International Journal of Multidisciplinary Research and Development
Online ISSN: 2349-4182, Print ISSN: 2349-5979, Impact Factor: RJIF 5.72
www.allsubjectjournal.com
Volume 3; Issue 9; September 2016; Page No. 125-132

Temporal variations in net primary production (NPP) and gross primary production (GPP) of three coniferous forests

[1] Mohamed AA Mohamed, *[2] Insaf S Babiker, [3] Tetsuya Hiyama

[1] College of Water and Environmental Engineering, Sudan University of Science and Technology, 11115, Khartoum, Sudan
[2] Department of Social Studies, Faculty of Arts, King Faisal University, Al-Hassa 31982, PO Box 1759, Kingdom of Saudi Arabia
[3] Hydrospheric Atmospheric Research Center, Nagoya University, Chikusa-ku, Furo-cho, 464-8601, Nagoya, Japan

Abstract

North latitudes temperate and boreal forests play an important role in the global carbon cycle. However, their responses to climate variability are not fully understood. Meteorological data including incident photosynthetic active radiation (PAR), absorbed photosynthetic active radiation (APAR), air temperature, precipitation, and relative humidity were obtained for three coniferous forests from the Euroflux network with 1-4 years data collected between 1997 and 2000. Net primary production was modeled using APAR and biome-specific conversion efficiency in order to investigate the variations and magnitude of vegetation responses to environmental variables. Seasonal variations of NPP reflected the typical phenology of temperate forests with peak productivity in spring-summer due to limiting growing season and changes in incoming radiations. Monthly NPP was tightly correlated to temperature, relative humidity and PAR while no relation was found with total precipitation. Temperature controls the productivity of coniferous forests by directly enhancing their metabolic activity and indirectly accelerating decomposition of organic matter in soil.

Keywords: Coniferous forests; Euroflux data, NPP; environmental controls

1. Introduction

Currently, the increasing atmospheric CO_2 concentration and the consequent global warming represent the greatest environmental issue (Hirano *et al*. 2003). This CO_2 increase is chiefly explained by anthropogenic emissions of CO_2 from fossil fuel burning, cement production, and land use change (deforestation) which are estimated to be 6.3 Pt C/y (Pt = 10^{15} gm) during the 1990s and was increasing. Balancing the annual carbon cycle taking into account the 2 Pt C/y dissolved into the ocean and the 3 Pt C/y accumulating in the atmosphere, results in a missing fraction of about 1.1 Pt C/y. The terrestrial biosphere is believed to incorporate this component (Houghton *et al*. 1998) [1]. However, conflict exists about allocating this sink to which part of the globe; the tropical, the northern mid and high latitude region or both (Keeling *et al*. 1996, Rayner *et al*.1999) [2, 3]. While CO_2 fluxes reflect the impacts of disturbance history (Law *et al*. 2002) [4], inter-annual differences in carbon sources and sinks are likely to be driven primarily by the effect of climate on ecosystem processes (Schimel *et al*. 2000) [5]. Therefore, it is essential to quantify the causal link between climate and CO_2 exchange for all major terrestrial ecosystems as a basis for model validation.

Data on atmospheric carbon dioxide and oxygen suggested that the terrestrial biosphere was largely neutral with respect to net carbon exchange during the 1980s and has become a net carbon sink in 1990s (Schimel *et al*. 2001) [6]. Willams *et al*. (1997) [7] stated that several processes including CO_2 fertilization (Idso & Idso 1994) [8], forest re-growth (Melillo *et al*. 1993) [9] and nitrogen deposition (Peterson & Melillo 1985) [10] may account for the budget imbalance.

The net carbon exchange between atmosphere and terrestrial biosphere is determined by the balance between the net primary production (NPP) and soil respiration (SR) which are likely to be affected by climate variability, CO_2 fertilization, nitrogen deposition and human-controlled land use changes. Early studies (McGuire *et al*. 1993, Melillo *et al*. 1993) [11,9] suggested that significant changes in patterns of terrestrial NPP are expected in response to the above mentioned factors. Forests at north and mid latitudes play an important role in the global carbon cycle (Keeling *et al*.1996, Fan *et al*. 1998) [2,12] particularly inter-annual studies have established a strong link between climatic variability and terrestrial carbon cycles of these ecosystems (Valentini et la. 2000, Mohamed *et al*. 2004) [13,14]. However, the processes that govern the carbon budget of northern forest ecosystems with respect to climate variability are not fully understood (Barr *et al*. 2002) [15].

This study was undertaken to investigate the temporal variations in NPP of one of the important northern high latitude ecosystems, coniferous forests. An attempt was also made to investigate the magnitude and variation in responses of this vegetation to environmental variables in order to increase our understanding on the factors governing their productivity.

2. Materials and methods

With technological advancement an international network has been established in 1996, the FLUXNET (Valentini *et al*. 2000, Baldocchi *et al*. 2001) [13, 16] representing regional collections of eddy covariance flux towers. FLUXNET hosts a data base of continuous measurements of ecosystem carbon and energy exchange, key meteorological variables and ancillary data describing location, vegetation and climate of the sites. The data sets cover multiple years (1992-2000) of flux tower measurements from the Ameriflux (23 sites) and EUROFLUX (16 sites, Valentini *et al*. 2000) [13] projects. The data represents the first four years of the project`s life.

