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Climatically induced interannual variability in aboveground production in forest-tundra and northern taiga of central Siberia

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Abstract To investigate the variability of primary production of boreal forest ecosystems under the current climatic changes, we compared the dynamics of annual increments and productivity of the main components of plant community (trees, shrubs, mosses) at three sites in the north of Siberia (Russia). Annual radial growth of trees and shrubs was mostly defined by summer temperature regime (positive correlation), but climatic response of woody plants was species specific and depends on local conditions. Dynamics of annual increments of mosses were opposite to tree growth. The difference in climatic response of the different vegetation components of the forest ecosystems indicates that these components seem to be adapted to use climatic conditions during the short and severe northern summer, and decreasing in annual production of one component is usually combined with the increase of other component productivity. Average productivity in the northern forest ecosystems varies from 0.05 to 0.14 t ha⁻¹ year⁻¹ for trees, from 0.05 to 0.18 t ha⁻¹ year⁻¹ for shrubs and from 0.54 to 0.66 t ha⁻¹ year⁻¹ for mosses. Higher values of tree productivity combined with lower annual moss productivity were found in sites in northern taiga in comparison with forest-tundra. Different tendencies in the productivity of the dominant species from each vegetation level (trees, shrubs, mosses) were indicated for the last 10 years studied (1990-1999): while productivity of mosses is increasing, productivity of trees is decreasing, but there is no obvious trend in the productivity of shrubs. Our results show that in the long term, the main contribution to changes in annual biomass productivity in forest-tundra and northern taiga

ecosystems under the predicted climatic changes will be determined by living ground cover.

Keywords Climatic change · Annual increment · Aboveground biomass · Inter-annual variability · Productivity

Introduction

The first stage of accumulation of atmospheric carbon in terrestrial ecosystems is the storage of C in living biomass. The rate of this process can be estimated through measuring of the annual primary production of ecosystems (Gower et al. 1999; Schulze 2000). Climate exerts a strong control on inter-annual variability of net primary production and carbon accumulation at the local, regional and global scale (Goulden et al. 1996; Kindermann et al. 1996; Schimel et al. 2000; Vukicevic et al. 2001; Scholze et al. 2003; Pleshikov et al. 2002). To assess the extent of these changes and estimate the main parameters of carbon balance for the vast territories, global and regional ecosystem models are used (McGuire et al. 2001). The local models of carbon exchange can give reliable results on inter-annual changes in carbon balance for single ecosystems. The best results are obtained if long-term field measurements of ecosystem carbon fluxes are used to calibrate the model. However, the number of studies on multi-year variability of the main parameters of carbon balance is limited. Investigation on year-to-year variability of carbon accumulation in different components of the same ecosystem is especially rare, because of the complexity of measurements and also the necessity of multi-year continuous observations. These difficulties are solved to some extent when chronosequences of ecosystem productivity are used (Schulze et al. 1995; Wirth et al. 2002a). However, the absolute values of productivity cannot be always accurately estimated by such an approach. There are few investigations of inter-annual variations of biomass productivity under changing

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environment in natural forest ecosystems in northern Asia—the region which is characterized by high sensitivity of ecosystems to temperature changes (Wirth et al. 2002b). In the present article, data on annual radial growth of trees and shrubs and linear increment of mosses were used: (1) to compare year-to-year variability of annual increment of the major vegetation components (trees, shrubs and mosses) in forest-tundra and northern taiga ecosystems in Siberia; (2) to analyse climatic response of the indicated vegetation components on yearly and intra-seasonal timescales in dependence on local conditions; (3) to compare trends and year-to-year variations in primary production of these vegetation components during the period 1990-1998.

Material and methods

Site description and material

The experimental sites were established under the International Geosphere-Biosphere Program (IGBP) as permanent plots in the north of central Siberia (Fig. 1). Two of the investigated sites FT-1 and FT-2 are located in the forest-tundra zone (68°20'N, 87°50'E), and site NT in the subzone of northern taiga (65°41'N, 89°37'E) (Pleshikov 2002). The regional climate is characterized as severe and continental. The average annual temperature in forest-tundra is -8.7°C and in northern taiga it increases up to -5.7°C (stations Dudinka and Turukhansk). The amount of annual precipitation is 463 mm in the region of forest-tundra and 500 mm in the northern taiga (Fig. 2).

Site FT-1 was selected to represent an unroofing terrace as a representative site of this area. FT-2 was chosen to characterize low-drainage sites in flat land. Site NT in the northern taiga represents the typical

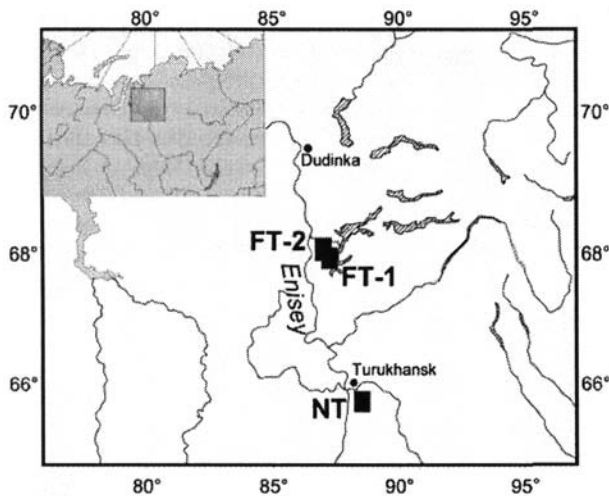


Fig. 1 Location of experimental sites at the forest-tundra zone (FT-1, FT-2) and northern taiga (NT), Dudinka and Turukhansk is climate station

conditions for this zone with drainage conditions comparable to FT-1. The main characteristics of the studied sites are shown in Table 1.

