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## Trends and variations in the activity of global vegetation in response to climate variability between 1987 and 1997

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### Abstract

Eleven-year (1987-1997) time series data of remotely sensed vegetation index (NDVI) and meteorological observations (temperature, precipitation, cloud cover and relative humidity) provided a powerful tool to illuminate the response of global terrestrial vegetation to short-and long-term climate variability. NDVI being a sensitive estimator of the amount of photosynthetic active radiation intercepted by the canopy has been treated as a proxy for above ground net primary production (ANPP). Analyses of trends, multiple regression and correlation analyses were employed. The main result indicates a considerable increase (0.7~1.9%/year) of monthly vegetation production in all ecosystems over the investigated period, allied with an analogous increase (0.9~15%/year) in precipitation. Additionally, several direct relationships were also observed on the intra- and inter-annual time scales suggesting that the increase and variation of ANPP in most biomes could be mainly linked to the corresponding increase and variation in precipitation. Overall, the four climate variables play a considerable role in the inter-annual variability of ANPP of global vegetation.

### المستخلص

بيانات زمنية متسلسلة لأحد عشر عاماً (1987-1997) عبارة عن مؤشر النباتات (NDVI) المستشعر عن بعد وبيانات الإحصاء الجوي (الحرارة، الهطول، السحب و الرطوبة النسبية) قدمت أداة فعالة لإلقاء الضوء على ردة فعل النباتات الأرضية على التغيرات المناخية على المدى القصير و الطويل. تم التعامل مع مؤشر النباتات و الذي يمثل مقياس حساس لكمية طاقة التمثيل الضوئي النشطة المعترضة بواسطة الغطاء النباتي ليمثل الإنتاج الأولي على سطح الأرض (ANPP). تمت معالجة البيانات المتسلسلة زمنياً باستخدام عدد من المعاملات الإحصائية مثل تحليل الميل، التراجع المتعدد و الارتباط. النتيجة الرئيسية أوضحت أن هناك تزايداً شهرياً مقدراً 0.7~1.9% في إنتاجية النباتات في كل الانظمة البيئية خلال فترة الدراسة منسجماً مع زيادة موازية في كمية الهطول (0.9~15%). بالإضافة للعديد من العلاقات الطردية على المقاييس بين و خلال السنوية مما يقترح أن الزيادة و التباين في الـ ANPP في أغلب البيئات النباتية مرتبط بزيادة أو تباين موازيين في معدلات الهطول. عموماً فإن المتغيرات المناخية الأربعة تلعب دوراً مقدراً في التغيرات بين السنوية في معدلات الإنتاج الأولي للنباتات في العالم.

**Keywords:** Terrestrial vegetation, NDVI, ANPP, climate variability, precipitation

### 1. Introduction

Terrestrial vegetation plays a key role in the global carbon storage and cycling by assimilating atmospheric CO<sub>2</sub> –and nutrients– in the photosynthetic process, converting carbon into plant tissue and accumulating it in the soil pool as litter fall. The anthropogenic emissions of CO<sub>2</sub> from fuel burning, cement production and land use change will be offset if terrestrial vegetation production increases. However, if terrestrial carbon is lost to the atmosphere the rate of accumulation of

CO<sub>2</sub> in the atmosphere will increase and the climate change problem will exaggerate. 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 [1]. This increase in carbon sequestration by terrestrial biosphere was attributed to nitrogen and CO<sub>2</sub> fertilization [2], forest regrowth [3; 4] and climate change in the northern mid and high-

latitudes and mainly to CO<sub>2</sub> fertilization in the tropics.

