Metabolic and Phenological Response of Vegetation to Temperature Gradient: Evidence Derived from AVHRR Data

Ye Qi and Peng Gong

Center for Assessment and Monitoring of Forest and Environmental Resources
Department of Environmental Science, Policy and Management,
University of California, Berkeley, CA 94720-3310, USA

Abstract
We studied the metabolic and phenological response of vegetation to the change in temperature using the latitudinal gradient to represent the temperature gradient. By comparing the seasonal curves of normalized difference vegetation index (NDVI) of northern latitudinal zones, we found that the annual peak value of the zonal NDVI average (MNDVI) increases as the latitude decreases from 75-56°N, with the greatest peak value occurring at 56°N. In the same latitude range, the arriving time (TNDVI) of the peak as measured by the Julian days when the MNDVI is reached decreases with latitude. These results imply that temperature increase in the high latitudes of the northern Hemisphere may increase the MNDVI and decrease TNDVI for the vegetation above 56°N, and therefore lower the trough of the seasonal curve of the atmospheric CO2 and make the trough arrive earlier. Because of the matching of spatial distribution of warming from 1965 to 1995 with the vegetation zone where the vegetation is sensitive to temperature, we conclude that the warming may have caused the metabolic enhancement and phenological shift for the vegetation in the high latitude region and which in turn causes the increase of seasonal amplitude of CO2 and its phase shift.

摘 要
本文根据标准化植被指数探讨了植被功能的地带特征及其与温度梯度的关系。结果表明在北半球高纬度地区NDVI的年最大值以及该值出现的时间与温度之间存在着密切的相关关系。但其定量关系因纬度而异。在较高纬度地带，两个参数对温度的反应更为敏感。由于这种温度作用的不均匀性，气温的增加将可能导致高纬度植被在功能上的趋同化，即较高纬度地带的植被在功能上更加接近较低纬度带上的植被。其结果将可能使大气CO2季节振幅增大，同时季节谷值出现时间提前。这一推论与大气CO2观测数据相吻合。

I. INTRODUCTION
The analyses of the seasonal and interannual variations of the atmospheric CO2 concentration have revealed that the seasonal amplitude of CO2 has been increasing since at least the mid-1970’s (Hall et al. 1975, Bacastow et al. 1985, Enting, 1987, Hall, et al. 1993). This increase suggests that both the net primary productivity (NPP) and respiration of the terrestrial ecosystems of the earth have been enhanced. A recent study (Keeling et al. 1996), while confirming the previous findings, further reveals a significant phase shift in the seasonal CO2 curve. The faster CO2 drawdown and the earlier arrival of the trough of the curve suggest that the maximum growth rate has been enhanced and the springing of the global vegetation may have shifted earlier. The presumed metabolic enhancement and phenological shift seem to exhibit a latitudinal variation with greater change occurring at high latitudes and smaller toward the Equator. Keeling et al. (1996) determined that between 1960 and 1989 the seasonal amplitude of CO2 increased about 20% and the trough shifted earlier by about 6 days at Mauna Loa, but for Point Barrow, Alaska they are 40% and 7 days, respectively (Keeling et al. 1996).

Earlier studies attribute the amplitude increase to the so-called beta effect, i.e. the enhancement of plant photosynthesis due to increased CO2 concentration in the atmosphere (Keeling et al. 1973, Goudriaan and Ajtay, 1979, Bacastow et al. 1985, Enting, 1987). However, the magnitude of the amplitude increase cannot be explained fully by the
beta-effect hypothesis alone. According to Luo and Mooney (1995), the beta effect can only account for up to 6% of the amplitude occurred at Mauna Loa (Keeling et al. 1996). In search for complementary hypotheses, it has been noted that the coincidence of the trend of CO₂ amplitude and the trend of global temperature at multiple time scales (Keeling et al. 1989, 1996) has lead to the speculation that the increasing temperature may have been the driving force for the metabolic enhancement and the phenological shift (Keeling et al. 1996 Qi, 1996a and b). In this paper we attempt to provide the rationale and evidence for the temperature-effect hypothesis based primarily on data derived from the NOAA meteorological satellites. Our objective is to offer an explanation on the cause and mechanism of the observed amplitude increase and phase shift of the atmospheric CO₂ concentration. Our proposition can be stated in two statements: (1) both the seasonal amplitude increase and phase shift of the atmospheric CO₂ concentration are caused by the metabolic enhancement and phenological shift of the vegetation at high latitudes of the northern Hemisphere; (2) The metabolic enhancement and phenological shift are the consequence of the temperature increase in the high latitude region. This hypothesis can be summarized in a simple diagram as follows:

