UC Irvine
Faculty Publications

Title

Beyond annual budgets: carbon flux at different temporal scales in fire-prone Siberian Scots pine forests

Permalink

https://escholarship.org/uc/item/0mc6p54x

Journal

Tellus B, 54(5)

ISSN

Authors

Wirth, Christian
Czimczik, Claudia I
Schulze, E.-Detlef

Publication Date

DOI

Copyright Information

Peer reviewed

Beyond annual budgets: carbon flux at different temporal scales in fire-prone Siberian Scots pine forests

By CHRISTIAN WIRTH*, CLAUDIA I. CZIMCZIK and E.-DETLEF SCHULZE, *Max-Planck-Institute for Biogeochemistry, P.O. Box 100164, 07743 Jena, Germany*

ABSTRACT

Along four chronosequences of fire-prone Siberian Scots pine forests we compared net primary production (NPP) and two different mass-based estimates of net ecosystem productivity (NEP_C and NEP_S). NEP_C quantifies changes in carbon pools along the chronosequences, whereas NEP_S estimates the short-term stand-level carbon balance in intervals between fires. The chronosequences differed in the mean return interval of surface fires (unburned or moderately burned, 40 yr; heavily burned, 25 yr) and site quality (lichen versus *Vaccinium* type). Of the *Vaccinium* type (higher site quality) only a moderately burned chronosequence was studied. NEP_C was derived from the rate of changes of two major carbon pools along the chronosequence time axes: (1) decomposition of old coarse woody debris (CWD) left from the previous generation after stand-replacing fire, and (2) accumulation of new carbon in biomass, CWD and soil organic layer by the regenerating stand. Young stands of all chronosequences were losing carbon at rates of -4 to -19 mol C m^{-2} yr^{-1} (-48 to -228 g C m^{-2} yr^{-1}). Depending on initial CWD pools and site-specific accumulation rates the stands became net carbon sinks after 12 yr (*Vaccinium* type) to 24 yr (lichen type) following the stand-replacing fire, and offset initial carbon losses after 27 and 70 yr, respectively. Highest NEP_C was reached in the unburned chronosequence (10.8 mol C m^{-2} yr^{-1} or 130 g C m^{-2} yr^{-1}). Maximum NEP_C in the burned chronosequences ranged from 1.8 to 5.1 mol C m^{-2} yr^{-1} (22 to 61 g C m^{-2} yr^{-1}) depending on site quality and fire regime. Around a stand age of 200 yr NEP_C was 1.6 ± 0.6 mol C m^{-2} yr^{-1} (19 ± 7 g C m^{-2} yr^{-1}) across all chronosequences. NEP_S represents the current stand-level carbon accumulation in intervals between recurring surface fires and can be viewed as a mass-based analogue of net ecosystem exchange measured with flux towers. It was estimated based on measurements of current woody NPP, modelled decomposition of measured CWD pools and organic layer accumulation as a function of time since the last surface fire, but ignores carbon dynamics in the mineral soil. In burned mature lichen type stands, NEP_S was 6.2 ± 2.6 mol C m^{-2} yr^{-1} (74 ± 31 g C m^{-2} yr^{-1}) and thus five times higher than NEP_C at the respective age (1.2 ± 0.6 mol C m^{-2} yr^{-1} or 14 ± 7 g C m^{-2} yr^{-1}). Comparing NEP_S and NEP_C of mature stands, we estimate that 48% of NPP are consumed by heterotrophic respiration and additional 35% are consumed by recurrent surface fires. As expected, in unburned stands NEP_C and NEP_S were of similar magnitude. Exploring a site specific model of CWD production and decomposition we estimated that fire reduces the carbon pool of newly produced CWD by 70%. Direct observation revealed that surface fire events consume 50% of the soil organic layer carbon pool (excluding CWD). We conclude that surface fires strongly reduced NEP_C. In ecosystems with frequent fire events direct flux measurements using eddy covariance are likely to record high rates of carbon uptake, since they describe the behaviour of ecosystems recovering from fire without capturing the sporadic but substantial fire-related carbon losses.

*Corresponding author.
e-mail: cwirth@bgc-jena.mpg.de

1. Introduction

Carbon flux measurements carried out over ecosystems (eddy covariance technique), landscapes (convective boundary layer budgeting) and whole continents (inversion modelling techniques) provide only a snap-shot view of the carbon cycle, although a very detailed one. Within the observational period, which very often captures only a few years, the temporal resolution is high. Since environmental variables are recorded with the same temporal resolution, these methods are ideal to explore short-term climatic controls of carbon exchange and are crucial to understand the mechanisms underlying interannual variability (Lloyd et al., 2002). However, the changes in carbon pools that are recorded over the few years are small wiggles compared to the large waves of carbon accumulation and decomposition that go along with forest stand succession or disturbance events (Krankina et al., 1999; Harden et al., 2000; Wirth et al., 2002a). In addition, direct flux measurements, even if they would cover several successional stages of a disturbance cycle (Schulze et al., 2000; Amiro, 2001), only describe the short-term behaviour of long-lived biological structures (namely forest ecosystems). In other words, the range of today's fluxes is predefined by forest structure that results from growth and mortality that happened in the past (ecological legacy). Understanding present fluxes thus also requires knowledge about environmental and biotic control of growth and regulation of stand density in terms of recruitment and survival.

Central Siberian Scots pine forests regenerate after stand-replacing fires, and from then on develop under a regime of recurring surface fires. The stand-replacing fire cycle lasts approximately 250 yr, whereas the lower intensity surface fires recur every 35 yr on average (Wirth et al., 1999; Arbatskaya and Vaganov, 1997; Furyaev, 1996). The same holds in principle for Siberian larch stands (Yevdokimenko, 1996) that cover half of the Siberian forest area. Stand-replacing fires usually consume all forest fuel types except fresh wood and mineral soil organic matter and lead to almost complete tree mortality. In contrast, surface fires only feed on the upper organic layer, including fragmented coarse woody debris, and exert a size-selective mortality regime (Wirth et al., 1999). Both types of fire have an important influence on ecosystem carbon dynamics. Fires induce an immediate direct carbon loss and a redistribution of carbon from the biomass into the necromass pool, thus favouring post-fire respiration losses of carbon. On the other hand, fires also initiate new growth by providing newly available growing space, mineral soil for regeneration and increased levels of nutrients for survivors. This paper aims at describing these dynamics by quantifying two independent trajectories of carbon stock changes over time. Each trajectory represents a different temporal resolution of net ecosystem productivity (NEP): (a) chronosequence-based net ecosystem productivity (NEP_C) describes the general patterns of carbon accumulation and decomposition along with stand development after stand-replacing fire, and (b) the short-term net ecosystem productivity (NEP_S) describes the carbon dynamics in intervals between surface fire events. NEP_C was derived from the changes of carbon pools in biomass, coarse woody debris and soil organic layer along the chronosequence time axes. NEP_S was estimated based on measured rates of wood accumulation, site-specific empirical functions of coarse woody debris decomposition and soil organic layer changes as a function of time since the last surface fire.

We hypothesise that NEP in ecosystems with repeated fire-related carbon losses strongly depends on the temporal scale of the observation and expect further that NEP_C is reduced in relation to NEP_S. Finally, the fraction of net primary production (NPP) accumulating as NEP_S versus NEP_C is calculated and inferences are made on the partitioning of carbon losses induced by heterotrophic respiration versus fire. As a diagnostic tool to explore the above questions simple empirical models of changes in carbon stocks and fluxes were developed that largely build upon and combine data that were presented in earlier publications of the authors (Wirth et al., 2002a; 2002b).

2. Methods

2.1. Study area and sites

The study area, located about 40 km west of the Yenisei river (60°43′N, 89°08′E), is characterised by monotypic Scots pine forests (*Pinus sylvestris* ssp. *sibirica* LEBED) that occur on alluvial sand dunes. The soils are podzols without underlying permafrost. The annual average air temperature is −3.7 °C, the average monthly air temperature is 17.3 °C in July and −22.9 °C in January (61°45′N, 91°13′E, Bor Met Station). The growing season (days with a mean daily temperature of >5 °C) typically lasts 147 days with a daily average temperature of 11.5 °C (Glebov, 1969).

Table 1. *Stand structure and fire regime of four chronosequences of central Siberian Scots pine forests*[a]

	Crown cover of stands older than 60 yr (%)	Basal area of stands older than 60 yr (m^2 ha^{-1})	Stand internal mean fire interval (yr)	Initial fire interval (yr)	Time since last non stand-replacing fire (yr)
Lichen type – unburned [lu]	81.0 [1; 95$_{lu}$]	40.3 [1; 95$_{lu}$]	No fire	No fire	No fire
Lichen type – moderately burned [lm]	61.0 ± 1.6 [4]	30.5 ± 2.3 [6]	43.2 ± 17.5 [6]	42.0 ± 25.5 [6]	46.5 ± 26.4 [6]
Lichen type – heavily burned [lh]	49.2 ± 14.7 [5]	17.0 ± 4.4 [5]	25.1 ± 9.9 [7]	27.5 ± 9.1 [7]	21.7 ± 17.3 [7]
Vaccinium type – moderately burned [vm]	128.8 ± 21.6 [2]	40.4 ± 12.2 [2]	41.4 ± 22.8 [3]	40.0 ± 25.6 [3]	36.3 ± 0.6 [3]

[a]To emphasise structural differences between the chronosequences the average crown cover and basal area of stands older than 60 yr is presented. For more information on structure and fire history of individual stands of all age classes see Wirth et al. (1999). The number of stands that entered the calculation of averages and standard deviations is given in square brackets.

Average annual precipitation is 565 mm (see also Schulze et al., this issue).

Four chronosequences of Scots pine forest were established based on differences in (a) site quality and (b) surface fire regime. Site quality was identified using understorey vegetation and height growth pattern [*Vaccinium* site type (subscript *v*) as opposed to lichen site type (subscript *l*), Cajander, 1926]. The fire regime was classified according to fire frequency as well as structure of individual stands reflecting the intensity of past fires as defined in Table 1 [unburned (subscript *u*), moderately burned closed forests (subscript *m*), heavily burned open woodlands (subscript *h*); see Wirth et al. 1999]. The following chronosequences were established (nomenclature of stands consists of stand age and subscript):

(1)   Unburned chronosequence of the lichen type: Dense forests with lichen understorey, which had not experienced surface fire since establishment (2$_{lu}$-, 14$_{lu}$-, 28$_{lu}$-, 31$_{lu}$-, and 95$_{lu}$-yr-old stands).

(2)   Moderately burned chronosequence of the lichen type: Closed forests with lichen understorey showing a homogeneous stand structure and a surface fire return interval of 43 ± 17 yr (moderately burned 67$_{lm}$-, 138$_{lm}$-, 200$_{lm}$-, 204$_{lm}$-, and 383$_{lm}$-yr-old stands). In our analysis we consider the young unburned 2$_{lu}$-, 14$_{lu}$-, 28$_{lu}$-, 31$_{lu}$-yr-old stands as also a starting point of the moderately burned chronosequence, since their stand age is below the average length of initial fire intervals measured in the moderately burned stands (Table 1, Wirth et al., 1999).

