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The Carbon Cycle in the Ecosystems of Thermal Springs in the Chukchi Peninsula as a Natural Model of Warming

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Abstract—Comparative studies on the ecosystems in the vicinity of thermal springs and in the typical tundra were performed in the southeastern Chukchi Peninsula in July and August 1997. Biogenic carbon fluxes during the greater part of the growing season were determined, the aboveground phytomass structure was studied, and the carbon reserve in the soil was estimated. It was demonstrated that the gross primary production and soil carbon in thermal ecosystems are greater than in similar permafrost ecosystems. The structural and ecophysiological changes leading to an increase in the gross production of plant communities were analyzed.

Key words: thermal and permafrost ecosystems, carbon cycle

Studies on the carbon cycle in the biosphere and its components have been considerably intensified due to the complex problems related to the accumulation of greenhouse gases in the atmosphere and a possible global warming. Efforts have been focused on the inventory of carbon reserves, natural sinks, and sources. Numerous studies have dealt with this problem in Russia (Isaev *et al.*, 1995; Kudeyarov *et al.*, 1995; Orlov *et al.*, 1996; *Uglerod v ekosistemakh…*, 1994). However, the focus has now shifted toward estimating the long-term effects of global change on the carbon cycle in natural ecosystems. The studies are aimed at answering the questions as to how the primary production and destruction change, what the trends in the total carbon reserve in ecosystems are, and whether natural ecosystems are able to compensate for the effects of global changes or, conversely, enhance them by the positive feedback mechanism.

The medium- and long-term effects of high temperatures and carbon dioxide concentrations may considerably differ from the short-term effects. This is a substantial obstacle to answering the aforementioned questions. One example concerns the results of the experiment on monitoring the carbon dioxide concentration in hermetic chambers that were set in the hummocky tundra (Oechel *et al.*, 1994). During the first year of the experiment, carbon sink was stimulated by a CO_2 concentration of 680‰; however, this stimulation ceased as soon as two years later.

Prolonged experiments on monitoring the main ecological factors (CO_2 concentration, temperature, and groundwater level) make it possible to estimate medium-term (over several years) effects of climatic changes on natural ecosystems. To estimate more long-term effects (decades or centuries), the researchers may use, in addition to paleoreconstructions, the ecosystems that have been naturally exposed to high temperatures and CO_2 concentrations for a long time. These are the ecosystems of geothermally active regions. During the past five years, the carbon cycle has been studied in these ecosystems located in various natural zones (Bettarini *et al.*, 1998; Cook *et al.*, 1998; Körner and Miglietta, 1994). Geothermal springs in the tundra are especially numerous in the Chukchi Peninsula. The purpose of this study was to assess the main components of the carbon cycle in the ecosystems affected by geothermal activity and to compare them with the same parameters for permafrost ecosystems.

MATERIALS AND METHODS

Field studies were conducted near the Chaplino thermal springs located in the Provideniya raion of the Chukot Autonomous Area (64°26′ N, 172°30′ W) in July and August 1997. This area is characterized by a low-mountain relief with the prevalence of hills and ridges rising to 300–650 m a.s.l. They are separated by glacial valleys with small rivers on the bottom, which form multiple channels. The microclimate of the area is severe because of its close proximity to the Bering Sea (4 km) and prevailing sea winds with an annual average speed of 7 m s^{-1}. Long-term average air temperatures at Cape Chaplino in July and January are +3.9 and –16.4°C; the annual average temperature is –6.2°C (Kozhevnikov, 1989). The annual average precipitation is 451 mm.

The outlets of the Chaplino springs are located on a terrace above the floodplain and in stony alluvial deposits on the right bank of the Ul’khum River, 10–20 m a.s.l. There is no permafrost around them, and the soil temperature at depths of 10 cm to 6.5 m is 22–24°C (Tikhomirov, 1957). An area of almost 70 ha is directly or indirectly affected by thermal springs. The thermal resources in this area are about 390 × 10^{12} J/day; water output is 16.6 l/s, which exceeds average values for all of the 18 groups of springs described in the Chukchi Peninsula (*Ekosistemy…*, 1981). The maximum temperature of hot water at the surface (+66°C) is also one of the highest. Regarding the relative concentrations of dissolved gases (1% CO_2 and 99% N_2), the springs are classified as nitrogen-gassing (*Ekosistemy…*, 1981).