The notion that vegetation is controlled, or at least greatly influenced, by climate has long been developed. Plant geographers in the early nineteenth century systematically described the relationship between the climate and vegetation (Humbold and Bonpland, 1805; Humbold, 1807; Schouw, 1823). Schimper (1898) discussed the importance of the basic physiological processes for explaining the control of climate on the vegetation. Holdridge (1947) and Box (1981) demonstrated the correlation between major physiognomic, or life form groups and two climatic characteristics — temperature and water availability. Woodward (1987) showed that the climate-vegetation relationship can be accurately formulated in a simulation model. The studies so far have focused on the physiognomy, species composition and geographical range. This study focuses on the functional response of the vegetation to the gradient of temperature. We choose temperature not only because it has traditionally been treated as the most important climate factor (Lieth 1975, Lieth and Box 1977, Holdridge, 1947), but more importantly, we try to use this analysis to explore the effect of the global warming on vegetation.

II. METHOD AND DATA

Satellite Data

In this study we use the data derived from the Advanced Very High Resolution Radiometer (AVHRR) aboard the meteorological satellites launched by the National Oceanic and Atmospheric Administration (NOAA). AVHRR data have demonstrated great potential for studying vegetation at regional and global scales (Tucker, 1979, 1991; Goward et al. 1991; Townshend 1992) because of its capability for daily global coverage. They are used to study the phenology and net primary productivity. The normalized difference vegetation index (NDVI) data, a primary product of the NOAA/NASA Pathfinder project, is processed by the Distributed Active Archive Center (DAAC) at NASA's Goddard Space Flight Center (James et al. 1994). We use NDVI as an indicator of leaf area index (LAI). A number of studies have demonstrated good correlation between NDVI and net primary productivity (NPP). As a first approximation, we assume NDVI is representative of NPP. We use the average NDVI of a region to represent the rate of NPP of the region at a certain time. We use the phase of NDVI in a manner similar to that in Fung et al. (1987)

Space-for-time substitute approach

The effect of global warming on vegetation is the consequences of the dynamic interactions between the climate and vegetation. As a result, vegetation changes over time as well as along the temperature
gradient. A logical approach to the study of vegetation response to global warming is to analyze the temporal pattern of vegetation changes as captured by NDVI. However, such a direct analysis is greatly hindered by two problems in the NDVI data. Firstly, the data record dates only back to 1981, covering a time span slightly longer than a decade. The time series is rather short for any rigorous statistical analysis of the trend and interannual variations. Secondly, the NDVI data is severely influenced by sensor replacement, degradation, and change of zenith and scan angle, all of which are important noise factors that may well obscure the signal to be sought, despite great effort has been made for sensor calibration and atmospheric correction (Vermote et al. 1990, Tanre et al. 1992, Rao 1993). To avoid these problems in temporal analysis, we adopt a space-for-time approach and conduct analysis of vegetation change with the latitude. This approach is viable because latitude from the Poles to Equator represents a temperature gradient from low to high. Figure 1a shows an approximately linear correlation between the temperature and latitude in the northern hemisphere between 20-80°N with either the annual average, January, or July temperature. Because of this strong correlation, we expect that the analysis result of vegetation changes with latitudes provides reliable information on vegetation response to temperature. Historically the space-for-time approach is commonly used in ecological research (Pickett, 1989). It has also been used in validation of large scale terrestrial ecosystem models (Rastetter, 1996). In this study, temperature is the common variable that connects the space (temperature increase with the latitude from the Poles to the Equator, Figure 1a) and time (temperature increase over time, Figure 1b).

Data processing

Original AVHRR images were captured twice a day at approximately 1.1km x 1.1km spatial resolution. The data were resampled to produce the Global Area Coverage (GAC) data which were further processed to generate the so-called “10-day” composites with 1° x 1° spatial resolution and 3 times per month (i.e. every 8 - 11 days for each grid). We used the data of all 12 complete years from 1982 through 1993. To minimize the deviation of individual years, all calculation in this study are based on the 12-year average. Our first step was to generate the seasonal pattern of NDVI for each latitudinal zone. Initial inspection suggested that low NDVI values might have great impact on the latitudinal average of NDVI because of their high occurrence. We did not include NDVI values lower than 0.1 in the calculation of the average NDVI's. Although the choice of the threshold of 0.1 is somewhat arbitrary, the sensitivity analysis has shown that this choice does not affect our conclusion.

