Ecosystem CO_2 exchange from the Sahel to the Arctic - in a global change perspective

Henrik Soegaard

Abstract

Within the framework of the IGBP(International Biosphere Geosphere Program) several field studies have recently focused on the interrelationship between the hydrological and the carbon cycles. The present paper summarizes results from four sites ranging in latitude from 15 °N to 75 °N and including: the Sahel, central Spain, boreal Sweden, and northeastern Greenland. Apart from the Greenland tundra site, the three other areas are agricultural. Based on eddy covariance measurements the average course in CO_2 exchange is presented for each site, and it is found that the least productive system is not located in the tundra as might be expected but rather in the wine-growing regions located in the driest part of Spain. The differences in carbon assimilation are related to the physiology of the vegetation; especially the stomatal control. The carbon dioxide budgets are compared to those of natural ecosystems, and for the growing season it is found that the seasonal carbon exchange is rather similar. By applying a photosynthesis model, the sensitivity of the ecosystems to temperature change is analysed and whereas the vegetation in the Sahelian and Tundra zones would appear to benefit from high temperatures, the carbon assimilation of Spanish vine rapidly approaches the zero level. Finally, the role of geographers as monitors and heralds of not only the possible consequences of a global warming but also the mechanisms at work is discussed.

Keywords

Net ecosystem exchange, climatic zones, carbon dioxide modelling.

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The interrelationship between climate, vegetation and landuse has been a major study theme among Danish geographers for nearly a century. This has resulted in the comprehensive work on world climatic zones and biochores (Vahl, 1911; Vahl and Humlum, 1949) and subsequently detailed local human ecological studies (e.g. Christiansen, 1975). In contrast to the renowned Köppen Climate Classification System (Köppen, 1936) which is defined purely in terms of measurable parameters (temperature and rainfall), the Vahl classification includes vegetation and landuse, but its broader application is limited because the boundaries between the zones lack a direct translation into climate parameters. Instead of trying to update the climatic criteria determining the boundaries between the individual climatic zones, it now seems more appropriate to use the ecosystem carbon dioxide exchange as a key parameter for characterizing the climatic zones; not only with respect to the present situation but also with respect to the consequences of a possible global warming.

Some noteworthy earlier studies of ecosystem carbon exchange concentrated on comparing the increase of drymatter and the decomposition rates (e.g. Müller and Nielsen, 1965), but recently the introduction of the eddy covariance technique for studying gas exchange has meant that the carbon cycling can be monitored with a much higher time resolution, and studies can thus be applied to specific processes (e.g. Baldocchi *et al.*, 1988). One of the lessons learnt from recent studies is that due to atmosphere-biosphere feedbacks, the individual processes need to be studied by an integrative approach. The stomatal control of water vapour and carbon dioxide diffusion cannot be studied in isolation because as soon as transpiration takes place, the humidity in the stomatal micro-environment will increase and thus change the diffusion rate which again will influence the stomatal aperture. Consequently, simulation models have become necessary tools during the last decade (e.g. Collatz *et al.*, 1991). Initially the models concentrated on leaf level processes. Later these models were elaborated to simulate vegetation at the global scale (Wang and Polglase, 1995; Haxeltine and Prentice, 1996).

Within the broad diversity of global vegetation types the present paper focuses on the carbon assimilation of four vegetation types whose locations range, from 75 °N to 15 °N. All four systems function under marginal conditions; limited either by heat or water supply. By combining eddy covariance measurements and CO_2 exchange modelling, the sensitivity of these systems related to temperature change is evaluated.

Areas of study

The major characteristics of the four selected study sites are listed in Table 1. The climatic zone of each site is classified according to Vahl and Humlum, 1949. At the three northernmost sites, the vegetation consists of C_3 plants whereas millet at the Sahel site is a C_4 plant. The terms C_3 and C_4 refer to the internal CO_2 pathway. C_4 plants lack photo-respiration and their leaf assimilation rate per unit absorbed light is 2-3 times higher than that of C_3 plants .

The tundra zone.

