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Needle, crown, stem, and root phytomass of *Pinus sylvestris* stands in Russia

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Abstract

With growing concern about predicted global warming, increasing attention is being paid to the phytomass (living plant mass) components of forest stands and their role in the carbon cycle. The ability to predict phytomass components from commonly available inventory data would facilitate our understanding of the latter. We focus on Scots pine (*Pinus sylvestris* L.) stands in Russia, with the objective of predicting stand phytomass (Mg ha^{-1}) for the four major stand components: needles, crown, stems, and roots. The study area includes regions in Russia where Scots pine is a stand-forming species: from European Russia (33°E) to Yakutia (130°E) in eastern Siberia. To ensure that results will be widely applicable, only variables consistently measured in forest inventories were considered as possible predictors: stand age, site quality class, and stocking (stand stem volume with bark, $\text{m}^3 \text{ha}^{-1}$). Stand phytomass data were obtained from numerous regional and local phytomass studies, and supplemented with additional unpublished data. This is the first comprehensive study synthesizing stand level phytomass relations for *P. sylvestris* for most of its range in Russia. The combined results from over 18 regional and local phytomass studies provide a level of generality that is not possible with individual local studies. In addition to estimating stand phytomass components across a wide range of conditions, these phytomass models can also be used to verify carbon allocation rules in process-based models.

Keywords: Biomass; Carbon allocation; Carbon cycle; Scots pine; Stand modeling

1. Introduction

Phytomass storage (live plant mass, above and below ground) is one of the major components determining the size of the terrestrial carbon pool. Russia is dominated by extensive reaches of taiga (boreal

forest) as well as temperate forest; it is a major center of phytomass storage. Kolchugina and Vinson (1993a) estimate that Russia contains nearly one-sixth of global phytomass. With growing concern about the role of the carbon cycle in predicted global warming (Houghton et al., 1990), increasing attention will be paid to the phytomass components of forest stands, and to their proper utilization.

We concentrate on one of the major components of taiga, Scots pine (*Pinus sylvestris* L.), which has a range spanning the entire width of Eurasia. Scots

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pine has a high requirement for light, and is therefore referred to as 'light-needed' (light-demanding) in the Russian literature, as is *Larix*. Because of its high level of tolerance of drought and frost, and a wide range of soil nutrient and soil moisture conditions, Scots pine is found in ecologically diverse locations throughout its range (Vorobyov, 1986; Safronova, 1993). For example, Scots pine is the dominant species in the sea of bogs in the taiga in western Siberia (Vorobyov, 1985) and is also dominant on sandy soils in central and eastern Siberia. Thus, it is found on the two soil moisture extremes, both of which have low soil nutrition. It cannot tolerate permafrost that does not melt to a depth of at least 2 m every growing season (Pobedinsky, 1965). Scots pine is not limited to these two moisture extremes, for it is a zonal species in taiga, found at various degrees of dominance in all taiga subzones (Walter, 1979). Its dominance is greatest in the warmer southern subzones, especially subtaiga (Smagin et al., 1980). It can even survive in isolated forest islands surrounded by steppe conditions too dry for other forest species in Kazakhstan (Usoltsev, 1985). Pravdin (1964) identified five distinct subspecies or geographic races of *P. sylvestris* in the former Soviet Union, an indication that genetic variability is high.

Impetus from the International Biological Program in the late 1960s produced a number of detailed phytomass studies in Russia, with strong emphasis on individual tree relations (Utkin, 1975). At the other extreme, several recent studies have focused on determining phytomass by region and biome for the former USSR (Kolchugina and Vinson, 1993a; Kolchugina and Vinson, 1993b), or by biome division for Siberia (Monserud et al., 1995). These large-scale studies are directed at questions of global carbon storage and changes from the past (mid-Holocene) to the present. Our emphasis is intermediate, at the stand level.