(3)   Heavily burned chronosequence of the lichen type: Open pine woodlands with lichen understorey and a surface fire return interval of 25 ± 10 yr (heavily burned 14$_{lh}$-, 32$_{lh}$-, 48$_{lh}$-, 50$_{lh}$,- 215$_{lh}$-, and 244$_{lh}$-yr-old stands).

(4)   Moderately burned stands of the Vaccinium type: Dense productive stands with an understorey of mosses and *Vaccinium* shrubs and a surface fire return interval of 41 ± 23 yr (12$_{vu}$-yr-old stand and moderately burned 53$_{vm}$- and 95$_{vm}$-yr-old stand).

A detailed description of the stands containing location, plot size, stand density and various other stand-level inventory data was presented in Wirth et al. (1999).

2.2. Chronosequence-based net ecosystem productivity (NEP_C)

NEP_C was calculated from rates of change in total ecosystem carbon pools along the chronosequences. *NEP* was originally defined as the physiological carbon balance of net assimilation and heterotrophic respiration (Aber and Melillo, 1991), while the carbon balance that also includes carbon export via fire and harvest was termed net biome productivity (NBP; Schulze and Heimann, 1998). However, in the present study we also define changes in ecosystem carbon along chronosequences affected by surface fires as NEP_C. The term NBP we reserve for the carbon balance at the biome level that also includes the effect of

stand-replacing fires on the age class distribution of a forest landscape.

The practical methods and statistical procedures used to estimate total and component ecosystem carbon pools were presented in detail in Wirth et al. (1999) and (2002a). Carbon pools are reported in the unit of mol C, which is converted to C by multiplying by the molar weight of carbon, 12 g mol^{-1}. Above-ground biomass carbon in various biomass components (sapwood, heartwood, bark, coarse and fine branches, twigs and needles) measured in 78 trees (5–8 trees per plot) by means of destructive sampling was scaled up to the stand level by use of allometric relationships. Breast height diameter over bark and tree height, which were inventoried for all trees within a sample plot, were used as biomass predictors. For the development of allometric relationships stands were grouped across chronosequences according to age classes. Coarse root biomass was calculated based on published root:shoot ratios specific for boreal Scots pine (Vanninen et al., 1996). Fine root and medium root biomass was sampled along with the soil studies from soil monoliths (see below). Carbon stored in dead standing trees was calculated using specific allometric relationships for stem biomass under bark assuming that wood fragmentation is negligible in dead trees that are still standing (Harmon et al., 1986). The volume of coarse woody debris (CWD) was either quantified by measuring the top and bottom diameter and length of lying logs within sample plots or by applying a line-intersect method. The CWD was assigned to one of three decomposition classes based on structural features and a succession of epiphytic cryptogams. The wood density of CWD of decomposition class 1 was assumed to be equal to the dry wood density of living wood (435 kg_{dw} m_{dw}^{-3}; Wirth et al., 2002a). The dry wood densities of decomposition classes 2 and 3 were approximated to be 66% (286 kg_{dw} m_{dw}^{-3}) and 33% (143 kg_{dw} m_{dw}^{-3}), respectively, of the dry wood density of living trees. Our system of three decay classes represents a simplified version of the system of five decay classes for Scots pine in boreal Russia established by Krankina and Harmon (1995). Our decay classes 1, 2 and 3 correspond to their decay classes 1 (402 kg_{dw} m^{-3} = 100%), 3 (234 kg_{dw} m^{-3} = 58%) and 5 (130 kg_{dw} m^{-3} = 32%). Carbon concentrations were measured in all dead and living tissues with an elemental analyser (Carlo Erba Comp., Milan, Italy and ELEMENTAR Vario EL, Hanau, Germany) to convert mass into carbon storage. We divided the forest floor CWD into two pools: one originating from the previ-

ous generation as a result of the stand-replacing fire (CWD_{old}) and the other pool originating from the current generation as a result of self-thinning and mortality due to surface fires (CWD_{new}). All CWD with a maximum diameter exceeding a threshold of two thirds of the diameter range of the living stand was regarded as old CWD left from the previous generation. Similarly, the CWD below this threshold was regarded as new CWD. The underlying assumption in this methodology is that smaller trees are preferentially subject to mortality due to surface fires. The existence of a size-selective mortality regime was demonstrated by Wirth et al. (1999). The carbon concentrations of living woody components were used to convert CWD necromass into carbon pools. Soil organic layer carbon content was sampled in 5–13 blocks of area 20 cm × 20 cm or 3 soil blocks of 30 cm × 30 cm. To obtain homogeneous subsamples for analysis with a minimum variation of carbon concentrations and bulk density we divided the organic layers into three horizons: litter, O_f-layer and O_h-layer. However, in reporting the data here we only present the total carbon content. Carbon pools of the mineral soil were not included in the analysis for reasons explained below. The border between the soil organic layer and the upper surface horizon of the mineral soil column (the A_h-horizon) was not always clear cut. Following standard definitions, any horizon whose carbon concentration exceeded 17% of sample dry weight was included in the organic layer (AG Boden, 1994).

To approximate the temporal course of carbon fluxes with stand development, generally the first derivatives of non-linear empirical functions fitted to carbon pools over time were calculated (Janisch and Harmon, 2001). In the study area stand regeneration is initiated by stand-replacing fires. These fires result in the death of the former tree generation, consume fine organic material like needles, twigs and fine organic layer but do not consume bulky woody tissues (Lobert and Warnatz, 1993). Therefore, young regenerating stands usually carry high initial loads of coarse woody debris but little fine organic matter on the forest floor. In practice, the dynamics of carbon loss resulting from the decomposition of old carbon (C_{old}) [exclusively comprising coarse woody debris (CWD_{old}) in our model] were thus treated separately from the dynamics of new carbon. New carbon (C_{new}) comprises new biomass (C_B), new coarse woody debris (CWD_{new}) and soil organic layer. Assignment of soil organic layer to C_{old} or C_{new} was practically impossible. Therefore, the soil organic layer was generally classified as C_{new}, although

Table 2. *Parameters of functions fitted to carbon pools* C_{old} *(old CWD – previous generation) and* C_{new} *(newly accumulated carbon in biomass, organic layer and new CWD) as shown in Fig. 2*[a]

C-pool	Chronosequence	Function	Age range (yr)	a	k	b	c	SEE	R^2
C_{old}	Lichen type – combined unburned and moderately burned	exp	2–383	570.13	0.0346	-	-	46.6	0.94
C_{old}	Lichen type – heavily burned	exp	14–244	277.23	0.0417	-	-	23.8	0.90
C_{old}	*Vaccinium* type – moderately burned	exp	12–266	590.31	0.0328	-	-	17.3	0.99
C_{new}	Lichen type – unburned	pow	2–95	3.695	-	1.209	-	22.9	0.98
C_{new}	Lichen type – moderately burned plus young unburned	logn	2–383	976.90	-	1.7097	498.68	66.3	0.97
C_{new}	Lichen type – heavily burned	hyp	14–244	737.49	-	126.25	-	72.1	0.90
C_{new}	*Vaccinium* type – moderately burned	hyp	12–266	2243.43	-	146.83	-	90.2	0.98
$C_B + CWD_s$	Lichen type – moderately burned plus young unburned	logn	2–383	715.68	-	1.5346	573.77	43.6	0.98
NPP_W	Lichen type – moderately burned plus young unburned	logn	2–383	7.276	-	1.128	96.903	1.85	0.66

[a]Carbon pools are expressed in mol C m^{-2}. A two-parameter exponential decay function was used to fit C_{old} decomposition ['exp'; $C_{old}(t) = a * e^{-k*t}$, with t representing stand age in years]. Accumulation of C_{new} was fitted either with a hyperbolic function ['hyp'; $C_{new}(t) = a * t/[(b + t)]$], a log-normal function ('logn'; $C_{new}(t) + a \exp\{-0.5[\ln(t/c)/b]^2\}$) or a power function ['pow'; $C_{new}(t) = a * t^b$] (Fig. 2). NPP_W and the sum of $C_B + CWD_S$ were both fitted with the log-normal function (Fig. 5). SEE = standard error of estimates.

even high intensity stand-replacing fires do usually not consume the complete pre-fire soil organic layer (Gorbachev and Popova, 1996; FIRESCAN science team, 1996; but see also Cromack et al., 2000). Mineral soil carbon was not included in the analysis, because soil carbon integrates over time-scales much longer than stand longevity and, again, assignment to C_{old} or C_{new} is therefore not possible. Furthermore, earlier studies did not reveal any dependencies of soil carbon on stand age (p-values for regressions along the four chronosequences ranged between 0.15 and 0.97) or on time-since-fire. Instead general differences between chronosequences existed (Wirth et al., 2002a). Ignoring the mineral soil carbon we approximately miss 15% of the ecosystem carbon pool in our study area if the upper 25 cm of the mineral soil column are considered (Wirth et al., 2002a), and about 25% if the upper 100 cm are considered (own unpublished data). NEP_C, i.e. the temporal change in ecosystem carbon (C), was calculated as

$$\frac{dC}{dt} = \frac{dCWD_{old}}{dt} + \frac{dC_{new}}{dt}.$$

Empirical non-linear functions were fitted to the carbon pool data over time using Sigma-Plot 4.0$^{\copyright}$, and

the resulting functions were then differentiated analytically. Decay of CWD_{old} was fitted with a negative exponential function. To ensure optimal fit different functions were used to fit C_{new} over time for the different chronosequences. We deliberately did not use sigmoidal growth functions, since we did not assume that stands would approach a maximum carbon pool within the age range of the chronosequences. Detailed results of the data-fitting procedure are presented in Table 2. For the calculation of 95% confidence intervals around predicted values for known parameters we used the standard procedure in Sigma-Plot 4.0$^{\copyright}$ that implements standard statistical theory, as outlined e.g. in Neter et al. (1996).