We quantified the annual growth increments of the dominant species for each vegetation component of the forest ecosystems: trees, shrubs, mosses. Larch (*Larix sibirica* Ledeb.) and spruce (*Picea obovata* Ledeb.) are dominant in the investigated stands in the forest-tundra. At the site in the northern taiga, larch is most common. The undergrowth consists of shrubby alder (*Duschekia fructifera* (Rupr.) Pouzar) and several species of willow (*Salix* sp.) are the dominant at all the sites among shrubs. Of the willows we used *Salix jenssensis* (Fr. Schmidt) B. Floder in our study because this species is one of the most widespread along the Siberian IGBP transect. It is also important in terms of biomass accumulated in understorey at the forest ecosystems of this territory. To characterize the annual growth of mosses, *Hylocomium splendens* (Hedw.) Schimp. in B.S.G., as the species which has a well-defined annual increment, was chosen for our investigation (Garibova et al. 1978).

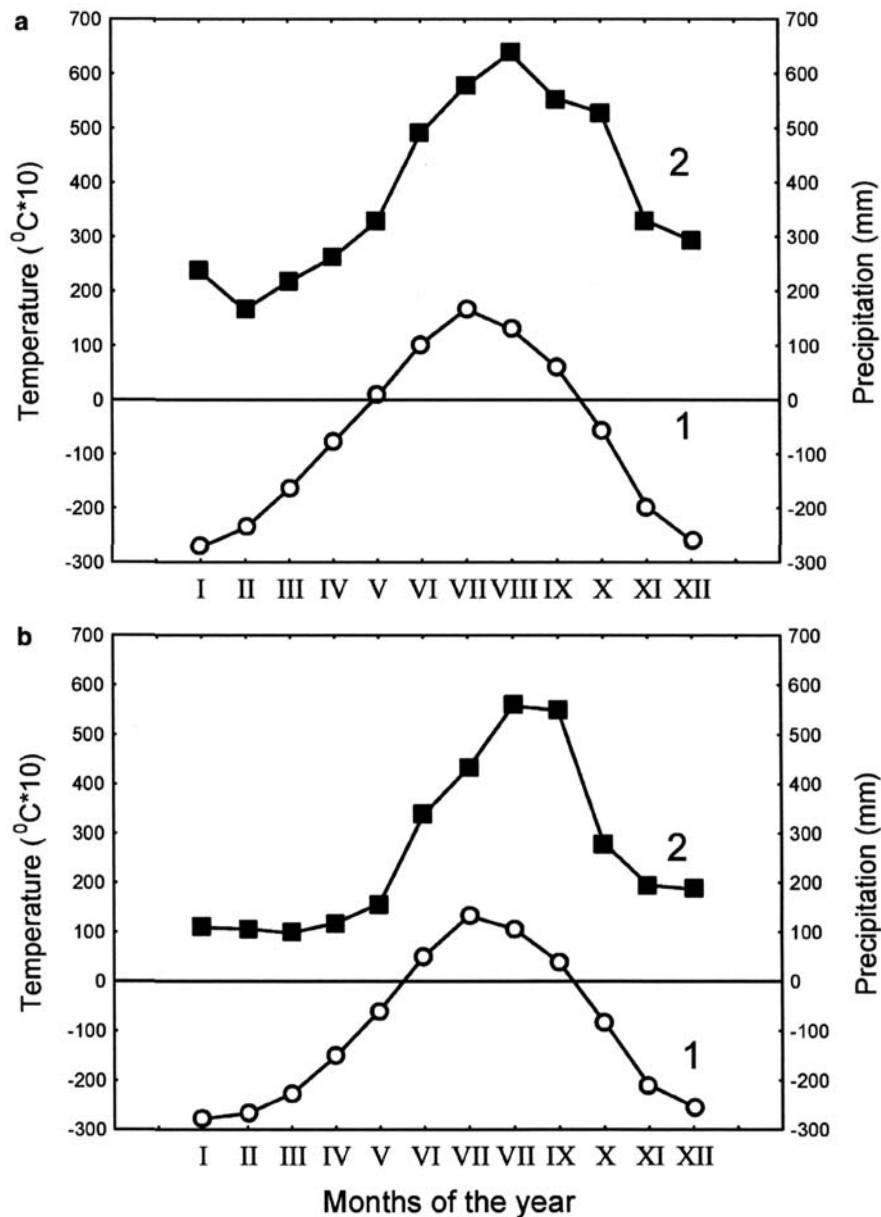
Sampling strategy and measurements of annual increment

To quantify radial growth of trees, we collected wood cores from 20 to 32 trees of each species at a site. Collected tree samples were equally distributed among the variety of diameters at breast height (DBH). The cores were sampled in accordance with the technique accepted in dendroclimatology (Schweingruber 1988). Measurements of tree-ring width and density profiles of wood radial increments were carried out with the use of a densitometer DENDRO-2003 (Walesch Electronics, Switzerland). The tree-ring data were processed in Dendrochronological Program Library (DPL) (Holmes 1992).

