Acclimation of Russian forests to recent changes in climate

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Abstract

Assessments made over the past few decades have suggested that boreal forests may act as a sink for atmospheric carbon dioxide. However, the fate of the newly accumulated carbon in the living forest biomass is not well understood, and the estimates of carbon sinks vary greatly from one assessment to another. Analysis of remote sensing data has indicated that the carbon sinks in the Russian forests are larger than what has been estimated from forest inventories. In this study, we show that over the past four decades, the allometric relationships among various plant parts have changed in the Russian forests. To this end, we employ two approaches: (1) analysis of the database, which contains 3196 sample plots; and (2) application of developed models to forest inventory data. Within the forests as a whole, when assessed at the continental scale, we detect a pronounced increase in the share of green parts (leaves and needles). However, there is a large geographical variation. The shift has been largest within the European Russia, where summer temperatures and precipitation have increased. In the Northern Taiga of Siberia, where the climate has become warmer but drier, the fraction of the green parts has decreased while the fractions of aboveground wood and roots have increased. These changes are consistent with experiments and mathematical models that predict a shift of carbon allocation to transpiring foliage with increasing temperature and lower allocation with increasing soil drought. In light of this, our results are a possible demonstration of the acclimation of trees to ongoing warming and changes in the surface water balance. Independent of the nature of the observed changes in allometric ratios, the increase in the share of green parts may have caused a misinterpretation of the satellite data and a systematic overestimation by remote sensing methods of the carbon sink for living biomass of the Russian forest.

Keywords: acclimation, carbon, climate change, forest

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Introduction

Analysis of satellite data has revealed an increase in the normalized difference vegetation index (NDVI) in Eurasia and North America as such observations began in the early 1980s (Myneni *et al.*, 2001; Slayback *et al.*, 2003). Russian forests, which account for more than 70% of all circumpolar boreal forests (FAO, 2001), have undergone substantial greening from the Taiga to the Forest Steppe on the west side of the Ural Mountains and along the zone of the Southern Taiga in Siberia. To the east of the

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Ural Mountains, in northern Siberia, the NDVI shows a slight downward trend. Despite negative trends over some regions, averaged over Eurasia as a whole, the seasonally accumulated NDVI shows an increase of $\sim 12\%$ during the 1982–1998 period (Myneni *et al.*, 2001). It has been suggested that this increase in NDVI reflects a large carbon sink in the living woody biomass of Russian forests of ~ 284 Tg of carbon per year (Tg C yr^{-1}) over the period 1995–1999 (Myneni *et al.*, 2001). For Russian forest conditions, this figure corresponds to ~ 560 Tg of dry matter or a net increment of about $1 \times 10^9 \text{ m}^3$ of growing stock per year (Shvidenko & Nilsson, 2003). Thus, in line with this estimate, the

forests should have increased in growing stock by $\sim 5 \times 10^9\,\mathrm{m}^3$ over this 5-year period. However, in a 1998 report, the national forest inventory shows a net increase of only $1.19 \times 10^9\,\mathrm{m}^3$ of growing stock as compared with the 1993 inventory (FFSR, 1999). In our view, the large discrepancy between forest inventories and satellite-based estimates arises, not from random errors, but from the changes in tree structure and some other changes in the Russian forests.

A possible clue, regarding how trees might have changed during the 20th century can be found through the analysis of tree ring records. In 1998, a study of more than 300 composite tree ring records from the Northern Hemisphere revealed a robust decline in the strength and structure of regression models for tree ring indexes and climatic variables (Briffa et al., 1998a, b). This breakdown in model performance included both, a systematic overestimate of growth, and a significant loss of correlation between tree rings and climate after 1960 (Cook & Zedaker, 1992; Briffa et al., 1998a). A similar decline in the apparent sensitivity of tree proxies to changes in climate was found in the south of Scandinavia (Briffa et al., 1998b) and in the Southern Taiga and the Mixed Forest of Eastern United States (Johnson & Siccama, 1983; Hornbeck & Smith, 1985; Cook & Zedaker, 1992). It is important to stress that the decline in annual tree ring growth was concurrent with significant increase in seasonally accumulated NDVI over Eurasia and the Eastern US. Thus, while during the last 40 years, the temperature and the NDVI of the Russian forest have been associated with a positive trend, there has been a decline in the sensitivity of the tree ring indexes to the increase in temperature. After the removal of trends in tree ring data, the interannual variability of the tree rings and the NDVI show a correlation only for June and July while there is an absence of correlation for spring and the fall months (Kaufmann et al., 2004). The latter indicates that, at the beginning of the growing season (April–May), trees accumulate carbon mainly in the production of leaves and only subsequently, in June–July, they begin to store carbohydrates in the stem wood while continuing the allocation to green parts. Over the past 40 years, the snow pack has started to melt earlier in the year and the growing season in boreal forests has become longer (Groisman et al., 1994; Brown, 2000). Therefore, one might speculate that the period of carbon allocation to green parts is taking a larger fraction of the entire growing season. Unfortunately, a more detailed comparison of climate and tree rings or NDVI and tree rings is limited because of the accessibility of tree ring records. Most tree ring data for the Russian territory are available up to around 1990–1992 (NOAA, 2005). The authors are aware of only one publication (Lawrence

et al., 2005) that analyzes the post-1992 relationship between the climate, NDVI, and tree ring data for the Russian forest (St Petersburg region). In that work, the strongest divergence between NDVI and tree ring data was found for the last two decades of the 20th century.

It is possible that because of the proximity of the latter study area to a large industrial city, this particular case of slower tree growth as well as some cases in the North-eastern US were caused by acid deposits and significant loss of soil calcium (Lawrence et al., 2005). However, this explanation is hard to apply in numerous cases of climate and tree rings decoupling along the unpolluted Siberian tree line border. Some authors believe that in the north of Siberia, a tree response to moisture and seasonal distribution of precipitation might change over time (Vaganov et al., 1999) or that the increase in the surface concentration of ozone and other air pollutants might suppress the growth of trees in boreal regions (Cook & Zedaker, 1992; Briffa et al., 1998a, b). However, all these suggestions only address the decline in the radial growth of the stem wood of trees and do not explain an apparent contradiction between a good correlation of changes in surface temperature with NDVI on the one hand (Zhou et al., 2003), and a divergence of decadal trends of climate and tree ring proxies on the other hand (Cook & Zedaker, 1992; Briffa et al., 1998a, b; Vaganov et al., 1999). In other words, until recently, the question of why, at the end of 20th century, the photosynthetic apparatus of trees might grow more vigorously than the stem wood has remained open.

We hypothesize that this 'tree ring–NDVI paradox' is caused by the fact that, over the last 40 years, the trees have increased the share of photosynthetic tissue at the expense of their water conducting tissue (stem wood and roots). Therefore, the NDVI, which reflects an abundance of green parts, has shown an increase, while the annual increments of tree rings from the same area have shown a relative decrease or a slower radial growth at the end of the 20th century in comparison with trees of similar age, as well as, in the years with about the same weather conditions that prevailed during the beginning of the 20th century.