Meteorological data including incident photosynthetic active radiation (PAR), absorbed photosynthetic active radiation (APAR), air temperature, precipitation, and relative humidity were obtained for three evergreen coniferous EUROFLUX sites with 1-4 years data collected between 1997 and 2000 which are available online at the EUROFLUX website: http://www-eosdis.ornl.gov/FLUXNET/. Site's description is provided in Table 1. Both original and gap filled data were provided. Eddy covariance flux towers usually reports half hourly data with the objective to collect data 24 hours a day and 365 days a year. However, violations in micrometeorological assumptions, instrument malfunction and poor weather will force investigators to reject a proportion of the data making the data coverage during a year only 65% (Falge *et al*. 2001) [17]. Although filling procedures help to provide complete data sets they are generally associated with errors increasing with the increase of data gab and decrease of randomness of gabs (Falge *et al*. 2001) [17].

Table 1: Site characteristics of the three evergreen coniferous forests. The values for "Tharandt" are means of four years (1997~2000) except for annual precipitation which is a mean of three years.

Name and symbol	Aberfeldy (AB)	Bordeaux (BO)	Tharandt (TH)
Country	Scotland	France	Germany
Location	56º 37' N, 3º 48' W	44º 05' N, 0º 05' E	50º 58' N, 13º 38' E
Elevation (m)	340	60	380
Climate	Oceanic	Mediterranean	Temperate
Species	*Sitka spruce*	*Maritime pine*	*Norway spruce*
Annual temperature (ºC)	8.25	14.92	8.97
Total precipitation (mm/y)	1208.4	941.4	714.5
Relative humidity (%)	91.58	76.8	74.63
Total PAR (mol/m^2/y)	5054	9835.79	7344.58
Total APAR (mol/m^2/y)	119.71	5127.68	3890.15
Leave area index, LAI (m^2/m^2)	8	2.6	6
Stem density (stem/ha)	2500	600	550
Analyzed period	97/8~98/12	97/1~98/6	96/8~00/12

In this study, only original data were used where the three FLUXNET sites (Aberfeldy, Tharandt and Bordeaux) were chosen according to the availability of APAR half-hourly measurements. Totally, 101 monthly data were available for the three sites, of which 78 months have complete APAR record, 10 months were accepted with missing data ranges from 0.8 ~ 18% per month, and 13 months were completely rejected. The selected 88 monthly data were further screened based on the other meteorological observations; incident photosynthetic active radiation (PAR), air temperature, precipitation, and relative humidity. Generally, 87.1% of the original data of the three sites had acceptable observation records of APAR, temperature, relative humidity and PAR measurements while 78.2% had acceptable precipitation record.

To estimate NPP a parametric model derived from (Monteith 1972, 1977) [18, 19] was used. The original model of crop growth remote sensing (Kumar & Monteith, 1981) [20] uses the efficiency concept to decompose NPP into independent parameters such as incoming solar radiation, radiation absorption efficiency and conversion efficiency of absorbed radiation into organic dry matter. Long and Hutchin (1991) [21] stated that the approach of predicting production from light interception and conversion efficiency is particularly promising. This approach was successfully employed over the last decades particularly, coupled with remotely sensed data (e.g. Ruimy *et al*. 1994, Maisongrande 1995, Knorr & Heimann 2001, Running *et al*. 2004) [22 - 25]:

$$NPP(t) = e f(t) c S_0(t) \qquad (1)$$

With t: time; *e*: conversion efficiency (organic dry matter produced/APAR); *f*: absorption efficiency (APAR/PAR); c: the climatic efficiency (PAR/incident global radiation) and S_0 is the incident global radiation.

Eq. (1) can be rewritten as:

$$NPP = e \times APAR \qquad (2)$$

The conversion efficiency *e* is usually assumed to be constant among plant formation of the same metabolic type (Monteith 1977, Kumar & Monteith 1981, Russell *et al*. 1989) [19, 20, 26]. Gamon *et al*. (1995) [27] argued that the assumption of relatively constant *e* may work well in annual and deciduous vegetation where canopy structure and light absorption change in synchrony with canopy-level fluxes however, their results showed striking seasonal variability in instantaneous photosynthetic radiation-use efficiency, *e*, in evergreen species. Heimann & Keeling (1989) [28] have used a constant *e* value of about 2.8 g dry matter produced per MJ of PAR absorbed on a global scale study. However, *e* varies with phenological stage, climatic conditions such as incoming radiation, temperature and water stress (Jarvis & Leverenz 1983) [29]. Maisongrande *et al*. (1995) [23] assumed that the dependence of *e* on temperature and biomass is actually due to autotrophic respiration while the 'photosynthetic efficiency, é, is more conservative. Ruimy *et al*. (1994) [22] have used biome-dependent values of *e* (conversion efficiency of absorbed PAR into total dry matter in g/MJ) calculated from literature. In this study the biome-specific conversion efficiency, *e*, of 1.5659 (g /MJ) from Ruimy *et al*. (1994) [22] was used, a mean value that corresponds to the temperate coniferous forests.

In order to obtain gross primary production, the respiratory losses, r, were first calculated based on the parameterization of Goward & dye (1987) [30]:

$$r(t) = (7.825 + 1.145T(t))/100 \qquad (3)$$

Where T is air temperature. GPP was then calculated according to the model of Maisongrande *et al* (1995) [23] who assumed that the temperature–dependent autotrophic respiration represents a fraction of assimilates photosynthesized:

$$NPP\ (t) = [1\text{-}r(t)]GPP(t) \qquad (4)$$

This formulation is particularly suitable for C_3 species (including coniferous vegetation) where photorespiration efflux of CO_2 rises as a proportion of light saturated net rate of CO_2 uptake per unit of leaf area with temperature (Long & Hutchin 1991) [21].

To gain insight into the controlling environmental factors on the temporal variations of coniferous ecosystems, monthly variations were correlated to the environmental parameters including temperature, precipitation, relative humidity and incident photosynthetic active radiation (PAR). Multiple regression analyses were performed between vegetation net primary production and the different environmental variables.

