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EFFECTS OF CLIMATE AND LIFEFORM ON DRY MATTER YIELD ( $\epsilon$ ) FROM SIMULATIONS USING BIOME-BGC

E. Raymond Hunt, Jr. and Steven W. Running

School of Forestry, University of Montana  
Missoula, Montana 59812, USA

**Abstract:** We used an ecosystem process simulation model, BIOME-BGC, in a sensitivity analysis to determine the factors that may cause the dry matter yield ( $\epsilon$ ), and hence, annual net primary production to vary for different ecosystems. At continental scales,  $\epsilon$  was strongly correlated to annual precipitation. At a single location, year-to-year variation in NPP and  $\epsilon$  was correlated to either annual precipitation and minimum air temperatures. Simulations indicated that forests had lower  $\epsilon$  than grasslands. The most sensitive parameter affecting forest  $\epsilon$  was the total amount of living woody biomass, which affects NPP by increasing carbon loss by maintenance respiration. Thus, a global map of woody biomass should significantly improve estimates of global NPP using remote sensing.

Introduction

Annual net primary production (NPP,  $g\ m^{-2}\ year^{-1}$ ) may be determined from satellite sensors such as AVHRR and MODIS using the Normalized Difference Vegetation Index (NDVI) to estimate the fraction of photosynthetically active radiation absorbed by the foliage. The dry matter yield ( $\epsilon$ ,  $g/MJ$ ) is used to calculate NPP from daily absorbed photosynthetically active radiation (APAR,  $MJ\ m^{-2}\ day^{-1}$ ), summed over the year:

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

where PAR is the incident photosynthetically active radiation [1,2,3,4,5,6]. Other studies use different words for dry matter yield; often,  $\epsilon$  is incorrectly termed an efficiency [2,4].

It is often assumed that differences in NPP resulting from year-to-year differences in climate will show up in  $\Sigma(APAR)$ . However, low temperatures, low relative humidities, and drought will reduce photosynthetic carbon uptake without affecting APAR. It has also been suggested that for practical purposes,  $\epsilon$  can be taken as constant for various ecosystems. There is considerable scatter in measured  $\epsilon$  for crops [4] and forests [6]. In the future with global climate change and increased atmospheric  $CO_2$ , current measurements of  $\epsilon$  may not be valid.

We developed a mechanistic ecosystem process model, BIOME-BGC (for Bio-Geochemical Cycles), for simulation of the carbon, nitrogen and hydrologic cycles of terrestrial ecosystems by generalizing the logic of a previous model, FOREST-BGC [6,7,8]. This model has been extensively validated for forests [9]. A major objective of BIOME-BGC is to predict NPP and APAR for various lifeforms (eg. grass, deciduous broadleaf, conifer) with a given climate. We performed a sensitivity analysis using BIOME-BGC to determine which factors could most affect  $\epsilon$  at global scales. We also determined the expected year-to-year variability of  $\epsilon$ .

Methods

BIOME-BGC was parameterized using data from the literature. For grasslands, we used studies primarily from the the Konza Prairie Long Term Ecological Research Site [6,10]. For deciduous broadleaf trees, we used values for various aspens and birches [6]. Climate data was obtained on compact disk from EarthInfo, Inc. (Boulder, CO), and extrapolated to a site using the model, MTCLIM [11]. Dry matter yield was calculated as:

$$\epsilon = NPP/\Sigma(APAR) \quad (2)$$

where NPP is defined as the annual carbon accumulation (sum of daily net photosynthesis minus daily maintenance respiration of the leaves, stems and roots minus growth respiration for synthesis of new tissue). Thus, NPP includes the carbon that may be lost due to litterfall and root turnover.

Results and Discussion

We found a strong interaction between lifeform and climate (Table 1). Annual net photosynthesis was only slightly higher for grass ecosystems compared to deciduous broadleaf or coniferous forests, but the higher  $\epsilon$  for grasses was due to larger total maintenance respiration for the forest ecosystems. For the grass and deciduous broadleaf lifeforms, phenology of leaf growth was simulated using reasonable yeardays for growing new leaves and shedding the old leaves, so APAR would not be increased (thereby decreasing  $\epsilon$ ) during drought and winter. However, there is still a strong effect of climate on these lifeform's  $\epsilon$  (Table 1).

The sensitivity analyses generally showed that  $\pm 50\%$  changes in physiological parameters affected  $\epsilon$  less than  $50\%$  (Table 2). One exception was lowering the optimum temperature for photosynthesis from  $20^\circ$  to  $10^\circ$  for the Florida climate. Increasing the specific rate of maintenance respiration decreased  $\epsilon$   $13\%$  for the cold, dry Montana climate and decreased  $\epsilon$   $36\%$  for the hot, wet Florida climate (Table 2). Warm temperatures increase the rate of maintenance respiration exponentially so  $\epsilon$  should generally be lower for warmer climates.

