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Geographical Gradients of Annual Biomass Production from Larch Forests in Northern Eurasia

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Abstract

From the vast collection of published data concerning larch forest biomass in northern Eurasia (390 plots), data from 17 plots selected from seven different regions were analyzed to determine how geographical differences influence the estimates of the annual net production rate. Nine plots were selected from four different regions of Siberia (southern and middle taiga, forest-steppe, forest-tundra), and the other eight plots were selected from three regions; Middle-Europe (Czechoslovakia, 1 plot), the Far East (northern China, 3 plots) and a Japanese Island (4 plots). Annual net production of each component (foliage, stem, branch, root and understory) was estimated separately using a multiple regression model, along with some parameters concerning stand characteristics (stand age, tree density, diameter and height), which had been developed previously for the regions in the Eurasian boreal larch forests. For this estimation, annual net production of each component was primarily assumed to be proportional to foliage biomass. Upon analysis, regional gradients of the estimated productivity from each of the larch forests could be determined. Specifically, the net production rates had increased from the northern (tundra) to the southern (steppe) parts of the Siberian taiga, and had decreased from the cool-temperate broad-leaf forest sub-zones (in Middle-Europe or northern Japan) to the central part of the Siberian taiga; which has been characterized as having an extremely continental climate (e.g. Yakutsk). Total and aboveground net production rates correlated highly with the continentality index; the values of coefficient of determination were 0.661 and 0.716, respectively.

Key words: continentality index, biomass, geographical gradient, larch forests, Northern Eurasia, productivity

Introduction

Forests generally play an important role in maintaining global carbon balance and climate (Schulze 2000). This function primarily depends on forest types with different productivity (Roy *et al.* 2001). Forest inventory of Russian territory has been established using so-called yield tables (i.e. stem volume basis) prepared for different forest types or regions (e.g. Kuusela 1990). However, a reliable data set for forest biomass and productivity (i.e. dry mass basis) determined for each component separately (e.g. stems, branches, foliage, roots, and understory) has provided too little information. (e.g. Schmidt *et al.* 1995, Lai *et al.* 2000, Roy *et al.* 2001). For assessing carbon stocks and/or carbon cycling in the forest ecosystems, it is important to compile data of biomass (or yield tables) obtained from sample plots from different regions.

Regarding the estimation of biomass, multiple regression models using some parameters concerning stand characteristics (e.g. stand age, tree density, diameter and height) have been proposed by Usoltsev (1997, 1998a, 1998b). Available data of net production rates of forest ecosystems have been considerably limited

in comparison with those of biomass (Roy *et al.* 2001). For an estimation of annual net production rate, extrapolation of the multiple regression model that was previously developed for biomass estimation, seems to have produced too many unstable estimates (Usoltsev 1998a). However, such a mathematical model may be suitable for the purpose of obtaining crude estimates when a regression model is applied using a simple (or individual) parameter (e.g. stand age) as suggested by Zamolodchikov and Utkin (2000). This kind of regression model has already been proposed for the estimation of net production rates of deciduous boreal forests (*Larix* spp.) using foliage biomass as an independent parameter. For this forest type, numerous foliage biomass data are available (i.e. 390 plots in total) (Usoltsev 1998b, Usoltsev and Koltunova 2001).

The final target of our study was to assess carbon stocks and carbon cycling in the Eurasian boreal larch (*Larix sibirica*, *L. gmelinii*, and *L. cajanderi*) forests (Abaimov 1995), and to clarify their regional-scale gradients in relation to differences in larch species, climate and other conditions (e.g. soils). As a result, the estimation method of the multiple regression model

(Usoltsev and Koltunova 2001) was initially reported, and in this paper, the geographical pattern of productivity from the larch forests in northern Eurasia was examined based on the estimates of some sample plots selected from seven different regions.