Tikhomirov (1957) published a detailed description of the vascular plants of both the thermal and the permafrost ecosystems in the vicinity of the Chaplino springs. Therefore, we will indicate only the dominant species of the ecosystems where the carbon cycle was studied. According to A.E. Katenin (personal communication), mosses are represented by *Bryum pseudotriquetrum* (Hedw.) Gaertn. *et al.*, *Brachythecium glaciale* Schimp., *Rhytidiadelphus subpinnatus* (Lindb.) T. Kop., *Lescuraea mutabilis* (Brid.) Lindb. ex J. Hag., and *Marchantia polymorpha* L. at thermal plots and by *Tomenthypnum nitens* (Hedw.) Loeske, *Oncophorus virens* (Hedw.) Brid., *Dicranum groenlandicum* Brid., *Polytrichum juniperinum* Hedw., *Sphagnum warnstorffii* Russ., *Torella fragilis* (Hook. et Wils.) Limpr., *Catascopium nigritum* (Hedw.) Brid., *Cratoneuron filicinum* (Hedw.) Spruce, and *Pseudocalliergon turgescens* (T. Jens.) Loeske in permafrost habitats.

When selecting experimental areas, we tried to find plots of zonal tundra ecosystems and similar tundralike plots directly affected by thermal activity. A shrub–dwarf shrub–herb–moss drained thermal ecosystem (DTE) was located 70–100 m away from the nearest thermal spring in a thermal tract of the right near-bed part of the Ul'khum River. A sedge–moss moist thermal ecosystem (MTE) was located 20 m away from the DTE. Note that we use the term “drained” in a comparative sense, as all the ecosystems studied were overmoistened.

The permafrost ecosystems studied were located on the left bank of the Ul'khum River, 1 km north of the thermal associations, on a gentle slope with a southern exposure (50 m a.s.l.). A shrub–dwarf shrub–herb–moss–lichen drained permafrost ecosystem (DPE) was located in elevated spots, and a sedge–moss moist permafrost ecosystem (MPE) was located in depressions with flowing damping.

The most common plants[1] of the DTE were *Betula exilis* Sukacz, *Salix chamissonis* Anderss., *S. pulchra* Cham., *Carex rariflora* (Wahlenb.) Smith, and *C. cryptocarpa* C.A. Mey. Shrubs, herbs, and mosses had coverage of 50, 30, and 80%, respectively. The only dominant plant in the DTE was sedge *Carex cryptocarpa* with a small admixture of *C. rariflora*. The total coverage of sedges and mosses was 65 and 80%, respectively; the grass stand was 25–30 cm high. The vegetation of the DPE was similar to that of the DTE; it consisted of *Betula exilis, Salix chamissonis, S. reticulata* L., *Carex aquatilis* Wahlenb., *C. gynocrates* Wormsk., *Ledum decumbens* (Ait.) Lodd. ex Steud., *Empetrum hermaphroditum* Hagerup, *Vaccinium vitis-idaea* L., and various mosses and lichens. The values of coverage for shrubs, dwarf shrubs, herbs, mosses, and lichens were 30, 25, 30, 70, and 30%, respectively. The MPE was characterized by a community of *Carex aquatilis* and *Eriophorum scheuchzeri* Hoppe with a total coverage of 50% and the moss layer coverage was 60%.

We measured ecosystem carbon fluxes in 40 × 40 cm permanent test plots (four plots in each DTE and DPE and two plots in each MTE and MPE). Carbon fluxes were measured with the use of a 42 × 42 × 30 cm portable plastic chamber, which was transparent for photosynthetically active radiation (PhAR). To perform the measurements, the chamber was mounted on the aluminum basis surrounding each test plot. To make the chamber airtight, we used a water lock. Changes in the CO_2 concentration in the chamber were measured using a Li-Cor 6200 gas analyzer. The net flux (*NF*) of carbon through an ecosystem was measured in the light, and gross respiration (*GR*) of the ecosystem, in the dark (under a coverlet). The gross primary production (*GPP*) was calculated as the difference between these values. The exposure time was only 1 min, and the CO_2 concentration and temperature in the chamber did not change significantly during this period. Therefore, we assumed that the effect of this procedure on the processes studied was negligible. The measurements were repeated every 1.5 h at each plot. During one 24-hour cycle, the procedure was performed in either all thermal or all permafrost plots. In each ecosystem, these cycles were repeated every seven to ten days, so that we obtained five 24-hour series for each ecosystem during the period of studies.