Climatic data have shown that the global warming has more impact on the high latitudes of the northern Hemisphere. In the thirty years from 1965 through 1995, the warming is most significant on northern Eurasian and Northwestern American continents (Figure 2). Therefore, we focus our analysis on latitudes above 45°N.

Figure 1. Temperature gradients in space and time. (a), correlation between temperature and latitudinal gradient. Evident is a general trend that air temperature (mean annual, January and July) decreases with latitude. (b), warming trend since 1950. Data show that global mean annual air temperature anomaly changes over time (GISS, 1997).
Figure 2. Spatial distribution of global warming from 1965-1995. A general pattern is shown that the warming of the time period occurs mainly in the high latitudes of the northern Hemisphere. (Adapted from data in GISS, 1997)

III. RESULT AND ANALYSIS

The seasonal pattern of NDVI by latitude

The 1° x 1° NDVI data were aggregated into 5-degree latitudinal zones. The average NDVI of each latitudinal zone for each 8-10 day period was calculated. For each 5-degree latitudinal zone, we obtained a curve of seasonal change of NDVI. Figure 3 shows all curves for 7 latitudinal zones from 45°N to 80°N. These curves share a similar pattern: each starts with a low NDVI value at the beginning of the year, goes up over time, and reaches the maximum in summer and then returns to a low value at the end of the year. This temporal pattern reflects the growth pattern of vegetation in the high latitudinal zones, i.e. a growth period during the warm season alternating with a dormancy period during the cold season. We are interested in two parameters for each curve, the maximum NDVI in the year, M_{NDVI}, and the time when the maximum NDVI is reached, T_{NDVI}. For example, for the 55°-60° N zone, M_{NDVI} is 0.46, and T_{NDVI} is 205. Comparing the M_{NDVI}s across these latitudinal zones, we see that the M_{NDVI} for 75°-80° N is the smallest in the graph, this parameter goes up as the latitude move down. However, when M_{NDVI} reaches the maximum at 55°-60° N, it goes down as it continues to move to lower latitudes as seen in 50°-55° N and 45°-50° N. The second observation of the curves has revealed that T_{NDVI} has a similar trend but in the opposite direction. T_{NDVI} decreases with the latitude, reaches minimum at the 55°-60° N latitudinal zone, and then increases.

Variation of the maximum NDVI along the latitude

M_{NDVI} is calculated for each degree of latitude of the northern Hemisphere and plotted in Figure 4. The greatest M_{NDVI} occurs at 56° N. The M_{NDVI}s at lower latitudes, while exhibiting fluctuation, do not change as sharply as their higher latitude counterparts. From 75° N to 56° N, the average rate of change is 0.0106 per degree of latitude, while from 40° N to 56° N, this parameter is only about half of that value. Compare to Figure 3, the seasonal amplitude of NDVI at around 56° N (55-60° N in Figure 3) is the greatest. From 75° N to 56° N, the seasonal amplitude of NDVI shows a monotone increases. Since M_{NDVI} is an indicator of photosynthetic activity of the vegetation, Figure 4 shows that the greatest rate of photosynthesis of vegetation occurs at 56° N.
Figure 3. Seasonal patterns of NDVI averages of northern latitudes. Each curve represents a 5-degree latitudinal zone. Shown in the graph are latitudes from 45 to 80°N.

Variation of the arriving time of the maximum NDVI along the latitude

$T_{\text{NDVI}}$ the time when NDVI reaches $M_{\text{NDVI}}$ is also calculated for each degree of latitude and plotted in Figure 5. A monotonic decreasing trend is clearly seen from 75 to 56°N. Then the trend stops to decline and begins to increase or level off. This curve shows that at 57°N the $M_{\text{NDVI}}$ comes the earliest at the northern half of the northern Hemisphere.

Figure 4. Latitudinal variation of the annual peak of zonal NDVI average. Between 56°N and 78°N the $M_{\text{NDVI}}$ monotonically decreases with latitude.

Implications

The linear correlation between the latitude and the temperature gradient shown in Figure 1a has the following implications for the vegetation change with temperature gradient.

1. $M_{\text{NDVI}}$ along temperature gradient: The annual peak value of NDVI may increase with temperature in the range corresponding to that in latitude above 56°C.

2. $T_{\text{NDVI}}$ along temperature gradient: The time it takes to reach the annual peak value of NDVI may decrease with temperature in the range corresponding to that in latitude above 56°C.

