Comparing the influence of site quality, stand age, fire and climate on aboveground tree production in Siberian Scots pine forests

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Summary   Temporal patterns of stem and needle production and total aboveground net primary production (ANPP) were studied at the tree and stand level along four chronosequences of Siberian Scots pine (*Pinus sylvestris* L.) forests differing in site quality (poor lichen type or the more fertile *Vaccinium* type) and in frequency of surface fires (unburned, moderately burned (fire return interval of ~40 years), or heavily burned (fire return interval of ~25 years)). The maximum range of variability in aboveground production was quantified for: (1) possible long-term changes in site quality; (2) stand age; (3) non-stand-replacing, recurring surface fires; and (4) interannual climate variability. For (1) and (2), total ANPP was low in the lichen-type chronosequence, reached a maximum of 170 g C m^{-2} year^{-1} after 100 years and decreased to 100 g C m^{-2} year^{-1} in older stands. Maximum ANPP in the *Vaccinium*-type chronosequence was 340 g C m^{-2} year^{-1} and occurred earlier in the 53-year-old stand than in the other stands. Along the lichen-type chronosequences, peak ANPP was paralleled by maximum carbon allocation to stem growth. (3) In mature trees, damage by recurrent surface fires decreased stem growth by $17 \pm 19\%$ over a 10-year period relative to pre-fire values. At longer timescales, ANPP was hardly affected by fire-related differences in mortality. (4) Needle- plus stem-NPP, reconstructed for a 3-year period, varied within a range of 15 g C m^{-2} year^{-1} in the lichen-type stands and 35 g C m^{-2} year^{-1} in the *Vaccinium*-type stands. For the same period, the coefficient of variance was higher for needle-NPP (20 ± 10 %) than for stem-NPP ($12 \pm 7\%$). Needle- and stem-NPP did not covary in time. Most 30-year time series of stem-NPP at the tree level exhibited strong autocorrelation. In older trees, stem-NPP was positively correlated with growing season precipitation. Thus, the factors driving variability in ANPP ranked according to their maximum influence as: stand age (controlled by the frequency of stand-replacing fires) > site quality > growth depression because of surface fire damage ≈ age-related reduction in ANPP > interannual variability ≈ long-term effects of fire (stand density reduction). In lichen-type forests, we found that ANPP at the landscape level declined sharply when the interval between stand-replacing fires was less than 120 years, illustrating that fire strongly influences ANPP of boreal Scots pine forests.

Keywords: age-related decline, allocation, autocorrelation, damage, interannual variability, mortality, net primary production, old-growth, rotation.

Introduction

Carbon fixation is manifested in ecosystems as net primary production (NPP). Net primary production is variable in time because plant growth depends on many internal and external factors that operate at different timescales. (1) Site quality determines long-term productivity and changes slowly in the absence of anthropogenic forcings. (2) In even-aged forest stands, NPP is a function of the developmental stage; it is close to zero during the seedling stage, peaks at the time of crown closure, and then decreases as the stand matures (Möller et al. 1954, Ryan et al. 1997). (3) Any disturbance that reduces the amount of photosynthetically active tissue (e.g., fire, insect outbreaks and commercial thinning) causes a decline in NPP over a period of years or decades depending on the resilience of the ecosystem. Disturbances usually recur and may cause mortality in plant parts, leading to growth reductions (Dietrich and Swetnam 1984, Gutsell and Johnson 1995, Arbatskaya and Vaganov 1997), or tree mortality (Harrington 1996, Waldrup and Brose 1999, Wirth et al. 1999). (4) Interannual variation in NPP, which fluctuates with interannual variation in climate, has been detected in aboveground yield of grasslands and agricultural lands (Morris and Haskin 1990, Briggs and Knapp 1995), in tree ring width series (Fritts 1971, D'Arrigo et al. 1987, Vaganov et al. 1996), in basal area increment and litter fall rates in permanent forest plots (Day et al. 1996, Knapp and Smith 2001) and in vegetation indices derived from satellite images (Prince 1991, Potter et al. 1999). Whereas foresters think in timescales of decades to centuries for harvest rotations and focus on managing long-term pro-

ductivity, atmospheric scientists are more interested in short-term interannual variability of plant production—mainly because terrestrial plant growth affects the seasonal oscillation of atmospheric CO_2 concentration in the northern hemisphere (Knorr 2000).

To understand long- and short-term variations in productivity, we studied aboveground net primary production (ANPP) of trees in chronosequences of pure Siberian Scots pine (*Pinus sylvestris* L.) stands that regenerate as even-aged cohorts after stand-replacing fires. We attempted to: (1) quantify current and past ANPP at the stand level and stem and needle production at the tree level; (2) compare the variability of ANPP at different temporal scales as induced by differences in site quality, stand age, fire and interannual climate variability; and (3) identify processes causing variability of ANPP at these different temporal scales. To analyze the age dynamics and sensitivity of ANPP, we compared four chronosequences differing in site quality and surface fire frequency. We also analyzed the dynamics of individual stem growth in relation to past fire events. Interannual variability of stem wood and needle production of 78 trees was measured by tree ring analysis and by estimating needle biomass of subsequent needle age classes.

Methods

Study area

The study area is located about 40 km west of the Yenisei River (60°43′ N, 89°08′ E) at the eastern edge of the west Siberian lowland, where monotypic *Pinus sylvestris* forests (ssp. *sibirica* Lebed) occur on alluvial sand dunes. The soils have a podzolic morphology. There is no underlying permafrost. Mean annual air temperature is −3.7 °C, and mean 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 mean daily temperature of 11.5 °C (Glebov 1969). Mean annual precipitation is 493 mm with 70% occurring as summer rainfall.

Study sites

Four chronosequences of Scots pine forest were established based on differences in site quality and fire regime. Understory vegetation and height growth pattern (Table 1) were used to identify site quality (*Vaccinium* type (subscript v) or lichen type (subscript l), Cajander 1926). The fire regime was classified primarily on historical fire frequency reconstructed by fire scar dating (Table 2). However, two stands with similar historical fire frequency may exhibit a different structure if they were subject to fires of differing intensity. Therefore, we also based our classification on stand structure data that can be regarded as a reflection of past fire effects (Table 1). The classification used was unburned forests (subscript u), moderately burned forests (subscript m) or heavily burned open woodlands (subscript h) (cf. Wirth et al. 1999). Four chronosequences were established based on measurements taken during field campaigns in 1995–2000 (nomenclature of stands

consists of stand age and the subscripts for site type and fire regime). (1) Unburned lichen-type chronosequence: closed forests with lichen understory that had not experienced fire since establishment (2_{lu}-, 14_{lu}-, 28_{lu}-, 31_{lu}-, 57_{lu}- and 95_{lu}-year-old stands). (2) Moderately burned lichen-type chronosequence: forests with lichen understory and a mean surface fire return interval of 43 ± 17 years. Mean crown cover in stands more than 60 years old was 61 ± 1.6%. Stand structure was homogeneous in that canopy gaps were of similar dimension to mean tree crowns (67_{lm}-, 138_{lm}-, 200_{lm}-, 204_{lm}- and 383_{lm}-year-old stands). (3) Heavily burned lichen-type chronosequence: open pine woodlands with lichen understory and a surface fire return interval of 25 ± 10 years. Crown cover was usually less than 60% (Table 1) and canopy gaps were much larger than mean tree crowns (14_{lh}-, 32_{lh}-, 48_{lh}-, 50_{lh}-, 215_{lh}- and 244_{lh}-year-old stands). (4) Moderately burned *Vaccinium*-type chronosequence: dense stands with an understory of mosses and *Vaccinium* shrubs and a surface fire return interval of 41 ± 23 years (12_{vu}-, 53_{vm}- and 95_{vm}-year-old stands).

Interannual variability of stem- and needle-NPP of individual trees

Stem-NPP_i   Stem wood production was measured in 78 trees. Discs were taken every meter along the stem in trees up to 10 m in height. In trees between 10 and 15 m high, the 3, 5, 7 and 9 m discs were not sampled, and in trees more than 15 m high, the 11 and 13 m discs were also omitted. The discs were dried and polished with fine sandpaper (grain size up to 1200). The age of each disc was determined with the aid of a dissecting microscope and fire scars were cross-dated. Dendrochronological analysis was carried out with a digital tree ring measurement device (spatial resolution 0.01 mm) in combination with the Time Series Analysis Program (TSAP, Frank Rinn Distribution, Heidelberg, Germany). For the last 20–30 years, ring width was measured annually, beginning from the outside, along two opposite radii if the discs had a circular shape. Four perpendicular radii were measured on discs with a more eccentric shape (ratio of maximum and minimum diameter > 1.1). Stem growth in earlier periods was measured at 10-year intervals to reconstruct the general growth pattern over the life span of the sample tree. Mean stem diameter increment, measured on the lower and upper disc of each 1- to 2-m segment, was used to calculate the increment of under-bark tree volume of stem segments based on the formula of a truncated cone. Stem volume increment was converted to biomass carbon by multiplying volume by wood density and carbon concentration, and is referred to as stem-NPP_i (where subscript i denotes individual). Cubes of heartwood and sapwood of known volume were prepared from 15 trees per site class and weighed. A paired *t*-test revealed that the difference between sapwood (415.4 ± 50.8 kg_{dw} m^{-3}_{dv}) and heartwood density (453.8 ± 55.5 kg_{dw} m^{-3}_{dv}) was significant (35.4 with 95% CI (19.3; 51.5), $t_{(15)}$ = 4.7, $P < 0.001$). Mean wood density of pooled sapwood and heartwood samples was 434.6 ± 56 kg_{dw} m^{-3}_{dv} (cf. 437 ± 23 kg_{dw} m^{-3}_{dv}; Klöhn 1999). We found no differences between site classes for sapwood density ($P = 0.49$) or heartwood den-

Table 1. Structural characteristics of Scots pine stands in central Siberia. Nomenclature of stands consists of stand age and the subscripts for site type and fire regime (compare Table 2). Abbreviation: D = diameter at breast height.

