In: Permafrost. Seventh International Conference. June 23-27, 1998.
Proceedings. Eds. A.G. Lewkowicz, M. Allard
National Academy of Sciences. Washington, D.C. P. 1207-1212.

POSTFIRE ALTERATIONS OF CARBON BALANCE IN TUNDRA ECOSYSTEMS: POSSIBLE CONTRIBUTION TO CLIMATE CHANGE

Dmitri G. Zamolodchikov, Dmitri V. Karelin, Andrei I. Ivaschenko

Center for the Problems of Ecology and Forest Productivity, Russian Academy of Sciences, 117418, Novocheryomushkinskaya, 69, Moscow, RUSSIA;

Biological department of Moscow State University, 119899, Vorobievy gory, Moscow, RUSSIA
e-mail: zamolod@glas.apc.org

Abstract

The adaptation of tundra ecosystems to warming will involve losses of carbon from storage. There are two main mechanisms of carbon cycle change. The first one is related to adaptive alterations in ecosystem respiration and production. The second one is connected with fires, which are more likely under global warming. In this context, three ecosystems were investigated in the summer of 1996 in north-eastern European Russia: (a) undisturbed dwarf-shrub moss-lichen tundra; (b) site burned in 1994; (c) site burned in 1988. Total carbon pool in (a) was estimated at 5.87 $kgC \cdot m^{-2}$. Site (b) had 67% and site (c) about 70% of that amount. The net carbon flux at site (a) was +13.7 $gC \cdot m^{-2} \cdot .day^{-1}$ (carbon source), at sites (b) and (c) -2.7 and -35.2 $gC \cdot m^{-2} \cdot .day^{-1}$, respectively (carbon sink). The restoration period of the carbon pool is estimated at 60 years.

Introduction

Large amounts of organic carbon are stored in permafrost and the active layer in tundra and forest tundra ecosystems. Under elevated temperatures, much of this carbon would be liberated from permafrost into the atmosphere due to an increase of CO_2 emissions (Billings et al., 1982). This could positively feed-back on global warming. Data obtained in Alaska (USA) show that the tundra has changed from a sink of CO_2 to a source to the atmosphere during the last 20 years (Oechel et al., 1993, 1995; Oechel and Vourlitis, 1994, 1995). Changes from sink to source were also observed in different regions of the Russian tundra zone (Zimov et al., 1991, 1993; Nazarov and Sivkov, 1995; Zamolodchikov et al., 1997a, 1997b). It is possible to conclude that the tundra biome could represent a significant carbon source during climate warming. On the other hand, it is evident, that the processes of carbon losses in tundra cannot increase endlessly in terms of ecosystem balance. Hence, the main questions are: (1) how long will the period of carbon emission last in tundra; (2) what will be the absolute amount of carbon lost by tundra ecosystems; and (3) what amount of carbon can be absorbed by tundra ecosystems after adaptation to new climate conditions.

There are two main mechanisms for carbon cycle change in tundra ecosystems. The first one is related to alterations in ecosystem respiration and production. Data, cited above, describe the different aspects of these alterations. The second mechanism is more rapid and desctructive to ecosystem functions and structure: tundra fires. The frequency of tundra fires is expected to increase during global warming. Data from the Alaska Fire Service confirm that the frequency of tundra fires is presently increasing (Oechel, 1993), possibly due to the reported elevation of surface temperature (Chapmen and Walsh, 1993). Carbon losses, induced by fires, and subsequent restoration of carbon pools in tundra ecosystems are the subject of the present study.

Materials and methods

DESCRIPTION OF STUDY AREA

Field investigations were performed on stationary plots in June-August of 1996. The study sites were established in the Vorkuta region (67°20'N, 63°44'E; north-eastern European Russia). The area belongs to the southern tundra subzone. The climate of the territory is wet, with cold summers and moderately cold winters (Rebristaya, 1977). Average annual temperature is -6.0°C. The warmest month is July (+12.4 °C) and the coldest one is February (-20.3°C). The mean number of days with air temperatures above 0°C is 125 per year with 90 days above +5°C. The annual precipitation is 548 mm with warm season (June - September) precipitation averaging 242 mm. Snow cover usually appears at the end of September, and snowmelt takes place from the end of May until early June. Depth of snow cover varies from 10 cm to 1.5 m, depending on micro-relief and vegetation. All study sites are in the continuous permafrost zone, and the maximum summer depth of soil thaw varies from 0.5 to 1.5 m.

