Implementing a Nitrogen-based Model for Autotrophic Respiration Using Satellite and Field Observations

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Popular Summary

Carbon accumulation by terrestrial vegetation is determined by the difference of two processes; photosynthesis and respiration. Plants acquire carbon from the atmosphere by the process of photosynthesis. Respiration is the process by which plants use a part of this acquired carbon for its maintenance and growth. The magnitude of these two processes depends upon the type of vegetation (broadly, for example, crop, grassland, forest) and the environmental conditions under which it is growing (broadly, for example, temperate, cold or tropical). Changes in vegetation type and environmental factors can alter carbon accumulation by the plant communities. While much has been learned about how different physiological and environmental factors affect these two processes, significant uncertainties still remain. For example, it is not clear, how climate change would affect the current state of the carbon balance. Also, the magnitude of interannual variation of these two processes under the current climate is poorly understood. A major difficulty in determining respiration has been that field studies show that some plant specific quantities which are needed to calculate respiration (called the specific respiration rates) are highly variable (different leaves within a canopy have different values and they also change with time, different for a leaf and roots, etc.). Thus, a major question has been, what factors determine this variability. It has been suggested that synthesis and maintenance of various protein compounds in plants determine respiration. This manuscript explores this suggestion quantitatively by calculating respiration for different types of vegetation over large areas and for several consecutive years using satellite and field observations.

Significant Findings

1. Maintenance and synthesis of proteins, as indicated by the nitrogen content of plant, provide a way to quantify respiration for different types of vegetation. This conclusion has been reached by comparing the calculated values of annual respiration with varied observations.

2. Interannual variation of the magnitude of the processes has been found to be generally less than 15%.

ABSTRACT

The rate of carbon accumulation by terrestrial plant communities in a process-level, mechanistic modeling is the difference of the rate of gross photosynthesis by a canopy (A_g) and autotrophic respiration (R) of the stand. Observations for different biomes often show that R to be a large and variable fraction of A_g, ca. 35% to 75%, although other studies suggest the ratio of R and A_g to be less variable. Here, R has been calculated according to the two compartment model as being the sum of maintenance and growth components. The maintenance respiration of foliage and living fine roots for different biomes has been determined objectively from observed nitrogen content of these organs. The sapwood maintenance respiration is based on pipe theory, and checked against an independently derived equation considering sapwood biomass and its maintenance coefficient. The growth respiration has been calculated from the difference of A_g and maintenance respiration. The A_g is obtained as the product of biome-specific radiation use efficiency for gross photosynthesis under unstressed conditions and intercepted photosynthetically active radiation, and adjusted for stress. Calculations have been done using satellite and ground observations for 36 consecutive months (1987-1989) over large contiguous areas (ca. 10^5 km^2) of boreal forests, crop land, temperate deciduous forest, temperate grassland, tropical deciduous forest, tropical evergreen forest, tropical savanna, and tundra. The ratio of annual respiration and gross photosynthesis, (R/A_g), is found to be 0.5-0.6 for temperate and cold adopted biome areas, but somewhat higher for tropical biome areas (0.6-0.7). Interannual variation of the fluxes is found to be generally less than 15%. Calculated fluxes are compared with observations and several previous estimates. Results of sensitivity analysis are presented for uncertainties in parameterization and input data. It is found that uncertainty in determining maintenance respiration for tropical biomes is such that R/A_g for these biomes could be similar to that for temperate biomes.

Keywords: Respiration, Photosynthesis, Net Primary Productivity, Nitrogen, Foliage, Fine Roots, Sapwood, Satellite Data, Inter-annual Variation, Modeling, Tropical, Temperate, Boreal, Tundra

INTRODUCTION

The rate of carbon accumulation by terrestrial plant communities is the difference of the rate of gross photosynthesis by a canopy (A_g) and autotrophic respiration (R, referred to below as respiration). Observations for different biomes often show that R to be a large and variable fraction of A_g, ca. 35% to 75% (Kira, 1975; Amthor, 1989, p. 116; Ryan et al., 1997; McKane et al., 1997; Waring and Running, 1998, p.95; Law et al., 1999), while other studies suggest substantially less variation (McCree, 1988; Gifford, 1994; Malhi et al., 1999). The maximum rate of gross photosynthesis by leaves (A_{max}) and photosynthetically active radiation intercepted by a canopy (IPAR) are major determinants of seasonal variation of A_g (Monteith, 1977), and such variation of R is determined by A_g, biomass accumulation per unit ground area by foliage, stem and roots, and their maintenance coefficients (Amthor, 1989; p.11). Since these maintenance coefficients generally increase with tissue temperature (Amthor, 1989; p.47), R has often been found to increase with temperature. Thus, considering that different biophysical factors exert important control on A_g and R, a better understanding of the effect of environmental or land use changes on carbon accumulation could be obtained by explicit evaluation of these two processes.

Lieth and Box (1977) produced a global map of long-term average annual gross photosynthesis by using a globally applicable empirical model which predicts net primary production of potential (i.e., undisturbed) vegetation from long-term average precipitation and air temperature, and a fitted relation between gross and net production developed from measurements for broad leaf forests at 17 locations. Using these empirical relations, Box (1978) calculated zonal variation of long-term average annual respiration (difference of gross and net production), which showed respiration to be 25% to 62% of annual gross production. Since these ground breaking studies providing spatially explicit global perspectives of gross photosynthesis and respiration, several bio-physically based models have been developed to calculate these processes at regional and global scales (for example, Raich et al., 1991; Warnant et al., 1994; Ruimy et al., 1996; Hunt et al., 1996). The difficulties in determining R and methods used for calibration have been elaborated by Ruimy et al. (1996).

Ruimy et al. (1996) have presented an approach for calculating A_g and R over the global land surface using satellite and ancillary data without calibrating the model parameters. The A_g was calculated as the product of radiation use efficiency and intercepted photosynthetically active radiation (IPAR). The radiation use efficiency was prescribed to be same for all biomes, while satellite observations were used to determine IPAR. The R was calculated as the sum of maintenance and growth respiration (R_m and R_g, respectively) according to the functional two component model of McCree (1974). The R_m was calculated from the "best guess" values of maintenance coefficient per unit dry matter of living foliage, sapwood and fine roots, and their dry matter. They noted that maintenance coefficients for many types of vegetation are not available, and the available data show much variability. Thus, the selected values of the maintenance coefficients of foliage, sapwood and roots were stated to be "best guess", and were assumed to be the same for all biomes. The root biomass was assumed to be equal to foliage biomass; the latter was determined as the product of a prescribed globally constant value of specific leaf weight and the leaf area index (L_o; m^2 projected leaf m^{-2} soil surface area). Spatial and temporal changes of L_o were derived from satellite observations. The sapwood biomass was estimated from stem and coarse root biomass, which was obtained as the difference of prescribed total biomass for potential vegetation and sum of the calculated seasonal maximum foliage and fine root biomass. The R_g was obtained as a constant fraction of the difference of A_g and R_m. Changes in A_g and R due to stresses were not considered. The calculated R/A_g for different biomes varied in the range 0.34 to 0.63. Equatorial rain forests were found to have lower net production compared to some areas of tropical savannas and northern temperate zones, which was not apparent in previous studies. In this context, Ruimy et al. noted that respiration in most previous studies was determined by calibration to match the production data or prescribed as an empirical fraction of gross photosynthesis. Substantial differences are also found for A_g. Box (1978) calculated gross production for the equatorial forest zone (0°-10°S) to be 4998 g m^{-2} yr^{-1}, while Ruimy et al. obtained 4409 g m^{-2} yr^{-1} for tropical rainforest.

The objective of the present study is to reassess gross and net production using independently derived parameters without model calibration. The radiation use efficiency for unstressed conditions (RUE) has been calculated for each biome considering their A_{max}, foliage temperature and fractional diffuse radiation incident on the canopy, because changes in these factors affect unstressed RUE (Monteith, 1977; Sinclair and Muchow, 1999; Choudhury 2001a,b). While maintenance coefficient per unit dry matter has been found to change during growth (McCree, 1988; Bunce, 1989) and show considerable variation within a canopy, among organs and species (Stockfors and Linder, 1998; Ryan, 1995; Brooks et al., 1991; Amthor, 1989, pp. 78-79), this variation decreases when maintenance coefficient is expressed per unit nitrogen content because protein turnover is considered to be a major determinant of maintenance respiration (McCree, 1983; Irving and Silsbury, 1987; Ryan, 1991; Reich et al., 1998). For example, field observations for *Lolium perenne* by Jones et al. (1978) showed that while maintenance respiration of sward per unit dry matter varied by a factor of five during growth, 79% of the variance could be explained by the variation of protein concentration. Observations (n=16) and analysis presented by Ryan (1991) show that while maintenance respiration per unit dry matter for different species and organs varied by three orders of magnitude, 58% of the variance can be explained by the variation of the associated nitrogen concentration. Thus, in this study, maintenance respiration of different biome has been determined from nitrogen content rather than from dry matter. Also, biomass of living fine root has not been assumed to be equal to foliage biomass. Effects of diurnal and seasonal variations of temperature on maintenance respiration have been considered, together with varied stresses affecting A_g and R. Calculations have been done for 36 consecutive months (1987-1989) for large contiguous areas (ca. 10^5 km^2) of boreal deciduous and evergreen coniferous forests, crop land, temperate deciduous forest, temperate grassland, tropical deciduous forest, tropical evergreen forest, tropical savanna, and tundra. The model and input data are discussed below, followed by comparisons with observations, those predicted by Lieth and Box's (1977) model, calculated by Ruimy et al. (1996) and several other estimates. Then, the results of sensitivity analysis are presented for uncertainties in parameterization and input data.

MODEL and PARAMETERS

Total Respiration

Following the functional two component model of McCree (1974), the daily total respiration per unit ground area at a temperature of T { R (T), mol CO_2 m^{-2} d^{-1} } has been calculated as the sum of growth (R_g) and maintenance (R_m) components (Amthor, 1989; pp.10-12):

$$R(T) = [R_g(T) + R_m(T)] \qquad (1)$$

where the growth respiration per unit ground area (R_g; mol CO_2 m^{-2} d^{-1}) is given by the following equation (Amthor, 1989; p.11, 145):

$$R_g(T) = (1 - Y_G)\{A_g - R_m(T)\} \qquad (2)$$

where Y_G is the growth conversion efficiency (mole C synthesized per mole input C; mol mol^{-1}) and A_g is actual daily total gross photosynthesis per unit ground area (mol CO_2 m^{-2} d^{-1}).

Although the dependence of respiration on temperature is shown explicitly in the above equations, one should note that varied stresses which affect A_g also affect R (Eq. 2).

Growth Conversion Efficiency

Chemical composition of plants is the principal determinant of Y_G, and, apart from any biome-specific differences, changes in chemical composition during growth can also introduce variations in Y_G (Merino et al., 1982; Lafitte and Loomis, 1988a; McCree, 1988; Griffin, 1994). It has been taken to be 0.74 for crops, and 0.69

for woody species (Table 1). The data in Table 1 do not include any value for natural grasslands. However, Baruch and Gomez (1996) have reported the construction cost (kg glucose required to produce unit kg of dry matter) determined by calorimetry for grassland species of a savanna during rainy and dry season. These data for construction cost would give the mean (n=24) and the coefficient of variation of Y_G as, respectively, 0.74 and 5%, if carbon content of dry matter is taken to be 40% (Dwivedi, 1971; Hughes et al., 1999). Thus, Y_G for natural grasslands has been taken to 0.74. These Y_G values are close to those used in previous regional and global studies; viz., 0.80 by Raich et al., (1991), Warnant et al. (1994) and Haxeltine and Prentice (1996), 0.72 by Ruimy et al. (1996), 0.67 by Hunt et al. (1996), although these studies considered all biomes to have the same Y_G. The coefficient of variation of Y_G appears to be about 12% (Table 1), and the effect of this variation on the fluxes has been addressed by sensitivity analysis.

Actual Gross Photosynthesis

The method used to calculate unstressed gross photosynthesis ($A_{g,o}$) is based on the concept proposed by Monteith (1977) and has been fully described in Choudhury (2000a, 2001a,b). The $A_{g,o}$ is obtained as the product of biome-specific values of RUE and IPAR, as briefly elaborated below.

The light response function for the rate of gross photosynthesis by leaves has been taken to be a non-rectangular hyperbola, in which the maximum rate of photosynthesis varies within a canopy as determined by the nitrogen content of leaves. The quantum efficiency varies with foliage temperature. The foliage is separated into sunlit and shaded fraction, and irradiance on these leaves has been determined from a solution of the radiative transfer equation for incident direct and diffuse PAR. The instantaneous canopy gross photosynthesis is obtained by summing the photosynthesis by sunlit and shaded leaves, and the instanteneous values have been integrated over the daylight period to obtain $A_{g,o}$. The RUE values for clear and overcast conditions are obtained as the ratio of $A_{g,o}$ and IPAR. Then, the RUE corresponding to the incident PAR is obtained by interpolating the RUE values for clear and overcast conditions using the diffuse fraction of the incident PAR. These RUE values for different biomes and IPAR, determined from satellite observations providing incident irradiance and fractional interception, have been used to calculate $A_{g,o}$.

Adjustment of gross photosynthesis due to stresses follows along previous studies (cf., McGuire et al., 1992; Hunt et al., 1996). The effect of soil water stress has been modeled by the following scalar multiplier to unstressed photosynthesis (Ritchie, 1981):

$$\Sigma_g = \min \{1, W/(0.4\, W_{max})\} \qquad (3)$$

where W is the root-zone available moisture, and W_{max} is its maximum value. The effect of this stress is essentially that the unstressed gross photosynthesis continues until the available moisture decreases to 40% of its maximum value, below which photosynthesis decreases linearly with the available moisture. A biophysical process based model, combining water and energy balance equations with input satellite and ancillary data, has been used to calculate W (Choudhury and DiGirolamo, 1998). Comparison of calculated soil moisture with observations at grassland sites over Illinois for 60 months period (1986-1990) is given in Choudhury (2000b); linear least square regression analysis gave r^2 of 0.73 for the moisture values, and r^2 of 0.50 for moisture anomalies (i.e., departure from the mean values).

In addition to soil water stress, photosynthesis is also suppressed when foliage temperature is less than optimum (McGuire et al., 1992; Potter et al., 1994), and for time lost to perform photosynthesis during the period when foliage was wet by the intercepted rainfall (Ishibashi and Terashima, 1995; Choudhury and DiGirolamo, 1998).

Maintenance Respiration

Maintenance respiration per unit ground area of foliage, sapwood and living fine roots at mean daily temperature of T_j (subscript j denoting foliage, sapwood and living fine roots; f, s, r), $R_{m,j}(T_j)$, has been calculated from their values at a reference temperature of 20°C { $R_{m,j}(20)$; mol CO_2 m^{-2} d^{-1} } and their temperature response function, $f_j(T_j)$,as (Ryan, 1991):

$$R_{m,j}(T_j) = R_{m,j}(20)\, f_j(T_j)\, I_o(\beta_j\, \Delta T_j / 2) \qquad (4a)$$

where $I_o(x)$ is the modified Bessel function, ΔT_j is the diurnal range of temperature (°C) for tissue j, and β_j is related to the generally quoted temperature response coefficient (Q_{10}) of tissue j, ($Q_{10,j}$), as,

$$\beta_j = ln\,(Q_{10,j})/10 \qquad (4b)$$

Both $f_j(T_j)$ and $I_o(x)$ are dimensionless quantities. The modified Bessel function accounts for the effect of diurnal variation of tissue temperature (taken to be sinusoidal) on respiration. Most previous regional and global studies have not considered this effect of diurnal variation, although ignoring this effect can underestimate respiration by 5% or more (Ryan, 1991).

The temperature response function of tissue j, $f_j(T_j)$, is often expressed in terms of Q_{10} of that tissue ($Q_{10,j}$) as:

$$f_j(T_j) = [\,Q_{10,j}\,]^{\{(T_j - 20)/10\}} \qquad (5)$$

Varied approaches have used to prescribe Q_{10} in regional and global studies. For example, McGuire et al. (1992) considered Q_{10} to vary with monthly mean air temperature (Q_{10} increased linearly from 2.0 to 2.5 as temperature decreased from 5^o to 0^oC, decreased linearly from 2.0 to 1.5 as temperature increased from 20^o to 40^oC and was constant at 2.0 for temperature between 5^o and 20^oC), while Hunt et al. (1996) considered Q_{10} to be 2.0 independent of temperature.

The value of Q_{10} is often observed to be about 2 in mid-temperature range (Amthor, 1989; pp. 47-48), while it increases at lower temperature and decreases at higher temperature because of limiting biophysical processes (Ryan, 1991; Criddle et al., 1994; Larcher, 1995; p. 106; Stockfors and Linder, 1998; Atkin et al., 2000). Field measurements over a 12-year-old cypress forest (*Chamaecyparis obtusa*) for three-year period (Paembnan et al., 1991) gave the following relation between Q_{10} for shoot (j=foliage and stem) and air temperature (T_a) (Fig. 1):

$$Q_{10j} = 3.38 - 0.079\ T_a \qquad (6)$$

with an explained variance (r^2) of 0.91, and T was in the range 2.5°C to 25.0°C.

The $f_j\ (\ T_j\ )$ derived from Eqs. (5) and (6) is shown in Fig. 2, where applicability of Eq. (6) has been assumed beyond the range of temperature data in Fig. 1. This figure also shows the linear response function used by Ruimy et al. (1996), although they did not report the measurements used to determine this linear function and the range of temperature over which this response function is valid. These two response functions differ by more than 10% below 16°C and above 28°C. For regional and global modeling, Raich et al. (1991), McGuire et al. (1992), Warnant et al. (1994) and Ruimy et al. (1996) did not distinguish temperature of foliage, sapwood and roots (which were taken to be equal to the monthly mean air temperature), while Hunt et al. (1996) distinguished the temperature of shoot and roots. Thus, baseline calculations have been done using Eqs. (5) and (6) (i.e., the non-linear function in Fig. 2), while the effect of changing the response function to be linear (as in Ruimy et al.) on the fluxes has been addressed by sensitivity analysis. Also addressed by sensitivity analysis is the effect of distinguishing the temperature of different tissues.

