Chapter 4
Carbon Cycles in Forests

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4.1 Introduction

The forests of eastern Siberia form one of the most natural borders in the cryolithozone and account for 45% of all Siberian forests. This forest ecosystem plays a significant role in terrestrial carbon cycles at the regional and global scale. Forest soils and plants act as a carbon pool, which is considered to be relatively stable because of the unfavourable conditions for decomposition. The vegetation and soil of the Siberian forest ecosystems retain 74 and 249 billion tons of carbon, respectively (Dixon et al. 1994). Almost 65% of the forest in eastern Siberia grows in the permafrost zone, and these forests have distinctive ecological characteristics enabling them to adapt to the physical environment in this region (e.g. Abaimov et al. 2002).

Studies of the carbon cycles in the eastern Siberian forest ecosystem (Central Yakutia) date back to the middle of the twentieth century (Chap. 1.3.2). The first multi-scale/multi-methodological carbon cycle study based on leaf- to canopy-scale observations in a *Larix gmelinii* forest in this region was conducted on the Aldan plateau (60°51′N, 128°16′E, 155 km south-west of the city of Yakutsk) under the guidance of Professor Ernst-Detlef Schulze (Germany). This comprehensive field campaign revealed the characteristics of the physiological and ecological responses of larch forest during the mid-growing season (Schulze et al. 1995; Hollinger et al. 1995; Arneth et al. 1996; Kelliher et al. 1997; Vygodskaya et al. 1997).

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Since the 1990s, multi-seasonal and multi-year field studies of *Larix cajanderi* forest have been continuously conducted at Spasskaya Pad scientific station at the Institute for Biological Problems of the Cryolithozone, of the Siberian Branch of the Russian Academy of Sciences (IBPC SB RAS) (Maximov et al. 2010). This series of ongoing studies is updating our knowledge of seasonal and annual variation in the function of carbon cycles in larch forest. Spasskaya Pad is located on the left side of the valley in the middle basin of the Lena River in Central Yakutia, Russia (62°14′N, 129°37′ E; 213 m a.s.l.). The station is situated in a 200-year-old cowberry larch forest (*Laricetum vacciniosum*), which stands on permafrost pale-solodic soil based on a light old-alluvial sandy loam. Soils in Spasskaya Pad have a high sand content and low porosity. The water retention capacity of these soils is relatively low. The thickness of the humus horizon does not exceed 5 cm. The second field site of Elgeeii station is located in a highly productive forest in south-eastern Yakutia, on the third terrace of the left bank of the Aldan River in south-eastern Yakutia, Russia (60°00′N, 133°49′E; 220 m a.s.l.). The surrounding environment is a 180-year-old cowberry larch forest on permafrost dark-humus pale-slightly solodic soils based on a carbonated loam. Soils in Elgeeii are heavier than at Spasskaya Pad due to their granulometric composition; in addition, the content of the medium and thin particles and silt in the soil is 2–3 times more than at Spasskaya Pad. Porosity is high and water retention capacity is relatively high. The thickness of the humus horizon is 10–15 cm on average. An additional description of these study sites was provided in Chap. 3.

Carbon budget is expressed in net biome production (NBP) as balance of net ecosystem production (NEP), ecosystem heterotrophic respiration (HR) which includes microbe respiration and decomposition of standing dead trees and coarse woody debris, flux due to natural and human-induced disturbance and consumption (Dtc), and lateral flux to the lithosphere and hydrosphere (LEh) (e.g. Dolman et al. 2012):

$$\mathrm{NBP} = \mathrm{NEP} - \mathrm{HR} - \mathrm{Dtc} - \mathrm{LEh}. \tag{4.1}$$

Focus on forest ecosystem, NEP is given as follows.

$$\mathrm{NEP} = -\mathrm{NEE} = \mathrm{NPP} - \mathrm{HR} = \mathrm{GPP} - \mathrm{ER} \tag{4.2}$$

$$\mathrm{ER} = \mathrm{AR} + \mathrm{HR} \tag{4.3}$$

where NEE is net ecosystem exchange, NPP is net primary production, GPP is gross primary production, ER is ecosystem respiration, and AR is autotrophic (above-ground and root) respiration. These terms are built up from carbon circulation between land surface and atmosphere including assimilation and respiration processes.

This chapter reports the distinctive features of leaf-scale photosynthesis (Sect. 4.2), soil respiration (Sect. 4.3), and net ecosystem exchange (NEE) of CO_2 (Sect. 4.4), mainly based on long-term (1998–2014) observations in Spasskaya Pad larch forest, which were then compared to the results for other boreal forests.

4.2 Photosynthetic Activity of Larch Forests

Since the early 1990s, many studies have investigated the ecological and physiological features of the larch photosynthesis process in Siberia (Maximov et al. 1994, 1995, 2004, 2005a, b, 2010; Maximov 2007; Maximov and Ivanov 2003, 2005; Tabuchi et al. 1994; Hollinger et al. 1995; Schulze et al. 1995; Arneth et al. 1996; Koike et al. 1998, 1999; Vygodskaya et al. 1997; Fujita et al. 1998; Saito et al. 2003; Suzuki et al. 2003). In these studies, the questions of daytime and diurnal photosynthesis dynamics and the influence of environmental factors were considered in detail.

4.2.1 *Diurnal Dynamics of Photosynthesis*

Regardless of the annual variation in moisture conditions, the daily intensity of net photosynthesis (A_{net}) of *L. cajanderi* generally increases from early morning (4–6 a.m.) until noon and then gradually decreases (approximately from 9 p.m.) to negative values (Maximov et al. 2005b). The daytime depression of photosynthesis, which is typical of annual cultural plants, is not observed in larch trees. This indicates that larch is well adapted to the arid climate. Although the photoperiod, with a positive gas exchange, is 16–17 h during summertime (from 5–6 to 20–22), the peak A_{net} only occurs for approximately 2 h.

The average photosynthetic daily assimilation of *L. cajanderi* is 3.99 g C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ (332.6 mmol CO_2 $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$) in wet years and 1.67 g C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ (139.5 mmol CO_2 $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$) in extremely arid years. This variability is larger than the range reported in previous studies for other species of larch, i.e. from 2.04 to 2.64 g C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ (from 170 to 220 mmol CO_2 $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$) (Benecke et al. 1981; Vygodskaya et al. 1997). Moreover, in late July of a wet year, a maximum of 5.95 g C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ (496 mmol CO_2 $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$) is observed. This means that in wet years, *L. cajanderi* takes up 2.4 times more CO_2 than in arid and extremely dry years. The difference in the daily assimilation of CO_2 among the dry years is insignificant, e.g. 1.8 and 1.7 g C $\mathrm{m^{-2}}$ $\mathrm{day^{-1}}$ in 2001 and 2002, respectively (Maximov et al. 2005b; Maximov 2007).

The variability of the photosynthesis rate is dependent not only on environmental conditions but also on the structure and physiology of the plants. For *L. gmelinii* (*cajanderi*), this has been reported from field studies on the Aldan plateau (Vygodskaya et al. 1997), where A_{net} is suppressed by 40% as a result of structural and physiological variation, but mainly due to the nitrogen distribution in crown leaves. In addition, A_{net} is suppressed by 12% due to the low levels of illumination in the morning and evening.

4.2.2 *Seasonal Dynamics of Photosynthesis*

Larch exhibits a high A_{net} from the beginning of needle growth on the shoots of previous years (the third week of May to the first week of June). Under favourable hydrothermal conditions (an abundance of precipitation and high temperatures) during the initial stages of growth and development, high levels of photosynthesis in *L. cajanderi* can also be observed in July. During dry years, it is usually limited to the previous month (June). During wet years, the maximum A_{net} value in July is higher than in June. The direct dependence of the photosynthetic activity of this species on summer precipitation has been clearly identified. Maximov (2007) reported that during dry and extremely dry periods, the correlation coefficient (r^2) for the relationship between larch photosynthesis intensity and the amount of precipitation in June–August is 0.33, whereas during wet years it increases to 0.77.

Trees in Yakutia prefer to use rainwater in wet years and thawed groundwater in dry years, as shown by our studies using stable isotopes (Sugimoto et al. 2002). This shows that these tree species use atmospheric and soil moisture. This is advantageous under cold soil conditions, where there can be a deficiency of moisture and nutrients. In Yakutia, the relatively high level of photosynthesis in larch is maintained mainly by precipitation, but in dry seasons it is maintained by the soil moisture accumulated during the preceding autumn and spring (there is a marked increase in photosynthesis at the beginning of the vegetative period in the growing season). The capillary rise of meltwater from deeper layers of soil and its use to support growth processes and photosynthesis are also possible in further periods of plant growth and development (e.g. July and August); however, the effect of this is much weaker than the use of atmospheric moisture. The high and stable level of xylem water potential (up to 3–4 MPa) contributes significantly to the increased consumption and absorption of water by the root system from the lower horizons of the soil (Maximov et al. 1996). The increase in the transpiration surface and well-developed root system also favours the effective use of water by plants.