Stand	Stand density (trees ha^{-1})	Mean D (m)	Mean tree height (m)	Crown cover (%)	Basal area (m^2 ha^{-1})	Aboveground biomass (kg C m^{-2})
2_{lu}	500[1]	–[2]	< 0.5	< 0.1	–[2]	< 0.1
14_{lu}	9900	–[2]	2.0 ± 0.7	40	–[2]	0.2
28_{lu}	9400	2.8 ± 1.4	3.4 ± 1.1	70	7.4	0.7
31_{lu}	10100	2.9 ± 1.4	3.9 ± 1.5	88	11.9	1.1
57_{lu}	6070	4.9 ± 2.8	5.7 ± 2.5	nd	24.0	1.5
95_{lu}	3800	10.9 ± 4.3	13.2 ± 3.5	81	40.3	6.5
67_{lm}	2840	10.8 ± 2.7	10.5 ± 1.6	61	27.4	3.9
138_{lm}	1100	18.3 ± 4.9	15.3 ± 2.0	61	31.6	5.3
200_{lm}	480	26.5 ± 6.9	17.9 ± 3.5	55	28.3	6.1
204_{lm}	800	22.0 ± 5.0	15.9 ± 2.4	60	31.8	5.4
383_{lm}	460	32.0 ± 7.0	18.4 ± 2.8	63	33.5	7.6
14_{lh}	290	–[2]	1.7 ± 1.1	5	–[2]	< 0.1
32_{lh}	1260	4.7 ± 1.8	3.7 ± 1.0	26	3.5	0.2
48_{lh}	1930	8.6 ± 4.3	7.6 ± 2.3	42	14.0	1.5
50_{lh}	210	7.3 ± 4.4	4.0 ± 2.0	9	1.2	0.3
215_{lh}	270	29.0 ± 7.0	16.7 ± 2.8	65	19.8	4.3
244_{lh}	230	26.9 ± 11.8	14.8 ± 4.2	31	13.5	3.3
12_{vu}	8600	4.1 ± 2.2	4.3 ± 1.4	> 100	14.5	1.2
53_{vm}	1830	10.2 ± 5.4	10.9 ± 4.7	> 100	27.4	3.4
95_{vm}	1790	13.2 ± 4.9	14.9 ± 3.6	> 100	31.7	5.7

[1] Stand 2_{lu} is a forest island in a bog and was subject to an experimental stand-replacing fire in 1993 (FIRESCAN science team (1996)). In 1995, regeneration seemed to be limited by seed input.

[2] In these stands the majority of trees had not yet reached breast height (1.30 m).

sity (P = 0.69). A reanalysis of the large data set compiled by Klöhn (1999) showed a similar result: although latewood percentage increased with site quality (Pearson's r = 0.79), this effect was offset by a parallel decrease in cell wall thickness of earlywood (r = –0.62), so overall wood density was constant. Carbon concentrations measured with an elemental C/N analyzer showed low variability (48.8 ± 0.7% of dry weight, n = 73; Wirth et al. 2002).

To quantify short-term variability of stem-NPP_i, independent of the long- and medium-term growth trend, the time series of individual trees were detrended. The most obvious long-term trend in volume growth of trees is a sigmoidal age trend. Depending on the position of the 30-year time window along the sigmoidal trend, the time series were fitted with both linear and simple polynomial functions, and the percentage deviation of the actual value from the predicted value was calculated.

Needle-NPP_i Interannual variability of needle production for individual trees (needle-NPP_i) was estimated from needle biomass of 1-, 2- and 3-year-old shoots. In a boreal climate with low nutrient availability, needles of Scots pine in Siberia are shed after 4 or 5 years, indicated by the absence of needle scars on young shoots. Maximum needle age was 8 years. Lamppu and Huttunen (2001) reported a mean needle age of 5.5 years for Siberian Scots pine trees. Because we harvested trees every year between 1995 and 1998, by pooling four overlapping 3-year-periods, we obtained a composite record of 6 years across all stands and trees. Interannual variability was expressed as a percentage and absolute deviation from any of the 3-year averages at the tree-level.

Biomass of needle age classes for all sample trees (n = 78) was determined by destructive harvesting according to a hierarchical procedure of repeated separation and subsampling. First, the complete crown of the harvested trees was separated

Table 2. Indicators of the surface fire regime in four chronosequences of Siberian Scots pine forests based on fire-scar dating of tree discs. The values in parentheses represent the number of stands.

Stand	Stand internal mean fire interval	Initial fire interval	Time since last non-stand-replacing fire
Lichen type unburned (lu)	No fire	No fire	No fire
Lichen type moderately burned (lm)	43.2 ± 17.5 (6)	42.0 ± 25.5 (6)	46.5 ± 26.4 (6)
Lichen type heavily burned (lh)	25.1 ± 9.9 (7)	27.5 ± 9.1 (7)	21.7 ± 17.3 (7)
Vaccinium type moderately burned (vm)	41.4 ± 22.8 (3)	40.0 ± 25.6 (3)	36.3 ± 0.6 (3)

into coarse branches (CB; > 5 cm diameter) and fine branches (FB; < 5 cm diameter). A subsample taken from fraction FB (SS-FB; every tenth branch) was further separated into green (G) and non-green (NG) fractions. A 20% subsample of fraction G (SS-G) was taken and separated into needles and shoots of different age classes. Fresh weights of the various fractions and subsamples were determined in the field and dry weights of subsamples were measured in the laboratory. To investigate whether needle biomass increased with age, 10 fascicles (short shoot bearing two needles) per needle age class and tree were collected and their dry weights measured.

Impact of fire on stem production at the tree level

To study the impact of historical recurring surface fires on changes in stem-NPP_i of all sample trees, production during the decade preceding the fire event was compared with production during the three decades following the fire. Because historical volume increments were measured in 10-year steps, fire events fell within the defined growth periods. A decade was defined as "decade before fire" if the fire occurred in the second half of the decade, otherwise it was defined as "first decade after fire." The stem-NPP_i of a tree was set as 100% for the period before each fire event and the relative change in the stem-NPP_i was then calculated for the three decades after fire. Taking into account age-related changes in relative growth rate and fire susceptibility, two developmental phases were distinguished: trees less than 60 years; and trees more than 60 years. Trees less than 60 years old generally increased in stem-NPP. Trees more than 60 years old tended to approach a plateau of stem-NPP and have thicker bark, thus increasing their ability to survive surface fires. All trees within a developmental phase were pooled for this analysis regardless of site quality and historical fire regime. We note that the decadal resolution of the time series acts as a filter for high frequency changes in ANPP, leading to an underestimation of variability.

Stand-level estimates of aboveground production

For scaling up productivity at the tree level (p) to the stand level, stand-specific allometric equations of the form $p = ax^b$ were established. For stem production, the diameter at breast height squared times tree height (D^2H) was chosen as best predictor, x. In the two 14-year-old stands, D_0^2H was used, where D_0 is base diameter. A preliminary study was performed based on data of harvest trees from seven stands (28_{lu}, 53_{vm}, 67_{lm}, 138_{lm}, 204_{lm}, 215_{lh} and 383_{lm}) to compare for each stand the suitability of the variables D, H, crown length (CL), crown projection (CP) and D^2H to predict needle biomass. The mean variance of needle biomass, explained by these predictors, was: 95.0% for CP, 94.4% for D, 94.4% for D^2H, 87.2% for H and 57.8% for CL. Although the variance explained by CP was slightly higher, we used D to predict needle and twig production because it is easier to measure in the field. Before fitting the data and applying Reduced Major Axis (RMA) regression, (LaBarbera 1989, Sokal and Rohlf 1995, p. 541 ff.) the values for p and x were ln-transformed. Bark-NPP was calculated using the stand-specific ratio of stem to bark biomass (Wirth et al. 2002). Branch-NPP cannot be considered a constant or a

biomass-proportional fraction of stem-NPP because self-pruning decreases with stand age (Albrektson 1980). We compiled measured and modeled data on branch- and stem-NPP in 28 pine stands, of which 15 stands are stocked by *P. sylvestris* (Appendix 1). A tight relationship between the branch-NPP to stem-NPP ratio (BSR; %) and stem biomass (x; Mg ha^{-1}) emerged with BSR = 4.95 + 112.57e$^{-0.0188x}$ ($R^2 = 0.85$).

Allometric equations were also developed for stem- and needle-NPP during historical periods (stem-NPP: 10 years before harvest; needle-NPP: 1 to 3 years before harvest).

To characterize the growth potential and carbon allocation patterns of individual trees in relation to age and available canopy space, a growth efficiency index for wood (GEI_S) and needles (GEI_N) was calculated and expressed as annual stem production (kg$_{dw}$) or annual needle production (kg$_{dw}$), respectively, per total needle biomass (kg$_{dw}$) (GEI_S = stem-NPP/ needle biomass; GEI_N = needle-NPP/needle biomass; Kuuluvainen 1991, Vanninen and Mäkelä 2000).