2.3. Short-term net ecosystem productivity (NEP$_S$)

The estimate of NEP_C outlined above implicitly captures the effect of recurring surface fires, but the real carbon pool trajectories triggered by surface fires remain hidden behind the long-term trend. To estimate NEP_S in intervals between fires we reconstructed current changes in ecosystem carbon, combining measurements and data-constrained empirical models according to the following three approaches:

(a) We estimated woody biomass increment at the stand level by means of tree-ring analysis. Current rates of wood accumulation are given as the average of only the last three years and can be viewed as an estimate of net primary production of woody tissues (NPP_W). For a better visualisation of the short-term carbon pool trajectories, the reconstruction of NPP_W was also extended to a period of ten years prior to the harvest date (Fig. 4). In practice, in each of five to eight sample trees per plot representing the range of diameters a complete stem analysis was performed. Ring-width measurements were carried out on two to four radii of wood discs taken every metre along the bole using a digital tree-ring measurement device (LINTAB III Digital Linear Table and software TSAP; Frank Rinn Distribution, Heidelberg, Germany). The average diameter increment measured on the lower and upper disc of each bole segment was used to calculate the increment of under bark tree volume in successive years. Volume increments were converted into carbon accumulation by multiplying with wood density (435 kg_{dw} m_{dw}^{-3}; Wirth et al., 2002b) and carbon concentration (48.8 ± 0.7% of dry weight, $n = 73$; Wirth et al., 2002a). Total wood increment was derived from stem growth by multiplication with stand-specific expansion factors (Table 3) that were based on biomass allocation ratios for bark (own data) and coarse roots (Vanninen et al., 1996) and on published productivity allocation ratios for branches in various pine species compiled in Wirth et al. (2002b). Short-term carbon accumulation in needles and fine roots was considered negligible based on the high turnover of these organs. To scale the growth information of individual sample trees to the stand level, for each stand allometric functions were developed that related wood increment of sample trees for each individual year during the pre-harvest decade to their diameter at breast height at the time of harvest (Wirth et al., 2002b). Since growth and mortality happen in parallel in most forest ecosystems (Peet and Christensen, 1987; Vygodskaya et al., this issue), reconstructing carbon accumulation in biomass based solely on information of survivors could lead to erroneous results. Wirth et al. (1999) could show that mortality in the studied stands was almost exclusively triggered by surface fires. Only in one mature stand (200_{lm}) that had not burned for 100 yr were standing dead trees observed that were not killed by fire. Assuming that trees that were lethally damaged by surface fires die within 15 yr after the fire, we decided to assign zero mortality to later periods within a surface fire interval. The recent fire history of every stand was

Table 3. *Stand-specific expansion factors used to convert woody stem NPP into NPP of other woody compartments (bark, branches, coarse roots) and total woody NPP*[a]

Stand	Stem NPP [mol C m^{-2}]	EF bark	EF coarse roots	EF branches	EFΣ
12_{vu}	9.9	0.2	0.32	0.86	2.37
53_{vm}	11.7	0.13	0.22	0.64	1.99
95_{vm}	7.9	0.10	0.19	0.23	1.52
14_{lu}	1.1	0.27	0.18	1.13	2.58
28_{lu}	2.2	0.23	0.18	1.01	2.41
31_{lu}	3.9	0.21	0.18	0.91	2.29
95_{lu}	6.7	0.10	0.18	0.18	1.46
67_{lm}	6.0	0.11	0.18	0.42	1.71
138_{lm}	7.2	0.08	0.18	0.26	1.52
200_{lm}	2.0	0.08	0.18	0.27	1.53
204_{lm}	3.3	0.08	0.18	0.28	1.54
383_{lm}	3.9	0.08	0.18	0.21	1.47
14_{lh}	0.1	0.25	0.18	1.17	2.61
32_{lh}	0.2	0.20	0.18	1.14	2.52
48_{lh}	3.4	0.16	0.18	0.75	2.09
215_{lh}	1.9	0.08	0.18	0.42	1.68

[a]EF bark = expansion factor for bark NPP approximated as the ratio of bark biomass to stem wood biomass; EF coarse roots = expansion factor for coarse root NPP based on published ratios of coarse root to stem wood biomass (Vanninen et al., 1996); EF branches = expansion factor for branch NPP according to Wirth et al. (2002b). Using published data for the genus *Pinus* the ratio of branch to stem wood NPP was regressed on stem wood biomass to predict the allocation of production to branches. EFΣ = overall expansion factor to convert stem wood NPP into total woody NPP.

reconstructed by dating fire scars on the wood discs (listed in Table 5).

(b) According to Wirth et al. (2002a) the soil organic layer carbon pool is highly dependent on the time since the last fire. After a fire the organic layer carbon pool was at a minimum (about 50 mol C m^{-2}) and recovered within 50 yr to a level of 190 mol C m^{-2}. The data presented in Wirth et al. (2002a) were reanalysed and five new data points had been added: two data points were adopted from the study of the FIRESCAN science team (1996) and three more profiles were studied in 2000 in a freshly burned stand and in two other stands that had burned 36 and 95 yr ago (Fig. 1). To obtain flux estimates unaffected from assumptions underlying logistic functions, the data were fitted with a cubic spline according to Reinsch (1967). In the
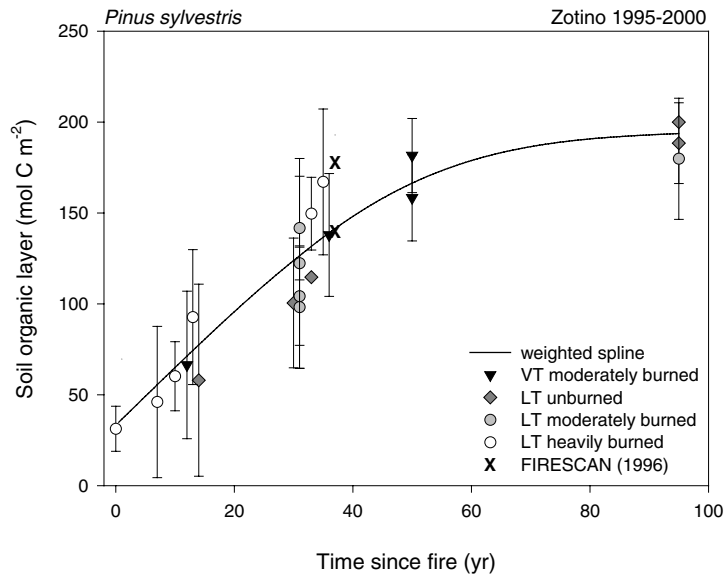
Fig. 1. Soil organic layer carbon pools as a function of time elapsed since the last fire event (stand-replacing crown fire or recurring surface fire). Error bars represent standard deviation of carbon content in either three soil monoliths of an area of 30×30 cm or five soil monoliths of an area of 20×20 cm per stand. Data were fitted with a cubic spline according to Reinsch (1967). In the regression individual points were weighted according to their standard deviation. VT, *Vaccinium* type; LT, lichen type. Crosses represent data taken from the FIRESCAN science team (1996).

regression individual points were weighted according to their standard deviation. In pooling stands of varying age, fire history and site quality, we accept a certain degree of bias introduced by differences in litter production rates associated with these factors. To lessen this bias we excluded stands with an *NPP* of needles (taken as a proxy for litter production rates) less than 1.5 mol C m^{-2} yr^{-1} with the average across all stands being 3.1 ± 1.9 (Wirth et al., 2002b). Consequently, the stands 2_{lu}, 14_{lh} and 26_{lh} were excluded from the analysis (needle $NPP = <0.1$, 0.2 and 0.6 mol C m^{-2} yr^{-1}, respectively).

(c) The amount of carbon currently lost by exponential decomposition of CWD is estimated applying a backward calculation with measured CWD carbon pool and decay constants as parameters. The decay constants of CWD were calculated for every chronosequence individually, with only the unburned and moderately burned lichen-type chronosequences being analysed together (Fig. 1; Table 4). The resulting decay constants were in agreement with decay constants reported for CWD of Scots pine in Russia of 0.033 yr^{-1} (Krankina and Harmon, 1995). Since decomposition rates of standing pine snags are very low (Krankina and Harmon, 1995), we entered as a mass

parameter only CWD that contacted the soil, i.e. lying logs and coarse dead roots. The latter were estimated based on the same root:shoot ratio as used for biomass (see above). NEP_S was then calculated as the sum of the measured rates of (a) woody biomass increment, (b) organic layer carbon accumulation as a function of time-since-fire and (c) carbon loss associated with CWD decomposition.

To estimate the fraction of *NPP* accumulating as short-term NEP_S in the ecosystem, the calculation had to be additionally performed for only the proportion of CWD that originated from the current stand (CWD_{new}), i.e. that resulted from *NPP* of the current stand. The difference between *NPP* and this form of NEP_S (new NEP_S) can be interpreted as carbon losses resulting from heterotrophic respiration.

2.4. Net primary production (NPP)

NPP of woody compartments (NPP_W) was estimated based on the same stem growth analysis as described above. In order to compare stands in which trees were harvested for this study in different years the interannual variability was removed by averaging

Table 4. *Cardinal points of chronosequence-based net ecosystem productivity (NEP$_C$) along different chronosequences of Siberian Scots pine forests*

Chronosequence	Stand age after which stands become a net sink for carbon (yr)	Time required to offset initial losses through decomposition of CWD_{old} (yr)	Stand age of maximum NEP_C (yr)	Maximum NEP_C (mol C m^{-2} yr^{-1})	NEP_C at stand age 200 yr (mol C m^{-2} yr^{-1})
Lichen type – unburned	24	58	95	10.8	-
Lichen type – moderately burned plus young unburned	23	77	72	3.1	1.3
Lichen type – heavily burned	25	70	71	1.8	0.9
Vaccinium type – moderately burned	12	27	69	5.1	2.7

stem-*NPP* estimates over three years before the harvest date. Again tree-level information was scaled up to the stand level using allometric relationships. Stand-specific expansion factors based on biomass relations were applied to convert stem growth into growth of all above- and belowground woody compartments (see above). Annual production of needles during the 3 yr before harvest was equated with the average stand level estimates of biomass of 1-, 2- and 3-yr-old needles. This approximation is considered valid since under boreal climate and low nutrient availability needles of Scots pine were not shed before 4–5 yr, as seen from needle scars. Detailed information on above-ground *NPP* in the studied stands is further provided in Wirth et al. (2002b). Annual fine-root production was not measured directly. Instead, we estimated fine-root production by dividing the measured fine-root biomass by a fine-root turnover time of 2 yr in the lichen-type stands and 1 yr in the *Vaccinium*-type stands. The value taken for the lichen-type stands represents the upper end of the range of longevity of Scots pine fine roots reported in Schoettle and Fahey (1994), taking into account the extreme continental climate and generally poor site quality in our study area. Furthermore, Mäkelä and Vanninen (2000) estimated fine-root longevity in Finnish Scots pine stands of the productive *Vaccinium* type and the poorer *Calluna* type to range between 0.5 and 0.8 yr and 0.9 and 2 yr, respectively. Accounting for the harsher continental climate in the study area and the even poorer site quality in the lichen-type stands we consider the assumed longevity values realistic. In our study the error associated with

the estimation of fine-root biomass is higher than in the estimation of needle production, although we did not attempt to quantify the errors. Fine root biomass was measured in conjunction with the soil sampling and was thus restricted to the area covered by the soil pits (<1 m^2 taken all pits together), which was much smaller than the area covered by the crowns of sample trees (between 5 and 150 m^2). It has been demonstrated by Vanninen and Mäkelä (1999) that fine-root production in boreal Scots pine is linearly related to needle production. To avoid propagating the uncertainty inherent in the fine-root production to the final stand-level estimate of *NPP*, we used this finding and expressed fine-root production as a linear function of needle production [fine-root production (mol C m^{-2} yr^{-1}) $= 1.38 \times$ needle production (mol C m^{-2} yr^{-1}); $R^2 = 0.70$, $p < 0.001$].

