SENSITIVITY OF TUNDRA CARBON BALANCE TO AMBIENT TEMPERATURE

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(Received 4 December 1997; accepted 6 May 1999)

Abstract. Summer field observations in the north-east European region of Russia (1995–1996) proved that natural local and temporal warming could cause similar reversible changes of carbon (C) balance pattern of south tundra ecosystems. Thirty-six diurnal chamber measurements of carbon dioxide fluxes at two different sites $(67^{\circ}57'N, 64^{\circ}40'E; 67^{\circ}20'N, 63^{\circ}44'E)$ in 4 main types of ecosystems were studied. Wide magnitude of ambient mean diurnal air temperature (from +4.1 to +20.2 °C) allowed to obtain significant linear relationship between this parameter and variation in ecosystems C net flux (from -2.6 (sink) to +2.0 (source) gC m⁻² d⁻¹, R² = 0.769). In the midst of the vegetative season, an increase of mean diurnal air temperature in the plant canopy over the critical value of +14 °C lead to a change in the C net flux from sink to source. This can revert with a temperature influenced increase of gross ecosystem respiration. The summer temperature induced changes may result in positive (C source) annual C balance in some studied ecosystems. The annual C loss of shrub-dwarf shrub community in 1996 was estimated at 45 gC m⁻² yr⁻¹. We consider our results to be another evidence of possible positive feed-back between climate warming and C emission to the atmosphere on short-term and regional scales.

Keywords: carbon balance, CO2, Russia, tundra, warming

1. Introduction

The concept of global warming postulates that a continuing technogenic increase in the atmosphere concentration of CO_2 and other greenhouse gases contributes to a further increase in the atmosphere temperature and corresponding global climate change. The hypothesis on positive feedback between global warming and growth of C emission to the atmosphere is one of the consequences of the concept (Billings *et al.*, 1982). Taking into account significant C pools in permafrost, soils and plant cover of tundra ecosystems (Billings, 1987; Kolchugina and Vinson, 1993; Melillo *et al.*, 1993; Oechel and Vourlitis, 1994; Orlov *et al.*, 1996), the growth of the corresponding C emission to the atmosphere could seriously reinforce the greenhouse effect. This was shown only for the native Alaskan tundra (Oechel *et al.*, 1993, 1995, 1997; Oechel and Vourlitis, 1994). Presently, very few evidences of



Water, Air, and Soil Pollution **119:** 157–169, 2000. © 2000 Kluwer Academic Publishers. Printed in the Netherlands. the process in Russian tundra regions are known. One area is the Kolyma lowland forest-tundra (Zimov *et al.*, 1991).

This study combined the data on C fluxes from a number of ecosystems in the East-European region of Russian tundra zone, relevant to verification of the hypothesis. The East-European tundra occupies Kola Peninsula and northern parts of Arkhangelsk province and Komi Republic with an area of 33.58 Mha, which is about 12% of the total tundra and forest tundra area in Russia (Karelin *et al.*, 1995). It contains 437.5 MtC, or 16% of total phytomass stocks in Russian tundra zone. The warmest climate among all other Russian tundra regions results in the highest total phytomass density (13 tC ha⁻¹). The long-term average for days with the air temperature below 0 °C in the East-European tundra is -10.4 °C, whereas a corresponding value for the entire Russian tundra is -15°C (Zukert and Zamolodchikov, 1997).

The ecosystems of the south tundra are the most common in East-European Russia, constituting about 50% of the total area in this tundra region. Therefore, any fluctuations of C cycle in the regional tundras can take considerable effect upon global climate changes.

2. Materials and Methods

2.1. STUDY AREA

Field investigations were carried out in July and August of 1995 and June to August 1996 in the north-east of European Russia (Komi Republic). In 1995 sample sites were situated in the vicinities of Khalmer-Yu settlement ($67^{\circ}57'N$, $64^{\circ}40'E$), 70 km to the north from the city of Vorkuta, and in 1996 – near the Talnik railroad station ($67^{\circ}20'N$, $63^{\circ}44'E$), 20 km to the south from Vorkuta.