3. Results

Temporal variation of NPP and GPP

Mean diurnal patterns of NPP and GPP (Fig. 1) were plotted for four seasons, spring (1/4 ~ 31/5), summer (1/6 ~ 30/9), autumn (1/10 ~ 30/11), and winter (1/12 ~ 31/3). The vegetation production is associated with a longer daytime during spring and summer (6:00~19:00 and 5:30~19:00, respectively) compared to autumn and winter (7:30~17:00, and 8:00~16:30, respectively). The daily NPP and GPP decrease in the sequence; spring, summer, winter then autumn at Aberfeldy and Bordeaux while at Tharandt the maximum daily NPP and GPP occurs in summer. The peak of NPP and GPP during the daytime occurs at around noon (12:30) except during autumn where the NPP and GPP peak around 11:00 o'clock. Generally, the Bordeaux site exhibits the maximum diurnal NPP (6.9 gC/m^2/d) and GPP (10 gC/m^2/d) followed by Tharandt (5 and 6.7 gC/m^2/d, of NPP and GPP, respectively) then Aberfeldy (0.14 and 0.17 gC/m^2/d of NPP and GPP, respectively). The later site has showed extremely low productivity rates particularly during autumn and winter (0.05 and 0.06 gC/m^2/d of NPP and GPP, respectively). In fact the average absorbed photosynthetically active radiation (APAR, the parameter used to model NPP) at Aberfeldy was an order of magnitude lower than at the other two sites while the total incident PAR was half of that of Bordeaux and one third of that of Tharandt. Moreover, Aberfeldy has significantly lower (0.03) "absorption efficiency" (the ratio between absorbed PAR and incident PAR) compared to Bordeaux and Tharandt (0.53).

In the three conifer sites, NPP and GPP peak during spring and summer but drop slightly in June at Bordeaux and in July at Tharandt. Inter-site comparison displays the difference in length of growing season between Aberfeldy and Tharandt sites at one hand and Bordeaux on the other hand (Fig. 2). At Bordeaux, site with the highest mean annual temperature (14.92 ºC), the growing season starts one month earlier (on March) and ends one month later (on October).

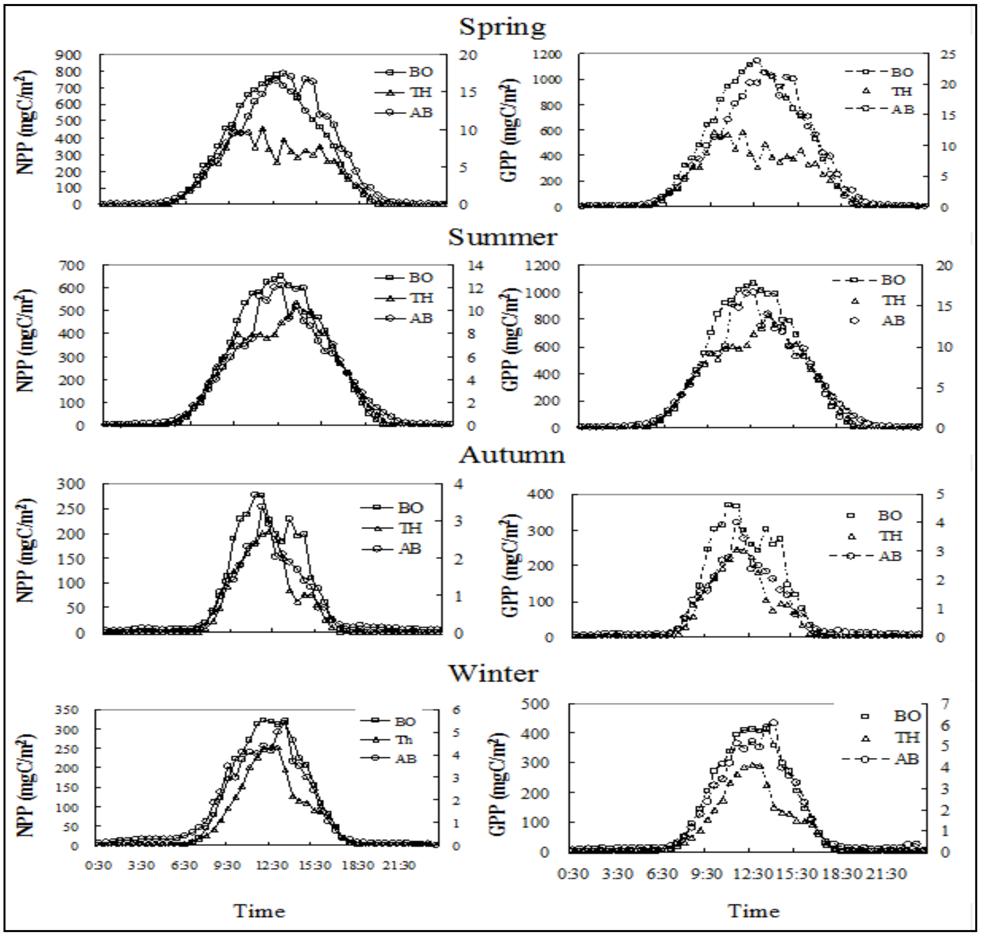

Fig 1: Spring summer, autumn and winter time diurnal variation of NPP and GPP at the three evergreen conifer sites; Aberfeldy, Bordeaux and Tharandt.

The four-year data set of Tharandt site enabled the inspection of inter-annual variation of NPP and GPP besides seasonal variations (Fig. 3). Slight variation in NPP (CV = 4.8%) and GPP (CV = 4.6%) was observed across the four-year period with the year 1997 has the maximum NPP (1980 gC/m^2) and GPP (2652 gC/m^2) and year 1998 has the minimum (1760 and 2373 gC/m^2 for NPP and GPP, respectively). The high NPP and GPP in 1997 were associated with the highest maximum annual temperature (19.6 ° C), the highest annual temperature amplitude (21.8 ° C) and the largest amount of photosynthetic active radiation (PAR) received (7893 mol/m2). Figure (3) also shows that during summer time the difference between NPP and GPP is larger than during winter.

