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Temperature sensitivity of nitrogen productivity for Scots pine and Norway spruce

**Svetlana Ladanai
&
Göran I. Ågren**

Department of Ecology and Environmental Research
Swedish University of Agricultural Sciences
P.O. Box 7072
SE-750 07 Uppsala
Sweden

tel.: +46 18 673401

fax: +46 18 673430

E-mail: Sveta.Ladanai@eom.slu.se

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Abstract

Environmental conditions control physiological processes in plants and thus their growth. The predicted global warming is expected to accelerate tree growth. However, the growth response is a complex function of several processes with both direct and indirect effects. To analyse this problem we have used the nitrogen productivity, which is an aggregate parameter for tree growth. Data on needle dry matter, production, and nitrogen content in needles of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) from a wide range of climatic conditions were collected and needle nitrogen productivities, defined dry matter production of needles per unit of nitrogen in the needle biomass, were calculated. Our results show that the nitrogen productivity for spruce is insensitive to temperature. However, for pine, temperature affects both the magnitude of nitrogen productivity at low needle biomass and the response to self-shading but the temperature response is small at the high end of needle biomasses. For practical applications it may be sufficient to use a species-specific nitrogen productivity parameter that is independent of temperature. Because temperature affects tree growth also indirectly through soil processes, the effects of temperature change on tree growth and ecosystem carbon storage should mainly be derived from effects on nitrogen availability through changes in nitrogen mineralization. In addition, this paper summarises data on dry matter, production and nitrogen content of needles of conifer along a temperature gradient.

Keywords: climate change, needle biomass, nitrogen productivity, conifers, growth of trees.

Introduction

Forest resources (e.g. Kuusela 1994; Kauppi et al. 1992) and tree growth (e.g. Spiecker et al. 1996; Mund et al. 2002) in Europe have been increasing during the past decades. In part this is a consequence of changes in management but improved growth conditions is another contributor. While the causes for the accelerating growth are still uncertain (e.g. Karjalainen et al. 1999), climate has been suggested as one of them.

Analyses of climate impact on tree increment started already in the middle of the 19th century (Bravais and Martins 1841; Beketov 1867; Pokorny 1869 (cited in Tarasov 1968)) and there is a huge literature dealing with this topic from very different perspectives. Most of this research has been directed towards deriving statistical and empirical relations between tree growth and climatic variables. However, these correlations showed no logical geographical or temporal patterns (Mäkinen 2003). Furthermore, the coming global climatic changes are likely to decrease the usefulness of existing yield tables for stand growth predictions (Chertov et al. 1999). That is, these models reflect our current understanding of growth of trees, but not how trees will respond in the future. Instead explanation must be emphasised (Andersson et al. 2000). Thus, process-based simulation models are developed to overcome the limitations set by empirical models. Nevertheless, when climatic variables have been tested as predictors of growth, the climatic variables correlate with short- and medium-term growth variation, but long-term trends cannot be predicted (Spiecker et al. 1996).

A mechanistic approach requires a strict relation between causes and consequences (Kryazhimskii 2001). Maps created by Churkina and Running (1998) of weighted climatic controls indicate that temperature must be a major measure of climate for use in growth models. However, the growth response is a complex function of several processes and temperature affects many processes of importance for growth, some of which operate directly on the plants and others that operate indirectly through soil processes. These two types of processes are likely to operate at different time scales. Long-term effects of temperature may, therefore, differ considerably from the short-term effects. Relationships between net production and mean annual climatic factors, which have been successful in predicting annual net production for a broad range of ecosystems in different climates (e.g. Lieth 1975), are purely statistical and do not separate the influence of different processes. There are just a few long-term studies of mechanisms of net carbon gain sensitivity to climatic conditions and these are generally focused on net photosynthesis (e.g. Teskey et al. 1994).