2.5. Modelling potential build up of CWD pools without fire

To explore the effect of fire on CWD pools a modelling analysis was performed to estimate how much carbon would be expected to accumulate as lying CWD if only carbon losses through heterotrophic respiration were to occur. This analysis was restricted to the moderately burned chronosequence of the lichen type because it contained most stands and covered the widest range of stand ages. In a first step, the temporal course of the production of decomposable lying CWD was calculated (dCWD_l/dt). Over the life-cycle, the cumulative woody net primary

production (NPP_W) of a stand produces more woody biomass than finally accumulates as biomass (C_B) in the ecosystem, i.e. $\int NPP_W(t) > C_B(t)$. The difference is the amount of carbon that was stored in trees that have become subject to mortality as the stand matured and thus been transferred into the coarse woody debris reservoir. Therefore,

$$NPP_W = \frac{dC_B}{dt} + \frac{dCWD}{dt}.$$

A freshly killed tree first enters the standing dead wood reservoir (CWD_s). Eventually, the snags fall over and enter the lying dead wood reservoir (CWD_l). The distinction of these two reservoirs of CWD is important, since it is known that in Scots pine the decomposition process starts only after the dead wood has contacted the soil (Harmon et al., 1986 and 2000). The change in CWD_l is then calculated as follows:

$$\frac{dCWD_l}{dt} = \\ NPP_W(t) - \frac{d(C_B + CWD_s)}{dt} - k \times CWD_l(t).$$

$NPP_W(t)$ was obtained by fitting the wood-NPP data along the chronosequence, and $d(C_B + CWD_s)/dt$ was obtained by analytical differentiation of the log-normal function fitted to the summed values of C_B and CWD_l that were measured in the chronosequence stands (Table 2). The last term $k \times CWD_l(t)$ reflects the circumstance that dead wood decomposes exponentially with a decay constant of k as soon as it enters the lying dead wood reservoir (Shvidenko and Nilsson, 2000). To solve for $CWD_l(t)$ it was necessary to sum up the overlapping decomposition trajectories of cohorts of carbon entering the lying dead wood reservoir at annual time-steps. This was done by numerical integration of:

$$CWD_l(\tau) =$$

$$\int_0^\tau \left[e^{-k(t-\tau)} \times \left(NPP(\tau) - \frac{d(C_B + CWD_s)}{d\tau} \right) \right] d\tau.$$

The resulting function $CWD_l(\tau)$ simulating the accumulation of CWD_l over time at given growth, mortality and decay rates can be compared to measured pools of CWD_l.

2.6. Direct fire losses from the soil organic layer carbon

The soil organic layer usually contains the most readily flammable materials in an ecosystem, and even fires of low intensity consume a certain portion of the organic layer and thus lead to direct carbon emissions (Gorbachev and Popova, 1996). To quantify direct carbon losses we compared burned and unburned sub-areas in three stands of the lichen type that were recently subject to fires: (1) A 235-yr-old stand of the heavily burned lichen type with a stand density of 156 trees per ha burned by a surface fire in 1990 was studied in 1997; (2) an approximately 200-yr-old stand with a stand density of 120 trees per ha burned by a surface fire in 2000 was studied directly after the fire; and (3) a 130-yr-old stand on Bor Island (a forest island in a bog) that was experimentally burned by a stand-replacing fire in 1993 was studied in 1995 and 1997 (FIRESCAN science team, 1996). Determination of soil organic layer carbon storage was performed using the same methods as outlined above.

3. Results

3.1. Chronosequence-based net ecosystem productivity (NEP_C)

The average decay constant of decomposition of CWD_{old} was 0.036 ± 0.002 (SE) (Table 2). In all chronosequences CWD_{old} was almost completely decomposed or indistinguishable from the organic layer after 100 yr (Fig. 2, upper panel). Accumulation of new carbon strongly differed between chronosequences (Fig. 2, lower panel). Carbon accumulation over time was highest along the moderately burned *Vaccinium*-type chronosequence and lowest along the heavily burned lichen-type chronosequence. Intermediate carbon accumulation was observed along the moderately burned lichen-type chronosequence. For comparison, the predicted values for C_{new} at the age of 200 yr ($\pm 95\%$ confidence interval) were 1293 ± 366 mol C m^{-2} in the moderately burned *Vaccinium* type chronosequence, 846 ± 76 mol C m^{-2} in the moderately burned lichen-type chronosequence and 452 ± 105 mol C m^{-2} in the heavily burned lichen-type chronosequence. Only under the absence of recurrent surface fires for an unusually long period of 95 yr did the oldest stand of the unburned lichen-type chronosequence (95_{lu}) reach the same level of C_{new} (908 ± 73 mol C m^{-2}) as the 95_{vm}-yr-old stand of the *Vaccinium* type (940 ± 264 mol C m^{-2}) that had burned at the age of 45 yr. None of the chronosequences seemed to reached a plateau of C_{new}. This may suggest that
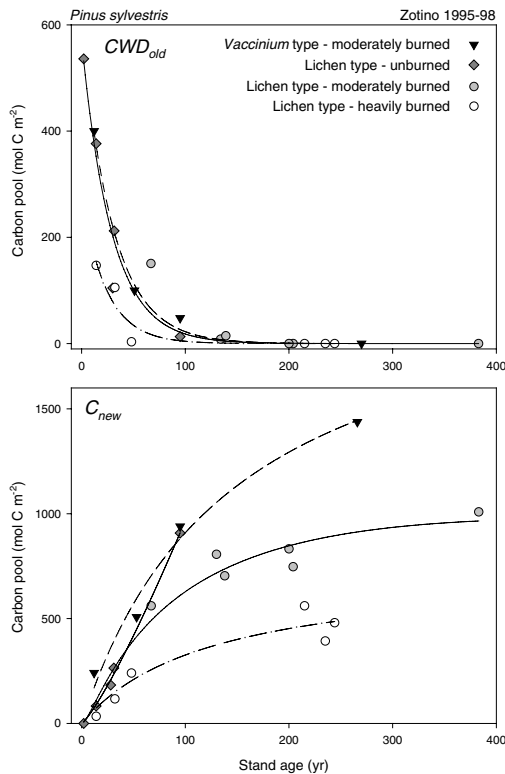
Fig. 2. Dynamics of carbon pools in four chronosequences of central Siberian Scots pine forests. The upper panel shows coarse woody debris left after a stand replacing fire (CWD_{old}). The lower panel shows carbon newly accumulated by the regenerating stand (C_{new}) including total biomass, coarse woody debris produced by the regenerating stand and soil organic layer. The types of functions used and their statistical indicators are presented in Table 2.

carbon accumulation continues even beyond the range of our chronosequences.

NEP_C as a function of stand age (t) was calculated for each chronosequence individually as the sum of the derivatives of the fitted functions for $CWD_{old}(t)$ and $C_{new}(t)$ over time. The resulting carbon fluxes $dC/dt = dCWD_{old}/dt + dC_{new}/dt$ are shown in Fig. 3. Stands of the lichen type acted as net carbon sources until a stand age of 24 yr irrespective of fire regime (Table 4). Comparing first the two burned lichen-type chronosequences, maximum NEP_C was higher in the moderately burned lichen type stands (3.1 mol C m^{-2} yr^{-1} at 72 yr) than in the heavily burned lichen type stands (1.8 mol C m^{-2} yr^{-1} at 71 yr). Despite this almost two-fold difference, the initial losses due to decomposition of

CWD_{old} were offset at the same time after about 75 yr (Table 4; downward arrows in Fig. 3) because initial CWD pools were much lower in the heavily burned lichen-type chronosequence. Under the absence of fire NEP_C had not yet reached a peak value along the unburned lichen-type chronosequence, and was as high as 10.8 mol C m^{-2} yr^{-1} at a stand age of 95 yr. This comparison illustrates the large negative impact of fire on NEP_C. Stands of the *Vaccinium* type became net carbon sinks already at a stand age of 12 yr due to about two times higher rates of carbon accumulation during this early period as compared to the lichen-type stands. Furthermore, initial losses of CWD_{old} were already offset after 27 yr, and a maximum NEP_C of 5.1 mol C m^{-2} yr^{-1} was attained after 69 yr. Figures 2 and 3 further illustrate that stands during their old-growth phase remain small but significant carbon sinks. 200-yr-old central Siberian pine stands were a net carbon sink of 1.63 ± 0.55 (SE) mol C m^{-2} yr^{-1}.

3.2. Short-term net ecosystem productivity (NEP_S)

NEP_S reflects the ecosystem carbon trajectories in periods between surface fires, i.e. direct losses of carbon from the soil organic layer through combustion and the transfer of carbon from the biomass to the CWD pool shortly after fire do not enter NEP_S. Therefore changes in biomass and organic layer carbon pools were always positive, while CWD was the only compartment exhibiting net losses of carbon (Table 5).

For NEP_S a comparable picture emerged as for NEP_C: young stands acted as net carbon sources whereas older stands were significant carbon sinks. While the pattern was similar compared to the chronosequence approach, the amplitude of the change in fluxes was higher: Very young stands appeared to be stronger carbon sources, while older stands generally were relatively stronger carbon sinks (Table 5). Site quality had a strong impact on sink–source dynamics during the early period of stand development. As an example, in the stand 12_{vu} of the *Vaccinium* type the magnitude of carbon losses from CWD (-15.3 mol C m^{-2} yr^{-1}) was greatly exceeded by carbon accumulation in woody biomass (19.8 mol C m^{-2} yr^{-1}) and organic layer carbon (3.2 mol C m^{-2} yr^{-1}), whereas in stand 14_{lu} losses from CWD of comparable magnitude (-18.4 mol C m^{-2} yr^{-1}) were not compensated for due to much lower rates of carbon accumulation in biomass (2.3 mol C m^{-2} yr^{-1}) and organic layer (3.1 mol C m^{-2} yr^{-1}).
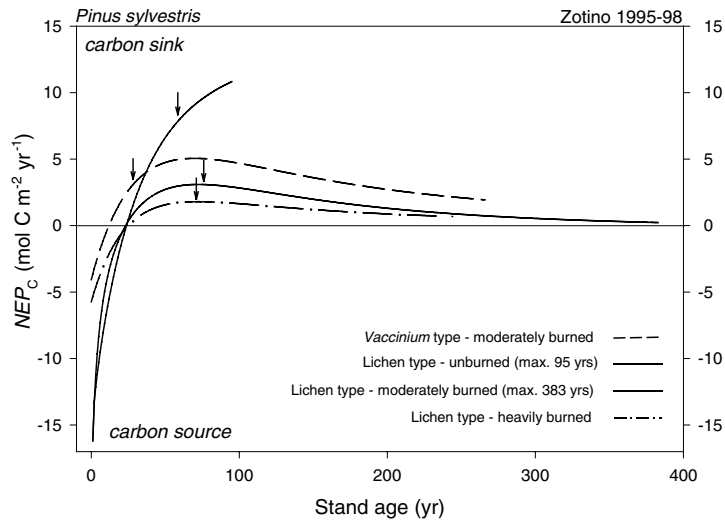
Fig. 3. Chronosequence-based net ecosystem productivity (NEP_C) calculated for each chronosequence individually as the sum of the derivatives of the fitted functions for CWD_{old} and C_{new} over time shown in Fig. 2 ($dC/dt = dCWD_{old}/dt + dC_{new}/dt$). Positive carbon flux values indicate net carbon uptake, negative values indicate carbon losses. Downward arrows indicate the time required to offset initial carbon losses that resulted from the decomposition of CWD_{old}.