The natural conditions, soils and vegetation of the region are examined in detail (Archegova, 1972; Rebristaya, 1977; Archegova *et al.*, 1991). Since these Russian papers are poorly known in the English-reading scientific community, it would be of interest to mention briefly this subject below.

Shrub communities are the most typical south tundra ecosystems in this region. Among them, the most common are different variants of dwarf birch, willow and dwarf shrub tundras combined with low-hilly bogs. Dryad, sedge and grass-mossy tundras with polygonal sedge bogs are not so abundant. Shrub tundras – the most widely distributed communities in the north-east of Europe – are represented by dwarf birch and willow ecosystems. Dwarf birch tundra (60–65% of total area) occupies elevated localities and uplands devoid of bogs. These habitats vary by species composition. Among them the dwarf birch, willow-dwarf birch mossy and moss-lichen communities are prevail. The vegetative cover is composed of shrub, grass-dwarf shrub and moss-lichen layers. Dwarf birch (*Betula nana*) and willow species (*Salix glauca, S. phylicifolia, S. lanata*) are forming shrub layer

(60–80 cm in height). In grass-dwarf shrub layer (20–25 cm) Ledum decumbens, Vaccinium uliginosum, V. vitis-ideae, Empetrum hermaphroditum and some others are predominate. Calamogrostis neglecta, Festuca ovina, Pedicularis labradorica, Polygonum bistorta and some other species are to be found in grass layer. The mossy-lichen cover is developed well (Pleurozium schreberi, Hylocomium splendens, species of Cladonia, Peltigera and Stereocaulon).

Willow tundra is not so common in the Vorkuta region, and occupies only 18% of total area. It usually covers river, lake and stream terraces, valleys, and hydromorphic low, boggy areas. Predominant willow species – *S. glauca, S. phylicifolia, S .lanata* and *S. lapponum* – often form dense thickets of 2.5 and even 4–5 m high. Grass vegetation is usually composed of *Geranium albiflorum, Trollius europaeus, Galium boreale, Veronica longifolia, Ranunculus borealis, Equisetum pratense, Viola epipsila*, and cereals. Moss cover is rather patchy and sparse, with some admixture of *Polytrichum spp.* and green mosses.

Sedge bogs are much less common inter-zonal elements of tundra landscape. They usually occupy small wet lowlands of $100-200 \text{ m}^2$ and have an expressed sphagnum and sedge layers. Predominant sedge species are *C.aquatica* and *Eriophorum scheuchzeri*.

Soil cover is usually represented by tundra peaty humus-surface-glevic, peatygleyic, or sandy and loamy sand soddy-alluvial soils. Severe temperature conditions fully determine pedogenesis in Vorkuta region, but in comparison with eastern Russian tundra regions the winter is not so cold here and the climate is more humid. The frost-free period averages 52 days, the average annual number of days with diurnal temperature above 0 °C is 125. Mean annual air temperature is -6.3 °C, mean annual precipitation is 550 mm (49% in form of snowfall), mean wind speed is 5.6 m s⁻¹. The warmest and coldest months are July and January–February (+12.7°C and -20.5°C, respectively). Freezing starts at the end of September and the following period of stable snow cover continues from mid October to late May (7–8 months). The depth of snow varies from 10 cm to 1.5 m, depending on local slope orientation, type of vegetation cover, wind speed and direction. Seasonally frozen soil layer normally joins the permafrost at the depth of 1.3-2 m. The permafrost demonstrates continuous geographical distribution in the study area with the thickness of 45–130 m. The upper limit of its distribution is 0.3–2 m deep from the soil surface in the upland tundra and peatlands, and may be 10-20 m at the lowlands and under stream bottoms. Seasonal soil thawing starts in June, following snow melt. Under high atmospheric humidity, the slow thawing of deeply frozen loamy soils is favourable to the development of surface gleying.