The vegetation cover of the studied area differs depending on local relief, solar and wind exposure and water table (Rebristaya, 1977; Archegova et al., 1991). One of the most representative types of tundra ecosystems is the dwarf-shrub moss-lichen tundra. This ecosystem has a layer of shrub plants (15-20 cm in height) dominated by *Betula nana, Empetrum hermaphrodium, Arctous alpina, Vaccinium uliginosum, V. vitis-idaea,* and *Ledum decumbens*. Graminoid cover is relatively poor, and includes *Calamagrostis holmii, C. lapponica, Festuca ovina,* and *Carex ensifolia*). Moss-lichen cover is formed by *Rhacomitrium lanuginosum, Hylocomium splendens, Polytrichum hyperboreum, Rhytidium rugosum, Sphaerophorus globosus, Cetraria cucullata, C. nivalis, Stereocaulon paschale, Cladonia mitis, C. gracilis, C. uncalis,* and *Thamnolia vermicularis*.

Two documented burned areas (2 and 8 years postfire) were located in the study area in dwarf-shrub tundra. The vegetation cover of the 2 years postfire site was sparse and consisted of mosses (height 2-3 mm, cover 40%), graminoids (grasses and *Chamaenerion angustifolium*) with cover 13%, and very few intact *Betula* and *Salix* shrubs. The 8 years postfire site possesses well developed *Polytrichum* mosses cover (height 4 cm, cover 100%) and about 15% cover of vascular plants (*Calamagrostis sp., Chamaenerion angustifolium, Vaccinium uliginosum, Salix sp.*).

SAMPLING METHODS

Sets of sample plots were established in each study site: in undisturbed dwarf-shrub tundra as characteristic of prefire state (site 1), 2 year burn (site 2), and 8 year burn (site 3). Each set consisted of 5 stationary sample plots, chosen as the most representative by plant composition. Aluminium square bases 40 x 40 cm that were previously dug 10 cm deep into the soil, made up the sample plots. The diurnal measurements of carbon fluxes were carried out on each plot using a portable cubic acrylic chamber transparent for photosynthetically active radiation (PAR) with a 40 x 40 cm base and 50 cm in height. During measurements, the chamber was alternately placed on the aluminium bases and sealed. A gas-tight seal of the chamber to a base was achieved using a water lock. For this purpose we put the chamber into an open channel welded around the perimeter of each aluminium base, and filled this channel with water. Changes in carbon dioxide concentration in the chamber were recorded in the field using a portable infra-red gas analyzer (Li-Cor 6200).

24-hour diurnal measurements of CO_2 fluxes were repeated every 7 to 10 days at each site. We performed 9 diurnal measurements from June 17 till August 3 at site 1, 6 diurnal measurements from June 19 until August 1 at site 2, and 5 from June 24 until July 30 at site 3.

During each diurnal measurement at one site all 5 sample plots (bases) were measured every 1 to 1.5 hours over a 24-hour cycle. The duration of an individual flux measurement at one plot was about 1 minute. We estimated an ecosystem Net Carbon Flux (NF) at natural PAR conditions, whereas a Gross Ecosystem Respiration (GR) was determined in the fully darkened chamber. Respiration measurements were made following each NF measurement by covering the chamber with an opaque blanket (Vourlitis et al., 1993). We assumed that Gross Primary Production (GPP) is consistent with the difference between absolute values of GR and NF.

In addition, chamber temperature, chamber relative humidity and ambient PAR were recorded. Diurnal carbon flux estimates were calculated by integrating all of the instantaneous flux values for each sample plot over a 24-hour measurement period using the trapezium method. Then the average values were calculated for each site. Additional ecological information was collected at the sampling sites in conjunction with the flux measurements. Temperatures in the air, at the soil surface temperature, and at depths of 1, 5 and 10 cm below the surface were determined using type-T thermocouples just prior to making an individual flux measurement. Depth of thaw at each site was determined using a steel rod inserted through the unfrozen soil at 20 random points, when flux measurements at a particular site were done. Soil moisture (0 to 5 cm) for each site was measured gravimetrically after completion of a regular diurnal measurement.