Terrestrial vegetation production is subject to changes at different time scales in response to variations in weather, radiation and nutrients in soil as well as to human influences. Regional and global patterns of net primary production (NPP) and their relation to mean climatic factors (mainly temperature and precipitation) have been described since the mid of last century [5; 6; 7]. However, recent endeavors [8; 9; 10] to identify significant relationships between inter-annual deviations in NPP and corresponding anomalies in their established mean climatic predictors, obtained conflicting results. Nevertheless, over the last two decades earth system -including terrestrial vegetation- experienced dramatic environmental changes such as the increase of global air temperature (1980s and 1990s), change in cloud and precipitation patterns and the more frequent and persistent El Niño events. Changes in the global hydrologic cycle are also a possible consequence of increasing concentrations of atmospheric greenhouse gases [11]. Accordingly, regional studies [12; 13; 14; 15; 16] have reported several increases in the productivity of terrestrial ecosystems. Nemani *et al.*, [17] reported an increase of global NPP between 1982 and 1999 resulting from climate changes which have eased critical climatic constraints to plant growth in several locations. They noted that global scale comprehensive analysis of the impacts of climate variability on vegetation production is still lacking. Here we attempt to investigate the climate-vegetation relationship of major terrestrial ecosystems over a one-decade period (1987~1997). Subsets of the Normalized Difference Vegetation Index, NDVI, of the Advanced Very High Resolution Radiometer, AVHRR, on board the National Oceanic and Atmospheric Administration's, NOAA satellites and historical meteorological data (temperature, precipitation, cloud cover and relative humidity) were used. The objectives are to (1) distinguish trends and variations in NDVI and climatic variables over the study period and to (2) investigate whether the variation in vegetation production could be linked to corresponding variations in climatic factors in the intra- and inter-annual time scales. Noting that plant growth is limited by a number of other factors such as the amount of solar radiation, nutrients in soil and permafrost, this contribution is primarily concerned with the constraints imposed by main climatic factors (e.g. temperature and precipitation).

## 2. Materials and methods

### 2.1. NDVI and climatic data

Recently, satellite-based vegetation indices became

recognized for their ability to report vegetation changes. They provide high spatial and temporal resolution coverage which allows monitoring dynamics of global and regional vegetation condition. NDVI is computed as the ratio between the difference between energy reflectance in the near-infrared waveband and the visible waveband and the sum of energy reflectance in both wavebands ( $NDVI = \frac{NIR - VIS}{NIR + VIS}$ ). This ratio provides a sensitive estimator of the amount of photosynthetic active radiation intercepted by the canopy and hence of the above ground net primary production (ANPP). Therefore the multi-temporal NDVI data are useful in studying temporal variation in phenology of natural vegetation due to inter-seasonal, inter-annual and episodic climatic variations.

Monthly NDVI measured by AVHRR on board NOAA 9, NOAA 11 and NOAA 14 polar-orbiting satellites and monthly mean temperature, precipitation, cloud cover and relative humidity derived from meteorological observations over land which were quality checked and compiled by the Office of Statistics in the Japan Meteorological Agency in collaboration with the World Meteorological Observation (WMO) were used. NDVI is preferred for monitoring global land vegetation because it partially compensates for changing illumination conditions, surface slope and viewing aspect. Here, a sub-set (1987-1997) of the C-level monthly NDVI data of the third generation version was used. This data has been obtained from NOAA/NESDIS's Office of Research and Application (ORA), Climate Research and Application Division (CRAD), Land Surface Team with a spatial resolution (pixel size) of 0.144° latitude by 0.144° longitude [18]. Three months data in 1994 (October, November and December) and one month in 1995 (January) were missing. The three corresponding months of 1993 were used for 1994 while the mean of February and March was taken to represent the missing January of 1995.