2.2. SAMPLING METHODS

We investigated 4 ecosystem types in the south tundra: (1) small shrub dwarf birch moss-lichen community; (2) tall shrub dwarf birch mossy community; (3) shrubdwarf shrub moss-lichen community, and (4) sedge bog. Our field work was based on the measurements of carbon dioxide exchange on the boundary between the atmosphere and ecosystem. All field measurements were held using a portable infrared CO₂-analyser (IRGA) LiCor-6200 (LiCor, Lincoln NE, U.S.A.). During the measurements, the sample plots in tundra were covered with a transparent acrilic chamber ($42 \times 42 \times 50$ cm). Carbon dioxide fluxes at natural sun light were assumed to be an estimate of net C flux (NF). The carbon dioxide flux measured in a darkened chamber was an estimate of gross ecosystem respiration (GR). The difference between GR and NF is the gross primary production (GPP). GR and GPP are opposing fluxes; in this study we present respiration data as a positive flux and gross production as negative.

The chamber exposure during each measurement was about 1 min. The average change in chamber CO_2 concentration during a single measurement was about 4 ppm min⁻¹ (maximum: -20 ppm min⁻¹) at natural sun light, whereas in the darkness it was +6 ppm min⁻¹ (maximum: +20 ppm min⁻¹). The corresponding average increase of air temperature inside the chamber was 0.2 °C min⁻¹ at light (maximum: 0.8) and 0.1 °C min⁻¹ in the dark (maximum: 0.6). Continuous stirring of the air during the measurements was attained by use of internal chamber fan. We calibrated zero channel of the IRGA by CO_2 -free air and reference channel – by ambient air, assuming that the average CO_2 concentration was 370 ppm.

In diurnal cycle, the fluxes from 6 (1995) or 8 sample plots (1996) were measured every 1.5–2 h. Total diurnal values of C fluxes were calculated by integrating the diurnal data. The mean of data on all sample plots gives the value of diurnal C flux in the ecosystem. Diurnal measurements in each ecosystem were repeated every 5–7 days at the same sample plots. In 1995 we carried out 8 diurnal measurements in small shrub dwarf birch tundra. In 1996, 13 diurnal measurements in tall shrub dwarf birch tundra, 9 measurements in shrub-dwarf shrub community, and 6 in sedge bog were held.

Simultaneously with C fluxes we registered a number of other ecological parameters: air and soil temperatures, intensity of photosynthetically active solar radiation (PAR), air and soil humidity, wind speed and direction (at the height of 1.3 m), and thaw depth. Air temperature was measured inside plant canopy; soil temperatures – at the surface and at the depth of 1, 5 and 10 cm.

3. Results and Discussion

3.1. DIURNAL DYNAMICS OF CARBON FLUXES

The net C flux in ecosystem was calculated as a difference between the gross ecosystem respiration and its gross primary production. The short-term studies of tundra ecosystems revealed that GPP is primarily determined by PAR, whereas GR – by air and soil temperatures (Tieszen, 1973; Lloyd and Taylor, 1994; and many others). Air temperatures influence the respiration of aboveground components of

ecosystem, while the soil temperature effects the respiration of underground biota including roots of vascular plants, soil micro-organisms and invertebrates. These data served as a basis for the following analysis of diurnal dynamics of C fluxes in shrub tundra.

At the peak of the growing season (July – beginning of August, 1995) the rate of PAR is sufficient for photosynthesis during almost entire daytime. Therefore, the values of GPP are close to zero only during 2–3 h at night-time (Figure 1). Moreover, if the air temperature is not high, tundra would act as C sink during the most of daytime (in Figure 1 the curve of NF passes below zero from 3 a.m. to 7 p.m.). Under the mean diurnal air temperature of only +4.1 °C the value of NF constitutes: -2.6, GPP: -5.1 and GR: +2.5 gC m⁻² day ⁻¹.

A week later, the measurements of C fluxes at the same sample plot had demonstrated a different pattern of diurnal dynamics (Figure 2). The average diurnal air temperature was significantly higher compared to the previous case (+19.6 °C). This resulted in the elevated GR during the day, which exceeded GPP by absolute value starting from 11 a.m. Hence in this case tundra has been depositing C only from 6 to 11 a.m. From 3 p.m. the PAR intensity decreased, which led to GPP reduction and, in its turn, accelerated the rate of C loss from the ecosystem. Finally, the above-mentioned processes resulted in C emission of +2.1 gC m⁻² d⁻¹ with GPP of -6.6 and GR of +8.7 gC m⁻² d⁻¹.