The results of a long-term observation at Spasskaya Pad have shown that a *L. cajanderi* forest absorbs up to 540 g CO_2 m^{-2} per growing season (May–August) in extremely dry years and up to 1440 gCO_2 m^{-1} $season^{-1}$ in humid years, which is 2.5 times more than in arid years. Recalculating these values as carbon gives 150 and 400 g C m^{-1} during the growing season in dry and humid years, respectively.

4.2.3 *The Maximum Intensity of Photosynthesis* (**A***max*)

The maximum intensity of photosynthesis ($A_{max)}$ of woody plants in eastern Siberia (Table 4.1) is well suited for both the theoretical (model) and experimental ranges of values in the boreal zone. Thus, according to the A_{max} allocation world biome map compiled by Woodward and Smith (1995), the theoretical values for our study area, predicted from the soil C and N content, are in the range of 12.6–15.1 μmol m^{-2} s^{-1}, while the experimental values are 7.6–10.1 μmol m^{-2} s^{-1}.

Table 4.1 Ecophysiological characteristics of larch (*Larix cajanderi* and *gmelinii*) in eastern Siberia (Yakutia)

Place, time, and tree age	Parameters							References
	A_{max} [µmol m^2 s^{-1}]	E [mmol m^2 s^{-1}]	I_C [µmol m^2 s^{-1}]	I_S [µmol m^2 s^{-1}]	N [mg g^{-1}]	NUE_I [µmol $mmol^{-1}$]	WUE_I [µmol mmol N^{-1} s^{-1}]	
Field observation								
62°15′N, 129°37′E					1.5%			Sassa (1993)
62°15′N, 129°37′E July	4.41* (~1.5)*	0.77* (~0.15)*		210 × 10^{-6} Em^{-2} s^{-1}*				Tabuchi et al. (1994)
60°51′N 128°16′E July, 125 ± 8 years	8.6–10.4*	22 mg m^{-2} s^{-1} (CL)		>300				Hollinger et al. (1995)
	5–6 (CL)							
60°51′N 128°16′ E July, 125 ± 8 years	10.1	3.9 (1 ± 0.8)		~500	15.6 ± 0.1			Vygodskaya et al. (1997)
	6.1 (CL) (2.7 ± 2.2)							
60°51′N 128°16′E July, 125 ± 8 years					16–22			Schulze et al. (1995)
62°18′N, 129°30′E; 62°13′N, 129°11′ E July, 23–171 years					16–20			Shibuya et al. (2001)
62°18′N, 129°30′E July, 200 years	13.6 ± 1.3^{a}**		29 ± 6^{a}	785 ± 166^{a}				Saito et al. (2003)
	9.6 ± 0.5^{b}**		18 ± 4^{b}	387 ± 47^{b}				

(continued)

Table 4.1 (continued)

Place, time, and tree age	Parameters							References
	A_{max} [μmol m^2 s^{-1}]	E [mmol m^2 s^{-1}]	I_C [μmol m^2 s^{-1}]	I_S [μmol m^2 s^{-1}]	N [mg g^{-1}]	NUE_I [μmol $mmol^{-1}$]	WUE_I [μmol mmol N^{-1} s^{-1}]	
62°15′N, 129°37′ E; 62°18′N, 129°30′ E	~7.5*			~700*				Suzuki et al. (2003)
Phytotron experiment	25–32.2*					0.014	1.1	Koike et al. (2000)

Modified by Maximov et al. (2010)

A_{max} maximum net assimilation (A_{net}), E transpiration rate, Ic light compensation point, Is light saturation point, N leaf nitrogen content, NUE_I instantaneous nitrogen use efficiency, WUE_I instantaneous water use efficiency

[a]light needle; [b]shade needle

[*]read from graphs or recalculation of data; [**]light saturated; ? mentioned but no data provided, *in brackets* average values, *CL* data scaled to canopy level

The values of the main photosynthetic parameters of larch at Spasskaya Pad that were investigated at the initial stage of the research period (from the 1990s to the early 2000s) are summarised in Table 4.1. Sometimes it is not easy, and often it is impossible, to compare the published data on a unified basis, because of the different methodological and temporal scales of measurements. Therefore, data were considered according to the authors' computations, with approximations from the graphs and recalculations, where possible. It should also be noted that during this period, overseas researchers did not distinguish between *L. gmelinii* and *L. cajanderi* but rather considered them to be one species: *Gmelin* or *L. gmelinii* (Abaimov et al. 2002).

In the artificial climate conditions of a growth chamber in a previous study, young larch had a very high A_{net} at 30 μmol m^2 s^{-1}, with a gradual increase in the concentration of CO_2 to 1500 ppm. When the CO_2 concentration was doubled and the air temperature was increased by 4 °C, all of the main tree species of Yakutia (*L. cajanderi*, *Pinus sylvestris*, and *Betula platyphylla*) had similar values and trends of A_{net} regardless of the growing conditions (Koike et al. 2000). There is a reason to believe that such a high A_{net} value is a common adaptive physiological feature of the Yakutian tree species that grow in arid climate conditions with a short vegetative period. The index of photosynthesis depends not only on environmental conditions but also on the structure and physiology of plants themselves and their organs (Mokronosov 1983; Tselniker et al. 1990). This has previously been reported for *L. gmelinii* (Vygodskaya et al. 1997); in that study, A_{net} was suppressed by 40% as a result of structural and physiological variation but mainly by the distribution of nitrogen in the leaves of the crown. In addition, A_{net} was reduced due to low lighting in the morning and in evening (by 12%) and low humidity (by 75%).

According to our measurements at Spasskaya Pad, the maximum A_{net} of maturated larch trees varies greatly during the growing season depending on the weather conditions. In our studies, during dry and extremely dry years (1998, 2001, and 2002), the maximum A_{net} was 6.3–7.5 μmol m^{-2} s^{-1}, while in wet years (1999, 2003, 2005, and 2006), it was 7.5–13.5 μmol m^{-2} s^{-1}. There was a clear difference in A_{net} (an average of 1.6 times) between wet and dry years. In very humid years, the highest A_{net} of *L. cajanderi* (13.5 μmol m^{-2} s^{-1}) was 1.3 times higher than that of larch forests in South Yakutia (Vygodskaya et al. 1997) and Central Siberia (Koike et al. 1998) and four times higher than that of European, Japanese, and American species (Maximov et al. 2010; Table 4.2). Vygodskaya et al. (1997) suggested that the high A_{net} values of the Yakut larch species are associated with high stomatal conductance and high transpiration intensity. The latter condition is necessary for the normal life of Yakut plants under drought conditions, because it prevents overheating and leaf heat stress (e.g. Stepanov 1976, Maximov 1989).

Geographical location within the bounds of Siberia makes no significant difference in the net photosynthesis of larch (Table 4.2). Vygodskaya et al. (1997) undertook a general comparison at the species level for *L. gmelinii* (*cajanderi*) in eastern Siberia and European *Larix decidua* (Table 4.3). In general, the needles of *L. cajanderi* and *L. decidua* share a similar anatomy, although the characteristics of the European species are more closely associated with those of the shade needles of Yakutian larch (Vygodskaya et al. 1997). *L. cajanderi* also shows wide intra-tree variation in the size and thickness of pine knot needles.

Table 4.2 CO_2 assimilation of *Larix* spp. in different regions (Maximov et al. 2010)

Region	Species	A_{net} [µmol CO_2 m^{-2} s^{-1}]	References
Europe	*Larix decidua*	3.0	Benecke et al. (1981)
Japan	*Larix leptolepis*	3.0	Matyssek and Schulze (1987) and Dang et al. (1991)
North America	*Larix laricina*	3.0	Matyssek and Schulze (1987) and Dang et al. (1991)
Moscow region	*Larix decidua*	25.0 ± 3.1[a]	Malkina (1995)
Central Siberia	*Larix gmelinii*	7.8–11.5	Koike et al. (1998)
Eastern Siberia (Irkutsk region)	*Larix sibirica*	22.0[a]	Shcherbatyuk et al. (1991)
Eastern Siberia (Central Yakutia)	*Larix gmelinii*	8.6–10.4	Hollinger et al. (1995), Schulze et al. (1995) and Vygodskaya et al. (1997)
Eastern Siberia (Central Yakutia)	*Larix cajanderi*	4.4–13.5	Data by the authors (SPA)

[a] A_{net} is calculated based on dry weight, mg CO_2 g^{-1} h^{-1}

Table 4.3 Physiological parameters of two larch species

	Larix decidua	*Larix gmelinii*	References
Stomatal density [mm^{-2}]	20	20–30	Meidner and Mansfield (1968) and Vygodskaya et al. (1997)
Stomatal aperture [µm]	20	20	Meidner and Mansfield (1968) and Vygodskaya et al. (1997)
Nitrogen content in leaves [mg g^{-1}]	24.7	15.6	Matyssek and Schulze (1987) and Vygodskaya et al. (1997)
Maximum net assimilation, A_{max} [µmol m^{-2} s^{-1}]	About 3	10.1	Benecke et al. (1981) and Vygodskaya et al. (1997)
Transpiration at VPD 1.5 KPa, E [mmol m^{-2} s^{-1}]	0.75	3.7	Benecke et al. (1981) and Vygodskaya et al. (1997)
Leaf conductance, g_s [mmol m^{-2} s^{-1}]	–	56 ± 60 (max 365)	Vygodskaya et al. (1997)
Light saturation, I_s [µmol m^{-2} s^{-1}]	About 500	About 500	Vygodskaya et al. (1997)
Average weight of needles [g m^{-2}]	–	138 ± 6	Vygodskaya et al. (1997)