A large number of models describe the different components (fractions) of stand phytomass in Russia. Working with Scots pine stands in the broad forest-steppe zone around Krasnoyarsk, Semechkina (1978) found that stem phytomass could be predicted best by a function of stand basal area, branch phytomass by a function of average stand diameter, and needle phytomass by a function of stand age. Gorbatenko

(1970) studied biological productivity of Scots pine forests along the Yenisey River and found that stand basal area and stand volume (stocking) were the best predictors of the phytomass of stems, roots, crowns, and needles. Kuzikov (1979) studied fir (*Abies siberica*) forests in the plains and mountains of Siberia. For each region, he found a number of linear and non-linear models that predicted phytomass as a function of stand age, height, and basal area. Pozdnyakov et al. (1969) studied the productivity of central Siberian forests, and found that leaf area index (LAI) per unit of stand phytomass was 4.5–5.1 m² kg⁻¹ for *P. sylvestris* stands.

A number of studies predict relative phytomass, the ratio P/V , where P is the phytomass of a given stand component, and V is the stem volume stocking (Pozdnyakov et al., 1969; Protopopov and Zubina, 1977). Onuchin and Borisov (1984) used the same approach to estimate phytomass components in Scots pine stands covering a wide range in productivity and stand conditions across Russia. Various combinations of age, site quality class, and volume stocking (V) were the predictors. Because V was used on both sides of the equation, fit statistics were artificially inflated and therefore unreliable. Very high variance inflation factors (Draper and Smith, 1981) are symptomatic of the multicollinearity problem induced by using a function of a variable to predict itself. Usoltsev (1988) studied the phytomass structure of Scots pine forests in southwestern Siberia and northern Kazakhstan based on this ratio approach. Combinations of stand age, number of trees per hectare, and site quality class were predictors; V was not.

Our objective was to predict stand phytomass (Mg ha⁻¹) for the four major stand components: needles, crown, stems, and roots. We confined our interest to regions in Russia where Scots pine is a stand-forming species: from European Russia (33°E) to Yakutia (130°E) in eastern Siberia (Table 1). We only used forest inventory variables consistently available in Russia: stand age, site quality class (Orlov, 1929), and stocking (stand stem volume with bark, m³ ha⁻¹). Of course, many more stand characteristics such as basal area per hectare are measured in a typical inventory, but these three stand characteristics were the only parameters consistently listed in all phytomass publications.

2. Methods

Because of the difficulty of conducting stand phytomass studies across most of Russia, we relied heavily on the literature for our data (Kulagina, 1968; Pozdnyakov et al., 1969; Gorbatenko, 1970; Ivanchikov, 1971; Kamenetskaya, 1971; Gorbatenko, 1975; Gabeev, 1976; Mitrofanov, 1977; Semechkina, 1978; Utkin and Ermolova, 1982; Utkin et al., 1982a; Utkin et al., 1982b; Utkin et al., 1982c; Mitrofanov, 1983; Atkin, 1984; Onuchin and Borisov, 1984; Pleshikov and Batin, 1984; Usoltsev, 1985; Kar-

manova et al., 1987; Usoltsev, 1988). These studies are either local or regional in nature (Table 1). We selected only stands of at least 80% Scots pine by volume. We desired a wide range in age, stocking, site quality, and geographic location. Generally, these were studies of healthy stands in the absence of serious damage by insects, disease, or pollution. We supplemented phytomass data from 140 stands described in the literature with 12 additional stands measured by Onuchin. This resulted in 152 stands with needle and crown phytomass determined. Stem phytomass was determined in 80 of these stands and

Table 1

Plot locations, number of plots per location, vegetation zone (Isachenko et al., 1988), climatological characteristics, and literature citations for phytomass plots. "Onuchin" refers to unpublished new phytomass plots added to this study. The Ural Mountains at 60°E separate European Russia from Siberia

