d. wt ha^{-1}, and then declined with stand development. The change in NPP was similar to that of GPP or R, but NPP tended to be constant at a biomass of between 40 and 60 Mg d. wt ha^{-1}. The CUE tended to increase with increases in the aboveground biomass of the stand, and then decreased gradually despite increases in the aboveground biomass. The CUE-value (0.28–0.39) of the seedling stage was much lower than that of (0.48–0.58) of the young or mature trees. The low value of CUE at the seedling stage was not due to the ratio of specific respiration rate to specific photosynthetic rate r/a, but was due to the low value of the leaf mass ratio y_L/y_T. In addition, the decline in CUE associated with older stages of stand development was due to the decreasing changes in y_L/y_T, and the r/a ratio did not influence the change in CUE. Because the range of y_L/y_T (0.079–0.43) was wider than the range of r/a (0.048–0.18), CUE was influenced more by y_L/y_T than by r/a. Therefore, the relationship between CUE and y_L/y_T was modeled by a hyperbolic function, and the results indicated that CUE reaches an upper limit of approximately 0.6 when y_L/y_T approaches its limit.