Comparing variability at different temporal scales

Table 3 summarizes the approaches used to quantify variability at different temporal scales: (1) site quality; (2) stand age; (3) fire cycle; and (4) interannual variability. Analysis of variance cannot be applied because, first, stands and trees were not sampled at random and, second, samples are not completely independent because different temporal resolutions of the same time series are compared with each other. To reduce the interference of variability occurring at different temporal resolutions, all trends occurring at timescales other than that of interest were removed by smoothing or detrending methods. For example, the influence of interannual variability on stand-level ANPP was removed by averaging ANPP for 3 years before harvest. The influence of stand age dynamics on the response of ANPP to the fire cycle was reduced by studying age-specific periods separately, and the influence of interannual variability was removed by looking at stem-NPP_i in decadal steps (Table 3). To quantify interannual variability of stem-NPP_i at the tree- and stand-level, long- and medium-term trends were removed by detrending the time series. To rank factors that occur at different timescales according to the variability they induce in ANPP, only the maximum range of values around the mean time series was considered.

Results

Short-term variability of NPP at the tree level

For stands not subjected to surface fires during the last 30 years (hereafter termed unburned), the detrended and standardized time series of stem-NPP_i were similar irrespective of differences in stand age, site type and stand structure that existed between stands and chronosequences (Figure 1). The time series showed distinct periods of lower and higher than average stem-NPP_i. Stem-NPP_i was below average in 1972–1974, 1981–1985, 1989–1991 and 1996. Stem-NPP_i was higher than average in 1976–1977, 1986–1988 and 1992–1993. Except for the two young stands (14_{lu} and 31_{lu}) and the

Table 3. Synopsis of the different approaches to quantify variability of ANPP in central Siberian Scots pine forests at four temporal scales.

Temporal scale	Time window	Proposed factor causing variability	Approach	Measure of variability
Site quality	Centuries to millennia	Differences in edaphic conditions only; the local climate conditions are similar for all stands	Compare general level of ANPP between moderately burned chronosequences of the lichen- and *Vaccinium*-type stands, independent of stand age	Absolute maximum difference of ANPP
Stand age	Up to 383 years maximum	Changes in allocation, hydraulic constraints or nutrient immobilization are discussed as possible factors	Change in ANPP with stand age along the chronosequences. To remove the effect of interannual variability, stand-level ANPP is calculated from mean stem- and needle-NPP averaged for the 3 years before harvest	Absolute maximum difference between: (a) ANPP at stand initiation (close to zero) and peak-ANPP (b) Peak-ANPP and ANPP at stand maturity
Surface fire cycle	Four decades	(a) Growth depression in damaged trees (b) Stand density reduction	(a) Compare tree-level stem-NPP_i in a decade before a fire and in three decades after the fire. Estimates based on mean decadal stem-NPP_i (b) Compare chronosequences of the lichen-type stand with different fire regimes (not done for the *Vaccinium*-type stand)	(a) Only relative deviation from pre-fire values of stem-NPP_i can be quantified (b) Absolute maximum difference of ANPP
Interannual variability	3–30 years	Interannual variability of the local climate controlling productivity; internal generative periodicity	(a) Tree-level stem-NPP_i during the last 30 years; long- and medium-term trends removed by detrending (b) Stand-level stem-NPP reconstructed for the last 3 and 10 years; detrended (c) Tree-level needle-NPP_i during 3 years before harvest (d) Stand-level needle-NPP during 3 years before harvest	(a) Relative deviation from 30-year mean after detrending (b) Absolute maximum difference, standard deviation and coefficient of variance (c) Relative deviation from 3-year mean (d) Absolute maximum difference, standard deviation and coefficient of variance

three stands that experienced surface fires during the last three decades (32_{lh}, 48_{lh} and 50_{lh}), all time series of stem-NPP_i were positively cross-correlated (Table 4). Interannual variability of stem-NPP was higher in younger stands than in older stands (Figure 1).

The average stem-NPP_i time series of the older stands of the lichen-type site (138_{lm}, 200_{lm}, 204_{lm} and 383_{lm}) revealed a significant autocorrelation at a lag time of 1 year (Table 5). Although only significant in stands 200_{lm} and 215_{lh}, the autocorrelation coefficients became negative at a lag time of 3 years, suggesting that periods of comparable growth performance recur about every 6 years and last at least 2 years. A similar but nonsignificant trend was observed in the stands of intermediate age (95_{lu}, 95_{vm} and 53_{vm}). In the young stands 12_{vm}, 14_{lu} and 28_{lu}, no resemblance to the above pattern or significant autocorrelation was detected. Total growing season precipitation and mean daily growing season temperature showed no autocorrelation, which explains why only a weak correlation existed between the time series of stem-NPP_i and climate (Table 4). Growing season temperature of the same year was not correlated with any of the stem-NPP_i time series. There was a significant positive correlation between growing season precipitation and stem-NPP_i in stands 95_{lu} and 138_{lm} and with mean stem-NPP_i time series of trees older than 60 years. These results suggest that growing season precipitation may influence interannual variability of stem-NPP_i in old stands. Previous-year climate did not show significant correlation with either of the stem-NPP_i time series. The magnitude of percentage deviation from the 30-year mean for the stand-wise averaged time series rarely exceeded 20% in the recently unburned stands. With few exceptions, the maximum percentage deviation (30%) occurred in 1992. Taking into account the standard deviation around the means of single years, it appears that the variability was generally higher in younger stands than in older stands.

Our estimate of interannual variability of needle-NPP_i could be confounded by two processes: (1) needles may have been shed from 1- to 3-year-old shoots; and (2) needle weight may increase substantially with needle age.

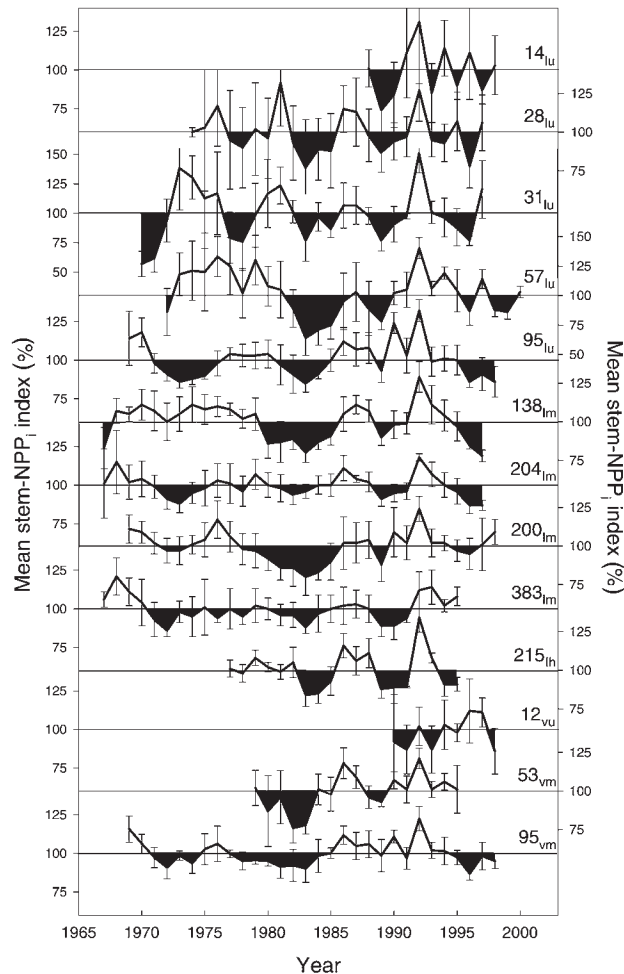(1) If early needle fall occurred, both shoot age and inter-

Figure 1. Interannual variability of stem-NPP$_i$ during the last two to three decades before harvest. None of the stands was subject to surface fires during this period. Stand-level time series are means calculated from 4 to 8 time series of individual sample trees (65 in total). These were detrended by linear and polynomial regression and standardized prior to analysis. Within stands, each sample tree represents a diameter at breast height class. Error bars represent ± 1 standard deviation.

annual variability should influence the percentage share of needle biomass carried by shoots (with 100% being the sum of 1- to 3-year-old needles). A two-way ANOVA with shoot age (range: 1–3 years) and calendar year (range: 1992–1997) revealed that calendar year had a highly significant effect on percentage needle biomass ($F_{(5;251)} = 15.5$, $P < 0.001$, percentages arcsine-transformed), whereas shoot age had no significant effect ($F_{(2;251)} = 0.2$, $P = 0.815$). However, if shoots older than 3 years were considered in a similar analysis, both shoot age ($F_{(6;444)} = 74.4$, $P < 0.001$, range: 1–8 years) and calendar year were significant ($F_{(9;444)} = 10.7$, $P < 0.001$, range: 1–8 years). These results suggest that, for shoots up to 3 years old, partial needle loss does not significantly contribute to the difference in needle biomass between shoot age classes.

(2) No significant differences in dry weight per needle pair existed between 1-, 2- and 3-year-old needles in nine out of 10

stands ($n = 5$ sample trees per stand, Figure 2). The slope of the regression relating needle dry weight to shoot age was significantly different from zero only in Stand 215$_{lh}$. The analysis does not reject the hypothesis that needles become heavier with age, but indicates that interannual variability overrides the effect of aging. In a two-way ANOVA with calendar year and shoot age as fixed factors and needle weight as dependent variable, neither factor showed a significant effect (calendar year: $F_{(5;149)} = 1.34$, $P = 0.26$ and shoot age: $F_{(2;149)} = 0.31$, $P = 0.73$)

Interannual variability of needle-NPP$_i$ during 1992–1997 was of comparable magnitude to that of stem-NPP$_i$ (Figure 3). The highest mean deviation from any of the 3-year means was 30%. Needle-NPP$_i$ was low in 1995 and high in 1994 and 1996. Comparing stem-NPP$_i$ averaged over all 53 trees of recently unburned stands with the dynamics of needle-NPP$_i$ indicated that wood and needle production do not occur in phase (Figure 3).