4.2.4 Ratio of Photosynthesis to Dark Respiration (R_{dark}) of Plants

Larch species use about 60% of the carbon they absorb to breathe. About a quarter of this is via respiration in needles, with 13–16% in branches, and there are approximately equal proportions of overall respiration in the stem and roots. Thus, about

40% of the carbon goes to the formation of biomass (Scherbatyuk et al. 1991). To understand carbon allocation in plants, and its role in growth and maintenance processes, the relationship between assimilation and respiration, specifically A_{net} and R_{dark}, needs to be determined. This can be characterised by the annual hydrothermal regime, which is critical for plants. Usually the ratio of R_{dark} to A_{net} reaches a maximum at the beginning of the growing season. At this time, plants need large amounts of energy to grow new shoots and needles (Zabuga and Scherbatyuk 1982; Sherbatyuk, 1976). We found that while the shoots grew and A_{net} increased, the R_{dark} of larch decreased slightly in July and stabilised in August (Maximov et al. 2005b). During the growing season, the R_{dark} costs of the larch needles varied from 22 to 57% of the maximum A_{net} (A_{max}), depending on the ambient temperature and moisture deficit. During this period, the average value of the respiratory costs was 36.4% of the A_{max}. Such a value for the ratio between A_{max} and R_{dark} of larch indicates a strong adaptation of *L. cajanderi* to extremely arid conditions.

We analysed the specific features of the R_{dark} of the leaves of the dominant tree species in Yakutia, i.e. *L. cajanderi*, *P. sylvestris*, and *Betula platyphylla* (Atkin et al. 2015). The leaf respiration rate of all tree species (measured in the dark) fell in response to the prolonged drought in June–July (Fig. 4.1). It is important to note that respiration rates significantly increased in August and September as a result of the frequent precipitation. The analysis showed that the decline of R_{dark} on a dry plot was not a thermal adaptation but rather was induced by water stress. During this dry spell, light respiration was about 30% lower than R_{dark}. These results show that precipitation plays an important role in regulating the scale and magnitude of the CO_2 released (in both light and dark) by the larch forest ecosystem, in which CO_2 released as a result of leaf respiration can account for 1/3 of the entire ecosystem respiration.

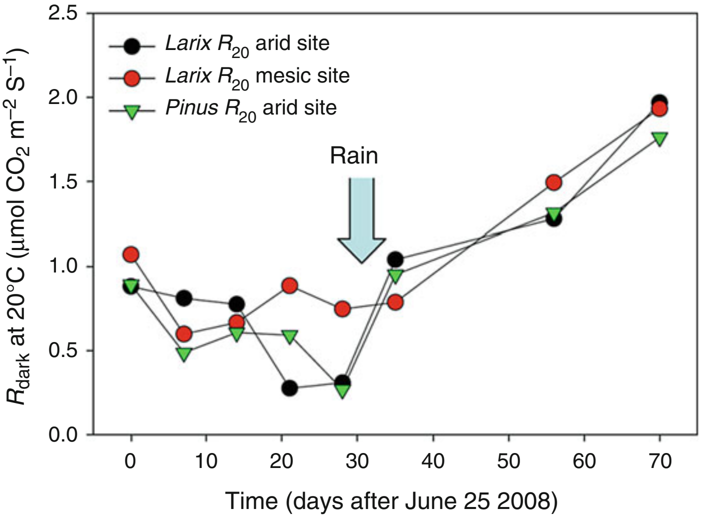

Fig. 4.1 Dark respiration of the larch (*L. cajanderi*) and pine (*P. sylvestris*) needles in different hydroclimatic plots of Spasskaya Pad station, June–September 2008

In other regions of Siberia where coniferous trees grow, R_{dark} amounts to 60% of $A_{\max}$ (Malkina 1995; Scherbatyuk et al. 1991). Compared to other conifers, such as spruce and pine, larch is distinguished by a high level of both photosynthetic activity and respiration in the light (Scherbatyuk et al. 1991). For pine and spruce, R_{dark} during the growing season is greater than light respiration, whereas in larch, light respiration dominates at this time. Photosynthesis and the release of CO_2 in the light are closely interrelated, and plants with a high intensity of photosynthesis are also characterised by high levels of light respiration (Laisk 1977; Bykov 1983, Atkin et al. 2015). Hence, with a high intensity of photosynthesis, the species of larch we studied may have low R_{dark} and high intensity of light respiration (Maximov 2007). As a result, Siberian larch is characterised by high daily photosynthesis productivity, e.g. 2.7 times higher than pine and 3.9 times higher than spruce (Ivanov and Kossovich 1932; Scherbatyuk et al. 1991).

The R_{dark} of Yakutian trees has been included as an integral part of a new global R_{dark} database based on leaf features (GlobResp), created from an assessment of 899 plant species in 100 sites from the Arctic to the tropics (Atkin et al. 2015). GlobResp data indicate that at ambient temperatures, R_{dark} increases only twofold from the Arctic to the tropics, although the temperature rises by 20 °C. At the same time, at a standard temperature of 25 °C, R_{dark} is three times higher in the Arctic than in the tropics and twice as high in dry plots compared to wet habitats. One of the interesting results of GlobResp is the high level of variation in R_{dark} among plant species and sites and along global gradients of temperature and aridity.

4.2.5 Light Dependence of Photosynthesis

The intensity of photosynthesis in larches in eastern Siberia indicates light saturation at a photosynthetic photon flux density (PPFD) of 300–500 μmol photons $m^{-2}\ s^{-1}$, which is about 20–25% of the maximum lighting (1500–2000 μmol photons $m^{-2}\ s^{-1}$) (Saito et al. 2003; Vygodskaya et al. 1997). A very high light saturation point (Is) of 1300 μmol photons $m^{-2}\ s^{-1}$ for larch was recorded at the river side of a branch stream of the Yenisei River in central Siberia (Koike et al. 1998), while the $A_{\max}$, light compensation point (I_C), and nitrogen content of the leaves were similar to those of Yakutian larch. The environmental conditions of the area require plant species growing there to be extremely light demanding, even for sciophilous species such as spruce, which has an I_S of about 500 μmol photons $m^{-2}\ s^{-1}$ (Koike et al. 1998).

The effects of sunflecks on photosynthesis inside a forest are important but are usually not taken into account when evaluating the carbon balance. Flecks penetrating the canopy may contribute 10–80% of the PPFD, despite being present for less than 10% of the time (Chazdon 1998). In a larch forest near Yakutsk, the daily sum of the PPFD penetrating the stand canopy was equivalent to 18–23% of the crown incident irradiance (Saito et al. 2003). The portion of the PPFD exceeding the I_S was 20% for a shaded canopy and 10% for the forest floor, with almost all sunflecks occurring in the second half of the day.

The sum of the sunfleck PPFD was at the lower limit of the range reported by Chazdon (1998). Because we were not aware of any data for the boreal zone, available values for tropical and temperate regions were used for comparison. According to some investigations, sunflecks in tropical forests could account for 30–65% of the daily carbon sequestration (Pearcy and Calkin 1983; Pearcy 1987), which is much higher than in temperate zones, where the figure may be as little as 6–19% in deciduous forests (Schulze 1972; Weber et al. 1985). There are two likely reasons for this difference (Pearcy and Pfitsch 1995): (1) the predominance of diffusive light in deciduous forests, which reduces the relative importance of assimilation due to sunflecks, and (2) the low leaf photosynthetic capacity of deciduous plants compared to tropical species.

4.2.6 Nitrogen and Nutrients in a Larch Forest

Sassa (1993) was the first investigator to measure the mineral elements in larch needles in eastern Siberia (as well as in birch and pine). The data for individual nutrients were reported as percentages, approximately 1.5, 0.35, 0.5, 0.20, and 1.3% for N, P_2O_5, CaO, MgO, and K_2O, respectively. A nitrogen content of 1.5% in needles is considered normal for conifers and deciduous trees (Larcher 1995).

Various studies have obtained similar values for the carbon content in aboveground biomass and the nitrogen content in leaves of larch (Shibuya et al. 2001; Koike et al. 1998; Schulze et al. 1995; Vygodskaya et al. 1997; Table 4.1). It can be concluded from these studies that the nitrogen available for growth is rapidly fixed in non-photosynthesising organs and appears to be the main limiting factor of aboveground biomass development, stand dynamics, and the carbon stock of larch. Great variation in leaf nitrogen content has also been observed, with up to a 40% difference reported (Vygodskaya et al. 1997). This has been explained by the high variability of gas-exchange rates, both within the crown and between separate trees. Under the natural conditions of larch forest in eastern Siberia (Central Yakutia), growth/respiratory processes are limited by nitrogen availability rather than CO_2 assimilation.