The total amount of maintenance respiration was most affected by the amount of woody biomass (Fig. 1). At low woody biomasses, conifers in Florida had higher  $\epsilon$  than Montana with its midseason drought. However, respiration increases rapidly in Florida due to the warm temperatures. With cool summer temperatures keeping the rate of respiration low, trees in Montana can have

TABLE 1  
Effect of Climate on Dry Matter Yield

	Yearday leaf on	Yearday leaf off	$\epsilon$ (g/MJ)
Missoula, MT 1984			
conifer	0	365	1.23
broadleaf	120	300	0.99
grass	120	240	1.55
Knoxville, TN 1984			
conifer	0	365	1.70
broadleaf	105	300	1.76
grass	105	300	3.11
Manhattan, KS 1989			
conifer	0	365	1.67
broadleaf	105	300	1.70
grass	105	244	2.85

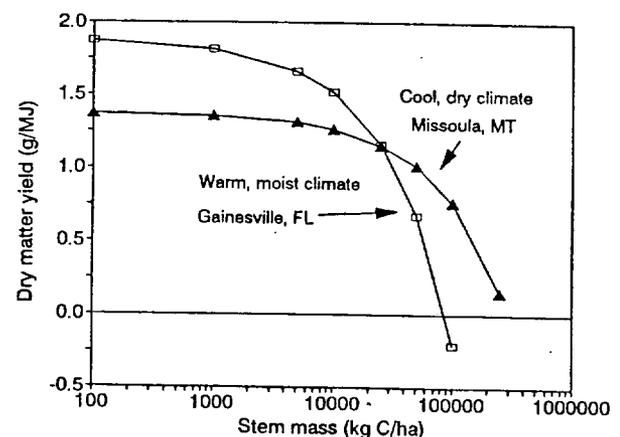


Fig. 1. Simulated dry matter yield ( $\epsilon$ ) for conifers with various amounts of woody biomass for two climates. This illustrates how climate and respiration interact to affect  $\epsilon$  of forest ecosystems. Thus, it is important to determine woody biomass for more accurate NPP estimates from NDVI/APAR using sensors like AVHRR or MODIS.

TABLE 2  
Sensitivity Analysis of Dry Matter Yield  
to BIOME-BGC Parameters for Conifers

	FL 1984		MT 1984	
	+50%	-50%	+50%	-50%
control	1.52		1.26	
photosynthesis ( $4 \mu\text{mol m}^{-2} \text{s}^{-1}$ )	1.94	1.10	1.61	0.89
growth respiration (0.35 kg/kg)	1.14	1.90	0.94	1.58
maintenance resp. ( $0.0002 \text{ kg kg}^{-1} \text{ day}^{-1}$ )	0.97	1.79	1.10	1.34
critical predawn $\Psi$ (-1.65 MPa)	1.52	1.51	1.29	1.18
stomatal conductance ( $1.0 \text{ mm/s}$ )	1.17	1.85	1.18	1.55
optimum temperature ( $20^\circ\text{C}$ )	1.52	0.23	1.11	0.82
PAR compensation pt. ( $482 \text{ kJ m}^{-2} \text{ day}^{-1}$ )	1.45	1.58	1.24	1.29
PAR saturation pt. ( $14850 \text{ kJ m}^{-2} \text{ day}^{-1}$ )	1.17	1.72	1.11	1.47
Atmospheric $\text{CO}_2$ (350 PPM)	1.82	0.91	1.46	0.77

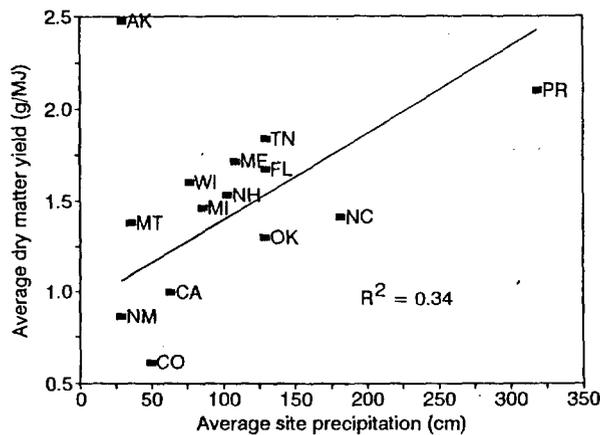


Fig. 2. Continental variation in average conifer  $\epsilon$  versus average annual precipitation. Variation in NPP caused by climate across the continent may be more related to  $\epsilon$  than  $\epsilon(\text{APAR})$ . Each climatic station was chosen to be close to an experimental forest or Long Term Ecological Research (LTER) site for validation data. National Weather Service stations are: Pasadena, CA (San Dimas Expt For); Albuquerque, NM (Sevilleta LTER); Missoula, MT (Lubrecht Expt For); Fraser, CO (Fraser Expt For); Idabel, OK (Ouachita Natl For); Gainesville, FL (Ocala Natl For); Knoxville, TN (Oak Ridge Natl Lab); Franklin, NC (Cowetta LTER); Grand Rapids, MN (Chippewa Natl For); Rhinelander, WI (Northern Lakes LTER); Pellston, MI (Michigan Biological Sta); Hanover, NH (Hubbard Brook LTER); Bangor, ME (Howland State For); Rio Piedras, PR (Luquillo LTER); and Fairbanks, AK (Bonanza Creek, LTER). AK and PR data points were not included in the regression.