We also measured the PhAR rate (using a Li-Cor 6200 instrument); the air temperature in the plant cover 10–20 cm above the ground; the soil temperature on the surface and at depths of 1, 5, and 10 cm (using Omega thermocouples); and the wind speed and direction 1.6 m above the ground surface (using a mechanical anemometer). After each 24-hour cycle, we measured the depth of the thawed-out soil layer in each test biotope using a steel probe. The soil humidity in all ecosystems was measured gravimetrically in samples of the top layer (0–5 cm).

The aboveground phytomass was collected immediately after seasonal measurements of the gas fluxes in all test plots. In addition, the phytomass was cut from five 0.16-m^2 plots in moist ecosystems. A total of four and seven samples of the cut phytomass were collected from each drained and moist ecosystem. The phytomass was divided into the main components (the foliage and woody parts of shrubs and dwarf shrubs, herbs, mosses, and lichens), dried to absolutely dry weight at +105°C, and weighed to an accuracy of 0.1 g.

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[1] Latin names of vascular plants are given according to Cherepanov (1995).

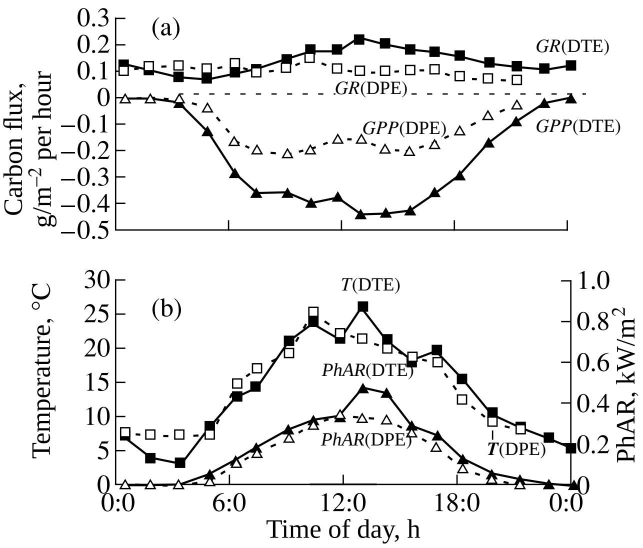

Fig. 1. Daily dynamics of (a) gross primary production (*GPP*) and gross respiration (*GR*); (b) air temperature (*T*) and photosynthetically active radiation (*PhAR*) in drained thermal (DTE) and permafrost (DPE) ecosystems measured on July 11 and July 23, 1997, respectively.

Soil sections in the ecosystems studied were made to a depth of 1 m or to the surface of the permafrost (in that period, soil thawed out to the depths of 80 and 73 cm in drained and moist ecosystems, respectively). We described and measured the boundaries of the horizons and took samples to measure soil moisture and density. The carbon content in the samples was measured as described by Tyurin (1937) at the Faculty of Soil Sciences of Moscow State University. The data obtained were used to calculate the carbon resources in the soil.

Daily carbon fluxes were estimated by integrating instant values for each test plot over 24 h by the trapezoid method. Afterwards, daily average estimates were calculated for each ecosystem. The standard error of the mean was calculated as follows: $\mathrm{SEM} = \mathrm{SD}/\sqrt{n}$, where SD is the standard deviation and n is the number of objects. Differences were tested for significance using Student's t test. Hereafter, the probability that the mean values are equal to each other (P) is indicated for such comparisons. The correlation between the characteristics measured was estimated using the Pearson rank correlation coefficient (R). The parameters of equations for primary production were calculated by the methods of nonlinear regression analysis.