Pixels of NDVI data (0.144° X 0.144°) which spatially overlap with meteorological stations on land were extracted and the corresponding meteorological measurements (temperature, precipitation, cloud cover and relative humidity) were taken to represent mean values of each cell. Pixels with meteorological station(s) positioned at or near the center were preferential. Generally, within a single pixel, maximum of two stations were located from which mean values of climatic parameters were computed. A total of 736 pixels were found to include meteorological stations with complete data record of 11 years. Pixels of NDVI data with their meteorological variables were then

aggregated into global land cover classes based on vegetation maps of Matthews [19] and Olson [20]. They were further regrouped into 8 broad vegetation classes adapted from IPCC [21]. 64 pixels were located in tropical evergreen forests, 52 in tropical deciduous forests, 116 in temperate forests, 53 in boreal forests, 131 in woodland, 166 in savanna, 51 in temperate grassland and 103 in deserts and semi-deserts. No pixels including meteorological stations with full data record were found in tundra class while pixels located in deserts and semi-deserts were grouped into one class. Therefore, pixels in each class were taken to represent sample measurements of the specific vegetation biome.

## 2.2. Analysis of trends in time series data

Here, trends in NDVI and climatic variables over the study period (1987~1997) were investigated. First, five-month running mean was applied on all data in order to smooth out any intra-seasonal variations. Because time series data usually contain seasonality that is usually much stronger than any other signal we wish to study, NDVI and meteorological variables were deseasonalized using Ratio-to-Moving Average method. For each vegetation biome, monthly NDVI, temperature and precipitation were obtained by averaging within biome data pixels. Linear trends in NDVI, temperature, precipitation, cloud cover and relative humidity were calculated by fitting linear functions through the time series data in each biome group. Monthly differences and change percentages over the eleven-year period were then computed for the statistically significant ( $P \leq 0.05$ ) trends.

## 2.3. Multiple linear regressions of NDVI and climatic variables

Multiple linear regression was used to examine the role of the four climatic parameters (temperature, precipitation, cloud cover and relative humidity) over the variability of monthly NDVI. For all data sets statistically significant trends were removed in order to produce approximately stationary time series. The dependent variable in the regression was NDVI and the independent variables were temperature, precipitation, cloud cover and relative humidity. Serial autocorrelation potentially exists between the independent variables (temperature, precipitation, cloud cover and relative humidity) therefore a “backward” selection process was performed [22]. The resultant regression model retains the combination of  $b_i$  terms corresponding to significant ( $P < 0.05$ ) temperature, precipitation, cloud cover or relative humidity. The standardized coefficients  $\beta$  were obtained by the transformation  $\beta_i = b_i S_i / S_y$  (for  $i = 1, 2, 3, 4$ ) where  $S_i$  denotes the standard deviation of the  $i$ th independent variable

$X_i$  and  $S_y$  denotes the standard deviation of NDVI values  $Y$ . Thus we present coefficients  $\beta$  that are “commensurate measure of response” of NDVI to climate variables [22; 23]. The regression analysis was performed excluding monthly data between June 1991 and February 1995 (NDVI possibly affected by the eruption of Mt. Pinatubo or satellite problems [24]). Therefore, 87 months in total were used in the regression analysis. These analyses use NDVI and climatic variables averaged over the entire vegetation biome where spatial variability has been smoothed out. We assumed that within biome pixels which are also morphologically and physiologically similar manifest similar responses to climate variability despite their spatial distribution.

## 2.4. Correlation analyses between annual means and coefficients of variation

In the second experiment the climate-NDVI relationship was examined over an inter-annual time scale using 11-year means and coefficients of variation (CV%) of NDVI and four climatic variables calculated for every data pixel. Correlations between means and coefficients of variation of NDVI and those of temperature, precipitation, cloud cover and relative humidity were computed using pixels of each biome (i.e., pixels were treated as replicate observations of the specific vegetation biome). We have adopted the assumption of Fang *et al.* [9] stating that; if the correlation between coefficient of variations of NDVI and those of temperature, precipitation, cloud cover or relative humidity were found statistically significant, the inter-annual variation in NDVI (the ANPP predictor) could be attributed to the inter-annual variation in these climatic parameters. The same approach was previously used to indicate that precipitation is the main determinant not only of ANPP of wheat in the Pampas region of Argentina but also of its inter-annual variability [25].