4.2.7 Assessment of the Biochemical Parameters that Limit Photosynthesis

Alongside investigations of gas exchange to and from needles, the primary biochemical parameters that limit photosynthesis have been estimated from the relationship between the intercellular CO_2 concentration and A_{net} (e.g. Farquhar et al. 1980). The maximum PPFD values were determined for activating the main enzyme involved in carboxylation of the Calvin cycle in photosynthesis, i.e. ribulose-1,5-

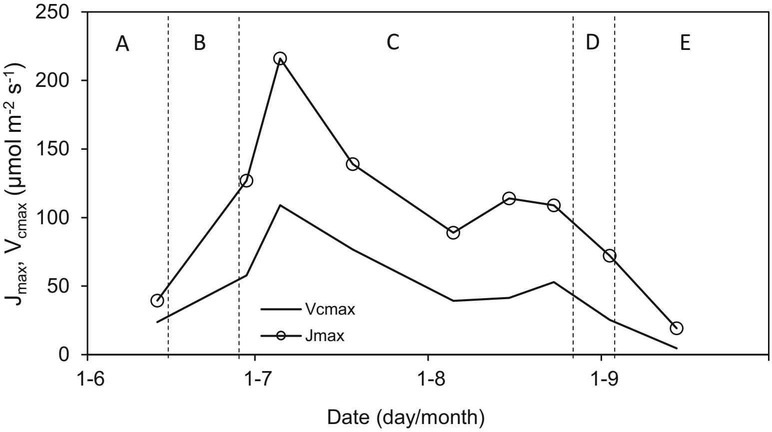

Fig. 4.2 Seasonal course of biochemical parameters (V_{cmax} and J_{max}) of *L. cajanderi* at Spasskaya Pad station. Data of 2008–2012 years are averaged. A. the beginning of active vegetation and buds' growth of the next year (needles have already completed their growth in early June); B, blooming of cones; C, the final phase of vegetation; D, the yellowing beginning of the needles and the buds formation of the next year; E, fallen needles

bisphosphate carboxylase/oxygenase (V_{cmax}), the electronic transport of regenerated ribulose-1,5-bisphosphate (J_{max}), and other related processes (the use of triose phosphate (TPU), light saturation (I_S), and so forth).

Long-term estimates (2000–2014) of V_{cmax} and J_{max} for *L. cajanderi* at Spasskaya Pad have shown that the seasonal variation in typical larch forests in central Yakutia is generally associated with the phases of needle and bud development, but in some years the seasonal trend may not be apparent. An example of the most complete and indicative seasonal course of the biochemical parameters of photosynthesis is shown in Fig. 4.2. These values (average of 40 and 94, maximum of 109 and 216 µmol m^{-2} s^{-1} for V_{cmax} and J_{max}, respectively) were within the range of theoretically expected and average values for similar plants and ecosystems (Wullschleger 1993).

4.3 Soil Respiration in a Larch Forest

Soil respiration result in the release of CO_2 produced by the living inhabitants of soil, i.e. microorganisms, other soil fauna, and plant organs (roots and rhizomes), from the soil surface to the atmosphere. Soil respiration reflects the respiratory activity of the soil biomass, during which soil organisms receive energy to sustain their life from the catabolism of dead organic matter.

Soil respiration is sometimes called underground or belowground respiration, as opposed to aboveground respiration, which refers to the production of CO_2 by plant organs that are located above the soil surface, i.e. stems, trunks, branches, and leaves. The generally accepted definition of soil does not include dead undecomposed plant residues located on the soil surface in the litter layer, but CO_2 produced as a result of litter decomposition is usually included in soil respiration.

In some circumstances, these patterns may be disrupted. For example, during heavy showers, the air spaces in the soil can be physically degassed by the incoming water, which leads to considerable CO_2 emission from soil surface. At the same time, soil moisture, which increases during rain, may directly affect soil respiration through the activation of soil biomatter. It should also be noted that the chemical reactions of carbonic acid or the activity of methanogenic microorganisms can also lead to changes in the equilibrium of CO_2 in the soil. Nevertheless, these processes do not have a significant influence on CO_2 emissions in the long term, but can affect the rate of CO_2 efflux from soils over shorter time intervals.

It has been widely reported that the recent changes in the average annual ground temperature in the northern hemisphere have begun to rise, particularly in north-eastern Russia (Fedorov et al. 2006; Oberman and Shesler 2009; Romanovsky et al. 2010). An increase in summer precipitation is also expected, together with other environmental and social changes (IPCC 2013). The observed changes in air temperature and precipitation are likely to substantially affect the intensity of soil respiration, which is a key component of the global carbon balance. Thus, with current climate trends, stimulation of soil respiration is expected, which could reduce the carbon uptake capacity of terrestrial ecosystems.

Soil CO_2 efflux (almost equal to soil respiration or soil CO_2 emission) is one of the most intense carbon flux components in the global carbon cycle. Even very small variation in soil respiration due to climate change will cause considerable changes in annual carbon emissions into the atmosphere. The strong sensitivity of soil respiration to variation in soil temperature and moisture is also an interesting and very important issue to study.

The intensity of the CO_2 release from soils depends on climatic variation and the hydrothermal conditions of soils and their properties. It can also be influenced by the physiological state of plants and microbial communities, species composition, and vegetation density. Thus, soil respiration, to a certain extent, characterises the functional state of the ecosystem during the growing season. An analysis of the daily, seasonal, and interannual dynamics of soil respiration in different forests, growing on distinctly different soils, and a subsequent comparison of soil respiration values with certain standard values could explain the mechanisms of ecosystem functioning and reveal their regional components (e.g. Prokushkin et al. 2000a, b; Maximov et al. 2005a).

To more clearly understand the carbon balance characteristics of permafrost larch forest ecosystems, we investigated the long-term response of permafrost soil CO_2-efflux processes in larch forests to changing climatic conditions, at two sites with different ambient and edaphic environments: Spasskaya Pad (medium-productivity larch forest) and Elgeeii (highly productive larch forest) in eastern Siberia.

4.3.1 Daily Dynamics of Soil Respiration

The diurnal variations in soil respiration at Spasskaya Pad and Elgeeii sites fit a bell-shaped curve (Fig. 4.3) and were strongly correlated with temperatures at a depth of 10–40 cm, which means that most soil biological activity originated at those depths. This has been proven by root density and microbial activity studies (Spasskaya Pad; Ivanova et al. 2006). Under relatively moist conditions (soil moisture content, SMC > 14%), the strong correlation between the respiration flux and the soil temperature resulted in the highest soil respiration during the daytime. During relatively dry periods, SMC < 10%, respiration was strongly linked to the SMC, and even small increases in the soil moisture of the upper soil horizons during the night, due to condensation effects, caused an increase in the CO_2 flux. During these conditions, the highest levels of soil respiration occurred at the beginning of the night when the rising soil moisture coincided with the still relatively high soil temperature.

Precipitation events rapidly increased the moisture content in the upper soil layers, which led in turn to a rapid short-term increase in the soil respiration rate, through the enhancement of soil biota activity (Kononov 2006). However, soon after rain, when soil was drying, the pattern of soil respiration again followed the seasonal trend of soil temperature. These CO_2 peaks had virtually no effect on the total CO_2 emission in the short term, with the total seasonal amount of precipitation being the main factor affecting the annual soil CO_2 flux. In both dry and wet years, rainfall after drought in midsummer caused a strong response in soil biological activity (expressed as soil CO_2 emissions). Very small amounts of precipitation

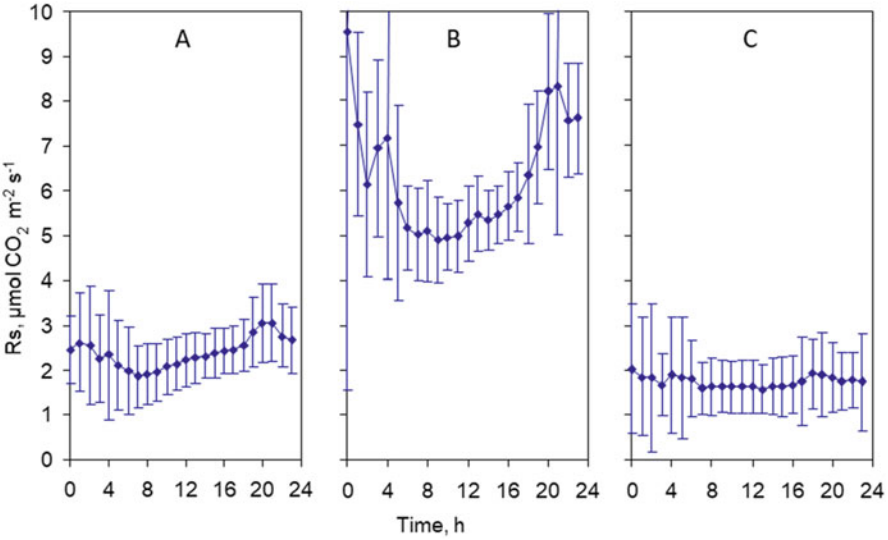

Fig. 4.3 Typical daily curves of soil respiration in Spasskaya Pad (SPA) station, 2006. (**a**) Early June, (**b**) mid-July, (**c**) late August (the error bars are standard deviations)

(2–3 mm day^{-1}) could cause an increase in the soil respiration rate (rise by 24–30%), whereas with much stronger rains (15–20 mm day^{-1}) during wet periods, the rise in the soil respiration rate was only 10–15%. Considerable amounts of precipitation during the cold period of late summer and early autumn did not have much effect on soil respiration, because the low soil temperatures would inhibit the respiratory metabolism of roots and soil organisms despite the abundance of soil moisture.