The spatial variation in the NDVI is a result of changes in the density of the forests' green canopy per unit ground area. However, for the purpose of carbon sink estimates, seasonally accumulated NDVI were calibrated on ground-based estimates of total living biomass (Myneni et al., 2001). This calibration holds true only if the percentage of foliage in the living biomass remains constant. In the study conducted over a north–south transect in Europe, it was found that the ratio between foliage biomass to sapwood area of *Pinus sylvestris* mature trees increases with an increase in the

annual mean temperature (Palmroth *et al.*, 1999). Studies of *P. ponderosa* and *P. taeda* seedlings growth revealed that the ratio of foliage to fine root biomass increases sharply as the growing season temperature at the place of origin of these seedlings increases (Bongarten & Teskey, 1987; Gregg, 1994). These data favorably agree with some computer models of the adjustment of tree structure to environmental changes under hydraulic constraints (Magnani *et al.*, 2002). However, the question remains whether the observed spatial distribution of the foliage to sapwood ratio of trees is the result of their ability to adjust to relatively fast changes in environment (phenotypic plasticity) or as a result of their long-term evolution strategy. Therefore, it is unclear as to what time scale is needed for these particular adaptations to occur. At the same time, in a changing environment (e.g., changes in temperature, nutrient supply, luminosity, water regime), plants are capable of maximizing their productivity by rapidly adjusting the carbon allocation (Bazzaz, 1997). A pronounced change in the structure of plants subjected to a changed environment was documented using *in situ* and *in vitro* experiments lasting from a few months to a decade (Reekie & Bazzaz, 1987; DeLucia *et al.*, 2000; LaDeau & Clark, 2001). Therefore, even during short periods, climatic and other environmental changes could affect the allometric ratios of trees, thereby altering the relationship between NDVI and the total living biomass.

During most of the 20th century, the Northern Hemisphere was subjected to industrial pollution, and changes in regional and global climate. Climatic trends and the atmospheric load of nitrogen and other chemicals were especially significant in Western Europe, Central and North-eastern US, and North-western Russia. In the following paragraphs, we describe our assessment of the changes in allometric ratios of the Russian forest, and analyze a possible link between these changes and trends in climate and atmospheric pollution during the last four decades of the 20th century.

Materials and methods

Data collection

In Russia, the main administrative units of the national forest inventory are the State Forest Management Enterprises (*Leskhozes* for short in Russian). Inside each Leskhoz there is a substantial number of primary inventory units (PIUs), which are represented by forest stands (forested areas) as well as by areas temporarily not covered by forests (burnt areas, etc.). There are more than 50 million PIUs within the 1830 Leskhozs in Russia (FFSR, 1999). A typical size of these units varies from 3

to 5 ha in European Russia to more than 50 ha in Siberia and the Russian Far East. Every 10–12 years these units are subject to a detailed survey by forest inventory teams. These teams assess the full biometric characteristics of each PIU, including the relative composition of species, the average diameter of trees at breast height (DBH), height of tree, relative stocking (RS, or basal area per hectare), growing stock (GS), and site index (SI). Forest inventory data at each PIU are used by the Leskhozes for planning forest management. Over the entire country, the PIU data are collected at each Leskhoz and presented at definite intervals (usually 5 years) in the State Forest Account. However, the routine forest inventories are not responsible for direct estimates of live biomass. The latter is measured at a much smaller number of sample plots through a destructive gravimetric technique employed by scientific research groups. During this process of destructive measurements, trees are cut and root systems are extracted from the ground (including fine roots where possible). Sample parts of trees are dried and weighed and the weight of each part is estimated independently from the others. Usually, it takes 2–4 weeks for three to five people to complete the measurements at a single sampling plot. As a rule, 10–30 randomly selected trees are subjected to destructive analysis. Our database contains information on 3196 sample plots (∼ 50 000 entries) and part of the data was collected through direct participation of the authors of this paper. Furthermore, the database contains all available archived and published data (Shvidenko & Nilsson, 2003). The distribution of data by major ecological regions (ecoregions) of Russia and groups of tree species is shown in Fig. 1 and Table 1.

The database of live biomass fractions of forest ecosystems

Following up the preceding discussion, it should be noted that the database does not directly represent the biomass inventory data for the whole Russian forest. Instead, this database contains multiple 'snapshots' of forest stands at selected sites. In the present study, we have used the latest version of this database, which contains data collected from 1953 to 2002. The seven biomass' fractions (stem wood and crown wood – both over bark, bark, foliage, roots, understory, green forest floor) are expressed as ratios of the mass of specific fractions to growing stock (i.e., stem volume of all living trees of a forest ecosystem). The data reflects all 28 ecoregions covering the Russian territory with forest growth and the major tree species of Russian forests (Fig. 1, Table 1).

In the Russian forests, coniferous species account for ∼ 80% of the growing stock and ∼ 70% by area (Alexeyev & Birdsey, 1998). In 1993, the average pan-
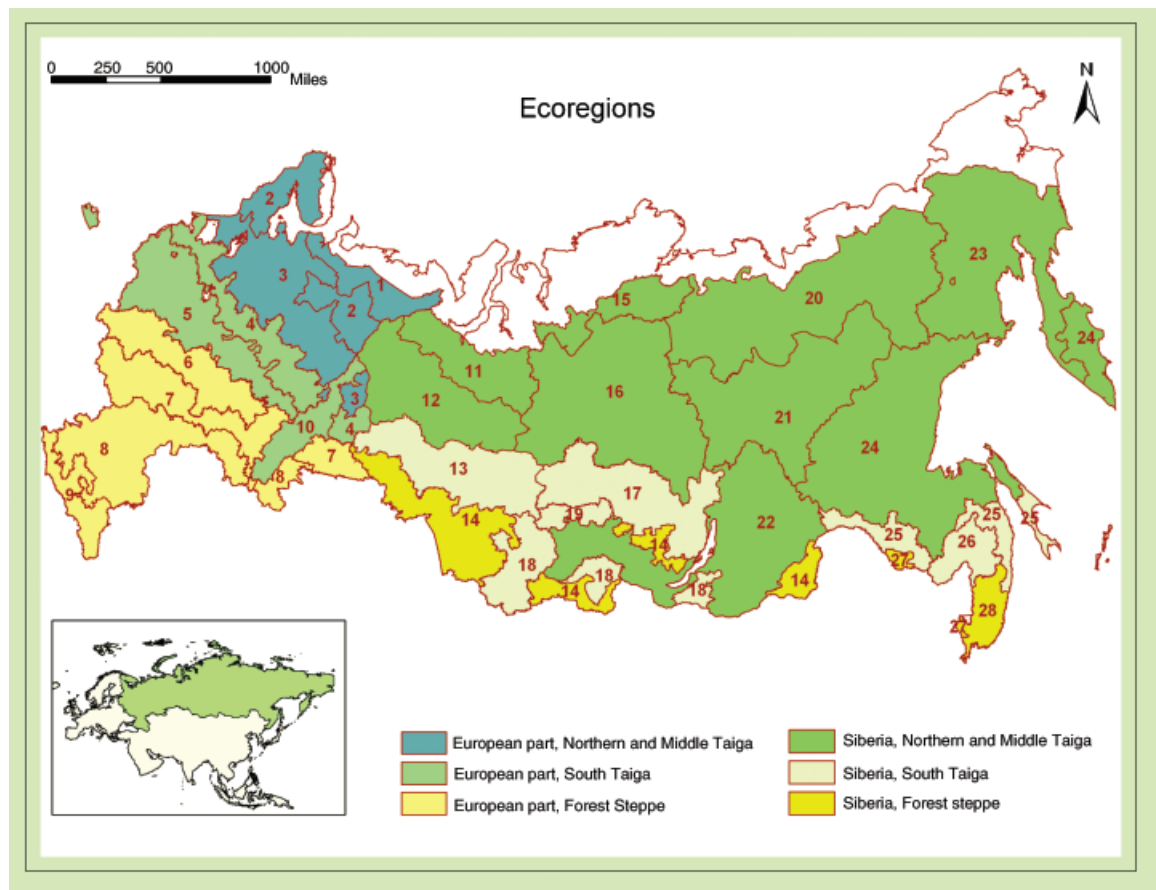
Fig. 1 Ecoregions of Russia (see details of distribution of sample plots and tree species in Table 1).