Materials and methods

Data source

In northern Eurasia, biomass and annual net production from larch forests have been studied by each tree component (stems, branches, needles, and roots), including understorey, for some *Larix* species growing on different regions; e.g. *L. leptolepis* in Japan (Hatiya et al. 1966, Satoo 1966), *L. decidua* in Czechoslovakia (Vyskot 1982), and *L. gmelinii* (Dahurian larch) in China (Lin and Yugong 1985, 1995) or Russia (Govorenkov 1972). For the present analysis, published data for biomass and annual net production rates of 17 sample plots from seven locations were selected. Specifically, nine plots were selected from four locations in Siberia (southern and middle taiga, forest-steppe, forest-tundra), and the other plots were chosen from Middle-Europe (Czechoslovakia, 1 plot), the Far East (northern China, 3 plots) and a Japanese Island (4 plots) (Fig. 1). Stand ages ranged from 13 to 250 years, and site conditions varied from Ia to Vc (i.e. site index of forest often used by Russian scientists), and tree densities were between about 300 to 6700 ha⁻¹ (Table 1).

Extrapolation model of net production rate

At first, the "stand age-biomass" table for each sample plot was constructed, i.e. estimates of biomass by each component at given stand ages (from 10 to 360 years). In this tabulation, use of the multi-factor regression of each component biomass was made using volume-forming indices as independent parameters: stand age (A), mean stem diameter at breast height (D_m) and mean tree height (H_m), and tree density (N). The regression was developed separately for each of the 21 regions in northern Eurasia by applying a multiple regression analysis (STATGRAPHICS plus 2.1) using the numerous biomass data sets from larch forests (in total 390 sample plots). Details of the regression of each region, such as the values of the four independent parameters and results of statistical analysis have been described elsewhere (Usoltsev 1998b, Usoltsev and Koltunova 2001).

Second, a "stand age-productivity" table was constructed for each sample plot by applying a similar mathematical regression model, which was developed for tabulating the "age-biomass" table for each region. However, the data set of annual net production rates for larch forests was too small to derive the same multifactor regression model. Thus, in the present analysis, a simple regression model was applied for the estimation of productivity using foliage biomass ($PF \text{ ton} \cdot \text{ha}^{-1}$) was regarded as an independent parameter:

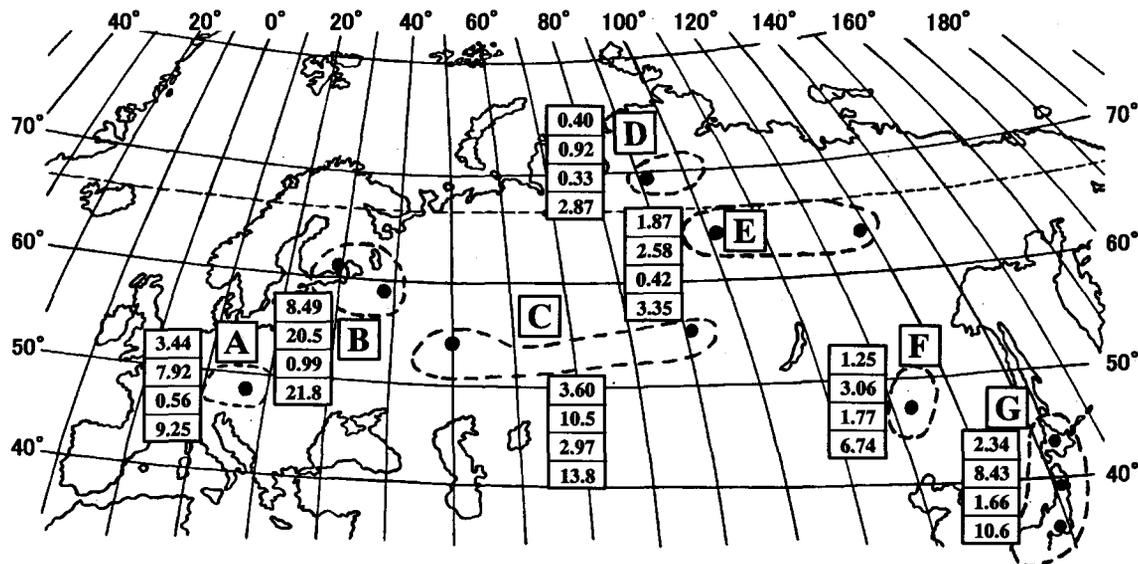


Figure 1. Geographical distribution of the 17 sample plots (black circles) of larch forests in seven locations (A-G) in northern Eurasia. Annual net production rates estimated at 100 years old are shown in each column: values of foliage biomass, aboveground-total, root and stand total (excluding understorey) (ton d.w. · ha⁻¹ · y⁻¹) are arranged from the top to bottom (see details of estimates at various ages in Table 4). Designation of the regions are as follows: A: a Middle-European province, a Broad-leaf forest subzone; B: a Scandinavian-Russian province, a Southern taiga subzone; C: Transvolga-Krasnoyarsk, a Forest-steppe subzone; D: Siberia, a Mountain forest-tundra; E: Siberia, a Middle taiga subzone; F: Far East, a Southern taiga subzone (the Great Xinganlin Mountains, China); G: the Japanese Islands' broad-leaf forests.

Table 1. Analyzed data of annual biomass growth rates obtained in 17 larch stands of seven different regions in Northern Eurasia

Region / forest zone	Stand no. ¹⁾	Forest type ²⁾ (Site index)	Species ³⁾ sharing	Stand age A (yrs-old)	Density (ha ⁻¹)	Diameter ⁴⁾ Dm (cm)	Height ⁵⁾ Hm (m)	Volume (m ³ ha ⁻¹)	Annual biomass growth rates (ton · ha ⁻¹ yr ⁻¹)					Data source	
									Stem		Branches	Foliage	Roots		Under-storey
									Total	Bark					
A. Middle-European province /Broad-leaved forest subzone															
Czechoslovakia	1	Nat. (Ia)	10L	36	959	14.6	16.4	100	1.35	-	0.076	0.96	0.247	0.7 [*]	Vyskot (1982)
B. Scandinavian-Russian province /Southern taiga subzone															
Leningrad region	2	Nat. (Ia)	10L	230	275	51.6	40.0	965	3.11	0.49	1.72	1.61	-	1.10	Govorenkov (1972)
Yaroslavl' region	3	Plant. (sand) (Ia)	10L	22	2450	12.4	12.7	194	6.67	0.87	2.37	3.87	-	-	Utkin <i>et al.</i> (1996)
	4	Plant. (sand) (Ia)	10L	29	1990	14.0	15.3	258	5.15	0.74	2.20	3.31	-	-	Utkin <i>et al.</i> (1996)
C. Transvolga-Krasnoyarsk /Forest-steppe subzone															
Samara region	5	Plant. (fresh) (I)	10L	21	3466	8.8	9.3	141	7.76	0.98	3.40	6.10	-	-	Utkin <i>et al.</i> (1980)
Krasnoyarsk territory	6	Loam-sand (II)	10L	25	4340	7.5	8.9	123	3.54	0.70	0.91	2.15	2.17	-	Vedrova <i>et al.</i> (2000)
D. Siberia /Mountain forest-tundra															
Krasnoyarsk territory	7	Alnos.-Vac. (V)	10L	155	485	19.5	15.3	104	1.47	-	0.09	1.23	0.58	2.74	Deeva (1985, 1987)
	8	Vac.-Clad. (V)	7L3B	155	275	8.0	7.0	5.6	0.12	-	0.02	0.10	0.16	0.95	Deeva (1985, 1987)
E. Siberia /Middle taiga subzone															
Evenkia	9	Led.-Arc.-Vac. (Vc)	10L	250	2090	6.8	5.5	33 [*]	0.26	-	0.06	1.00	0.48	-	Kajimoto <i>et al.</i> (1999)
Yakutia	10	? (V)	10L	169	900	19.3	16.9	213	0.67	-	0.16	1.68	0.23	0.44	Kanazawa <i>et al.</i> (1994)
F. Far East /Southern taiga subzone															
China, Inner Mongolia	11	Rhodod. (III)	10L	186	792	24.6	24.3	450	2.49	0.47	0.15	1.96	2.15	0.56	Lin and Yugong (1985, 1995)
	12	Led. (V)	10L	175	811	17.3	17.4	164	2.27	0.56	0.21	1.46	4.04	1.87	Lin and Yugong (1985, 1995)
	13	Sphagn.-Led. (Vb)	10L	107	2934	8.0	8.1	75.1	0.68	0.11	0.05	0.53	0.54	6.52	Lin and Yugong (1985, 1995)
G. Japanese Islands /Broad-leaved forest subzone															
Hokkaido Island	14	Plant. (moist.) (Ia)	10L	21	1240	15.1	15.3	169	6.70	-	3.00	4.90	-	0.30	Satoo (1974)
	15	Plant. (moist.) (Ia)	10L	21	-	-	-	-	7.80	-	3.66	4.90	2.83	0.16	Satoo (1966)
Northern Honshu Island	16	Plant. (moist.) (Ia)	10L	39	1155	19.9	19.4	355	5.80	-	3.26	3.59	1.96	1.06	Satoo (1970)
	17	Plant. (moist.) (Ia)	10L	13	6738	7.1	8.4	125	8.00	-	4.60	5.30	3.10	-	Hatiya <i>et al.</i> (1966)