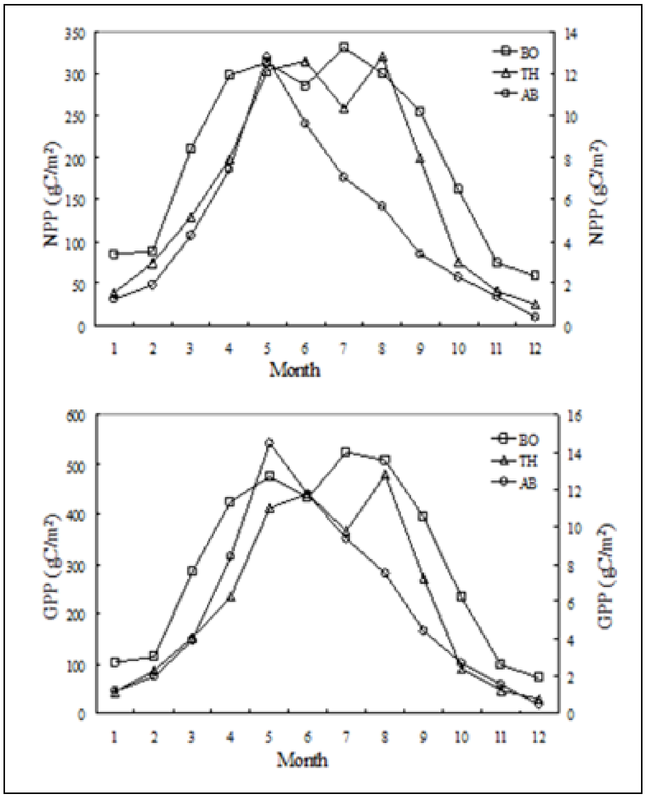

Fig 2: Seasonal variations of NPP and GPP at the three sites. The right side Y-axis corresponds to productivity values (NPP and GPP) at Aberfeldy.

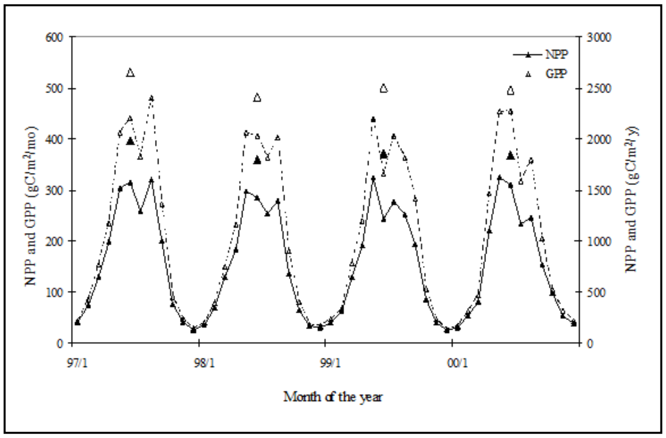

Fig 3: Seasonal and inter-annual variations of NPP and GPP over four years (1997 ~ 2000) at Tharandt. Closed large triangles refer to the annual NPP while open large triangles refer to the annual GPP. The right side Y-axis corresponds to the annual values.

Environmental controls over NPP

Since GPP was basically derived from NPP and plant respiration which was modeled as a function of temperature (one of the environmental variables considered here), in characterizing the relationships between photosynthetic production of coniferous vegetation and different climatic variables, only the NPP will be analyzed unless otherwise mentioned. Figures (4) and (5) show that while monthly mean temperature explained about 60% of the variation of NPP, no significant relationship exists between monthly NPP and precipitation in the three coniferous forests.

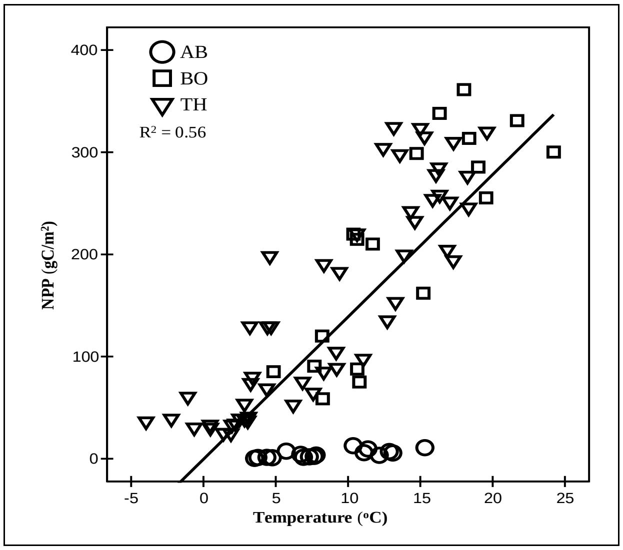

Fig 4: Relationship between monthly NPP and mean temperature. The entire monthly data set was used (88 months). P < 0.001.