Russian forest living biomass consisted of ~ 6.2% green parts, ~ 71.8% aboveground wood, and ~ 22% roots (Shvidenko & Nilsson, 2002).

Because these measurements were designed for estimating the characteristics of various forest ecosystems and not for detecting temporal trends, the distribution of measurements in time occurred randomly. To obtain representative temporal statistics, these data must be aggregated within regions with sufficient numbers of measurements for each age group of tree species with similar plant physiology and for a wide range of forest conditions. We aggregated all database entries into six geographic regions for three biomass fractions within four major groups of species. These geographic regions represent the zones: the Northern and Central Taiga (including Forest Tundra, Northern, Sparse, and Middle Taiga); the Southern Taiga and Mixed Forest; and the Forest Steppe and Steppe. Each of these zonal belts is separated into two regions: west of the Ural Mountains (European Russia) and east of the Ural Mountains (Siberia and the Russian Far East) (Fig. 1). The three biomass fractions that we used are photosynthetic tissue or green parts such as leaves and needles; above-

ground wood (stems and branches); and belowground biomass (roots). The understory and green forest floor were excluded from this analysis of tree fractions. The four groups of species that we analyzed are the bulk composition of the forest (all species combined), dark coniferous, light coniferous, and deciduous species. These species are predominant in different Geographical areas. The dark coniferous species are most common in the Northern and Central Taiga, west of the Ural Mountains. The light coniferous species are predominant in the Northern and Central Taiga east of the Ural Mountains. The deciduous species are most numerous in the Forest Steppes and Steppes in the Southern Taiga zone.

Changes in climate and the Palmer Drought Severity Index (PDSI) dataset

The factors influencing the allocation of growth and carbon among tree components are active mostly in the summer months. However, it was shown that the mean annual temperature can be used as a predictor of the ratio of foliage biomass to sapwood area in *P. sylvestris*

Table 1 Distribution of 3196 sample plots by ecoregions and groups of species.

	Number of sample plots			
Ecoregions	Ecoregion (see map)	Dark coniferous	Light coniferous	Deciduous
European Forest Tundra	1	3	2	1
European Northern Taiga	2	18	7	1
European Middle Taiga	3	152	91	19
European Southern Taiga	4	50	103	15
European Mixed Forests	5	26	26	230
European Deciduous Forests	6	42	201	313
European Forest Steppe	7	1	197	171
European Steppe	8	0	38	42
Caucasus Mount. Broadleaves Forests	9	0	0	8
Ural Mount. Southern Taiga	10	14	4	2
West Siberian Sparse Taiga	11	–	17	–
West Siberian Middle Taiga	12	4	14	14
West Siberian Southern Taiga	13	12	30	27
West Siberian Forest Steppe	14	20	278	218
Middle Siberian Sparse Taiga	15	3	8	3
Middle Siberian Northern and Middle Taiga	16	28	160	6
Middle Siberian Southern Taiga	17	6	30	8
Middle Siberian Mount. Southern Taiga	18	89	107	42
Middle Siberian Forest Steppe	19	37	58	68
East Siberian Sparse Taiga	20	–	17	–
East Siberian Middle Taiga	21	1	41	3
East Siberian Mount. Middle Taiga	22	37	20	3
Far Eastern Sparse Taiga	23	–	14	0
Far Eastern Mount. Middle Taiga	24	8	41	2
Far Eastern Southern Taiga	25	28	6	5
Far Eastern Coniferous Broadleaves Forests	26	4	1	0
Far Eastern Forest Steppe	27	11	1	5
Far Eastern Mount. Coniferous Broadleaves Forests	28	12	0	8
Total	–	569	1512	1115

Dark coniferous forests: spruce (*Picea* ssp.), fir (*Abies* ssp.), and Russian cedar (*Pinus sibirica* and *P. koraiensis*). Light coniferous forest: Scotch pine (*P. sylvestris* L.) and larch (*Larix* ssp.). Deciduous forests: birch (*Betula* ssp.), aspen (*Populus tremula L.*), oak (*Quercus* ssp.), ash (*Fraxinus* ssp.).

mature trees. An increase in the annual mean temperature leads to an increase in this ratio (Palmroth *et al.*, 1999). However, an increase in vapor pressure deficit and a decrease in soil moisture lead to a decrease in the leaf-to-sapwood area ratio (Mencuccini, 2003). Under the assumption that the wood density does not change, the changes in the foliage to the sapwood area should be proportional to the changes in the ratio of foliage mass to the mass of sapwood.

Over the past few decades, all regions of the Russian forests have been subjected to an increase in mean annual temperature (Gruza *et al.*, 2000). Although, in the 20th century, average winter temperatures in the Northern Hemisphere increased at a faster rate than summer temperatures (Folland *et al.*, 2001), during the period 1960–2000, the Northern hemispheric summer temperatures became warmer by at least ~ 1 °C.

Furthermore, the region of the Northern and Central Taiga and the tree line zone (latitudes > 60°N) exhibit a stronger summertime temperature increase than the Northern Hemisphere as a whole or only the lower latitudes (Lugina *et al.*, 2003).

In fact, during the last 40 years, the maximum increase in average summer temperatures of ~ 2 °C was reached in Eastern Siberia (Jones & Moberg, 2003). On the west side of the Ural Mountains, the increase in summer temperature was accompanied by frequent wet spells, resulting in 10–20% increases in mean annual precipitation (Sun & Groisman, 2000), as well as, significant increases in summer soil moisture (Robock *et al.*, 2000), river runoff, and groundwater level (Georgievsky *et al.*, 1996). A smaller increase in mean annual precipitation has occurred in forest ecosystems in the watershed regions of the large Siberian rivers in the

Southern Taiga. A substantial decrease in the number of summer days with precipitation and a weak trend of decreasing annual precipitation was observed in the Northern Taiga of Siberia (Gruza *et al.*, 2000; Sun & Groisman, 2000). Overall, we can conclude that the surface temperature has increased over all areas of Russian forests, while the precipitation has increased in the Southern Taiga zone of European Russia and parts of west Siberia, and has decreased in the Northern and Central Taiga in Siberia.

One of the integral climatic indicators often used to detect possible water stress (or its absence) in plants is the PDSI. The PDSI can be calculated from monthly temperature and rainfall data (Palmer, 1965). The negative PDSI values reflect prolonged drought, while values greater than zero reflect normal or wet spell conditions. Analysis of empirical orthogonal functions of this index reveals that, since 1950 most changes in PDSI in Siberia can be explained by linear trends towards drier conditions. Within European Russia and the Southern Taiga of Siberia, the index has remained constant or increased slightly towards wetter conditions (Dai *et al.*, 2004). The PDSI is positively correlated with changes in vapor pressure deficit, soil moisture, and runoff (Dai *et al.*, 2004). Therefore, we can use temporal changes in this index as a potential indicator of resulting changes in the water regime of trees. Here, we have employed the Global Data Set of the PSDI for 1870–2002 (Dai *et al.*, 2004), and calculated linear trends of PDSI within practically the same geographic regions where

we estimated trends in the allocation of carbon among tree parts (Fig. 2, Table 2). Our analysis indicates that regional trends in PDSI are closely correlated with changes in green parts of living forest biomass.

Statistical model

Overall, within the whole forest (average of all regions and species), we detect a significant increase in the fraction of green parts (Fig. 3).