A high amplitude of daily soil respiration was observed in the mid-growing, with an increase in soil CO_2 emissions at day- or night-time during wet and dry years, respectively. At the beginning and end of the season, the daily curve was smoothed and almost flat, which could be explained by the stable soil temperature regime during these periods.

4.3.2 *Seasonal Dynamics of Soil Respiration*

There are not many soil respiration data under larch forests worldwide, and almost all the studies were carried out in boreal conifer forests, such as pine, fir, or spruce, mainly in Canada, Alaska, and Scandinavian Peninsula. For instance, in black spruce forests of Manitoba and Saskatchewan (Canada, latitude 54–55°N, sporadic permafrost), soil respiration rates vary from 0.60 to 3.20 μmol m^{-2} s^{-1} (Bond-Lamberty et al. 2004), while in Sweden (Scotch pine and Norway spruce forests, latitude 60–64°N, continuous permafrost), reported soil respiration rates are 1.45–10.51 μmol m^{-2} s^{-1} (Bhupinderpal-Singh et al. 2003; Högberg et al. 2001; Eliasson et al. 2005; Moren and Lindroth 2000; Widen and Majdi 2001). In Russian climatic research station Zotino (ZOTTO) in the Krasnoyarsk Krai (Siberia, latitude 61°N, continuous permafrost), soil respiration rate was reported to be 1.90 μmol m^{-2} s^{-1} (Kelliher et al. 1999). Thus, estimation of soil respiration rates in boreal conifer forests varies widely, and the average value is around 2.7 μmol m^{-2} s^{-1}.

Data on eastern Siberian permafrost forests (Spasskaya and Elgeeii sites) show that the seasonal pattern of soil CO_2 efflux has a dome-like shape (Fig. 4.4). Minor detectable soil CO_2 releases began immediately after the snow cover started to melt

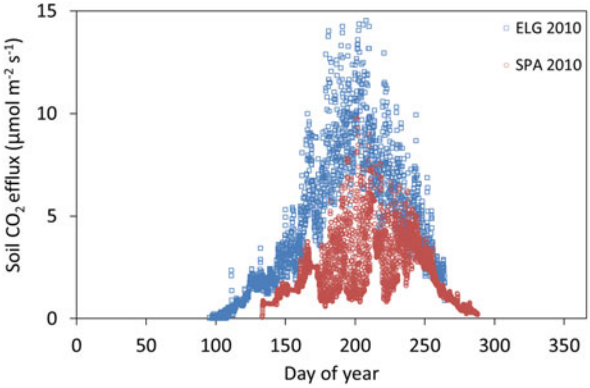

Fig. 4.4 Typical seasonal curves of soil respiration in Spasskaya Pad (SPA) and Elgeeii (ELG) stations, 2010

around the end of April–early May. Observable soil CO_2 emissions began at almost the same time at both sites, in the second week of May, but in Elgeeii they started a few days earlier (DOY 125–135). The maximum soil CO_2 emission in Spasskaya Pad was usually observed in late July–early August (DOY 199–232), with an average of 6.8 μmol CO_2 m^{-2} s^{-1}. In the highly productive Elgeeii site, the highest CO_2 emission (interannual mean: 12.5 μmol CO_2 m^{-2} s^{-1}) was recorded at the end of the second week in July (DOY 188 ± 3), which was 2–3 weeks earlier than at the medium-productivity Spasskaya site. This indicates the early occurrence of optimal conditions for the soil biota in the south-eastern site and can be explained by the physical properties of soils in south-eastern Yakutia (e.g. fast soil warming due to the higher thermal conductance and higher soil porosity of 48.8% versus 40.9% in central Yakutia).

The soil CO_2 efflux at SPA usually stopped in the middle of October (DOY 285–290). At Elgeeii, we measured soil respiration until early October, but based on an analysis of the timings, when the soil temperature reached freezing point, soil biological activity ended at a similar time, i.e. around the end of October.

The seasonal temporal trends of soil respiration mostly corresponded to the temporal variability of the CO_2 concentration along the soil profile. During late autumn and winter, bursts of CO_2 were observed aboveground, accompanied by a corresponding decrease in the CO_2 concentration in the deep soil layers. This could be explained by the release of CO_2 gas, which had previously become trapped under pressure between the upper soil layer and permafrost during the simultaneous freezing of soil horizons. Then the pressurised gas was released to the atmosphere through cracks in the soil that appeared during frost heave. The seasonal magnitude of soil respiration increased significantly with the rise of soil temperature and soil moisture. However, in waterlogged soil, soil respiration was reduced due to the inhibition of aerobic soil biota by over-wetting.

4.3.3 Interannual and Spatial Variation in Soil Respiration

Long-term observations of soil CO_2 emissions in larch forests during the warm period of the year (May–September) revealed significant interannual variation in CO_2 emissions from soils, which were mostly driven by weather conditions during the warm period (air and soil temperatures and precipitation). This was strongly correlated with the moisture reserve of soils, which in turn was highly dependent on the autumn precipitation of the previous year and the water reserves in the current year's snow cover. The long-term (2001–2014) trend of soil CO_2 emissions at Spasskaya Pad had a tendency to decrease slightly. The reasons for this were most likely connected to the general decrease in photosynthetic activity in larch forests that we had observed in the last 10 years, which were determined by plant physiology.

Substantial differences were identified in the magnitude of seasonal and annual CO_2 fluxes from soils in the medium-productivity larch forests at Spasskaya Pad

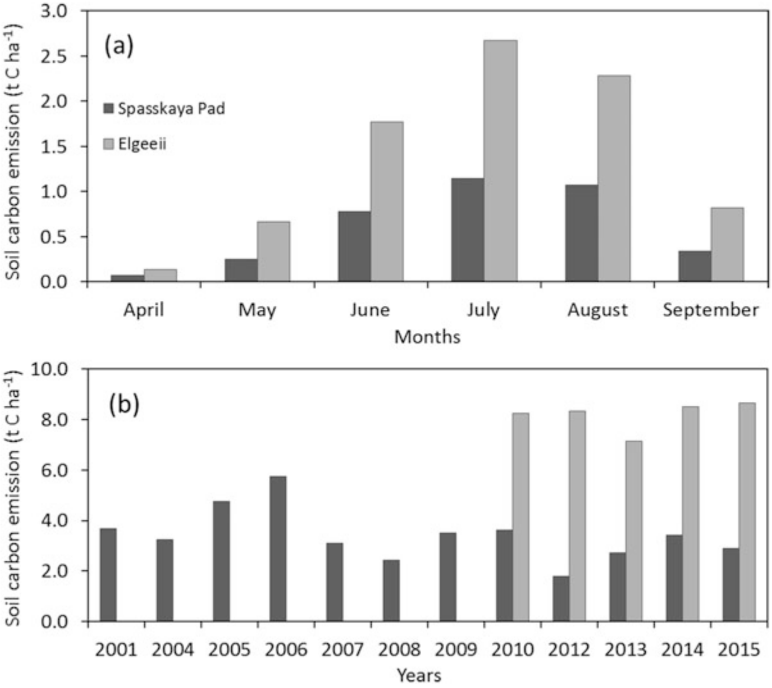

Fig. 4.5 Cumulative carbon fluxes at Spasskaya pad station (SPA, mid-productive forests), 2001–2015, and Elgeeii station (ELG, high-productive forest), south-eastern Yakutia, 2010–2015. (**a**) Long-term monthly averages of carbon emission from soils during the warm period of the year (April–September); (**b**) the interannual amounts of carbon emissions from soils

(central Yakutia) and highly productive larch forests at Elgeeii (south-eastern Yakutia) (Fig. 4.5). The mean annual cumulative carbon emissions from soils at Elgeeii were twice as high as those than at Spasskaya Pad (7.91 and 3.54 t C ha^{-1}, respectively, Fig. 4.6). The main reasons for this difference were as follows: (1) the soils at Elgeeii have a higher porosity and a greater water retention potential than soils at Spasskaya Pad; (2) the higher soil moisture was accompanied by a larger precipitation amount at Elgeeii than at Spasskaya Pad; (3) a longer frost-free period at Elgeeii, with a higher activity of soil biota (156 ± 14 days in Elgeeii vs. 145 ± 12 days in the Spasskaya Pad); and (4) a large biomass and high activity of soil biota (including roots, fungi, actinomycetes, and so forth) in the south-eastern region.