In the five mature stands of the moderately and heavily burned lichen-type chronosequences (138_{lm}, 200_{lm}, 204_{lm}, $215l_{lh}$ and 383_{lm}) NEP_S was found to be five times higher than NEP_C. Average NEP_S in these stands was 6.2 ± 2.6 mol C m^{-2} yr^{-1} and average NEP_C was only 1.2 ± 0.6 mol C m^{-2} yr^{-1}. Among this group the highest NEP_S was reached in the stand 138_{lm} (9.6 mol C m^{-2} yr^{-1}). Four of the five mature lichen-type stands had been exposed to the same large-scale surface fire event 31 yr prior to the time of investigation (Table 5). Since changes in soil carbon were modelled as a function of time-since-fire, these stands accumulate carbon in the organic layer at the same rate of 2.6 mol C m^{-2} yr, while in stand 200_{lm} that had not burned for 95 yr organic layer carbon was close to equilibrium (cf. Fig. 1). Since in these stands pools of lying CWD were small the losses from the CWD component were also small. A similar pattern was found in the two older stands of the *Vaccinium* type chronosequence (53_{vm} and 95_{vm}) with NEP_S as high as 23.4 and 5.0 mol C m^{-2} yr^{-1}, respectively, as opposed to estimates of NEP_C of 4.8 and 4.7 mol C m^{-2} yr^{-1}.

The difference between short-term and chronosequence-based *NEP* is also illustrated in Fig. 4, where the recent development of ecosystem carbon pools was reconstructed for a period of 10 yr prior to the investigation. The resulting short-term carbon pool trajectories (small symbols in Fig. 4)

approached the trend lines of respective chronosequences from below indicating higher current *NEP* as compared to the long-term trend in ecosystem carbon accumulation. In general, NEP_S was very sensitive to the current level of decomposable CWD (i.e. excluding standing dead trees). For example, despite high rates of woody biomass accumulation (6.0 mol C m^{-2} yr^{-1}) the stand 67_{lm} was carbon neutral due to high loads of CWD (240 mol C m^{-2}), causing a carbon efflux of -8.2 mol C m^{-2} yr^{-1}. For the same reason the stand 31_{lu} was still a source after 31 yr. Comparing young and old stands of the unburned and the moderately burned lichen type chronosequence it emerged that age-related variability of wood accumulation was generally smaller than variability of losses from CWD decomposition.

3.3. Partitioning the losses of carbon

The fraction of *NPP* consumed by either ecosystem respiration or by fire can be inferred by comparing the ratios of NEP_S to NPP ($=r_S$) and NEP_C to NPP ($=r_C$). Since NEP_S is a measure of carbon accumulation in periods without fire, the expression $1 - r_S$ can be viewed as fraction of *NPP* lost to heterotrophic respiration (R_h). NEP_C on the other hand includes the effect of many recurring surface fires along a chronosequence. Therefore $1 - r_C$ is equivalent to the fraction of *NPP*

Table 5. *Carbon fluxes at different temporal scales in four chronosequences of Siberian Scots pine forests*[a]

Stand	Time since last fire (yr)	Decomposable CWD (mol C m^{-2})	Decomposable new CWD (mol C m^{-2})	Short-term (mol C m^{-2} yr^{-1})						Chronosequence-based (mol C m^{-2} yr^{-1})			
				Accumulation of woody biomass (1)	Changes in soil carbon (2)	Decay of all CWD (3)	Decay of new CWD only (4)	NEP_S (1 + 2 + 3)	"new" NEP_S (1 + 2 + 4)	"new" NEP_C dC_{new}/dt (5)	$dCWD_{old}$ /dt (6)	NEP_C (dC/dt) (5 + 6)	NPP ("")
12$_{vu}$	12[b]	446	0	23.6 ± 4.3	3.2	-15.3	0	**11.5**	26.8	13.1	-13.1	<	32.6
53$_{vm}$	36	116	20	23.3 ± 2.0	2.4	-4.0	-0.7	**21.7**	25.0	8.2	-3.4	**4.8**	45.1
95$_{vm}$	50	221	165	12.0 ± 0.8	1.5	-7.6	-5.7	**5.9**	7.8	5.6	-0.9	**4.7**	23.7
266$_{vm}$	50	68	43	n. d.	n. d.	n. d.	n. d.	**n. d.**	*n. d.*	1.9	<	**1.9**	n.d.
2$_{lu}$	2[b]	536	<	<	<	-19.0	<	**-19.0**	<	<	-18.4	**-18.4**	<
14$_{lu}$	14[b]	437	<	2.9 ± 0.7	3.1	-15.0	<	**-9.0**	*6.0*	7.7	-12.1	**-4.4**	6.9
28$_{lu}$	28[b]	122	<	5.3 ± 0.7	2.7	-4.2	<	**3.8**	*8.0*	9.0	-7.5	**1.5**	10.8
31$_{lu}$	31[b]	246	<	8.8 ± 0.8	2.6	-8.4	<	**3.0**	*11.4*	9.2	-6.7	**2.4**	17.2
95$_{lu}$	95	50	35	9.8 ± 1.0	0.1	-1.7	-1.2	**8.2**	*8.7*	11.6	-0.7	**10.8**	21.9
67$_{lm}$	31	240	66	10.6	2.6	-8.2	-2.3	**5.0**	*10.9*	5.0	-1.9	**3.1**	24.7
138$_{lm}$	31	52	35	11.0 ± 1.1	2.6	-1.8	-1.2	**11.8**	*12.4*	2.4	-0.2	**2.2**	20.3
200$_{lm}$	95	14	8	3.1 ± 0.01	0.1	-0.5	-0.5	**2.7**	*2.7*	1.3	<	**1.3**	11.8
204$_{lm}$	31	23	23	5.1 ± 0.3	2.6	-0.8	-0.8	**6.4**	*6.4*	1.3	<	**1.3**	13.1
383$_{lm}$	31	28	28	5.7 ± 0.3	2.6	-1.0	-1.0	**7.3**	*7.3*	0.3	<	**0.3**	16.9
14$_{lh}$	14[b]	172	2	0.4 ± 0.05	<	-5.9	-0.1	**-5.5**	*0.3*	4.7	-6.5	**-1.7**	0.9
26$_{lh}$	14	138	15	0.6 ± 0.1	<	-4.7	-0.5	**-4.1**	*0.1*	3.7	-3.0	**0.7**	2.0
48$_{lh}$	10	5	1	7.0 ± 1.6	3.1	-0.2	0	**9.9**	*10.1*	3.1	-1.5	**1.5**	15.7
215$_{lh}$	32	6	6	3.2 ± 0.6	2.6	-0.2	-0.2	**5.6**	*5.6*	0.8	<	**0.8**	12.1

[a]Short-term net ecosystem productivity (NEP_S) was calculated as the sum of (1) accumulation of woody biomass that was derived from stem analysis (average of 3 yr prior to measurement date ±SD), (2) changes in soil carbon including organic layer calculated as a function of time-since-fire according to Fig. 1 and (3) decay of coarse woody debris (CWD) calculated backwards using site-specific exponential decay functions and measured current CWD pools as input (also compare Table 4). Decomposable CWD comprises lying dead wood and dead coarse roots. In addition, NEP_S was also expressed based on decomposition of only newly produced CWD. The component fluxes of chronosequence-based net ecosystem production (NEP_C) resulting from decay of old CWD ($dCWD_{old}$/dt) and accumulation of new carbon in biomass, CWD and organic layer ("new" $NEP_C = dC_{new}$/dt) are given for the respective stand ages. The estimation of NEP_C was based on the chronosequence approach (compare Fig. 2). Negative signs indicate loss of carbon from the ecosystem to the atmosphere, NEP = net primary productivity, <= value below 0.01.
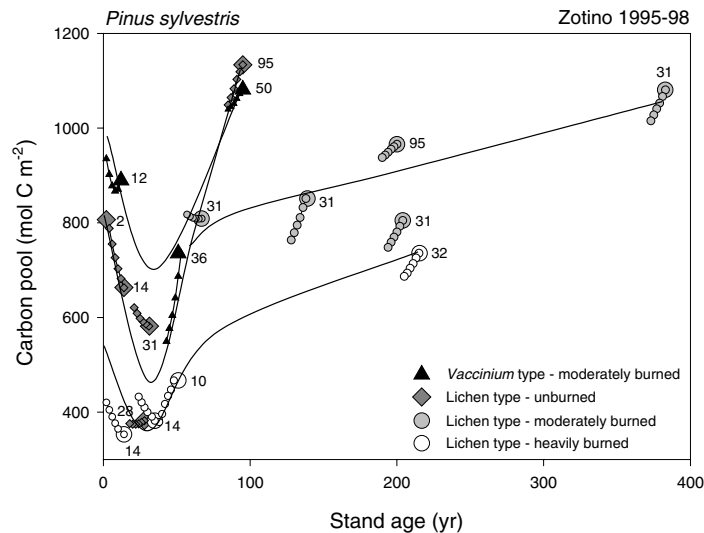[b]Last fire was a stand-replacing crown fire.