Fire-related variability of NPP at the tree and stand level

Surface fires markedly increased the variability of stem-NPP$_i$. Figure 4 compares the stem-NPP$_i$ time series of all recently unburned sample trees with mean stem-NPP$_i$ time series of stands that experienced fire during the last 30 years. Fire damage led to growth depressions in trees in Stands 32$_{lh}$ and 50$_{lh}$, and stem-NPP$_i$ consequently varied by a factor of two to three around the 30-year mean. Triggered by the severe fire event in 1982, a high degree of autocorrelation was induced in Stands 32$_{lh}$ and 50$_{lh}$, with autocorrelation coefficients being significantly positive at lag times of 1 to 3 years. The fire effect was less pronounced in Stand 48$_{lh}$. Although subject to four fires, the time series of stem-NPP$_i$ in Stand 48$_{lh}$ was positively correlated with the time series of Stands 28$_{lu}$ and 53$_{vm}$, suggesting that the four dated fires in Stand 48$_{lh}$ were patchy and of low intensity.

Stem-NPP$_i$ of trees more than 60 years old was significantly reduced by $17 \pm 19\%$ on average during the first decade after surface fire (Figure 5). Stem-NPP$_i$ recovered toward pre-fire values during the second decade after fire and significantly exceeded pre-fire values during the third decade after fire by $24 \pm 40\%$. When trees less than 60 years old were in their phase of maximum stem wood production, no growth depression relative to pre-fire values was detected. However, stem-NPP$_i$ was significantly reduced relative to trees that were not subject to fire during this period (Figure 5, trees < 60 years).

Recurring surface fires usually lead to repeated stand density reductions. The effect of this thinning regime on surviving trees is illustrated in Figure 6 by comparing tree growth in three, approximately 200-year-old, lichen-type stands (204$_{lm}$, 200$_{lm}$ and 215$_{lh}$) with differing fire histories. The historical course of stem-NPP$_i$ (five to eight sample trees per stand) was averaged. Because trees were sampled to represent the range of diameters within a stand, errors are large. Lowest mean stem-NPP$_i$ was found in the moderately burned stand 204$_{lm}$. This stand experienced only three surface fires (downward arrowheads, Figure 6) and had the highest stand density (800 trees ha^{-1}). Higher mean stem-NPP$_i$ was measured in the

Table 4. Correlation matrix of climate variables and stem-NPP_i time series that represent the mean of four to eight sample trees per stand. Time series of stem-NPP_i were detrended before analysis. Coefficients of significant correlations are printed in bold letters. Abbreviations: GS-Precip = sum of growing season precipitation (mm); GS-Temp = median of averaged daily temperatures during growing season (°C); all/-fire = mean stem-NPP_i of all investigated sample trees not subjected to fire during the last 30 years ($n = 65$); old/-fire = mean stem-NPP_i of recently unburned trees older than 60 years; * $P < 0.05$; ** $P < 0.01$. Previous growing season precipitation and temperature correlated with neither of the stem-NPP_i time series (data not shown).

	GS-Temp	all/-fire	old/-fire	14_{lu}	28_{lu}	31_{lu}	57_{lu}	95_{lu}	138_{lm}	200_{lm}	204_{lm}	383_{lm}	32_{lh}	48_{lh}	50_{lh}	215_{lh}	53_{vm}	95_{vm}
GS-Precip	**−0.35***	0.30	**0.41***	0.12	0.13	0.27	0.11	**0.4***	**0.37***	0.26	0.34	0.04	0.11	0.29	−0.14	0.35	0.11	0.40
GS-Temp		0.05	0.07	0.17	0.15	0.09	0.10	−0.03	−0.01	−0.16	0.12	−0.07	0.27	−0.08	0.31	−0.04	0.23	0.02
all/-fire			**0.86****	**0.62***	**0.80****	**0.69****	**0.84****	**0.59****	**0.72****	**0.75****	**0.67****	**0.63****	0.10	0.32	**0.50***	**0.83****	**0.78****	**0.72****
old/-fire				0.51	**0.60***	0.30	**0.56****	**0.80****	**0.84****	**0.82****	**0.84****	**0.70****	−0.18	0.12	0.22	**0.85****	**0.78****	**0.86****
14_{lu}					0.38	0.53	0.56	0.32	0.39	**0.62***	0.51	0.39	**0.69***	0.05	0.55	0.58	**0.72***	0.28
28_{lu}						**0.76****	**0.59****	**0.45***	**0.46***	**0.49***	**0.53***	0.40	0.08	**0.45***	0.39	**0.64****	**0.58***	**0.49***
31_{lu}							**0.67****	0.04	0.23	0.25	0.18	0.28	0.07	0.36	**0.47***	**0.72****	0.45	0.29
57_{lu}								0.34	**0.51***	**0.58****	0.32	**0.46***	−0.11	0.36	0.47	**0.72****	**0.55****	**0.39***
95_{lu}									**0.55***	**0.6****	**0.69****	**0.45***	0.07	0.04	−0.12	**0.62****	**0.75****	**0.81****
138_{lm}										**0.79****	**0.60****	**0.41***	−0.36	0.12	0.34	**0.75****	**0.77****	**0.64****
200_{lm}											**0.48***	**0.43***	**−0.50***	0.23	**0.47***	**0.63****	**0.77****	**0.72****
204_{lm}												**0.74****	0.32	0.05	0.01	**0.84****	**0.69****	**0.67****
383_{lm}													0.07	−0.11	0.19	**0.65****	**0.51***	**0.55***
32_{lh}														−0.07	**−0.38***	−0.02	−0.21	−0.12
48_{lh}															0.32	0.22	**0.50***	0.07
50_{lh}																0.37	0.33	−0.04
215_{lh}																	0.47	**0.63****
53_{vm}																		**0.82****

other moderately burned stand 200_{lm}, which had a lower stand density (480 trees ha^{-1}). Here, the first fire occurred early during stand development, when trees are most susceptible to fire-related mortality. Probably as a result of this early heavy thinning, individual trees sustained high rates of stem-NPP_i until the next fire occurred 60 years later. Highest mean stem-

Table 5. Coefficients of autocorrelation (r_{ac}) for detrended time series of stem-NPP_i. Asterisks indicate significant deviation from zero at $\alpha = 0.05$ (which is given if r_{ac} exceeds the double standard error; Legendre and Legendre 1998). Abbreviations: n = number of cases of time series; Lag = length of lag time (years); GS-Precip = sum of growing season precipitation (mm); GS-Temp = median of averaged daily temperatures during growing season (°C); all/-fire = mean stem-NPP_i of all investigated sample trees not subjected to fire during the last 30 years; old/-fire = mean stem-NPP_i of recently unburned trees older than 60 years. The time series of Stand 12_{vu} was too short ($n = 8$) for meaningful autocorrelation analysis.

| Site	n	Lag = 1	Lag = 2	Lag = 3	Lag = 4	Lag = 5	Lag = 6
GS-Precip	30	0.08	0.14	0.13	−0.04	0.06	0.25
GS-Temp	30	0.08	0.13	0.11	−0.08	0.03	**−0.36***
all/-fire	30	0.27	−0.04	**−0.38***	−0.27	0.108	0.16
old/-fire	30	**0.37***	0.12	**−0.33***	**−0.31***	−0.11	0.10
14_{lu}	11	−0.20	−0.02	−0.38	0.24	−0.20	0.02
28_{lu}	24	−0.05	−0.25	−0.29	−0.35	**0.48***	0.30
31_{lu}	30	0.31	−0.20	**−0.51***	**−0.39***	0.07	0.24
57_{lu}	30	**0.45***	0.24	0.04	−0.14	−0.11	−0.22
95_{lu}	30	0.33	0.32	−0.19	−0.20	−0.21	−0.24
138_{lm}	30	**0.52***	0.14	−0.12	−0.22	−0.13	−0.02
204_{lm}	30	**0.38***	−0.01	**−0.39***	**−0.44***	−0.24	0.14
200_{lm}	30	**0.49***	**0.36***	−0.04	0.01	−0.04	0.04
383_{lm}	29	**0.50***	0.08	−0.30	−0.32	−0.08	0.05
32_{lh}	28	**0.81***	**0.60***	**0.40***	0.24	0.13	−0.07
48_{lh}	30	0.30	−0.11	**−0.42***	−0.17	0.05	0.10
50_{lh}	30	**0.80***	**0.56***	**0.34***	0.18	0.01	−0.20
215_{lh}	19	0.12	−0.34	**−0.54***	−0.01	0.11	**0.34***
53_{vm}	17	0.33	0.23	−0.12	−0.26	−0.01	0.15
95_{vm}	20	0.24	0.28	−0.15	−0.13	−0.12	0.01
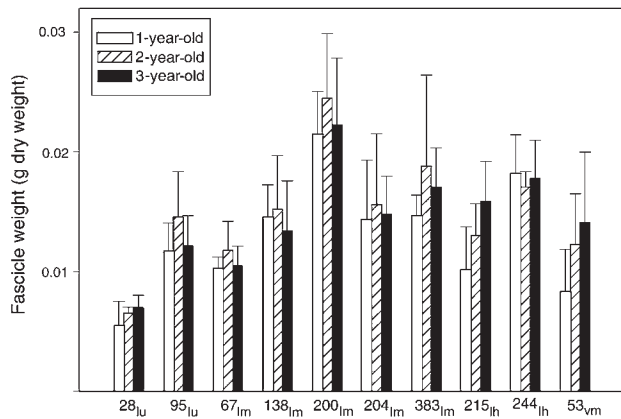
Figure 2. Mean dry weight of 1-, 2- and 3-year-old fascicles (short shoots bearing two needles) measured in 10 chronosequence stands. Error bars represent + 1 standard deviation. In Stand 215_{lh} there was a significant increase in fascicle dry weight with fascicle age.