According to available data in Russian scientific literature, the cumulative soil carbon flux is 1.7–15.7 t C ha^{-1} per growing season in northern and southern Russian taiga, respectively (Kudeyarov et al. 1995).

As for eastern Siberian permafrost forests, the absolute value of soil CO$_2$ emissions significantly varies on a spatial basis, even within the central Yakutia region. Comparative studies there made in 2005–2006 (Kononov 2006) show that there are

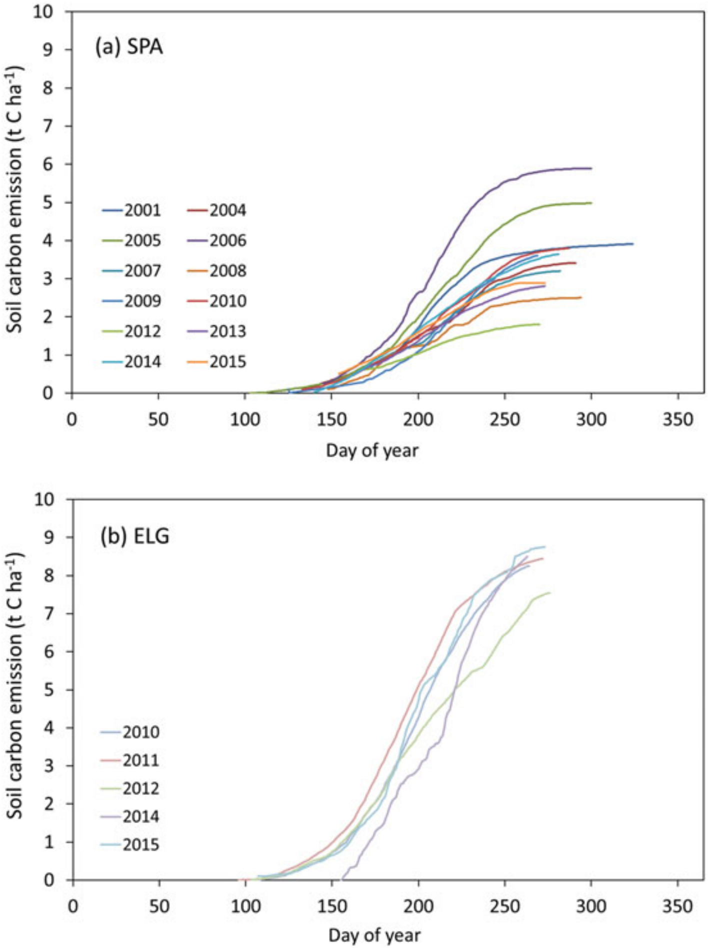

Fig. 4.6 Carbon fluxes from soils of larch forests at Spasskaya pad stations, Central Yakutia, 2001–2015, in (**a**) SPA site (mid-productive forest) and Elgeeii, south-eastern Yakutia, 2010–2015, in (**b**) ELG site (high-productive forest)

15–20% differences in soil respiration in the larch forests on the right and left banks of the Lena River central basin. At the same time, in the south-eastern part of the investigated region (Elgeeii), the cumulative emission of CO_2 reached 8.5 t C ha^{-1} during the growing season, which was more than twice as high as that recorded at sites along the Lena River in central Yakutia. These differences were largely due to hydrothermal conditions, but the pivotal factor was the soil type and its associated properties.

4.3.4 Environmental Dependencies of Soil Respiration

Several environmental dependencies of soil respiration were identified, which showed that the soil CO_2-efflux values during the growing season (F_s) had a strong positive correlation with the trend of soil temperature (T_s) at both sites ($r^2 = 0.74$ for Spasskaya Pad and $r^2 = 0.79$ for Elgeeii). The response of soil respiration to temperature (long-term average Q10 values) at Spasskaya Pad was 4.89 and was almost identical to that at Elgeeii (4.85), but base respiration (T_0) was 1.5 times higher at Elgeeii (1.53 vs. 0.99 at Spasskaya Pad). This indicates that the bigger CO_2 flux at the Elgeeii site could be explained not only by the relatively higher T_s but also by some endogenous factors, for example, a more massive microbial and fungal community. An analysis of other environmental dependencies showed that there were no soil CO_2-efflux correlations with net radiation, photosynthetically active radiation (PAR), or soil heat flux. A soil physics study indicated that the soils at Elgeeii had a higher porosity and water retention capacity compared to that of Spasskaya Pad soil. These soil qualities at Elgeeii led to a relatively stable soil moisture regime during the whole season. As a consequence, the soil conditions at Elgeeii were much more comfortable for soil biota, and therefore a higher annual soil carbon release (cumulative CO_2-flux) was observed at Elgeeii. It was also found that at the Spasskaya Pad site, the cumulative soil carbon efflux in early summer was strongly dependent on the precipitation levels in the autumn of the previous year. For example, if there was a large amount of precipitation registered in autumn, then in early summer of the following year, the soil CO_2 efflux would also be high. In late summer, the CO_2 efflux was mainly correlated with the current precipitation levels.

A comparative analysis of the properties and hydrothermal regime of soils of larch forests in different bioclimatic zones in Yakutia showed that the main factor limiting the seasonal biological activity of the ecosystem was the soil moisture in the upper soil horizons (0–20 cm), which corresponded to the specific properties of soils (porosity, texture, and composition) and the amount of precipitation. At the same time, precipitation (and accordingly soil moisture) also played an important role on a seasonal scale. The early summer soil CO_2 efflux had a strong correlation with the previous year's autumn precipitation. Soil respiration in the second half of summer was mainly correlated with the current year's late summer rains.

Based on an analysis of our data, obtained along the meridional transect, it was found that soil CO_2 emissions in the middle taiga of central Yakutia could be limited by the hydrothermal conditions of the season; however, the main factors were the types and properties of soils. The crucial endogenous factors that determined the soil respiration rate were the depth of the humus layer and accordingly the carbon content of the soil. The difference in soil respiration values of typical sod-pale-yellow solodic and pale-yellow solodic soils in larch forests of the middle Lena River Basin in central Yakutia was 15–20% (the humus reserves in the 0–50 cm layers of each soil type were 108.3 and 97.2 t C ha^{-1}, respectively). The soil respiration of sod-pale-yellow typical soils along the middle Aldan River basin in the south-eastern part of central Yakutia (Elgeeii), with humus reserves of 137.0 t C ha^{-1}, was more than twice as high than the respiration of soils with a lower humus content. In the northern ecosystems, every change in the soil carbon stock (increase or decrease) may lead to rapid changes in the carbon balance of the whole ecosystem.

Thus, it must be concluded that the expected changes in precipitation and soil temperature in high latitudes are likely to cause an increase in soil biological activity, together with fluctuations in the levels of soil carbon. Therefore, an enhancement of the soil dead organic matter decomposition rates, accompanied by the intensification of CO_2 emissions from soils, could occur. Finally, we considered that these processes could lead to drastic changes in the carbon exchange in northern forest ecosystems.

4.4 NEE of CO_2 in Larch Forest

According to our calculations, in the Yakutian forest ecosystems, the total carbon reserves are 13.3–15.7 billion tons of carbon (Table 4.4). The carbon content in the vegetation and soil of forest ecosystems exceeds that of the tundra by an average of 63 and 2 times, respectively. Accumulated carbon stocks in the soils of forest and tundra ecosystems in eastern Siberia (Yakutia) are total 17.1 billion tons in a total area of 125.5 million hectares of forest and 37 million hectares of tundra. This is about 7 and 25% of the total carbon stock in the forest soils of Siberia and Russia, respectively (Maximov et al. 1996).

There has been an increase in the demand for wood that has coincided with changes in management practices to increase forest outcomes. Because the NEE in the forest is the balance of carbon uptake as the result of tree growth and carbon release as a result of soil respiration, management strategies oriented only to tree growth can have negative consequences for the capacity of the entire ecosystem to accumulate and emit carbon.

Table 4.4 Carbon pool of eastern Siberia, Republic of Sakha (Yakutia) (Maximov 2007)

	Carbon stocks [Gt C]
Forest ecosystem (126 million ha)	13.3–15.7
Vegetation	2.2–4.5
Soil	11.2
Tundra ecosystem (37 million ha)	5.9
Vegetation	0.053
Soil	5.9
Total	19.2–21.6

Table 4.5 Monthly average of net ecosystem exchange (NEE), as well as day- and night-time estimates, observed in larch forest of the scientific station “Spasskaya Pad”. The duration of the daytime is from 5:00 a.m. to 21:00 p.m. of Yakutsk local time. Data of 2000–2014 years are averaged

	NEE [μmol m^{-2} s^{-1}]		
Month	All day	Daytime	Night-time
May	0.51	0.55	1.72
June	−3.20	−4.34	1.07
July	−2.01	−3.32	1.92
August	−1.24	−2.94	1.85
September	0.31	−0.49	1.12

4.4.1 The Daily and Seasonal Dynamics

According to eddy covariance flux observations in a larch forest in eastern Siberia, seasonal CO_2 uptake has a distinct pattern. In typical hydrothermal conditions, the Yakutian larch forest absorbs CO_2 mostly in June. Some decrease in the uptake is expected at the end of July and August (Table 4.5). When the needles fall in September, trees and soils continue to breathe and emit CO_2 before the soil freezes. When night and day conditions were reviewed separately, it was clear that the high uptake in June was mainly caused by a significant daytime uptake. June is the month with the highest physiological activity in this ecosystem (see Sect. 4.2). The largest positive values in night-time occurred in July and August.