3. The effect of warming on vegetation: If the two implications above are true, the warming primarily occurring in the land areas of this latitudinal zone would have two effects: first, it increases the seasonal amplitude of the photosynthetic rate of the vegetation in the region; second, it makes the peak of the photosynthetic rate arrives earlier than what it did before.

4. The effect of warming on the atmospheric CO$_2$: The enhancement of plant photosynthesis lowers atmospheric CO$_2$ concentration. The increased peak value of photosynthesis corresponds to the decreased trough of the seasonal CO$_2$ concentration. An early peak of photosynthesis results in an early drawdown of the CO$_2$ concentration. Qualitatively speaking, both the increase of seasonal amplitude of CO$_2$ concentration and the earlier drawdown are caused in part by the warming in the high latitudinal zone, mainly on the land area above 56°C.
Quantitative analysis

A quantitative analysis is needed in order to assess the magnitude of the effect of warming on vegetation growth and on the seasonal pattern of CO₂ concentration. We attempt to quantify the change in the seasonal amplitude of NDVI and CO₂ concentration as the latitude and temperature change by 1 degree. However, we must bear in mind that the result of such a quantitative analysis can be influenced by the choice of NDVI threshold value. With the threshold of 0.1, we have calculated using Figure 4 that from 75°N to 56°N the rate of change of M_{NDVI} is 0.0106 per degree of latitude. In the same range of latitude, the change of temperature is 0.9575 °C per degree of latitude. Therefore, equivalent temperature effect on M_{NDVI} is 0.0106/0.9575 = 0.01107 °C. The relative rate of change is about 3.04% per degree of latitude or 3.18% per °C of temperature, with a range of 1-7%. T_{NDVI} decreases 1.63 days per °C of temperature. Compare to the change of CO₂ amplitude in the period 1973-90, the amplitude at Mauna Loa increased by 19 ± 4% with respect to land temperatures north of 30°N, and Point Barrow by 26 ± 6% per °C with respect to temperature north of 50°N. Note that half of each value (i.e. 9.5% at Mauna Loa and 13% at Point barrow) is attributed to the change in NPP and the other half to respiration. Using Mauna Loa as the signal of the global average, we may conclude that the temperature increase at 56-75°N alone would explain one third of amplitude increase, and about one half of the phase shift, suppose that the NDVI is proportional to NPP.

IV. DISCUSSION

Apart from the result of quantitative analysis, it is evident that the 50-60°N latitudinal zone is ecologically special since both the greatest M_{NDVI} and the lowest T_{NDVI} occur in this zone. While there appear to be no simple explanation for this phenomena, it is of interest to note that this latitudinal zone coincides with the distribution of boreal forest. As shown in Figure 6, the 55-60°N zone is dominated by boreal forest, with over 60% of land area taken by closed-crown boreal forest and 7.4% by Taiga. As latitude moves further north, closed-crown boreal forest is replaced by tundra. Taiga serves as a transitional type of vegetation. It has been noted that boreal forests tend to have a higher leaf area index than broad leafed forests, because the needles of conifers may stay on trees for two years or more (Walter, 1985). On the contrary, tundra, consisting of grasses and shrubs, not only are sparsely distributed vegetation, but also the leaf area of each plant is much smaller than trees. This may explain the change in M_{NDVI} with the latitudinal gradient.

The reason for the shift in T_{NDVI} is less obvious. We note that the M_{NDVI} for 55-60°N occurs at early July (i.e. 181-190th Julian day. See Figure 5), when the temperature approaches its annual maxima. In fact, in most latitudinal zones, T_{NDVI} falls in 181-200 when high temperature occurs. As the latitude moves north the M_{NDVI} comes later and later. This may be caused by the cold temperature in the high latitude. Plant growth starts late and it takes certain time for plants to reach their maximum leaf area.

The transition of boreal forest-taiga-tundra occurs where the tree line is drawn. This type of ecotone is sensitive to the change in temperature because it is temperature that often constitutes the limiting factor for growth. Moisture is generally sufficient due to high precipitation and/or low evaporation. The climate of the boreal zone is humid, i.e. precipitation exceeds potential evapotranspiration (Havranek and Tranquillini, 1995). Numerous evidence has been made available on the shift of the tree line and the composition of vegetation in response to climatic change. According to Sirois (1992), during the warming period between 12000BP and 8100BP, a general northward movement of tree line and afforestation in the present taiga and tundra is evidenced by Holocene pollen and macrofossil records. Subsequent global cooling after 8000 BP