An important criterion when choosing a representation of a system is that it can be done with as few qualitatively different processes as possible (Ågren 1984). Hence, a possible approach is to use the strong relationship between growth and nutrients, notably nitrogen, in the plant (Ingestad 1979, 1980, 1981; Ågren 1983a; Wikström 1995) with nutrient supply as the link between plants and soil. Ågren (1983ab, 1985, 1998) formalized the growth response to nutrients in the nutrient productivity concept, which states that the relation between the plant's absolute growth rate and its content of nitrogen is linear. He also proposed that the proportionality factor in this relation (the nitrogen productivity) was conservative with respect to climate, but this

suggestion has until now never been tested against empirical data. However, the practical advantage of such a simple predictor of plant growth is obvious. Furthermore, given that environmental conditions control physiological processes in plants and thus their growth, there is a potential for temperature-driven changes in nitrogen productivity. In view of the concern about climatic change, it is important to test the temperature sensitivity of this parameter.

The primary objective of the present study is to test the temperature sensitivity of nitrogen productivity for different species. A second aim has been to collect biomass data from different climatic conditions.

Materials and methods

Collection of the published data

We have relied on literature data for conifers. Our analyses require information on needle biomass, needle growth, needle nitrogen content and temperature. We have only accepted needle data that have been obtained with direct sampling (trees were felled and needle were separated and weighted) and ignored data that have been derived from allometric equations. Some studies lacked climatic information and in this case we have relied on data from nearby meteorological stations. The result is data from 57 stands of Scots pine (*Pinus sylvestris* L.) and 46 stands of Norway spruce (*Picea abies* [L.] Karst.) see Appendix. Data for other species were not sufficient to allow further analysis.

Nitrogen productivity

The nitrogen productivity expresses quantitatively the limiting effect of nitrogen on growth (Ågren 1983a, 1985, 1988, 1994) through the following basic growth equation

$$\frac{dW}{dt} = P_N (N - c_{N,min}) W \quad (1)$$

where W is the dry weight of foliage, N is the amount of nitrogen in foliage, t time, $c_{N,min}$ a certain minimum concentration of nitrogen in the foliage that is not active in growth and thus discounted, and P_N is the nitrogen productivity, i.e., the growth rate is proportional to the amount of nitrogen in the plant, with the nitrogen productivity as a proportionality factor. A plant is thus characterised by two parameters, P_N and $c_{N,min}$, which under constant environmental conditions are constant. The parameter $c_{N,min}$ is for most species small and can be neglected. On the other hand, because canopy size and architecture influences light interception, self-shading becomes important for larger canopies and the nitrogen productivity go down with the size of the canopy. Ågren (1983a) showed that this could be expressed as

$$P_N = a - bW \quad (2)$$

Where a and b are species-specific parameters. Using this model we will test the temperature sensitivity of nitrogen productivity by analysing the temperature sensitivity of the parameters a and b .

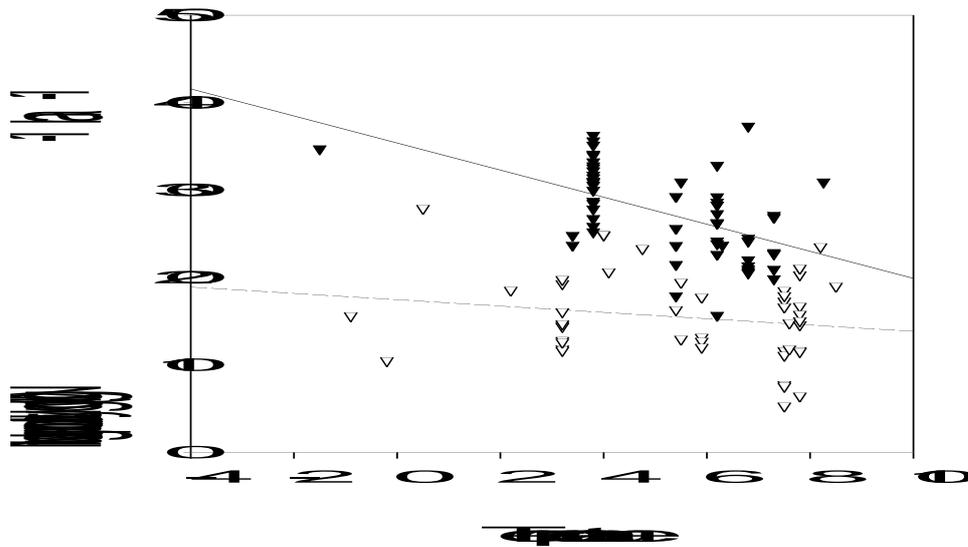
Calculations

The nitrogen productivity for a given stand, defined as the amount of biomass produced per amount of nitrogen in the plant per unit of time (Ågren 1983a), was calculated as (current needle biomass)/(total nitrogen in needle biomass). We used mean annual air temperature (T) as climatic variable because this is the only temperature variable generally available.