It appeared that the flux dynamics on Figure 2 are characteristic for days with a high mean diurnal air temperature. At such days tundra stores C only during the morning hours. In the afternoon, C balance changes its pattern to the opposite, and the ecosystem becomes a C source to the atmosphere.

3.2. CRITICAL TEMPERATURE FOR DIURNAL CARBON BALANCE

The analysis of diurnal total C fluxes reveals a strong correlation between temperature and general pattern of C balance. In the field season of 1995 the weather conditions were rather diverse and average diurnal air temperature varied in the range from +5.9 to +20.2 °C. With that, the gross respiration of shrub little dwarf birch tundra altered from 1.9 to 7.3 gC m⁻² d⁻¹, gross primary production – from 2.7 to 5.3 gC m⁻² d⁻¹, and net flux – between –2.0 and +2.0 gC m⁻² d⁻¹. The tundra served either as C sink or as source depending on temperature regime (lower or higher, respectively; Figure 3). The mean diurnal air temperature responsible for the change of general C balance pattern was determined as +14 °C. Since we measured the air temperature inside the plant canopy, it was close to the actual temperature of leaves surface and the above-mentioned critical value possibly reflects a real physiological temperature limitation. The correlation between net C flux (gC m⁻² d⁻¹) and mean diurnal temperature (T, °C) was significant:

$$NF = -3.46 + 0.265T$$
, $R^2 = 0.769$, $n = 8$, $p = 0.004$



Figure 1. Diurnal dynamics of carbon fluxes in shrub tundra (Halmer-Yu site, July 16, 1995). Carbon fluxes (A: GR = Gross Ecosystem Respiration, GPP = Gross Primary Production, NF = Net Flux), photosynthetically active radiation (PAR) and mean diurnal air temperature (T) are shown on the Y axes, time of the day is shown on the X axis.

Variations of ecosystem net flux were mostly determined by gross respiration, whereas gross primary production was not affected by temperature:

The change in C balance pattern of the south tundra ecosystems in response to rise in air temperature was reversible, i.e. the tundra turns into the sink of C again, as the temperature decreases. Over the summer, in some cases changes in PAR-dependent GPP fluxes along with almost equal respiration rates can cause differences between

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Figure 2. Diurnal dynamics of carbon fluxes in shrub tundra (Halmer-Yu site, July 23, 1995). See Figure 1 for abbreviations.

absolute NF values under similar temperatures (Figure 3: compare the dates 7/16 and 8/3).

In 1996 we extended the period of observations (from the middle of June till the beginning of August), as well as the range of studied ecosystem types (shrub tundra, shrub-dwarf shrub tundra, sedge bog). In all studied cases the excess of +14 °C by mean diurnal air temperature in the midst of the season resulted in emission of carbon dioxide to the atmosphere (Figure 4). The rate of PAR, thaw depth, soil and air humidity, wind speed, and other ecological factors were not affecting the above-mentioned threshold value. Nevertheless all these parameters are linked with the C fluxes and can change their values, the general pattern of ecosystem C balance (sink or source of C) is closely correlated with the air temperature only.

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Figure 3. Diurnal carbon fluxes, mean diurnal air temperature (T) and PAR in shrub tundra (Halmer-Yu site, July–August, 1995). Negative fluxes values are carbon sink, positive – are carbon source. Average values \pm standard errors are shown, n = 6. See Figure 1 for abbreviations.

Therefore, the value of +14 °C is believed to be the threshold mean diurnal air temperature for the C balance in the south tundra ecosystems.