Location	No. of plots	Vegetation zone	Annual precipitation (mm)	Mean temperature (°C)			Lat. (°N)	Long. (°E)	Literature citation
				Annual	January	July			
Turuhansk	5	Northern taiga	671	-7.6	-28.4	15.4	65	89	Pozdnyakov et al., 1969
South Karelia	10	Middle taiga	500	2.4	-11.0	16.0	62	33	Ivanchikov, 1971
Komsomolsky	1	Middle taiga	540	-0.8	-19.0	17.0	62	68	Mitrofanov, 1977
Khanty-Mansysk	1	Middle taiga	569	-1.0	-20.0	17.0	62	69	Mitrofanov, 1977
Surgut	1	Middle taiga	676	-2.7	-22.0	18.0	62	74	Mitrofanov, 1977
Pokamennaya Tunguska	8	Middle taiga	671	-4.7	-25.3	16.5	62	90	Pozdnyakov et al., 1969; Mitrofanov, 1983
Nazimovo	5	Middle taiga	667	-3.2	-23.0	18.1	60	90	Pleshikov and Batin, 1984
Baikit	1	Middle taiga	518	-7.0	-31.5	16.5	62	96	Mitrofanov, 1977
Chunskaya Strelka	2	Middle taiga	475	-8.0	-32.5	15.7	62	103	Mitrofanov, 1977
Bratsk	3	Southern taiga	406	-2.3	-23.6	18.2	56	102	Kulagina, 1968
Sunatar	1	Middle taiga	308	-7.8	-34.2	17.7	62	118	Mitrofanov, 1977
Yakutsk	4	Middle taiga	247	-10.2	-43.2	18.8	62	129	Mitrofanov, 1977
Yaroslavl	4	Subtaiga	600	3.3	-10.0	17.5	57	39	Kamenetskaya, 1971
Tomsk	6	Subtaiga	637	-0.6	-19.2	18.1	57	85	Utkin et al., 1982c; Gabeev, 1976
Bolshaya Murta	7	Southern taiga	465	-1.4	-21.0	18.0	58	91	Semechkina, 1978; Onuchin
Suhobuzimo	7	Subtaiga	444	-1.8	-21.8	17.6	57	93	Pozdnyakov et al., 1969; Semechkina, 1978; Onuchin
Minusinsk	7	Forest-steppe	362	-0.1	-20.3	19.7	53	91	Pozdnyakov et al., 1969
Kyzyl	8	Steppe	253	-4.9	-33.9	19.9	51	94	Pozdnyakov et al., 1969
Naryn-Gorhon	5	Subtaiga	453	-3.7	-26.1	16.3	51	105	Onuchin
Ulyanovsk	4	Forest-steppe	500	3.0	-13.0	20.0	54	48	Utkin and Ermolova, 1982
Kuibyshev	4	Forest-steppe	460	3.4	-15.0	21.0	54	52	Utkin et al., 1982a
Novosibirsk	16	Forest-steppe	514	-0.1	-19.4	18.7	55	82	Gabeev, 1976
Irbeiskoye	5	Forest-steppe	484	-1.3	-21.1	18.3	55	95	Semechkina, 1978
Tayejny	4	Subtaiga	293	-2.8	-25.4	17.7	51	105	Onuchin
Podmoskovye	6	Subtaiga	600	3.4	-10.0	18.0	55	38	Karmanova et al., 1987
Vladimir	5	Subtaiga	600	3.4	-10.0	18.0	56	41	Utkin et al., 1982b
Ust-Charysh	2	Forest-steppe	527	1.2	-17.5	18.9	53	82	Gabeev, 1976
North Kazakhstan	15	Forest-steppe	340	1.1	-16.8	18.3	53	68	Atkin, 1984; Usoltsev, 1985
South Kazakhstan	5	Steppe	313	2.5	-15.2	20.6	49	73	Usoltsev, 1985

root phytomass was determined in 61. Unfortunately, all four phytomass components were measured on only 24 of the 152 stands.

Table 1 reveals that the 152 stands represent a broad spectrum in climatic conditions and geographic locations, from moderate climates in European Russia to extreme continental climates (very cold and dry) in Yakutia (eastern Siberia) and in mountain basins in Tuva (southern Siberia). Precipitation ranges from 250–350 mm in eastern Siberia and Kazakhstan to 600 mm in European Russia to nearly 700 mm in central Siberia. All major vegetation zones containing Scots pine are represented, from middle taiga and southern taiga to the warmer subtaiga and forest–steppe, and even forest islands surrounded by steppe in Kazakhstan. Scots pine stands penetrating into northern taiga along the Yenisey River Valley are also represented (Pozdnyakov et al., 1969).