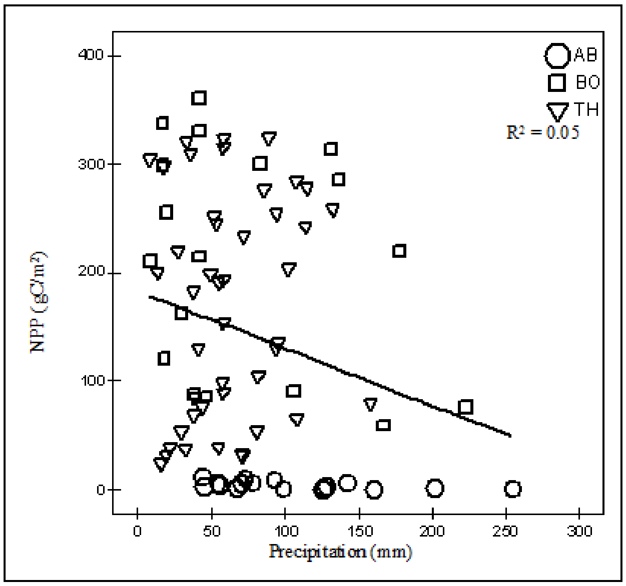

Fig 5: Relationship between monthly NPP and total precipitation. 79 monthly data were used.

Significant negative correlation was found between monthly NPP and relative humidity ($R^2 = 0.65$, Fig. 6). The correlation with monthly GPP was also strong ($R^2 = 0.6$, data not shown). For a given solar elevation angle, decreases in total incident photosynthetic active radiation indicate changes in sky conditions from clear to cloudy, along with an increase in diffuse radiation where as air and soil temperature and vapour pressure deficit tend to decrease (Gu *et al*. 1999)[31]. Here, we have plotted monthly anomalies of incident PAR against NPP (Fig. 7). As expected, the results indicate a strong direct relationship between anomaly of incident PAR and NPP ($R^2 = 0.62$) i.e. NPP tends to increase during clear sky conditions and decrease during cloudy ones.

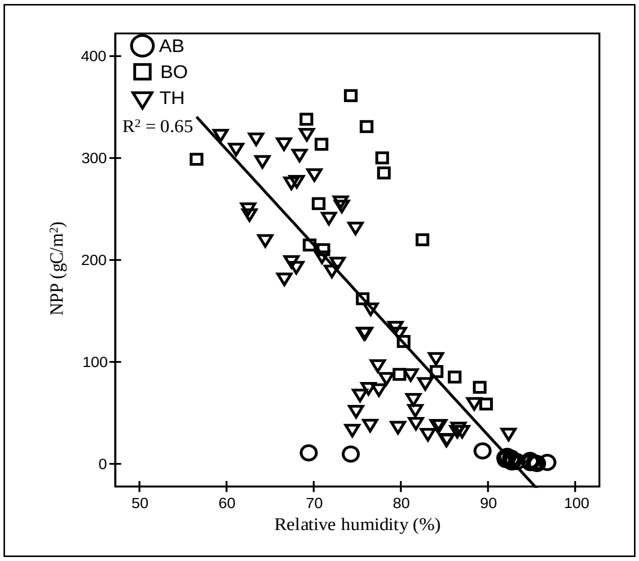

Fig 6: Relationship between monthly NPP and mean relative humidity. The entire monthly data set was used (88 months). $P < 0.001$.

Table 2 displays the result of multiple regression analyses performed between the dependent variable NPP and the four independent climatic variables; temperature, total precipitation, relative humidity and PAR anomaly. The resultant multiple regression equation is:

$$\mathrm{NPP}\ (t) = 5.145 \times \mathrm{TEM} + 0.214 \times \mathrm{PPT}_{tot} - 6.483 \times \mathrm{RH} + 0.069 \times \mathrm{PAR}_{an} + 577.242 \qquad (5)$$

Where NPP, the net primary production; t, time; TEM average temperature; PPT_{tot}, total precipitation; RH, average relative humidity and PAR_{an}, incident photsynthetically active radiation anomaly.

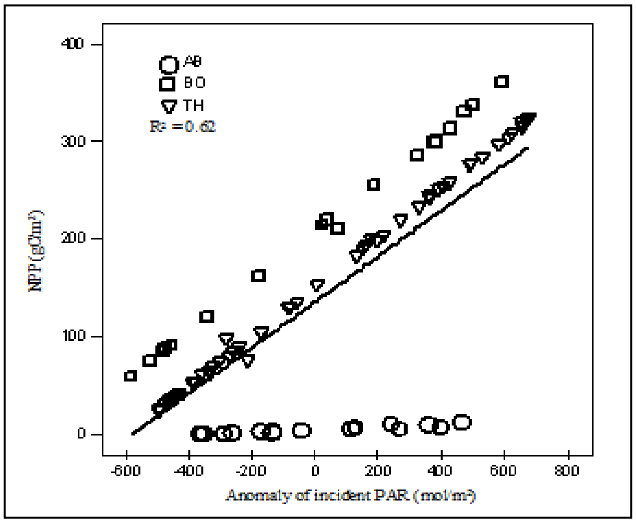

Fig 7: Relationship between monthly NPP and anomaly of incident PAR. The entire monthly data set was used (88 months). $P < 0.001$.

Table 2: Regression analysis result for the dependent variable NPP and the independent variables; TEM, average temperature; PPT_{tot}, total precipitation; RH, average relative humidity and PAR_{an}, incident photsynthetically active radiation anomaly. The data set size, n =78.

Coefficients					**Model summary**		
Predictors	**Regression coefficient**	**Std. Error**	**t**	***P***	**R^2**	**F**	***P***
TEM	5.145	1.804	2.85	<0.01	0.8	74.19	<0.0001
PPT_{tot}	0.214	0.141	1.52	0.13			
RH	-6.483	0.910	-7.126	<0.0001			
PAR_{an}	0.069	0.028	2.47	<0.05			
Constant	577.242	73.63	7.84	<0.0001			

4. Discussion

The seasonal variation of NPP and GPP (Fig. 2) in the three coniferous forests reflects the typical phenology of temperate and boreal forests with a peak activity in spring-summer because of limited growing season and seasonal variations in incoming radiation (Ruimy *et al*. 1994) [22]. The latter is clear from the increase of daytime during spring and summer compared to autumn and winter while the differences in mean annual temperature and incident photosynthetically active radiation among sites have explained the variation in their diurnal, seasonal and annual production. The cumulative impacts of air temperature over plant photosynthesis and respiration is indicated by the larger difference between NPP and GPP in summer where the increase in gross CO_2 assimilation with increase in temperature is increasingly offset by photorespiration (Long 1985) [32].