These conclusions are only true for the period of active plant growth. During the entire warm season (June–September), CO_2 emission to the atmosphere can take place even under relatively low diurnal air temperatures. This takes place in the spring, from the beginning of the warm season till the beginning of active plant growth (Figure 4; open markers). Tundra gains the capacity to deposit C only after formation of vascular plants foliage, and the spring C emission is due to the predominance of GR flux over GPP in this period. Similar pattern is well known for the end of warm season due to the plant senescence (the so called 'autumnal C emission'; see: Oechel *et al.*, 1995; and many others). Therefore, during the warm



Figure 4. Net flux (NF) versus mean diurnal air temperature (T) in different south tundra ecosystems (Talnik site, June–August, 1996). Data are means \pm S.E., $n = 3 \div 5$. Circles = shrub tundra, squares = dwarf shrub tundra, triangles = sedge bog. Open markers = spring C emission, solid = period of active plant growth.

TABLE I

Integrated carbon fluxes, average air temperature and average diurnal sum of PAR for the periods of observations in the south tundra ecosystems. Fluxes values \pm standard errors are given. See text for abbreviations

Tundra	Year	Period	Т	PAR	GPP ^a	GR	NF
ecosystems				(MJm^{-2})			
			$(^{\circ}C)$	d ⁻¹)	$(gC m^{-2})$	$(gC m^{-2})$	$(gC m^{-2})$
Shrub ^b	1995	July 14–August 5	10.5	8.1	-95±13	89±10	-6 ± 10
Dwarf shrub ^c	1996	June 17–August 3	12.6	8.4	$-118{\pm}20$	132 ± 20	14±9
Shrub ^c	1996	June 17–August 3	11.4	7.4	$-218{\pm}20$	188 ± 15	$-30{\pm}14$
Sedge bog ^c	1996	June 19-August 1	10.2	6.3	$-139{\pm}16$	96±11	-43 ± 9

^a GPP values were calculated as a difference between NF and GR.

^b Halmer-Yu site.

^c Talnik site.

period south tundra ecosystems under temperatures below +14 °C can act either as a C sink or source, and only as a C source – at temperatures above +14 °C. In the period of active plant growth the relation between temperature and C balance pattern simplifies: below threshold value tundra functions as a C sink and above the threshold as its source (Figure 4).

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3.3. SEASONAL BALANCE OF CARBON IN THE SOUTH TUNDRA

The correlation between diurnal C balance and air temperature almost fully predicts values of total seasonal C fluxes. Table I shows the integrated values of GPP, GR, and NF for the sampling period. The values were calculated by integrating the data on seasonal dynamics of diurnal fluxes by method of trapezium. Therefore, the values of NF characterise an amount of C, being taken up or lost during a period of observations. It was found that the shrub-dwarf shrub tundra is a seasonal C source, while the other studied ecosystems had demonstrated a sink pattern. All the seasonal NF values in the table are significantly differ from zero. The integrated seasonal estimates can be somewhat affected by weather variations due to some shift of the periods of observations between different types of ecosystems. Thus, the observations in shrub-dwarf shrub site were carried out during the warmer days (Figure 4), which resulted in the highest mean air temperature and positive seasonal estimate of net flux in this ecosystem (Table I).

According to the outlined regularity, any short-term excess of the threshold mean diurnal air temperature in shrub tundra leads to change in diurnal C balance (Figures 3 and 4), nevertheless, this does not result in seasonal C source (Table I). We found the maximum seasonal value of C deposition for the sedge bog ecosystem (43 gC m⁻²), which is mostly due to the fact, that in the days of observation at this site there were not recorded any high air temperatures (Figure 4).

4. Discussion

Physiologically the phenomenon of the threshold temperature of diurnal C balance in the south tundra is explainable from the position of low temperature optimums of photosynthesis in many species of arctic plants (Gerasimenko and Shvetsova, 1989). At absence of limitation by PAR, maximum rates of photosynthesis are in the range of +7: +12 °C, and further rise of temperature can even suppress the process. At the same time, gross respiration of plants and micro-organisms follows the increase of ambient temperature, which leads to the observed transformation of the C balance.