Results

The calculated nitrogen productivities for two conifer species are given in the Appendix, Table 2 and Table 3. There is no suggestion for a relationship between temperature and nitrogen productivity for spruce in Fig. 1 ($r^2 = 0.03$).

Fig.1 Nitrogen productivity as a function of temperature. Regressions: solid line and filled triangles (*P. sylvestris*) $P_N = 35.38 - 1.55T$, $r^2 = 0.27$; broken line and open triangles (*P. abies*) $P_N = 17.44 - 0.36T$, $r^2 = 0.03$



On the other hand, there is a weak trend of decreasing P_N with T for pine but there is a lot of scatter around the regression lines and much of the trend depends also on the single point at $T = -1.5$ °C. The scatter is a result of differences in canopy size for a given temperature. To remove the influence of canopy size, we have used Eq. (2). Because of the limited size of the data sets we have tested the effect of temperature by splitting each of the two data into two almost equally large parts by looking at $T < 5$ °C and $T > 5$ °C. Figures 2 and 3 display the relation $P_N - W$ for pine and spruce stands, respectively.

Fig.2 The relation between nitrogen productivity and needle biomass for *P. sylvestris* stands. Regressions: solid line and filled circles ($T < 5$) $P_N = 37.82 - 1.52W$, $r^2 = 0.38$; solid line and open circles ($T > 5$) $P_N = 31.70 - 1.16W$, $r^2 = 0.26$; broken line and all circles (all T) $P_N = 35.8 - 1.57W$; $r^2 = 0.33$

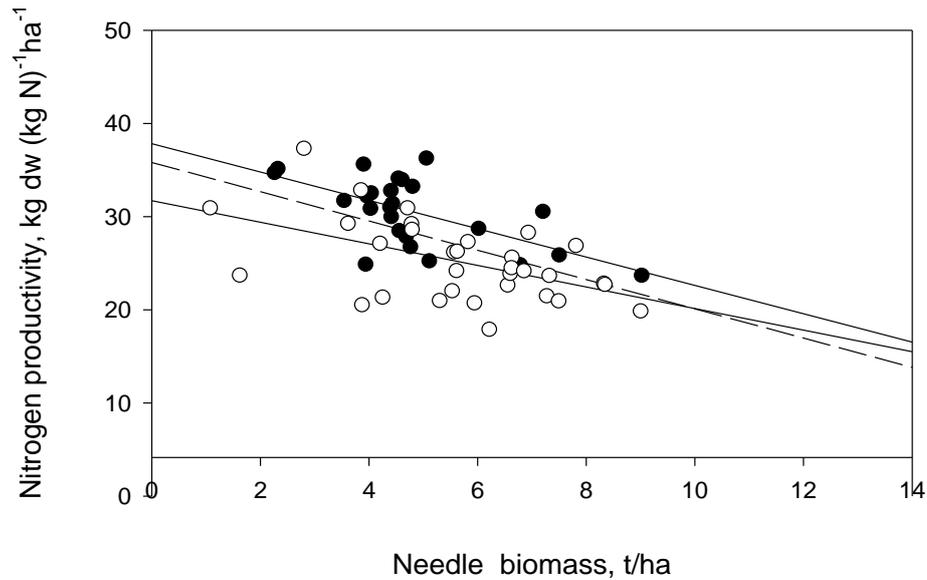
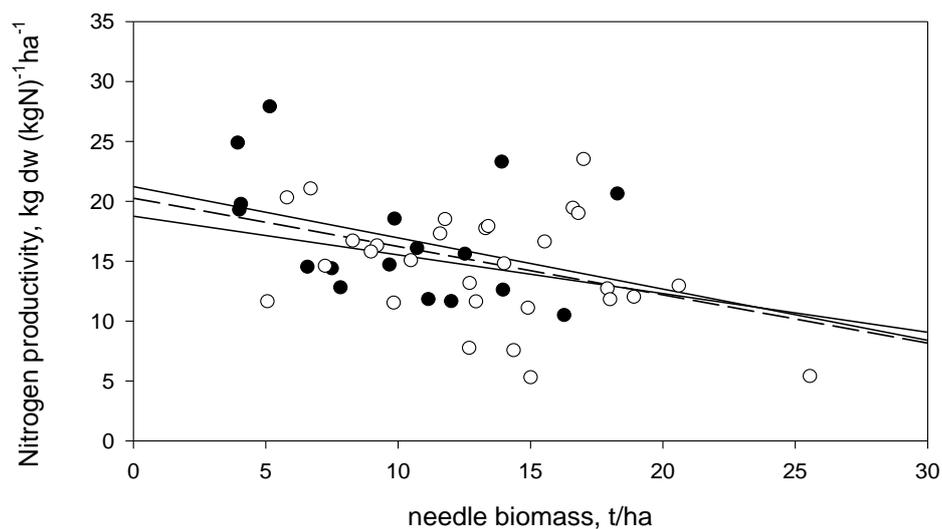