## 3. Results and discussion

### 3.1. Trends in NDVI and climatic variables over one decade

The one-decade study period of 1987 to 1997 witnessed some important environmental events such as; the strong La Niña of 1988-1989, the prolonged El Niño of 1991-1995, the eruption of Mt. Pinatubo (1991) and the developing historical El Niño of 1997. Over this period, monthly NDVI has increased in all vegetation biomes (0.7~1.9%/year) with the largest change percentages found in deserts, boreal forests and savanna vegetation and the least found in tropical evergreen and temperate forests (Table 1).

Similarly, except in boreal forests, precipitation has significantly increased over the eleven-year period particularly in deserts where monthly precipitation over doubled. Relative humidity on the other hand,

has slightly decreased in all vegetation biomes. Cloud cover decreased in boreal forests, woodland and temperate grasslands but slightly increased in tropical evergreen forests and savanna. Therefore, it is more likely that increase of precipitation has contributed to the increase of ANPP in most biomes especially tropical and water-limited biomes (deserts, grasslands and woodlands). In arid ecosystems, changes in regional precipitation patterns associated with El Niño were found to increase plant cover several folds by massive germination of annuals and increase of seed bank in the soil. Notably, wet ENSO events might also cause long-lasting effects on arid and semi-arid environments by encouraging recruitment of trees and shrubs [26]. The considerable increase of monthly NDVI in boreal forests (18.8% over 11

years) may be attributed to growth stimulation from other mechanisms such as; lengthening of active growing season [12], nitrogen deposition and forest regrowth [17]. Increase of NDVI in the different biomes may not indicate similar increase in their net primary production relative to each other due to the intrinsic differences in their greenness (measured by NDVI) and production potential. Thus although deserts show large relative pulse in NDVI the absolute ANPP response is biotically constrained because of low plant density and leaf area [10]. Similarly, a relatively small increase of NDVI in the tropical region implies large increase of net primary production (high production potential) and consequently a sizable contribution to the overall increase of global NPP.

Table 1: Trends and change percents (over 11-year period) of NDVI and four climatic variables across eight vegetation biomes. Negative values indicate decreasing trends. Only significant trends are shown. Probability values less than 0.05 are indicated with a single asterisk and those less than 0.01 with double asterisk. TEG stands for tropical evergreen forests, TDC for tropical deciduous forests, TMF for temperate forests, BOR for Boreal forests, WOO for woodlands, SAV for Savannah, TMG for temperate grasslands and DES for deserts.

Biome	NDVI		Temperature		Precipitation		Cloud cover		Relative humidity	
	Trend /month	Change (%)	Trend /month	Change (%)	Trend /month	Change (%)	Trend /month	Change (%)	Trend /month	Change (%)
TEG	$2 \times 10^{-4*}$	7.8			0.171**	19.8	0.0016**	3.1	-0.015**	2.5
TDC	$3 \times 10^{-4**}$	15.1	0.002**	1.1	0.117**	29.0			-0.011**	2.0
TMF	$2 \times 10^{-4**}$	10.3			0.049**	9.14			-0.022**	3.9
BOR	$3 \times 10^{-4**}$	18.8					-0.0006*	1.2	-0.013**	2.3
WOO	$2 \times 10^{-4**}$	11.7			0.119**	27.2	-0.002**	4.3	-0.014**	2.7
SAV	$3 \times 10^{-4**}$	16.6	0.0014*	0.75	0.072**	20.0	0.0009**	2.45	-0.006*	1.2
TMG	$2 \times 10^{-4**}$	13.6	0.004*	6.63	0.086**	36.1	-0.0021*	6.1	-0.034**	7.1
DES	$2 \times 10^{-4**}$	21.1			0.122**	131.1			-0.012**	3.2