Table 1. Parameters of equations $GPP = a_1^* a_2^* \mathrm{PhAR}/(a_1^* \mathrm{PhAR} + a_2)$, which describe the relationship between *GPP* values (calculated per unit area and unit dry weight of vascular plant foliage) and the PhAR rate (kW/m^2)

Ecosystem	Number of measurements	Parameters of the equations					
		g/m^2 h			g/kg h		
		a_1	a_2	R^2	a_1	a_2	R^2
DTE	360	4.43	0.557	0.97	38.4	4.93	0.96
MTE	218	7.77	0.847	0.97	47.8	5.21	0.97
DPE	361	4.75	0.265	0.81	42.4	2.37	0.76
MPE	217	3.75	0.230	0.90	41.0	2.47	0.89

RESULTS

Daily dynamics of carbon fluxes. Typically, the daily *GPP* dynamics of the *GPP* in tundra ecosystems is mainly determined by PhAR dynamics. However, Arctic plants and plant communities exhibit a so-called daytime photosynthesis depression (Gerasimenko and Shvetsova, 1989; Zamolodchikov *et al.*, 1997; Politova and Luk'yanova, 1994). The *GPP* is decreased in the warmest time of the day possibly because the temperature is higher than optimum for most species. The *GPP* curve is in this case bimodal. We observed this type of the *GPP* daily dynamics in the DPE on July 23, 1997 (Fig. 1a). A distinct decrease was observed between 11 a.m. and 2 p.m. In the following figures and tables simultaneously showing the *GR* and *GPP*, they are assigned plus and minus signs, respectively. Such a depression was not observed in thermal ecosystems with similar vegetation (Fig. 1a; July 11, 1997) in days with similar weather (Fig. 1b). At the maximum PhAR, the absolute value of the *GPP* in thermal ecosystems was more than two times greater than in permafrost ecosystems.

These characteristic features of the *GPP* daily dynamics suggested that the plant communities of the thermal ecosystems have a more effective photosynthesis and higher temperature optimums of photosynthesis. To test the first suggestion, we analyzed a set of instantaneous *GPP* measurements for all test plots in the ecosystems studied. The parameters of the *GPP* illumination curve were determined for each ecosystem (Monsi and Saeki, 1953) by the following formula:

$$GPP = a_1 a_2 \mathrm{PhAR}/(a_1 \mathrm{PhAR} + a_2),$$

where a_1 is the tangent of the initial slope and a_2 is the saturation "plateau" of the curve. The data obtained (Table 1) indicate that, at light saturation (the value of parameter a_2), the *GPP* values calculated either per unit area or unit weight of the assimilating parts of vascular plants were almost two times higher in thermal ecosystems than in permafrost ecosystems.

To estimate the optimum temperatures of photosynthesis, we determined the mean *GPP* values at light saturation (PhAR ≥ 0.15 kW/m^2) for the temperature ranges <16, 16–20, 20–24, and >24°C (Fig. 2). The *GPP* proved to decrease significantly ($P < 0.01$) as the temperature increased to pessimum in permafrost ecosystems and to increase significantly ($P = 0.06$) and insignificantly ($P = 0.77$) in the MTE and DTE, respectively. Thus, the temperature optimum of photosynthesis in thermal ecosystems was shifted towards higher temperatures.

In the example considered (Fig. 1a), the *GR* in the DTE was higher than in the DPE; however, this difference was considerably smaller than the difference between the *GPP* values in these ecosystems. The *GR* increased in the daytime, this increase being most closely associated with temperature changes (the average correlation coefficient for all ecosystems studied was $R = 0.53$, $P < 0.05$). The correlations of respiration with the PhAR and *GPP* were also significant ($R = 0.49$, $P < 0.05$ and $R = 0.45$, $P < 0.05$, respectively). In permafrost ecosystems, respiration obviously depended on the *GPP*: the daytime photosynthesis depression was accompanied by a decrease in the *GR* (Fig. 1a).

Seasonal dynamics of carbon fluxes. The aforementioned differences between carbon fluxes in permafrost and thermal ecosystems were typically observed at the peak of plant growth (early and middle July). The relative values of carbon fluxes in different ecosystems changed during the growing season. The daily absolute values of the *GR* and *GPP* substantially decreased in drained ecosystems since late July (Fig. 3a). This decrease might be related to either the decrease in PhAR (Fig. 3b) or purely phenological changes. The absolute *GPP* values in the DPE also decreased by the end of the growing season (Fig. 3a), but this decrease was less pronounced than that in the DTE. These characteristic features of the *GPP* seasonal dynamics confirmed that photosynthesis was more efficient in the thermal ecosystems under conditions of light saturation, which occurred in early and middle July.