Fig.3 The relation between nitrogen productivity and needle biomass for *P. abies*. Regressions: solid line and filled circles ($T < 5$) $P_N = 21.22 - 0.43W$, $r^2 = 0.14$; solid line and open circles ($T > 5$) $P_N = 17.59 - 0.23W$, $r^2 = 0.11$; broken line and all circles (all T) $P_N = 19.80 - 0.37W$; $r^2 = 0.16$



The negative relationship between nitrogen productivity and needle biomass is clear. An analysis of variance (Table 1) shows that the two temperature groups are significantly different only for Scots pine and that this difference can be attributed to both the intercepts and the slopes of the lines describing the relation between nitrogen productivity and needle biomass.

Table 1 Analysis of variance to compare a single regression line with separate regressions lines for $T < 5\text{ }^{\circ}\text{C}$ and $T > 5\text{ }^{\circ}\text{C}$

Source of variation	Regressions for <i>P. abies</i>	Regressions for <i>P. sylvestris</i>
Single line versus two different lines	All data: $P_N = 19.80 - 0.37 W$ $T < 5\text{ }^{\circ}\text{C}$: $P_N = 21.22 - 0.43 W$ $T > 5\text{ }^{\circ}\text{C}$: $P_N = 17.59 - 0.23 W$ F = 0.98	All data: $P_N = 35.8 - 1.57 W$ $T < 5\text{ }^{\circ}\text{C}$: $P_N = 37.8 - 1.52 W$ $T > 5\text{ }^{\circ}\text{C}$: $P_N = 31.7 - 1.16 W$ F = 10.4***
Single line versus two lines with equal slopes	All data: $P_N = 19.80 - 0.37 W$ $T < 5\text{ }^{\circ}\text{C}$: $P_N = 20.08 - 0.31 W$ $T > 5\text{ }^{\circ}\text{C}$: $P_N = 18.55 - 0.31 W$ F = 1.83	All data: $P_N = 35.8 - 1.57 W$ $T < 5\text{ }^{\circ}\text{C}$: $P_N = 36.7 - 1.27 W$ $T > 5\text{ }^{\circ}\text{C}$: $P_N = 32.4 - 1.27 W$ F = 15.2***
Single line versus two lines with equal intercept	All data: $P_N = 19.80 - 0.37 W$ $T < 5\text{ }^{\circ}\text{C}$: $P_N = 19.43 - 0.27 W$ $T > 5\text{ }^{\circ}\text{C}$: $P_N = 19.43 - 0.37 W$ F = 1.24	All data: $P_N = 35.8 - 1.57 W$ $T < 5\text{ }^{\circ}\text{C}$: $P_N = 34.2 - 0.84 W$ $T > 5\text{ }^{\circ}\text{C}$: $P_N = 34.2 - 1.56 W$ F = 12.5***

