

## Relationship between woody biomass and PAR conversion efficiency for estimating net primary production from NDVI

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(Received 25 November 1993; in final form 1 February 1994)

**Abstract.** Terrestrial net primary production (*NPP*) may be determined from remotely-sensed vegetation indices by estimating the amount of photosynthetically active radiation (*PAR*) absorbed by vegetation. Studies from the literature were used to determine the upper limit of the *PAR* conversion efficiency ( $\epsilon$ ) as a function of woody biomass for forest vegetation. Without climatic or other limitations, the upper limit was about  $3.5 \text{ g MJ}^{-1}$  of absorbed *PAR* at very low values of stem biomass. Because of increased maintenance respiration with increasing woody biomass, the upper limit decreased to  $2.0 \text{ g MJ}^{-1}$ . Therefore, global estimates of *NPP* based on vegetation indices should include a classification among established forest, young forest and non-forest ecosystems to account for differences in  $\epsilon$ .

### 1. Introduction

The contribution of forest ecosystems toward the global carbon budget may be estimated using data from sensors onboard satellite platforms such as the Advanced Very High Resolution Radiometer (AVHRR). Goward *et al.* (1985) and Tucker *et al.* (1986) showed vegetation indices, such as the Normalized Difference Vegetation Index ( $NDVI = (NIR - R)/(NIR + R)$ , where *NIR* and *R* are the near-infrared and red reflectances, respectively) are related to net primary production (*NPP*,  $\text{g m}^{-2} \text{ year}^{-1}$ ).

Monteith (1972, 1977) suggested that *NPP* under non-stressed conditions is linearly related to the amount of photosynthetically active radiation (*PAR*,  $\text{MJ m}^{-2}$ ) that is absorbed by the green foliage (*APAR*,  $\text{MJ m}^{-2}$ ). Furthermore, Kumar and Monteith (1981) showed how the fraction of *PAR* absorbed relates to the ratio of red reflectance (*R*) to near-infrared reflectance (*NIR*). Asrar *et al.* (1984) subsequently related the *NDVI* to the fraction of *PAR* absorbed; hence, *NDVI* may be used to estimate *NPP* at global scales by:

$$NPP = \epsilon \Sigma(APAR) = \epsilon \Sigma(NDVI \times PAR) \quad (1)$$

where  $\Sigma(APAR)$  is the annual sum of *APAR* and  $\epsilon$  is the *PAR* conversion efficiency ( $\text{g MJ}^{-1}$ ). The term for  $\epsilon$  is in a state of transition, as  $\epsilon$  is not a true thermodynamic efficiency (Russell *et al.* 1989, Prince 1991). There are problems using *NDVI* to calculate *APAR*, which are not addressed here (Goward and Huemmrich 1992 and Asrar *et al.* 1992).

Jarvis and Leverenz (1984) present a simple model of  $\epsilon$ , which is used to separate the factors controlling *NPP*:

$$\epsilon = \epsilon_{max} f Y_m Y_g d \quad (2)$$

where  $\varepsilon_{max}$  is a maximum *PAR* conversion efficiency ( $\text{g MJ}^{-1}$ ),  $f$  is the fraction when photosynthesis is not reduced by climatic factors (such as drought, high vapour pressure deficits or cold temperatures),  $Y_m$  is a term for maintenance respiration,  $Y_g$  is a term for growth respiration, and  $d$  is the fraction dry matter not lost by death, turnover and herbivory. Based on the quantum yield of photosynthesis, Jarvis and Leverenz (1984) and Russell *et al.* (1989) calculate  $\varepsilon_{max}$  should be about  $5.0 \text{ g MJ}^{-1}$  for plants with the  $C_3$  photosynthetic pathway (including all forest tree species).  $Y_m$  and  $Y_g$  (dimensionless) are defined:

$$Y_g = 1 - R_g/P \quad (3a)$$

$$Y_m = 1 - R_m/PY_g \quad (3b)$$

where  $P$  is the amount of net photosynthesis ( $\text{g m}^{-2} \text{ year}^{-1}$ ),  $R_m$  is the amount of non-foliar maintenance respiration ( $\text{g m}^{-2} \text{ year}^{-1}$ ), and  $R_g$  is the amount of growth respiration ( $\text{g m}^{-2} \text{ year}^{-1}$ ). As forests age and accumulate dry matter,  $y_m$  should decrease because of increased  $R_m$ , thereby decreasing  $\varepsilon$  (Jarvis and Leverenz 1984, Hunt and Running 1992).

The objectives of this study were to determine the importance of estimating standing forest biomass for remotely-sensed NPP and establish an upper limit of  $\varepsilon$  for forest ecosystems. To achieve these objectives, data from the literature were used to estimate  $\varepsilon_{max}Y_gY_m$ . Equation (1) is applicable to both forest and non-forest ecosystems, it may be important to have a forest/non-forest classification for remotely-sensed NPP.