It is generally recognized that much of the maintenance cost is due to turnover of protein in live plant tissue (Amthor, 1989; p. 49). A synthesis of observations relating maintenance respiration to nitrogen content for crops and uncultivated species from temperate and Mediterranean climate gave (Ryan, 1991; Choudhury, 2000c):

$$R_m\ (20) = 0.21\ (\ N_f + N_s + 2\ N_r\ ) \qquad (7a)$$

where N_f, N_s and N_r are nitrogen content per unit ground area (mol N m^{-2}) of foliage, sapwood and living fine roots. The first, second and third term on the right hand side of Eq. (7a) are, respectively, the respiration of foliage, sapwood and roots, $R_{m,f}$, $R_{m,s}$ and $R_{m,r}$. Higher respiration observed for roots, as compared to shoot, is thought to be due to the additional cost of ion uptake (Amthor, 1989; p. 97).

Ryan (1995) observed that maintenance respiration per unit nitrogen content for leaves of sub-alpine and boreal trees and shrubs to be 1.8 times higher than that for temperate species, which was suggested by Ryan (1995) to be in response to adaptation to colder climate. Thus, the equation used for boreal and tundra vegetation is the following:

$$R_m(20) = 0.38\,(N_f + N_s + 2\,N_r) \qquad (7b)$$

Measurements used in developing Eqs. (7a) and (7b) did not include any data for tropical biomes. If, at the reference temperature of 20°C, R_m per unit nitrogen content of boreal species is higher as compared to temperate species in response to adaptation to colder climate (Ryan, 1995), one may hypothesize that R_m per unit nitrogen content of tropical species at that reference temperature could be lower as compared to that for temperate species in response to adaptation to warmer climate. The impact of decreasing the numerical coefficient in Eq. (7a) for tropical biomes due to possible adaptation to growing at higher temperature has been addressed by sensitivity analysis.

Estimation of R_m (20) for different biomes is presented below.

By periodic harvest of fertilized stands of *Zea mays* during the period from emergence to one week before silking, Plenet and Lemaire (1999) found the following linear relation (r^2=0.98, n=23) between nitrogen content of shoot per unit ground area (i.e, $N_f + N_s$) and projected leaf area index (L_o; m^2 leaf m^{-2} soil surface area), up to the observed maximum L_o of 6:

$$N_f + N_s = 0.206\,L_o \qquad (8a)$$

while the relation for plants growing under limiting nitrogen conditions and L_o greater than 1.5 was,

$$N_f + N_s = 0.145 + 0.073\,L_o \qquad (8b)$$

Fig. 3 shows Eq. (8), together with total respiring nitrogen content appearing in Eq. (7a) (i.e., $N_f + N_s + 2\,N_r$) and L_o determined from harvest data during the vegetative phase of fertilized stands of *Triticum aestivum* (Choudhury, 2000c), *Sorghum bicolar* (Szeicz et al., 1973; Sivakumar et al., 1979; Eck and Musick, 1979; Myers, 1980; Lafitte and Loomis, 1988b), *Glycine max* (Hanway and Weber, 1971a; Rochette et al., 1995), *Gossypium hirsutum* (Bassett et al., 1970; Halevy, 1976; Mauney et al., 1994; Pettigrew, 1999), and *Phaseolus* *vulgaris* (Peck and MacDonald, 1984; Lynch et al., 1992). A constrained linear least square regression analysis gave the following relation (r^2=0.86, n=58):

$$N_f + N_s + 2\,N_r = 0.226\,L_o \qquad (9)$$

A practical constraint for annual crops is that ($N_f + N_s + 2\,N_r$) be zero when L_o is zero. Observations and analysis presented by Plenet and Lemaire (1999) and in Fig. 3 suggest that L_o can be considered to be an indicator of nitrogen content of a stand of some agricultural crops. Billore (1973) (quoted in Singh and Joshi, 1979) had found a linear relation between L_o and chlorophyll content for a grassland community, although both linear and non-linear relations between L_o and chlorophyll content have been noted depending upon the degree of shading and structural, non-photosynthetic tissue (Singh and Joshi, 1979).

An equation for estimating R_m (20) of cultivated areas can be obtained by substituting Eq. (9) in Eq. (7a) as:

$$R_m\,(20) = 0.047\,L_o \qquad (10)$$

Assuming that ($N_f + N_s + 2\,N_r$) scales with L_o of temperate grasslands as (Appendix A):

$$N_f + N_s + 2\,N_r = 1.395\,L_o \qquad (11)$$

one can obtain the following relation for R_m (20) of temperate grasslands (substituting Eq. 11 in Eq. 7a):

$$R_m\,(20) = 0.293\,L_o \qquad (12)$$

The equation for R_m (20) of tropical grasslands is found to be (Appendix B):

$$R_m\,(20) = 0.189\,L_o \qquad (13)$$

Attempt to apply Eq. (7) in totality to woody vegetation was not very successful because of very limited data for sapwood nitrogen content per unit ground area for different biomes needed to determine stem maintenance respiration. Following Hunt et al. (1996), the concept of pipe model was considered to estimate stem maintenance respiration. From available data on above ground standing biomass and an estimate of this biomass constituting sapwood, Haxeltine and Prentice (1996) proposed the following equation for sapwood maintenance respiration in terms of the seasonal maximum L_o ($L_{o,\,max}$) :

$$R_{m,\,s}\,(\,20\,) = 0.011\,L_{o,\,max} \qquad (14a)$$

Based on a synthesis of data relating sapwood maintenance respiration to leaf area index (Table 2), we have used the following relations for sapwood maintenance respiration of trees and shrubs based on the foliage shape:

Needle leaf: $R_{m,\,s}\,(\,20\,) = 0.009\,L_{o,\,max}$ (14b)

Broad leaf: $$R_{m,s}(20) = 0.014\ L_{o,\ max} \qquad (14c)$$

Waring and Schlesinger (1985; Table 2.2) have tabulated percentage of living cells in sapwood for eight species each of conifer and broad leaf trees, which gives mean (standard deviation, n=8) of live cells as, respectively, 7.1 (1.4)% and 16.0 (7.2)%. For the same sapwood volume, the cost of maintaining a lower percentage of live cells would be expected to be lower (Eqs. 14b,c).

Note that Eq. (14a), derived independently considering sapwood biomass and its maintenance coefficient, is consistent with the data in Table 2 when needle leaf and broad leaf species are not separated. Haxeltine and Prentice (1996) did not discuss the uncertainty associated with Eq. (14a) due to variability in the maintenance coefficient and uncertainty in determining the sapwood biomass. The impact of this uncertainty on the fluxes has been assessed by sensitivity analysis.

Then, maintenance respiration at 20°C of foliage and living fine roots is calculated from Eq. (7a) as:

$$R_{m,f} + R_{m,r} = 0.21\ (N_f + 2\ N_r) \qquad (15a)$$

for all biomes, except for boreal forests and tundra, for which the following equation is used (Eq. 7b):

$$R_{m,f} + R_{m,r} = 0.38\ (N_f + 2\ N_r) \qquad (15b)$$

Maintenance respiration of foliage and living fine root per unit L_o can be expressed as:

$$R_{m,f} + R_{m,r} = (\phi_f + \phi_r)\ L_o \qquad (16)$$

where $\phi_f = 0.21 N_f / L_o$ or $0.38 N_f / L_o$, and $\phi_r = 0.42 N_r / L_o$ or $= 0.76 N_r / L_o$. ϕ_f and ϕ_r determined from field observations for different biomes are given in Table 3, and elaborated in Appendix C.

From "best guess" values of the maintenance coefficients for foliage and fine roots, and assuming that fine root biomass to be equal to foliage biomass, Ruimy et al. (1996) had developed the following equation for calculating $R_{m,f} + R_{m,r}$ at 20°C for all biomes:

$$R_{m,f} + R_{m,r} = 0.047\ L_o \qquad (17)$$

The present independent calculations (Eq. 16 and Table 3) agree reasonably well (within 10%) with Eq. (17) for tropical evergreen forests and temperate deciduous forests, but not for other biomes. Eq. (10) derived for crops (including stem) is also in good agreement with Eq. (17), although Ruimy et al. (1996) did not consider crops to be a separate biome (their calculations are for potential vegetation). The present calculations are based on field data for fine root biomass, instead of the assumption that fine root biomass being equal to foliage biomass.

Net Carbon Accumulation

Net carbon accumulation per unit ground area per day (C; mol m^{-2} d^{-1}) has been calculated as the difference of gross photosynthesis (A_g) and respiration (R):

$$C = A_g - R \qquad (18)$$

By inserting Eqs. (1) and (2) in Eq. (18), one can also write C as:

$$C = Y_G (A_g - R_m) \qquad (19)$$

Note that, while IPAR is a major determinant of A_g, R_m is independent of IPAR. A radiation use efficiency corresponding to C (defined as the ratio of C and IPAR) would be conservative under conditions when respiration varies in proportion to photosynthesis (Choudhury, 2001b). Attempt to determine C without explicit calculation of A_g and R would require that C be parameterized in a way which can account for different sensitivities of A_g and R to biophysical factors.

INPUT DATA AND METHODS

Calculations have been done at a spatial resolution of 0.25°x0.25° (latitude x longitude cell dimension) for 36 consecutive months (1987-1989) using spatially representative, geo-referenced data derived from satellite and surface observations (Choudhury and DiGirolamo, 1998; Choudhury, 2001a). The leaf area index (L_o) has been determined following the algorithm of Los et al. (2000) using monthly maximum composite of visible and near infrared observations by the Advanced Very High Resolution Radiometer (AVHRR) on board the NOAA satellites after correcting the reflectances for the atmospheric effects (Rayleigh and aerosol scattering, and absorption by ozone, mixed gases and water vapor) and sensor degradation (Choudhury and DiGirolamo, 1998). The algorithm for L_o was derived and tested against field data (Los et al., 2000). Observations by the Tiros Operational Vertical Sounder (TOVS) on board the NOAA satellites have been used to determine air temperature (Choudhury and DiGirolamo, 1998). Comparison with surface observations for 12 months period (year 1988) at globally distributed 134 stations, which were selected to be away from large water bodies (viz., major lakes and oceans) and mountainous areas, gave the RMS error of 2.9°C and explained variance of 96% (the range of temperature was –40°C to 40°C). The diurnal temperature range needed for calculating maintenance respiration (Eq. 4a) is based upon climatologic data (Muller, 1982).

The input data used for calculating gross photosynthesis ($A_{g,o}$ and Σ_g) are fully described in Choudhury (2001a) and Choudhury and DiGirolamo (1998), which include the maximum rate of photosynthesis by leaves, incident photosynthetically active radiation, air temperature, precipitation, vapor pressure deficit of air, fractional cloud cover, surface albedo, and friction velocity. A large part of these data are needed for solving water and energy balance equations, which provide root-zone soil moisture needed for determining Σ_g (Eq. 3). The maximum rate of photosynthesis by leaves has been determined from compilations given in Medina (1986), Korner (1994), Vygodskaya et al. (1997), among others.

Calculations have been done for three consecutive years (1987-1989) for large contiguous areas (ca. 10^5 km^2) of boreal deciduous coniferous forest (BDF), boreal evergreen coniferous forest (BEF), crop land (CL), temperate deciduous forest (TDF), temperate grassland (TG), tropical deciduous forest (TrDF), tropical evergreen forest (TEF), tropical savanna (TS), and tundra (T), based on consulting vegetation maps of Olson et al. (1983), Matthews (1983) and Haxeltine and Prentice (1996) (Table 4). The vegetation types for these areas, according to the land cover data of Matthews (1983) following the UNESCO classification system, are given in Table 4. These are: cold-deciduous forest, without evergreens (Type #11 in Matthews; UNESCO code, 1.B.3) for BDF area; temperate/sub-polar evergreen needle-leaf forest (Type #8; code 1.A.10) for BEF area; cultivation (Type #32) on nearly 100% of the area for the CL area; cold-deciduous forest, with evergreens (Type #10; code 1.B.2) for the TDF area; meadow, short grassland, no woody cover (Type #28; code 5.C.5, 5.C.6, 5.C.7) for the TG area; tropical/sub-tropical drought deciduous forest (Type #9; code 1.B.1) for the TrDF area; tropical evergreen rainforest, mangrove forest (Type #1; code 1.A.1, 1.A.5) for the TEF area; tall/medium/short grassland with 10-40% area woody tree cover (Type #23; code 5.A.1, 5.B.1, 5.C.1) for the TS area; arctic/alpine tundra, mossy bog (Type #22; code 4.D, 4.E, 5.C.8) for the T area. Annual total precipitation and mean air temperature for the three years over the study areas are given in Table 4, together with long-term average data at selected locations for reference (Wernstedt, 1972; Muller, 1982).

The maintenance respiration of each biome has been calculated from the biome specific equations given in the previous section (e.g., Eq. 10 for CL, Eq. 12 for TG, etc.). For the tropical savanna (TS) area, a fractional area weighted sum of tropical deciduous forest {R_m (20) (TrDF)} and tropical grassland {Eq. 13; R_m (20) (TrG)} has been used, as follows:

$$R_m(20) = f_w * R_m(20)\,(\mathrm{TrDF}) + (1-f_w) * R_m(20)\,(\mathrm{TrG}) \qquad (20)$$

where f_w is the fractional woody vegetation cover. A mean value of 0.25 has been assigned to f_w, based on the description of this vegetation type given by Matthews (1983), namely 10-40% woody tree cover, as noted above. The growth conversion efficiency (Y_G) for the TS area has also been prescribed as the weighted average of values for woody vegetation (=0.69) and grassland (=0.74). The effect of uncertainty in prescribing f_w (i.e., variability between 10% and 40%) on the fluxes has been addressed by sensitivity analysis.

To compare with the present results, the following equations from Lieth and Box (1977) (LB's model) have been used to calculate net primary production (NPP) and gross primary production (GPP), both in units of g (dry matter) m^{-2} yr^{-1}, for all biomes except crop land (since these equations have been designed for potential vegetation):

$$\mathrm{NPP} = \min \{ \mathrm{NPP}(T), \mathrm{NPP}(P) \} \quad (21a)$$

$$\mathrm{GPP} = -4140\, ln \{ 1 - (\mathrm{NPP}/3000) \} \quad (21b)$$

where,

$$\mathrm{NPP}(T) = 3000/\{1 + exp(1.315 - 0.119\, T)\} \quad (21c)$$

$$\mathrm{NPP}(P) = 3000 \{ 1 - exp(-0.000664\, P) \} \quad (21d)$$

P and T are, respectively, annual total precipitation (mm) and mean air temperature (°C). Eq. (21a) attempts to capture limitations in productivity due to soil water stress (precipitation) and length of the growing season (temperature). Although biophysical basis of Eq. (21b) is not apparent, one can verify that this equation predicts the ratio (NPP/GPP) to decrease monotonically or (R/GPP) to increase monotonically with increasing NPP.

The P and T values for the three years given in Table 4 have been averaged for calculating NPP and GPP. Since the present calculations give the fluxes in carbon rather than dry matter equivalent, it was necessary to prescribe the carbon content of dry matter to compare with the results derived from LB's model. Thus, the carbon content of dry matter has been taken to be 40% for grasslands (Dwivedi, 1971; Hughes et al., 1999), 45% for savanna (Ajtay et al., 1979), and 48% for all other biomes (Raich et al., 1991) to convert NPP and GPP to, respectively, C and A_g. This conversion of the fluxes introduces an uncertainty of 5-10% because of variability of the carbon content (Singh and Singh, 1991). Then, R has been calculated as the difference of A_g and C. Note that the ratio of the fluxes (R/A_g) is not affected by the choice of carbon content of dry matter.

RESULTS and DISCUSSION

Model Results

Temporal variations of actual gross photosynthesis, total respiration and the ratio of maintenance respiration and total respiration are shown in Figs. (4a) for crop land (CL), (4b) for temperate grassland (TG), and Fig. (4c) for tropical evergreen forest (TEF) areas. Because of differences in the seasonality of leaf area index, incident radiation, temperature and soil moisture, which are the major driving forces for photosynthesis and respiration, the temporal variations of the fluxes are significantly more pronounced for CL and TG areas as compared to TEF area.

The seasonal maximum photosynthesis (total respiration) for the CL area is calculated to be 23 (12), 16 (9), and 23 (11) mol m^{-2} mo^{-1} for respectively, 1987, 1988, and 1989 (Fig. 4a). Precipitation during 1988 was about 150 mm lower than that during 1987 and 1989 (Table 4), and thus affecting the fluxes. For example, it is seen in Fig. 4a that during 1987 both photosynthesis and respiration reach their maximum during June, then they decrease during July, followed by increase in August, and then progressive decrease. This temporal pattern for the fluxes match the temporal variation of the soil water stress factor (Fig. 5). The ratio of maintenance respiration and total respiration attains its maximum during July in 1987 (Fig. 4a), when leaf area index (L_o) reaches its maximum (Fig. 5). Respiration exceeds photosynthesis during July 1988 (Fig. 4a).