Sampling of material from shrubs was carried out for willow and alder separately. These shrubs grow in groups constituted by several shoots of one species. To represent the variety of local conditions in the site, we collected material from each group of shrubs. The branch (shoot) with average parameters of height and diameter was sampled in each group and the number of living branches in the group was calculated. Annual radial increment was measured with the accuracy of 0.01 mm at several heights (every 50 cm along the stem). Gravimetric density of wood of shrubby alder was measured as the mass of oven-dried pieces of wood divided by their volume.

To study annual growth of mosses at each site, 8-10 columns (10.2 cm²) of *Hylocomium* were sampled in three micro-topographic strata: elevated micro-relief (EMR), flat micro-relief (FMR) and micro-depression (MD). Annual linear increment was measured for 25 individual stems from each element of micro-relief at every site. Annual mass increment of mosses was measured for the same samples only for non-decomposed parts of moss stem for the last 10 years with the accuracy of 0.001 g.

Fig. 2 Average values of temperature-1 and precipitation-2 of meteorological stations **a** Turukhansk (1906-1999) and **b** Dudinka (1892-1990)



Climatic response

The climatic response of radial growth of trees and shrubs was estimated in accordance with the standard in dendroclimatology techniques (Fritts 1976; Cook et al.

1990a, b). Indices for the radial growth of woody plants were calculated from the raw data on radial growth of woody plants to eliminate non-climatic signals in ring-width chronologies (especially, age trend) (Cook and Peters 1981). Modified negative exponent or linear

Table 1 Characteristics of studied sites

Site	Tree's density (number/ha)	Average <i>D/H</i> of trees (cm/m)	Aboveground phytomass ^a			Aboveground NPP (t ha ⁻¹ year ⁻¹)	Thawing soil layer (cm)
			Trees (kg/m ²)	Shrubs (kg/m ²)	Mosses and lichens (kg/m ²)		
FT-1 (434)		23/14	3.16	0.18	0.36	2.3	40-60
FT-2 (667)		13,8/9,7	1.91	0.13	0.53	2.0	40-60
NT (401)		21,7/14,7	4.08	0.28	0.72	4.5	>60

^aAboveground biomass (Vedrova et al. 2002) and NPP (Pleshikov et al. 2002) represents a total of all species of each vegetation component in the studied ecosystems

regression approaches were used to fit ring-width data. Dimensionless indices were produced by dividing the measured ring width by the fitted value.

To compare the obtained time series and to characterize the strength of their climatic signal, standard dendrochronological statistics were calculated: the mean correlation coefficient between individual and mean chronology, coefficient of sensitivity, standard deviation. Coefficient of sensitivity and standard deviation allow estimation of environmental impact on tree growth. These parameters range from 0 to 1. The stronger and more correspondent is the response of tree-ring growth to environmental changes, the higher these two dendrochronological statistics.

Correlation coefficients of index chronologies with monthly temperature and precipitation were calculated for the period from September of the previous year until August of the current year. Data from station Dudinka (69°40'N, 86°17'E) for the period 1907-1990 were used for the analysis of chronologies in forest-tundra zone and from Turukhansk (65°78'N, 87°93'E) for the period from 1902 till 1999, for the site in the northern taiga. The detailed dendroclimatic analysis was carried out to understand the intra-seasonal dynamics of temperature influence on radial growth in trees. For this, correlation coefficients were calculated between tree ring-width index chronologies and mean temperature of five consecutive days (pentads) (Vaganov et al. 1999; Kirilyanov et al. 2003; Wang et al. 2002).

Annual production of the vegetation components of forest ecosystems

Evaluation of wood production of stems in trees was carried out separately for different tree classes. Trees of the same species at each site were divided in five classes by DBH. The classes and their number were chosen to have at least one tree with data on ring width and density for each of the classes. Tree-ring data were transferred to data on wood biomass produced annually by each measured tree. We assumed the form of tree stem to be cone shaped, and annual stem wood production (ASWP) was calculated according to:

$$ASWP = \frac{\pi}{12} \left[\frac{H^3 D^2}{(H - 1.3)^2} - \frac{h^3 d^2}{(h - 1.3)^2} \right] \text{Dens,}$$

where, H is the height of a tree in year i , D the DBH in year i , h the height of tree in previous year $i-1$, d the DBH year $i-1$, Dens the average density of tree ring formed in year i . D and d were calculated from tree ring-width data (TRW). For each tree ring, average value of two TRW obtained for different cores from the same tree was used to eliminate the difference in TRW in different directions from pith to bark. Dens was calculated from the density profile of each tree ring measured by means of densitometer DENDRO-2003. H and h were obtained based on tree height measured and

approached that linear stem growth is in direct relation to radial tree-ring growth. The assumptions used in the model are quite rude, but the results obtained are in good agreement with inventory data and tree biomass measurements (Pleshikov et al. 2002; Knorre 2003). Production of these trees was re-calculated to data on wood biomass for each DBH class and then to total stem production of trees in the ecosystem using the inventory data (Osawa et al. 2000).