The climate of the polar tundra is characterized by a short growing season (approximately 50 days with a daily mean temperature of around 6 °C. The evapotranspiration is generally low (50 mm/year) and even though the annual rainfall is typically below 200 mm, only vegetation on coarse sediments with low field capacity suffers from water shortage during the growing season. The snow cover during the long winter season reduces the exchange of gases and heat. Several studies have emphasized the sensitivity of the Arctic climate with respect to possible global warming. The present case study was conducted at the Zackenberg Research Station in northeast Greenland during the months of June and July 1996.

The boreal zone

In the Vahl classification, the coldest part of the temperate zone is denoted as the coniferous forest. To avoid any confusion with regard to the vegetation in the present study, the equivalent term, boreal, is used instead. The boreal forest is often considered as one of the most important CO_2 sinks as a response to global warming. For the present study, however, the focus is on the agricultural land found within the boreal zone. The study site was located in the NOPEX research area near Uppsala (Halldin *et al.*, 1999, Soegaard and Thorgeirsson, 1999) and data collection was conducted in two periods (May-June 1994, May-July 1995).

The subtropical zone

The subtropical study site is located on a plateau SE of Madrid close to the town of Tomelloso. Table 1 shows the area to have a very low annual rainfall and this fact combined with a warm and extremely dry summer makes it a perfect site for the study of potential desertification in Europe (Bolle *et al.*, 1993). An extensive use of irrigation has caused a drop in the groundwater level in the region during the last two decades. In the non-irrigated areas, viticulture is a predominant landuse. The data presented here were collected during a field experiment in June-July 1994.

The savanna zone

The coupling between hydrological and carbon cycling was studied intensively during the Hapex Sahel project.

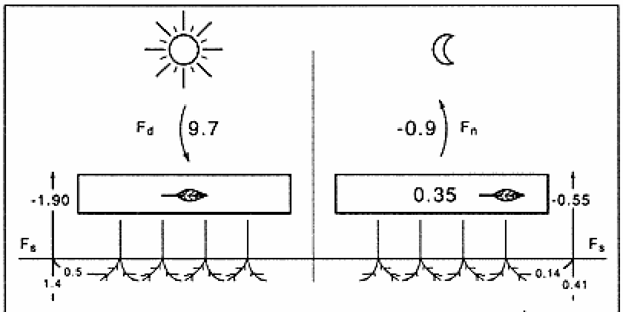
Type (Vahl's system)	*Location*	*Coordinates (°)*	*Land use*	*Growing season*					*Annual precipitation mm/year*
				NEE gC m^{-2}	*Evapotranspiration mmd^{-1}*	*Air temperature °C*	*Length days*	*Average LAI*	
Polar tundra	*Zackenberg Greenland*	*74N 21W*	*fen grass*	*96*	*1.3*	*5*	*50**	*0.8*	*223*
Boreal	*Uppsala Sweden*	*60N 17E*	*grain*	*261*	*2.8*	*17*	*60**	*1.7*	*570*
Sub-tropical	*Tomelloso Spain*	*39N 3W*	*vine*	*32*	*0.55*	*24*	*120**	*0.2*	*450*
Savanna	*Foundou Beri, Niger*	*14N 3W*	*millet*	*154*	*3.3*	*28*	*80**	*0.3*	*420*

***Table 1**: Landuse and climate characteristics at the four study sites. * = estimated value.*

(Goutorpe *et al.*, 1997) conducted in Niger in August-October 1992. In the rainy season, which is concentrated in the months of August and September, the area receives 400-500 mm precipitation. The most important agricultural crop is millet which typically covers 10% of the land surface.

Methods

The carbon dioxide which is assimilated by the vegetation originates from two sources, namely the atmosphere and the soil. For a developed crop (LAI>1), approximately 80% of the carbon dioxide comes from the atmosphere. The carbon dioxide flux from the atmosphere to the canopy is measured by use of the eddy covariance technique where the equipment consists of a sonic anemometer for measuring wind speed, and an infrared gas analyser for measuring CO_2 and water vapour. When integrated over time, the CO_2-flux is denoted NEE (net ecosystem exchange). The contribution from the soil is either measured using chambers mounted on top of the soil or estimated by modelling (Lloyd & Taylor, 1994). Fig. 1 shows how the contribution from each part of the plant-soil-atmosphere system adds to the carbon balance. The numbers are based on mean values from a wheat crop in the Swedish boreal zone. The unit is g Carbon m^{-2} d^{-1}. In a similar way, the gross primary production (GPP) can be calculated as the daytime numerical sum of carbon fluxes originating from both above and below the canopy. As shown in Fig. 1, the net primary production (NPP) can be calculated by subtracting the respiration loss from GPP.