The seasonal maximum photosynthesis for the TG area is calculated to be 14, 18, and 18 mol m^{-2} mo^{-1} for respectively, 1987, 1988, and 1989 (Fig. 4b). The seasonal maximum L_o was found to be 0.9 in 1988, but somewhat lower in 1987 and 1989 (L_o = 0.7). The annual total precipitation for the TG area was maximum in 1989, followed by 1987 and 1988 (Table 4). Temporal variation of precipitation is shown in Fig. 6. Precipitation during the initial growing period (May-June) was 73, 68, and 84 mm for 1987, 1988 and 1989. Thus, while L_o was lower in 1989, the available water was higher. Both L_o and soil water stress are contributing to the interannual variation of gross photosynthesis. The seasonal maximum total respiration is calculated to be 9, 12, and 11 mol m^{-2} mo^{-1} for respectively, 1987, 1988, and 1989, and, of this total, maintenance respiration contributed, respectively, 83, 79, and 69%. These seasonal maximum values of respiration and photosynthesis temporally coincide for 1988 and 1989, but are offset by one month in 1987. With the onset of the growing season, the fraction of total respiration due to maintenance increases because of vegetation growth, but then the fraction decreases because of senescence. It is seen in Fig. 4b that photosynthesis increases from zero to the seasonal maximum in two months, but then it decreases to zero in three months during all three years. Such temporal variation is also seen for total respiration during 1988 and 1989, but not during 1987.

The seasonal maximum gross photosynthesis for the TEF area is calculated to be about 25 mol m^{-2} mo^{-1}, while the seasonal minimum photosynthesis is found to be 16 mol m^{-2} mo^{-1} (Fig. 4c). The seasonal maximum total respiration is found to be about 15 mol m^{-2} mo^{-1}, while the seasonal minimum to be about 12 mol m^{-2} mo^{-1}.

Thus, the seasonal range of photosynthesis and total respiration are, respectively, about 9 and 3 mol m^{-2} mo^{-1}. The maintenance respiration is found to contribute about 80% of the total respiration.

Calculated annual fluxes of gross photosynthesis, maintenance and growth respiration, and net carbon accumulation are given in Table 5 for all three years. It is seen that maintenance respiration exceeds growth respiration for all biomes. Averaged for the three years, the ratio of annual maintenance respiration and annual total respiration is found to be highest for TEF (0.81), followed by TS (0.75), TrDF (0.72), TG (0.71), CL (0.71), BDF (0.66), TDF (0.65), BEF (0.61), and T (0.58). Ryan (1991) has summarized the ratio of maintenance and total respiration for two stands each of temperate grasslands and temperate forests, giving the range as 0.75-0.88. The ratio of annual total respiration and gross photosynthesis is found to be highest for TEF (0.70), followed by TS (0.63), TG and TrDF (0.62), BDF (0.57), TDF (0.56), CL (0.55), BEF (0.54), and T (0.52). Interannual variation of the fluxes is generally within 15%, except for the CL area for which C during 1988 is about 62% lower than the other two years. During 1989, the C for the BDF area is about two times that for other two years, and the C for the TS area is about 32% higher than the other two years. The C for the T area differs significantly for each of the three years due primarily to differences in A_g and R_g caused by soil water stress; June-September precipitation for 1987, 1988 and 1989 were, respectively, 92, 76, and 142 mm.

Comparison with Observations and Previous Estimates

The present results (averaged for the three years), together with those predicted by Lieth and Box's (1977) model (Eq. 21) and calculated by Ruimy et al. (1996) are given in Table 6. This table also includes the data presented by Ajtay et al. (1979; Table 5.5) based on approximate averages of published values or chosen subjectively as possible values.

The calculated C for the BDF area is 30% lower than the value given by Ajtay et al. for open boreal coniferous forest, but it is 42% higher than that predicted by Lieth and Box's (LB's) model, and less than half the value calculated by Ruimy et al. (Table 6). It is, however, not clear whether the value given by Ajtay et al. is appropriate for boreal deciduous coniferous forest or boreal forest – tundra ecotone (forest tundra). Potter et al. (1993) calculated C to be 13 mol m^{-2} yr^{-1}, which is 31% lower than the present result. Hunt et al. (1996) calculated C to be 17 mol m^{-2} yr^{-1}, which is in agreement with the present result. Lloyd (1999) calculated C to be 19 mol m^{-2} yr^{-1}, which is 11% higher than the present result. For deciduous and evergreen coniferous forests in Siberia, Schulze et al. (1999) determined above ground production to be 7 mol m^{-2} yr^{-1}, and depending upon the assumption used to determine below-ground production (turnover of fine roots), C was estimated to be 9-12 mol

m^{-2} yr^{-1}. For a deciduous coniferous stand near Tura (64.3°N, 100.2°E), Kajimoto et al. (1999) determined above ground production to be 6 mol m^{-2} yr^{-1}, and depending upon the assumption used to determine below-ground production (turnover of fine roots), C was estimated to be 8-31 mol m^{-2} yr^{-1}. The present values of C for 1987 and 1988 are fairly consistent with these estimated values, and, although the result for 1989 is somewhat higher, it is within the range of estimated values (Table 5). While there are substantial differences in A_g calculated in the present study and those determined from LB's model and calculated by Ruimy et al. (Table 6), there does not appear to be any measured gross production or respiration against which to evaluate these calculated results. The present R/A_g compares well with Ruimy et al., but substantially higher than that predicted by LB's model.

The calculated for C for the BEF area is 9% higher than the value given by Ajtay et al. and that predicted by LB's model, and 25% higher than the value calculated by Ruimy et al. (Table 6). Using a calibrated process-based model McGuire et al. (1992) calculated C to be 19 mol m^{-2} yr^{-1} for boreal forest, which is 84% lower than the present calculation. Also using a calibrated process-based model Warnant et al. (1994) calculated C to be 35 mol m^{-2} yr^{-1} for needle-leaf forest, which agrees well with the present calculation. Using a calibrated radiation use efficiency based model, Potter et al. (1993) calculated mean C for needle-leaf evergreen trees to be 19 mol m^{-2} yr^{-1}, which is about half the value calculated in this study. Lloyd (1999) calculated C to be 10 mol m^{-2} yr^{-1}, which is about one-third the value calculated here. The calculated A_g is 49% and 25% higher than that from LB's model and estimated by Ruimy et al., respectively. The calculated ratio R / A_g is much higher than that predicted by LB's model, but agrees well with that calculated by Ruimy et al. Ryan et al. (1997) have given carbon balance data for two boreal coniferous stands each of *Picea mariana* and *Pinus banksiana*, while Malhi et al. (1999) have given such data for one stand of *Picea mariana*. The mean (standard deviation, range, n=5) of A_g is 80 (11, 64-91) mol m^{-2} yr^{-1}, C is 26 (10, 19-43) mol m^{-2} yr^{-1}, R is 54 (14, 37-69) mol m^{-2} yr^{-1}, and (R /A_g) is 0.67 (0.12, 0.46-0.77). The present A_g is 5% lower, the C is 35% higher, while (R /A_g) is 19% lower than the mean values from these carbon balance data, although the present results for C and (R /A_g) are within the range of the carbon balance data. It appears that the present calculations are underestimating R by about 20%.

The calculated C for the CL area is 18% lower than the value given by Ajtay et al. (Table 6). Considering the specific crops which are grown within and around the study area and field measurements of dry matter production of these crops, the C for the CL area is estimated to be about 49 mol m^{-2} yr^{-1} (Appendix D), and the calculated C is 24% lower. Warnant et al. (1994) calculated C to be 64 mol m^{-2} yr^{-1}, which is 42% higher than the present result. Potter et al. (1993) calculated mean C for all cultivated areas to be 24 mol m^{-2} yr^{-1}. Lloyd

(1999) calculated C to be 106 mol m^{-2} yr^{-1}, which is about a factor of two higher than the present result. The results in Table 5 show that C for 1988 is substantially lower than the other two years. The average C for 1987 and 1989 is 47 mol m^{-2} yr^{-2}, which is 4% higher than the value given by Ajtay et al., but 4% lower than the estimated value for the area (Appendix D). Considering available measurements, Amthor (1989; p. 115) has suggested that annual respiration (R) for CL is about 50% of A_g. The present calculations, averaged over the three years, are giving this fraction as 55% (Table 6). Again, if the results for 1988 are excluded, the R / A_g for the other two years agrees well with that suggested by Amthor (1989) (Table 5).

The present result for C for the TDF area agrees well with the value given by Ajtay et al., but is 20% and 9% higher than that derived from LB's model and calculated by Ruimy et al., respectively (Table 6). McGuire et al. (1992) calculated C to be 61 mol m^{-2} yr^{-1}, which is 21% higher than the present result. Warnant et al. (1994) calculated C to be 55 mol m^{-2} yr^{-1}, which is 13% higher than the present result. Potter et al. (1993) calculated mean C for broad-leaf deciduous and mix of broad-leaf and needle-leaf trees to be 26 mol m^{-2} yr^{-1}, which is 85% lower than the present value. The present A_g is, respectively, 59% and 13% higher than that derived from LB's model and calculated by Ruimy et al. The carbon balance data given in Kira (1975), Ryan (1991) and Malhi et al. (1999) give mean (standard deviation, range, n=10) of A_g as 113 (41, 56-181) mol m^{-2} yr^{-1}, C as 57 (14, 30-79) mol m^{-2} yr^{-1}, R as 56 (31, 26-120) mol m^{-2} yr^{-1}, and (R / A_g) as 0.48 (0.09, 0.37-0.66). These mean A_g and C are, respectively, 4% and 16% higher, while the mean (R / A_g) is 17% lower than the present results. These carbon balance data data suggest that R is being overestimated by about 10%.

The present result for C for the TG area is 5% lower than the value given by Ajtay et al., but it is 18% and 56% lower than that derived from LB's model and calculated by Ruimy et al., respectively (Table 6). McGuire et al. (1992) calculated C to be 17 mol m^{-2} yr^{-1} for temperate short grassland, which is 6% lower than the present result. Potter et al. (1993) calculated C to be 15 mol m^{-2} yr^{-1} for perennial grassland, which is 20% lower than the present result. Warnant et al. (1994) calculated C to be 28 mol m^{-2} yr^{-1} for grassland, which is 36% higher than the present result. Lloyd (1999) calculated C for grasslands to be 27 mol m^{-2} yr^{-1}, which is 33% higher than the present result. The present A_g is 35% higher than that from LB's model, and 31% lower than that calculated by Ruimy et al. The present R / A_g (viz., 0.62) is substantially higher than that from LB's model and determined by Ruimy et al. (ca. 0.37). Sims and Coupland (1979; Table 5.6) have presented measurements for net primary production at 10 locations for one to three years periods, which give mean (standard deviation, range, n=24) as 0.80 (0.30, 0.23-1.43) kg (dry matter) m^{-2} yr^{-1}. These measurements at the Matador (50.7°N, 107.8°W) site, which is at the similar latitude as the present study area and has similar annual precipitation (338 mm), reported for three years give mean and the range of C, respectively, as 0.70 and 0.54-0.87 kg (dry matter) m^{-2} yr^{-1}. The mean (range) NPP at Matador would correspond to C of 23 (18-29) mol m^{-2} yr^{-1}, if the carbon content of dry matter is taken to be 40% (Dwivedi, 1971; Hughes et al., 1999). The present result for C is 22% lower than the mean value at Matador, but it is at the lower end of the range. Heslehurst and Wilson (1974) have present field data for R / A_g of *Panicum maximum* as 0.57, while Ryan (1991) has reported two studies giving this ratio as 0.53 and 0.61. While the present result for R / A_g averaged over the three years (viz., 0.62; Table 6) is little higher than these reported measurements, the results for C and R/A_g for 1987 and 1989 are more along the line of above quoted measurements (Table 5).

The calculated C for the TrDF area is 10% higher than the value given by Ajtay et al., but it is 11% lower than that from LB's model and 20% higher than that calculated by Ruimy et al. (Table 6). Warnant et al. (1994) calculated C to be 59 mol m^{-2} yr^{-1}, which is 12% lower than the present result. Using a process-based model Raich et al. (1991) determined C to be 70 mol m^{-2} yr^{-1}, which is 6% higher than the present result. Estimates from the measurements reported at four sites give C in the range 44-80 mol m^{-2} yr^{-1} (Appendix E), which averages to 58 mol m^{-2} yr^{-1}. The present result (66 mol m^{-2} yr^{-1}) is 14% higher than this average. The present value of R / A_g (viz., 0.62) agrees well with Ruimy et al. (viz., 0.60), but 17% higher than that predicted by LB's model (0.53). Brown and Lugo (1982) have given gross and net dry matter production for a stand of sub-tropical dry forest near Ensenada (18.0°N, 65.9°W) as, respectively, 19.0 and 11.0 t ha^{-1} yr^{-1}, which would give R / A_g as 0.58.

The present result for C for the TEF area is 21% lower than the value given by Ajtay et al., and 31% lower than that from LB's model, but 10% higher than that calculated by Ruimy et al. (Table 6). Warnant et al. (1994) calculated C to be 77 mol m^{-2} yr^{-1}, which is 12% higher than the present result. Potter et al. (1993) calculated C to be 86 mol m^{-2} yr^{-1}, which is 21% higher than the present value. Modeling by Raich et al. (1991) had given C as 81 mol m^{-2} yr^{-1}, which is 16% higher than the present result. The present A_g is 21% lower than that from LB's model, but 39% higher than that estimated by Ruimy et al. Mearements at Khao Chong (7.6°N, 99.8°E) reported by Kira (1975) give A_g as 334 mol m^{-2} yr^{-1}, while gross ecosystem production at Reserva Jaru (10.1°S, 61.9°W) and near Manaus (2.5°S, 60.1°W) were determined to be, respectively, 204 and 250 mol m^{-2} yr^{-1} (Lloyd et al., 1995; Malhi et al., 1998). The present value of A_g is within the range of these reported measurements, and it agrees well with the average of two measurements within the Amazonian forest (viz., 204 and 250 mol m^{-2} yr^{-1}). The ratio (R / A_g) was determined to be 0.66 at Khao Chong (Kira, 1975), and 0.46 near Manaus (Malhi et al., 1999). At El Verde (18.3°N, 65.8°W), net and gross dry matter production were determined to be, respectively, 28.9 and 100 t ha^{-1} yr^{-1} (Lieth and Box, 1977), giving (R / A_g) as 0.71. For Pasoh Forest (3.0°N, 102.3°E), net and gross dry matter production have been determined to be, respectively, 22.5 and 81 t ha^{-1} yr^{-1} (Aoki et al., 1975; Cannell, 1982, p.196; Yoda, 1983), which would give (R / A_g) as 0.72. Allen and Lemon (1976) have reported the average gross and net CO_2 assimilation for two days of measurements for a stand near Turrialba (9.9°N, 83.6°W) as, respectively, 41.6 and 17.0 g (CO_2) m^{-2} d^{-1}, which would give (R / A_g) as 0.59. While the present result for R / A_g (viz., 0.70) is within the range of reported values, measurements near Manaus reported by Malhi et al. (1999) and comparison in Table 6 suggest that respiration is being overestimated by about 20%.

The calculated C for the TS area is 28% lower than the data given by Ajtay et al., and it is 19% lower than that from LB's model but 15% higher than that calculated by Ruimy et al. (Table 6). Using an empirical model, Scholes and Hall (1996) estimated C to be 53 mol m^{-2} yr^{-1}, which is 17% lower than the present result. Warnant et al. (1994) calculated C to be 54 mol m^{-2} yr^{-1}, which is 15% lower than the present result. Modeling by Raich et al. (1991) had given C to be 78 mol m^{-2} yr^{-1}, which is 21% higher than the present result. Scholes and Hall (1996) have summarized available measurements of C by TS areas. According to this summary, the data is available at Nylsvley (24.7°S, 28.7°E) and three sites near Lamoto (6.2°N, 5.0°E). By taking the carbon content of dry matter for trees and grasses as, respectively, 48% and 40%, one obtains the value of C at Nylsvley as 35 mol m^{-2} yr^{-1} (of which 46% was contributed by the grass layer), while it averages to be 104 mol m^{-2} yr^{-1} (range 93-110 mol m^{-2} yr^{-1}) for sites near Lamoto (of which 94% was contributed by the grass layer). For a TS within the Chandraprabha sanctuary (25.9°N, 83.2°E), Singh (1989) has given C to be 39 mol m^{-2} yr^{-1} (of which 78% was contributed by the grass layer). The present value of C is within the range of these measurements. The average of the C values at Nylsvley, Lamoto and Chandraprabha is 59 mol m^{-2} yr^{-1}, which is 5% lower than the calculated C. The present A_g agrees well with that calculated from LB's model, but it is 48% higher than the value calculated by Ruimy et al.. The present R / A_g is higher than that predicted by LB's model and calculated by Ruimy et al. by about 17%. I could not find any reported measurements for A_g and R, which might allow a better understanding of the discrepancy of 28% for C (Table 6). However, based on some assumptions, McGuire et al. (1992) determined carbon balance at Nylsvley, which gives R/A_g as 0.60. The present R/A_g is 5% higher.