Fig. 4. Development of total ecosystem carbon pools along the four chronosequences (large symbols). Chronosequence-based net ecosystem productivity (NEP_C is approximately equivalent to the slope of the fitted lines (manually fitted here; exact calculation see text and Table 2). Small symbols illustrate the recent course of carbon pools reconstructed for a period of ten years before the time of investigation in time-steps of 2 yr. Notably in older stands that have experienced surface fires, the resulting trajectories of recent changes in carbon pools (short-term net ecosystem productivity NEP_S, small symbols) approach the trend lines of respective chronosequences from below illustrating higher NEP_S in intervals between fires as compared to NEP_C. Figures close to data points indicate the time since the last fire.

lost to both heterotrophic respiration and fire. The fraction lost by combustion f_{Fire} in the simply calculated as $f_{Fire} = (1 - r_C) - (1 - r_S) = r_S - r_C$. In general, this comparison requires one to remove the effect of decomposition of old CWD from both NEP_S and NEP_C (giving "new NEP_S" and "new NEP_C", Table 5), since this process feeds on carbon that did not originate from NPP of the current stand. Both ratios, r_S and r_C, exhibited an exponentially decreasing trend with stand age and reached a constant low baseline in mature stands after about 150 yr (Fig. 5). Despite considerable scatter it appears that in mature stands r_S stabilises at 0.42, i.e. about 58% of NPP is lost to heterotrophic respiration ($1 - r_S = 0.58$). In contrast, r_C stabilises at 0.07 in mature stands, suggesting that in old stands only 7% of NPP accumulates in the ecosystem. The fraction of NPP additionally lost by combustion f_{Fire} was 0.35 or 35%. In those stand that have never burned both expressions $1 - r_S$ and $1 - r_C$ quantify heterotrophic losses only and should therefore be of comparable magnitude. Indeed, in the 95-yr-old unburned stand of the lichen type the chronosequence-based estimate of the fraction of NPP lost by heterotrophic respiration

$(1 - r_C = 0.47)$ was even lower than the short-term estimate ($1 - r_S = 0.60$).

3.4. Estimates of direct carbon losses during fire

In three partly burned stands, 235_{lh}, 200_{lh} and 130_{lm}, the magnitude of carbon losses due to burning of the organic layer was quantified to be 69, 49 and 39%, respectively, relative to the pre-fire status (Table 6). Thus, approximately half of the organic layer carbon was consumed by fires. It is interesting to note that the experimental stand-replacing fire initiated by the FIRESCAN science team (1996) in stand 130_{lm} caused less relative reduction than the surface fires in the two other stands.

The role of fire in controlling dead wood pools was further explored in a modelling analysis using the moderately burned chronosequence of the lichen type. The two lines in the upper panel in Fig. 6 show the temporal course of woody biomass production, $NPP_W(t)$ (cf. Table 5), and the combined rate of carbon accumulation in woody biomass dC_B/dt and standing dead wood $dCWD_s/dt$, respectively. The difference between production and accumulation, illustrated as the
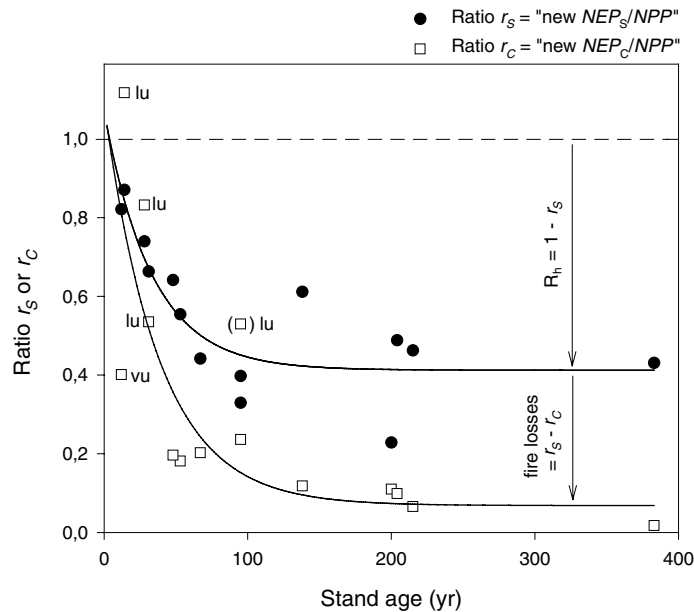
Fig. 5. The ratios of NEP_C and NEP_C over NPP (r_S and r_C, respectively) as a function of stand age based on the data presented in Table 5. Data of all stands were pooled for the analysis and fitted with a negative exponential function with a constant term added. The fraction of NPP lost by heterotrophic respiration (R_h) at a given stand age can be approximated by the quantity $1 - r_S(t)$, while the direct fire loss through combustion is given by $r_S(t) - r_C(t)$. Unburned stands that were included in fitting r_C are marked with either *lu* or *vu*, depending on the site quality of the respective chronosequence.

Table 6. *Comparison of soil organic layer carbon pools in burned and unburned parts of recently burned stands of the lichen type in central Siberian Scots pine forests*

Stand	Status	Type and date of fire	n^a	Organic layer average $\pm$ SD (mol C m^{-2})	Relative reduction (%)
235_{lh}	Unburned		2	150 ± 20	
	Burned	Surface fire 7 yr ago	3	46 ± 42	-69
200_{lh}	Unburned		5	61 ± 33	
	Burned	Fresh surface fire	5	31 ± 12	-49
130_{lh}	Unburned		3	247 ± 56	
	Burned	Stand-replacing fire 2 yr ago	3	150 ± 47	-39

[a]n indicates the number of soil profiles sampled per spatial subunit.

shaded area, yields the rate ($dCWD_l/dt$) at which carbon is transferred into the lying coarse woody debris pool (CWD_l). The solid line in the lower panel in Fig. 6 represents the modelled pools of CWD_l, if the carbon cohorts that continuously enter the forest floor according to $dCWD_l/dt$ decompose exponentially with the measured rate of 0.036 yr^{-1}. The model behaviour for extreme values of k (0.03 yr^{-1} and 0.045 yr^{-1}) is also

shown in Fig. 6. With the appearance of lying CWD at a stand age of about 50 yr the modelled and measured pools soon diverge. From then on the measured CWD_l are only about 30% of the modelled pools for k = 0.036 yr^{-1}. This result suggests that recurring surface fires reduce the amount of lying CWD by as much as 70% and therefore consume lying CWD at a three times higher rate than heterotrophic respiration.
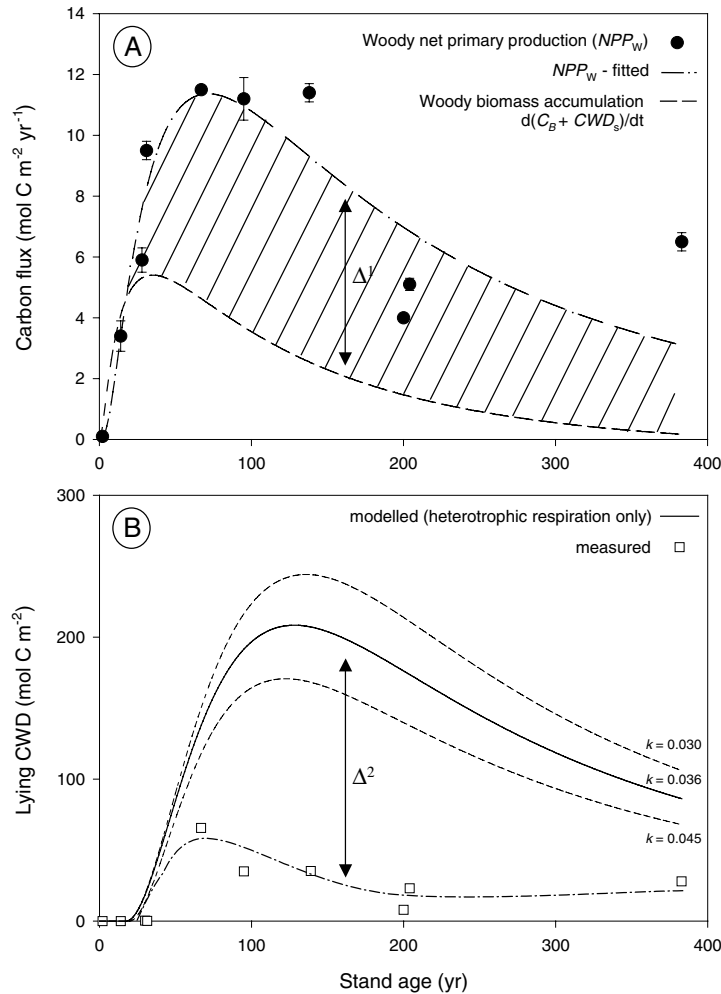
Fig. 6. The upper panel shows the age trend of annual production of woody biomass (NPP_W, filled circles or dashed-dotted line) and the summed accumulation rates of carbon in biomass and standing dead wood [$\mathrm{d}(C_B + CWD_s)/\mathrm{d}t$] (dashed line) along the moderately burned chronosequence of the lichen type, including the young unburned lichen-type stands as a realistic starting condition. Data points of NPP_W are shown as average of 3 yr before harvest ± standard deviation. The shaded area is the rate at which coarse woody debris enters the forest floor over time, including dead roots of standing dead trees. This rate was used as input function to model the accumulation of newly produced CWD with stand age. Cohorts of new CWD_l entering the forest floor at an annual time-step are assumed to decompose exponentially with a decay rate of $k = 0.036$ yr^{-1}. The resulting build up of new CWD_l is shown as a solid line in the lower panel. Measured actual pools of new CWD_l are shown as open squares. The difference between the modelled and measured values Δ^2, suggests that about 70% of new CWD_l is consumed by surface fires.

4. Discussion

4.1. Validity of model assumptions

Clearly, our estimates of NEP_C, NEP_S and the build up of CWD_l pools are sensitive to variations in the

decay constants k that were derived from our data to model fluxes related to decomposition of CWD. Using NEP_C as an example, with a decay constant half of the estimated average value (0.018 yr^{-1} instead of 0.036 yr^{-1}), the moderately burned chronosequence of the lichen type would become a net sink after 7 instead

of 23 yr and would offset initial carbon losses after 20 instead of 72 yr. Deriving a decay constant from fitting the disappearance of CWD_{old} along a chronosequence implicitly assumes that all stands of the chronosequence started off with same initial mass of CWD. In turn, the initial mass of CWD_{old} after a stand-replacing fire is directly dependent on the coarse woody biomass of the previous stand, because this represents a fraction of ecosystem carbon that is not even consumed by high intensity fires (Lobert and Warnatz, 1993). However, because accumulation rates of woody biomass started to decrease after about 120 yr (Wirth et al., 2002a), a variability in stand-replacing fire cycles beyond that age becomes less and less important. For example, doubling a 150-yr fire cycle to a 300-yr cycle would increase the initial CWD mass by only 30% from about 480 to 630 mol C m^{-2}. This range also shows that the initial CWD mass in stand 2_{lu} of 536 mol C m^{-2} well represented the starting point in a system with an average stand-replacing fire cycle of about 250 yr.

Apart from variation in initial mass of CWD_{old}, bias would be introduced if recurring surface fires speeded up decomposition of CWD_{old}. This seemed to be of minor importance though. If a decay constant was derived from the unburned chronosequence of the lichen type (0.038 yr^{-1}) this did not significantly differ from the decay constants given in Table 4 that include burned stands. Furthermore, our decay constants are in close agreement with estimates of Krankina and Harmon (1995) and Harmon et al. (2000), who report 0.033 and 0.035 yr^{-1}, respectively, for CWD in Scots pine forests of European Russia that were not subject to surface fires. It seems therefore, that the decomposition dynamics of the initial CWD mass, from which the decay constants were derived, were indeed dominated by the activity of heterotrophic organisms.