Discussion

Comments on the collected database

In spite of already existing large databases on forest biomass and production (Cannell 1982; Bazilevich 1993; Usoltsev 2001) there is rarely enough information available in these databases to allow estimations of parameters (Young and Beven 1994). Much of published data can be unsuitable because they correspond to specific forestry problem and vital pieces of information can be missing for certain further analyses. This study is the first one synthesising stand level needle biomass (total and current) and foliage nitrogen of Scots pine and Norway spruce for most of their temperature range. This database covers most of the natural geographical distribution of these species, spanning the entire width of Eurasia, although a wider range of climatic conditions would have been desirable. The estimation of needle biomasses is a problem due to lack of accurate methods. The mean tree method, which is the most common way to estimate biomass components, may introduce some uncertainty to stand-level needle biomass estimates (Zavitkovski et al. 1974 cited in Kuuluvainen 1990).

Sensitivity of nitrogen productivity

We found that temperature has no effect on the nitrogen productivity for Norway spruce. On the other hand, the nitrogen productivity for Scots pine is sensitive to temperature and the sensitivity affects both the magnitude at low needle biomass and the response to self-shading. What is surprising is that the nitrogen productivity seems

to decrease with temperature except at the high end of the needle biomasses. We see two possible explanations.

First of all, it should be observed that nitrogen productivity represents the net carbon gain of a canopy and is therefore a balance between photosynthesis and respiration (Ågren 1996). Calculations with a model parameterised for *Pinus taeda* by Lou et al. (2001) indicate that under certain conditions net assimilation might go down with temperature and that, in general, the temperature response of net assimilation might not be that large anyhow. The observed decrease in temperature sensitivity of nitrogen productivity with increasing needle biomass and thus increasing canopy size, when shelf shading becomes important, support the suggestion that self-shading could limit the response of carbon assimilation to temperature (Ziska 1997). Ellsworth (2000), who found that warming affected the net carbon assimilation only during sunny days, provides a further indication. In natural environments changes in temperature are often accompanied by changes in light intensity. Our observation suggests that the pronounced impact of light availability on net assimilation exceeded the impact of temperature. This is in consistent with Hennessey's observation (1991) that non-stomatal processes were a significant component of the rhythm in carbon assimilation, which did not occur spontaneously but must be induced and co-ordinated by an external stimulus. However, while cycles of light during growth entrained circadian rhythm in assimilation, a temperature cycle under constant light did not induce this rhythm.

Secondly, we are using temperature as a substitute for all climatic variables. However, increasing temperature may also be accompanied by water stress, which could lead to decreasing production with increasing temperature as a result of increased evaporative demands. Climatic changes, where current patterns of temperature and precipitation are altered, may therefore require a revision of our analyses.

It should be noted that the predicted higher sensitivity at low needle biomass depends on stands with either very young or very old trees (Appendix, Table 2). The observed decrease of sensitivity towards the high end of the needle biomasses could be a shift from a juvenile to an adult phase. That is, the net production of adult trees is less sensitive to changes in temperature than that of juvenile trees. Another observation pointing in this direction is provided by Ermolenko (1981) who found that the dry weight production of a unit of needles became independent of temperature at the age of a tree coinciding with the life span of needles for the species. Similarly, the higher sensitivity at the low needle biomass for the very old trees, might be attributable to ageing effects, when decline in needle mass is usual. However, these results must be taken with caution because they are based on only a small number of stands. Also, the main part of the ecophysiological knowledge is derived from measurements on seedlings during the juvenile phase and less is known about the response of mature trees to climate change (Källomäki 2000).

Finally, although the observed effect of temperature on nitrogen productivity for Scots pine seems to indicate a decrease with increasing temperature, there is a lot of scatter in the data, and over large ranges of needle biomasses the difference between high and low temperature is small. Moreover, much of the difference at low needle biomasses depends on a few data points. Therefore, for practical application it may be sufficient to use a nitrogen productivity that is independent of temperature. These

results are obtained for two conifer species, but as these two species have rather different physiologies (e.g. sensitivity to shade) it is possible that other conifers also should show a similar insensitivity in nitrogen productivity.