larger stem woody biomass (Fig. 1). Ponderosa pine forests in Missoula, MT, have a measured  $\epsilon$  of  $1.1 \text{ g/MJ}$  for stands with  $70000 \text{ kg C/ha}$  (S. T. Gower and E. R. Hunt, Jr., unpublished results) and slash pine stands with  $40000 \text{ kg C/ha}$  stem biomass near Gainesville, FL, have measured  $\epsilon$  of  $0.4 \text{ g/MJ}$  [12]; the simulated values are close to these data.

Overall, average  $\epsilon$  for conifer lifeforms was correlated with mean annual precipitation for sites across the United States (Fig. 2). This should be expected as many studies have demonstrated a correlation between NPP and precipitation. During winter months, the cold temperatures inhibit photosynthesis but the canopies are still absorbing PAR. The biggest outlier was for Fairbanks, AK (Fig. 2), which had low NPP and even lower APAR. During the winter, there is little PAR absorption because of the high latitude.

An objective of the Oregon Transect Terrestrial Ecosystem Research (OTTER) experiment was to validate the use of APAR models for NPP. Simulated  $\epsilon$  was limited in Corvallis and Bend by lack of precipitation (Fig. 3) caused by rain shadow effects of the coastal and Cascade

mountains, respectively. Belknap Springs and Santiam Pass are located on the west side of the Cascade Mountains and have the highest amounts of precipitation of the transect (mainly as snow in winter); simulated photosynthesis was limited by cold temperatures at the high elevations (Fig. 3). The highest simulated  $\epsilon$  was for the mild, coastal site at Newport, OR. The experimental data show the same qualitative trend as Fig. 3 (Richard Waring and John Runyon, personal communication).

The effects of annual variation of climate on  $\epsilon$  are especially important for use with satellite data such as the AVHRR or MODIS because of the limited number of years in a mission. For dry climates such as Missoula, MT (Fig. 4), there is a large variance in annual precipitation. This variation in precipitation causes large changes in annual growth rings [9] and in the simulated value of  $\epsilon$  (Fig. 4). The regression between  $\epsilon$  and precipitation on an annual basis for Missoula is significantly different than the regression in Fig. 2, so a simple regression between precipitation and  $\epsilon$  can not be used to improve estimates of NPP.

For cool, moist climates such as Bangor, ME, there is no correlation between simulated NPP or  $\epsilon$  with annual precipitation (data not shown). However, there is a large variation in simulated  $\epsilon$  that is correlated with the yearly mean minimum temperature (Fig. 5). These simulated variations in  $\epsilon$  are as large as those in the sensitivity analyses. For sites with warm, moist climates such as Gainesville, FL, there was essentially

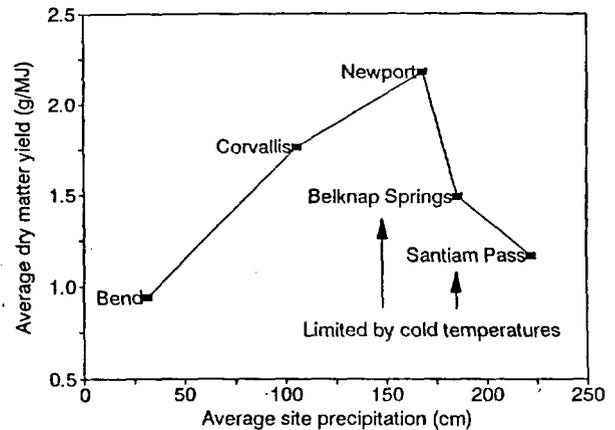


Fig. 3. Variation in  $\epsilon$  for 5 sites of the Oregon Transect Terrestrial Ecosystem Research (OTTER) experiment. These results show that  $\epsilon$  is not a simple correlate of annual precipitation.