NPP_i (> 1 kg C $year^{-1}$ $tree^{-1}$) was found in the heavily burned stand 215_{lh}, where it increased almost linearly over 200 years. Trees in Stand 215_{lh} had survived seven fires and stand density was low (270 trees ha^{-1}). In summary, we observed an inverse relationship between tree volume growth and stand density. Stand density was mainly a function of the fire history of the stand (Wirth et al. 1999).

Aboveground net primary production at the stand level

A comparison of the moderately burned and unburned lichen-type chronosequences (Figure 7A, Table 6) indicates that total
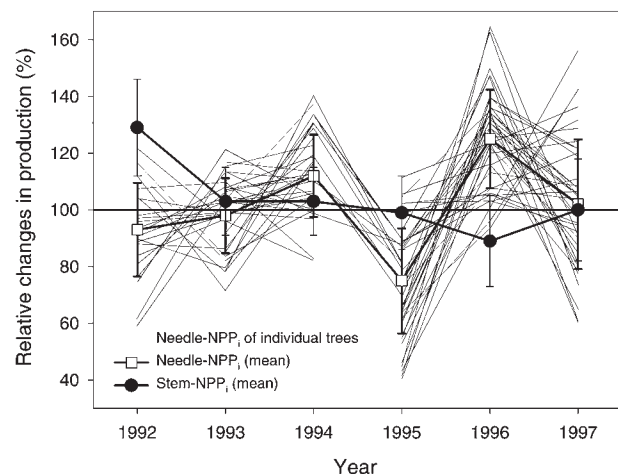
Figure 3. Comparison of interannual variability of needle-NPP_i and stem-NPP_i. Thin lines: percentage deviation of NPP_i of 1-, 2- and 3-year-old needles from the mean value of NPP_i during 3-year periods before harvest for each sample tree. Thick line, □: annual mean relative change in needle-NPP_i averaged for all sample trees. Thick line, ●: mean stem-NPP_i of 65 trees in recently unburned stands. It is shown that needle- and stem-NPP_i do not covary over time. Error bars represent ± 1 standard deviation.
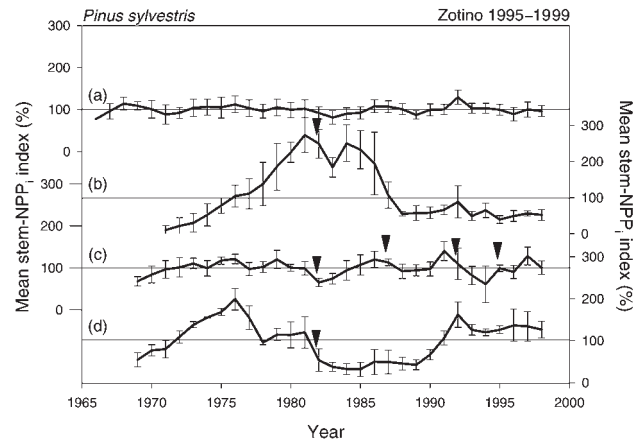

Figure 4. Interannual variability of stem-NPP_i in central Siberian Scots pine trees in relation to fire during the last two to three decades before harvest. (a) Average of all recently unburned stands shown in Figure 1. (b–d) Average time series of sample trees in stands that experienced surface fires during the last 30 years: (b) Stand 32_{lh}; (c) Stand 48_{lh}; and (d) Stand 50_{lh}. The series of individual sample trees were detrended by linear regression and standardized before analysis in the same way as for Figure 1. Within stands, each tree represents a diameter at breast height class. Fire events are indicated by downward arrowheads. Error bars represent ± 1 standard deviation.

ANPP peaked at about 170 g C m^{-2} $year^{-1}$ at a stand age of about 100 years. This was followed by an immediate decline by 40% until Age 200 with no further decrease until Age 383. Stands that were more than 200 years old had an ANPP around 100 g C m^{-2} $year^{-1}$. Aboveground net primary production was higher in the *Vaccinium*-type stands than in the lichen-type stands and reached a maximum of 343 g C m^{-2} $year^{-1}$ in the 53_{vm}-year-old stand. This high ANPP was not sustained and collapsed to the value found for lichen-type stands at Age 100. If enhanced growth of individual trees in response to fire compensates for a negative effect of reduced stand density on production caused by fire-related mortality, it would explain why ANPP in heavily burned stands reached values similar to those in unburned and moderately burned stands, whereas basal area was lower by a factor of two (see Table 1), with basal area being proportional to biomass.

Figure 7b illustrates the change in carbon allocation pattern with stand age. In stands less than 50 years old, the ratio of aboveground stem- to needle-NPP was less than 1. This ratio increased to about 1.8 during the period of maximum ANPP between Ages 50 and 150. In older stands, the ratio again dropped below 1. *Vaccinium*-type stands invested relatively more carbon in stem wood production than lichen-type stands. The ratio of 3 found in the 12_{vu}-year-old stand was considered an outlier. Heavily burned lichen-type stands allocated relatively more carbon to needles. Growth efficiency index for stem wood production (GEI_S) expressed as stem-NPP per total needle biomass, another indicator of overall productivity, was highest in *Vaccinium*-type stands (Table 7). Growth efficiency index for stem wood production was positively correlated with percentage crown cover (Pearson's $r = 0.73$; $P = 0.002$), but
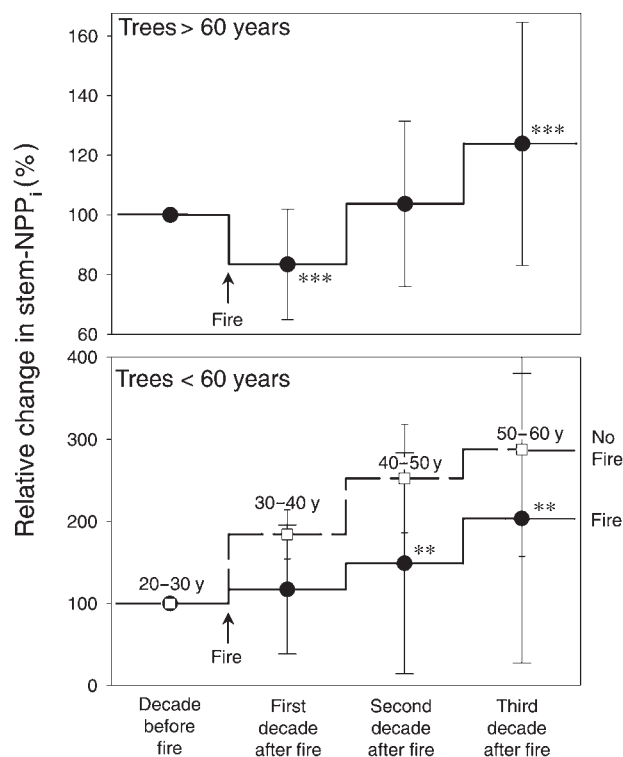
Figure 5. Impact of fire events on individual tree growth. Percentage changes in tree-level stem-NPP$_i$ relative to the decade before the fire are shown. The growth response is followed over three decades following the fire. The upper panel comprises fire events ($n = 79$) affecting trees older than 60 years, being in or close to the phase where stem-NPP generally levels off under undisturbed conditions. The lower panel comprises fire events ($n = 32$) affecting trees younger than 60 years still showing generally increasing stem-NPP. Error bars represent ± 1 standard deviation. Asterisks indicate significant deviation from pre-fire growth values (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$). Abbreviation: y = years.
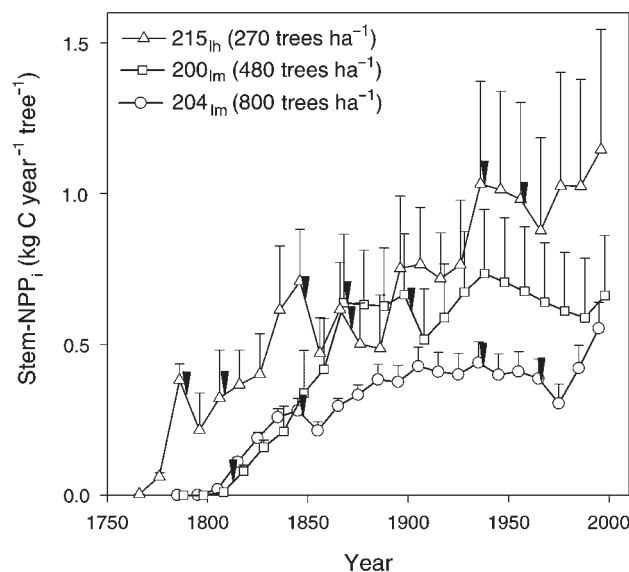

Figure 6. Historical course of stem-NPP$_i$ of sample trees in decadal time steps of three, approximately 200-year-old, lichen-type stands. The three stands 204_{lm}, 200_{lm} and 215_{lh} differed in the regime of recurring surface fires but not in site quality. Downward arrowheads indicate historical fire events. The stands 204_{lm} and 200_{lm} belong to the same category of fire regime (moderately burned) based on their fire return interval. However, in Stand 200_{lm}, the first fire occurred much earlier when trees are still more susceptible to fire, leading to contrasting growth responses. Error bars represent + 1 standard error.

not with stand age ($r = -0.137$; $P = 0.149$). Denser stands with higher crown cover had higher GEI$_S$ values than sparser stands with lower crown cover. Open stands of the heavily burned lichen-type chronosequence had GEI$_S$ values only half those in the denser stands of the moderately burned chronosequence. In contrast to GEI$_S$, the ratio of needle-NPP to total needle biomass (GEI$_N$) was constant, irrespective of differences in crown cover, stand age and site quality.