During the growing period of 2001, the total NEE obtained by summing the daily values was estimated to be −206.4 g C m^{-2} (−17.2 mol C m^{-2}) in the larch forest at Spasskaya Pad (Dolman et al. 2004). By considering the CO_2 from soil respiration trapped in the unfrozen soil layer, which is created by the freezing of soils from both above and below in autumn (after September), a small emission of 1.6 mol C m^{-2} (19.2 g C m^{-2}) was estimated (Dolman et al. 2004). In a similar manner, we estimated the total NEE of the growing season in the larch forest to be −164 to −223 g C m^{-2} (−1.6 to −2.2 t C-CO_2 ha^{-1}) during 2001–2015. From these estimates, the annual uptake of CO_2 was determined to be 170 g C m^{-2} $year^{-1}$ (1.7 t C ha^{-1} $year^{-1}$) in an extremely dry year (2001) and 270 g C m^{-2} $year^{-1}$ (2.7 t C ha^{-1} $year^{-1}$) in a wet year (2006). It should be noted that this is not a long-term deposit of carbon into the ecosystem, but represents net biome production (NBP). The values of NEE that we calculated can be described optimally as net ecosystem production (NEP) (Körner 2003, Dolman et al. 2004). To assess the long-term NBP, the influence of disturbances such as fires should be taken into account. It has been established that forest fires, deforestation, and other disturbances significantly reduce NEP; about 10% of the NEP is locked into soil carbon in the form of NBP. According to Shvidenko and Nilsson (1994), the total area of larch forests in eastern Siberia is 168.8 × 10^3 km^2. We estimated the regional total of the annual carbon storage capacity to be 0.28 Gt C $year^{-1}$, which is probably not the upper limit and can vary significantly from year to year (Dolman et al. 2004).

These results obtained in a larch forest in eastern Siberia (central Yakutia) can be compared to other Siberian ecosystems. The overall NEE was comparable to values reported for birch and mixed forests in central Siberia (Röser et al. 2002), but they were slightly higher than our results for eastern Siberia. The most distinctive finding in eastern Siberia was a sharp increase in negative NEE (uptake) after the needles began to grow. The forest was completely dormant for 9 months, with photosynthesis suddenly beginning in June. June was definitely the month with the greatest absorption, whereas for the central Siberian forest, it is July (Röser et al. 2002).

The rate of CO_2 uptake in summer at Spasskaya Pad was quite high (18 μmol m^{-2} s^{-1}). The maximum negative NEE in a birch plot in central Siberia and at two plots in a mixed stand were −13, −10, and −8 μmol m^{-2} s^{-1}, respectively (Röser et al. 2002). For larch forest investigated in this study, Hiyama et al. (2001) reported a maximum rate of uptake in July of −15.9 μmol m^{-2} s^{-1}, which is comparable with the results of our measurements. High daily rates are supported by independent measurements of photosynthesis in 2003, which showed that at the leaf level, the maximum NEE was 12 μmol m^{-2} s^{-1} in July. With a leaf area index of about 2, a maximum rate of about 24 μmol m^{-2} s^{-1} was determined at the level of the canopy. Such a value lends credence to current estimates and suggests that the rate of CO_2 uptake by larch forests in eastern Siberia during the peak periods may be higher than those in pine forests growing in central Siberia (Dolman et al. 2004).

Then forests of the intracontinental areas in eastern Siberia have developed in severe conditions, with extremely low temperatures, low annual precipitation, and a strong nitrogen deficit. However, as our studies have shown, water stress was not observed, even in dry years, because soil water is accessible to trees and flows to the active root zone during thawing of the seasonally thawed layer (STL) that stabilises transpiration (Sugimoto et al. 2003). The maximum net carbon uptake occurs at the beginning of the summer (June) and then decreases in the hotter midsummer, while uptake rises on cool days at the end of summer.

4.4.2 Contribution of Permafrost Forest in the Terrestrial Carbon Cycle of Russia

Long-term studies of NEE in the larch forest and tundra zone in eastern Siberia are summarised in Fig. 4.7. There is significant interannual variation in cumulative NEE in the medium-productivity larch forest of central (Spasskaya Pad) and southern (Elgeeii) Yakutia (range from −170 to −270 g C m^{-1} $year^{-1}$). In the tundra ecosystem, the variation in NEE is small (range from −50 to −90 g C m^{-2} $year^{-1}$), due to the influence of the maritime climate in the tundra zone of Yakutia (Chokurdakh), where the climatic conditions are less variable than in the continental central Yakutia.

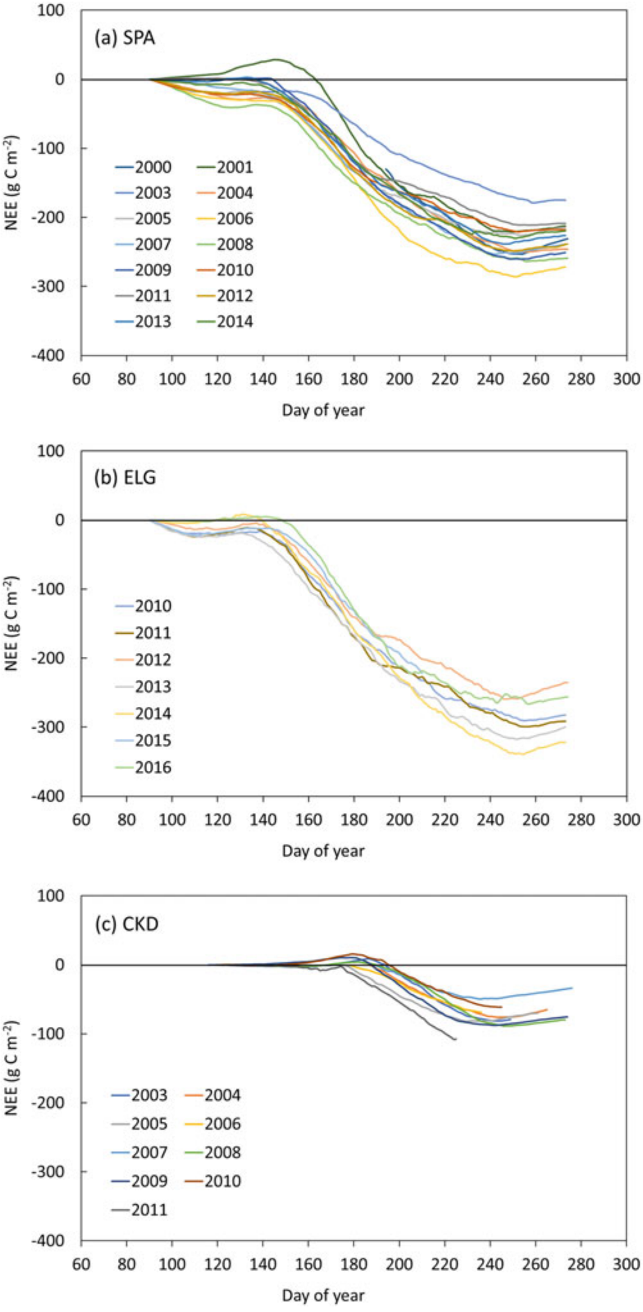

Fig. 4.7 Cumulative carbon accumulation in eastern Siberia, 2000‾2014, by forest ecosystems in (**a**) SPA and (**b**) ELG sites and by tundra ecosystem in (**c**) CKD site

According to long-term eddy-correlation data, the annual NEE at Spasskaya Pad was 212 ± 34 g C m^{-2} $year^{-1}$, at Elgeeii was 243 ± 23 g C m^{-2} $year^{-1}$, and in Chokurdakh was 75 ± 14 g C m^{-2} $year^{-1}$.

Preliminary studies have estimated the drainage capacity of the Siberian forest to be between 50 and 250 g C m^{-2} $year^{-1}$, which is well within the limits indicated in the United Nations Framework Convention on Climate Change (UNFCC) proposal and the value obtained by an atmospheric inversion model (Schulze et al. 1999). Recent estimates using these atmospheric modelling methods assume a carbon flow capacity of 1.5 billion tons $year^{-1}$ for north Asia. This estimate includes all changes in land use over a 10-year period and is based on measurements of atmospheric CO_2 (Bousquet et al. 1999).