Intergrated	Daytime Flux	Nighttime Flux	Day + Night
GPP	$F_d - F_s = A_n$		9.7 - (-1.9)=11.6
NPP	$F_d - F_s$	$F_n - F_s(1-f_r)$	9.7 - (-1.9)-0.9+ 0.41=11.1
NEE	F_d	F_n	9.7-0.9=8.8

Figure 1: Calculation of carbon budget for a plant canopy. The numbers are based on mean values for wheat in the Swedish boreal area. The unit is g Carbon m^{-2} d^{-1}. GPP is the Gross Primary Production, NPP is Net Primary Production, NEE is the Net Ecosystem Exchange, f_r is the fraction of respiration originating from roots, here 0.25 = 0.14/(0.41+0.14).

Carbon dioxide fluxes directed towards the ecosystem are here calculated as positive numbers whereas fluxes directed upwards (i.e. ecosystem loss) are calculated as negative numbers in the budget, in accordance with Ruimy *et al.* (1995).

Not only CO_2 fluxes but also heat and water vapour fluxes are measured by the eddy covariance technique. In most of the experimental studies, the flux data are supplemented by standard meteorological measurements. In addition, are the photosynthetically active radiation (PAR) is measured with a quantum sensor, the vegetation density

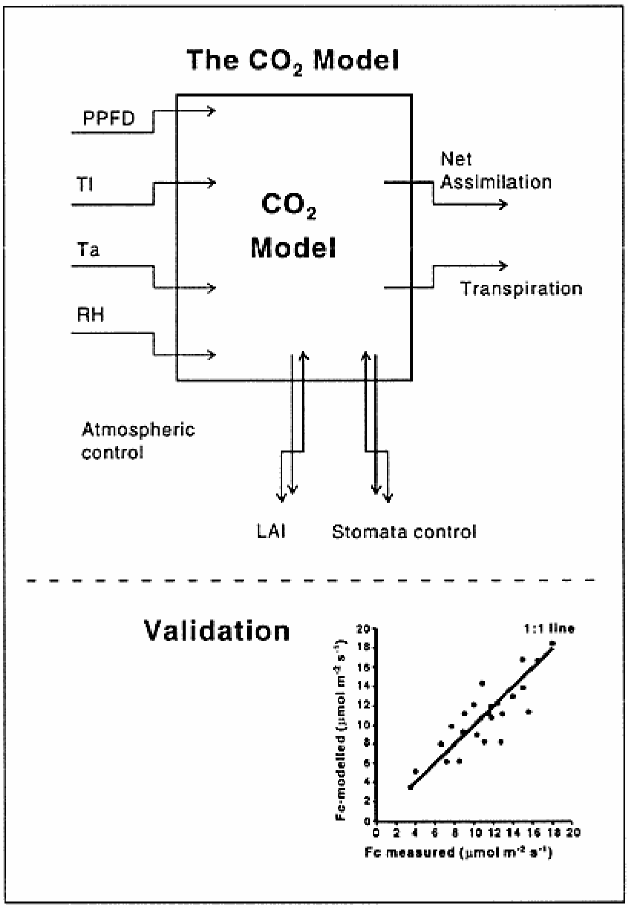


Figure 2: Input and output structure of the applied photosynthesis model. PPFD is the light intensity (Photosynthetic Photon Flux Density) ,Tl is leaf temperature, Ta is air temperature, and RH is Relative Humidity. The lower half of the box shows the model estimates plotted against flux measurements from the boreal zone in Sweden in 1994.

(LAI) with handheld optical sensors, and the stomatal resistance with a porometer.