Annual production of shrubs was estimated based on the same approach for the shape of the model branches as for tree stems and data on average density for the branch. However, TRW in shrubs was measured for each model branch at several heights (every 0.5 m) in 2-4 directions and the formula for truncated cone was used to estimate wood produced each year in the lower parts of model branch. The data for single branch were multiplied to the number of branches in the group from which the branch was taken. The data from each group at site were summed up to evaluate the site production of shrubs (Knorre 2003).

Annual production of mosses was simply obtained as the average mass growth of mosses from different elements of micro-relief multiplied by the area covered by mosses. Comparative analysis of annual production of all the components of ecosystem was difficult to carry out for the whole span of chronologies because of the lack of data on loss of individual trees, shrubs and decomposition of mosses. We assumed that during the last 10 years, these processes did not influence our results significantly and the data that are presented here are on primary production for the last 10 years only.

Results

Statistics of radial increment of trees, in relation to climate

The longest tree-ring chronologies were obtained for spruce (366 years) and larch (360 years) from the site FT-1 in the forest-tundra zone (Table 2). The lowest values of average tree-ring width were found for spruce from FT-2 and larch at the northern taiga site. Coherence in tree-ring growth indicated by correlation coefficients of individual chronologies with mean time series is high at all the sites and for both larch and spruce. Sensitivity of tree-ring chronologies which indicates the strength of environmental impact on tree growth is also high.

Dendroclimatic analysis of tree-ring chronologies shows that summer temperature regime is the main climatic factor influencing tree radial growth in both regions (Table 3). But, trees of different species growing at the same site react to climate in different ways. Thus, larch shows approximately equal high correlation with June and July temperature, but tree-ring width of spruce is more dependent on the temperature of July.

At the site NT in northern taiga, radial growth of larch is also positively correlated with temperature

Table 2 Statistical parameters of tree-ring width chronologies (raw data)

Site	Species	Period (years)	The number of trees measured	Tree-ring width (mm)		The mean correlation coefficient between individual and mean chronology	Coefficient of sensitivity	Standard deviation (mm)
				Max.	Mean			
FT-1	<i>Larix sibirica</i>	1638-1998	52	2.21	0.51	0.78	0.42	0.32
	<i>Picea obovata</i>	1632-1998	51	2.43	0.35	0.68	0.27	0.19
FT-2	<i>Larix sibirica</i>	1723-1998	29	2.24	0.43	0.71	0.37	0.27
	<i>Picea obovata</i>	1676-1998	46	1.36	0.24	0.66	0.30	0.13
NT	<i>Larix sibirica</i>	1657-1998	33	2.67	0.34	0.67	0.42	0.22

of June and July. Additionally, a negative correlation of radial growth to April temperature is found. Influence of precipitation on larch and spruce radial growth in forest-tundra is insignificant. Chronology from the site in northern taiga correlates negatively with April precipitation ($R = -0.24$, $P < 0.05$).

Detailed dendroclimatic analysis—correlation of tree-ring chronologies with pentad temperatures (Fig. 3)—shows that radial growth in larch on the drier site is connected to the temperature of the period started from 7 June. In spruce at the same site it starts 5 days later. But under wetter conditions tree-ring width of both larch and spruce correlates with temperature of the later period (from 27 June). In the northern taiga the growth of larch shows a positive correlation with temperature already from June, 2. Periods with significant influence of temperature on tree radial growth end during the first decade of July at site FT-1 and by the end of July at two other studied sites (FT-2, NT).

Statistics of radial increment of shrubs, in relation to climate

The lengths of the ring-width chronologies of willow and alder range from 40 to 70 years (Table 4). The average annual increment of shrubs is comparable to that of trees and decreases with increasing wetness of the sites. In contrast to trees, correlation coefficients between individual and mean chronologies of shrubs are lower at wetter sites. Sensitivity of the chronologies obtained for shrubs from sites with different conditions is quite high.

Dendroclimatic analysis of shrubs indicates that climatic response of their ring growth is species specific and depends on local conditions (Table 5). Thus, at the drier site FT-1 in the forest-tundra zone significant correlation was found for ring width of willow with June

Table 3 Correlation coefficients of tree-ring index chronologies with monthly temperature

Site	Species	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII
FT-1	<i>Larix sib.</i>	0.31								0.57	0.52		
	<i>Picea ob.</i>									0.30	0.44		
FT-2	<i>Larix sib.</i>									0.55	0.55		
	<i>Picea ob.</i>									0.38	0.43		
NT	<i>Larix sib.</i>								-0.24	0.36	0.24		

and July temperature, and for alder—with the temperature of July. At the wetter site FT-2, a negative correlation of ring width of alder with spring temperature was observed. Ring width of willow from the same site showed significant correlation with the temperature of June. For the site in the northern taiga only a positive correlation of the alder chronology with the temperature of July was found. Patterns of ring growth of shrubs to precipitation also depend on species and site.

Annual growth of mosses

Minimal annual increments of mosses are mostly observed for micro-depressions (1.8-3.0 mm in the forest-tundra and 1.2 mm in the northern taiga). But the maximum values of linear increment of mosses do not change significantly from one position in micro-relief to another in the site. In general, there is a slight difference between maximal values of linear increment in forest-tundra (20.5-24 mm) and northern taiga (22.5-26.6 mm). Mean values of increment obtained for the sites increase in north-south direction from 10.3 mm on FT-1 and 8.7 mm on FT-2 to 11.4 mm on NT.