At first glance, the increase in the share of green parts agrees favorably with regional studies and some models which predict an increase in the leaf-to-sapwood ratio with an increase in the annual mean temperature (e.g., Palmroth *et al.*, 1999; Magnani *et al.*, 2002). However, in addition to temperature and water regime factors, there are a few other possible explanations of the apparent changes in average tree fractions shown in Fig. 3. As shown in past studies, the share of leaves and needles in tree biomass of the Russian forest depends on tree age and the relative stocking of stands (Alexeyev & Birdsey, 1998; Shvidenko & Nilsson, 2002). As a rule, the aging of trees leads to a reduction in the share of green parts. The increase in the relative stocking of trees (forest density) also leads to a reduction in the share of green parts, while the impact of site indexes (forest landscape) is nonmonotonous and less significant (Shvidenko & Nilsson, 2002). The strong correlation between a stand's *Age* and average *DBH* or average height of trees, or between *RS* and average *DBH*, makes *Age* and
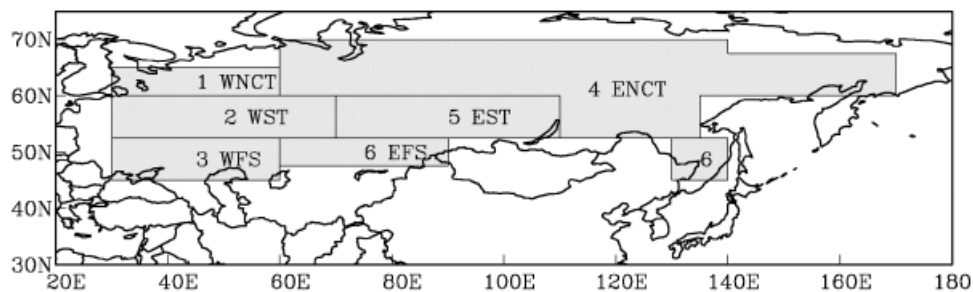

Fig. 2 Six major regions of Russian forest where Palmer Drought Severity Index trends were estimated.

Table 2 Estimates of the area-averaged, 1950–2000 mean annual PDSI, their standard deviations and trends

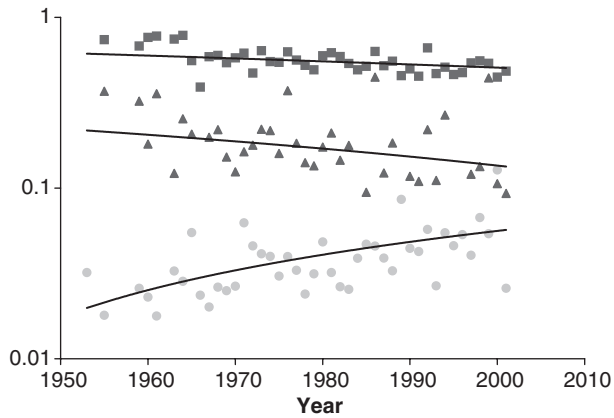| Region (see Fig. 2)	Mean annual (1950–2000)	Standard deviation (1950–2000)	Trend/50 years
1. West North and Central Taiga	0.04	1.46	−0.50
2. West South Taiga	0.10	1.26	0.60
3. West Forest Steppe	0.09	1.25	0.53
4. East North and Central Taiga	−0.63	0.98	−2.08
5. East South Taiga	−0.41	1.13	−1.74
6. East Forest Steppe	−0.13	1.60	−0.70
Area average for all regions	−0.27	0.74	−1.01

Fig. 3 Apparent changes in living biomass fractions at sample plots in the Russian forests (tons per m^3 of growing stock). The data were averaged over all 28 ecoregions and for each year across species for available sample plots. Green circles represent the fraction of green parts; red squares, the fraction of aboveground wood (stem and branches); and blue triangles, the fraction of roots.

RS the two primary forest parameters (Shvidenko & Nilsson, 2002). Therefore, an apparent increase in the fraction of green parts in the Russian forest could be a result of a decline in average *Age* or *RS* of stands as well as a result of changes in the carbon allocation within trees over *Time* in response to the changing climate.

In order to separate the possible effect of *Time* from the effect of other variables, we had to include *Age* and *RS* of tree stands into the analysis. Because the dominating part of trends in surface temperature and PDSI can be explained by linear trends (Dai *et al.*, 2004), it makes sense to look for a possible response of green parts (as the fraction most sensitive to changes in temperature and hydrologic balance) in the same functional form.

Therefore, we used a simple multiple linear regression model with intercept:

$$R_i = a \times Age + b \times RS + c \times Time + d, \quad (1)$$

where R_i is an aggregated *i* biomass fraction expressed in metric tons per cubic meter of growing stock of the green parts (R_1), aboveground wood (R_2), and roots (R_3); *Age* and *RS* are age (20–200 years) and relative stocking of stands (0.3–1.0), respectively; *Time* is the year of measurement from 1953 to 2002; and *a, b, c, d* are regression coefficients, where *c* is the estimate of temporal trend of tree fraction R_i.

Analysis of uncertainties

Measurement errors. A detailed discussion of various errors and accuracy of inventory-based estimates of growing stock and phytomass can be found in numerous publications (e.g., Vompersky, 1982; Shvidenko & Nilsson, 2002, 2003). The errors depend substantially on the complexity of forest stands, share of the fraction of the biomass under consideration and the number of measured trees. However, the key conclusion is that the methods used for the assessment of living biomass by fractions do not have any systematic errors (biases) (Shvidenko & Nikitin, 1978; Vompersky, 1982). Typically, the fractions of living biomass can be measured at a sample plot with an average standard error of ±10–15% (Shvidenko & Nilsson, 2002). This error can be much lower (less than ±5%) for the fraction of stem wood of uniform stands, and can be larger (up to ±50%) for the fraction of roots at sampling plots with a large diversity of tree species (Alexeyev & Birdsey, 1998).

Spatial heterogeneity and error of aggregation. The spatial scale of our analysis was limited by the adequate number of PIUs required for the construction of a reliable regression model. The multidimensional biomass equations for a given species or group of species can be favorably determined for an adequate size of sampling (Shvidenko, 2001). The exact number of tree stands required to estimate the biomass equation at a statistically significant level varies substantially according to the diversity of given stands, species composition of forest, and other factors. In average Russian forest conditions, however, the number of stands required to derive a multidimensional forest biomass equation for an individual species and region with a statistical probability of 0.9 (R^2 test) is ∼ 50–100 PIUs (Shvidenko, 2001). In this paper, we introduced a new variable: the *Time* of measurement. This variable adds a new degree of freedom into the analysis and causes some additional errors. Below is our estimate of the adequate size of samples required for estimating the parameters in the multiple regressions model (see Eqn (1)).

All four regression coefficients in Eqn (1) can be estimated if one has at least five measurements of *Age*, *Time*, *RS* and fraction R_i. However, it is clear that the odds of choosing four representative measurements of the whole dataset of tree stands are slim. We have used a random numbers generator to choose 10, 50, 100, 150, 200, 300, 400, 600, 800, 1000, and 1200 PIUs from the total of 1512 sample plots of light conifers species from the database. Light conifers show the highest variability of the green part fraction among all of the other species. Therefore, the results for light conifers can be accepted as the upper bound estimates of maximum error in the estimates of multiple regression coefficients caused by the spatial heterogeneity of data. For each set of

samples, we derived linear multiple regression with intercept, and calculated the fraction of green parts and the fraction of aboveground wood for four different *Age* groups: (30, 60, 90 and 120 years), three *RS* values (0.3, 0.6, 0.9), and three different *Times* (1980, 1990, 2000). Thus, we generated 12 ($4 \times 3 \times 3$) matrices with 36 elements. Subsequently, we calculated the residuals between the current matrices and their final estimate ($\Delta_{ij} = R_{i,j} - R_{i,1512}$). These experiments were repeated five times. The example of changes in distributions of normalized residuals (deviations of matrix elements from the elements of the matrix derived from all 1512 measurements) is shown as Box–Wishker plots (Fig. 4).