To improve the interpretation, the CO_2 fluxes are often analysed using a mathematical model which handles both the individual processes (e.g. the light absorption) and the feedback between processes. In the present study, the carbon assimilation in the canopy is modelled by use of a photosynthesis model elaborated by Collatz *et al.*(1991). Fig. 2 shows that the model predicts the carbon assimilation from four atmospheric variables and regulates through two plant characteristic variables (stomatal resistance and Leaf Area Index, LAI). In the CO_2 model box (Fig. 2), the carbon assimilation is calculated as the minimum of three potential limitations for plant growth namely 1) the absorption of light, 2) the availability of CO_2 through the stomata, and 3) the removal of the assimilates. When the model is calibrated against flux data it may also be used for estimating the CO_2 exchange in the part of the season when no direct flux measurements are available.

Results

Diurnal course in carbon dioxide fluxes.

Fig. 3 shows the average diurnal patterns in CO_2-flux. The diagram is based on averaged fluxes recorded in the middle of the growing season at all four study sites. The highest average fluxes were measured at the Swedish barley site. During the daytime, when the carbon dioxide flux is directed from the atmosphere towards the plant canopy, the maximum flux occurs close to noon. Because of the higher temperatures in the afternoon, the respiration loss is also higher in the afternoon which gives the curve a slightly asymmetric shape. Due to the northern location, there is a net carbon uptake for nearly 16 hours per day. The higher level of carbon dioxide fluxes observed for barley is to some extent linked to the fact that its average LAI is up to 8 times as high as those of millet and vine (Table 1).

The diurnal variation for millet at the Sahelian site is quite comparable to that of the Swedish site except for the longer nights. Equally true of millet, the diurnal curve is asymmetric, with higher values in the morning than in the afternoon. The midday maximum is two-thirds of that at the barley site even though the average leaf density is only one-fifth. This clearly emphasizes the effectiveness of carbon assimilation by C_4 plants. The light response curves prove that C_4 plants are far less influenced by light saturation than C_3 plants, and they are therefor better suited to utilize the high midday radiation in the Sahel.

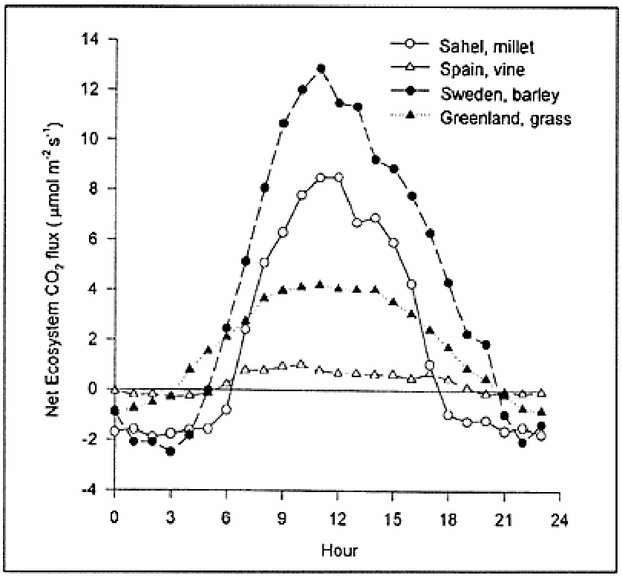


Figure 3: Diurnal variation of the carbon dioxide flux between plant canopy and the atmosphere.

The diurnal pattern of NEE at the Polar tundra site is characterized by an upper maximum level which is due partly to less variation in solar radiation throughout the day and partly to the limitation in biochemical processes because of insufficient nitrogen content in the leaves (Soegaard and Nordstroem,1999). At the summer solstice, the tundra site receives 24 hours of sunlight, allowing the carbon flux to be directed downwards, even at midnight. At the end of the growing season, the tundra ecosystem becomes a carbon dioxide source at night. Calculated as an average for the whole season, the carbon flux is directed towards the plants for 18-19 hours per day (see Fig. 3).

The most striking deviation from the general pattern is observed at the Spanish vine site for which the fluxes are low both night and day. The soil is extremely dry; which limits soil respiration. The midday fluxes average 1 µmol m^{-2} s^{-1} ;corresponding to only 43 mg C m^{-2} h^{-1}.