The direct linear relationship between NPP and temperature indicates the enhancement of vegetation productivity in response to increase of temperature. In many northern and temperate ecosystems increase of temperature during summer may increase NPP metabolically by enhancing photosynthesis or increasing nutrient availability (particularly inorganic nitrogen) through higher rates of decomposition (Ruimy *et al*. 1994) [22]. Law *et al*. (2002) [4] have found a similar relationship between annual temperature and gross primary production across several vegetation types of Euroflux and Ameriflux sites. Global scale studies (Braswell *et al*. 1997, Mohamed *et al*. 2004) [33, 14] have also outlined this characteristic immediate positive response of north latitudes temperate vegetation to the increase of annual mean temperature.

Effects of temperature on photosynthesis may be separated into two categories: instantaneous effects and temperature effects from previous gross periods (Long & Hutchin 1991) [21]. In conifers where the long–lived leaves must literally survive years of fluctuating temperatures acclimation of the photosynthetic apparatus is essential. Elevated temperatures may greatly reduce the period during which natural acclimation results in depression of photosynthetic capacity particularly during the winter and spring. Furthermore, increased winter and spring temperatures will reduce the incidence of low-temperature-dependent photoinhibition in conifer forests and hence increase the ability of leaves to respond to light during late winter and early spring periods (Long & Hutchin 1991) [21].

Although actual evepotranspiration is considered as a strong predictor of patterns of NPP across large regions (Rosenzweig 1968, Webb *et al*. 1983) [34, 35], annual precipitation is also strongly related to NPP with accurate records readily available for all biomes. Water stress is the most common limitation to gross of vegetation (Kozlowski *et al*. 1991) [36]. It is well known that stomatal conductance declines under water stress resulting in reduction of both photosynthetic activity and respiration. The result presented here might therefore; indicate that vegetation productivity in temperate coniferous forests is limited by other environmental factors (e.g. temperature, inorganic nutrients) rather than water stress. Agreeing with this result, a study by Mohamed and others (2004) [14] found no link between annual variation of NPP and precipitation but has found significant relationships between the variation in temperature and cloud cover and NPP in the mid northern latitude vegetation.

A study on annual water balance across several Euroflux and Ameriflux sites (Law *et al*. 2002) [4] showed that more precipitation is entering most of the sites than the amount of water lost through evaporation and transpiration i.e. plenty of water is available in soil. Laboratory studies and theories (Doran *et al*. 1990, Skopp *et al*. 1990) [37, 38] reveal that high water content can impede diffusion of oxygen which impedes decomposition of organic matter and CO_2 production. Davidson *et al*. (1998) [39] suggested that the effect of the temperature–dependent function, Q_{10}, usually used to model soil respiration, may include within it and may mask a negative correlation between water content and soil respiration at high water contents hence reducing the availability of inorganic nutrients for plant growth. The low productivity during autumn at Aberfeldy and Bordeaux and during spring at Tharandt might hence be related to the precipitation events over these periods which reduce soil decomposition and availability of inorganic nitrogen in soil, which further confirms that NPP in northern and temperate ecosystems are highly limited by availability of nitrogen in soil (Melillo *et al*. 1993) [9]. The above discussion is supported by Valentini *et al*. (2000) [13] who showed that respiration is the main determinant of the C balance in European forests.

Relative humidity describes the degree of water saturation of the air and is the ratio of the quantity of water vapour actually present to the saturation vapour pressure, the greatest amount possible at the given temperature. It is inversely proportional to the water vapour deficit, temperature and eveapotranspiration (important determinant of NPP). Therefore, The inverse relationship between NPP and relative humidity observed here is in harmony with the result of Law *et al*. (2002)[4] which shows significant positive correlation ($R^2 = 0.58$) between GEP and eveapotranspiration in evergreen coniferous forests. Moreover, the modeled and measured results of Arain *et al*. (2002) [40] showed a linear relationship between monthly GEP and evaporation in boreal deciduous and conifer forest. The increase in relative humidity is expected to decrease the temperature which will have direct negative impact on vegetation productivity as well as respiration. It might also increase light scattering and consequently reduces the incoming of photosynthetic active radiation further reducing NPP and GPP.

Changes in cloud cover are predicted, however, the directions and patterns of change and their exact implications for surface solar radiation are unclear. Given, however, the linear dependence of leave photosynthesis on incident light, at low light, any change in total solar radiation will be of significance particularly in closed canopies where light is limiting to photosynthesis in a high proportion of leaves. Law *et al*. (2002) [4] found that daily net carbon uptake was greater under diffuse sky conditions in both Aspen and coniferous boreal forests. They provided two explanations; first, the cloud cover results in a greater proportion of diffuse radiation and constitutes a higher fraction of light penetrating to lower depths of the canopy, and second, ecosystem respiration decreases with air and soil temperatures, when water is not limiting, and leads to more net carbon uptake for a constant level of growth photosynthesis. Our results show, however, that monthly vegetation production (NPP) is negatively impacted by the reduction of incident photosynthetic active radiation as the sky condition changes from clear to cloudy. NPP might further be reduced by the decrease of air temperature and vapour pressure deficit. The difference between the two results might also rise from the difference in time scale of the data used. Berbigier *et al*. (2001) [41], found that at daily scale, diffuse APAR (absorbed fraction of PAR) is only weakly linked to total APAR while the relationship is much tighter at the monthly scale meaning that at the daily scale there is a clear difference between sunny and cloudy days but when averaged over a month this difference is smoothed so that the diffuse APAR depends more on the seasonal trend than on differences in cloud cover.