Based on these experiments, we found that a sample size of ~ 300 and ~ 100 stands (sample plots) is sufficient to derive a multiple regression model significant at the 0.9 level for green parts and stem wood fractions, respectively. Noting that (a) our experiments were geographically 'blind' (regression did not account for geographic location of a specific PIU), and that (b) the light coniferous species we chose exhibit more variability in green part fractions than the dark coniferous or deciduous species, it can be asserted that our experiments have revealed the upper bound estimate of a minimal number of sample plots required

to derive a statistically significant regression model with a *Time* variable. We analyzed six geographic regions (three each the from east and west of the Urals) with ~ 250–300 PIUs of dominant species: dark coniferous, light coniferous and deciduous. Our attempts to increase the number of geographic regions (e.g., from three to four from each side of the Ural Mountains, for a total of eight regions) leads to the loss of statistical significance of the regression model for most regions.

Covariance among variables. The estimates of temporal trends might be altered by covariance between *Time* and *Age* variables or between *Time* and *RS*. The mean annual *Age* of stands and the average *RS* for the whole database demonstrate pronounced interannual variability ($\pm 40\%$ over the whole period from 1960 to 2000), but show no statistically significant trends. Therefore, in most of the data, we found no statistically significant covariance between the independent variables of *Age* and *Time* and between *RS* and *Time*. However, a more detailed analysis of the same variables inside the six geographic regions demonstrated a statistically significant covariance between *Age* and *Time* variables inside regions 2, 3 and 6 (Table 3).

In regions 2 and 3 the covariance coefficients are low, while in region 6 the negative correlation between *Time*
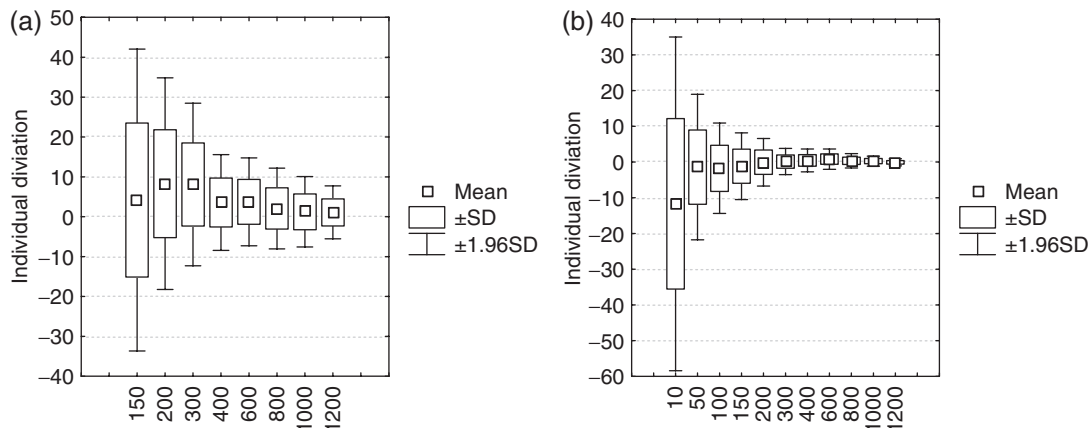

Fig. 4 Estimates of resulting errors caused by the spatial heterogeneity of sample plots data. The data presented for two tree fractions: (a) green parts and (b) stem wood fractions of light conifer species (see text for details). The horizontal axes represent the number of primary inventory units used in the analysis.

Table 3 The estimates of standardized covariance (Pearson's correlation coefficient) between *Time* of measurements, *Age* and *RS* of forest stands in six regions of Russian forest

	Region 1		Region 2		Region 3		Region 4		Region 5		Region 6	
	Age	*RS*	*Age*	*RS*	*Age*	*RS*	*Age*	*RS*	*Age*	*RS*	*Age*	*RS*
Time	−0.17	0.16	**0.20**	**0.26**	**−0.20**	**−0.21**	0.04	0.01	0.04	0.07	**−0.45**	0.08

Statistically significant results ($P < 0.05$) are shown in bold font.

and *Age* of stands is relatively high ($r = -0.45$) (Table 3). The most sensitive component to changes in *Age* and *RS* fraction of trees is the fraction of green parts. In the ± 20 year range of changes in the average age of stands (~ 50–70 years in region 2 and ~ 75–55 years in region 3) empirical biomass models suggest a very small (less than $\pm 10\%$) change in the fraction of green parts, and less than $\pm 5\%$ changes in stem wood and roots (Alexeyev & Birdsey, 1998; Shvidenko *et al.*, 2001). In region 6, however, the average *Age* of stands decreased from 90 in 1960 to less than 45 years in 1998, which might cause ~ 30–50% increase in the fraction of green parts. A strong decline in the average *Age* of stands can be explained by the selective harvest of mature trees, and active reforestation of this particular region during the last 40 years (Pavlovsky, 1986). Because the Siberian Forest Steppe represents only $\sim 5\%$ of the total area of the Russian forest, we decided to exclude the estimates of temporal trends of this region from further discussion.

Resulting errors. By suggesting statistical independence of individual errors discussed above, the resulting random error of temporal trends of living biomass fractions (σ_R) can be approximately estimated as the geometric sum of errors sampling or methodological (M), heterogeneity (H) and covariance (C) errors (Kheshgi & Lapenis, 1996):

$$\sigma_R = \sqrt{(\sigma_M^2 + \sigma_H^2 + \sigma_C^2)}. \quad (2)$$

The estimates of the resulting errors of tree fractions for five geographic regions are shown as 0.9 confidence intervals in Fig. 5.

The standard errors of the area-averaged trends in the PDSI were estimated through the interannual variability of this index (Dai *et al.*, 2004) and are shown in Fig. 6.

Calculations of the area-averaged carbon density of green parts fraction

The average Russian forest carbon density of total living biomass was estimated by Shvidenko & Nilsson (2003) and was based on the total growing stock and other proxy data of forest inventories from 1961, 1966, 1973, 1978, 1983, 1988, 1993, and 1998. Following a different approach from this work, where we consider only changes in leaves and needles, in their analysis Shvidenko & Nilsson (2003) included the data on biomass of understory (bushes + undergrowth) and green forest floor. The application of the modeling technique known as 'restored dynamic' (multidimensional regression equations that link biometric characteristics of major
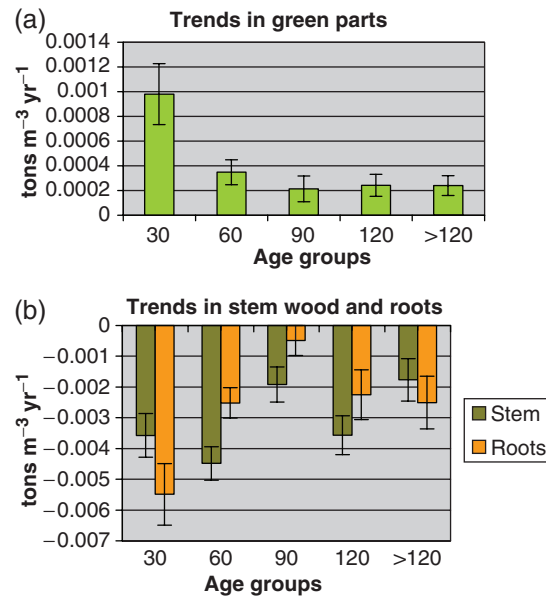