![Figure 6. Latitudinal distribution of vegetation of upper northern latitudes. A clear transition pattern is seen from closed-crown boreal forest to taiga and then to tundra.](image-url)
resulted in a marked southward shift of the forest and transformation of northern taiga into forest-tundra in the western part of Russia. Another phase of forest progression occurred during the second half of the Atlantic period (6000-4600 BP). Spruce stumps from this epoch suggest that the tundra zone disappeared almost completely in the northwestern Russia. Larch stump macrofossils substantiate forest encroachment 300, 100 and some tens of kilometers north of the present forest limit in the Yamal and Taimyr peninsulas and in the eastern maritime region, respectively. Pollen and macrofossil evidence suggests a northern forest recession between 4600 and 4100 BP, a new advance between 4100 and 3200 BP and a degradation between 3200 and 2500 BP (Khotinsky 1984). Northern forest vegetation of Russia has responded positively to the global warming trend in the twentieth century. Northward migratorial trends have been observed in tree species, and forests are now found on patterned ground generated under a former tundra environment (Tikhomirov 1961, 1963). In places, the movement of forest onto previously treeless areas is reported to be as rapid as 700 m per year (Uspenskii 1963 in Bray 1971).

Because of the great temperature response of vegetation from boreal forest to tundra, we may speculate that when the temperature increases in these zones, a broad northward expansion of vegetation would occur. The metabolism and phenology of vegetation in higher latitudes would change so as to be similar to those at lower latitude. If this is true as we believe, we would expect to observe greater $M_{\text{NDVI}}$ and smaller $T_{\text{NDVI}}$ at latitude above 56°N during the warming period. Although it is yet to determine the relative rates of metabolic enhancement and phenological shift of different vegetation in response to temperature increase, we may speculate that the vegetation in zones at higher latitudes has greater response.

Now let us revisit the spatial pattern of warming from 1965 to 1995 (Figure 2), we see that the warming occurs primarily at above 50°N, coinciding with the boreal-tundra zone. This coincidence further confirms our hypothesis and is the key to explain why the amplitude of atmospheric CO$_2$ has been increasing and the phase has been shifting forward. It is because the warming in the high latitude of the northern Hemisphere, that the vegetation in the region has responded with an increased annual peak of photosynthetic capacity and earlier peaking time, which, in turn, lowered the trough of the seasonal curve of the atmospheric CO$_2$ and make the trough occurs earlier.

Two questions remain. Is the change in the vegetation of high latitude zones big enough to explain the change in the seasonal curves of CO$_2$ concentration at low latitudes, e.g. Mauna Loa at 20°N? What is the effect of temperature on respiration. This study concentrates on photosynthesis and production, implicitly assuming the effect of change in respiration would not be big enough to revert the conclusion drawn from this study. In fact, Hall et al. (1993) found that the increasing seasonal amplitude of CO$_2$ is caused by the increase in both production (P) and respiration (R), but the P-R ratio has remained constant (P/R=1). Nevertheless, the effect of temperature on respiration merit further scrutinizing. Although it is beyond the scope of this paper to explore the answer to the first question, we would like to point out two facts. Firstly, the area of the vegetation above 50°N constitutes over one half of the total area of vegetation on the earth. Secondly, the vegetation in this region has the greatest seasonal fluctuation among vegetation of all regions.

V. CONCLUDING REMARKS

We studied the metabolic and phenological response of vegetation to the change in temperature using the latitudinal gradient to represent the temperature gradient. By comparing the seasonal curves of normalized difference vegetation index (NDVI) of northern latitudinal zones, we found that the annual peak of the zonal NDVI average ($M_{\text{NDVI}}$) increases as latitudes decrease from 75-56°N, with the greatest peak occurring at 56°N. In the same latitude range, the arriving time of the peak as measured by the Julian days when the $M_{\text{NDVI}}$ is reached decreases with latitude. These results imply that temperature increase at high latitudes in the northern Hemisphere may increase the $M_{\text{NDVI}}$ and decrease $T_{\text{NDVI}}$ for the vegetation above 56°N, and therefore lower the trough of the seasonal curve of the atmospheric CO$_2$ and make the trough arrive earlier. Because of the matching of spatial distribution of warming from 1965 to 1995 with the vegetation zone where the vegetation is sensitive to temperature, we conclude that the warming may have caused the metabolic enhancement and phenological shift for the vegetation in the high latitude region and which in turn causes the increase of seasonal amplitude of CO$_2$ and its phase shift. The results are derived based on a major assumption that NDVI is
representative of NPP of a large region. This assumption is yet to be confirmed by further study.

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