Our simple exponential model of CWD decomposition assumes a constant decay rate. However, it was found by Harmon et al. (2000) that because decomposers slowly colonise standing dead pine wood the decay rate is initially lower. Own field observations suggest a lag-time of about 5 yr until trees fall over and the decomposition process commences. However, these dynamics are difficult to derive from chronosequence data and require direct long-term observation. Accounting for a lag-time in the decomposition model would probably dampen the long-term carbon dynamics. The early minimum of ecosystem carbon at a stand age of 25 yr would become less pronounced, since at

the delayed onset of decomposition the accumulation rates of new carbon are already high.

Fine-root NPP is a significant component of total NPP (Jackson et al., 1997; Makkonen and Helmisaari, 2001). The accuracy of the estimate of total NPP is thus dependent on the quality of the indirect estimation based on measured fine-root biomass and assumptions regarding fine-root turnover. Fine-root biomass in stands of the lichen type (12.4 $\pm$ 4.5 mol C m^{-2}) was in good agreement with published values for seven boreal Scots pine stands of varying age on poorer site types averaging 12.7 $\pm$ 3.2 mol C m^{-2} (Persson, 1978; Axelsson and Brakenhielm, 1980; Linder and Axelsson, 1982; Helmisaari, 1995; Vogt et al., 1996). Assuming a fine-root turnover of 2 yr resulted in stand-level average root:shoot ratio of NPP of 0.39 $\pm$ 0.04 ($n = 17$) which was consistent with root:shoot ratios of NPP reported for eight other boreal Scots pine forests by Gower et al. (2001) that averaged 0.42 $\pm$ 0.18, suggesting the appropriateness of the above approach.

It is important to note that the carbon pool of the mineral layer did not enter the calculation of NEP_C and NEP_S. While Wirth et al. (2002a) could show that there was no significant trend in mineral layer carbon pools along any of the four chronosequences, they found indications for a downward transport of dissolved organic carbon shortly after fire. Thus, ignoring the mineral layer carbon dynamics it is possible that we miss a small but significant sink. Ongoing research aims at quantifying the magnitude of this unaccounted sink in the deeper soil layers. Ignoring the mineral soil layer we account only for a part of the fine-root NPP, namely the fraction that enters the organic layer. Approximately half of the fine-root NPP is deposited in the mineral soil compartment, and any carbon accumulation due to this carbon input is not detected.

4.2. The importance of the temporal scale

The discrepancy between long- and short-term estimates of NEP in pole stands as well as mature stands illustrates the pitfalls of using short-term flux estimates like those obtained from eddy covariance measurements as a means to quantify carbon exchange in disturbed ecosystems. Disturbance by recurring surface fires has multiple effects: (a) Through combustion of flammable material surface fires cause a carbon export from the system (Lobert and Warnatz, 1993;

FIRESCAN science team, 1996). (b) By causing tree mortality surface fires lead to an increase of CWD pools as well as a decrease of green biomass (Matveev and Usol'tzev, 1996; Yevdokimenko, 1996). This results in a transient shift of the ecosystem carbon balance towards respiratory carbon losses (Shvidenko and Nilsson, 2000; Wirth et al., 2002a). (c) Surface fires usually improve growing conditions for survivors by opening up space and increasing nutrient availability (Raison, 1979; Neary et al., 1999). Thus, the carbon balance of a surface fire cycle is characterised by three stages: (1) direct carbon losses, (2) initial dominance of post-fire carbon losses over carbon uptake and (3) recovery of survivors sequestering carbon at high rates by filling newly available growing space and restoration of the organic layer. Since stage 3 is long in comparison with the duration of stages 1 and 2, any short-term flux measurement campaign in disturbance-prone ecosystems is likely to hit the period of net carbon uptake. We believe that this is the reason why our mass based estimate of NEP_S in formerly burned mature stands is so much higher than the estimates of NEP_C that reflect the longer-term carbon accumulation along the chronosequence. Since the majority of mature stands were affected by the same fire event in 1964 these stands were well in the recovery stage (stage 3) at the time of the investigation and exhibited high actual rates of carbon accumulation until high stand ages (Fig. 4). Based on our findings, we assume that at least part of that carbon will be consumed by direct and indirect carbon losses associated with the next fire event to come.

Indeed, eddy covariance measurements of short-term carbon exchange in boreal pine forests exhibited high rates of carbon uptake. For a 35-yr-old boreal Scots pine forest of the *Vaccinium* site type regenerating after harvest, Markkanen et al. (2001) reported a 3-yr average of 19 mol C m^2 yr^{-1}. Eddy flux measurements carried out in the 200_{lm}-yr-old stand of the lichen type resulted in a 2-yr average of 13.5 mol C m^2 yr^{-1} (Lloyd et al., this issue). This flux estimate exceeded our mass-based NEP_S in stand 200_{lm} (2.7 mol C m^2 yr^{-1}) by a factor of 5, and the average short-term NEP_S of all mature stands of the lichen type (6.5 $\pm$ 3.0 mol C m^2 yr^{-1}) by a factor of 2. At the moment we are not able to explain this discrepancy. Eddy covariance studies that were designed to capture the carbon balance during stage 2 of a disturbance cycle (dominance of post-disturbance carbon losses) indeed evidenced net losses of carbon to the atmosphere after

fire (Amiro, 2001), harvest (Schulze et al., 1999) and wind-throw (Knohl et al., 2002).

4.3. Partitioning carbon losses into respiration and combustion

Once carbon appears in an ecosystem as net primary production it may be lost again through heterotrophic respiration or it may be exported by processes that by-pass respiration, like fire or harvest (Schulze and Heimann, 1998). Employing an indirect analysis that follows the ratios of NEP_C and NEP_S to NPP with stand age, respectively, we estimated that in mature stands older than 150 yr some 58% of NPP is lost by heterotrophic respiration and that surface fire consumes another 35% in the long term (Fig. 5). The remaining 7% of NPP accumulates in the ecosystem of mature fire-prone pine ecosystems. A rough calculation may prove that the above partitioning is in the right order of magnitude. Given an average NPP of mature lichen type stands of 14.8 $\pm$ 3.7 mol C m^2 yr^{-1} (stands 138_{lm}, 200_{lm}, 204_{lm}, 215_{lh} and 383_{lm}) and a mean fire return interval of 35 yr (Wirth et al., 1999), the average surface fire should consume 180 mol C m^{-2} (=14.8 mol C m^2 yr^{-1} $\times$ 35 yr $\times$ 0.35). This loss rate is comparable to fire emissions observed in North American pine forests that ranged between 91 and 208 mol C m^{-2} per fire (Stocks and Kauffmann, 1997). The average fuel consumption rate for Canada was reported to be 108 mol C m^{-2}, with a range of 75–170 mol C m^{-2} (Amiro et al., 2001), and according to Shvidenko and Nilsson (2000) in the forested area of Russia the direct fire losses in burned areas averaged 110 mol C m^{-2}. Our estimate of fractional carbon loss to fire is further confirmed by Harden et al. (2000), who estimated that in Canadian *Pinus banksiana* forests of the lichen type considering a time-scale of millennia about 25% of NPP is consumed by fire. We note that the fraction of carbon lost to heterotrophic respiration (58%) in mature stands was remarkably low, which defies the wide-held notion of mature stands being carbon neutral. As we pointed out earlier, all mature stands accumulated significant amounts of carbon and were thus far away from steady-state conditions.

Forest fires do not only emit carbon but also produce recalcitrant black carbon (Kuhlbusch, 1998). Published conversion efficiencies expressed as percent black carbon produced per fuel mass burned range between 0.6 and 8% across biomes (Kuhlbusch et al., 1996; Fearnside et al., 1999; Tinker and Knight, 2000;

own data of C. Czimczik in preparation), i.e. each fire may set aside between 1 and 14 mol C m^{-2} as recalcitrant black carbon that may accumulate in deeper soil layers over time. Ignoring this flux we may miss a small but significant and persistent sink.

We conclude that in fire ecosystems as they are typical for large areas of the boreal forest biome a significant proportion of *NPP* is lost from the system by combustion. We proposed a framework according to which these losses can be quantified based on data on inventoried changes in carbon pools and fire history. We suggest that any short-term flux measurement carried out in disturbed ecosystems should be accompanied by mass-based analyses that allow the reconstruction of long-term trajectories of carbon pools.

5. Abbreviations

C = ecosystem carbon pool

C_b = carbon stored in biomass

C_{new} = carbon pool produced and accumulated by the current stand

C_{old} = carbon pool produced and accumulated by the previous stand

CWD_{old} = carbon left over from the preceeding stand after stand-replacing fire comprising mainly CWD

CWD_l = lying coarse woody debris

CWD_s = standing coarse woody debris

NEP = net ecosystem productivity

NEP_C = chronosequence-based net ecosystem productivity

NEP_S = short-term net ecosystem productivity

NPP_W = net primary productivity of woody biomass components only

R_h = heterotrophic respiration

r_C = ratio of NEP_C to NPP

r_S = ratio of NEP_S to NPP

6. Acknowledgements

REFERENCES

Aber, J. D. and Melillo, J. M. 1991. *Terrestrial ecosystems*. Saunders College Publishing, Philadelphia, 429 pp.

AG Boden. 1994. *Bodenkundliche Kartieranleitung*, 4th edn. Schweizerbart'sche Verlagsbuchhandlung Hannover, 392 pp.

Amiro, B. D. 2001. Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. *Glob. Change Biol.* **7**, 253–268.

Amiro, B. D., Todd, J. B., Wotton, B. M., Logan, K. A., Flannigan, M. D., Stocks, B. J., Mason, J. A., Martell, D. L. and Hirsch, K. G. 2001. Direct carbon emissions from Canadian forest fires, 1959–1999. *Can. J. For. Res.* **31**, 512–525

Arbatskaya, M. K. and Vaganov, E. A. 1997. Long-term variation in fire frequency and radial increment in pine from the middle taiga subzone of central Siberia. *Russ. J. Ecol.* **28**, 291–297.

Axelsson, B. and Brakenhielm, S. 1980. Investigation sites of the Swedish Coniferous Forest project – biological and physiographical features. In: *Structure and function of northern coniferous forests – an ecosystem study* (ed. T. Persson). *Ecol. Bull.* **32**, 25–64.

Cajander, A. K. 1926. The theory of forest types. *Acta For. Fenn.* **29**, 1–108.

Cromack, Jr., K., Landsberg, J. D., Everett, R. L., Zeleny, R., Giardina, C. P., Strand, E. K., Anderson, T. D., Averill R. and Smyrski, R. 2000. Assessing the impacts of severe forest fire on forest ecosystem recovery. In: *Mapping wildfire hazard and risks* (eds. R. N. Sampson, R. D. Atkinson and J. W. Weiss). Food Products Press, Binghampton, NY, 177–228.