Quite a different pattern is observed for mosses, if their annual mass increments are compared. There is no clear dependence of this parameter from position in micro-relief. Minimal values of mass increment observed

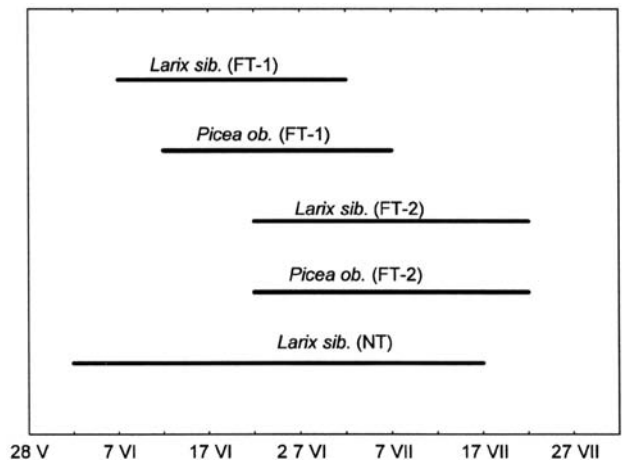
**Fig. 3** Periods with significant influence of temperature on radial tree growth defined for pentads

Table 4 Statistical parameters of radial increments of shrubs (raw data)

Site	Species	Period (years)	The number of samples measured	Tree-ring width (mm)		The mean correlation coefficient between individual and mean chronology	Coefficient of sensitivity	Standard deviation
				Max.	Mean			
FT-1	<i>Duschekia fruticosa</i>	1959-2000	13	2.73	0.58	0.60	0.42	0.31
	<i>Salix jenisseensis</i>	1974-2000	12	1.60	0.51	0.46	0.42	0.23
FT-2	<i>Duschekia fruticosa</i>	1937-2000	14	1.71	0.41	0.26	0.48	0.25
	<i>Salix jenisseensis</i>	1936-2000	16	1.8	0.42	0.39	0.49	0.28
NT	<i>Duschekia fruticosa</i>	1931-2000	25	1.97	0.51	0.46	0.52	0.29

at each forest zone are quite close (approximately 0.5 mg), but in general maximum values of mass increment increase from forest-tundra (33.0 mg) to northern taiga (42.4 mg). The tendency of increase in north-south direction is also observed for annual mass increment averaged for each site (from 6.7 mg and 5.4 mg on FT-1 and FT-2, respectively to 8.9 mg on NT).

Variability of tree-ring width, annual increment of shrubs and mosses

Comparative analysis of tree ring-width chronologies obtained for different sites shows that the highest correlation was found for larch index chronologies from sites FT-1 and FT-2 in the same vegetation zone ($R = 0.85$, $P < 0.005$). Relationship between time series of spruce from these two sites is lower, but still very high ($R = 0.75$, $P < 0.005$). Fewer correlations were found between larch chronologies obtained for sites in different vegetation zones ($R = 0.47$ for FT-1 and NT and $R = 0.26$ for FT-2 and NT).

Results in Table 6 indicate that correlation between tree-ring chronologies of larch and spruce from the same site does not depend significantly on local conditions. However, the latter can greatly influence the relation of radial growth series of shrubs. Moreover, relation of shrub chronologies with time series of conifers is different for the sites with various local conditions. Thus, time series of alder strongly and positively correlate with chronologies of conifers on the drier site FT-1. But in case of the wet site FT-2, correlation of alder chronologies with chronologies of conifers is insignificant. Willow does not show such a tendency. Their correlation with time series of other species is either insignificant or

week on both sites. It is necessary to note that there is no significant relationship between chronologies obtained for shrubs. Significant correlation was found neither for chronologies of the same species from different sites nor for chronologies of different species from the same site.

Correlation of the annual linear increment of mosses with chronologies of woody plants is negative in most of the cases (Table 7). It is especially well pronounced for elevated elements of micro-relief and for shrubs at the drier site FT-1 in the forest-tundra.

Comparative analysis of productivity of different components of the ecosystems

Annual production of different components of ecosystems was calculated only for site FT-1 and NT to allow comparison of production at sites with similar local conditions (i.e. wetness). Period of consideration covered 1990-1999 only. It could be obtained based on maximum length of moss production data (Table 8).

Average wood productivity of larch and spruce in forest-tundra zone during the last 10 years (1990-1999 year) was very similar—about $0.05 \text{ t ha}^{-1} \text{ year}^{-1}$ (standard deviation was $0.02 \text{ t ha}^{-1} \text{ year}^{-1}$ for larch and $0.01 \text{ t ha}^{-1} \text{ year}^{-1}$ for spruce). However, productivity greatly varies from year to year. Thus, in larch it was 0.01 t ha^{-1} for 1997, but in 1996 wood production was 0.07 t ha^{-1} and in 1998 0.06 t ha^{-1} . In spruce during these years wood productivity changed from 0.01 to $0.05 \text{ t ha}^{-1} \text{ year}^{-1}$. In the northern taiga zone the average productivity (\pm standard deviation) of larch is higher ($0.14 \pm 0.04 \text{ t ha}^{-1} \text{ year}^{-1}$) and the mean annual NPP per site ranges between 0.06 and $0.18 \text{ t ha}^{-1} \text{ year}^{-1}$ during the last 10 years.