During the 3-year period before harvest, relative variability was higher in needle-NPP than in stem-NPP except in the heavily burned lichen-type stands (see Table 8; for further explanation, see Table 3). Mean CV for all stands was 20 ± 10% for needle-NPP, 12 ± 7% for stem-NPP and 10 ± 6% for total ANPP. The range of stem- and needle-NPP was dependent on the absolute magnitude of stand-specific production (see error bars in Figure 7a). Therefore, the mean ranges of needle- and stem-NPP were higher in the three *Vaccinium*-type stands (30 ± 13 and 26 ± 17 g C m^{-2} year^{-1}, respectively) than in the lichen-type stands (15 ± 11 and 8 ± 5 g C m^{-2} year^{-1}, respectively, ignoring stands 2_{lu} and 14_{lh}). Although not significant, it appears that, in lichen-type stands, the 3-year ranges of

stem-NPP were lower than the 3-year ranges of needle-NPP ($P = 0.06$; t-test for dependent samples, $n = 9$). However, over the 10-year period the ranges of stem-NPP reached a value comparable with the 3-year ranges of needle-NPP variation ($18 ± 12$ g C m^{-2} year^{-1}). The mean range of stem- plus needle-NPP for the 3-year period was $35 ± 13$ g C m^{-2} year^{-1} in *Vaccinium*-type stands and $15 ± 10$ g C m^{-2} year^{-1} in lichen-type stands. The range of needle- plus stem-NPP was not significantly different from the mean range of needle-NPP ($P = 0.52$, $n = 13$) and the mean range of stem-NPP during the 10-year period ($P_{(13)} = 0.80$). However, it was significantly higher than the range of stem-NPP during the 3-year period ($P_{(13)} = 0.002$). Therefore, stand-level needle- and stem-NPP did not covary in time (see Figure 3).

Discussion

Aboveground net primary production of Siberian Scots pine forests exhibited variability at different temporal scales in response to (1) long-term changes in site quality (e.g., a shift from lichen- to *Vaccinium*-type site), (2) stand age as controlled by frequency of stand-replacing fires, (3) recurring surface fires and (4) interannual climatic variability.

Stand age

The variability in ANPP associated with stand aging was large. We note that the stand age in our study region is purely a function of the frequency of stand-replacing fires. In lichen-
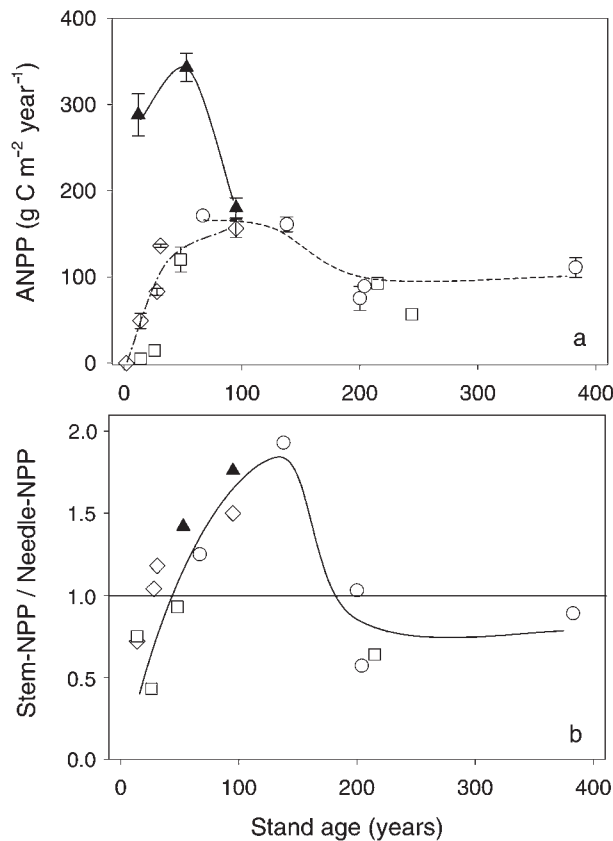
Figure 7. (a) Aboveground net primary productivity versus stand age along the four studied Scots pine chronosequences: ◇ = unburned liched type; ○ = moderately burned lichen type; □ = heavily burned lichen type; and ▲ = moderately burned *Vaccinium* type. Error bars represent the range of ANPP (joint range of stem- and needle-NPP) during the 3-year period before harvest. (b) Aboveground allocation pattern versus stand age expressed as the ratio of stand-level stem-NPP to needle-NPP. Trend lines were fitted manually.

type stands, ANPP was close to zero shortly after stand-replacing fire and increased to a maximum of 171 g C m^{-2} $year^{-1}$ after about 100 years. The low initial ANPP may be associated with poor site conditions, preventing the development of an early-successional herbaceous vegetation (Reed et al. 1999). Because ANPP in *Vaccinium*-type stands rarely drops below 80 g C m^{-2} $year^{-1}$ (Gabeev 1990), we assume that the range of ANPP along the *Vaccinium*-type chronosequence (peak ANPP: 343 g C m^{-2} $year^{-1}$) is less than 250 g C m^{-2} $year^{-1}$ (Figure 8). Peak ANPP in lichen-type stands was low. Aboveground net primary production measured in 27 Scots pine forests across boreal Eurasia averaged 394 ± 111 g C m^{-2} $year^{-1}$ (basal area ranging from 8 to 40 m^2 ha^{-1}; see reviews by Gower et al. 1994, 2001).

An age-related decline in ANPP (Ryan et al. 1997) of about 70 g C m^{-2} $year^{-1}$, or 40% relative to the peak value, was observed in the lichen-type chronosequence and thus contributed much less to age-related variability than the initial increase. There is much debate about the possible causes of the age-related decline in forest productivity. Currently, increased hy-

draulic constraints in larger trees (Magnani et al. 2000), immobilization of nutrients (Gower et al. 1996), changes in allocation patterns (Gower et al. 1994) and canopy structure (Smith and Long 2001) are proposed as mechanisms. We found that peak ANPP in the lichen-type chronosequence coincided with the period of maximum crowding and maximum carbon allocation to stem-NPP. Similar results were obtained for Scandinavian Scots pine chronosequences (Albrektson 1988, Kuuluvainen 1991). In accordance with Vanninen and Mäkelä (2000), we found that trees in stands with dense canopies produced more stem wood per unit needle biomass (higher GEI_S). It is therefore possible that, besides successional changes related to the degree of canopy density, a peak in ANPP shortly after crown closure results from pronounced changes in allocation to stem-NPP.

Site quality

Under natural conditions, site quality changes slowly with successional processes, and its variability is therefore perceived as a spatial rather than a temporal phenomenon. However, anthropogenic impact such as drainage, litter raking or nitrogen deposition may alter site quality within decades to years (Spieker et al. 1996, Schulze et al. 2000, Mund et al. 2002). Maximum variability related to differences in site quality (lichen-type versus *Vaccinium*-type) was about 200 g C m^{-2} $year^{-1}$. The change in ANPP along the lichen-type chronosequence was therefore about as high as the difference between the two site types (Figure 8).

Recurring surface fires

The instantaneous effects of past fire events on ANPP could be approximated by up-scaling decadal growth information on surviving trees. In trees more than 60 years old, surface fires were estimated to induce a growth depression of 17% and a recovery to 24% relative to the pre-fire values of stem-NPP_i. Arbatskaya and Vaganov (1996) report that recurrent fires explained 40–60% of the variability present in tree ring width chronologies of southern Taiga pine stands. If we assume that most trees more than 60 years old survive surface fires (Wirth et al. 1999), and that the extent of depression and recovery is similar for all aboveground tree components, we can calculate a variability range of ANPP at chronosequence time t according to RANGE = ANPP(t)1.24 – ANPP(t)0.83. The resulting ranges around the ANPP values of the chronosequence stands over 40 years old were 46 ± 18 g C m^{-2} $year^{-1}$ ($n = 9$) in lichen-type stands and 97 ± 35 g C m^{-2} $year^{-1}$ ($n = 2$) in *Vaccinium*-type stands. We note that these results are based solely on information on surviving trees and historical stand density dynamics are unknown. Surface fires not only reduce production by damaging trees, but also by selectively killing trees that otherwise would have contributed to NPP. Density reductions would not change the range drastically, because they would intensify the initial depression in ANPP, but also weaken the extent of recovery. The confounding effect of stand density reduction is further reduced by the fact that fires selectively kill small trees (Wardrup and Brose 1999, Wirth et al. 1999), which contribute little to overall production (De Kort 1993).

Table 6. Component and total aboveground NPP in central Siberian Scots pine stands (g C m^{-2} year^{-1}). Abbreviation: nd = no data.