Although the material on stand phytomass was collected by different authors at different times and locations, examination of their reported procedures revealed a nearly uniform methodology. The most detailed methods can be found in Pozdnyakov et al. (1969), Smirnov (1971), Semechkina (1978), and Onuchin (1985). A description of the field procedure used by Onuchin (1985) follows; this procedure is similar to that used in most of the existing phytomass studies.

All trees on the plot were enumerated by 2- or 4-cm diameter classes. Plot size was not less than 0.25 ha, with at least 150–200 trees per plot in the main canopy. In mature stands, a minimum of 10–15 sample trees were selected for felling; these trees covered the observed range in diameter. If the stand was extremely young and uniform then the number of sample trees was reduced to not less than six. These sample trees were felled and component parts were separated and weighed. Needle phytomass included only green needles. Crown phytomass included needles and all live branches, but not the main bole or dead branches (weighed separately). Stem phytomass was the main bole of the tree; root biomass was the below-ground woody phytomass. To eliminate seasonal variation, all measurements were made in August and September.

To estimate needle phytomass, sample branches were taken equally from each third of the crown of

the tree. If canopy phytomass was less than 5 kg, all branches were sampled; between 5 and 10 kg, half of the branches were sampled; over 10 kg, 20% of all branches were sampled. Needles were removed and weighed. The ratio of needle phytomass to branch phytomass provided an estimator of total needle phytomass.

Stem phytomass was determined by the product of wood density and stem volume. First, the volume of all sample trees was measured in 2 m sections for the length of the main bole. Volume inside bark and volume outside bark were determined for each section. Next, all sections from each of three to six sample trees were weighed; the ratio of mass to volume yielded density (kg m^{-3}). Bark was peeled from every other section on each of the weighed trees; the bark was weighed separately and bark density determined. Based on the density and the volume of bark and wood, the total phytomass of bark and wood was estimated for each sample tree.

Root phytomass was determined by excavating and weighing the root system from two to three sample trees in the medium diameter classes. Most studies used the techniques of Remezov et al. (1963). All roots were excavated, washed, and weighed from an area at least 3 m on a side, centered on the subject tree. No lower size limit was imposed, and all roots that were encountered were measured. Although some investigators divided roots into size classes (Semechkina, 1978; Atkin, 1984), we only used total root phytomass.

Stem and crown subsamples were removed from each sample tree and oven-dried (105°C until weight was stable) to determine dry weight; all phytomass estimates were converted to the corresponding dry weight.

The frequency distribution of diameters determined the number of trees per hectare represented by each diameter class. A mean curve of phytomass vs. diameter was derived from the sample trees. The summation of the phytomass value corresponding to the midpoints of the diameter classes multiplied by the corresponding diameter frequency produced the final estimate of stand phytomass for each of the four phytomass components.

Dominant stand age was determined by counting rings on felled sample trees. Dominant stand height was measured and site quality was determined using

Orlov (1929). In Orlov's classification, class I is good, III is intermediate, and V is poor. In addition, Ia is better than I and Ib is better than Ia, while Va is worse than V and Vb is worse than Va.

3. Results

Examination of the data revealed that relations between the phytomass components and the various stand parameters such as age, stocking, and site quality class were linear. A simple logarithmic transformation of an independent variable occasionally improved the performance of the equations. These three stand parameters are required in Russian forest inventories and are always available.

For needle phytomass, a linear combination of the logarithms of stocking and age was significant, with different intercepts for the best site quality class and all poorer site quality classes:

$$N = 1.4935\ln(V) - 1.3520\ln(A) + 3.7623S_1 + 2.5815S_2 \quad (1)$$

where N is needle phytomass (Mg ha^{-1}), V is stocking (stand bole volume with bark, $\text{m}^3 \text{ha}^{-1}$), A is stand age (years), $\ln(x)$ is the natural logarithm of x (base e), and S_1 and S_2 are site quality class dummy variables: $S_1 = 1$ if site quality class equals Ia or I, and $S_1 = 0$ otherwise; $S_2 = 1$ if site quality class is II or poorer and $S_2 = 0$ otherwise. We use the same notation in all equations. This regression