During the sampling period, above-ground components of plant and litter mass (green and woody parts of shrubs, graminoids, mosses, lichens, dead parts of shrubs and graminoids) were cut from random sample plots (40 x 40 cm), oven-dried and than weighed. We obtained data from 20 sample plots at site 1, 11 plots at site 2 and 8 at site 3. After the last measurement at each site, the above-ground standing crop of the sample plots was cut and sorted, as described above. The biomass data were converted to carbon content using ratio of 0.50 for living plants and 0.53 for dead plants and litter.

ESTIMATION OF UNDERGROUND CARBON STORAGE

We did not measure directly the carbon storage in the underground part of the ecosystems in our study, which includes carbon of living roots, dead plant tissues and organic matter of soil upper layer. In the field, we confined ourselves to the measurements of surface soil horizon thickness. For this purpose, 5 pits 20 cm deep were dug at each site. In order to estimate total

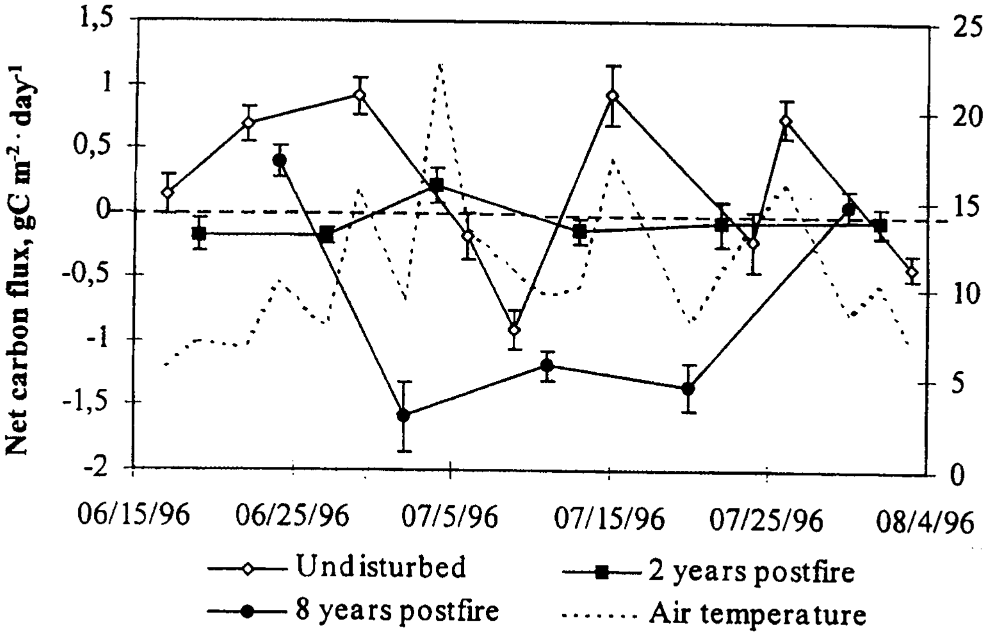

Figure 1. Seasonal dynamics of net carbon flux and air temperature at undisturbed and postfire sites in dwarf-shrub moss-lichen tundra (Vorkuta region, Russia).

carbon storage in soil and underground biomass, we used published data by Archegova (1972), who investigated the underground structure of dwarf-shrub moss-lichen tundra. The data in this paper allowed us to calculate the ratio of living root mass to above-ground biomass of vascular plants (5.13 ± 0.91 ± SE)), and the ratio of underground dead plant mass to the mass of living roots (1.34 ± 0.64). The above-mentioned ratios were used for estimating the underground plant biomass at all sites. In addition, using the same data source, we calculated the values of humus content per 1 cm of the upper soil horizons, which constitute 464.9 ± 69.9 g C$\cdot$m^{-2} for the first organic horizon, 426.0 ± 17.0 g C$\cdot$m^{-2} for the second, 115.7 ± 13.9 g C$\cdot$m^{-2} for the gleic horizon and 58.3 ± 6.6 g C$\cdot$m^{-2} for the mineral horizon. We recalculated the humus content using our data on horizon thickness and then converted the values by the ratio of 0.57 to get the carbon storage.