The average annual stem production of shrubby alder at the forest-tundra site is $0.19 (\pm 0.06) \text{ t ha}^{-1} \text{ year}^{-1}$. In the northern taiga it is much higher and reaches $0.36 (\pm 0.09) \text{ t ha}^{-1} \text{ year}^{-1}$. Variations of stem productivity in shrubby alder in adjoining years can be from 0.07 to $0.26 \text{ t ha}^{-1} \text{ year}^{-1}$ on site FT-1 and from 0.26 to $0.52 \text{ t ha}^{-1} \text{ year}^{-1}$ on NT. Wood production may differ from year to year by factor 3 in the forest-tundra and by factor 2 in the northern taiga. It is interesting that annual radial increment of shrubs in forest-tundra and northern taiga is quite close, but annual production is

Table 5 Correlation coefficients of ring-width index chronologies of shrubs with monthly temperature

Site	Species	IX	X	XI	XII	I	II	III	IV	V	VI	VII	VIII
FT-1	<i>Dusch. frut.</i>											0.53	
	<i>Salix jen.</i>										0.49	0.50	
FT-2	<i>Dusch. frut.</i>							-0.38		-0.59			
	<i>Salix jen.</i>										0.33		
NT	<i>Dusch. frut.</i>									-0.33		0.25	

Table 6 Correlation coefficient between tree-ring width index chronologies and standardized time series of radial increment of shrubs from the same sites in forest-tundra and northern taiga

	FT-1			FT-2			NT
	<i>Larix sib.</i>	<i>Picea ob.</i>	<i>Dusch. fr.</i>	<i>Larix sib.</i>	<i>Picea ob.</i>	<i>Dusch. fr.</i>	<i>Larix sib.</i>
<i>Picea ob.</i>	0.47*			0.52*			
<i>Duschekia fr.</i>	0.75*	0.76*		-0.27	-0.09		0.06
<i>Salix jen.</i>	0.39*	0.36*	0.19	0.38*	0.06	0.08	

*Correlation significant at $P < 0.05$

Table 7 Correlation coefficients of linear increment of mosses with ring-width chronologies of woody species in forest-tundra and northern taiga

	Site	Woody species	Position of mosses in micro-relief		
			EMF	FMF	MD
	FT-1	<i>Larix sibirica</i>	-0.66*	-0.21	-0.18
		<i>Picea obovata</i>	-0.48*	-0.22	-0.03
		<i>Duschekia fruticosa</i>	-0.67*	-0.55*	-0.45*
		<i>Salix jenisseensis</i>	-0.83*	-0.45*	-0.58*
Mosses were sampled in three micro-topographic strata: <i>EMF</i> elevated micro-relief; <i>FMF</i> flat micro-relief; and <i>MD</i> micro-depression	FT-2	<i>Larix sibirica</i>	-0.15	-0.22	0.38*
		<i>Picea obovata</i>	-0.30	-0.45*	-0.21
		<i>Duschekia fruticosa</i>	-0.38	-0.30	0
		<i>Salix jenisseensis</i>	-0.26	-0.44*	0.45
*Correlation significant at $P < 0.05$	NT	<i>Larix sibirica</i>	-0.01	-0.02	0.29
		<i>Duschekia fruticosa</i>	-0.40*	-0.32	0.18

almost two times higher in northern taiga. The difference in annual production is caused by the height and thickness of the stems of shrubby alder. Thus, individual stems of alder in northern taiga can reach 3.5 m in height and can be thicker more than 30 mm.

The average annual production of mosses at the site in forest-tundra is $0.66 (\pm 0.13) \text{ t ha}^{-1} \text{ year}^{-1}$. It is much higher in comparison with stem production of trees and shrubs. Moss productivity is even higher for elevated elements of micro-relief and can reach $0.95 \text{ t ha}^{-1} \text{ year}^{-1}$. Productivity of mosses in forest-tundra averaged for the site varies from year to year more than two times: from 0.43 to $0.87 \text{ t ha}^{-1} \text{ year}^{-1}$. In northern taiga mean annual growth of moss biomass is lower $0.54 (\pm 0.10) \text{ t ha}^{-1} \text{ year}^{-1}$. The highest contribution is made by mosses at micro-depressions (up to $0.90 \text{ t ha}^{-1} \text{ year}^{-1}$) and moss production averaged for the ecosystem here varies from 0.37 to $0.64 \text{ t ha}^{-1} \text{ year}^{-1}$.

Table 8 Average annual production of the studied components of the ecosystems*, $\text{t ha}^{-1} \text{ year}^{-1}$

	FT-1	NT
Trees stem wood (larch)	0.045	0.143
Shrubs stem wood (alder)	0.191	0.359
Mosses (hylocomium)	0.659	0.539
Total	0.941	1.041

*Average values for 10 years for trees and shrubs, for 8 years for mosses

In Fig. 4 inter-annual variations of stem biomass production of trees and shrubs and also variations of moss productions during the last 10 years are presented. In spite of difference in values of stem production of trees in forest-tundra and northern taiga, there is a tendency for it to decrease in both zones. On the contrary, production of biomass of mosses clearly shows a positive trend in both vegetation zones. There is no distinct evidence for changes in stem productivity of shrubs on a decadal scale during the considered period.