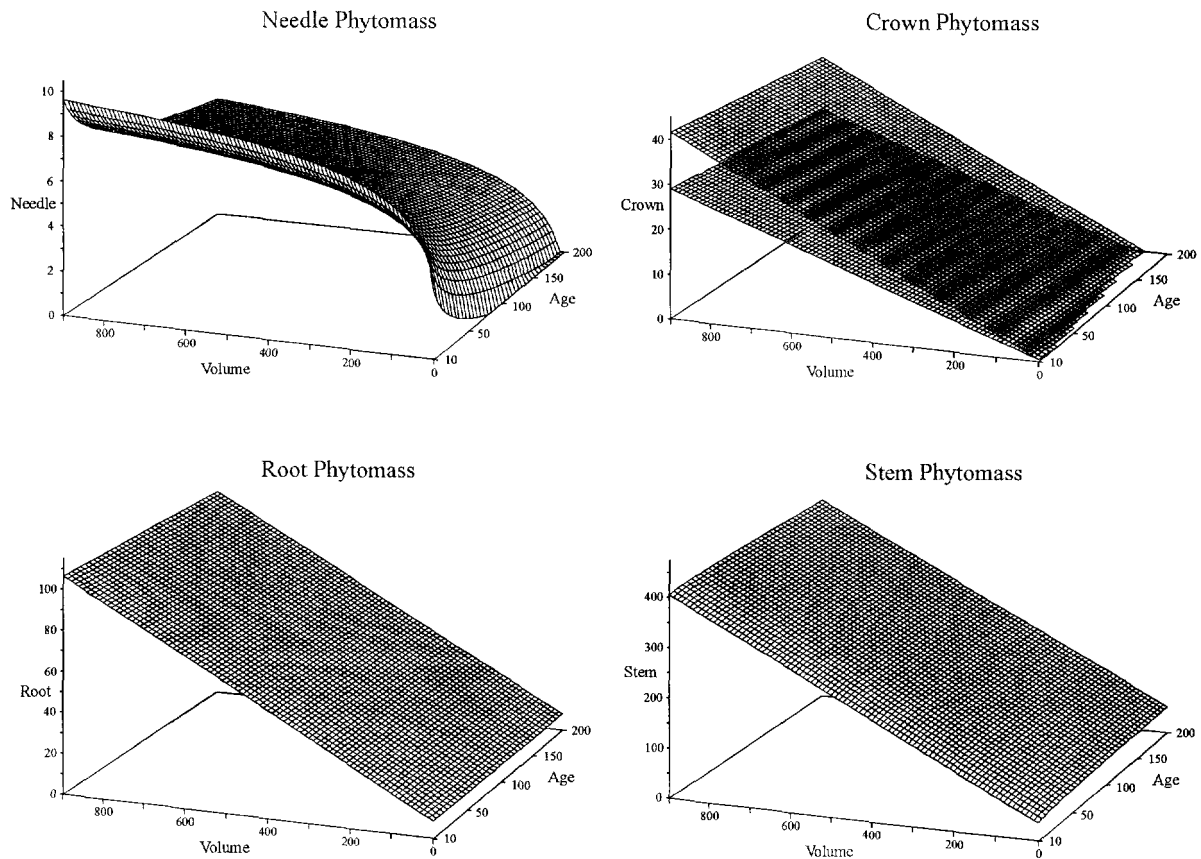


Fig. 1. Phytomass components (Mg ha^{-1}) predicted as a function of stocking volume ($\text{m}^3 \text{ha}^{-1}$) and stand age (years). Needle phytomass as predicted by Eq. 1 for intermediate site quality classes (II–V) is shown; predicted needle phytomass for the best site quality classes (I or Ia) is 1.18 Mg ha^{-1} higher. Crown phytomass is predicted by Eq. 2 for the best site quality class (I or Ia) (upper plane) and intermediate site quality classes II–V (lower plane). Root phytomass is predicted by Eq. 3, and stem phytomass by Eq. 4.

explained 56.5% of the variation ($100 \times R^2$). The root mean square residual (s) was 1.18 Mg ha^{-1} , and the number of observations (n) was 152 stands.