Results

CARBON FLUXES

The seasonal dynamics of the net carbon flux in undisturbed moss-lichen tundra was significantly different (t-test, p=0.05) from the postfire sites in the same ecosystem (Figure 1). From snowmelt to the end of vascular plants foliage formation (mid-June - late June), the undisturbed tundra was a source of carbon to the atmosphere, or, in other words, the estimated net carbon fluxes were "positive". This means that Gross Ecosystem Respiration (carbon loss) exceeded Gross Primary Production (carbon capture). Net carbon flux from 8 year burn was also "positive", while the net flux from the 2 year burn was found to be "negative" (carbon sink) just after snowmelt.

In the middle of the growing season (maximum of plant biomass) undisturbed tundra exhibited both negative and positive values of net carbon flux. As was shown in our earlier studies, this pattern of the dynamics is fully explained by variations in air temperature (Zamolodchikov et al., 1997b). At low mean diurnal temperatures (from +5 to +14°C), tundra acted more as a sink (Figure 1), and when temperature rose above +14°C, it was converted to a source of carbon. This change in carbon balance pattern was mainly caused by increasing Gross Ecosystem Respiration and the variation in Gross Primary Production was not as great.

At the height of the growing season, both burn sites demonstrated negative values of NF, constituting on average -0.10 g C$\cdot$m^{-2} $\cdot$day^{-1} in the 2 year burn and -1.38 g C$\cdot$m^{-2} $\cdot$day^{-1} in the 8 year burn. Nevertheless the increase of air temperature to +15°C (July 4) led to change of the NF pattern into positive for the 2 year postfire site also.

The observation period covered more than two-thirds of the vegetative season, therefore the integrated observed values of carbon fluxes (Table 1) satisfactorily represent the estimation of seasonal total fluxes. The undisturbed site during the sampling period was acting basically as a carbon source and lost a total of about 14 ± 7 g C$\cdot$m^{-2}. The value of GPP of the ecosystem constituted -118 ± 21 g C$\cdot$m^{-2} and GR +132 ± 20 g C$\cdot$m^{-2}. Hence, we can conclude that primary production

Table 1 Seasonal carbon fluxes, weather characteristics of the sampling period and depth of soil thaw at undisturbed and postfire sites in dwarf-shrub moss-lichen tundra (Vorkuta region, Russia)[1]

Parameters	Undisturbed	2 years postfire	8 years postfire
Date of the first observation	06/17/96	06/19/96	06/24/96
Date of the last observation	08/03/96	08/01/96	07/30/96
Sampling period, days	47	43	36
Seasonal respiration, g C m^{-2}	132 ± 20	56 ± 9	73 ± 7
Seasonal net flux, g C m^{-2}	14 ± 7	-3 ± 5	-35 ± 6
Seasonal gross production, g C m^{-2}	-118 ± 21	-59 ± 10	-108 ± 9
Average PAR, MJ m^{-2} day^{-1}	16.8 ± 2.3	12.7± 2.5	12.4 ± 2.5
Average air temperature, °C	12.6 ± 1.5	12.0 ± 2.3	9.1± 0.4
Average soil temperature at 5 cm depth, °C	8.0± 1.1	7.8± 0.9	7.3 ± 0.3
Average soil temperature at 10 cm depth, °C	5.2 ± 0.4	6.1± 0.3	6.5 ± 0.4
Maximum depth of thaw, cm	79± 2	107 ± 2	115 ± 2

[1] means ± SE

Table 2 Carbon content in main ecosystem components at undisturbed and postfire sites in dwarf-shrub moss-lichen tundra (Vorkuta region, Russia)