The present result for C for the T area is 15% higher than the value given by Ajtay et al., and 25% higher than the values from LB's model and that calculated by Ruimy et al. (Table 6). Calculation of Warnant et al. (1994) had given C to be 18 mol m^{-2} yr^{-1}, which is 17% higher than the present result. Potter et al. (1993) calculated C to be 7 mol m^{-2} yr^{-1}, which is less than half of the present result. McGuire et al. (1992) calculated C to be 8 mol m^{-2} yr^{-1} for wet/moist tundra, which is 88% lower than the present result. Considering available measurements, Bliss (2000; Table 1.5) has given net primary production to be in the range, 0.15-0.45 kg (dry matter) m^{-2} yr^{-1}, which would be equivalent to C of 6-16 mol m^{-2} yr^{-1} if carbon content of dry matter is taken to be 48%. The present result is at the high end of this range (Table 6). Using a calibrated ecosystem-level model, Hobbie et al. (1998) determined C during one year (1995) for the Kuparuk River basin (ca. 69°-70°N, 149.2°-149.8°W) to be 8 mol m^{-2} yr^{-1}, which is about half the value calculated here for three year average (15 mol m^{-2} yr^{-1}) but agrees with the result for 1988 (Table 5). The values C for 1987 and 1988 are within the range suggested by Bliss (2000), but it is outside the range for 1989 (Table and 5). The present A_g is 88% and 60% higher than, respectively, from LB's model and that calculated by Ruimy et al. The present R / A_g is higher than that calculated from LB's model and obtained by Ruimy et al. Considering available data, McGuire et al. (1992) reported C and A_g for wet tundra near Toolik Lake (68.6°N, 149.6°W) to be, respectively, 10 and 37 mol m^{-2} yr^{-1}, giving R / A_g as 0.73. Based on measurements and ecosystem-level modeling, McKane et al. (1997) determined A_g for *Carex-Eriophorum* meadow vegetation at Barrow (71.3°N, 156.7°W) and tussock tundra at Toolik Lake (68.6°N, 149.6°W) to be, respectively, 17 and 39 mol m^{-2} yr^{-1}, and the present A_g for three year average (32 mol m^{-2} yr^{-1}; Table 6) is within this range, but A_g for 1989 is outside this range (Table 5). Rather high A_g for 1989 is because of significantly higher precipitation during this year (Table 4), and thus minimizing stress. McKane et al. (1997) determined R / A_g for these two sites to be, respectively, 0.57 and 0.76, and, while the present result for three year average (0.52; Table 6) is outside the range, the result for 1988 is within the range (Table 5). Both A_g and R/A_g for 1989 are outside the range determined from measurements and results from a calibrated model (Table 5). If we exclude the results for 1989, the average C for the other two years, viz., 12 mol m^{-2} yr^{-1}, is 8% lower than the value given by Ajtay et al., and R/A_g (0.56) is closer to the range of values determined by McKane et al. (1997).

From the above comparisons, the calculated C (averaged for the three years) differ by about 30% from the measurements summarized by Ajtay et al. (1979) for the BDF and TS areas; the discrepancy for all other biome areas is generally less than 20%. There are more reported measurements for C than for A_g or R. These data suggest that R is being underestimated for the BEF area, and overestimated for TEF area by about 20%.

Results of Sensitivity Analysis

Sensitivity analysis has been done for variability in the growth conversion efficiency (Y_G; Table 1), differences in the temperature response function for maintenance respiration { f (T); Eq. 4 and Fig. 2}, distinguishing the temperature of shoot and root (Eq. 4), variability in the sapwood maintenance respiration per unit seasonal maximum leaf area index (Eq. 14 and Table 2), the effect of variations in the fraction of tree cover in the TS area (f_w, Eq. 20), and decreasing R_m of foliage and roots per unit nitrogen content for tropical biomes as compared to temperate biomes (i.e., decreasing the values of φ in Table 3 for tropical biomes) due to possible adaptation to growing temperature (Ryan, 1995).

Any variability in Y_G can directly translate to an equivalent variability in R_g (Eq. 2) and C (Eq. 19). Thus, 12% increase (decrease) in Y_G can increase (decrease) the calculated C values by 12%. Any discrepancy between the calculated and observed C up to about 12% may not be resolved satisfactorily because of the uncertainty in prescribing Y_G (Table 1). Modeling of Choudhury (2000c) showed that R/A_g decreased during growth when Y_G was assumed not to change during growth, but variations in R/A_g decreased considerably when changes in Y_G during growth was taken into consideration. These sensitivity results suggest that a better quantification of Y_G is desirable for a more accurate assessment of R/A_g.

The impact of changing the temperature response function from non-linear to linear on R_m, R, and C (averaged for the three years) is given in Table 7. The impact is found to be generally less than 5%, except for the BDF, TDF and T areas, for which R increased by about 10% and C decreased by 10%.

The results presented above were obtained by taking shoot and root temperature to be equal to air temperature, as was done in the studies reported by Raich et al. (1991), McGuire et al. (1992), Warnant et al. (1994) and Ruimy et al. (1996), although Hunt et al. (1996) distinguished the temperature of shoot and roots. Measurements reported by Toy et al. (1978), Zheng et al. (1993), among others, show that mean soil temperature at 0.1-0.3 m depth in grass-covered ground can differ from air temperature by 1-3°C. Calculations done by taking root temperature to be equal to soil temperature, rather than air temperature, showed that R is not affected by more than 3% (Table 8). Changes of less than 1% are calculated for crop land (CL) and tropical evergreen forest (TEF) areas. For CL, nitrogen content of roots is about 15% of that in shoot (Fig. 3; Eqs. 8 and 9) and thus its contribution to the maintenance respiration of a stand is small. For TEF, soil temperature did not change significantly for being in moist condition and because of high vegetation cover (leaf area index of about 5). Measurements of temperature for a typical day (November 22, 1973) above and within a rainforest (Pasoh Forest; 3.0°N, 102.3°E) reported by Aoki et al. (1975) show that mean daily temperature above the canopy and at soil surface to be almost identical (respectively, 23.5° and 23.4°C). Thus, it is reasonable to approximate mean daily root temperature by the corresponding air temperature for TEF area.

The sapwood maintenance respiration per unit seasonal maximum leaf area index was found to have a coefficient of variation of 33% and 58%, respectively, for needle leaf and broad leaf vegetation (Table 2). The impact of increasing stem maintenance respiration by 35% on total R_m, R, and C (averaged for the three years) is given in Table 9. The total R_m was found to increase by 1% for the TS area to 9% for the TDF and TrDF areas, while C decreased by 1% for the TS and T areas to 11% for the TEF area. Thus, uncertainty in estimating stem maintenance respiration could be introducing an uncertainty in determining C of about 10%.

The percent tree cover in the TS area was taken to be 25%, as being the average of the range of tree cover (10% to 40%) according to the description of Matthews (1983). When the tree cover was decreased to 10%, R decreased by 8% and C increased by 14% as compared to the values given in Table 5. When the tree cover was increased to 40%, R increased by 5% and C decreased by 9%. Thus, for the same change in fractional tree cover, C increases more when the fractional cover is decreased as compared to decrease in C when the fractional cover is increased. Several field studies have reported concave relations between above ground herbaceous production and tree cover (Beale et al., 1973; Jackson and Ash, 1998). The discrepancy between the present calculations for C and the data reported by Ajtay et al. (1979) in Table 6 decreases from 28% to 19% when fractional tree cover is decreased from 25% to 10%. While much discrepancy still remains between the present C and the value given by Ajtay et al. (1979), available observations are rather limited (Scholes and Hall, 1996) to quantify this discrepancy more objectively.

Eq. (7a), developed from observations for temperate and Mediterranean species, has been applied to tropical biomes. However, R_m per unit nitrogen content for boreal species has been observed to be higher compared to temperate species (Eq. 7b vs. Eq. 7a), presumably in response to adaptation to colder climate (Ryan, 1995). Then, one may hypothesize that R_m per unit nitrogen content for tropical biomes would be lower compared to that for temperate biomes in response to adaptation to warmer climate. The impact of decreasing R_m of foliage and roots of tropical biomes (φ in Table 3) by a factor 1.5 on the fluxes is given in Table 10. It is seen that the total maintenance respiration (R_m) decreases by 25% (for TrDF area) to 32% (for TS area), R decreases by 12% (for TrDF area) to 18% (for TS area), and C increases by 20% (for TrDF area) to 36% (for TS area). Considering this sensitivity, it is desirable to know the extent to which Eq. (7a) applies to tropical biomes. It is also clear that R/A_g of tropical biome areas (particularly, the tropical evergreen forest) can be rather comparable to that for the temperate areas, and thus the variability of R/A_g among biomes can be lower.

SUMMARY and CONCLUSIONS

The rate of net carbon accumulation per unit area by plant communities is the difference of the rate of gross photosynthesis by a canopy and the rate autotrophic respiration of the stand per unit ground area. While seasonal changes in the maximum rate photosynthesis by leaves and radiation intercepted by a canopy are the major determinants of the rate of gross photosynthesis by a canopy, seasonal changes in biomass of organs, their specific respiration coefficient and temperature are important determinants of the rate of respiration by the stand, in addition to photosynthesis. A better understanding of the carbon balance of plant communities, and how this balance might change due to changes in land cover or environmental conditions requires explicit evaluation of the rates of photosynthesis and respiration.

The autotrophic respiration (R) was calculated as the sum of maintenance (R_m) and growth (R_g) components using satellite and field observations. The R_m of foliage and living fine roots per unit ground area for different biomes was determined objectively from observed nitrogen content of these organs per unit ground area, and taking into consideration of diurnal and seasonal variations of temperature. The R_m of stems of herbaceous crops and natural grasslands was also determined from the nitrogen content. An empirical equation for sapwood maintenance respiration was derived according to pipe model, which was found to be consistent with an equation derived independently considering sapwood biomass and its maintenance coefficient. The R_g was calculated from the difference of gross photosynthesis by a canopy per unit ground area (A_g) and R_m. The A_g was expressed as a product of biome-specific radiation use efficiency for gross photosynthesis under unstressed conditions (RUE), intercepted photosynthetically active radiation (IPAR), and stress factors to account for soil water stress and temperature away from optimum. The unstressed RUE for different biomes was determined from the maximum rate of photosynthesis by leaves, foliage temperature and fractional diffuse incident radiation. All stresses which affect A_g also affect R. The rate of net carbon accumulation per unit ground area (C) was determined as the difference of A_g and R.

Calculations were done using spatially representative, synchronous data for 36 consecutive months (1987-1989) derived from satellite and field observations for large contiguous areas (ca. 10^5 km^2) of boreal deciduous coniferous forest (BDF), boreal evergreen coniferous forest (BEF), crop land (CL), temperate deciduous forest (TDF), temperate grassland (TG), tropical deciduous forest (TrDF), tropical evergreen forest (TEF), tropical savanna (TS), and tundra (T).

On annual basis, R_m was found to exceed R_g for all biome areas. Averaged for the three years, the ratio of R_m and R was found to be highest for TEF (0.81), followed by TS (0.75), TrDF (0.72), TG (0.71), CL (0.71), BDF (0.66), TDF (0.65), BEF (0.61), and T (0.58). The ratio of R and A_g was found to be highest for TEF (0.70), followed by TS (0.63), TG and TrDF (0.62), BDF (0.57), TDF (0.56), CL (0.55), BEF (0.54), and T (0.52). Interannual variation of the fluxes was generally within 15%, except for the BDF area for which C during 1989 was about a factor two higher than the other two years, while C for the CL area during 1988 was about 62% lower than the other two years. The C for the TS area during 1989 was about 32% higher than the other two years. The C for the T area for 1988 was half the value found for 1987, and nearly one-third the value for 1989. Previous large-scale modeling studies did not addressed interannual variations of respiration and net carbon accumulation for different biomes.

The calculated C (averaged for the three years) was found to be about 30% lower for the BDF and TS areas, when compared against a synthesis of observed and likely values of C. However, in the absence of observed A_g and R, it could not be determined which of these two fluxes is contributing more, and/or which way, to this discrepancy. The discrepancy for C for other biome areas was generally less than 20%. Aggregately for all biome area, the calculated C was about 10% lower than the reported data. The calculated A_g values were generally within the range of measurements, where available. The present calculations for R might be underestimating the flux for BEF area, and overestimating it for TEF area by about 20%.

Sensitivity analysis was done to assess the impact of variability in the growth conversion efficiency (Y_G), differences in the temperature response function for maintenance respiration, differences in shoot and root temperature, variability in the sapwood maintenance respiration per unit of the seasonal maximum leaf area index, the effect of variations in the fractional cover of trees in the TS area, and uncertainty in determining maintenance respiration per unit nitrogen content of tropical biomes from measurements on temperate species.

Any variability in Y_G directly translates to equivalent variability in C. Variability of Y_G was found to be about 12%, and, if this variability is assumed to be due only to differences in biochemical composition of plants, any discrepancy between the calculated and observed C up to about 12% cannot be resolved satisfactorily.

The impact of changing the temperature response function was found to be generally less than 5%, except for the TDF and T area, for which R increased by about 10% and C decreased by 10%. Calculations done by taking root temperature to be equal to soil temperature, rather than air temperature, showed that R is not affected by more than 3%.

The effect of increasing sapwood maintenance respiration by 35% was to increase total respiration by 1% (for the TS and T areas) to 5% (for the TrDF area), while C decreased by 1% (for the TS and T areas) to 11% (for the TEF area).

The fraction of woody cover in the TS area was taken to be 25%, being the average of the range of woody cover (10% to 40%) suggested for the area. When the woody cover was decreased to 10%, R decreased by 8% and C increased by 13%. When the woody cover was increased to 40%, R increased by 5% and C decreased by 9%.

Relationships between maintenance respiration and nitrogen content used in the present study are based upon observations for temperate, Mediterranean, and boreal species, and their applicability to tropical species is not known. When maintenance respiration foliage and roots per unit nitrogen content for the tropical biome areas was decreased by a factor of 1.5 as compared to that for temperate species, R for tropical biome areas decreased by 12-18% and C increased by 20-36%. Considering this sensitivity, it is desirable to determine variation of maintenance respiration with nitrogen content for tropical biomes. If maintenance respiration per unit nitrogen content for tropical species is observed to be lower than that for temperate species, R/A_g for the tropical biome areas could become comparable to that for the temperate regions.

The results presented in this study can be improved, for example, by quantifying, (a) temporal variation of biomass and nitrogen content of living fine roots in relation to those of foliage, and (b) foliage maintenance respiration per unit nitrogen content for species growing in the tropics.

Appendix A

This appendix elaborates on the data used to relate total respiring nitrogen content per unit ground area to the projected leaf area index (L_o) of ungrazed temperate grasslands.

By synthesizing available measurements, Jackson et al. (1997) and Gordon and Jackson (2000) have given average (standard deviation, n) living fine roots (less than 2 mm in diameter) biomass as 0.95 (0.078, 21) kg m^{-2} and its nitrogen concentration as 1.11 (0.002, 54)%, which would give the average nitrogen content of living fine roots per unit ground area (N_r) as 0.753 mol m^{-2} (= 0.95 x 10^{3} x 1.11 x 10^{-2} / 14). They have also given the percentage of total roots to be living fine roots as 63%.

The above data for nitrogen content of living fine root needs to be supplemented by the nitrogen content of living foliage and stem (N_f and N_s). Sims and Coupland (1979; Tables 5.3 and 5.5) have tabulated peak green shoot biomass and peak root biomass (live and dead) for grasslands at several locations according to the year of measurements (two to three years). There are 14 concurrent pairs of such data near five locations (Cottonwood, Matador, Osage, Pantex, and Pawnee). These data give the mean (standard deviation; n=14) peak green shoot biomass as 0.176 (0.082) kg m^{-2}, while mean peak root (live and dead) biomass as 1.461 (0.614) kg m^{-2}. Taking 63% of this mean peak root biomass one obtains 0.921 kg m^{-2}, which agrees well with the value for living root biomass given by Jackson et al. (1997) quoted above. Thus, the living fine root biomass data given by Jackson et al. might correspond to an average live shoot biomass of 0.176 kg m^{-2}.

Measurements by Risser and Parton (1982) near Osage gave nitrogen concentration of live shoot at its peak biomass as 0.89%. This concentration would give the average nitrogen content of live foliage and stem per unit ground area ($N_f + N_s$) as 0.112 mol m^{-2}.

Thus, the average respiring nitrogen content per unit ground area, ($N_f + N_s + 2\ N_r$), appears to be 1.618 mol m^{-2}.

Considering that leaf area index might provide an indicator of the above ground biomass (Singh and Joshi, 1979), we wanted to relate the mean live shoot biomass to L_o. Measurements near Pawnee during 1970 gave peak L_o as 0.55 (Knight, 1973), while the peak green shoot dry biomass as 0.091 kg m^{-2} (Sims and Coupland, 1979; Table 5.3). Measurements near Matador gave the peak L_o during 1970 and 1971as, respectively, 1.5 and 1.0 (Ripley and Redmann, 1976), while the peak green shoot biomass was, respectively, 0.187 and 0.163 kg m^{-2} (Sims and Coupland, 1979; Table 5.3). Measurements near Manhattan by Middleton (1992) at two sites dominated by grass species gave mean (standard deviation) L_o as 2.06 (0.44) and 1.43 (0.41), while the corresponding mean green shoot dry biomass were, respectively, 0.282 and 0.245 kg m^{-2}. These data give the mean (standard deviation, n=5) ratio of green shoot biomass and L_o as 0.152 (0.020) kg m^{-2}. Thus, L_o corresponding to the average green shoot biomass of 0.176 kg m^{-2} has been taken to be 1.16 (=0.176/0.152).

The data presented above suggests that ($N_f + N_s + 2\ N_r$) of 1.618 mol m^{-2} might correspond to L_o of 1.16. If ($N_f + N_s + 2\ N_r$) is considered to scale with L_o , one can write the following equation:

$$N_f + N_s + 2\ N_r = 1.395\ L_o \qquad \text{(A1)}$$

where the numerical coefficient is obtained as the ratio of 1.618 mol m^{-2} for ($N_f + N_s + 2\ N_r$) and 1.16 for L_o. While there is rather limited data for the dynamics of living fine root biomass or its nitrogen content (Singh and Singh, 1981; Waring and Schlesinger, 1985, p.46), the above parameterization does not assume fine root biomass to be equal to foliage biomass (Ruimy et al., 1996; Hunt et al., 1996). The data presented above clearly show that the average living fine root biomass to be substantially higher than that for foliage biomass. It is recognized that seasonal variation of above ground biomass (and nitrogen content) can differ from that of below ground biomass (Singh and Krishnamurthy, 1981; Garcia-Moya and Castro, 1992).

Appendix B

This appendix elaborates on the data used to determine the maintenance respiration per unit ground area of tropical grasslands at 20°C.