Needle phytomass increased with an increase in stocking (Fig. 1). This relation is especially clear with low stocking, but is not so obvious beyond $300 \text{ m}^3 \text{ ha}^{-1}$. Under the same stocking, young stands were characterized by greater phytomass than older stands. Decreasing needle phytomass with increasing age under equal stocking was distinctly expressed in the age range 20–50 years. This was characteristic of both high and low site quality classes. However, under the same stocking in stands of the same age, needle phytomass was slightly greater (1.2 Mg ha^{-1}) in stands of the best (Ia–I) site quality classes than in stands of the lower (II–Va) site quality classes.

Although all possible points in the respective phytomass–volume–age space are plotted in Fig. 1, not all combinations are possible. The largest predictions for needle phytomass in Fig. 1 were for young ages and high stocking, a combination that simply does not occur in Scots pine stands. For young stands below age 30, the largest observed stocking in our data was $250 \text{ m}^3 \text{ ha}^{-1}$.

Crown phytomass, which was a combination of needle and live branch phytomass, was best expressed as a simple linear combination of stocking and age. The slope of stocking was positive and that of age negative. However, the slope for stocking differed between site quality groups, with the best site quality classes producing greater crown phytomass for a given age and stocking:

$$C = 0.6507 + V(0.04577S_1 + 0.03171S_2) - 0.01668 A \quad (2)$$

where C is crown phytomass (Mg ha^{-1}), with $R^2 = 0.70$, $s = 4.96 \text{ Mg ha}^{-1}$, and $n = 152$. With very slight improvement in overall fit, we also found that the slope for the age term differed by site group in the above formulation, with the age slope for S_1 positive and for S_2 negative. Because of a limitation in the distribution of stand ages in the best site group (maximum age only 110 years), we rejected separate slopes for age. As is clear from Fig. 1, the age effect is very minor.

For root phytomass, no amount of effort could squeeze out more than the simplest linear regression in stocking:

$$R = 8.3206 + 0.1089V \quad (3)$$

where R is root phytomass (Mg ha^{-1}), with $R^2 = 0.77$, $s = 10.7 \text{ Mg ha}^{-1}$, and $n = 61$. Root phytomass increases linearly with stocking, unrelated to age or site quality class (Fig. 1).

The strongest relationship described stem phytomass:

$$S = 21.0995 + 0.4105V + 6.2162 \ln(A) \quad (4)$$

where S is stem phytomass (without bark, Mg ha^{-1}), with $R^2 = 0.963$, $s = 10.8 \text{ Mg ha}^{-1}$, and $n = 80$. This relation reflects the strong correlation between weight and volume when wood is fairly homogeneous (Fig. 1). Additional but minor variation is also explained by age, for tree boles monotonically increase their phytomass with time, until death. Using the logarithm of age rather than age itself keeps predictions from growing indefinitely large over time after the range of our data is passed (our maximum age is 200 years). As with Eq. 2, the age effect is significant but unimportant when explaining variation in phytomass (Fig. 1).

Alternately, confounding between weight and volume was resolved by calculating density $D = S/V$. Density averaged $0.42 \pm 0.05 \text{ Mg m}^{-3}$. The best predictor was the logarithm of age:

$$D = 0.2716 + 0.0380 \ln(A) \quad (5)$$

with $R^2 = 0.283$, $s = 0.044 \text{ Mg m}^{-3}$, and $n = 80$. Site quality did not explain a significant amount of variation. Stocking V was not considered a predictor because it is in the denominator of the dependent variable.

All phytomass equations performed well and showed no indication of multicollinearity, as all variance inflation factors are less than 3 (Draper and Smith, 1981). Linear regression insures that all estimates are unbiased.

We were also interested in examining the proportion of total phytomass in each of the four major components. The data could not support a detailed analysis, for all four phytomass components were measured on only 24 of the 152 stands. On average, the percentage of total phytomass that was in crown,

stems, and roots was 12%, 71%, and 17%, respectively. Furthermore, needle phytomass, which was approximately one-third of crown phytomass, was 4% of total phytomass. In these 24 stands, stocking was the most significant predictor of percentage of total phytomass; the slope was positive when predicting the percentage of phytomass in stems, and negative when predicting the percentage of phytomass in needles, crown, or roots.