Temperature is also influencing tree growth indirectly by its effect on decomposition of soil organic matter and mineralization of soil nutrients (Eberhardt et al. 2000). Our result suggests that this might be the mechanism through which long-term temperature effects operate. Unfortunately, there are no clear mechanisms explaining the response of nutrient uptake to soil temperature. Ingestad (1979) showed that the efficiency of the nutrient solution to supply nutrients is independent of temperature of the nutrient solution. Not surprisingly, there is a lot of contradiction in empirically derived relationships between net assimilation and soil temperature (e.g. Landhauser 2001; Man and Lieffers 1997; Day et al. 1990; DeLucia 1986; Grossnickle 2000). However, the major issue is probably how to obtain a correct estimation of the rate of nitrogen mineralization and thus the supply of nitrogen to the trees.

Conclusion

We have analysed the temperature response of the nitrogen productivity. Our main result is that the nitrogen productivity of conifers is not sensitive to temperature. This result supports the hypothesis that effects of temperature on the growth of trees are mediated by nutrient availability (Eberhardt et al. 2000). Indirect effects can be more important than direct one and efforts should therefore be focused on the processes occurring in the soil when estimating future growth stand.

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Appendix

Table 2 Mean annual temperature T ($^{\circ}\text{C}$), total and current needle biomasses (t/ha), amount of nitrogen in needle biomass (kg/ha), nitrogen productivity (P_N) in *Pinus sylvestris* stands of different ages (years)