Ecosystem components	Carbon content at different sites (± SE)				
	Undisturbed	2 years postfire		8 years postfire	
	g C m^{-2}	g C m^{-2}	% of undisturbed	g C m^{-2}	% of undisturbed
Wood of vascular plants	90 ± 29	2 ± 2	2	6 ± 5	7
Foliage of vascular plants	28 ± 9	11 ± 6	39	10 ± 4	36
Mosses	139 ± 26	23 ± 8	17	223± 16	160
Lichens	107 ± 37	0	0	15 ± 6	14
Above-ground dead matter	129 ± 41	35 ± 17	27	17 ± 8	13
Total above-ground organic matter	493 ± 54	70 ± 22	14	271± 12	55
Living roots	606 ± 225	65 ± 37	11	81 ± 41	13
Dead roots	861 ± 410	92 ± 57	11	114 ± 66	13
Humus in upper organic soil horizons	1261 ± 273	1034 ± 232	82	980 ± 257	78
Humus in all horizons	3913 ± 374	3687 ± 361	94	3633 ± 383	93
Total underground organic matter	5381 ± 627	3844 ± 320	71	3828 ± 341	71
Total	5874 ± 567	3914 ± 287	67	4099± 305	70

returned more rapidly to undisturbed values, than ecosystem respiration. This explains why postfire sites in tundra act as carbon sinks. Thus, during the observation period the 2 year burn took up 3 gC•m^{-2}, while the 8 years postfire site took up 35 g C•m^{-2}.

It should be mentioned, that differences in weather conditions on days of measurement can affect the estimates of carbon fluxes at different sites. For instance, the average air temperatures during sampling days at the undisturbed tundra and 2 year burn was higher, than at 8 years postfire site (t-test, $p \leq 0.05$; table 1). At the same time, the observed photosynthetically active radiation (PAR) wasn't significantly higher at the undisturbed site, than at the burns ($p > 0.05$). However, under similar temperature conditions, the 2 years postfire site was acting as carbon sink, while the undisturbed site was a carbon source.

Soil temperatures at the depth of 10 cm depend more on site conditions than on local weather fluctuations. This temperature shows a maximum for the 8 years postfire site and a minimum for the undisturbed site (t-test, $p \leq 0.05$). Maximum seasonal thaw was also deeper at the 8 year burn (t-test, $p \leq 0.01$; Table 1).

CARBON POOLS

The most noticeable differences in carbon storage were found for above-ground components of the ecosystems. The above-ground plant biomass in 2 year and 8 year burns was 10 and 34%, respectively, compared to 100% at the undisturbed site (t-test, $p \leq 0.01$). The structure of biomass also differed among the sites. In undisturbed tundra, plant biomass is distributed more evenly among the different components (8% - foliage of vascular plants, 25% wood of vascular plants, 38% mosses, 29% lichens), whereas at the 2 years postfire site, 31% of total plant biomass is the foliage of vascular plants and 65% are mosses. At the 8 year burn the corresponding numbers are 4 and 88%, with the highest values of mosses biomass (Table 2). Therefore, the major renewal of above-ground plant biomass at the postfire sites is initially taking place as mosses.

Since we estimated the biomass of living and dead roots from values of above-ground biomass of vascular plants, the calculated values of carbon storage in these components of the ecosystem change in a similar manner at all sites in the study. Possibly this approach can lead to a small underestimate of dead root biomass in the postfire sites.

The total thickness of upper organic soil horizons in the studied tundra ecosystem is rather small and constitutes only 5.0 ± 1.1 cm in the undisturbed site. After fire, the thickness of upper organic horizons decreased to 4.0 ± 1.4 cm at the 2 years postfire site and 3.8 ± 1.1 cm at the 8 year burn, effecting a decrease in the carbon storage in the upper organic layers by some 20% (Table 2).

Our data do not allow to estimate the difference in carbon content in mineral soil horizons, therefore we assumed the content to be the same at all sites, and equal to carbon storage in a 70 cm layer of the above-mentioned horizons.

The total carbon storage in the undisturbed dwarf-shrub tundra is 5.87 ± 0.57 kg C•m^{-2} (Table 2). The total carbon content was 67% and 70% of that value at the 2 year and 8 year postfire sites, respectively. Therefore, fire in the dwarf-shrub moss-lichen tundra can lead to the loss of one-third of the initial carbon content.