In close conifer canopies the maximum quantum efficiency, Ø, of photosynthesis will be the measure determinant of canopy photosynthesis. However, Ø is very sensitive to CO_2, temperature, light quality, soil moisture and vapour pressure deficit (Long & Hutchin 1991) [21]. Generally, the empirical observation that CO_2 uptake by close canopies response linearly to increase light flux, sometimes to the level sunlight, provide clear evidence that light at most levels in the canopy must be limiting. This might explain the very small absorption efficiency at Aberfeldy (LAI =8 and stem density is 2500 stem/ha) and the low productivity values observed.

Finally, in the multiple regression result the large F value indicates that the regression equation is useful in estimating NPP. In particular, the absolute values of t are greater than t-critical (1.99) for three independent variables; temperature, relative humidity and incident photsynthetically active radiation while total precipitation seems to be insignificant predictor of NPP in evergreen coniferous forests.

5. Conclusion

A one-four years data collected between 1997 and 2000 from three EUROFLUX sites (Aberfeldy, Tharandt and Bordeaux) was modeled using an efficiency-based approach thought to be suitable for C3 species (including coniferous vegetation). The Objective was to estimate net primary production, gross primary production and to study the environmental factors (temperature, precipitation, relative humidity and incident photosynthetic active radiation, PAR) controlling the temporal variability of coniferous ecosystems. The typical phenology of temperate and boreal forests was clearly obvious from the seasonal variation of NPP and GPP in the three coniferous forests. A direct linear relationship between NPP and temperature was observed indicating the enhancement of vegetation productivity in response to increase of temperature. Obviously, vegetation productivity in temperate coniferous forests is limited by environmental factors such as temperature and inorganic nutrients rather than water stress. The main reason is that, plenty of water is available in soil which may affect soil respiration hence reducing the availability of inorganic nutrients (such as nitrogen) for plant growth. Also, the multiple regression indicated significant dependence of NPP on three independent variables; temperature, relative humidity and incident photsynthetically active radiation while total precipitation seems to be insignificant predictor of NPP in evergreen coniferous forests. At last, forests at north and mid-latitudes may play an important role in the global carbon cycle as suggested by earlier studies where particular climatic variables such as temperature variability will significantly govern the variability of their net primary productivity

Generally, despite the need for more revisions to photosynthetic parameters and their temperature dependency in global flux modeling, estimations based on FLUXNET data were considered valuable for terrestrial biosphere modeling (Bonan *et al*. 2011) [42].

6. Acknowledgment

We acknowledge the efforts of all of the individual technicians, scientists and web managers of the FLUXNET who helped in compiling data and making it available online to support different researchers. The authors are very grateful to the PIs of Aberfeldy, Bordeaux and Tharandt; (Prof. Paul Jarvis &John Moncrieff & Robert Clement), (Prof. Berbigier & Denis Lousteau) and Prof. Christian Bernhofer, respectively, for their precious efforts to maintain these data. Thanks also extended to the anonymous reviewers for their valuable comments to increase the quality of the manuscript.

7. References

1. Houghton RA, Davidson EA, Woodwell GM. Missing sinks, feedbacks, and understanding the roll of terrestrial ecosystems in the global carbon balance. Global Biogeochem. Cycles. 1998; 12:25-34.
2. Keeling RF, Piper SC, Heimann M. Global and hemispheric CO2 sinks deduced from changes in atmospheric CO2 concentration. Nature. 1996; 381:218-221.
3. Rayner PJ, Enting IG, Francey RJ, Langenfelds R. Reconstructing the recent carbon cycle from atmospheric CO2, δ13C and O2/N2 observations. Tellus, 1999; 51B:213-232.
4. Law BE, Falge E, Gu L, Baldocchi DD, Bakwin P, Berbigier P *et al*. Environmental control over carbon dioxide and water vapor exchange of terrestrial vegetation. Agric. For. Meteorol. 2002; 113:97-120.
5. Schimel D, Melillo J, Tian H, McGuire AD, Kicklighter D, Kittel T *et al*. Contribution of increasing CO2 and climate to carbon storage by ecosystems in the United States. Science. 2000; 287:2004-2006.
6. Schimel DS, House JI, Hibbard KA, Bousquet P, Ciais P, Peylin P *et al*. & others. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature. 2001; 414:169-172.
7. Williams M, Rastetter EB, Fernandes DN, Goulden MI, Shaver GR, Johnson LC. Predicting gross primary productivity in terrestrial ecosystems. Ecol. Appl. 1997; 7:882-894.
8. Idso KE, Idso SB. Plant responses to atmospheric CO2 enrichment in the face of environmental constraints: A review of the last 10 years' research. Agri. Fors. Meteorol. 1994; 69:153-203.
9. Melillo JM, McGuire AD, Kicklighter DW, Moore III B, Vorosmarty CJ Schloss AL. Global climate change and terrestrial net primary production. Nature.1993; 363:234-240.
10. Peterson BJ, Melillo JM. The potential storage of carbon caused by eutrophication of the bioshere. Tellus. 1985; 37B:117-127.
11. McGuir e AD, Joyce LA, Kicklighter DW, Melillo JM, Esse r G, Vorosmarty CJ. Productivity responses of climax temperate forests to elevated temperature and carbon dioxide: a North American comparison between two global models. Clim. Change. 1993; 24:287-310.
12. Fan S, Gloor M, Mahlman J, Pacala S, Sarmiento J, Takahashi T *et al*. A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. Science. 1998; 282:442-446.
13. Valentini R, Matteucci G, Dolman AJ, Schulze ED, Rebmann C, Moors EJ *et al*. Respiration as the main determinant of carbon balance in European forests. Nature. 2000; 404:861-865.
14. Mohamed AAM, Babiker IS, Chen ZM, Ikeda K, Ohta K, Kato K. The role of climate variability in the inter-annual variation of terrestrial net primary production (NPP). The sci. Tot. Environ. 2004; 332(1-3):123-137.
15. Barr AG, Griffis TJ, Black TA, Lee X, Staebler RM, Fuentes JD *et al* Comparing the carbon budgets of boreal and temperate deciduous forest stands. Can. J For. Res. 2002; 32:813-822.
16. Baldocchi DD, Falge E, Gu L, Olson RJ, Hollinger D, Running S *et al*. A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. Bull. Am. Meteorol. Soc. 2001; 82:2415-2434.
17. Falge E, Baldocchi DD, Olson RJ, Anthoni P, Aubinet M, Bernhofer C *et al*. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agric. For. Meteorol. 2001; 107:43-69.
18. Monteith JL. Solar radiation and productivity in tropical ecosystems. J of Applied Ecology. 1972; 9:744-766.
19. Monteith JL. Climate and the efficiency of crop production in Britain. Physiological Transactions of the Royal Society of London. 1977; B281:277-294.
20. Kumar M, Monteith JL. Remote sensing of crop growth. In Smith, H. (ed). Plants and the daylight spectrum. Academic Press. London, New York, Toronto, Sydney, San Francisco, 1981, 133-144.
21. Long SP, Hutchin RP. Primary production in grasslands and coniferous forests with climate change: an overview. 1991; 1(2):139-156.
22. Ruimy A, Saugier B, Dedieu G. Methodology for the estimation of terrestrial net primary production from remotely sensed data. J Geophys. Res. 1994; 99(D3):5263-5283.
23. Maisongrande P, Ruimy A, Dedieu G, Saugier B.