To clarify to what extent the difference in CO_2 fluxes among the sites can be attributed to stomatal performance, the diurnal course in the stomatal resistance has been analysed and plotted in Fig. 4. Stomatal resistance is known to depend on environmental factors (water availability and light) as well as the stage of plant development. To improve the comparability, the diurnal courses shown in Fig. 4 are all from the early vegetative stage with low vegetation density (LAI= 0.25) at all sites. Whereas both millet and barley exhibit low resistance during midday hours (150-200 s m^{-1}), the vine shows a totally different picture; the course being strongly asymmetric, with low values in

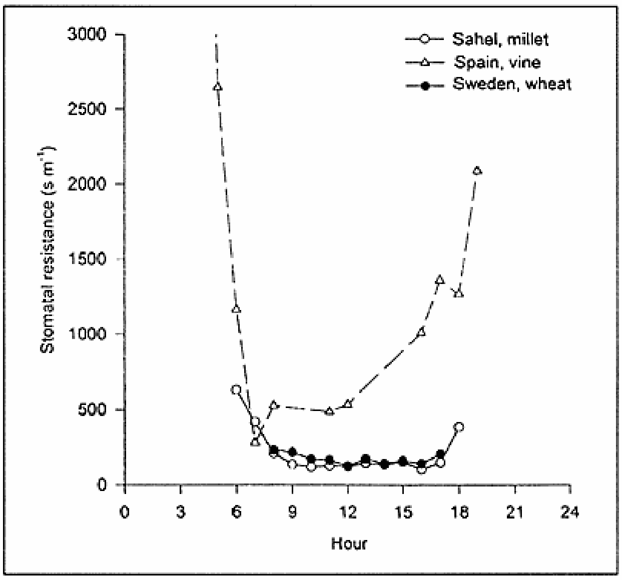


***Figure 4:** Diurnal variation in stomatal resistance at three of the study sites.*

the early morning followed by a rapid increase associated with increases in leaf temperature and vapour pressure density. Together with a midday resistance 3-4 times larger than recorded at the two other canopies, the vine shows an obvious sign of severe water stress. Measurements of the Greenlandic cotton grass stomatal resistance were not conducted due to the insufficient leaf width.

Growing season budgets

The growing season net ecosystem exchange for the four sites (Table 2) shows the same features as depicted in Fig. 3. Due to the longer growing season, the vine reaches arelatively higher level compared to the average values given in Fig. 3.

However, the four selected sites should not be considered as representative of their respective latitudes. The conditions at Zackenberg produce far above the average values for latitude 70-80 °N, whereas for the vine in Spain the NEE is much below the latitudinal average. To elaborate the latitudinal dependency, the NEE-values are compared with corresponding results obtained in other ecosystems when applying the same technique. The results are presented in Table 2.

As can be seen, there is a general trend towards a maximum in growing-season NEE with respect to the mid-latitudes (40-50 °N), whereas a decline is observed towards both the pole and the equator. The table underlines that the tropical ecosystem has by far the largest assimilation, but due to the high respiration loss, the turnover (= NEE) is only 100 g C m^{-2} as found in dry parts of the Sahel.

In general, these results should be treated with caution as most of the data are only based on one year of observations. In most cases, only the fluxes during the growing season were actually measured whereas the fluxes during the rest of the year were modelled, as already discussed. As shown in several studies (e.g. Lindroth et al, 1998), large differences in NEE may occur from year to year due to the strong temperature dependency.

The temperature dependency of the carbon budget.

By use of the photosynthesis model, it is possible to study the stability of the carbon balance with respect to temperature and thus evaluate the likely effects of a warmer or colder climate. Most climate modellers predict the greenhouse effect cause a temperature increase in the order of 1-5°C by the year 2030 (e.g. Warrick *et al.*, 1990), and the calculations have therefore been made here based on a slightly broader range (-4° C to +8°, relative to today).