Jackson et al. (1997) and Gordon and Jackson (2000) have given the mean (standard deviation, n=5) living fine root biomass as 0.51 (0.13) kg m^{-2}, and its nitrogen concentration as 1.11 (0.002)%. These data give mean nitrogen content of living fine roots per unit ground area (N_r) as 0.404 mol m^{-2}. They also give the mean (standard deviation, n=5) total root biomass as 0.99 (0.24) kg m^{-2} (fraction of living roots being about 52%).

Strugnell and Pigott (1976) have tabulated temporal variations of total (live and dead) root biomass for a tropical grassland near Mweye (0.2°S, 29.9°E), which show that the biomass during January and February to be, respectively, 0.73 and 1.16 kg m^{-2}. These root biomass values encompass the mean total root biomass given above (0.99 kg m^{-2}).The mean (standard deviation) of live shoot biomass during these two months has been given as 0.21 (0.11) and 0.19 (0.08) kg m^{-2} , which averages to about 0.20 kg m^{-2}. The average nitrogen concentration of live shoot during these two months has been given as, respectively, 1.83% and 1.96%. For a mean nitrogen concentration of 1.90%, one obtains nitrogen content of live shoot per unit ground area ($= N_f + N_s$) as 0.271 mol m^{-2}. The mean (standard deviation) L_o for these two months has been tabulated as, respectively, 0.96 (0.31) and 1.45 (0.54), suggesting an average L_o of 1.2.

From the data given above, $R_{m,o}(20)$ is obtained as:

$$R_{m,o}(20) = 0.189\ L_o \qquad \text{(B1)}$$

where the numerical coefficient has been calculated by taking ($N_f + N_s + 2\ N_r$) as 1.079 mol m^{-2} and L_o as 1.2 in Eq. (6a) (0.21x1.079/1.2=0.189).

Appendix C

The data given in Table 3 are elaborated in this appendix.

Unless stated otherwise, average biomass and nitrogen concentration of living fine roots given by Jackson et al. (1997) and Gordon and Jackson (2000) have been used to determine the nitrogen content of living fine roots per unit ground area for each biome (N_r; mol N m^{-2}) given in Table 3. These data for root nitrogen content have been supplemented by projected leaf area index (L_o) and foliage nitrogen content per unit ground area (N_f; mol N m^{-2}) as follows.

For a stand of boreal deciduous coniferous forest (*Larix gmelinii*), Vygodskaya et al. (1997) have given L_o, specific leaf weight and nitrogen concentration as, respectively, 1.5, 138 g m^{-2} and 1.56%. These data give foliage biomass and nitrogen content as, respectively, 207 g m^{-2} and 0.231 mol m^{-2}. The fine root biomass has been taken to be 1.5 times the foliage biomass (Kajimoto et al., 1999), and nitrogen concentration has been taken to be 1.11% (Gordon and Jackson, 2000). Thus, nitrogen content of fine roots is obtained as 0.246 mol m^{-2}.

The foliage biomass and L_o values of boreal evergreen coniferous forest have been determined from the paired data for these two canopy characteristics given in Cannell (1982) and Gower et al. (1997). When several such paired values were available from a locality, they have been averaged first so as to minimize possible bias introduced by that specific locality on the overall average. Thus, for example, the data for 17 stands of *Picea abies* at 62°N, 34°E given in Cannell (1982; pp. 361-364) have not been counted individuality, but as one average pair of values. The mean (standard deviation; n=6) L_o and foliage biomass were found to be, respectively, 5.2 (3.8) and 0.867 (0.426) kg m^{-2}. The mean (standard deviation) obtained by excluding the highest and the lowest values are, respectively, 4.0 (0.8) and 0.750 (0.134) kg m^{-2} (n=4). Variability in the stand characteristics decreases considerably when the highest and the lowest values are excluded; the variability for L_o decreases from 73% to 20%, and for foliage biomass from 49% to 18%. These mean L_o and foliage biomass suggest an average specific leaf weight of 0.188 kg m^{-2} (=0.750/4.0). The foliage nitrogen concentration of boreal conifer species given in Schulze et al. (1994) and Middleton et al. (1997) give the mean concentration (standard deviation; n=7) as 0.97 (0.13)%. The data presented by Middleton et al. (1997) give average (n=2) specific leaf weight and foliage nitrogen concentration of *Picea glauca* as, respectively, 0.193 kg m^{-2} and 0.95%. Thus, N_f has been calculated from biomass and nitrogen concentration as 0.520 mol m^{-2} ($= 0.750 \times 10^3 \times 0.97 \times 10^{-2} / 14$).

For a desert shrub community, Chew and Chew (1965) have reported L_o to be in the range 0.9 and 1.3, from which an average value of 1.1 has been taken. They have also reported the specific leaf weight as 0.230 kg m^{-2}, which gives foliage biomass as 0.253 kg m^{-2} (= 1.1 * 0.230). For *Larrea tridentata*, which was the dominant species of this community, Reich et al. (1999) have given the nitrogen concentration of leaf as 1.94%, and thus N_f is calculated to be 0.351 mol m^{-2}. For a desert community dominated by *Larrea divaricata*, Whittaker and Niering (1975) have given L_o as 0.6 and foliage chlorophyll content as 0.34 g m^{-2}. By taking molar weight of chlorophyll as 900 g mol^{-1} and the molar ratio of chlorophyll and nitrogen as 0.004 mol mol^{-1} (Pons et al., 1994; Ishida et al., 2000), we get N_f as 0.095 mol m^{-2}. The average L_o and N_f for these two desert communities are, respectively, 0.9 and 0.223 mol m^{-2}.

For sclerophyllous shrubs, Rundel (1981; Tables 10.5 and 10.7) has given L_o, foliage biomass and nitrogen concentration of leaves for seven dominant species (five evergreen and two deciduous) growing at Fundo Santa Laura (Chile). Mooney and Miller (1985; Table 10.1) have given L_o, specific leaf weight, and nitrogen concentration of leaves for seven dominant evergreen shrub species growing at Echo Valley (USA). The L_o and N_f for these 14 species vary between, respectively, 0.9 to 4.4, and 0.140 to 0.607 mol m^{-2}. The mean (standard deviation, n=14) of L_o is 2.2 (0.9) and N_f is 0.334 (0.147) mol m^{-2}. The mean (standard deviation, n=12) obtained by excluding the highest and lowest values are, 2.1 (0.7) for L_o, and 0.328 (0.124) mol m^{-2} for N_f.

For temperate evergreen coniferous forests, Webber (1977) has given foliage biomass and N_f for a stand of *Pseudotsuga menziesii* and L_o was determined from the foliage biomass using the specific leaf weight given by Turner et al. (2000). Ando et al. (1978) have given L_o and N_f for stands of *Abies firma* and *Tsuga sieboldii*. Alban et al. (1978) have given foliage biomass and N_f for stands of *Pinus resinosa*, *P. banksiana* and *Picea glauca*. For these stands L_o has been determined from foliage biomass using specific leaf weight data (Cannell, 1982, Reich et al., 1998). Grier et al. (1981) and Vogt et al. (1982) have given L_o and N_f for two stands of *Abies amabilis*, which have been averaged to form one pair. Gower et al. (1994) have given foliage biomass, among other data, for several stands of pine growing in temperate and other climate. These data for three stands (*Pinus palustris*, *P. rigida*, and *P. strobus*) growing in temperate climate were supplemented by specific leaf area and nitrogen concentration given by Reich et al. (1998). Foliage biomass and L_o data for three stands (*P. sylvestris*, *Abies lasiocarpa*, and *Taxodium distichum*) growing in temperate climate given by Cannell (1982) were supplemented by nitrogen concentration given by Reich et al. (1998). Pertinent data for *P. radiata* have been given by Ryan et al. (1996), while Law et al. (2000) have given such data for *P. ponderosa*. For these 15 stands, L_o varies between 1.1 and 11.4, while N_f from 0.196 to 1.192 mol m^{-2}. The mean (standard deviation, n=15) L_o is 4.8 (2.7) and N_f is 0.783 (0.300) mol m^{-2}. The mean (standard deviation, n=13) obtained by excluding the highest and the lowest values are, 4.6 (1.9) for L_o and 0.798 (0.249) mol m^{-2} for N_f.

For temperate broad-leaf deciduous forests, Khanna and Ulrich (1991) have given mean (standard deviation, n=19) of L_o, and foliage biomass as, respectively, 5.2 (0.3) and 0.350 (0.029) kg m^{-2}, while the nitrogen concentration of leaves for different species and sites quoted by Khanna and Ulrich (1991) give the average concentration as 2.23% (n=22).

The L_o and foliage biomass values of tropical broad-leaf deciduous forests have been determined from the paired data given in Cannell (1982). The mean (standard deviation; n=10) of L_o was found to be 3.8 (1.5), and these for foliage biomass as 0.360 (0.139) kg m^{-2}. The mean (standard deviation) obtained by excluding the highest and the lowest values was 3.8 (1.2) for L_o and as 0.350 (0.117) kg m^{-2} for foliage biomass (n=8). These data give an effective specific leaf weight of 0.092 kg m^{-2}. The mean (standard deviation, n=46) foliage nitrogen concentration given by Schulze et al. (1994) is 2.71 (0.10)%. The data presented by Sobrado (1991) and Kitajima et al. (1997) give an average (n=22) specific leaf weight and nitrogen concentration as, respectively, 0.087 kg m^{-2} and 2.62%. Thus, a nitrogen concentration of 2.71% has been used for calculating the foliage nitrogen content.

The L_o and foliage biomass of tropical evergreen forests within Brazil and Venezuela have been determined from the paired data given in Cannell (1982), Schulze (1982), Medina and Cuevas (1989) and Malhi et al. (1999), and foliage nitrogen concentration in Schulze et al. (1994). The mean (standard deviation; n=7) of L_o was found to be 5.3 (1.3), and these for N_f as 0.740 (0.270) mol m^{-2}. The mean (standard deviation; n=5) obtained by excluding the highest and the lowest values is found to be 5.1 (0.4) for L_o and 0.769 (0.157) mol m^{-2} for N_f.

Shaver and Chapin (1991) have given L_o and N_f of vascular plants, among other data, for four tundra communities; tussock, shrub, wet sedge, and heath. The below-ground biomass of these four communities are given as, respectively, 0.482, 0.962, 0.349, and 0.103 kg m^{-2}. Because of substantial differences in L_o and N_f among these communities some thought was given in using data so as to be consistent with the data for living fine root biomass and nitrogen concentration given by Jackson et al. (1997) and Gordon and Jackson (2000). The root biomass of the shrub community (0.962 kg m^{-2}) is comparable to the value quoted by Jackson et al. (1997) (viz., 0.96 kg m^{-2}) and Jackson et al. (1996) (viz., 1.2 kg m^{-2}). This would suggest that L_o and N_f of the shrub community would be appropriate for associating with the living fine root data given by Jackson et al. However, Shaver and Chapin (1991) have noted that all roots were not extracted in their study. Thus, equally weighted average of L_o and N_f of tussock, shrub and wet sedge communities was considered in determining L_o and foliage nitrogen content. These weighted average values are given in Table 3, together with the calculated ϕ. For reference, we note that the L_o, N_f and ϕ for the shrub community are found to be, respectively, 1.4, 0.240 mol N m^{-2} and 0.211 mol CO_2 m^{-2} d^{-1}, while these for the tussock community are found to be, respectively, 1.1, 0.211 mol m^{-2} and 0.257 mol m^{-2} d^{-1}, and for the wet sedge community are found to be, respectively, 0.4, 0.074 mol m^{-2} and 0.322 mol m^{-2} d^{-1}.

Appendix D

This appendix elaborates on the data and methods used to determine net carbon accumulation (C) for the crop land area.

The study area for crop land includes a major portion of the State of Iowa and smaller portions of the States of Missouri, Nebraska, South Dakota, and Minnesota. Important crops for the State of Iowa, with respect to land area, are *Zea mays*, *Glycine max* and hays (primarily *Madicago sativa* and mixture), constituting respectively, about 56%, 36% and 8% of the total area of these crops (over 92,000 km^2).

Considering the reported above ground dry matter production at locations within and around the study area, the mean (standard deviation) production for *Zea mays*, *Glycine max* and *Madicago sativa* is found to be, respectively, about 13.90 (2.99), 8.95 (0.73) and 8.78 (0.83) t ha^{-1} yr^{-1} (Table D1). Determination of above ground production of *Glycine max* is somewhat difficult because leaves begin to fall from the plants during the later stages of reproductive growth period, and the biomass of these leaves is often not quantified or included in the reported data (Hanway and Weber, 1971; Beaver and Cooper, 1982). Although there are many reports providing grain yield, these data have not been used to calculate above ground production because of variability of the harvest index (Johnson and Major, 1979; DeLoughery and Crookston, 1979; Schapaugh and Wilcox, 1980). Production of root (taken here to be root dry biomass for annual crops), as percent of above ground production, is about 9% for *Zea mays* (Foth, 1962), 13% for *Glycine max* (Mayaki et al., 1976), and 56% for *Madicago sativa* (Pearce et al., 1969; Pettersson et al., 1986). Thus, the mean (standard deviation) total dry matter production for *Zea mays*, *Glycine max* and *Madicago sativa* is found to be respectively, as 15.15 (3.26), 10.11 (0.82) and 13.70 (1.29) t ha^{-1} yr^{-1}.

By taking the carbon content of dry matter to be 44% for *Zea mays* (Ajtay et al., 1979; Loomis and Lafitte, 1987), 48% for *Glycine max* (Watanabe, 1976), and 45% for *Madicago sativa* (Ajtay et al., 1979; Dubach and Russelle, 1994), the mean (standard deviation) C for *Zea mays*, *Glycine max* and *Madicago sativa* is obtained as, respectively, 56 (12), 40 (3), and 51 (5) mol m^{-2} yr^{-1}. When these C values are weighted by the fractional area of these crops (56%, 36%, and 8%, respectively) one obtains an area average mean (standard deviation) C as 50 (8) mol m^{-2} yr^{-1}.

There are other uncertainties in the above value of C because of, (a) not considering several other crops like *Avena sativa*, *Secale cereale*, *Sorghum bicolar*, *Triticum* sp. which are also grown, and land use categories like woodland, land under conservation, and urban areas, and (b) the study area includes parts of several States other than the State of Iowa, where the cropping patterns are different.

According to Ajtay et al. (1979), C for temperate woodlands and urban areas are, respectively, 56 and 19 mol m^{-2} yr^{-1}.

Changes in the cropping pattern can affect the value of C. For example, *Zea mays*, *Glycine max* and hays are also the major crops for the State of Missouri, but the fractional areas occupied by these crops are, respectively, 25%, 41% and 34%. For these fractional areas, the weighted mean C would be 48 mol m^{-2} yr^{-1}. The major crops for the State of Nebraska are *Zea*, hays, *Glycine*, *Triticum*, and *Sorghum*, which occupy, respectively, 47%, 18%, 14%, 11%, and 10% of the total area for these crops (over 64,000 km^{2}). If the mean values of C for *Triticum* and *Sorghum* are taken to be, respectively, 38 and 47 mol m^{-2} yr^{-1} (unpublished preliminary synthesis of production data within and around the area), the area weighted mean C would be 50 mol m^{-2} yr^{-1}. The major crops for the State of Minnesota are *Zea*, *Glycine*, *Triticum*, and hays, which occupy, respectively, 40%, 31%, 16%, and 13% of the total area for these crops (over 66,000 km^{2}). The area weighted mean C would be 48 mol m^{-2} yr^{-1}.

The above results suggest that the C for the crop land area is about 49 mol m^{-2} yr^{-1}, with an uncertainty of about 15%.

Appendix E

This appendix elaborates on the estimate of net production of tropical deciduous forests.

Cannell (1982; p. 81) has given above ground dry matter production for a stand near Varanasi (25.3°N, 83.0°E) as 14.87 t ha^{-1} yr^{-1}, and litterfall dry matter as 6.78 t ha^{-1} yr^{-1}.

By synthesizing the available data, Nadelhoffer and Raich (1992) have suggested that annual fine root production (FRP; g (carbon) m^{-2} yr^{-1}) can be estimated from litterfall (LFC; g (carbon) m^{-2} yr^{-1}) using the following empirical equation:

$$\mathrm{FRP} = (130 + 1.92\ \mathrm{LFC}) / 3 \qquad (\mathrm{D1})$$

Additionally, for synthesizing the available data, they converted all organic matter fluxes to carbon units by taking 48% as conversion factor.

Thus, for LFC of 325.4 (=6.78 x 100 x 0.48) g (carbon) m^{-2} yr^{-1}, Eq. (D1) gives FRP = 251.6 g (carbon) m^{-2} yr^{-1} or 21 mol m^{-2} yr^{-1}. Adding this root production to the above ground production gives net carbon accumulation as 80 mol m^{-2} yr^{-1}.

For another forest near Varanasi (24.9°N, 83.2°E), Cannell (1982; p. 84) has given above and below ground net dry matter production as, respectively, 9.50 and 3.54 t ha^{-1} yr^{-1}, which gives the total net production as 13.04 t ha^{-1} yr^{-1}. This net production corresponds to C of 52 mol m^{-2} yr^{-1}, when carbon content of dry matter is taken to be 48%.

Brown and Lugo (1982) have given net dry matter production for a stand of sub-tropical dry forest near Ensenada (18.0°N, 65.9°W) as 11.0 t ha^{-1} yr^{-1}. This corresponds to C of 44 mol m^{-2} yr^{-1}, when carbon content of dry matter is taken to be 48%.

Measurements in the Marihan range of East Mirzapur Forest Division (24.9°-25.2°N, 82.5°-82.8°E) by Singh and Singh (1991) gave net carbon accumulation as 6.7 (+/- 1.0) t ha^{-1} yr^{-1} or 56 (+/- 8) mol m^{-2} yr^{-1}.