## 2. Review of the literature

### 2.1. Assumptions

Reviewing the literature,  $\varepsilon$  was determined for a wide range of tree species, and from a wide range of climates: boreal, temperate, subtropical, and tropical. Occasionally, the amount of woody biomass was not given in these studies, so woody biomass had to be estimated from companion studies. When density and carbon concentration data were not available, wood volumes were converted to mass assuming a density of  $0.5 \text{ Mg m}^{-3}$  and mass carbon values were doubled to obtain wood mass in terms of dry matter. For all of the studies,  $d$  was assumed to be unity.

Among the different datasets compiled, there were differences in the units of measured  $\varepsilon$  from total grams dry matter produced per  $\text{MJ APAR}$  (1) to above-ground-only dry matter produced per  $\text{MJ}$  intercepted solar radiation (Russell *et al.* 1989). For conversion of  $\varepsilon$  to a common set of units, I assumed all intercepted radiation was absorbed. Moreover, when below-ground production was not measured, any measured  $\varepsilon$  was doubled with units of above-ground dry matter to estimate  $\varepsilon$  in terms of total dry matter (Santantonio 1989). Finally, any  $\varepsilon$  with units of per  $\text{MJ}$  solar radiation was doubled to estimate  $\varepsilon$  with units of per  $\text{MJ APAR}$  (Russell *et al.* 1989).

### 2.2 Results

At low woody biomass reported for saplings grown in pots,  $\varepsilon$  reached a maximum of  $3.5 \text{ g MJ}^{-1}$  (figure 1). This is in the upper range reported for  $C_3$  herbaceous plants (2.5 to  $3.5 \text{ g MJ}^{-1}$ ; Prince 1991). For older stands (about

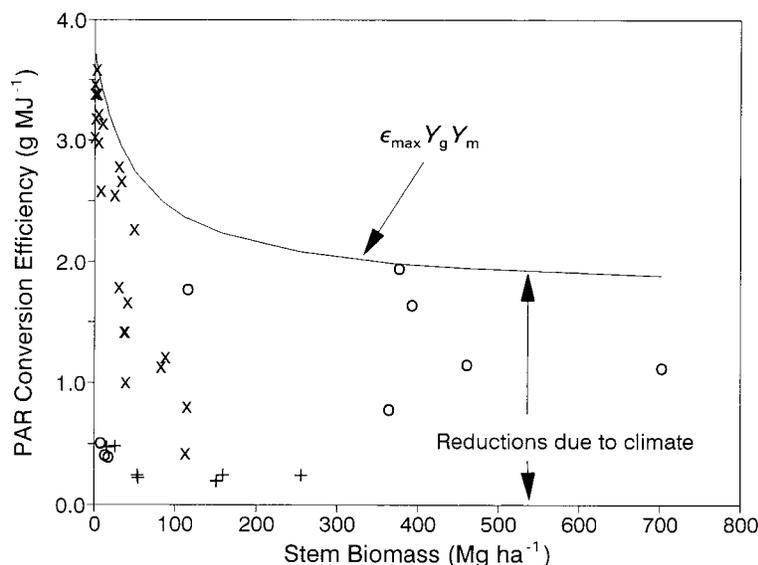


Figure 1. Relationship between the upper limit of the *PAR* conversion efficiency ( $\epsilon$ , equal to  $\epsilon_{\max} Y_g Y_m$ ) and woody biomass. The line is a hyperbolic function of woody biomass bounding the measured  $\epsilon$  to account for reductions due to herbivory and climate (Eq. 2). Woody biomass and  $\epsilon$  were estimated for the following studies: apple orchards ( $\times$ : Monteith 1977, Palmer and Jackson 1977); tropical rainforest ( $+$ : Saldarriaga and Luxmoore 1991, Saldarriaga *et al.* 1988), *Eucalyptus spp.* and *Pinus sylvestris* ( $\times$ : Linder 1985); *Eucalyptus spp.* ( $\times$ : Turnbull *et al.* 1988); *Pinus radiata* ( $\times$ : Grace *et al.* 1987); *Salix viminalis* and *Populus trichocarpa* ( $\times$ : Cannell *et al.* 1988); *Populus* hybrids ( $\times$ : Landsberg and Wright 1989); *Pinus elliotti* ( $\times$ : Gholz *et al.* 1991); *Pinus ponderosa* ( $\times$ : Gower *et al.* 1993, E. R. Hunt, Jr., S. T. Gower and S. W. Running, unpublished results); *Eucalyptus camaldulensis*, *Gliricidia sepium*, *Leucaena diversifolia*, and *Acacia auriculiformis* ( $\times$ : Harrington and Fownes, 1993, and R. A. Harrington and J. H. Fownes, unpublished data); *Pinus radiata* ( $\times$ : Biology of Forest Growth Experiment, Raison and Myers 1992, Snowdon and Benson 1992); coniferous forest stands in Oregon, U.S.A. ( $O$ : Runyon *et al.*, 1994).