If it is assumed that the rate of carbon restoration in these ecosystems corresponds to the rate of net flux at the 8 year burn (-35 g $C \cdot m^{-2}$), it would take approximately 50 years to replace the carbon deficiency of 1.77 kg $C \cdot m^{-2}$, with full renewal in about 60 years. We can check the accuracy of this approach by using the estimate of restoration period of carbon storage difference between the 8 and 2 years postfire sites (185 g $C \cdot m^{-2}$). If the value of net flux at the 8 year burn is accepted as the rate of restoration, we get 5 years. But if we use the average value of net flux for the 2- and 8 year burns, we get 9 years. The real age difference between these two burned sites is 6 years, which is intermediate between the two estimates.

Discussion

The alterations in carbon storage at the tundra sites after the fire were mainly due to changes in plant biomass and the thickness of upper organic soil horizons. It is evident that, in the first place, the renewal of carbon content depends on the rate of vegetative cover restoration. Tundra burn sites in this study differ from the other known tundra burns mainly by the pattern of vegetative cover restoration. It has been reported that the rapid renewal of vascular cover occurs in Alaska during the first 2-3 years following fire (Johnson and Viereck, 1983). An 8 years postfire site in tussock tundra in Alaska recovered 80% of vascular plant biomass (Racine et al., 1983). In our case the restoration of vascular cover occurs rather slowly; the biomass storage of foliage of vascular plants at both the 2- and 8 year burns was equal and constituted 37% of the undisturbed state. At the same time, the proportion of total vegetation biomass as mosses at the 8 year burn was 1.5 times greater than at the undisturbed site.

In the Alaskan tundra, the loss of the organic soil horizon after severe and moderate fires is more considerable. For example, at the fire in birch shrub tundra, the organic horizon of 5 cm thick was fully burnt. In tussock tundras with organic soil layer depths of 15-30 cm, moderate fires can burn up to 15 cm (Racine, 1981). In our study, only about 1 cm of the upper organic horizon was lost. We did not find any indications of restoration of the organic soil layer during the 6-year period between these two fires, which is consistent with the other tundra studies, where postfire recovery of the organic horizons is not rapid (Racine et al., 1983).

We estimated the full period of carbon content restoration to its initial state at 60 years as derived from a constant rate of carbon deposition. However, the rate of net primary production can increase along with vegetative cover restoration, and even exceed net production in undisturbed ecosystems. Thus, a 13 year postfire site in tussock tundra in Alaska had a rate of aboveground net primary production almost 1.5 times higher in comparison with the undisturbed state (Oechel, 1993). In our research the GPP at the 8 year burn constituted 92% of that of undisturbed site, and it may possibly increase in the near future. Nevertheless, GPP of the 2 years postfire site was only 50% of the undisturbed state, which is rather less than analogous estimates for tundras of Alaska (Oechel, 1993).

In our study, the undisturbed dwarf-shrub tundra acted as carbon source during the warm season. In the summer of 1996, many days had mean air temperatures greater than +14°C, which led to a change of carbon balance pattern from sink to source in native undisturbed tundra (Zamolodchikov et al., 1997b). During the same period, the burns were acting as carbon sinks. Thi leads to the conclusion, that carbon content restoratio on a postfire sites can occur rather successfully eve under conditions of climate warming. Possibly, plan communities recovering from recent fires will be bette adapted to climate warming than undisturbed tundr ecosystems.

Conclusions

1. Fire in dwarf-shrub moss-lichen tundra may resu in the loss of one-third of total carbon content in th ecosystem.

2. The period of full carbon storage restoration burned tundra sites is about 60 years.

3. Seasonally, postfire sites serve as a carbon sin even when undisturbed tundra ecosystems function carbon sources due to local warming.

Acknowledgments

The research was funded by the Program No "Climate" (Russian Ministry of Science Policy) and t Supplementary program of National Scienti Foundation (USA). Help of A. V. Skichko in the fie investigations is greatly appreciated.

References

Archegova I.B. (1972). *The features of humus creation in soils of the East European tundra.* Syktivkar, Institut Biologii Komi filiala Akademii Nauk (60 pp).

Archegova, I.B., Kotelina, N.C., Grunina L.K. et al. (1991). *Ecological bases of management of agricultural plant communities productivity in the East European tundra.*Leningrad, Nauka, (152 pp).

Billings, W.D., Luken, J.O., Mortensen, D.A. and Peterson, K.M. (1982). Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? *Oecologia,* **53,** 7-11.