According to our data, the interannual variation in the NEE in the forest ecosystem of the permafrost zone is 1.7–2.7 t C ha^{-1} $year^{-1}$, which leads to an upper limit of annual deposition capacity of 0.45–0.71 Gt C $year^{-1}$ for 257.1 million ha area of these forests in Russia. In larch forests in eastern Siberia, there is an annual accumulation from 0.4 to 1.0 Gt C, which is comparable to the equivalent values for European and tropical forests. This calculation does not include the emissions from forest fires. According to Isaev et al. (1995), the carbon flux for the post-fire loss from Russian forests ranges from 0.053 to 0.058 Gt C $year^{-1}$. From satellite observations, CO_2 emissions after fires are estimated to be 0.14 Gt for area of Russia (Rödenbeck et al. 2003). The contribution of Siberian forests (located to the east of the Ural mountain) to this CO_2 budget excluding forest fire is estimated to be 55–62% of all Russian forests. The annual sink of the permafrost larch forests in Siberia is almost half that of all Russian forests (55%), and soil emissions are about 27% of all Russian forests (Table 4.6).

Comparing our experimental data with earlier studies using satellite data (Schimel et al. 2001; Goodale et al. 2002), it was clear that the earlier data were undervalued,

Table 4.6 Annual carbon budget of larch forests in Siberia and Yakutia (Maximov 2007)

Territory	CO_2 flux [Gt C $year^{-1}$]	Profit [%]
Assimilation		
Siberia[a]	1.3	100
Larch in Siberia	0.4–1.0	54
Larch in eastern Siberia (Yakutia)	0.2–0.4	23
Emission		
Russia's soil[b]	2.6–3.0	100
Larch in Siberia	0.8–0.9	27
Larch in eastern Siberia (Yakutia)	0.4	12
Net ecosystem gas exchange (NEE)		
Russia[b]	0.82	100
Larch in Siberia	0.45	55
Larch in eastern Siberia (Yakutia)	0.18	22

Without marks – our data

[a] Schimel et al. (2001), Goodale et al. (2002)

[b] Kudeyarov et al. (1995)

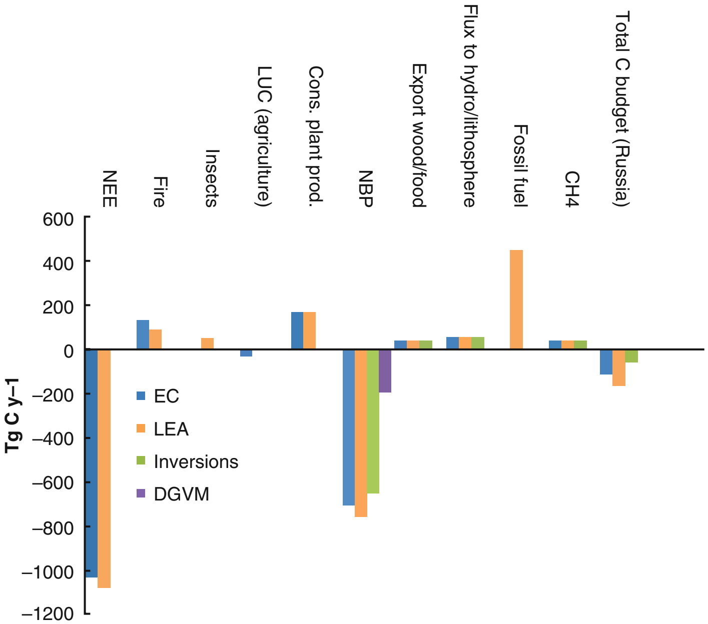

Fig. 4.8 Assessment of carbon budget of Russian 5 biome using three models, LEA (Land Ecosystem Assessment), Inversions and DGVM (Dynamic Global Vegetation Model), and tower experimental eddy covariance method (EC). (Dolman et al. 2012)

with a value of 0.7 Gt C year^{-1} (Dolman et al. 2012) against 1.3 Gt C year^{-1}. In recent years, an increase in the absorptive capacity of larch forests could be traced to climate warming, with an increase in the duration of the growing season, amendments in land use (afforestation or reforestation), and the nutrient fertilising effects of a CO_2 increase (Maximov 2007).

The net CO_2 flux from land to atmosphere in Russia, including Ukraine, Belarus, and Kazakhstan, was evaluated using inventory-based, eddy covariance, and inversion methods (Dolman et al. 2012). Our upper estimate (Dolman et al. 2012) was −0.342 G t C year^{-1} from the eddy covariance method, which is close to the upper bounds of the inventory-based Land Ecosystem Assessment (LEA) and inverse model estimates (Fig. 4.8). Our lower estimate was −1.3 Gt C year^{-1} from the inversion models. The average of the three methods was −0.6 Gt C year^{-1}. The methane emission was estimated separately, with a positive value of 0.041 Gt C year^{-1} derived. These three methods agreed well within their respective error bounds. There was thus good consistency between bottom-up and top-down methods. From the LEA, the forests of Russia had a net atmosphere to land flux of 0.7 Gt year^{-1}. It was remarkable that the three methods produced such close estimates (0.61, 0.66, and 0.55 Gt C year^{-1}) for the NBP, given the inherent uncertainties in all of the approaches.

The lack of recent forest inventories, the limited numbers of eddy covariance sites, and the associated uncertainty with upscaling and under-sampling of concentrations for the inversions were among the prime causes of the uncertainty. The dynamic global vegetation models suggested a much lower uptake of 0.091 Gt C year^{-1}, which we argue that it is caused by a high estimate of heterotrophic respiration compared to the other methods.

4.5 Concluding Remarks

During the short growing season in eastern Siberia, the growth and development of woody plants are provided by high levels of physiological processes (photosynthesis and transpiration) with relatively low R_{dark} and night respiration rates supporting growth and maintenance. The large interannual variability of the photosynthesis and R_{dark} for *L. cajanderi* plants indicates its excellent adaptability to the peculiar cryolithozone climatic conditions.

The seasonal maximum of photosynthetic activity of forest plants is observed in June in dry years and in July in wet years. It was found that in the eastern Siberia permafrost region, under natural conditions the $A_{\max}$ was substantially higher than the $A_{\max}$ of similar vegetation species in warmer regions, including Europe. The key morphophysiological adaptation to these conditions was a high stomatal conductance. The range of diurnal photosynthesis had a single peak, with no midday depression. Seasonal and annual fluctuations were reduced to a single pattern, clearly showing the difference in CO_2 assimilation dynamics over the year, with the most active month being July and the least active being May.

Long-term estimates of V_{cmax} and $J_{\max}$ have shown that in a larch forest in Yakutia, their seasonal character generally followed the phenological phases of needle, cone, and bud development. The variation in these parameters, which was not related to phenology, was caused by the nitrogen dynamics in the needles. The V_{cmax} and $J_{\max}$ values of *L. cajanderi* were within the theoretical ranges and were similar to the average values for the other plant species and ecosystems under similar environmental conditions. Both the initial and modelled relationships between V_{cmax} and $J_{\max}$ as well as their ratio with $A_{\max}$ had a strong correlation, providing a basis for the mutual analysis of the values.

Based on a study of 899 plant species from 100 sites (from the Arctic to the tropics), a new global database of the R_{dark} of plants (GlobResp) was created (Atkin et al. 2015), part of which includes the R_{dark} results for larch, pine, and birch in the taiga ecosystem of eastern Siberia.

With regard to the daily dynamics of the soil carbon emission, the main environmental factor affecting the soil respiration rate in the larch forests of eastern Siberia was the soil temperature, while the humidity of the upper soil horizons was only an additional factor contributing to the temperature sensitivity of soil respiration. A large amplitude in the daily soil respiration was observed in the mid-growing season, with an increase in the soil CO_2 emission during day and night in wet and dry years, respectively. At the beginning and the end of the season, the curve showing the daily pattern of soil respiration was smooth and almost flat.

The maximum soil CO_2 emissions in permafrost soils during the growing season were observed from mid-July to mid-August, when the soil temperature reached a maximum and the soil moisture in upper soil horizons was minimal. At that time, the source of CO_2 was the deeper layers of soil. If the precipitation at that time was insufficient, the influence of the overnight soil moisture increase became stronger, but in years with a large rainfall during July and August, the soil moisture variation was not a factor limiting soil respiration. Early in the season, when the moisture content in the upper soil horizons was still high, the soil temperature played a dominant role. The heavy rains in the cold period of late summer and autumn were not able to affect the general seasonal course of soil respiration because the activity of soil biota at that time was suppressed by low soil temperatures despite the presence of sufficient soil moisture.

In future, the crucial endogenous factors that determine the soil respiration rate are the depth of the humus layer and, accordingly, the carbon content in the soil. In northern ecosystems, every change in the soil carbon stock (increase or decrease) may lead to rapid changes in the carbon balance of the whole ecosystem.

It must be concluded that the expected changes in precipitation and soil temperatures in high latitudes are likely to cause an increase in soil biological activity together with fluctuations in the soil carbon content. Therefore, soil organic matter decomposition rates could be enhanced, accompanied by the intensification of CO_2 emissions from soils. We considered that these processes could lead to drastic changes in the carbon exchange in northern forest ecosystems.

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