Stand	12$_{vu}$	53$_{vm}$	95$_{vm}$	2$_{lu}$	14$_{lu}$	28$_{lu}$	31$_{lu}$	57$_{lu}$	95$_{lu}$	67$_{lm}$	138$_{lm}$	200$_{lm}$	204$_{lm}$	383$_{lm}$	14$_{lh}$	32$_{lh}$	48$_{lh}$	215$_{lh}$	244$_{lh}$
Year of harvest	1998	1996	1998	1998	1998	1995	1997	2000	1998	1995	1995	1998	1995	1995	1998	1998	1998	1996	1995
Stem 3-year mean ± SD[1]	119 ± 22	142 ± 12	95 ± 6	< 0.1	13 ± 3	26 ± 4	46 ± 4	51 ± 7	81 ± 8	74[5]	87 ± 9	24 ± 0.5	39 ± 3	47 ± 3	1.5 ± 0.3	3 ± 0.5	40 ± 9	23 ± 4	19[5]
Stem harvest																			
1 year	141	152	99		15	25	41	59	78		82	24	37	44	1.8	3.2	47	24	
2 years	120	142	88		16	24	49	47	74		81	24	39	47	1.3	2.7	44	18	
3 years	97	128	98		10	30	49	47	90		97	24	42	49	1.5	2.3	30	26	
4 years	90	145	101		22	25	44	56	86		68	26	33	40	2.0	3.3	20	30	
5 years	59	115	99		14	22	54	42	84		66	26	32	36	1.2	2.6	32	20	
6 years	51	111	113		15	19	35	45	117		61	32	30	36	1.0	4.2	41	19	
7 years	31	86	87		9	20	33	51	88		71	26	32	40	0.5	3.4	60	18	
8 years	16	81	100		3	21	24	43	109		68	28	32	41	0.3	3.2	42	22	
9 years	5	87	88		2	19	28	54	79		66	22	34	40	0.1	2.8	39	21	
10 years	3	84	94		1	13	26	37	95		51	26	30	36	0.1	2.8	36	22	
Needle 3-year mean ± SD[1]	36 ± 12	100 ± 21	54 ± 13	< 0.1	18 ± 6	25 ± 1	39 ± 3	nd	54 ± 18	59 ± 7	45 ± 4	42 ± 14	38 ± 4	53 ± 14	2 ± 0.5	7 ± 1	43 ± 8	36 ± 8	26
Needle harvest																			
1 year	31	77	61		16	24	42		60	65	50	44	43	67	2	7	53	30	
2 years	49	120	62		25	22	37		70	58	42	55	37	54	3	8	38	46	
3 years	26	102	39		13	24	39		34	52	44	27	35	39	2	6	40	32	
Twigs (measured)	27	20	15	< 0.1	6	6	9	nd	8	10	6	6	7	10	0.5	1	1	6	3
Branches[2]	102	91	22	< 0.1	15	26	42	27	15	31	23	6	11	9	2	3	30	10	11
Bark[3]	30	11	10	< 0.1	3	6	9	nd	8	8	7	3	2	4	0.5	1	7	24	1
Total[4] 3-year mean ± SD	288 ± 27	343 ± 19	181 ± 12	< 0.1	49 ± 9	83 ± 4	136 ± 2	nd	156 ± 11	172	162 ± 9	76 ± 14	90 ± 3	112 ± 12	5 ± 1	14 ± 1	120 ± 15	93 ± 5	57

[1] Averaged over 3 years previous to harvest to allow for comparison with variability of needle-NPP.

[2] Branch-NPP (including twigs) was calculated as a variable fraction of stem-NPP. This fraction was modeled as a function of stem biomass that was established based on published data for 28 pine stands.

[3] Bark-NPP was calculated proportional to stem-NPP using the stand-specific ratios of stem biomass to bark biomass (Wirth et al. 2001).

[4] Aboveground net primary productivity as the sum of the aboveground components (stem, needles, branches and bark). Note that the standard deviation is calculated only from the annual sum of stem- and needle-NPP during 3 years previous to the harvest year, ignoring the contribution of branches and bark. Stem- and needle-NPP together make up 73 ± 11% of ANPP.

[5] Stem-NPP was calculated as increment during the decade previous to harvest divided by 10.

Table 7. Growth indices of stem wood and needle production (GEI$_S$ and GEI$_N$) calculated for individual trees as stem-NPP$_i$ or needle-NPP$_i$ in (kg$_{dw}$ year^{-1}) per unit total needle mass per tree (kg$_{dw}$). Means of n sample trees per plot ± 1 standard deviation are shown. Lowercase letters indicate statistically homogeneous subgroups using Hochberg's GT2 post-hoc test.

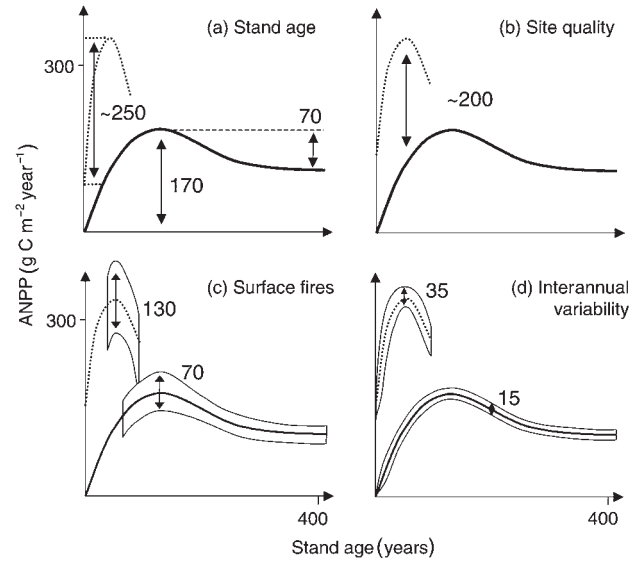| Plot	Crown cover (%)	n	GEI$_S$	GEI$_N$
14$_{lu}$	40	5	0.39 ± 0.15 cd	0.21 ± 0.02 a
28$_{lu}$	70	5	0.26 ± 0.19 abcd	0.21 ± 0.01 a
95$_{lu}$	81	5	0.30 ± 0.05 abcd	0.23 ± 0.01 a
67$_{lm}$	61	5	0.14 ± 0.09 a	0.18 ± 0.02 a
138$_{lm}$	61	3	0.15 ± 0.07 ab	0.19 ± 0.01 a
200$_{lm}$	55	5	0.21 ± 0.10 abc	0.18 ± 0.09 a
204$_{lm}$	60	4	0.15 ± 0.07 ab	0.19 ± 0.01 a
383$_{lm}$	63	5	0.20 ± 0.05 abc	0.21 ± 0.02 a
14$_{lh}$	5	5	0.10 ± 0.06 a	0.14 ± 0.06 a
32$_{lh}$	26	5	0.09 ± 0.02 a	0.19 ± 0.03 a
48$_{lh}$	42	5	0.22 ± 0.12 bc	0.23 ± 0.02 a
215$_{lh}$	65	4	0.14 ± 0.01 a	0.20 ± 0.04 a
244$_{lh}$	31	5	0.11 ± 0.03 a	–
12$_{vu}$	100	5	0.51 ± 0.05 d	0.37 ± 0.33 a
53$_{vm}$	100	5	0.43 ± 0.13 cd	0.20 ± 0.01 a
95$_{vm}$	100	5	0.34 ± 0.07 abcd	0.19 ± 0.02 a

Figure 8. Schematic comparison of external and internal factors influencing ANPP at different temporal scales. The comparison is based on the maximum range of absolute variability they induce in ANPP. Solid line = ANPP along lichen-type chronosequence, dotted line = ANPP along *Vaccinium*-type chronosequence (as in Figure 7a). (a) Vertical arrows and adjacent figures (g C m^{-1} year^{-1}) indicate maximum range in ANPP as induced by changes in stand age. The so-called age-related decline in ANPP along the lichen-type chronosequence was 70 g C m^{-1} year^{-1}. (b) The vertical arrow indicates the position and magnitude of the largest difference in ANPP due to differences in site quality. (c) The band around the ANPP trend lines illustrates the maximum range of ANPP caused by short-term effects of surface fire on tree growth. The range was calculated as an interval of –17 to +24% around the ANPP trend line of stands older than 60 years (see Figure 5). The long-term effect of surface fires calculated as the difference in stand-level ANPP between heavily burned and unburned/moderately burned stands is less than 20 g C m^{-2} year^{-1}. (d) Interannual variability of ANPP was calculated as: maximum ANPP – minimum ANPP during 3 years previous to the year of harvest.

Interannual variability and climate

The interannual variability of ANPP was estimated from the temporal growth patterns in the stem and needle compartments that comprised 73 ± 11% of total ANPP averaged for all stands. The mean coefficient of variation (CV) of ANPP based on a 3-year period before harvest was 13 ± 9%, corresponding to a maximum range of 18 ± 13 g C m^{-2} year^{-1} averaged over all stands. If only stands close to the chronosequence peak of ANPP were considered, the maximum range increased to 24 ± 7 g C m^{-2} year^{-1} (Table 8). An analysis based on 12-year records of ANPP has shown that interannual variability in natural temperate and boreal forest ecosystems is generally low when compared with other biomes (Knapp and Smith 2001). The CV of forest ANPP over time was 8% on average (n = 3), whereas the mean CV of ANPP in grasslands exceeded 30%. Knapp and Smith (2001) proposed that this difference arises because forests are (a) less susceptible to changes in rainfall because they are generally less limited by water and (b) subject to lower interannual variability of rainfall (CV of about 14%) than grassland. However, variability of growing season precipitation was high in our study region (CV = 26%) but CV of ANPP was low (13 ± 9%). Based on our finding that needle- and stem-NPP did not vary in parallel (Figure 3), we suggest that forests have low variability of ANPP because the different aboveground meristem types (needle primordia, cambial meristem) react to a varying climate with different time constants. For example, if needle- and stem-NPP covary exactly in time, the maximum range averaged for all stands would increase from 18 to 28 g C m^{-2} year^{-1}.

Because our estimates of interannual variability patterns of ANPP may be influenced by generative growth cycles, we did not quantify carbon allocated to cone production. Published values for cone production as a proportion of ANPP in mature pine range between 0.2 and 12% (Malkönen 1974, Albrektson and Valinger 1984, Cremer 1992, Valinger 1993). Valinger (1993) and Cremer (1992) reported that there was no positive relationship between cone production or needle or stem production, suggesting that in the genus *Pinus*, the climate trigger of interannual variability of stem- and needle-NPP is not severely affected by superimposed cycles of mass cone production.