### 3.2. Climatic controls over the variability of monthly NDVI

Table 2 shows that monthly variations of NDVI are closely related to climate variability-particularly temperature and precipitation- in the various vegetation biomes. The four climatic variables were relatively good predictors of monthly ANPP in temperate forests and deserts, moderate predictors in temperate grassland, savanna and woodlands but were weak predictors in tropical

forests. In boreal forests there was no sufficient evidence to indicate that either of the four climatic factors has control over the monthly variations in vegetation growth. Several mechanisms may be responsible. Although vegetation in cold regions is limited by temperature [27] the response is complicated by effects from previous growth periods [28]. Precipitation, on the other hand plays little role in modulating the vegetation growth in regions where precipitation usually exceeds the

minimum threshold above which vegetation is unresponsive [27]. Nevertheless, northern and

temperate ecosystems are known to be highly limited by the availability of nitrogen in soil.

Table 2: Summary of results of multiple regression analyses between dependent variable NDVI and independent variables; temperature, precipitation, cloud cover and relative humidity. The indicated regression models are significant at  $p < 0.001$ . Biome codes are explained in the caption of Table 1.

Biome code	Regression coefficient ( $R^2$ )	Standardized coefficient and significance level of independent variables							
		Temperature		Precipitation		Cloud cover		Relative humidity	
		$\beta$	$p$	$\beta$	$p$	$\beta$	$p$	$\beta$	$p$
TEG	0.20					0.61	0.000	-0.43	0.002
TDC	0.22	-0.22	0.027	0.53	0.000			0.24	0.039
TMF	0.50			0.46	0.000	-0.35	0.000	0.46	0.000
BOR									
WOO	0.29	0.26	0.010	0.60	0.000				
SAV	0.30	-0.39	0.000			0.70	0.000	-0.33	0.043
TMG	0.32	0.24	0.023	0.67	0.000				
DES	0.41	-0.20	0.042	0.66	0.000	0.40	0.000		

The highly significant correlations between NDVI and precipitation coincide with the assumption introduced in the previous section that the increase of ANPP over the study period (1987~1997) is more likely attributed to the concurrent increase in precipitation. Monthly NDVI in arid ecosystems (deserts and savanna) are also controlled by temperature and cloud cover. This might indicate that plant growth in these biomes is regulated not only by direct increase of rainfall but also by the increase of water use efficiency through reduction of water loss by evapotranspiration (decrease of air temperature and increase of cloud cover). In tropical evergreen forests the increase of monthly NDVI is related to the increases in cloud cover which does not conflict with the fact that tropical vegetation is radiation-limited [17], instead may rather indicate a two-way feedback between vegetation and climate. Berbigier *et al.* [29], 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.

### 3.3. Patterns of inter-annual variation of NDVI and climate variables

While the previous section reveals several relationships between monthly deviations of ANPP and climatic variables across different biome groups, the following sections examine the pattern of inter-annual variations in NDVI - the predictor



of ANPP – and whether these variations can also be related to corresponding deviations in these factors. In Table 3, the mean annual NDVI is directly related to annual temperature in boreal forests, temperate forests and grasslands but is inversely related to annual temperature in savanna. The former three relationships indicate that annual vegetation growth in boreal and temperate ecosystems is limited by temperature [27]. In many northern and temperate ecosystems increase of temperature during summer may increase ANPP metabolically by enhancing photosynthesis or increasing nutrient availability (particularly