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Table 1. A summary of growth conversion efficiency (Y_G, in units of mol C mol^{-1} C, with percent coefficient of variation in parenthesis) for whole plant, shoot, leaf, stem, and roots of cultivated herbaceous and woody species (growing under natural or controlled conditions), together with their sources.

Species	Y_G	Sources
Cultivated herbaceous (n=29)	0.74 (14)	1
Woody species:		
Whole plant:		
Arctostaphylos glauca	0.68	2
Adenostoma fasciculatum	0.73	2
Ceanothus greggii	0.67	2
Rhus ovata	0.68	2
Colliguaya odorifera	0.69	2
Lithraea caustica	0.66	2
Satureja gilliesii	0.67	2
Trevoa trinervis	0.68	2
Trema guineensis	0.64	3
Shoot:		
Pinus silvestris	0.66	4
Chamaecyparis obtusa	0.52	5
Sapwood:		
Populus tremuloides	0.78	6
"	0.73	6
Pinus banksiana (old)	0.81	6
"	0.75	6
Pinus banksiana (young)	0.80	6
"	0.72	6
Picea mariana	0.58	6
"	0.57	6
Roots:		
Pinus silvestris	0.80	4
Leaves:		
Lepechinia calycina	0.70	7
Diplacus aurantiacus	0.69	7
Heteromeles arbutifolia	0.73	7
Summary statistics (n=23):		
Mean	0.69	
Coeff. of variation (%)	11	

Sources: 1 (Amthor, 1989; Table 5.1); 2 (Oechel and Lawrence, 1981); 3 (Lehto and Grace, 1994); 4 (Szaniawski, 1981); 5 (Adu-Bredu et al., 1997); 6 (Lavigne and Ryan, 1997); 7 (Merino et al., 1982)

Table 2. A compilation of maximum projected leaf area index ($L_{o,\ max}$) and stem maintenance respiration per unit ground area of woody species under the prevailing soil water conditions ($R_{m,\ s}$ mol CO_2 m^{-2} d^{-1}) at 20°C using the reported Q_{10} values and available meteorologic data, together with their sources. Species with asterisk are needle leaf, while others are broad leaf species. The carbon content of dry matter has been taken to be 48% when it was not given.

Species	$L_{o,\ max}$	$R_{m,\ s}$	$R_{m,\ s}$ / $L_{o,\ max}$	Sources
Arctostaphylos glauca	3.0	0.072	0.024	1
Adenostoma fasciculatum	1.2	0.015	0.013	1
Ceanothus greggii	1.6	0.034	0.021	1
Rhus ovata	2.2	0.012	0.006	1
Colliguaya odorifera	2.3	0.058	0.025	1
Lithraea caustica	3.2	0.009	0.003	1
Satureja gilliesii	3.6	0.027	0.007	1
Trevoa trinervis	2.3	0.025	0.011	1
Populus tremuloides	2.2	0.041	0.019	2
"	3.3	0.058	0.018	2
*Pinus banksiana** (old)	2.2	0.016	0.007	2
"	1.3	0.015	0.012	2
*Pinus banksiana** (young)	1.8	0.016	0.009	2
"	2.8	0.026	0.009	2
*Picea mariana**	4.9	0.071	0.014	2
"	5.6	0.038	0.007	2
Acer, Quercus	5.0	0.026	0.005	3
*Pinus resinosa**	6.2	0.029	0.005	4
*Pinus ponderosa**	2.7	0.022	0.008	4
*Pinus elliottii**	2.2	0.027	0.012	4
*Tsuga heterophylla**	8.7	0.054	0.006	4
Floresta Ombrofila	4.0	0.047	0.012	5

Summary statistics:

Needle leaf (n=10)			
Mean	3.8	0.032	0.009
Coeff. of variation (%)	63	58	33
Broad leaf (n=12)			
Mean	2.7	0.034	0.014
Coeff. of variation (%)	39	60	58
All (n=22)			
Mean	3.3	0.034	0.012
Coeff. of variation (%)	55	57	55

Sources: 1 (Oechel and Lawrence, 1981; Rundel, 1981; Mooney and Miller, 1985); 2 (Ryan et al., 1997); 3 (Edwards and Hanson, 1996); 4 (Ryan et al., 1995); 5 (Lloyd et al., 1995; Haxeltine and Prentice, 1996)

Table 3. The data for projected leaf area index (L_o), foliage nitrogen content per unit ground area (N_f ; mol N m^{-2}), effective nitrogen content of a leaf ($N_l = N_f / L_o$; mol N m^{-2}) and nitrogen content of live fine roots (less than or equal to 2 mm in diameter) per unit ground area (N_r ; mol N m^{-2}), and the calculated daily maintenance respiration per unit ground area at 20°C for foliage and roots per unit L_o (ϕ_f and ϕ_r ; mol CO_2 m^{-2} d^{-1}) appearing in Eq. (16), and sources of these data (elaborated in Appendix C). The data for nitrogen content of roots are from Jackson et al. (1997) and Gordon and Jackson (2000), unless noted otherwise in the text. Biomes are arranged in alphabetical order.

Biome	L_o	N_f (N_l)	N_r	ϕ_f	ϕ_r	Sources
Boreal deciduous forests	1.5	0.231 (0.154)	0.246	0.0585	0.1246	1
Boreal evergreen forests	4.0	0.520 (0.130)	0.182	0.0494	0.0346	2
Deserts shrubs	0.9	0.223 (0.248)	0.103	0.0520	0.0481	3
Sclerophyllous shrubs	2.1	0.328 (0.156)	0.222	0.0328	0.0444	4
Temperate coniferous forests	4.6	0.798 (0.173)	0.396	0.0364	0.0362	5
Temperate deciduous forests	5.2	0.558 (0.107)	0.349	0.0225	0.0282	6
Tropical deciduous forests	3.8	0.678 (0.178)	0.222	0.0375	0.0245	7
Tropical evergreen forests	5.1	0.769 (0.151)	0.262	0.0317	0.0216	8
Tundra	1.0	0.174 (0.174)	0.270	0.0661	0.2052	9

Sources: 1 (Vygodskaya et al., 1997; Kajimota et al., 1999); 2 (Cannell, 1982; Schulze et al., 1994; Gower et al., 1997; Middleton et al., 1997); 3 (Chew and Chew, 1965; Whittaker and Niering, 1975; Reich et al., 1999; Ishida et al., 2000); 4 (Rundel, 1981; Mooney and Miller, 1985); 5 (Webber, 1977; Alban et al., 1978; Ando et al., 1978; Grier et al., 1981; Vogt et al., 1982; Cannell, 1982; Ryan et al., 1996; Gower et al., 1994; Reich et al., 1998; Law et al., 2000; Turner et al., 2000); 6 (Khanna and Ulrich, 1991); 7 (Cannell, 1982; Schulze et al., 1994); 8 (Cannell, 1982; Schulze, 1982; Medina and Cuevas, 1989; Schulze et al., 1994; Malhi et al., 1999); 9 (Shaver and Chapin, 1991).

Table 4. The biome areas for which calculations have been done, together with the land cover type number according to the land cover classification of Matthews (1983), annual total precipitation (mm) and mean air temperature (°C) for individual years. The long-term averages (LT) at selected stations from Wernstedt (1972) and Muller (1982) are given for reference. The biomes are arranged in alphabetical order. The UNESCO codes for the biome areas are given in the text.

Biome	Type #	Precipitation (mm)				Air Temperature (°C)			
		LT	1987	1988	1989	LT	1987	1988	1989
Boreal Decid. Forest (60°-63°N, 114°-134°E)	11	213^{*a}	284	366	391	-10.2^{a}	-9.4	-6.1	-6.8
Boreal Evergn. Forest (50°-53°N, 91°-95°W)	8	517^{b}	503	637	447	2.5^{b}	3.8	2.1	1.3
Crop Land (40°-45°N, 92°-97°W)	32	693^{c}	696	517	656	9.1^{c}	11.7	10.8	9.7
Temp. Decid. Forest (45°-47°N, 66°-71°W)	10	1058^{d}	826	927	1082	4.4^{d}	5.2	5.4	5.2
Temp. Grassland (51°-53°N, 72°-76°E)	28	299^{e}	362	257	483	1.6^{e}	4.4	5.6	5.5
Trop. Decid. Forest (20°-24°S, 45°-50°W)	9	1499^{f}	1506	1319	1509	20.0^{f}	21.1	21.1	20.2
Trop. Evergn. Forest (0°-5°S, 65°-70°W)	1	2800^{g}	2744	2820	2556	24.9^{g}	24.5	24.2	23.5
Trop. Savanna (13°-17°S, 55°-59°W)	23	1400^{h}	1514	1578	1768	24.9^{h}	24.0	24.0	22.5
Tundra (69°-70°N, 147°-162°W)	22	126^{i}	124	116	285	-11.6^{i}	-7.8	-8.0	-6.8

*Location name and coordinate for the long term data: a (Jakutsk (62.1N, 129.8E); b (Winnipeg (49.9N, 97.3W)); c (Mapleton (42.2N, 95.8W)); d (Quebec City (46.8N, 71.4W)); e (the average of data at Omsk (54.9N, 73.4E) and Karaganda (49.8N, 73.1E)); f (Franca (20.6S, 47.4W)); g (Fonte Boa (2.5S, 66.2W)); h (Coxipo (15.6S, 56.0W)); i (Wainwright (70.6N, 160.0W)).

Table 5. Calculated annual total gross photosynthesis (A_g), maintenance (R_m) and growth (R_g) respiration of a stand, and net carbon accumulation (C) per unit ground area (mol C m^{-2} yr^{-1}), and the ratio of total respiration (R) and gross photosynthesis (R / A_g). The biome areas are given in Table 4. The biome names have been abbreviated below as: BDF for Boreal Deciduous (coniferous) Forest, BEF for Boreal Evergreen (coniferous) Forest, CL for Crop Land, TDF for Temperate Deciduous Forest, TG for Temperate Grassland, TrDF for Tropical Deciduous Forest, TEF for Tropical Evergreen forest, TS for Tropical Savanna, and T for tundra. All fluxes have been rounded to integers.

Biome	Year	A_g	R_m	R_g	C	R/A_g
BDF	1987	30	15	5	11	0.65
"	1988	38	17	7	15	0.62
"	1989	52	13	12	26	0.49
BEF	1987	75	23	16	36	0.52
"	1988	81	29	16	36	0.56
"	1989	71	23	15	33	0.54
CL	1987	98	33	17	48	0.51
"	1988	59	34	7	18	0.69
"	1989	91	30	16	45	0.50
TDF	1987	103	38	20	45	0.57
"	1988	116	40	24	52	0.55
"	1989	107	40	21	46	0.57
TG	1987	47	20	8	19	0.60
"	1988	47	26	7	14	0.70
"	1989	44	15	9	20	0.54
TrDF	1987	179	83	30	67	0.63
"	1988	167	77	29	61	0.63
"	1989	178	74	32	71	0.60
TEF	1987	227	132	29	65	0.71
"	1988	238	136	32	70	0.71
"	1989	222	121	31	70	0.69
TS	1987	166	83	25	57	0.65
"	1988	157	78	25	54	0.65
"	1989	183	80	29	74	0.60
T	1987	33	9	7	17	0.50
"	1988	22	10	4	8	0.62
"	1989	40	10	9	21	0.48

Table 6. The present results (averaged over the three years), together with those determined from Lieth and Box's (1977) model using precipitation and temperature data in Table 4 (averaged for the three years), calculated by Ruimy et al. (1996) and a synthesis of measurements given by Ajtay et al. (1979). The carbon content of 45% given by Ajtay et al. has been used to convert their fluxes quoted in units of dry matter to its carbon equivalent. Percent discrepancy (%) between the present value of C and the value given by Ajtay et al. is given. The fluxes are in units of mol C m^{-2} yr^{-1}, and abbreviation for biome names and symbols are as given in Table 5.

Biome	Present			Lieth and Box			Ruimy et al.			Ajtay et al.	%
	A_g	C	R / A_g	A_g	C	R / A_g	A_g	C	R / A_g	C	
BDF	40	17	0.57	17	12	0.31	77	35	0.55	24^{*a}	-30
BEF	76	35	0.54	51	32	0.38	61	28	0.55	32^{b}	+9
CL	82	37	0.55	-	-	-	-	-	-	45^{c}	-18
TDF	108	48	0.56	68	40	0.41	96	44	0.54	49^{d}	-2
TG	46	18	0.62	34	22	0.35	67	41	0.39	19^{e}	-5
TrDF	175	66	0.62	159	74	0.53	136	55	0.60	60^{f}	+10
TEF	229	68	0.70	289	99	0.66	165	62	0.63	86^{g}	-21
TS	169	62	0.63	167	74	0.56	114	54	0.53	86^{h}	-28
T	32	15	0.52	17	12	0.31	20	12	0.39	13^{i}	+15

* a (Boreal coniferous, open); b (Boreal coniferous, closed); c (Temperate annuals); d (Temperate deciduous/mixed); e (Temperate dry grassland); f (Tropical seasonal forest); g (Tropical humid forest); h (Grass dominated savanna); i (Low arctic/alpine).

Table 7. Results of sensitivity analysis for the effect of changing the temperature response function for maintenance respiration (Fig. 2) on the maintenance respiration of a stand (R_m), total respiration (R) and net carbon accumulation (C) for the biome areas, averaged for the three years. Percent changes are positive when the effect of changing the response function was to increase the flux relative to the standard case (Tables 5 and 6). Abbreviation for the biome names is as noted in Table 5.

Biome	ΔR_m (%)	ΔR (%)	ΔC (%)
BDF	+13	+7	-10
BEF	+9	+4	-5
CL	+6	+4	-4
TDF	+19	+9	-11
TG	+4	+2	-4
TrDF	0	0	0
TEF	-2	-2	+2
TS	-2	-1	+1
T	+28	+12	-12

Table 8. Results of sensitivity analysis for distinguishing shoot and root temperature for calculating their maintenance respiration. Percent change from the base values (Tables 5 and 6) for maintenance respiration of the stand (ΔR_m), total respiration (ΔR) and net carbon accumulation (ΔC) of the biome areas, averaged for the three years, when root temperature was taken to be soil temperature rather than air temperature.

Biome	ΔR_m (%)	ΔR (%)	ΔC (%)
BDF	+3	+2	-2
BEF	+3	+1	-2
CL	0	0	0
TDF	+4	+2	-2
TrDF	+2	+1	-2
TEF	0	0	-1
TS	+1	0	0
T	+5	+2	-2

Table 9. Results of sensitivity analysis for uncertainties in the sapwood maintenance respiration. Percent change from the base values for total maintenance respiration (ΔR_m), total respiration (ΔR) and net carbon accumulation (ΔC) of the biome areas, averaged for the three years, due to 35% increase in the sapwood maintenance respiration.

Biome	ΔR_m (%)	ΔR (%)	ΔC (%)
BDF	+2	+1	-2
BEF	+6	+2	-3
TDF	+9	+4	-5
TrDF	+9	+5	-7
TEF	+8	+4	-11
TS	+1	+1	-1
T	+3	+1	-1

Table 10. Results of sensitivity analysis for decreasing the maintenance respiration of foliage and roots of tropical biomes by a factor of 1.5. Percent change from the base values (Tables 5 and 6) for total maintenance respiration (ΔR_m), total respiration (ΔR) and net carbon accumulation (ΔC), averaged for the three years.

Biome	ΔR_m (%)	ΔR (%)	ΔC (%)
TrDF	-25	-12	+20
TEF	-26	-14	+33
TS	-32	-18	+36

Table D1. Selected data for above ground dry matter production (DM; t ha^{-1}) of *Zea mays*, *Glycine max* and *Medicago sativa* within and around the study area for crop land. Data given are: location name and coordinate, number of data values (n), mean (standard deviation) and range of DM, and the sources for these data. Summary statistics for DM of each crop based on the mean values at all locations, and those obtained by excluding the highest and the lowest DM values are also given.