In the calculation, it is assumed that all other climatic parameters including radiation, relative humidity and wind speed remain unaffected by a temperature change. Furthermore, it is assumed that the air, leaf, and soil temperatures

Vegetation/land-use	***Growing season NEE gC m^{-2}***	***Annual NEE gC m^{-2}***	***"Dry/cold" season NEE gC m^{-2}***	***Latitude (°)***	***Longitude(°)***	***Reference***
Polar fen	*96*	*64*	*-32*	*75 N*	*21W*	*Soegaard and Nordstroem,1998*
Temperate deciduous	*470*	*600*	*-130*	*41 N*	*14 E*	*Valentini et al. (1996)*
Boreal deciduous	*350*	*130*	*-220*	*54 N*	*106 W*	*Black et al.(1996)*
Tropical rainforest	*102*	*102*	*0*	*10 S*	*62 W*	*Lloyd et al. (1995)*
Bush-grass in savanna	*110*	*29*	*-81*	*14 N*	*3 W*	*Hanan et al. (1998)*
Agricultural systems						
Millet in savanna	*150*	*69*	*-81*	*14 N*	*3 W*	*Friborg et al.(1995) Boegh et al.(1998)*
Barley in boreal	*260*	*na*	*na*	*60 N*	*17 E*	*Soegaard and Thorgeirsson,1998*
Vine in subtropical	*32*	*na*	*na*	*39 N*	*3 W*	*Preliminary data*

***Table 2:** Net ecosystem carbon exchange estimated by eddy covariance technique. Na menotes not available. Values read from graphs has been rounded to nearest 10. For the millet dry season, the data from the neighbouring bush grass savanna are used.*

are changed by the same amount. To improve the comparability between the sites, the calculations are conducted on one single sunny day when the LAI was at the same level at all four sites (LAI=0.25).

When evaluating the temperature dependency, it should be noted that both gross assimilation and respiratory loss from the plant tend to increase with increasing temperature. The increase in photosynthesis with rising temperature will occur until a point above which it will begin to decrease through inhibition. As long as air humidity is kept constant, an increase in temperature will also cause the VPD (vapour pressure deficit) to increase, and plants can be assumed to react by reducing their stomatal apertures.

Due to the exponential shape of the saturation vapour curve with temperature, the effect on stomatal resistance will be most significant at high temperatures.

The plots in Fig. 5 show the resulting net assimilation. Three of the four sites display similar patterns; namely, that a temperature decrease compared to present-day figures would cause a decrease in carbon assimilation, whereas a slight temperature increase would increase the net carbon uptake. However, when the temperature increases even further, net carbon assimilation starts to decline. The only exception from this rule is found at the vine site where the temperature is already so high that any temperature increase would force the net assimilation towards the zero level.

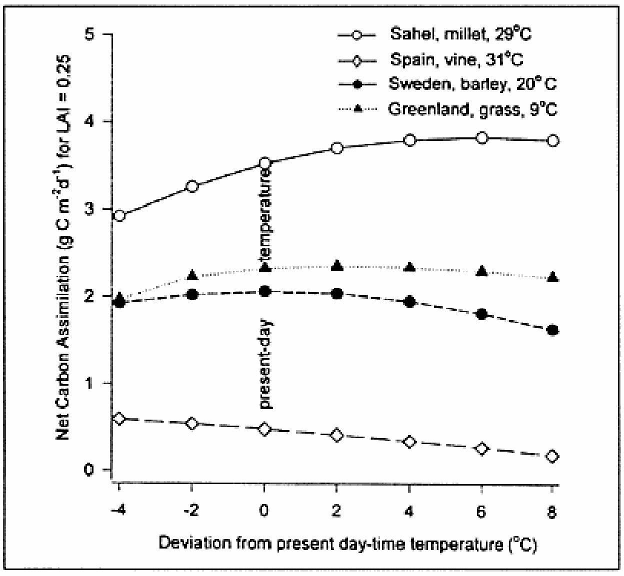


Figure 5: Net carbon assimilation for a crop with LAI=0.25 at temperature scenarios ranging from 10 °C below to 10 °C above present. The legend shows the day-time leaf temperature at the time when the vegetation had a LAI=0.25.

Because the simulations in Fig. 5 are based on canopies with the same leaf area index (LAI=0.25), the graph is able to quantify the assimilation efficiency. It is clear that the C_4-plant, millet, is by far the most efficient with regard to assimilation of C.