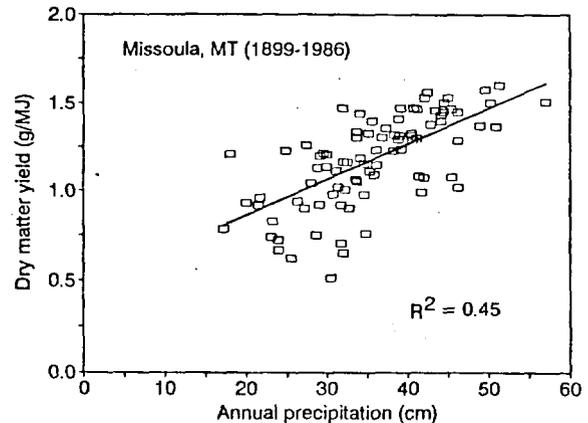


Fig. 4. Annual variation in  $\epsilon$  with annual precipitation for conifers in a cold, dry climate (Missoula, MT). The regression equation can not explain most of the variation in  $\epsilon$  and is significantly different than the regression presented in Fig. 2, so annual precipitation can not be used for a simple correction of  $\epsilon$ .

no annual variation in  $\epsilon$ , with a mean of 1.4 g/MJ and a range of 0.3 g/MJ (data not shown). The simulations indicated that no reduction of photosynthesis occurred due to cold temperatures, low relative humidity, or low soil moisture contents. However, hot temperatures there increase maintenance respiration so average  $\epsilon$  in Florida is lower than the average  $\epsilon$  in Bangor, ME (Fig. 5). So, the temperature responses of photosynthesis and respiration must be considered separately.

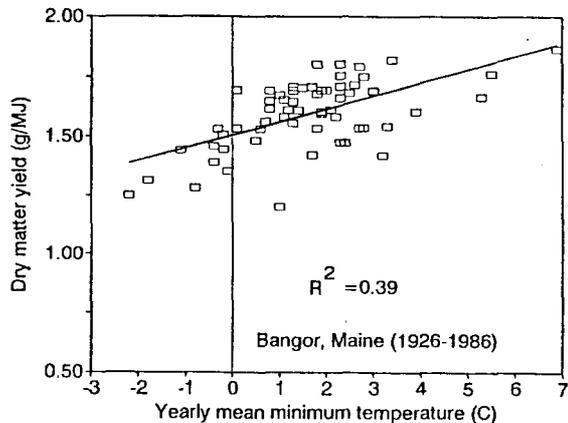


Fig. 5. Annual variation in  $\epsilon$  with annual mean minimum temperature for conifers in Bangor, ME. For cold, moist sites, variation in  $\epsilon$  is correlated to reduction of photosynthesis by cold temperatures. However, average  $\epsilon$  is high for forests because cool summer temperatures reduce maintenance respiration.

#### Conclusions

Ecosystem lifeform seems to have a greater influence on NPP, APAR and  $\epsilon$  than does variation in physiology. The amount of respiring woody biomass may be one of the most important determinants of ecosystem NPP, accounting for the much higher  $\epsilon$  for grasslands compared to forests at a given site. A global map of woody biomass is therefore essential for prediction of NPP from satellite NDVI data. Woody biomass may possibly be remotely-sensed using active microwave sensors such as a Synthetic Aperture Radar. Currently, we can not specify the necessary accuracy for estimates of woody biomass from radar data, because the effect of woody biomass on  $\epsilon$  is a strong non-linear function of climate. Perhaps all that is needed is simply a value within an order of magnitude (Fig. 1).

The influence of climate on  $\epsilon$  is at least as much as the influence of climate on E(APAR) for conifers. However, the seasonality of daily PAR increases with latitude, which may be confused with the effects of cool summer temperatures that decrease maintenance respiration, unless an ecosystem simulation model is used to separate the two processes. Without some sort of correction for  $\epsilon$ , estimates of NPP from NDVI will be in error. Besides cool summer temperatures affecting respiration, the climatic influences on photosynthesis are largely low temperatures, low relative humidity and drought (low soil moisture). Moreover, these three influences may be remotely-sensed in the future using thermal infrared data [13, R. Nemani, personal communication]. How accurately do we need to know global climate data for estimates of global NPP from satellite NDVI? It depends on the type of climate (Figs. 3,4,5).

Clearly, these simulations demonstrate that a single, globally-averaged  $\epsilon$  is inappropriate for use in APAR/NDVI models of NPP. Furthermore, simple regressions of  $\epsilon$  with climatic variables do not appear promising. The question is then how to get the appropriate value of  $\epsilon$ ? One approach is to use ecosystem process models in the future to calibrate  $\epsilon$ , that is nesting small-scale models within the large-scale APAR models. There may be a computational limit to the total area simulated by small-scale models. However, small-scale ecosystem process models can be used to sample  $\epsilon$  within a bioclimatic region for a given lifeform (if woody biomass is included as well). This approach may be powerful when the small-scale models are well validated, and may be necessary with increased atmospheric CO<sub>2</sub> changing ecosystem response to climate, when measured values of  $\epsilon$  are no longer valid.

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