Location	n	Mean (sd)	Range	Sources
***Zea mays*:**				
Ames (42.0N, 93.6W)	48	15.19 (3.60)	6.17-22.80	1
Goodhue (44.4N, 92.6W)	22	13.93 (1.62)	10.00-16.90	2
Lamberton (44.2N, 95.3W)	45	13.63 (3.17)	7.42-17.24	3
Lancaster (42.8N, 90.8W)	9	14.28 (2.22)	9.50-16.90	4
Lincoln (40.8N, 96.7W)	6	21.50 (3.14)	18.43-26.52	5
Madison (44.0N, 97.1W)	12	8.68 (1.22)	7.02-10.50	6
Manhattan (39.1N, 96.6W)	2	21.75 (-)	18.60-24.90	7
Mead (41.2N, 96.5W)	100	11.82 (3.13)	5.70-20.40	8
Nashua (42.9N, 92.5W)	15	13.34 (3.76)	7.00-18.53	9
Rosemount (44.7N, 93.1W)	36	10.38 (2.03)	6.90-15.30	10
St. Paul (44.9N, 93.1W)	48	12.40 (5.70)	6.60-26.10	11
Waseca (44.1N, 93.5W)	62	12.57 (3.79)	4.40-19.50	12
Summary	12	14.12 (3.92)	8.68-21.75	
"	10	13.90 (2.99)	10.38-21.50	
Glycine max:				
Ames (42.0N, 93.6W)	8	9.42 (0.87)	8.16-10.77	13
Castana (42.1N, 95.9W)	1	9.96 (-)		14
Columbia (38.9N, 92.3W)	4	8.51 (1.03)	6.65-10.07	15
Lincoln (40.8N, 96.7W)	4	7.69 (2.81)	5.15-11.38	16
Manhattan (39.1N, 96.6W)	2	9.10 (-)	7.60-10.60	7
Mead (41.2N, 96.5W)	8	7.12 (0.40)	6.72-7.91	17
Rosemount (44.7N, 93.1W)	9	9.33 (0.57)	8.56-9.98	18
Urbana (40.1N, 88.2W)	10	9.67 (1.21)	8.30-11.80	19
Summary	8	8.85 (1.00)	7.12-9.96	
"	6	8.95 (0.73)	7.69-9.67	
Medicago sativa:				
Ames (42.0N, 93.6W)	6	8.95 (0.73)	8.20-9.84	20
Arlington (43.3N, 89.4W)	11	8.05 (0.52)	7.45-8.99	21
Aurora (44.3N, 96.7W)	4	10.18 (0.66)	9.30-10.90	22
Becker (45.4N, 93.9W)	6	8.50 (3.01)	4.30-11.30	23
Lancaster (42.8N, 90.8W)	6	7.03 (1.43)	5.00-8.40	24
Lincoln (40.8N, 96.7W)	4	8.97 (0.88)	8.03-10.02	25
Madison (43.1N, 89.4W)	18	10.33 (2.34)	5.25-13.08	26
Marshfield (44.7N, 90.0W)	11	7.62 (0.39)	6.94-8.05	21
Rosemount (44.7N, 93.1W)	12	9.20 (0.80)	8.00-10.10	27
Summary	9	8.76 (1.10)	7.03-10.33	
"	7	8.78 (0.83)	7.62-10.18	

Sources: 1 (Hanway and Russell, 1969; Helsel and Wedin, 1981; Blackmer and Sanchez, 1988); 2 (Jokela and Randall, 1989); 3 (Voorhees et al., 1989); 4 (Zemenchick et al., 2000); 5 (Perry et al., 1977); 6 (Olson, 1971); 7 (Hattendorf et al., 1988); 8 (Russelle et al., 1983; Peterson and Varvel, 1989); 9 (Blackmer amd Sanchez, 1988); 10 (DeLoughery and Crookston, 1979; Schmid et al., 1976); 11 (Crookston et al., 1978; DeLoughery and Crookston, 1979); 12 (DeLoughery and Crookston, 1979; Jakela and Randall, 1989; Voorhees et al., 1989); 13

(Hanway and Weber, 1971b); 14 (Sivakumar et al., 1977); 15 (Johnson and Major, 1979); 16 (Power and Koerner, 1994); 17 (Clawson et al., 1986); 18 (Ham and Caldwell, 1978); 19 (Beaver and Cooper, 1982; Beaver et al., 1985; Smith et al., 1988); 20 (Buxton and Wedin, 1970); 21 (Sulc and Albrecht, 1996); 22 (Curran et al., 1993); 23 (Lory et al., 1992; Blumenthal and Russelle, 1996); 24 (Zemenchik et al., 1996); 25 (van Riper and Owen, 1964; Peterson et al., 1993); 26 (Rominger et al., 1976); 27 (Juan et al., 1993)

CAPTION TO THE FIGURES

Figure. 1. Observed variation of the temperature response coefficient (Q_{10}) for a cypress forest tree with air temperature from Paembonan et al. (1991), together with the result of linear least square regression.

Figure 2. The temperature response function for maintenance respiration normalized to be 1 at 20°C based on Q_{10} regression equation in Figure 1 for the temperature range 2.5° to 25.0°C, and extrapolated beyond this range of values. The temperature response function used by Ruimy et al. (1996) is also shown.

Figure 3. Scatter plot of projected leaf area index and total respiring nitrogen content of shoot and root per unit ground area (mol N m^{-2}) determined from periodic harvests of stands of *Triticum*, *Sorghum*, *Glycine*, *Gossypium* and *Phaseolus*. The regression result obtained by Plenet and Lemaire (1999) for the relation between leaf area index and the nitrogen content of shoot per unit ground area for fertilized stands of *Zea* is also shown.

Figure 4. Temporal variations of calculated monthly total actual gross photosynthesis, total respiration, and the ratio of maintenance respiration and total respiration for, (a) crop land, (b) temperate grassland, and (c) tropical evergreen forest. The fluxes are in units of mol C m^{-2} mo^{-1}.

Figure 5. Temporal variations of leaf area index for the crop land area during 1987, and the calculated actual gross photosynthesis, and soil water stress factor

Figure 6. Monthly total precipitation (mm) and daily mean air temperature (°C) for the temperate grassland area for the three years.

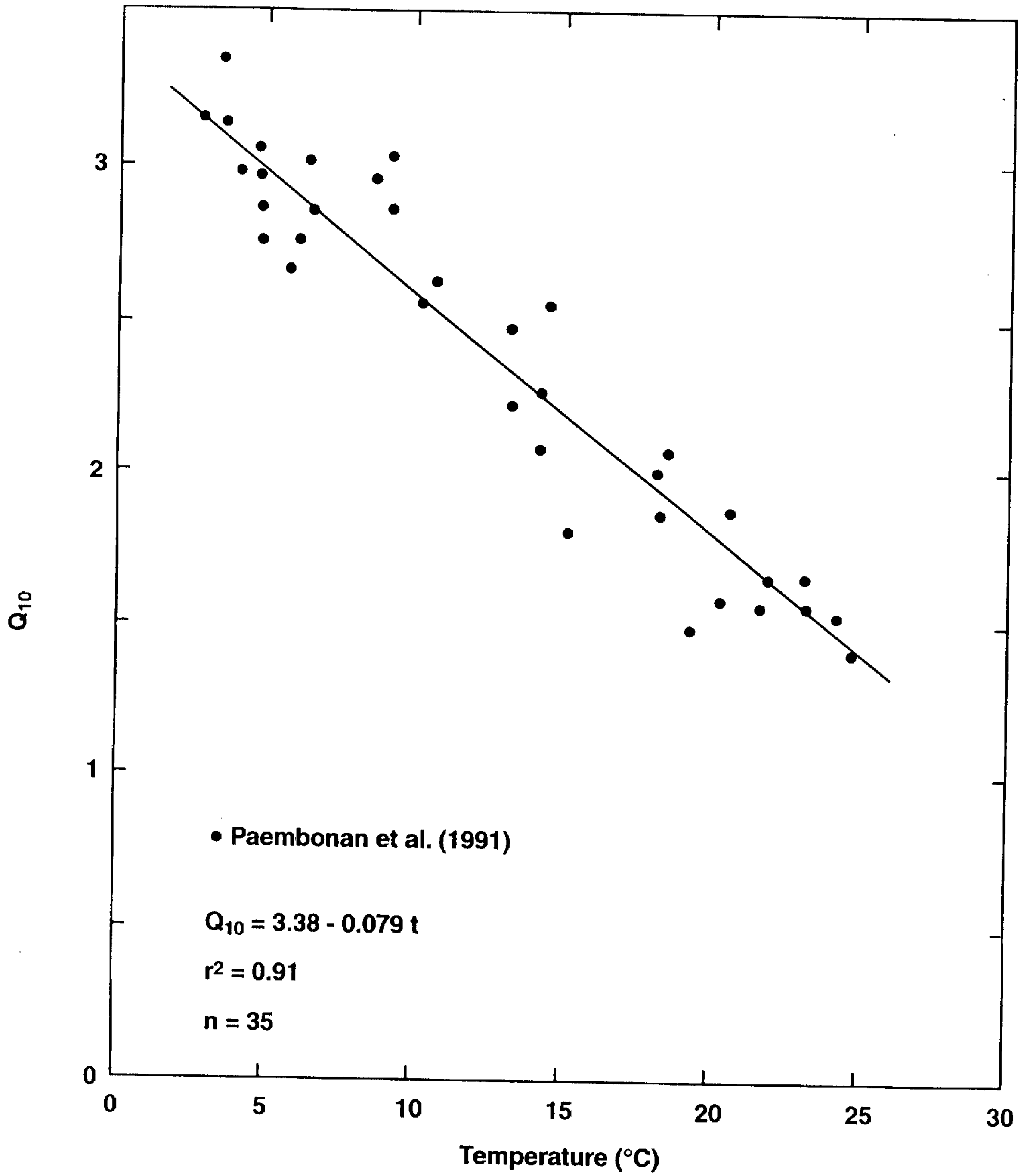

Q10
3
2
1
0
0
5
10
15
20
25
30
Temperature (°C)
● Paembonan et al. (1991)
Q10 = 3.38 - 0.079 t
r2 = 0.91
n = 35

Fig. 1

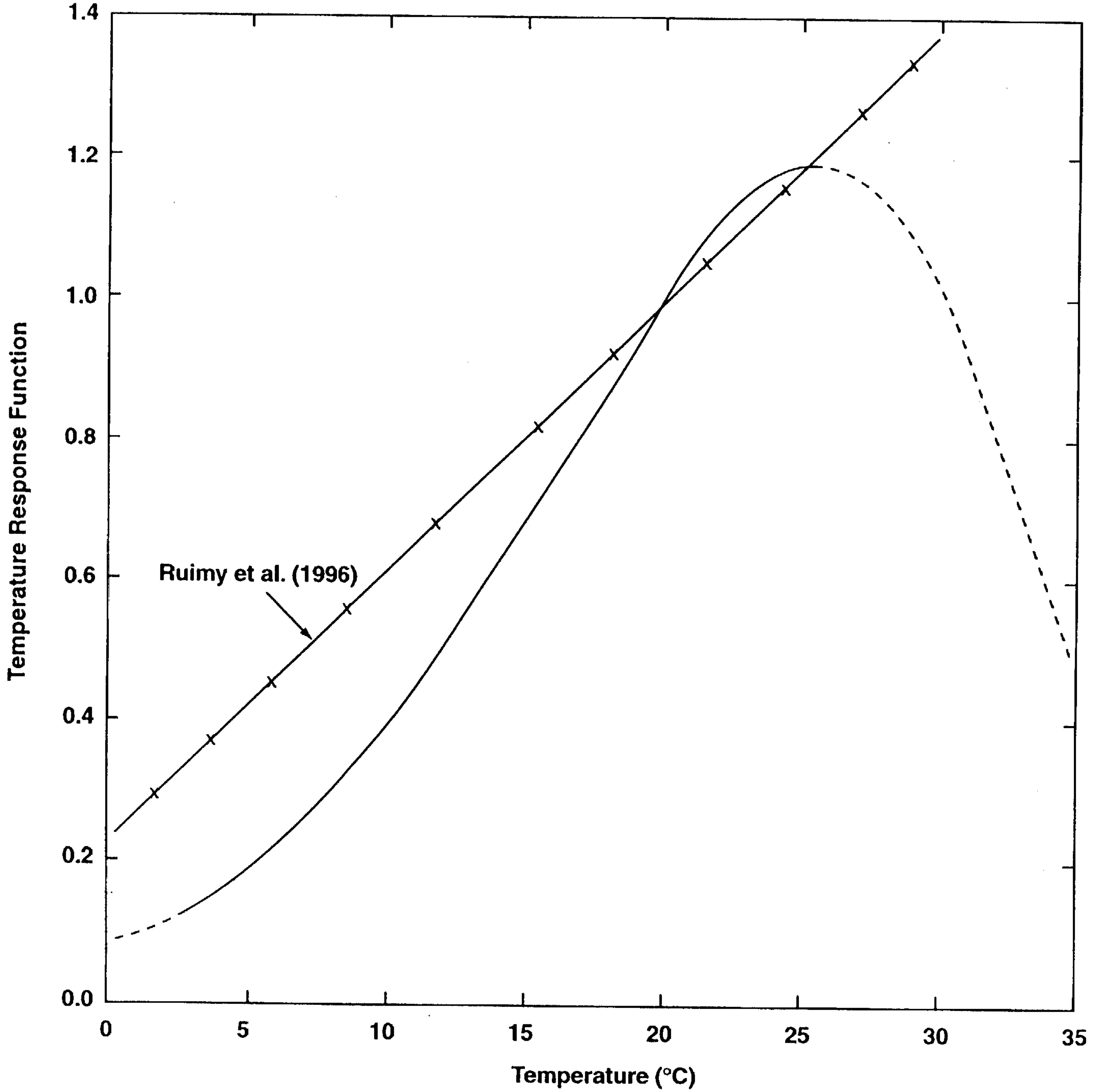
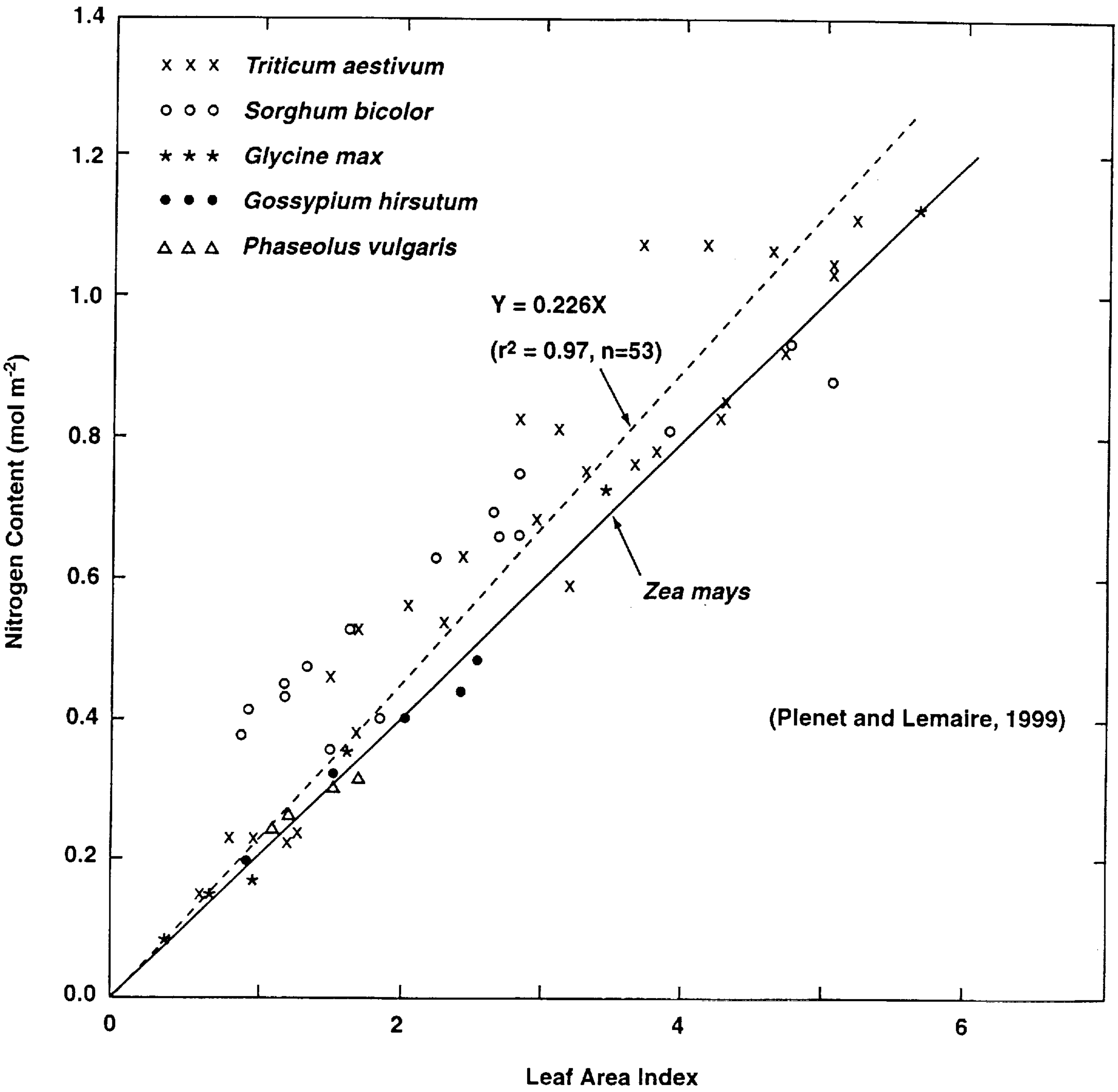