According to plant geometry, a sparse canopy will absorb radiation more efficiently when light travels at lower solar angles. By contrast, a larger fraction of the light pass straight down to the soil at higher solar angles. Together with the long summer daylight hours with sufficient light the lower solar angles allow the Greenlandic vegetation to reach high daily assimilation rates. The barley found in the boreal zone seems to be the only crop which grows at its optimal temperature. This is, however, only valid in the early part of the growing season when the sparseness of the canopy causes the amount of absorbed light to be the main limitation. At later stages of plant development the optimal temperature would occur at temperatures approximately 2 °C above the present-day level. For millet, the optimal temperature is found at approximately 6 °C above the 29 °C which figures in the data set.

Discussion

During the last couple of decades, a number of theories have been proposed with respect to the carbon cycling in a natural ecosystem context and its temperature dependency. The hypothesis that higher mean temperatures would increase the carbon sink function is debatable when considering the boreal forest. Long-term measurements from the NOPEX area in Sweden (Lindroth *et al.*, 1998) show the boreal forest to function as carbon source. Moreover, observations (Oechel *et al.*, 1993) from Alaska to prove that the high latitudes have changed from carbon sink to source is not substantiated by recent research on the Greenland polar tundra (Soegaard and Nordstroem, 1998).

The present analysis indicates that carbon budget sensitivity to temperature change can vary greatly, even in regions with similar growing season temperatures and annual rainfall. Whereas the C_4 plants in the Sahelian zone would to some extent benefit from a warmer climate as long as the water supply was not limited, the driest parts of the Mediterranean zone would become extremely marginalized and the desertification-threatened-area concept is likely to become a reality.

In the boreal zone where small agricultural fields are found within extensive forest areas, the present agricultural landuse seems to be in balance. The carbon uptake is of the

same order of magnitude as found in the mid-latitude forest ecosystems. The carbon sink potential would only increase should more heat-resistant crops (e.g. maize) be grown on a larger scale.

The tundra study site clearly indicates that annual mean values are of little use when trying to estimate the carbon balance. Even though the annual air temperature is as low as -20 °C, the northernmost study site shows a carbon gain as high as 96 g C m^{-2} in the growing season . The wintertime loss is limited due to the very low temperature, so as a result the annual carbon surplus is significant. High assimilation rates in Greenland were also reported by Eckardt et al., 1982.

It is obvious that the terrestrial carbon and hydrological cycling consists of a complex set of processes which should be studied by scientists in close cooperation transcending traditional biogeographical boundaries. Within this framework, ranging from plant physiological studies at leaf level to global circulation models, the role of geographers seems to be related to the scaling of processes from the canopy up to landscape level. At the larger scale, the human activities as expressed through different types of landuse and management (including artificial fertilization and irrigation) are of major importance. In the current preference to utilize large scale approaches to study processes, remote-sensing data have for long been demonstrated to be important and their useful application has been quickly recognized by geographers. In conclusion, it seems inevitable that geographers will play an important role contributing to our understanding of the interrelationship between man and the environment.

Acknowledgment

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same order of magnitude as found in the mid-latitude forest ecosystems. The carbon sink potential would only increase should more heat-resistant crops (e.g. maize) be grown on a larger scale.

The tundra study site clearly indicates that annual mean values are of little use when trying to estimate the carbon balance. Even though the annual air temperature is as low as -20 °C, the northernmost study site shows a carbon gain as high as 96 g C m^{-2} in the growing season . The wintertime loss is limited due to the very low temperature, so as a result the annual carbon surplus is significant. High assimilation rates in Greenland were also reported by Eckardt et al., 1982.

It is obvious that the terrestrial carbon and hydrological cycling consists of a complex set of processes which should be studied by scientists in close cooperation transcending traditional biogeographical boundaries. Within this framework, ranging from plant physiological studies at leaf level to global circulation models, the role of geographers seems to be related to the scaling of processes from the canopy up to landscape level. At the larger scale, the human activities as expressed through different types of landuse and management (including artificial fertilization and irrigation) are of major importance. In the current preference to utilize large scale approaches to study processes, remote-sensing data have for long been demonstrated to be important and their useful application has been quickly recognized by geographers. In conclusion, it seems inevitable that geographers will play an important role contributing to our understanding of the interrelationship between man and the environment.

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