Monitoring seasonal and interannual variations of gross primary productivity using a diagnostic model and remote-sensed data. Tellus. 1995; 47B:178-190.

24. Knorr W, Heimann M. Uncertainities in global bioshere modeling, Part II: Global constraints for a process-based vegetation model. Glob. Biogeoch. Cyc. 2001; 15(1):227-246.
25. Running SW, Nemani RR, Heinch FA, Zhao M, Reeves M, Hashimoto H. A continuous satellite-derived measure of global terrestrial primary production. Bioscience. 2004; 54(6):547-560.
26. Russel G, Jarvis PG, Monteith JL. Absorption of radiation by canopies and stand growth. In Russel, G., Marshal, B. & Jarvis, P.G (eds). Plant canopies: their growth, form and function. Cambridge University Press. Cambidge, England, 1989, 21-30.
27. Gamon JA, Field CB, Goulden ML, Griffen KL, Hartlcy AE, Jocl G, *et al*. Relationship between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. Ecolog. Appl. 1995; 5(1):28-41.
28. Heimann M, Keeling CD. A three-dimensional model of atmospheric CO2 transport based on observed winds, 2, Model description and simulated tracer experiments, in Aspects of climate variability in the Pacific and the Western Americas, edited by D.H. Peterson. Geophys. Monogr. 1989; 55:237-274.
29. Jarvis PG, Leverenz JW. Productivity of temperate, deciduous and evergreen forests. In Lange, O.L., Nobel, P.S., Osmond, C.P. & Ziegler, H. (eds). Encyclopedia of plant physiology, New series, Springer-Verlag. New York. 1983; 12d:233-280.
30. Goward SN, Dye DG. Evaluating North-American net primary productivity with satellite observations. Adv. Space Res. 1987; 7:165-174.
31. Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA. Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: results from two North American deciduous forests. J Geophys. Res. 1999; 104:31421-31434.
32. Long SP. Leaf gas exchange. In Barber, J & Baker, N.R. (eds). Photsynthetic mechanisms and the environment. Elsevier, Amsterdam, the Netherlands, 1985, 453-500.
33. Braswell BH, Schimel DS, Linder E, Moore IIIB. The response of global terrestrial ecosystems to interannual temperature variability. Science. 1997; 278:870-872.
34. Rosenzweig ML. Net primary productivity of terrestrial communities: prediction from climatological data. Am. Nat. 1968; 102(923):67-74.
35. Webb WL, Lauenroth WK, Szarek SR, Kinerson RS. Primary Production and Abiotic Controls in Forests, Grasslands, and Desert Ecosystems in the United States Ecology. 1983; 64:134-151.
36. Kozlowski TT, Kramer PJ, Pallardy SG. The physiological ecology of woody plants. Academic press, San Diego, USA. 1991, 390.
37. Doran JW, Mielke LN, Power JF. Microbial activity as regulated by soil water-filled pore space. In: transaction of the 14th. International congress of soil science. Symposium III-3; Ecology of soil microorganism in the microhabital environments. 1990, 94-99.
38. Skopp J, Jawson MD, Doran DW. Steady-state aerobic microbial activity as a function of soil water content. Soil Science Society of Am. J. 1990; 54:1619-1625.
39. Davidson EA, Belk E, Boone R. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob. Change biol. 1998; 4:217-227.
40. Arain MA, Black TA, Barr AG, Jarvis PG, Massheder JM, Verseghy DL, *et al* Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. Can. J For. Res. 2002; 32:878-891.
41. Berbigier P, Bonnefond JM, Mellmann P. CO2 and water vapour fluxes for 2 years above Euroflux forest site. Agri. Fors. Meteorol. 2001; 108:183-197.
42. Bonan GB, Lawrence PJ, Oleson KW, Levis S, Jung M, Reichstein M *et al*. Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data, J Geophys. Res. 2011; 116, G02014, doi:10.1029/2010JG001593.