Fig. 5 The average for regions 1, 2, 3, 4 and 5 estimates of temporal trends in fractions of (a) green parts and (b) stem wood (aboveground wood) and roots. The possible changes in tree fractions caused by changes in average *Age* and *RS* of tree stands were removed by the multiple regression. Error bars represent 90% confidence interval of our estimates.

forest forming species in Russia with proxy inventory data) allows for a reduction in the biases and estimation of the changes in the average carbon density over most regions of Russian forests within an accuracy of ± 3–5% and a confidence probability 90% (for each year of the State Forest Account during the last 40 years) (see details in Shvidenko & Nilsson, 2002). In this study, we used the earlier estimate of total carbon density of living biomass to estimate the changes in the component of total carbon density related to the changes in fractions of green parts, aboveground wood and roots. Specifically, we estimated the changes in the average carbon density of green parts (C_{Green}), aboveground wood (C_{Above}), and roots (C_{Roots}) by multiplying the earlier estimate of total carbon density for specific ecoregions (C_{Total}) by the fraction of living biomass (R_i) found in this work. In the case of the green parts fraction, for example, our calculations were

$$C_{Green} = C_{Total} \times R_{Green}. \quad (3)$$

The relevant fraction of tree parts (R_i) was calculated for each year of inventory by Eqn (1).

Results and discussion

In Fig. 5, we show the estimates of temporal trends in tree fraction for the whole database derived by applying

the multiple regression technique (estimates of regression coefficient c in Eqn (1)). In addition, as in the case of bulk of data trend (Fig. 3), the *Time* component of changes in tree fractions demonstrates an increase in the fraction of green parts and a decline in the fractions of stem wood and roots (Fig. 5). The temporal trends were found to be stronger among younger trees as compared with the older trees.

A more detailed statistical analysis revealed a strong increase in the fraction of green parts in European Russia among the dark coniferous species of the Northern and Central Taiga (region 1 in Fig. 2), the light coniferous species of the Southern Taiga (region 2), and the deciduous species of the Forest Steppe (region 3). A smaller but statistically significant increase in the fraction of green parts among light coniferous species was found in the Siberian Southern Taiga (region 5). A decline in the fraction of green parts and an increase in the fractions of aboveground wood and roots were detected in the predominantly larch forests of the Northern and Central Taiga in Siberia (region 4). The Siberian Forest Steppe (region 6) was excluded from the analysis (see above).

The area-averaged trends in PDSI show direct proportionality to regional trends in green parts (Fig. 6).

These results are in agreement with the current theory of resource allocation in plants (Reekie & Bazzaz, 1987). According to this theory, a nonstructural carbon (e.g., sugars) is considered the appropriate currency of allocation and cost, and is used to 'purchase' other

resources essential for plant functions (Grifford & Evans, 1981). Analysis of a large quantity of data demonstrates that trees increase their investment in photosynthetic tissue relative to the water-conducting tissue in the stem (sapwood) as the environment becomes wetter (Mencuccini & Grace, 1995; DeLucia et al., 2000; Mencuccini, 2003). Earlier works have shown that the leaf area index is driven mostly by the local water balance (Grier & Running, 1977; Gholz, 1982). The overall conclusion of all these studies is that a given species of tree can afford a larger crown in moist regions than in arid regions where it must invest more carbon in roots and sapwood.

The alternative explanation of observed trends in green parts could be increase in longevity of leaves and needles. In other words, one might suggest that trees allocate the same amount of carbon to their green parts, but individual leaves and needles stays longer on trees. Such an assumption, however, is difficult to justify taking into account the decline in the air quality and increase in the surface temperature.

In our opinion, the resources allocation theory mentioned above, fits our data better than any other theory. As an example, to the west of the Ural Mountains, in accordance with this theory, trees cheaply (from the perspective of carbon trade) 'purchased' large photosynthetic apparatus, while to the east of the Ural Mountains (Northern and Central Taiga) they had to invest in carbon to maximize the growth of other parts such as roots and stems. Thus, a decrease in aridity over western Russia has caused an increase in the allocation of carbon to leaves and needles, while a significant increase in aridity over northern Siberia has resulted in an increase of carbon allocation to roots and stems.

However, in three of the five regions of the Russian forests that we analyzed, the PDSI demonstrates a trend towards aridity (regions 1, 3, 4 in Fig. 6) even though regions 1 and 3 showed increased greenness for negative PDSI values. Therefore, if the water regime was the only factor influencing changes in the allocation of carbon to green parts, the relationship shown in Fig. 6 would cross the center of the coordinates and we would see a decline in the average fraction of green parts in the Russian forests. Because this relationship passes above the center of the coordinates at zero PDSI (a result that is statistically significant for the average among species – black circles in Fig. 6), we conclude that a small increase in aridity over the Northern Taiga and over the Forest Steppe region of western Russia was compensated by some other environmental change, which caused an increase in carbon allocation to green parts. As stated above, analysis of the geographic distribution of allometric ratios demonstrate that coniferous species has a tendency to increase the allocation to foliage as the
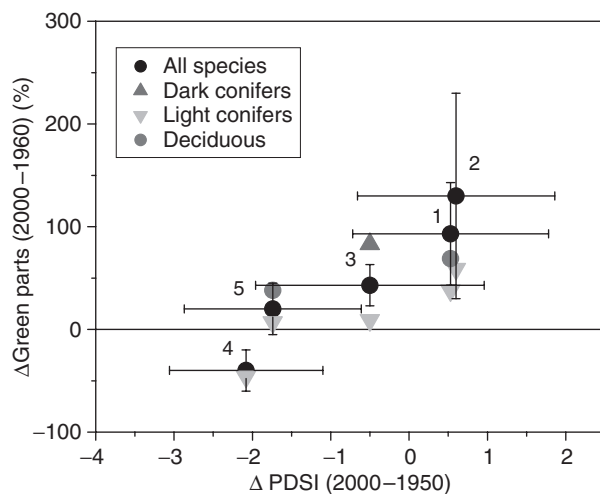

Fig. 6 The area-averaged trends in green parts vs. Palmer drought severity index (PDSI) trends as estimated over regions 1–5 (Fig. 1). Significant trends were found in each of the five regions for the majority of species (all species combined) and for the dominant groups of species in a given region. Horizontal and vertical error bars represent the 0.9 confidence interval of estimates for PSDI and the green parts, respectively.

2100 A. LAPENIS *et al.*

annual mean temperature increases (Bongarten & Teskey, 1987; Gregg, 1994; Palmroth *et al.*, 1999). This fact can be explained by the temperature-induced decline in the hydraulic resistance of stems and roots (Mencuccini, 2003). Thus, it might be 'cost efficient' for trees to support a larger crown as the temperature increases. As some modeling studies have shown, depending on the soil moisture and structure, an increase in the mean annual temperature of $\sim 2\,°C$ might cause 10–100% increase in the leaf-to-sapwood ratio (Magnani *et al.*, 2002). Therefore, the increase in surface temperatures could be the main factor that caused the overall increase in the fraction of green parts in living biomass. Some other factors, such as atmospheric depositions of nitrogen (particularly in European Russia) or an increase in the atmospheric concentration of CO_2, might contribute to the increase in the fraction of green parts. Metaanalysis of long-term experiments on the fertilization of boreal forests with nitrogen demonstrates a decline in the hydraulic efficiency of trees, which allows for the development of a larger photosynthetic apparatus and increases the resistance of trees to drought (Mencuccini, 2003). An increase in atmospheric CO_2 effects stomata opening and improves the drought resistance of plants as well (Mencuccini, 2003). A significant increase in atmospheric CO_2 (doubling the preindustrial concentration) might lead to early maturation of plants and an increase in their fecundity. For example, in 4-year CO_2 fertilization experiments (Duke Forest, NC USA), the average stem diameter of loblolly pine trees reaching maturity declined, while the allocation of carbon to cones increased by ~ 30–100% (LaDeau & Clark, 2001). However, since 1960, the atmospheric CO_2 concentration has increased by only 18% (Keeling & Whorf, 2004).