Discussion

It is well established in dendroclimatic literature that summer temperature (especially, June-July temperature) is the main environmental factor influencing conifer radial-growth in the north of Eurasia (Vaganov et al. 1996; Briffa et al. 2001). Our results confirmed this. However, we have found clear evidence for the differences in the climatic response of different species growing under the same conditions. Thus, in forest-tundra the period with significant correlation between tree-ring width and temperature of pentads for larch starts one pentad earlier than for spruce. A difference in response was also observed in the same species from different conditions. For example, radial growth of larch and spruce from the wetter site FT-2 in forest-tundra correlates with the temperature of later period than at the drier site FT-1. The shift is about 15 days.

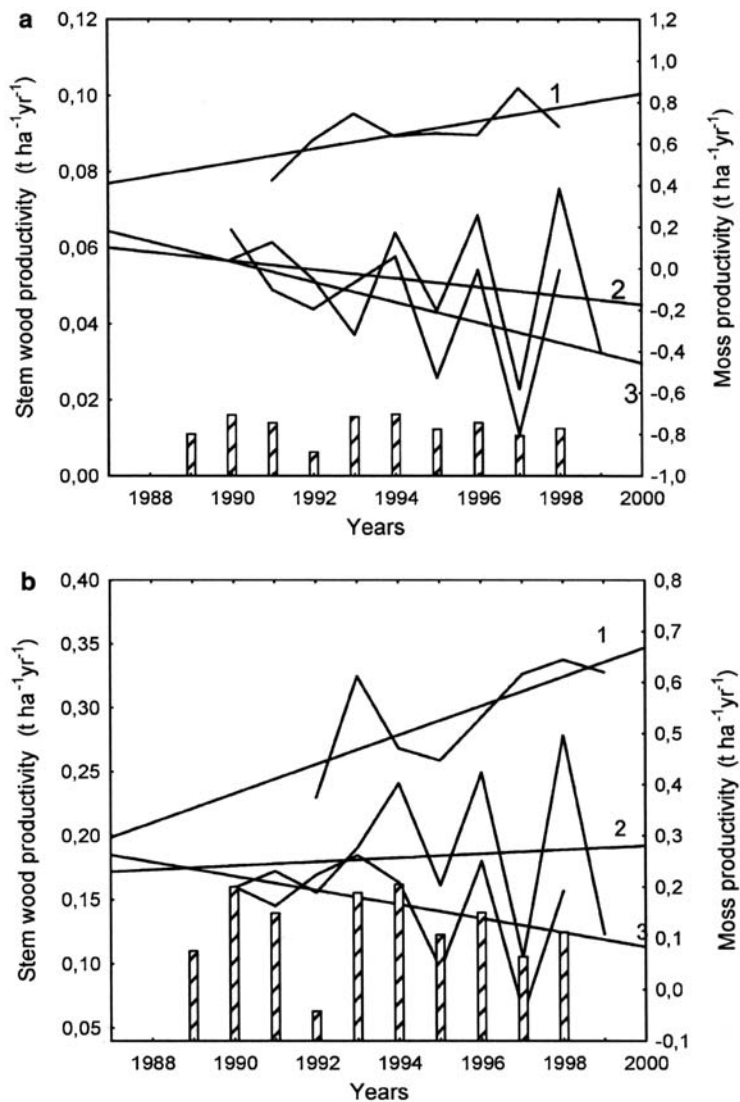
One of the possible reasons for the difference in climatic response of larch and spruce may be various

physiological features of these species. It is well known that larch is the most adapted conifer to grow in the north of Asia under continental climate. *Larix* spp. is characterized by better ability to use light and thermal conditions at the beginning of growing season because of lower temperature threshold of growth initiation than in other species. Temperature increase at the beginning of vegetation period leads to earlier initiation of the assimilatory apparatus. In turn, it means larger amounts of photosynthate that could be produced during the season and used for tree radial growth (tree-ring width) in larch.

Radial growth of trees was shown to be dependent on June-July temperatures both in northern taiga and in the forest-tundra of Middle Siberia. However, in northern taiga there is a 5-day shift to the earlier dates for the period when temperatures are important for tree-ring growth in comparison to that of in forest-tundra. More south location of the site defines earlier snow

melting and, consequently earlier warming of soil above 0°C. Negative influence of April temperature is likely to become apparent due to a number of years with much higher monthly temperatures than the average for the period by records. Extremely high temperature in April for several years (up to 1.5°C) is followed by temperature decrease in May. It can lead to cessation of growth processes which started in April and damage the cambium and surface roots. Negative influence of April temperature on larch tree-ring growth is typical for the region (Panyushkina et al. 1996). It is necessary also to note that during the last 10 years, mean April temperatures in this region increased approximately as much as 1°C in comparison with the average for more than a 100-year period of instrumental observations. The negative influence of April precipitations on tree radial growth is likely to be defined also by the features of snow cover formation and melting. Snow cover was shown to be important for the initiation of cambium (Vaganov

Fig. 4 Changes in annual production (lines) of mosses (1) and stem wood of shrubs (2) and trees (3) during the last decade in forest-tundra (a) and northern taiga (b) in relation to mean June-July temperature (column, $T/1000$ for a and $T/100$ for b)



et al. 1999; Kirdyanov et al. 2003), because it defines snow-melting time and temperature regime at the beginning of growing season. It also plays a great role as a source of water at the beginning of vegetation period.