Fearnside, P. M., Graca, P. M. L. A., Filho, N. L., Rodrigues, F. J. A. and Robinson, J. 1999. Tropical forest burning in Brazilian Amazonia: measurement of biomass loading, burning efficiency and charcoal formation at Altamira, Pará, *For. Ecol. Manag.* **123**, 65–79.

FIRESCAN science team. 1996. Fire in ecosystems of boreal Eurasia: The Bor Forest Fire Experiment, Fire Research Campaign Asia-North (FIRESCAN). In: *Biomass burning and global change*, Vol. II (ed. J. S. Levine). MIT Press, Cambridge, MA, 848–873.

Furyaev, V. V. 1996. Pyrological regimes and dynamics of the Southern Taiga forests in Siberia. In: *Fire in ecosystems of boreal Eurasia* (eds. J. G. Goldammer and

V. V. Furyaev). Kluver Academic Publishers, London, 168–185.

Glebov, F. Z. 1969. Bogs and wetlands of the forest zone of the Yenisei left-bank (in Russian). Nauka, Moscow, 132 pp.

Gorbachev, V. N. and Popova, E. P. 1996. Fires and soil formation. In: *Fire in ecosystems of boreal Eurasia* (eds. J. G. Goldammer and V. V. Furyaev). Kluver Academic Publishers, Dordrecht, 331–336.

Gower, S. T., Krankina, O., Olson, R. J., Apps, M., Linder, S. and Wang, C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* (in press).

Harden, J. W., Trumbore, S. E., Stocks, B. J., Hirsch, A., Gower, S. T., O'Neill, K. P. and Kasischke, E. S. 2000. The role of fire in the boreal carbon budget. *Glob. Change Biol.* **6(Suppl. 1)**, 174–184.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* **15**, 133–276.

Harmon, M. E., Krankina, O. N. and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. *Can. J. For. Res.* **30**, 76–84

Helmisaari, H.-S. 1995. Nutrient cycling in *Pinus sylvestris* stands in eastern Finland. *Plant Soil* **168/169**, 327–336

Jackson, R. B., Mooney, H. A. and Schulze, E.-D. 1997. A global budget for fine-root biomass, surface area and nutrient contents. *Proc. Natl. Acad. Sci. USA* **94**, 7362–7366.

Janisch, J. E. and Harmon, M. E. 2001. Succesional changes in live and dead wood stores: implications for net ecosystem productivity. *Tree Phys.* (in press).

Knohl, A., Kolle, O., Minayeva, T. Y., Milyukova, I. M., Vygodskaya, N. N., Foken, T., Schulze, E.-D. 2002. Carbon exchange of a Russian boreal forest after disturbance by windthrow. *Glob. Change Biol.* **8**, 231–246.

Krankina, O. N., Harmon, M. E. and Griazkin, A. V. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. *Can. J. For. Res.* **29**, 20–32.

Krankina, O. N. and Harmon, M. E. 1995. Dynamics of the dead wood carbon pool in Northwestern Russian boreal forest. *Water Air Soil Poll.* **85**, 227–238.

Kuhlbusch, T. A. J., Andreae, M. O., Cachier, H., Goldammer, J. G., Lacaux, J.-P., Shea, R. and Crutzen, P. J. 1996. Black carbon formation by savanna fires: measurements and implications for the global carbon cycle. *J. Geophys. Res.* **101(D19)**, 23651–23665.

Kuhlbusch, T. A. J. 1998. Black carbon and the carbon cycle. *Science* **280**, 1903–1904.

Linder, S. and Axelsson, B. 1982. Changes in carbon uptake and allocation patterns as a result of irrigation and fertilisation in a young Pinus sylvestris stand. In: *Carbon*

uptake and allocation: key to management of subalpine forest ecosystems* (ed. R. H. Warring). IUFRO Workshop. For. Res. Lab., Oregon State University, Corvallis, OR, 38–44.

Lloyd, J., Shibistova, O., Zolotoukhine, D., Kolle, O., Arneth, A., Wirth, C., Styles, J. M., Tchebakova, N. M. and Schulze, E.-D. 2002. Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest. *Tellus* **54B**, this issue.

Lobert, J. M. and Warnatz, J. 1993. Emissions from the combustion process in vegetation. In: *Fire in the environment* (eds. P. J. Crutzen and J. G. Goldammer). Dahlem Workshop Reports, Environmental Sciences Research Report 13, John Wiley and Sons Ltd., Chichester, 15–38.

Mäkelä, A. and Vanninen, P. 2000. Estimation of fine-root mortality and growth from simple measurements: a method based on systems dynamics. *Trees* **14**, 316–323.

Makkonen, K. and Helmisaari, H.-S. 2001. Fine root biomass and production in Scots pine stands in relation to stand age. *Tree Physiol.* **21**, 193–198.

Markkanen, T., Rannik, U., Keronen, P., Suni, T., and Vesala, T. 2001. Eddy covariance fluxes over a boreal Scots pine forest. *Bor. Environ Res.* **6**, 65–78.

Matveev, P. M. and Usol'tzev, V. A. 1996. Post-fire mortality and regeneration of *Larix sibirica* and *Larix dahurica* in conditions of long-term permafrost. In: *Fire in ecosystems of boreal Eurasia* (eds. J. G. Goldammer and V. V. Furyaev). Kluwer Academic Publishers, Dordrecht, 366–371

Neary, D. G., Klopatek, C. C., DeBano, L. F. and Ffolliott, P. F. 1999. Fire effects on below-ground sustainability: a review and synthesis. *For. Ecol. Manag.* **122**, 51–71.

Neter, J., Kutner, M. H., Nachtsheim, C. J. and Wassermann, W. 1996. *Applied linear statistical models*. WCB McGraw-Hill, Boston, 1408 pp.

Peet, R. K. and Christensen, N. L. 1987. Competition and tree death. *BioScience* **37**, 586–594.

Persson, H. 1978. Root dynamics in a young Scots pine stand in central Sweden. *Oikos* **30**, 508–519.

Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. *Plant Soil* **51**, 73–108.

Reinsch, C. H. 1967. Smoothing by spline functions. *Numer. Math.* **10**, 177–183.

Schoettle, A. W. and Fahey, T. J. 1994. Foliage and fine-root longevity of pines. In: *Environmental constraints on the structure and productivity of pine ecosystems: a comparative analysis* (eds. H. L. Gholz, S. Linder and R. E. McMurtie). *Ecol. Bull.* **43**, 136–154.

Schulze, E.-D. and Heimann, M. 1998. Carbon and water exchange of terrestrial systems. In: *Asian change in the context of global climate change* (eds. J. Galloway and J. Mellilo). Cambridge University Press, Cambridge, 363 pp.

Schulze, E.-D., Lloyd, J., Kelliher, F. M., Wirth, C., Rebmann, C., Lühker, B., Mund, M., Knohl, A., Milyukova, I., Schulze, W., Ziegler, W., Varlagin, A., Sogachov, A., Valentini, R., Dore, S., Grigoriev, S., Kolle, O.,

Tchebakova, N. and Vygodskaya, N. 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink – a synthesis. *Glob. Change Biol.* **5**, 703–722.

Schulze, E.-D., Wirth, C. and Heimann, M. 2000. Managing forests after Kyoto. *Science* **289**, 2058–2059.

Schulze, E.-D., Vygodskaya, N. N., Tchebakova, N. Czimczik, C. I., Kozlov, D. Lloyd, J., Mollicone, D., Parfenova, E., Siderov, K., Varlagin, A. and Wirth, C. 2002. The Eurosiberian transect: an introduction to the experimental region. *Tellus* **54B**, this issue.

Shvidenko, A. and Nilsson, S. 2000. Fire and the carbon budget of Russian forests. In: *Fire, climate change, and carbon cycling in the boreal forest* (eds. E. S. Kasischke and B. J. Stocks). Springer, New York, 289–311.

Stocks, B. J. and Kauffmann, J. B. 1997. Biomass consumption and behaviour of woodland fires in boreal, temperate, and tropical ecosystems: parameters necessary to interprete historic fire regimes and futuer fire scenarios. In: *Sediment records of biomass burning and global change* (eds. J. S. Clark et al.). NATO ASI Series 51, Springer, Berlin.

Tinker, D. B. and Knight, D. H. 2000. Coarse woody debris following fire and logging in Wyoming Lodgepole Pine forests. *Ecosystems* **3**, 472–783.

Vanninen, P., Ylitalo, H., Sievänen, R. and Mäkelä, A. 1996. Effects of age and site quality on the distribution of biomass in Scots pine. *Trees* **10**, 213–238

Vanninen, P. and Mäkelä, A. 1999. Fine root biomass of Scots pine stands differing in age and site fertility in southern Finland. *Tree Physiol.* **19**, 823–830

Vogt, K. A., Vogt, D. J., Palmiotto, P. A., Boon, P., O'Hara, J. and Asbjornsen, H. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* **187**, 159–219.

Vygodskaya, N. N., Schulze, E.-D., Tchebakova, N. M., Karbachevskii, L. O., Kozlov, D., Sidorov, K. N., Panfyorov, M. I., Abrazko, M. I., Shapschnikov, E. S., Solnzeva, O. N., Minaeva, T. I., Jeltuchin, A. S., Wirth, C. and Pugachevskii, A. V. 2002. Climatic control of stand thinning in unmanaged spruce forests of the southern taiga in European Russia. *Tellus* **54B**, this issue.

Wirth, C., Schulze, E.-D., Schulze, W., von Stünzner-Karbe, D., Ziegler, W., Miljukowa, I. M., Sogatchev, A., Varlagin, A. B., Panvyorov, M., Grigorev, S., Kusnetzova, W., Siry, M., Hardes, G., Zimmermann, R. and Vygodskaya, N. N. 1999. Above-ground biomass and structure of pristine Siberian Scots pine forests as controlled by competition and fire. *Oecologia* **121**, 66–80.

Wirth, C., Schulze, E.-D., Lühker, B., Grigoriev, S., Siry, M., Hardes, G., Ziegler, W., Backor, M., Bauer, G. and Vygodskaya, N. N. 2002a. Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forests. *Plant Soil* **242**, 41–63.

Wirth, C., Schulze, E.-D. Kusznetova, V., Milyukova, I., Hardes, G., Siry, M., Schulze, B., B. and Vygodskaya, N. N. 2002b. Comparing the influence of site quality, stand age, fire and climate on above-ground production in Siberian Scots pine forests. *Tree Physiol.* (in press).

Yevdokimenko, M. D. 1996. Fire-induced transformations in the productivity of light coniferous stands of the Trans-Baikal region and Mongolia. In: *Fire in ecosystems of boreal Eurasia* (eds. J. G. Goldammer and V. V. Furyaev). Kluver Academic Publishers, Dordrecht, 211–218.