Discussing the relationships between temperature and C fluxes, we used values of easily determined air temperature, although it is evident, that partial respiration of different ecosystem components directly depends on their own specific temperatures. At most this relates to the temperatures of underground components of ecosystems, such as roots of vascular plants, fungi, bacterium etc. Thus, in the south tundra 60–70% of root biomass is located in soil within the upper layer of 0–15 cm (Archegova, 1972). The observed average air temperature, during both field seasons, was estimated at +10.8 °C, while the soil temperature at the depth of 1 cm was +10.1 °C, at 5 cm: +7.8 °C, and at 10 cm: +5.9 °C. Nevertheless, the

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dynamics of soil and air temperatures were found to be rather similar. Thus, the coefficient of correlation between the air temperature and soil temperature at the depth of 5 cm was +0.77. Hence we may conclude, that air temperature is related to the most components of ecosystem.

A similar reverse in the C balance pattern in response to the ambient temperature has been reported for different tundra plant species (Nazarov and Sivkov, 1995). But the existence of the constant (independent on season or type of ecosystem) threshold mean diurnal air temperature was the first to be established on the ecosystem level. The similarity of the found value to the metabolic temperature limit of microbial communities in tundra soils is also of interest. When the temperature decreases below +15 °C, the anaerobic processes in such microbial communities change from methanogenesis to a hydrogen acetogenesis (Zavarzin *et al.*, 1993).

It is especially important to estimate annual C balance of individual ecosystems, landscapes, regions etc., under investigation of greenhouse effect. In this regard we can make the following assumptions on annual pattern of C balance of studied ecosystems. Our observation period covered 2/3 of vegetative season from the moment of snow melt. We have no information on C fluxes at the end of warm season and during 'cold period' (from the midst of September till the end of May). But normally, in the late August an autumn reverse of C balance takes place, thereafter tundra ecosystems and entire landscape function only as C source (Oechel et al., 1995; Zamolodchikov et al., 1997). Therefore, the C balance in the tundra, at the end of a warm period, can be shifted only towards the source of C. In the winter time, C emission continues even from fully frozen soils. The direct measurements of CO₂ emission from tundra soils in the winter period showed that C losses during cold season constitute about 10-70 gC m⁻² (Zimov et al., 1991; Fedorov-Davidov and Gilichinski, 1993; Oechel et al., 1997). Assuming that the winter C emission in the south tundra ecosystems was about 30 gC m⁻², we can estimate the annual C loss of shrub-dwarf shrub community in 1996 at some 44 gC m⁻² (net fluxes in 1996 were significant; see Table I). If the estimation of the winter emission is correct, the C balance of shrub tundra was close to an equilibrium and sedge bog deposited about 13 gC m⁻² yr⁻¹ in that year (Table I). Shrub and dwarf shrub communities are predominate by area in the studied region (Rebristava, 1977), hence we may consider, that natural tundra landscape of north-east European Russia in 1996 was acting as C source to the atmosphere. Besides this conforms well to some ascending trend of summer temperatures over the territory of the East-European tundra from middle eighties till nowadays (Zukert and Zamolodchikov, 1997). Nevertheless the correct interpretation needs better accuracy in the estimation of ecosystem winter C fluxes.

The results of C fluxes investigations in the north-east European Russia could provide new arguments in favour of the hypothesis of positive feedback between climate warming and increase of C emission in the tundra. But it should be clearly stated here, that our findings are valid only on the short-term scale of ecosystem functioning (days–months). The observed short-term, reversible sensitivity of carbon balance to warming does not tell us much about the long-term response of ecosystems (years). This question is beyond the scope of this study. As a long-term process, climate warming could cause considerable shifts and complicated changes in nutrient mineralization, thawing, water balance and other valuable characteristics, finally resulted in a new composition, distribution, or acclimation of plant species.

Acknowledgements

This study was supported by the Project 4.3.3. of the Program 18 'Global changes of Natural Environment and Climate' (Russian Ministry of Science Policy) and Supplemental Grant of National Scientific Foundation (U.S.A.). Special thanks to Dr. I. B. Archegova (Syktyvkar, Komi Republic, Russia), and V. P. Krylov (Vorkuta, Komi Republic, Russia) for logistical help, and also to A. V. Skichko (Moscow, Russia) for assistance in the field.

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