Because increased temperature, atmospheric CO_2, and nitrogen deposition are all favorable to the allocation to leaves and needles, any of these factors could contribute to the observed changes in biomass fractions in the Russian forest. At the same time, taking into account the magnitude of these changes, the increase in the annual mean temperature and variations in the aridity are the two most probable explanations of the strong linear proportionality between the area-averaged PDSI trends and regional trends in green parts (Fig. 6). Therefore, we conclude that over the last four decades, the Russian forests have demonstrated an acclimation to recent climate change through the increase in the share of foliage (leaves and needles) and some decrease in the shares of stem wood and roots. The latter explains the 'tree ring–NDVI paradox'. Independent of the nature of the observed increase in the share of photosynthetic tissue of trees, this phenomenon may have caused misinterpretations of satellite data on the changes in leaf indices.

It has been shown that any type of forest can be characterized by a relatively consistent number of specific leaf area indexes or a typical area of green parts per kilogram of foliage mass. On the average, the Russian forest produces $\sim 8.5\,m^2\,kg^{-1}$ of green parts, although the variability of this value is high (from about 4–$20\,m^2\,kg^{-1}$, (Ermolova & Utkin, 1998). Therefore, changes in carbon density of green parts reflect changes in the leaf area. Changes in the leaf area change the reflectivity of the vegetation and, thus, values of NDVI. According to some calculations, the area-averaged NDVI and forest biomass density in tons per hectare, might be linked with each other as a logarithmic function with possible saturation at high NDVI values (supplementary information by Myneni *et al.*, 2001). However, within the range of 50–65° of latitude (the range of 90% of Russian and Scandinavian forests), the relationship between biomass density and the area-averaged NDVI is very close to a linear function, with a slope of ~ 1 (supplementary information by Myneni *et al.*, 2001). Therefore, it is most likely that the changes in the carbon density of live biomass in Russian forests occur at about the same rate as the increase in the satellite-based estimate in the seasonally accumulated NDVI.

According to our estimates of changes in the carbon density of various tree parts, however, the rates of increase in carbon density of stem wood and roots are three to five times smaller than the rate of increase in the carbon density of green parts and the rate of increase in the seasonally accumulated Eurasian NDVI (Fig. 7).

The difference in the geographic area of carbon density and NDVI estimates (the Russian forest vs. the whole of Eurasia) is unlikely to be a reason for such a large difference as the Russian forest represents most of Eurasian forests. At the same time, the normalized trend in carbon density of green parts practically coincides with the area-averaged normalized NDVI trend. Therefore, our data provide the only known independent line of evidence in support of the Eurasian NDVI trend to date. In other words, our data point to the fact that ~ 12% increase in the Eurasian NDVI coincided in time with a similar (~ 10%) increase in the biomass of green parts of the whole Russian forest. Because the green parts are responsible for up to 90–100% of the net primary production (NPP) (Shvidenko & Nilsson, 2003), our results suggest that the recently observed significant increase in the apparent NPP of Russian forests (Nemani *et al.*, 2003; Slayback *et al.*, 2003) has been mostly caused by the shift of carbon allocation towards the leaf tissues. This particular type of 'greening' through changes in the shape of trees is quite similar to the phenomenon of the 'green revolution' in
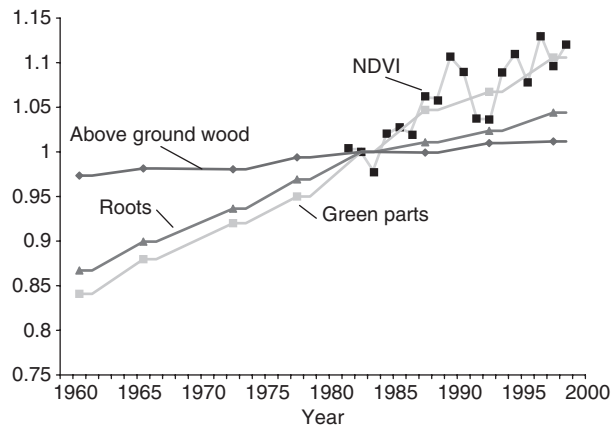
Fig. 7 Estimates of area-averaged carbon densities of green parts (leaves, needles as well as understory and green forest floor), aboveground wood, and roots in the Russian forests based on data of national forest inventory (see Calculations of the area-averaged carbon density of green parts fraction). These results reflect on changes in the allometric ratios as well as all documented changes of Russian forests in regions 1–5 (Methods), which explain some differences of the relationships comparatively to Fig. 3. All data, including the area-averaged seasonally accumulated normalized difference vegetation index over Eurasia (Myneni *et al.*, 2001), were normalized to their 1983 values.

agriculture. The increase in the productivity of agricultural plants during the last four to five decades was mostly achieved, not through the increase in the rates of photosynthesis per unit leaf area, but by the shift in the allocation of carbon (Ericsson *et al.*, 1996). In productive cultivars a larger fraction of carbohydrates is now used for the growth of leaves and reproductive organs at the expense of stems and roots (Ericsson *et al.*, 1996).

However, it should be noted that the greening of Russian forests was not only caused by the shift in the allocation of carbohydrates. During the 1961–1998 period, the total carbon density of the living biomass stock of the Russian forests increased by $\sim 9\%$ from 4.08 to 4.44 $(\mathrm{kg\,C\,m^{-2}})$ (Shvidenko & Nilsson, 2003). Our estimates indicate that the corresponding values for aboveground wood, roots, and green parts increased by 4%, 21%, and 33%, respectively (Fig. 7). As already mentioned above, during the 1981–1998 period, the increase in the growth rate of green parts almost closely coincided with the rate of increase in the NDVI-derived greening of the Russian forests and was approximately three to five times higher than the increase in the carbon density of aboveground wood (Fig. 7). Taking into account the uncertainty of our estimates and the increase in the area of the Russian forests (from $695.5 \times 10^{10}\,\mathrm{m^2}$ in 1961 to $774.2 \times 10^{10}\,\mathrm{m^2}$ in 1998; (FFSR, 1999)), we can approximately estimate the carbon sink attributable to the living biomass during the 1961–1998 period:

$$((4.44 - 4.08) \times 10^3 \mathrm{g} \times m^{-2} \times 735 \times 10^{10} m^2) \div 37\ yr$$
$$= 72 \pm 50\ \mathrm{Tg\,C\,yr^{-1}}.$$

According to Fig. 7, however, this estimate would be at least three times higher if changes in the allometric ratios were neglected and green parts (or NDVI) were used as the only proxy for changes in the total living biomass of Russian forest.

Acknowledgments

References

Alexeyev VA, Birdsey RA (1998) USDA General Technical Report NE-244, 137 pp.

Bazzaz FA (1997) In: *Plant Resource Allocation* (eds Bazzaz FA, Grace J), Academic, CA.

Bongarten BC, Teskey RO (1987) Dry weight partitioning and its relationship to productivity in loblolly pine seedlings from seven sources. *Forest Science*, **33**, 255–267.

Briffa KR, Schweingruber FH, Jones PD *et al.* (1998a) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature*, **391**, 678–682.