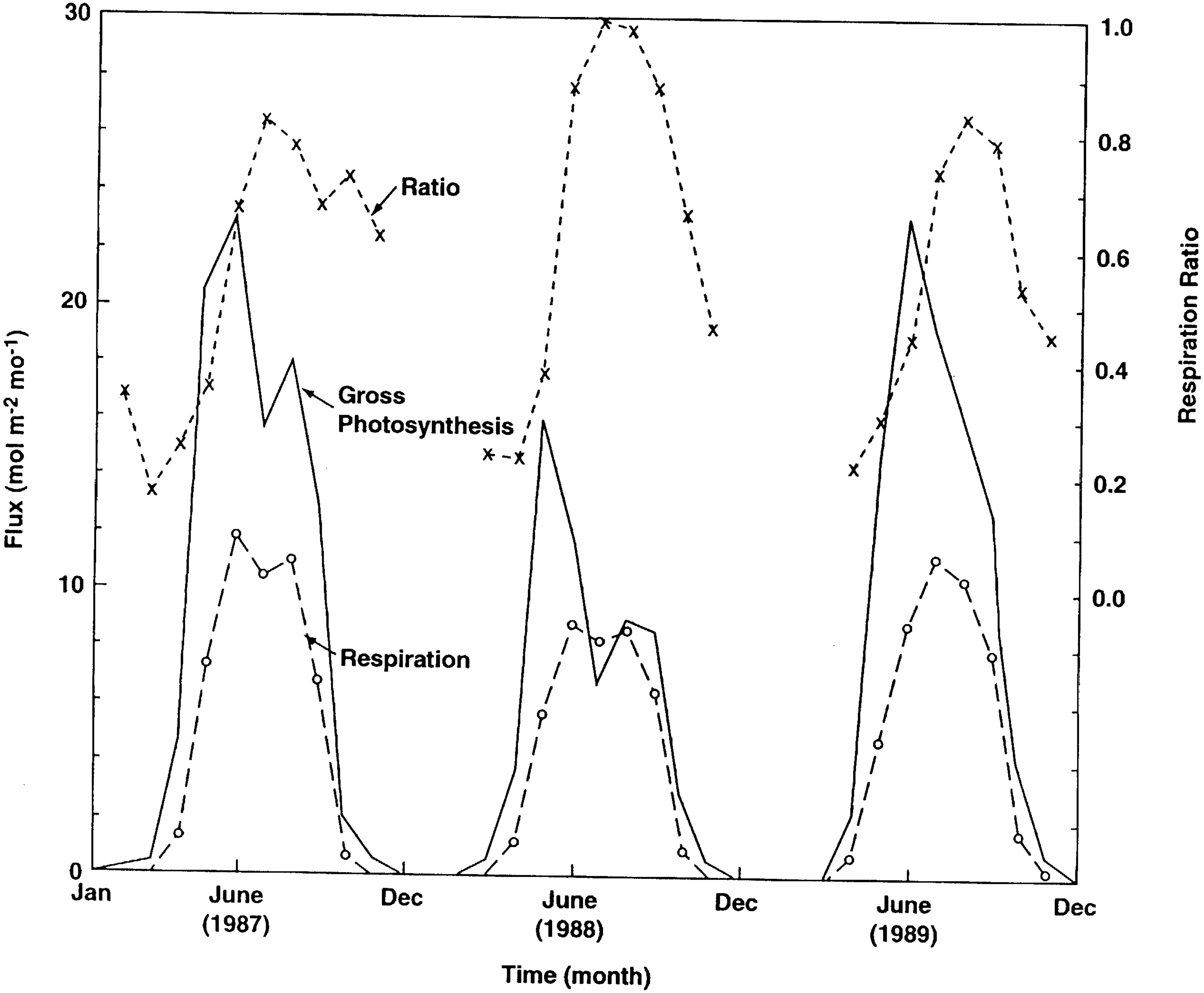
Fig. 2

E1557.007



1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Nitrogen Content (mol m-2)
0
2
4
6
Leaf Area Index
x x x Triticum aestivum
o o o Sorghum bicolor
★ ★ ★ Glycine max
● ● ● Gossypium hirsutum
△ △ △ Phaseolus vulgaris
Y = 0.226X
(r2 = 0.97, n=53)
Zea mays
(Plenet and Lemaire, 1999)

Fig. 3



Crop Land [40° - 45° N, 92° - 97°W]

Fig. 4a

E1557.003

Temperate Grassland [51° - 53° N, 72° - 76°E]

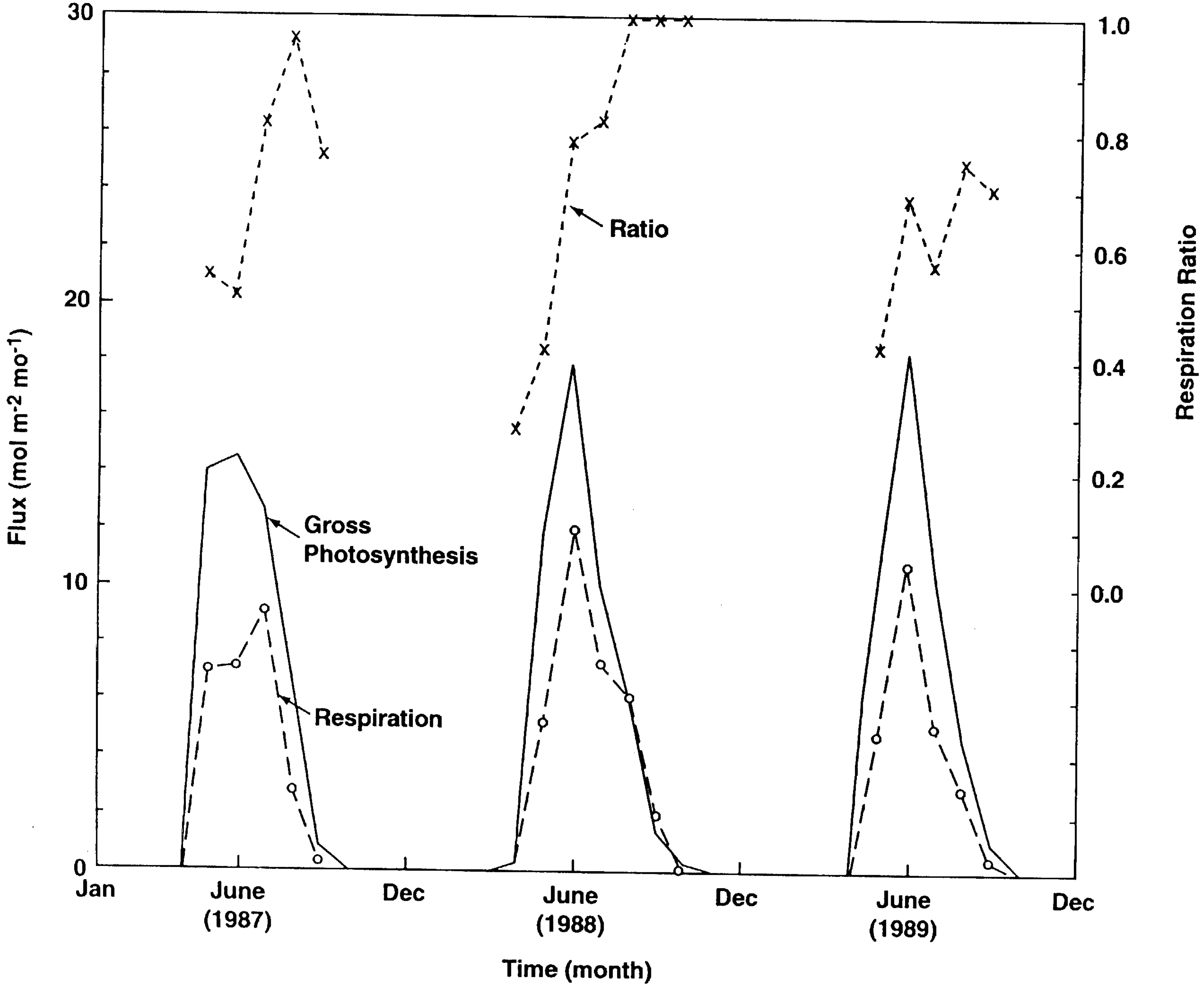


Fig. 4b

E1557.002

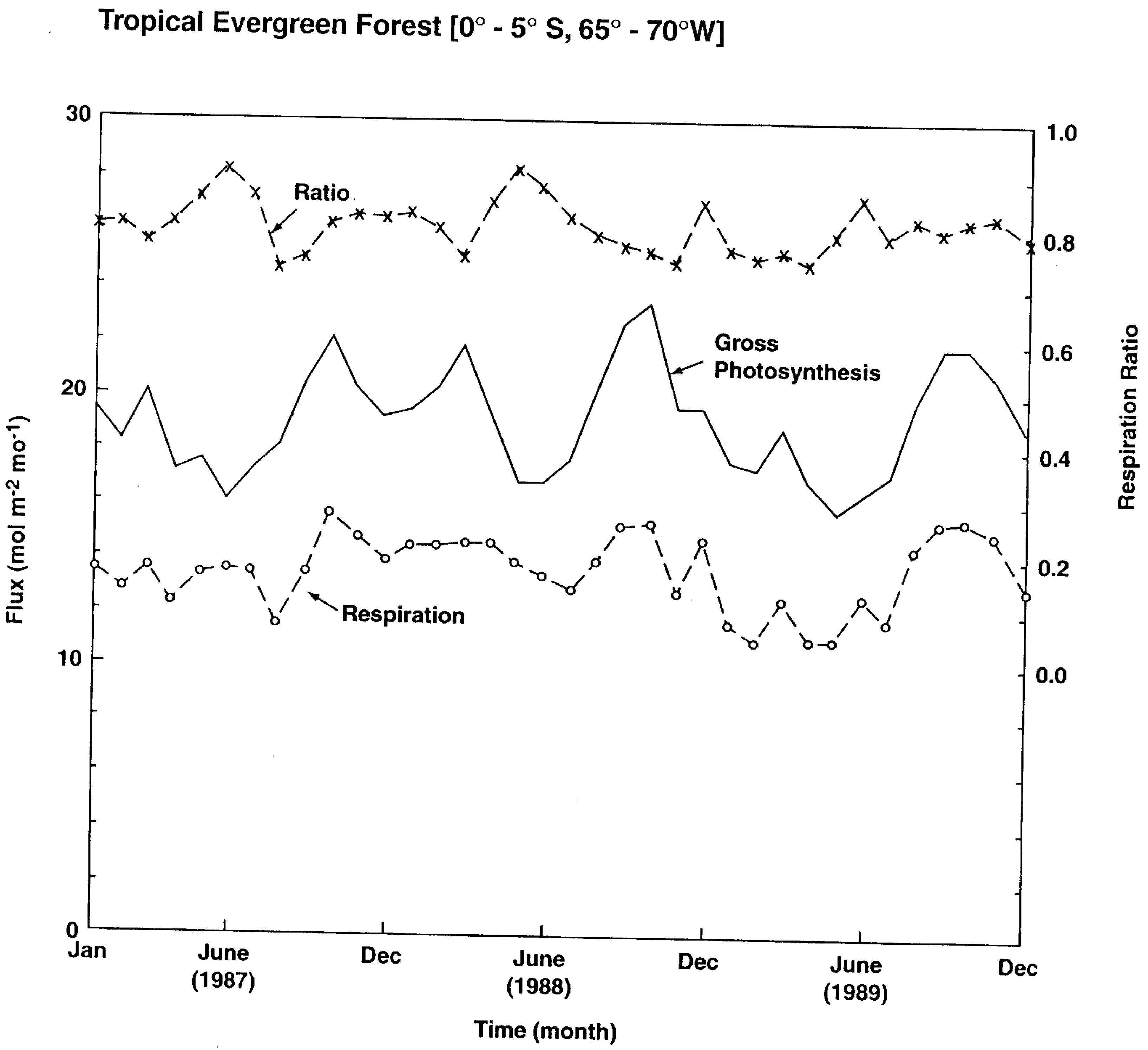


Fig. 4c

F1557.001

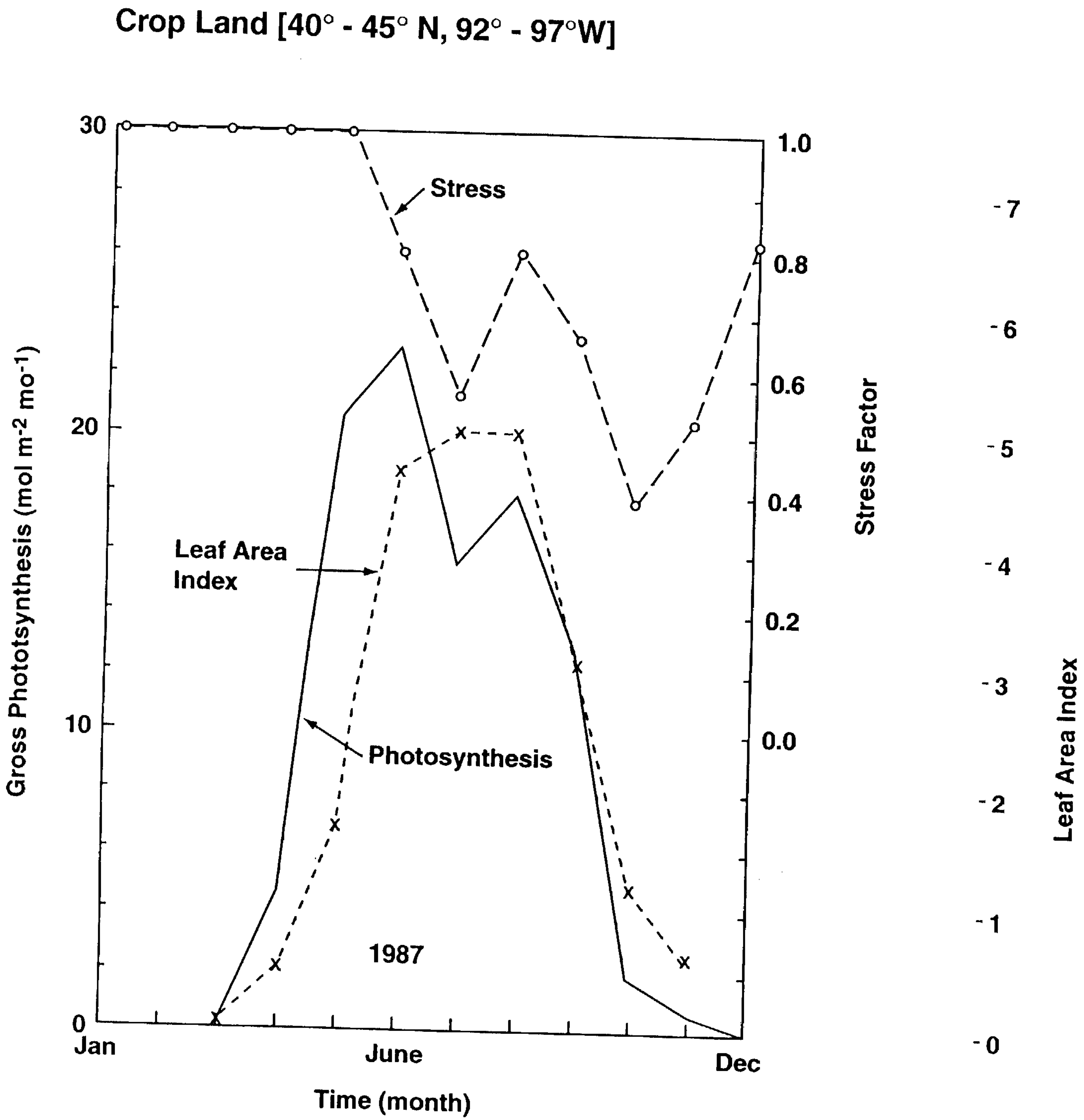
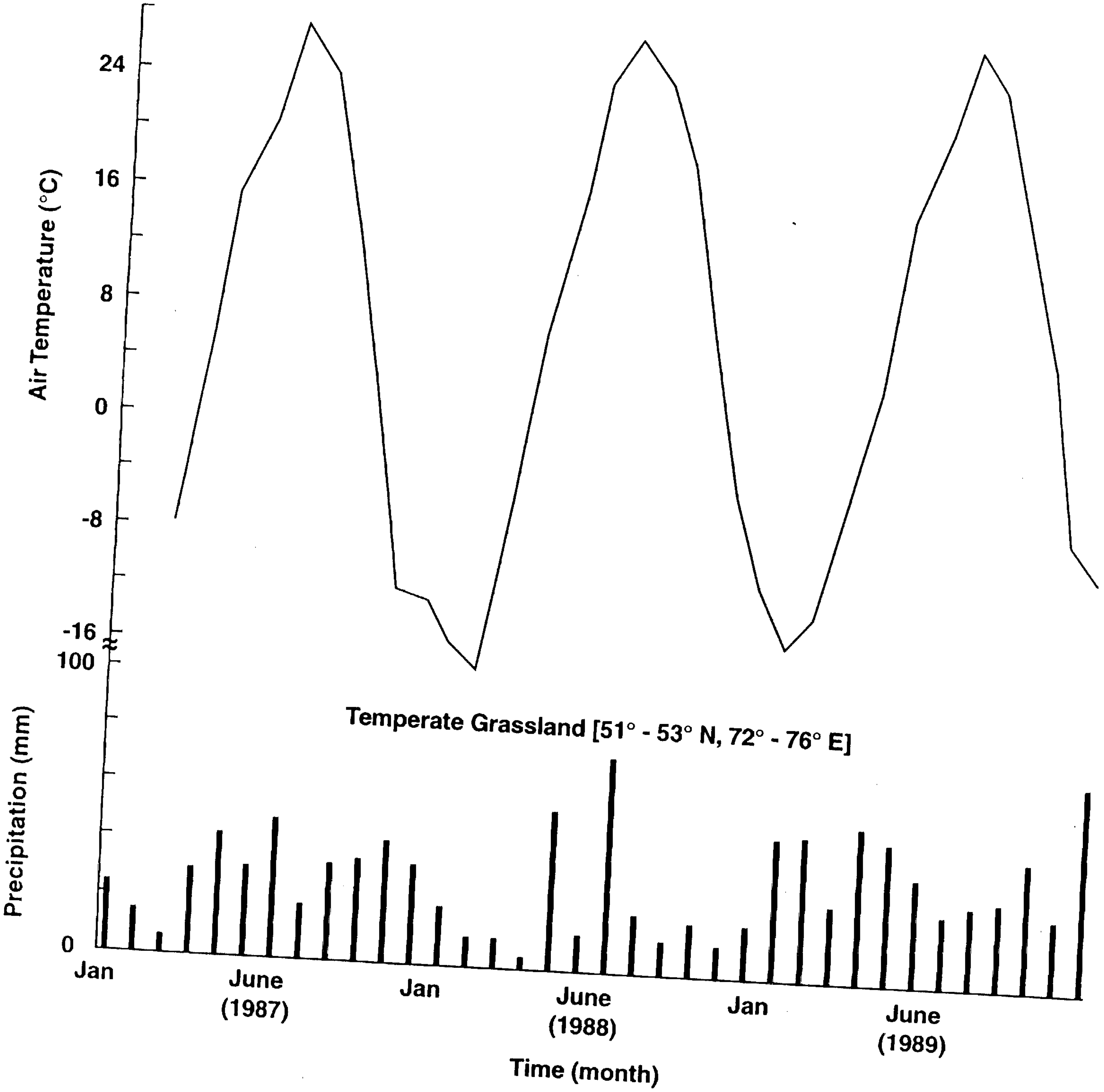


Fig. 5

:1557.005



Temperate Grassland [51° - 53° N, 72° - 76° E]

Fig. 6

1557.006