In the DTE, the *GR* (Fig. 3a) also decreased in the second half of the period studied. The temperature varied in this period but did not exhibit any distinct trend. Thus, the observed decrease of respiration was apparently related primarily to the decrease of the *GPP.* Note that the relationship between the *GPP* and the *GR* was determined by many ecophysiological and biochemical mechanisms, from a higher respiration rate of intensely photosynthesizing leaves to a higher rate of organic matter release by the roots. At the same time, respiration in the DPE changed insignificantly during the entire period of studies (Fig. 3a). This was explained by both constant the temperature and the relatively small changes in the *GPP.*

The net carbon flux (*NF*) is the balance between the *GPP* and *GR* fluxes. The DTE (Fig. 3a) had a negative *NF* value in July and a positive value in August, thus being a carbon sink and a carbon source, respectively. The DPE was a carbon sink only on the date when the first 24-hour measurements were made (July 11); on all other days, it lost carbon.

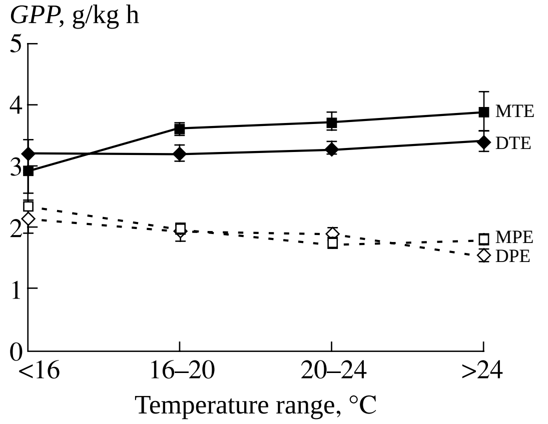

Fig. 2. Average gross primary production (*GPP*) values per unit weight of photosynthesizing organs of vascular plants for different temperature ranges. DTE, MTE, DPE, and MPE are drained thermal, moist thermal, drained permafrost, and moist permafrost ecosystems, respectively.

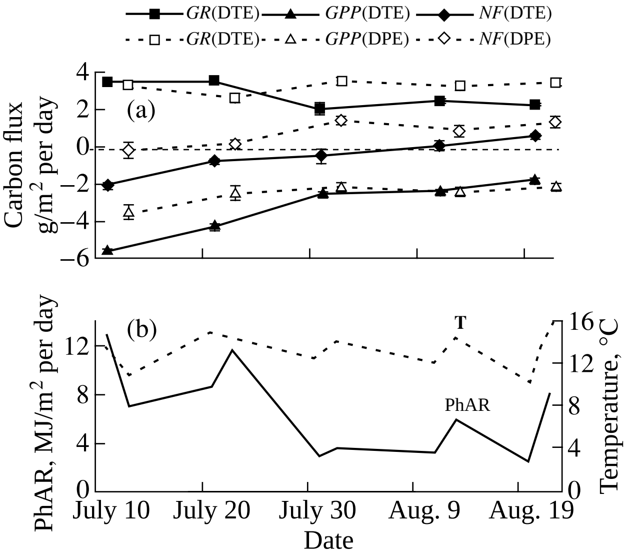

Fig. 3. Seasonal dynamics of (a) gross primary production (*GPP*), gross respiration (*GR*), and net carbon flux (*NF*); (b) PhAR and temperature of ground air (*T*) in the drained thermal (DTE) and permafrost (DPE) ecosystems.

In general, the aforementioned patterns of the seasonal dynamics of carbon fluxes were also characteristic of moist ecosystems, except for the ratio between the absolute *GR* and *GPP* values. In the MTE, the absolute *GPP* was higher than the absolute *GR* throughout the season, which was reflected in negative *NF* values (Fig. 4). In the MPE, the *NF* was negative during the first half of the period of measurements and close to zero during the second half (Fig. 4).

Seasonal carbon fluxes and resources. Regarding the carbon fluxes during the entire season, both the DTE and the MTE were distinct carbon sinks. Between July 11 and August 20, they absorbed 77 and 21 g of carbon per square meter, respectively (Table 2). The MPE was also a carbon sink (13 g of carbon per m^2), whereas the DPE lost 29 g of carbon per m^2. Note that the DPE slightly differed from the thermal ecosystems

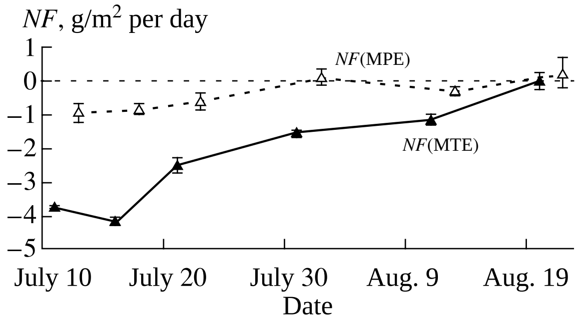

Fig. 4. Seasonal dynamics of net carbon flux (*NF*) in moist thermal (MTE) and permafrost (MPE) ecosystems.

with respect to the *GR*, whereas the *GR* value in the MPE was considerably lower. The *GPP* was maximum in the MTE and minimum in the MPE.