Location	Age	T	Total needle	Current needle	Amount of N in needle	P_N	Literature citation
Russia, W.Siberia, Tomsk	130	- 1.5	2.26	0.85	24.48	34.72	Pyavchenko,1967
Russia, Yaroslavl	57	3.4	6.78	2.39	96.28	24.82	Utkin, 1988
Russia, Yaroslavl	41	3.4	9.02	3.42	144.32	23.70	Utkin, 1988
Finland, South	28	3.8	2.32	0.90	25.60	35.16	Mälkönen, 1974
Finland, South	45	3.8	3.54	1.38	43.50	31.72	Mälkönen, 1974
Finland, South	48	3.8	3.90	1.75	49.11	35.63	Mälkönen, 1991
Finland, South	48	3.8	3.96	1.72	55.27	32.21	Mälkönen, 1991
Finland, South	47	3.8	4.03	1.57	50.73	30.87	Mälkönen, 1974
Finland, South	47	3.8	4.04	1.66	50.87	32.53	Mälkönen, 1974
Finland, South	48	3.8	4.39	1.72	55.27	31.03	Mälkönen, 1991
Finland, South	48	3.8	4.40	1.82	55.46	32.78	Mälkönen, 1991
Finland, South	47	3.8	4.41	1.67	55.55	29.99	Mälkönen, 1974
Finland, South	47	3.8	4.43	1.67	55.55	31.41	Mälkönen, 1974
Finland, South	48	3.8	4.54	1.72	55.27	34.13	Mälkönen, 1991
Finland, South	47	3.8	4.55	1.64	57.37	28.50	Mälkönen, 1974
Finland, South	48	3.8	4.60	1.97	58.02	33.97	Mälkönen, 1991
Finland, South	68	3.8	4.68	1.64	58.99	27.85	Mälkönen, 1974
Finland, South	68	3.8	4.76	1.61	59.99	26.75	Mälkönen, 1974
Russia, Moskva	17	3.8	4.80	2.24	67.40	33.24	Sudnitsyna, 1967
Finland, South	48	3.8	5.05	2.31	63.68	36.28	Mälkönen, 1991
Finland, South	68	3.8	5.11	1.62	64.35	25.24	Mälkönen, 1974
Finland, South	68	3.8	6.02	2.18	75.80	28.73	Mälkönen, 1974
Russia, Moskva	17	3.8	7.20	2.74	89.70	30.55	Sudnitsyna, 1967
Russia, Moskva	17	3.8	7.50	2.61	100.90	25.87	Sudnitsyna, 1967
Sweden, Jädraås	120-150	4.0	3.94	1.26	50.70	24.89	Bringmark, 1977
Sweden, Lisselbo E40	25	5.4	3.61	1.19	40.70	29.26	Albrektson, 1977
Sweden, Lisselbo E40	25	5.4	6.21	2.42	134.90	17.90	Albrektson, 1977
Sweden, Lisselbo E40	25	5.4	6.63	2.53	98.80	25.62	Albrektson, 1977
Sweden, Lisselbo E40	25	5.4	7.27	2.50	116.10	21.49	Albrektson, 1977
Sweden, Lisselbo E40	25	5.4	7.31	2.30	97.10	23.67	Albrektson, 1977
Byelorussia, Smolevichi	6	5.5	1.08	0.43	13.90	30.94	Yurkevich, 1974
Byelorussia, Vasilevichi	53	6.2	3.85	1.91	58.14	32.85	Smoljak, 1978
Byelorussia, Vasilevichi	44	6.2	4.78	2.11	72.18	29.23	Smoljak, 1978
Byelorussia, Vasilevichi	43	6.2	4.79	2.07	72.33	28.62	Smoljak, 1978
Byelorussia, Vasilevichi	42	6.2	5.56	2.20	83.96	26.20	Smoljak, 1978
Byelorussia, Vasilevichi	27	6.2	5.61	2.05	84.71	24.20	Smoljak, 1978
Byelorussia, Vasilevichi	56	6.2	5.62	2.23	84.86	26.28	Smoljak, 1978
Byelorussia, Vasilevichi	36	6.2	5.82	2.40	87.88	27.31	Smoljak, 1978
Byelorussia, Ozarichi	54	6.2	6.55	2.24	98.91	22.65	Smoljak, 1978
Byelorussia, Ozarichi	51	6.2	6.60	2.38	99.66	23.88	Smoljak, 1978
Byelorussia, Ozarichi	51	6.2	6.93	2.96	104.63	28.29	Smoljak, 1978
Byelorussia, Osipovichi	8	6.3	1.62	0.50	21.06	23.71	Yurkevich, 1974
Ukraina, Roven´	90	6.8	2.80	1.90	50.90	37.33	Smoljaninov, 1969
Byelorussia, Ivacevichi	43	6.8	3.87	1.20	58.44	20.53	Smoljak, 1978
Byelorussia, Ivacevichi	60	6.8	4.25	1.37	64.18	21.35	Smoljak, 1978
Byelorussia, Ivacevichi	47	6.8	5.30	1.68	80.03	20.99	Smoljak, 1978
Byelorussia, Ivacevichi	64	6.8	5.53	1.84	83.50	22.04	Smoljak, 1978
Byelorussia, Ivacevichi	43	6.8	5.94	1.86	89.69	20.74	Smoljak, 1978
Byelorussia, Ivacevichi	44	6.8	6.62	2.45	99.96	24.51	Smoljak, 1978
Byelorussia, Ivacevichi	45	6.8	6.85	2.50	103.44	24.17	Smoljak, 1978
Byelorussia, Kobrichi	47	7.3	4.20	1.72	63.42	27.13	Smoljak, 1978
Byelorussia, Kobrichi	49	7.3	7.49	2.37	113.10	20.96	Smoljak, 1978
Byelorussia, Kobrichi	50	7.3	7.81	3.17	117.93	26.88	Smoljak, 1978
Byelorussia, Kobrichi	50	7.3	8.32	2.87	125.63	22.84	Smoljak, 1978
Byelorussia, Kobrichi	49	7.3	8.34	2.86	125.93	22.71	Smoljak, 1978
Byelorussia, Kobrichi	40	7.3	9.00	2.70	135.90	19.87	Smoljak, 1978
Scotland, Morayshire	64	8.2	4.71	1.56	50.44	30.93	Wright et al., 1958

Table 3 Mean annual temperature T ($^{\circ}\text{C}$), total and current needle biomasses (t/ha), amount of nitrogen in needle biomass (kg/ha), nitrogen productivity (P_N) in *Picea abies* stands of different ages (years)