Chapman, W.L. and Walsh, J.E. (1993). Recent variations of sea ice and air temperatures in high latitudes. *Bulletin of the American Meteorological Society,* **74,** 33-47.

Fetcher, N., Beatty, T. F., Mullinax, B., and Winkler D. S. (1984). Changes in Arctic tussock tundra thirteen years after fire. *Ecology,* **65,** 1332-1333.

Johnson, L. and Viereck L. (1983). Recovery and active layer changes following a tundra fire in northwestern Alaska. In *Proceedings 4th International Conference on Permafrost, Fairbanks, Alaska.* National Academy Press, Washington, DC. pp. 543-547.

Nazarov, S.K. and Sivkov, M.D. (1995). Effect of climatic warming on the carbon balance and geographical distribution of some tundra plants. In *Global change and Arctic terrestrial ecosystems.* Brussels, Luxembourg, ECSC-EC-EAEC, pp. 221-226.

Oechel, W.C. (1993). *Net ecosystem carbon flux of age specific subarctic tussock tundra stands following fire: implications for Alaska interagency fire management.* PNW 92-0253. Report to the National Park Service. Branch on fire and aviation management. (26 pp).

Oechel, W.C., Hastings, S.J., Jenkins, M., Riechers, G., Grulke, N. and Vourlitis, G. (1993). Recent change of arctic tundra ecosystems from a carbon sink to a source. *Nature,* **361,** 520-523.

Oechel, W.C. and Vourlitis, G.L. (1994). The effects of climate change on arctic tundra ecosystems. *Trends in Ecology and Evolution,* **9,** 324-329.

Oechel, W.C. and Vourlitis, G.L. (1995). Effects of Global Change on Carbon Storage in Cold Soils. In Lai, R., Kimble, J., Levine, E. and Stewart, B.A., (Eds.), *Soils and Global Change.* Lewis Publishers, London, pp. 117-129.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J. and Bochkarev, S.A. (1995). Change in arctic CO_2 flux over two decades: effects of climate change at Barrow, Alaska. *Ecological Applications,* **5,** 846-855.

Racine C.H. (1981). Tundra fire effects on soils and three plant communities along a hill-slope gradient in the Seward Peninsula, Alaska. *Arctic,* **34,** 71-84.

Racine, C.H., Patterson III, W.A., and Dennis, J.G. (1983). Permafrost thaw associated with tundra fires in northwest Alaska. In *Proceedings 4th International Conference on Permafrost, Fairbanks, Alaska.* National Academy Press, Washington, DC, pp. 1024-1029.

Rebristaya O.V. (1977). *Vegetation of the East of Bolshezemelskaya tundra.* Leningrad, Nauka, (334 pp).

Vourlitis, G.L., Oechel, W.C., Hastings, S.J. and Jenkins M.A. (1993). A system for measuring in situ CO_2 and CH_4 flux from unmanaged ecosystems: An arctic example. *Functional Ecology,* **7,** 360-379.

Zamolodchikov, D. G., Karelin, D. V. and Ivaschenko, A.I. (1997a). Carbon balance of tundra landscapes in Central Siberia: observations, simulation and GIS-modeling. *Journal of General Biology, Russian Academy of Sciences,* **58,** 2, 15-33.

Zamolodchikov, D. G., Karelin, D. V. and Ivaschenko, A.I. (1997b). The critical temperature for carbon balance patterns in southern tundra ecosystems. In Lewkowicz, A.G. and Kokelj, S. (eds.), *27th Arctic Workshop. Program and Abstracts.* Ottawa, University of Ottawa, p. 245.

Zimov, S.A., Davidov, S.P., Prosiannikov, S.F., Voropaev, Y.V. and Semiletov, I.P. (1991). Soils of the North - generator of carbon dioxide. *Herald of Soviet Academy of Sciences,* **8,** 71-83.

Zimov, S.A., Zimova, G.M., Davidov, S.P., Voropaev, Y.V., Voropaeva, Z.V., Prosiannikov, O.V., Semiletov, I.V. and Prosiannikova, I.P. (1993). Winter biotic activity and production of CO_2 in Siberian soils: A factor of greenhouse effect. *Journal of Geophysical Research,* **98,** 5017-5023.