The soil carbon resources were extremely large in both the thermal and permafrost ecosystems. They varied from 48 to 69 kg of carbon per m^2 in the MPE and DTE, respectively (Table 3). The abundance of carbon was determined by the considerable thickness of the peat-bearing horizons (32–88 cm) and the high carbon content in them (24.1–45.8%). The carbon resources in the aboveground components of the ecosystems, including the aboveground plant organs and plant detritus, were as small as only 0.3–0.5% of the underground resources. The carbon resources of the thermal ecosystems were nonsignificantly ($P = 0.20$) higher than those of the permafrost ecosystems.

Table 2. Carbon fluxes in ecosystems as integrated over the period of study (40 days, from July 11 to August 20, 1997)

Ecosystem	Seasonal carbon fluxes, g/m² per season		
	GR	*GPP*	*NF*
DTE	108 ± 8	–129 ± 4	–21 ± 8
MTE	131 ± 5	–209 ± 7	–77 ± 7
DPE	128 ± 8	–98 ± 11	29 ± 10
MPE	67 ± 7	–80 ± 9	–13 ± 9

Table 3. Characteristics of peat-bearing horizons and total soil carbon resources in the ecosystems studied

Ecosystem	Peat-bearing horizons			Carbon resources*, kg/m²
	thickness, cm	density, g/cm³	carbon content, %	
DTE	88	0.171 ± 0.009	45.8 ± 0.9	69 ± 5
MTE	81.5	0.293 ± 0.036	24.1 ± 0.8	58 ± 7
DPE	44	0.245 ± 0.006	35.3 ± 1.0	61 ± 5
MPE	32	0.231 ± 0.019	29.0 ± 1.4	48 ± 7

* Soil carbon resources of permafrost ecosystems include carbon of gleyed horizons underlying peat-bearing horizons above the top of the permafrost.

The data obtained were insufficient for revealing any distinct relationship between the underground resources and the seasonal fluxes of carbon. The closest correlation found was that between the soil carbon resource and the *GR* ($R = 0.61$), but even this correlation was nonsignificant ($P = 0$).

DISCUSSION

Data extrapolation to the conditions of expected global warming is the most controversial problem in discussing the results obtained. Global warming primarily involves an increase in the air temperature, whereas changes in the soil temperature patterns are secondary. However, the situation with the thermal ecosystems studied is different. The soil is heated from underneath due to geothermal activity, and the profile of soil temperatures is inverse to that in permafrost ecosystems. The differences between the studied ecosystems with respect to the temperature patterns of the ground air layer and the soil surface were nonsignificant ($P = 0.2$); however, soil temperatures at depths exceeding 1 cm differed significantly ($P < 0.07$). Thus, soil temperature patterns primarily determined the differences between the ecosystems studied.

At the same time, changes in the temperature and hydrologic patterns of soils in permafrost ecosystems induced by atmospheric warming may considerably activate destructive processes in them. It is generally thought that the possible increase of primary production will not counterbalance the increase of the destruction; hence, much carbon that is now in a passive form will be released into the atmosphere. This is the essence of the hypothesis concerning positive feedback between global warming and the change in the carbon balance from the sink to the source of atmospheric carbon dioxide in tundra ecosystems (Billings *et al.*, 1982; Oechel *et al.*, 1993). The results of our study indicate that the long-term functioning of thermal ecosystems at predominantly positive soil temperatures (by the centigrade scale) does not prevent the accumulation of organic matter in amounts exceeding carbon reserves in the soils of permafrost ecosystems.