The high degree of inter-correlation between the time series of mean stem-NPP$_i$ of recently unburned stands indicated that the interannual pattern of stem production was determined by common external factors other than fire (Table 4). As in other dry boreal pine ecosystems (Larsen and MacDonald 1995, Arbatskaya and Vaganov 1997), stem-NPP$_i$ was positively correlated with growing season precipitation, but not with

Table 8. Measures of interannual variability of stem- and needle-NPP and total ANPP (g C m^{-2} year^{-1}) in Siberian Scots pine stands. Abbreviations: nd = no data; CV = coefficient of variation (%).

	Stand																
	12_{vu}	53_{vm}	95_{vm}	14_{lu}	28_{lu}	31_{lu}	57_{lu}	95_{lu}	67_{lm}	138_{lm}	200_{lm}	204_{lm}	383_{lm}	14_{fh}	32_{lh}	48_{lh}	215_{lh}
Stem-NPP																	
3-year mean ± SD[1]	119 ± 22	142 ± 12	95 ± 6	13 ± 3	26 ± 4	46 ± 4	51 ± 7	81 ± 8	74	87 ± 9	24 ± 0.5	39 ± 3	47 ± 3	1.5 ± 0.3	3 ± 0.5	40 ± 9	23 ± 4
CV (%) (3-year period)	18	8	6	23	15	9	14	10		10	2	8	6	20	17	23	17
3-year range (max − min)	19[2]	22[2]	11	6	3	7[2]	12[2]	16		16	0	5	5	0.3[2]	1	17	8
10-year range (max − min)	23[2]	41[2]	25	14	9	24[2]	16[2]	42		27	10	9	10	1[2]	2	38	13
Needle-NPP																	
3-year mean ± SD	36 ± 12	100 ± 21	54 ± 13	18 ± 6	25 ± 1	39 ± 3	nd	54 ± 18	59 ± 7	45 ± 4	42 ± 14	38 ± 4	53 ± 14	2 ± 0.5	7 ± 1	43 ± 8	36 ± 8
CV (%) (3-year period)	33	21	24	33	4	8		33	12	9	33	10	26	20	14	19	22
3-year range (max − min)	23	43	22	12	2			36	13	8	27	8	27	1	2	15	16
Total ANPP																	
3-year mean ± SD[3]	288 ± 27	343 ± 19	181 ± 12	49 ± 9	83 ± 4	136 ± 2	nd	156 ± 11	172	162 ± 9	76 ± 14	90 ± 3	112 ± 12	5 ± 1	14 ± 1	120 ± 15	93 ± 5
CV (%) (3-year period)[4]	17	8	8	29	8	2		8		7	21	4	12	28	10	18	8
3-year range (max − min)	49	33	23	18	8	4		20		18	28	4	23	1	2	30	10

[1] Averaged over 3 years previous to harvest to allow for comparison with variability of needle-NPP.

[2] In the stands 12_{vu}, 14_{fh}, 53_{vm}, 57_{lu}, 31_{lu} and 138_{lm}, there was a significant temporal trend in stand-level stem-NPP. For these stands the range of the residuals of a linear regression is given.

[3] Note that the standard deviation and the range of the total is based only on the variability of stem- and needle-NPP during 3 years previous to the harvest year (ignoring the contribution of branches and bark). Stem- and needle-NPP together make up 73 ± 11% of ANPP.

[4] The coefficient of variation for ANPP was calculated with the sum of needle- and stem-NPP and not total ANPP set as 100%.

growing season temperature. Needle-NPP_i time series were too short to allow statistically meaningful correlations with climate parameters. Our stem-NPP_i time series were in good agreement with local ring width chronologies constructed by Vaganov et al. (1996) ($r = 0.61$, $P < 0.001$, temporal overlap = 24 years). Their chronology exhibited the same pronounced temporal autocorrelation. Arbatskaya and Vaganov (1997) suggested that autocorrelation results from longer-term fluctuations in the groundwater table that result from the buffering effect of the large peat body in adjacent bogs.

Conclusion

Large variability in ANPP was associated with differences in stand age and site quality, whereas differences in the historical surface fire regime had less influence (Figure 8). Recurring surface fires led to tree damage and induced short-term growth depressions. Interannual variability of ANPP was low because stem- and needle-NPP did not vary in parallel and therefore the individual time response of the two compartments partly cancelled each other out at the tree and stand levels. Stem growth was controlled by precipitation rather than temperature. Because of the importance of stand age on ANPP, shifts in the age class distribution within a boreal forest landscape may have a strong impact on ANPP at the landscape level (Gower et al. 2001). Fires also act as stand-replacing disturbances and have multiple effects on ANPP by shaping the age class distribution. Long intervals between stand-replacing fires increase the proportion of old stands but do not reduce landscape ANPP, whereas shortening the fire interval to less than 120 years leads to a sudden drop in landscape ANPP (Figure 9). In addition, reducing the mean stand age greatly increases the risk of surface fire damage to individual trees. We

conclude that any direct effect of a changing precipitation regime on ANPP in response to global change is likely to be overruled by indirect effects of growing season precipitation on the fire regime.

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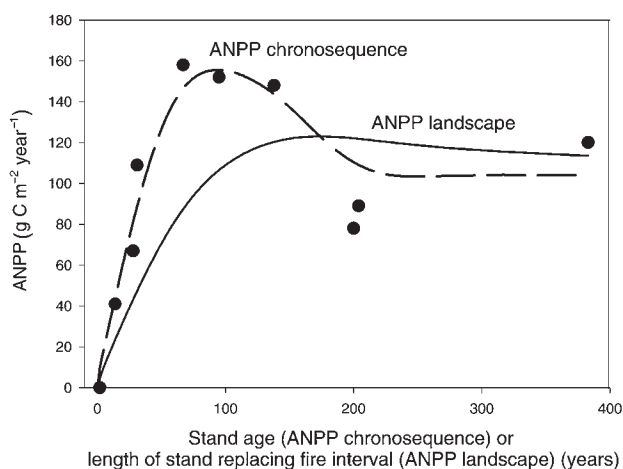

Figure 9. Mean landscape ANPP (solid line) in Scots pine forests as a function of the interval of stand-replacing fires or—in case of management—harvest rotation. Assuming even distribution of age classes in the landscape, mean ANPP was calculated by averaging ANPP as it changes along the unburned and moderately burned chronosequences (dashed line) over successively longer intervals up to stand age 383 years.

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Appendix 1

Table A1. Published data on stem- and branch-NPP of pine species.

Species	Country	Stand age (years)	Stand height (m)	Stand density (trees ha⁻¹)	Basal area (m² ha⁻¹)	Stem biomass including bark (Mg ha⁻¹)	Stem-NPP (Mg ha⁻¹ year⁻¹)	Branch-NPP (Mg ha⁻¹ year⁻¹)	Branch-NPP relative to Stem-NPP (%)	Type of data	Source
P. sylvestris	Sweden	20	6	–	–	11.9	0.78	0.68	87.2	Measured	[1]
P. sylvestris	Sweden	20	7	–	–	19.1	1.06	0.86	81.1	Measured	[1]
P. sylvestris	Sweden	20	8	–	–	31.4	1.92	1.56	81.3	Measured	[1]
P. sylvestris	Sweden	20	8	–	–	36.2	2.29	1.74	76.0	Measured	[1]
P. sylvestris	Finland	28	6	2911	8	9.6	0.78	0.75	96.2	Measured	[2]
P. sylvestris	Finland	47	12	845	12	27.1	1.79	0.96	53.6	Measured	[2]
P. sylvestris	Finland	45	15	1420	20	55.6	2.35	1.19	50.6	Measured	[2]
P. sylvestris	Northern Sweden	16	5	7145	–	37.8	3.2	1.9	59.4	Measured	[3]
P. sylvestris	Northern Sweden	16	6	20964	–	36.9	3.7	3.4	91.9	Measured	[3]
P. sylvestris	Germany	60	20	1043	–	145.8	–	–	13.6	Modelled	[4]
P. sylvestris	Germany	64	16	788	–	89.4	–	–	15.0	Modelled	[4]
P. sylvestris	Germany	41	18	852	–	104.1	–	–	14.8	Modelled	[4]
P. sylvestris	Sweden	10	–	–	–	10.0	–	–	100.0	Estimated	[5]
P. sylvestris	Sweden	50	–	–	–	70.0	–	–	28.1	Estimated	[5]
P. sylvestris	Sweden	100	–	–	–	90.0	–	–	33.3	Estimated	[5]
P. taeda	NC, USA	16	15	2243	49	124	5.6	1.9	33.9	Measured	[6]
P. taeda	NC, USA	15	12	1470	41	74	9.5	0.8	8.3	Measured	[6]
P. strobus	NC, USA	15	12	1760	23	42	6.8	3.0	46.6	Measured	[7]
P. nigra	Netherlands	22	–	–	–	45	4.1	2.0	48.8	Measured	[8]
P. contorta	BC, Cananda	70	–	1900	–	107	2.1	0.2	9.5	Measured	[9]
P. contorta	BC, Cananda	70	–	3580	–	108	1.9	0.2	10.5	Measured	[9]
P. contorta	BC, Cananda	70	–	1770	–	195	4.2	0.3	7.1	Measured	[9]
P. contorta	BC, Cananda	78	–	1900	–	285	4.2	0.4	9.5	Measured	[9]
P. radiata	Southern Australia	10	14	625	24	55	8	4	50.0	Measured	[10]
P. radiata	Southern Australia	10	14	599	24.7	53	8	6	75.0	Measured	[10]
P. radiata	Southern Australia	10	16	703	27.7	69	13	4	30.8	Measured	[10]
P. radiata	Southern Australia	10	16	704	36.6	93	18	6	33.3	Measured	[10]
P. radiata	Southern Australia	10	16	746	38.2	87	23	6.5	28.3	Measured	[10]

[1] Axelsson and Axelsson 1986.
[2] Malkönen 1974.
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