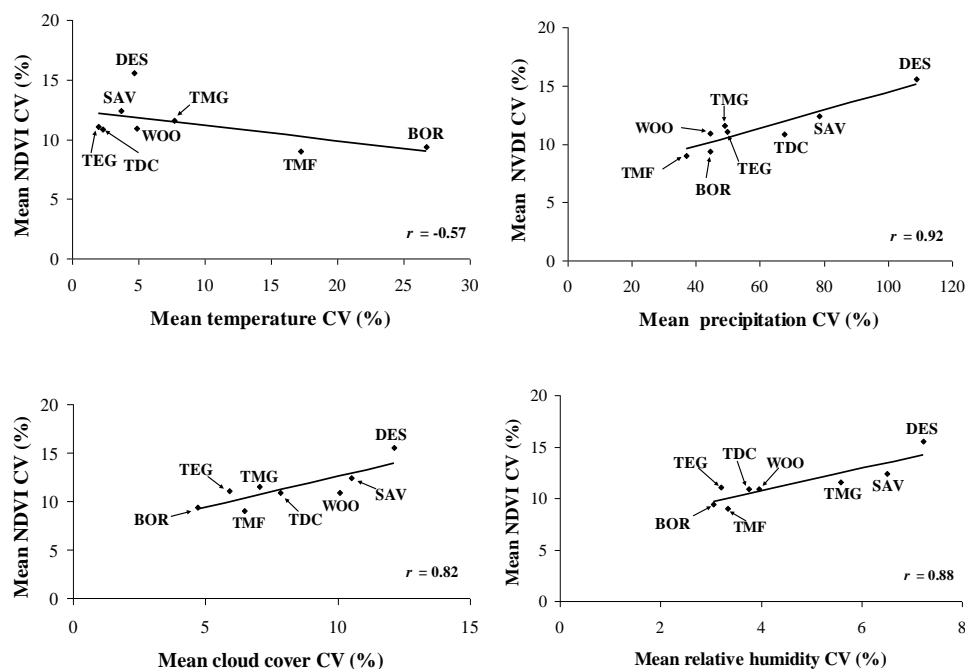
inorganic nitrogen) through higher rates of soil decomposition [12; 30]. The same results were also identified by Braswell *et al.* [22], Law *et al.* [31] and Mohamed *et al.* [32]. On the other hand, high annual temperatures imply lower vegetation growth in the water-limited savanna may be due to increase of water stress [22]. The positive correlations between mean annual NDVI and precipitation, cloud cover and relative humidity in most biomes indicate the control of water availability over plant growth which concurs with the acknowledged hypothesis that water stress is the most common limitation to vegetation [33; 34].

Table 3: Correlations between mean NDVI and mean climatic variables across eight biome groups. Only significant ( $P=0.05$ ) coefficients are shown. Numbers between brackets indicate number of observations. Biome codes are explained in the caption of Table 1.

Biome code	Climatic parameter			
	Temperature	Precipitation	Cloud cover	Relative humidity
TEG (64)	--	--	--	0.33
TDC (52)	--	0.44	--	0.37
TMF (116)	0.22	0.32	0.30	0.57
BOR (53)	0.51	0.50	0.49	0.63
WOO (131)	--	0.60	0.42	0.71
SAV (166)	-0.56	0.50	0.25	0.75
TMG (51)	0.52	0.83	0.41	0.61
DES (103)	--	0.72	0.54	0.57

Over an inter-annual time scale, NDVI was most variable in deserts (mean CV%=15.5), followed by savanna (12.4) and grasslands (11.6) and was least variable in forests (Fig. 1). These results agree with those of Knapp and Smith (10) and Fang *et al.* (9). Temperature was typically most variable in boreal forests (mean CV%=78.4) followed by temperate forests (17.3) while least variable in tropical forests

and savanna (mean CV%=3.7). Regions with high annual mean temperature usually show less variation in this factor. Precipitation was highly variable in all biomes with the largest variation occurred in desert biome (mean CV%=108.8), followed by savanna (78.4) and tropical deciduous forests (67.6) while temperate forests were the least (37).



**Fig.1:** Relationship between mean NDVI CV versus mean CV of temperature, precipitation, cloud cover and relative humidity of all eight biome groups. Biome codes are explained in the caption of Table 1.