Note that the soil carbon resources revealed in both thermal and permafrost ecosystems are considerably higher than the average resources in other regions of the Russian tundra zone (Orlov *et al.*, 1996; Chestnykh *et al.*, 1999). It is unclear why such great resources of soil organic matter have been accumulated. Apparently, this is associated with the climate and the paleoecological history of the eastern Chukchi coastal zone.

The conclusion that soil warming in thermal ecosystems does not lead to a considerable increase in the *GR*, compared to that in permafrost ecosystems, is an important result of this study. However, it should be noted that the study lasted for only a half of the growing

Table 4. Fraction composition of absolutely dry aboveground phytomass (grams dry matter per m^2) in the ecosystems studied

Ecosystem	Shrubs		Dwarf shrubs		Herbs	Mosses	Lichens	Total
	foliage	wood	foliage	wood				
DTE	45 ± 9	125 ± 11	0.5 ± 0.5	0.2 ± 0.2	70 ± 4	152 ± 49	0	393 ± 55
MTE	0	0	0	0	174 ± 7	101 ± 15	0	275 ± 14
DPE	19 ± 5	107 ± 28	41 ± 7	39 ± 10	57 ± 11	166 ± 59	65 ± 23	494 ± 56
MPE	0.4 ± 0.3	0.9 ± 0.6	2.7 ± 1.8	0.3 ± 0.2	95 ± 5	150 ± 17	0	249 ± 17

season. The annual gross respiration in thermal ecosystems may be substantially greater than in permafrost ecosystems due to a high *GR* in the cold season.

The gross production is considerably higher in thermal than in permafrost ecosystems. Therefore, gross production of tundra ecosystems may, in principle, considerably increase in the case of warming. What causes the increase of primary production? Data on the structure of aboveground phytomass in the ecosystems studied (Table 4) may partly clarify this question. In MTEs, the mass of assimilating organs of herbs is almost twice greater than in permafrost ecosystems, with this phytomass being almost entirely accounted for by *Carex cryptocarpa*. The photosynthetic efficiency of this species is higher than that of *C. aquatilis*, which dominates permafrost ecosystems (our unpublished data). The drained ecosystems studied were similar in the composition of shrub and dwarf shrub species (*Betula exilis*, *Salix chamissonis*, *Empetrum hermaphroditum*, and *Vaccinium vitis-idaea*) and the total masses of assimilating plant organs. However, assimilating organs of shrubs prevailed in the thermal ecosystem, whereas those of dwarf shrubs prevailed in the permafrost ecosystem. It is known (Gerasimenko and Shvetsova, 1989) that the photosynthetic efficiency of deciduous shrubs is considerably higher than that of evergreen dwarf shrubs. Moreover, the photosynthetic efficiencies of the same shrub and dwarf shrub species in thermal ecosystems are higher than in permafrost ones (our unpublished data).

Thus, plant communities use a set of mechanisms to adapt themselves to geothermal heat. These are (1) changes in the species structure, (2) changes in the relative abundance of dominant species, and (3) changes in ecophysiological characteristics of species. Adaptation of permafrost ecosystems to global warming may involve all of these mechanisms.

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REFERENCES

Bettarini, I., Vaccari, F.P., and Miglietta, F., Elevated CO_2 Concentrations and Stomatal Density: Observations from 17 Plant Species Growing in a CO_2 Spring in Central Italy, *Global Change Biol.*, 1998, vol. 4, no. 1, pp. 17–22.

Billings, W.D., Luken, J.O., Mortensen, D.A., and Peterson, K.M., Arctic Tundra: A Source or Sink for Atmospheric Carbon Dioxide in a Changing Environment?, *Oecologia*, 1982, vol. 53, no. 1, pp. 7–11.

Cherepanov, S.K., *Sosudistye rasteniya Rossii i sopredel’nykh gosudarstv* (Vascular Plants of Russia and Neighboring States), St. Petersburg: Mir i Sem’ya-95, 1995.

Chestnykh, O.V., Zamolodchikov, D.G., and Karelin, D.V., Resources of Organic Carbon in the Soils of Tundra and Forest–Tundra Ecosystems in Russia, *Ekologiya*, 1999, no. 6, pp. 428–436.

Cook, A.C., Tissue, D.T., Roberts, S.W., and Oechel, W.C., Effects of Elevated CO_2 from Natural CO_2 Springs on *Nardus stricta*: Photosynthesis, Biochemistry, Growth and Phenology, *Plant, Cell Environ.*, 1998, vol. 21, no. 4, pp. 417–425.