4. Discussion

Because of the enormous geographic extent of the sample plots and the wide range of stand conditions covered, we expect these phytomass equations to perform well for most locations in Russia where stands of Scots pine are found. We used plots across the taiga zone from European Russia to eastern Siberia. Sample plots covered the full range of site quality classes, from the best (Ia) to the poorest (V). The range in stand age was wide, from 10 to 210 years; stocking also had a broad range, from 16 to 840 m³ ha⁻¹. Because only healthy stands were studied, predictions for damaged stands (e.g. from insects, disease, pollution) will be of unknown accuracy. Also, there were not any very old stands in our dataset, the maximum age being 210 years. It is possible that old-growth Scots pine stands with their very distinctive crown structure have different phytomass relations than typical stands younger than 210 years. The equations should not be applied to sparse old stands with very low stocking ($V < 90$ m³ ha⁻¹), as they are not represented in the dataset. Such conditions do not indicate normal forest stand development, although they can be found in specific low productivity sites (e.g. the bogs of western Siberia, stony soils at the southern distribution limit in Kazakhstan, and very poorly drained soils in middle and northern taiga).

The equations performed reasonably well. Because the entire complement of needles is replaced regularly (mean life expectancy is 4 years; Pobedin-sky, 1965), needle phytomass cannot increase as rapidly as components containing long-lasting woody tissue. This limitation is reflected by logarithmic relations between needle phytomass and both stocking and age in Eq. 1. Needle phytomass is a far more

ephemeral system, with needle birth and death a normal process occurring annually throughout a tree's life. It is also reasonable that the least amount of variation explained ($R^2 = 0.565$) was for needle phytomass, the only component without long term retention of heavy tissues.

In contrast to the logarithmic transformations of stocking and age that slowed the increase in needle phytomass in dense, mature stands, crown phytomass was linearly related to stocking and age in the entire range of both parameters. Crown branches, like boles, must continue to accumulate phytomass until individual branches die. On average, 34% of the crown phytomass was in needles.

Stem and root phytomass are both dominated by the steady accumulation of woody tissue. Such effects are represented in Eqs. 3 and 4 by positive coefficients for stocking. In addition, stem phytomass also increases linearly with age.

Difficulties measuring root phytomass should be considered. During excavation, small and fine roots can be missed; the greater part of the data will be concentrated on structural roots whose function is largely mechanical, not nutritional. Thus, it is not surprising that the root phytomass equation is a simple function of the volume of the trees in the stand. Eq. 3 describes the physical requirement for a root system to be of a given size to mechanically support a corresponding amount of phytomass above ground. Soil properties such as depth, type, texture, and the amount of stones affect the development of the root system. Unfortunately, we found no consistent parameter of soil properties in the root phytomass literature.

Site quality effects were useful in explaining variation in both needle and crown phytomass. Because site quality attempts to quantify some important characteristics of the nutritional and moisture status of a stand, the phytomass of the stand canopy should be related to site quality. The better site quality classes also should produce more needle and crown phytomass than less productive ones. This behavior is found in Eqs. 1 and 2.

This is the first comprehensive study synthesizing stand level phytomass relations for *P. sylvestris* for most of its range in Russia. The combined results from over 18 regional and local phytomass studies provide a level of generality not possible with indi-

vidual local studies. The underlying factors determining phytomass development are certainly more complex than the relatively simple relations expressed here. Key climatic and soil factors influencing moisture and nutrient regimes cannot be explicitly considered in a study attempting to summarize phytomass relations for most of Russia using only standard inventory parameters. Detailed local studies have a greater chance of capturing such detailed interactions, but will lack the generality and utility needed to meet our objective.

In addition to estimating stand phytomass components across a wide range of conditions in Russia, these phytomass models can also be used to verify carbon allocation rules in process-based models such as found in Dixon et al. (1990). The carbon budget is usually the foundation of process-based stand models, and carbohydrate allocation for growth of different tree parts is a crucial, albeit poorly understood, step (Nikinmaa and Hari, 1990). Our independently derived models for estimating stand phytomass components are a tool that could be used to increase confidence in process-based models.

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