Location	Age	T	Total needle	Current needle	Amount of N in needle	P_N	Literature citation
Sweden, Stråsan, E26A	10-15	3.2	4.06	0.87	44	19.77	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	4.00	0.83	43	19.30	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	7.49	1.57	109	14.40	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	10.71	2.51	156	16.09	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	13.96	3.43	272	12.61	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	7.82	1.96	153	12.81	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	11.14	2.78	235	11.83	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	12.00	2.95	253	11.66	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	9.67	2.78	189	14.71	Tamm, 1974
Sweden, Stråsan, E26A	10-15	3.2	6.57	1.86	128	14.53	Tamm, 1974
UK, Thetford Chase	11	3.2	5.80	2.54	125	20.32	Ovington, 1957
UK, Thetford Chase	14	7.8	6.69	3.16	150	21.07	Ovington, 1957
UK, Thetford Chase	17	7.8	8.97	3.95	250	15.80	Ovington, 1957
UK, Thetford Chase	20	7.8	10.48	4.37	290	15.07	Ovington, 1957
UK, Thetford Chase	23	7.8	5.06	2.62	225	11.64	Ovington, 1957
Sweden, Hökaberget, E1	23	7.5	13.4	2.60	145	27.85	Mälkönen, 1974
Sweden, Hökaberget, E1	23	7.5	11.77	2.35	127	26.75	Mälkönen, 1974
Sweden, Hökaberget, E1	23	7.5	11.58	2.25	130	33.24	Sudnitsyna, 1967
Sweden, Hökaberget, E1	23	7.5	15.53	2.91	175	36.28	Mälkönen, 1991
Sweden, Hökaberget, E1	23	7.5	12.94	2.56	220	25.24	Mälkönen, 1974
Sweden, Hökaberget, E1	23	7.5	14.9	2.81	253	28.73	Mälkönen, 1974
Sweden, Hökaberget, E1	23	7.5	12.68	2.45	316	30.55	Sudnitsyna, 1967
Sweden, Hökaberget, E1	23	7.5	14.36	2.71	358	25.87	Sudnitsyna, 1967
UK, Thetford Chase	31	7.8	8.28	4.01	240	16.70	Ovington, 1957
Sweden, Skogaby	31	7.6	14.00	2.50	169	14.81	Persson, 2000
Germany, Solling	34	5.9	18.9	2.98	248	12.02	Cole, 1981
UK, Thetford Chase	35	7.8	9.83	3.46	300	11.53	Ovington, 1957
Italy, Monte di Mezzo	37	8.5	16.8	2.80	147	19.01	Persson, 2000
Sweden, Skåne	55	7.6	18.00	2.60	220	11.82	Nihlgård, 1972
UK, Thetford Chase	55	7.8	7.24	3.58	245	14.61	Ovington, 1957
Czechoslovakia	70	5.5	20.6	3.25	251	12.95	Klimo, 1980
Denmark, Klosterhede	76	7.5	15.00	1.00	188	5.31	Persson, 2000
Russia, Valday	80	5.0	25.55	2.85	526	5.41	Grishina, 1974
Germany, Hoeglwald	85	8.2	17.00	5.60	238	23.53	Recognition
Russia, north Dvina	50	-0.9	12.52	2.19	140	15.62	Bazilevich, 1983
Russia, Onezhskoe see	50	2.2	9.86	2.20	119	18.55	Bazilevich, 1983
Russia, Valday hejgt	50	4.75	13.91	2.95	127	23.31	Bazilevich, 1983
Russia, Chibiny, 500 m	50	0.5	5.15	1.38	49	27.91	Bazilevich, 1983
Russia, Gulf Finsky	50	4.1	18.28	3.39	164	20.65	Bazilevich, 1983
Germany, Solling	87	5.9	17.9	2.90	228	12.72	Cole, 1981
France, Aubure	92	5.4	9.20	2.10	129	16.32	Persson, 2000
Germany, Solling	115	5.9	12.7	2.12	161	13.17	Cole, 1981
Sweden Jädraås	120-150	4.0	3.94	1.26	51	24.89	Bringmark, 1977
Germany, Waldstein	142	5.5	16.60	4.70	242	19.45	Persson, 2000
Czech Republic, Nacetin	568	5.9	13.3	3.60	203	17.75	Persson, 2000
Russia, Arhangel province	200	-0.2	16.27	2.20	210	10.49	Marchenko, 1962