Ekosistemy termal’nykh istochnikov Chukotskogo poluostrova (Ecosystems of Thermal Springs in the Chukchi Peninsula), Yurtseva, B.A., Ed., Leningrad: Nauka, 1981.

Gerasimenko, T.V. and Shvetsova, V.M., Main Results of Ecophysiological Studies on Photosynthesis in the Arctic, in *Ekologo-fiziologicheskie issledovaniya fotosinteza i dykhaniya rastenii* (Ecophysiological Studies on Photosynthesis and Plant Respiration), Leningrad: Nauka, 1989, pp. 65–114.

Isaev, A.S., Korovin, G.N., Sukhikh, V.I., *et al.*, *Ekologicheskie problemy pogloshcheniya uglekislogo gaza posredstvom lesovosstanovleniya i lesorazvedeniya v Rossii* (Ecological Problems of Carbon Dioxide Absorption by Means of Reforestation and Forest Cultivation in Russia), Moscow: Tsentr Ekologicheskoi Politiki Rossii, 1995.

Kozhevnikov, Yu.P., *Geosistemnye aspekty rastitel’nogo pokrova Chukotki* (Geosystems Aspects of the Plant Cover of the Chukchi Peninsula), Vladivostok: Akad. Nauk SSSR, 1989.

Körner, C. and Miglietta, F., Long-Term Effects of Naturally Elevated CO_2 on Mediterranean Grassland and Forest Trees, *Oecologia*, 1994, vol. 99, nos. 3–4, pp. 343–351.

Kudeyarov, V.N., Khakimov, F.I., Deeva, N.F., *et al.*, Assessing Respiration of Russian Soils, *Pochvovedenie,* 1995, no. 1, pp. 33–42.

Monsi, M. and Saeki, T., Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion, *Jpn. J. Bot.,* 1953, vol. 14, no. 1, pp. 22–56.

Oechel, W.C., Cowles, S., Grulke, N., *et al.*, Transient Nature of CO_2 Fertilization in Arctic Tundra, *Nature*, 1994, vol. 371, no. 6497, pp. 500–503.

Oechel, W.C., Hastings, S.J., Jenkins, M., *et al.*, Recent Change of Arctic Tundra Ecosystems from a Carbon Sink to a Source, *Nature*, 1993, vol. 361, no. 6421, pp. 520–523.

Orlov, D.S., Biryukova, O.N., and Sukhanova, N.I., *Organicheskoe veshchestvo pochv Rossiiskoi Federatsii* (Soil Organic Matter in the Russian Federation), Moscow: Nauka, 1996.

Politova, N.Yu. and Luk'yanova, L.M., Sulfur Dioxide Exchange and Productivity of Mountain Tundra Communities in the Khibiny Mountains, in *Plodorodie pochv i produktivnost' fitotsenozov* (Soil Fertility and Productivity of Phytocenoses), Apatity: Kola Res. Center Ross. Akad. Nauk, 1994, pp. 72–85.

Tikhomirov, B.A., On the Flora and Vegetation of Thermal Springs in the Chukchi Peninsula, *Bot. Zh.* (Leningrad), 1957, vol. 42, no. 9, pp. 1425–1427.

Tyurin, I.V., *Organicheskoe veshchestvo pochv i ego rol' v pochvoobrazovanii i plodorodii: Uchenie o pochvennom gumuse* (Soil Organic Matter and Its Role in Soil Formation and Fertility: A Theory of Soil Humus), Moscow: Sel'khozgiz, 1937.

Uglerod v ekosistemakh lesov i bolot Rossii (Carbon Storage in Forests and Peatlands of Russia), Alexeyev, V.A. and Birdsey, R.A., Eds., Krasnoyarsk: Inst. Lesa im. Sukacheva, Ross. Akad. Nauk, 1994. Published in English by the USDA Forest Service, Northern Research Station, GTR NE-244, 1998.

Zamolodchikov, D.G., Karelin, D.V., and Ivashchenko, A.I., Carbon Balance of Biogeocenoses in the Russian Tundra Zone, in *Uglerod v biogeotsenozakh: XV Chteniya pamyati akademika V.N. Sukacheva* (Carbon in Biogeocenoses: XV Academician V.N. Sukachev Memorial Lectures), Moscow: Ross. Akad. Nauk, 1997, pp. 99–121.