### 3.4. Influences of climate variables over inter-annual variation of NDVI

Table 4 reveals the relationships between coefficient of variation of NDVI and that of four climate variables, for the different biome groups. Three significant weak relationships ( $p=0.05$ ) between CV of NDVI and CV of precipitation were observed; in tropical evergreen forests, in boreal forests and in temperate grasslands. In Table 3, annual mean NDVI was not related to precipitation in tropical evergreen forests which implies that although the annual mean precipitation does not limit the vegetation growth inter-annual variations in precipitation might be partially responsible for the inter-annual variation in ANPP. In a previous work [32], we have observed significant relationship between CV of NPP and that of precipitation in the entire tropical zone. Fang et al. [9] also observed highly significant correlations between inter-annual variations in NDVI and precipitation in six vegetation ecosystems across China including forest, grassland, desert, alpine vegetation and cropland. However, other attempts did not find significant relation between the inter-annual variability of NDVI and equivalent anomalies in annual precipitation over a wide range of vegetation types in North America [8] and in Africa ([8; 35]. Generally, the differences between results lie on the inherent tradeoffs between data

quality and spatial extent [36] since the localized nature of precipitation anomalies complicates their effect at global scale [22]. The inter-annual variation of NDVI in savanna was also correlated to inter-annual variation of relative humidity. A similar relationship was observed in the intra-annual time scale (Table 2).

Generally, Fig. 1 shows significant correlations between mean NDVI CV and mean precipitation CV ( $r=0.92$ ,  $p=0.001$ ), mean cloud cover CV ( $r=0.82$ ,  $p=0.001$ ) and mean relative humidity CV ( $r=0.88$ ,  $p=0.001$ ) for all eight biome groups while displays insignificant relation with mean temperature CV ( $r=-0.57$ ). The former result agrees well with the result of Fang et al. [9] who have identified a similar relationship across six different biome groups in China. Nevertheless, the statistically significant correlations between mean NDVI and mean temperature, precipitation, cloud cover or relative humidity indicate that although these climatic variables may not contribute to the inter-annual variation of ANPP in many ecosystems they remain as essential predictors of mean ANPP.

Atmospheric CO<sub>2</sub> inversion models [21] have shown that recently northern mid-latitude vegetations have been consistently large carbon



sinks while the tropics are either neutral or small sources. Differently, our result indicates a considerable increase (0.7~1.9%/year) of vegetation production in all ecosystems over the investigated eleven-year period (1987~1997) allied with an analogous increase (0.9~15%/year) in

precipitation (except in boreal forests). Monthly variations of NDVI on the other hand were closely related to climate variability-particularly temperature and precipitation- in the various vegetation ecosystems.

Table 4. Correlations between CV of NDVI and CV of four climatic variables across eight biome groups. Only significant ( $P= 0.05$ ) coefficients are shown. Numbers between brackets indicate number of observations. Biome codes are explained in the caption of Table 1.

Biome code	Climatic parameter			
	Temperature	Precipitation	Cloud cover	Relative humidity
TEG (64)	--	0.27	--	--
TDC (52)	--	--	--	--
TMF (116)	--	--	--	--
BOR (53)	--	0.3	0.49	--
WOO (131)	0.17	--	--	0.32
SAV (166)	0.17	--	0.17	0.63
TMG (51)	--	0.52	--	--
DES (103)	--	--	--	--

In this contribution, NDVI which represents a sensitive measure of photosynthetically active radiation intercepted by plant canopy was used as proxy of (ANPP). This approach has been criticized by Knapp and Smith [40]. They argued that although NDVI can be related to chlorophyll content, leaf area, and standing crop biomass in most biomes [41] and also NPP in some instances, NDVI-based relationships are typically calibrated with standing crop biomass data, not NPP. Because standing crop biomass and NPP are positively related across broad spatial scales, it is common in the remote sensing literature for these very different ecosystem attributes to be treated as synonymous. Unfortunately NDVI-NPP relationships are not robust under many conditions. In grazed grasslands for example where standing

crop is low but NPP is high NDVI can only accurately estimate standing crop [42]. Worldwide it is likely that a majority of the grasslands remotely sensed are grazed. In addition to that background soil reflection in arid regions further complicates NDVI-relationships in deserts [39]. Relationships observed in such biomes should therefore be treated with caution.

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