Briffa KR, Schweingruber FH, Jones PD *et al.* (1998b) Trees tell of past climates: but are they speaking less clearly today? *Philosophical Transaction of Royal Society*, **B353**, 65–73.

Brown RD (2000) Northern Hemisphere snow cover variability and change, 1915–1997. *Journal of Climate*, **13**, 2339–2355.

Cook ER, Zedaker SM (1992) The dendroecology of red spruce decline. In: *Ecology and Decline of Red Spruce in the Eastern United States. Ecological Studies 96* (eds Eagar C, Adams MB), pp. 192–231. Springer Verlag, New York.

Dai A, Trenberth KE, Qian T (2004) A global data set of Palmer Drought Severity Index for 1870–2002: relationship with soil moisture and effects of surface warming. *Journal of Hydrometeorology*, **5**, 1117–1130.

DeLucia EH, Maherali H, Carey EV (2000) Climate-driven changes in biomass allocation compromise the ability of pines to store atmospheric carbon. *Global Change Biology*, **6**, 587–593.

Ericsson T, Rytter L, Vapaavuori E (1996) Physiology of carbon allocation in trees. *Biomass and Bioenergy*, **11**, 115–127.

Ermolova LS, Utkin AI (1998) Specific leaf area of major forest forming species of Russia. *Ecology*, **3**, 178–183.

FAO (2001) *Global forest resource assessment 2000*. Main Report. Food and Agriculture Organization of the United Nations, Rome, FAO Forestry Paper 140.

FFSR (1999) *Forest Fund of Russia (state by 1 January 1998).* Federal Forest Service of Russia, Moscow (in Russian).

Folland CK, Palmer TN, Parker DE (2001) Climate change 2001: the scientific basis. In: *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds Houghton JT *et al.*), Cambridge University Press, Cambridge, UK.

Georgievsky VY, Ezhov AV, Shalygin AL *et al.* (1996) Assessment of predicted climatic change impact on hydrological regime and river water resources across the territory of former USSR. *Meteorology and Hydrology*, **11**, 89–99.

Gholz HL (1982) Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology*, **63**, 469–481.

Gregg BM (1994) Carbon allocation, gas exchange, and needle morphology of *Pinus ponderosa* genotypes known to differ in growth and survival under imposed drought. *Tree Physiology*, **14**, 883–898.

Grier CC, Running SW (1977) Leaf area of mature Northwestern coniferous forests: relation to site water balance. *Ecology*, **58**, 893–899.

Grifford RM, Evans LT (1981) Photosynthesis, carbon partitioning, and yield. *Plant Physiology*, **32**, 485–509.

Groisman PY, Karl TR, Knight RW (1994) Changes of snow cover, temperature and radiative heat balance over the Northern Hemisphere. *Journal of Climate*, **7**, 1633–1656.

Gruza GV, Rankova EYA, Razuvaev V *et al.* (2000) *Third National Communication of the Russian Federation.* Inter-Agency Commission of the Russian Federation on the Climate Change, Moscow.

Hornbeck JW, Smith RB (1985) Documentation of red spruce growth decline. *Canadian Journal of Forest Research*, **15**, 1199–1201.

Johnson AH, Siccama TG (1983) Acid deposition and forest decline. *Environmental Science and Technology*, **17**, 294A–305A.

Jones PD, Moberg A (2003) Hemispheric and large-scale surface air temperature variations: an extensive revision and an update to 2001. *Journal of Climate*, **16**, 206–223.

Kaufmann RK, D'Arrigo R, Laskowski R *et al.* (2004) The effect of growing season and summer greenness on northern forests. *Geophysical Research Letters*, **31**, L09205, doi: 10.1029/2004GL019608.

Keeling CD, Whorf TP (2004) *Trends Online: A Compendium of Data on Global Change.* Carbon Dioxide Information Analysis Center, Oak ridge, TN.

Kheshgi HS, Lapenis AG (1996) On the accuracy of the Russian paleoclimate reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **121**, 221–237.

LaDeau S, Clark J (2001) Rising CO_2 levels and the fecundity of forest trees. *Science*, **292**, 95–98.

Lawrence GB, Lapenis AG, Berggren D *et al.* (2005) Climate Dependency of Tree Growth Suppressed by Acid Deposition Effects on Soils in Northwest Russia. *Environmental Science and Technology.* ASAP Article 10.1021.

Lugina KM, Groisman PYA, Vinnikov KYA *et al.* (2003) *Trends Online: A Compendium of Data on Global Change.* Carbon Dioxide Information Analysis Center, Oak Ridge, TN.

Magnani F, Grace J, Borghetti M (2002) Adjustment of tree structure in response to the environment under hydraulic constraints. *Functional Ecology*, **16**, 385–393.

Mencuccini M (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic cost of stature across plant life forms. *Plant, Cell and Environment*, **26**, 163–182.

Mencuccini M, Grace J (1995) Climate influences the leaf area-sapwood relationship in Scots pine (*Pinus sylvestris* L.). *Tree Physiology*, **15**, 1–10.

Myneni RB, Dong J, Tucker CJ *et al.* (2001) A large carbon sink in the woody biomass of Northern forests. *Proceedings of the National Academy of Sciences, USA*, **98**, 14784–14789.

Nemani RR, Keeling CD, Hashimoto H *et al.* (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, **300**, 1560–1563.

Palmer WC (1965) *Meteorological Drought, Research Paper No. 45, 58.* Department of Commerce, Washington, DC.

Palmroth S, Berninger F, Nikinmaa E *et al.* (1999) Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climates. *Oecologia*, **121**, 302–309.

Pavlovsky A (1986) *Artificial Forests of USSR.* Nauka, Moscow.

NOAA (2005) http://www.ngdc.noaa.gov/paleo/ftp-treering.html

Reekie EG, Bazzaz FA (1987) Reproductive effort in plants. II. Does carbon reflect the allocation of other resources? *American Naturalist*, **129**, 897–906.

Robock A, Vinnikov KY, Srinivasan G *et al.* (2000) The Global Soil Moisture Data Bank. *Bulletin of American Meteorological Society*, **81**, 1281–1299.

Shvidenko A, Shepaschenko D, Nilsson, S (2001) Aggregared models of phytomass for major forest forming species. *Forest Inventory and Forest Planning, Russia*, **1**, 50–57.

Shvidenko A, Nikitin K (1978) *Methods and Technique of Processing Forest Information, Forest Industry.* Moscow (in Russian).

Shvidenko A, Nilsson S (2002) Dynamics of Russian Forests and the carbon budget in 1961–1998: an assessment based on long-term forest inventory data. *Climatic Change*, **55**, 5–37.

Shvidenko A, Nilsson S (2003) A synthesis of the impact of Russian forest on the global carbon budget for 1961–1998. *Tellus*, **55B**, 391–415.

Slayback DA, Pinzon J, Los S *et al.* (2003) Northern hemisphere photosynthetic trends 1982–1999. *Global Change Biology*, **9**, 1–15.

Sun B, Groisman PY (2000) Cloudiness variations over the former Soviet Union. *International Journal of Climatology*, **20**, 1097–1111.

Vaganov EA, Hughes MK, Kirdyanov AV (1999) Influence of snowfall and melt timing on tree growth in sub-arctic Eurasia. *Nature*, **400**, 149–151.

Vompersky SE (1982) *Biological Productivity of Forests of Povolgia.* Nauka, Moscow (in Russian).

Zhou L, Kaufmann RK, Tian Y *et al.* (2003) Relation between interannual variations in satellite measures of vegetation greenness and climate between 1982 and 1999. *Journal of Geophysical Research*, **108**, *(D1)*, doi: 10.1029/2002 JD002510.