Summer temperatures are important not only for tree-ring growth but also for radial growth of shrubs. As with trees, various species of shrub are influenced by temperature of different periods. Thus, June-July temperature is important for willow, but only the July temperature for alder at FT-1.

An important finding of our investigation is that dominant species of each vegetation component of ecosystems in forest-tundra and northern taiga in Middle Siberia are characterized by different responses to climate variations. Thus, growth of mosses shows negative correlation with radial growth of trees and shrubs which is possibly due to a negative influence of high early summer temperature. It can also be connected to water loss of the upper soil horizons. At low summer temperatures, growth of mosses does not considerably decrease because the depth of the thawed soil horizon (including litter) is enough for mosses to realize their growth potential. In contrast, narrow (and the so-called 'missing') rings are formed in trees in cold years because of low air temperature. Temperature stress is usually combined with the effect of small depth of soil horizon melted (Jarvis and Linder 2000). Taking into account the difference in climatic response of the different vegetation components of northern forest ecosystems, we can conclude that these components are adapted to use climatic conditions during the short and severe northern summer. Thus, for the considered forest-tundra ecosystem, loss in annual production of stem wood in trees in a cold year ($-0.14 \text{ t ha}^{-1} \text{ year}^{-1}$) is compensated by an increase in annual moss production ($+0.20 \text{ t ha}^{-1} \text{ year}^{-1}$).

The results obtained provide us with the ability to predict changes in vegetation growth in the north under possible regional climate changes. Taking into account the contribution of every vegetation component of ecosystem to total carbon budget, we can suggest that the main changes in overall net primary production under increasing temperature are caused by changes in production of trees and shrubs. This conclusion follows from high inter-annual variability of stem productivity obtained both for trees and shrubs and low year-to-year variability of annual productivity in mosses.

In the case of a temperature increase accompanied by an increase in water deficit due to higher evapotranspiration, the mean annual productivity of mosses will decrease. At the same time, the increase of water deficit will lead to a decrease of annual wood productivity in shrubs and trees. It will be more pronounced in shrubs because their root system is located at upper soil horizons which are more affected by air temperature variations and, consequently faster dehydration under temperature increase. On the other hand, warming will lead to melting of deeper soil horizons and better availability of water and nitrogen from these horizons

for trees. It will partly compensate the possible water deficit of trees and, consequently decrease wood production of trees. Anyway, total annual productivity in forest-tundra ecosystems under combined effect of both increasing temperature and water deficit will decrease because of suppression of moss growth.

In the long term, losses of total primary production under climatic changes will be compensated by the increase of both tree growth and stand density in the existing forest areas. There will also be expansion of forest into tundra which will lead to a change of forest-tundra ecosystems to that typical for the northern taiga.

Meridional changes in ratio of annual productivity between woody plants and mosses can be well understood from the biology of forest vegetation and are likely to be connected to the three main factors which define composition and distribution of species in high latitudes: climatic conditions, pattern of permafrost and fire regime. Increase of annual stem productivity of trees and shrubs obtained for the southern site in northern taiga, in comparison with that in forest-tundra, is related to the improvement of climatic conditions (temperature, length of vegetation and frost-free periods, etc). This has an opposite effect on the productivity of mosses, which decreases from the north to the south; however, their contribution in cumulative ecosystem productivity is still much higher than that of trees and shrubs.

In the forest-tundra zone only upper horizons of soil are melted and seasonal depth of melted soil limits the activity of root systems. Therefore, species with surface root system (shrubs) and without roots (mosses) have an advantage under these conditions in comparison with trees. In northern taiga the depth of seasonally thawed soil is much greater. Consequently, suppressed impact of permafrost on the development of root system of trees is much less and trees can better use minerals and nutrients from soil. So, in northern taiga, trees have the higher potential to grow than in forest-tundra.

Frequency of forest fires also changes along the Yenisey meridian (Furyaev et al. 2001). The mean inter-fire interval in forest-tundra zone is up to 275 years but in northern taiga—only about 80 years (Arbatskaya 1998; Ivanova 1996). The major types of fires in the north of Siberia are surface fires. They almost destroy all living ground cover and, therefore, remove 60-70% of annual production of ecosystems. When several years are needed for the ecosystem to recover after fire (Abaimov et al. 1997; Sofronov and Volokitina 1998), total losses in productivity of the forest ecosystem can be up to $4\text{-}5 \text{ t ha}^{-1} \text{ year}^{-1}$. The magnitude of losses of annual production due to forest fires shows how important the question about the increase of fire regime under predicted climatic changes, which lies in the estimation of the carbon budget of boreal forests.

In general, our results show that the main contribution to changes in annual biomass productivity in forest-tundra and northern taiga ecosystems under

the predicted climatic changes will be determined by living ground cover.

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