200–400  $\text{Mg ha}^{-1}$ ), the upper limit of  $\epsilon$  was about  $2 \text{ g MJ}^{-1}$  (figure 1), because further accumulation of woody biomass would be in non-respiring heartwood and not in sapwood. Not shown in figure 1 is a coastal redwood stand with a biomass of  $3461 \text{ Mg ha}^{-1}$ ,  $\epsilon$  was estimated to be  $1.5 \text{ g MJ}^{-1}$  (Richard Waring, personal communication). Whereas maintenance respiration is strongly affected by temperature (Ryan 1991), there was no significant difference (one-way ANOVA,  $\alpha=0.05$ ) in measured  $\epsilon$  among species from tropical, subtropical, temperate and boreal climates.

The range in measured  $\epsilon$  at any value of woody biomass (figure 1) may be due to the reduction of photosynthesis by climate ( $f$  in equation (2)). For the nine stands from Oregon (symbol:  $O$ , figure 1), Runyon *et al.* (1994) calculated the reduction in photosynthesis due to climate, concluded all stands had  $\epsilon_{\max} Y_g Y_m$  of about  $2 \text{ g MJ}^{-1}$ . However, climate cannot explain the low  $\epsilon$  reported by Saldarriaga and Luxmoore (1991) for a chronosequence of a moist, tropical forest (symbol:  $+$ , figure 1). Saldarriaga *et al.* (1988) suggested these forests had low NPP because of poor mineral nutrition.

### 3. Discussion

The maximum, measured  $\epsilon$  of  $3.5 \text{ g MJ}^{-1}$  may be very close to  $\epsilon_{\max} Y_g$ . The ratio of  $R_g/P$  for most plants ranges from 0.2 to 0.5, so a good average of  $Y_g$  would be about 0.75 (Jarvis and Leverenz 1984). Thus, for a tree with little woody biomass, or climatic and other reductions,  $\epsilon_{\max} Y_g$  should be about  $3.8 \text{ g MJ}^{-1}$ , close to the maximum value in figure 1 for many different species.

The fraction of non-respiring heartwood of stem biomass was estimated using a hyperbolic function of stem biomass in order to determine  $Y_m$ . The equation for the line in figure 1 is:

$$\epsilon_{\max} Y_g Y_m = 5.0 \times 0.75 \times [1 - 0.4/0.75 \times B/(B + 50)] \quad (4)$$

where  $B$  is the stem biomass, 5.0 is  $\epsilon_{\max}$ , 0.4 is the ratio  $R_m/P$  (3 b), 0.75 is  $y_g$ , and  $50 \text{ Mg ha}^{-1}$  is a constant related to the amount of sapwood. The constants, 0.4 and 50 respectively, were selected to provide an upper bound to the data from the literature (figure 1).  $R_m$  may be about 40 per cent of  $P$  when stem biomass is greater than  $100 \text{ Mg ha}^{-1}$ , and the upper limit of  $\epsilon$  is about  $2.0 \text{ g MJ}^{-1}$ . Ryan and Waring (1992, personal communication) estimated respiration of sapwood alone is about 5 to 20 per cent of photosynthesis. Thus, the decrease in  $Y_m$  is due also to increases in root mass, which is correlated with the increase of sapwood mass.

The sensitivity of backscatter ( $L$  band or  $P$  band) from a synthetic aperture radar (SAR) to woody biomass is high at low values of woody biomass, and backscatter saturates at about  $200 \text{ Mg ha}^{-1}$  (Ranson and Sun 1992, Dobson *et al.* 1992). Thus, SAR data may prove useful in the estimation of  $\epsilon_{\max} Y_g Y_m$  for remote-sensing models of NPP. Perhaps a simple determination of woody-biomass classes ( $0$ – $100 \text{ Mg ha}^{-1}$  and  $> 100 \text{ Mg ha}^{-1}$ ) is all that is required given the climatic and other limitations on  $\epsilon$ . More research in relating SAR backscatter to woody biomass and integration with optical sensors is required.

Forests grow to  $100 \text{ Mg ha}^{-1}$  within 10 to 40 years after cutting (depending on climate), so much of the world's forests may be expected to have a  $\epsilon_{\max} Y_g Y_m$  of  $2.0 \text{ g MJ}^{-1}$ . As this upper limit for  $\epsilon$  for forest ecosystems is much less than that of herbaceous vegetation (Prince 1991), a classification of ecosystems into established forest, and non-forest ecosystems is essential to improve estimates of NPP by remote sensing. However, classification alone is not sufficient to estimate actual NPP as  $\epsilon$  is reduced even more by climate and other factors.

### Acknowledgments

I thank R. A. Harrington, J. H. Fownes and S. T. Gower for providing unpublished data, and R. H. Waring for valuable discussions. Funding was provided by NASA Earth Observing System contract NAS5-31363 and National Science Foundation grant BSR-8919649 to S. W. Running, and a Natural Resources Canada, Canadian Forest Service Science and Technology Opportunities Fund grant to M. B. Lavigne and S. E. Franklin.

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