1) More detailed location of each stand are as follows; 1:Brno, Blansko. (470 m a.s.l., 49° 19'N, 16° 40'E), 2:Karelian Isthmus (50 m a.s.l., 60° 30'N., 30° E.), 3-4: Rybinsk. (105 m a.s.l., 58° 06'N, 38° 42'E), 5:Krasnyi Yar. (53° 30'N, 50° 20'E), 6:Kemchug river (56° 13'N., 92° 19'E), 7-8: Plateau Putorana (70-290 m a.s.l., 70° N., 90° E), 9:Kochechum river, Tura (160 m a.s.l., 64° 19'N, 100° 13'E), 10: Yakutsk, Spasskaya Pad (220 m a.s.l., 63° N, 129° E), 11: Great Xinganlin Mountain, Genher (47° N, 123° E), 14: near Mount Asibetu (300 m a.s.l., 43° 13'N, 142° 23'E), 15: Hokkaido (unknown), 16: Iwate Pref., Koiwai (360 m a.s.l., 39° 45'N, 141° 08'E), 17: Nagano Pref., near Mt. Asama (1000 m a.s.l.).

2) Abbreviations of forest type are as follows; Alnos.: *alnosum*, Arc.: *arctosum*, Clad.: *cladinosum*, Led.: *ledosum*, Rhod.: *rhododendrosom*, Sphagn.: *sphagnosum*, Vac.: *vaccinosum*, Nat.: natural forest, Plant.: plantation.

3) Relative dominance of tree species, e.g., 10L means *Larix* sp. occupied almost 100%. 4), 5) Mean values of stem diameters at 1.3m (Dm) and tree heights (Hm).

* Values are calculated according to the original data

$$\ln ZP_i = f(\ln PF), \quad (1)$$

where ZP_i ($\text{ton} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$) means current biomass production of each component: stems (ZPS), branches (ZPB), roots (ZPR), and understorey (ZPU). In this estimation, it was assumed that current biomass production of each component was proportional to the current production of foliage (i.e. foliage biomass).

For geographical analysis, the 17 sample plots were grouped together into seven regions (A-G) taking into consideration the zonal-provincial division system of the Eurasia territory, as proposed by Russian scientists (Bazilevich and Rodin 1967, Kurnayev 1973, Smagin et al. 1978). According to this division system, some plots (i.e. 2 plots of forest-steppe of Transvolga and Krasnoyarsk, and 2 plots of Siberian taiga zones of both middle- and eastern-parts) were dealt with as samples of different locations. However, for applying this system, the number of samples was too small (each location contained 1 plot). Thus, these sample plots were temporally joined into an integrated location (C and E) respectively (Fig. 1).

To analyze regional differences in the estimates of annual net production rates, the fitness of the equation (1) of each component was compared. It is known that understorey biomass and its current production generally increase with stand age due to reduction of crown density (e.g. Assmann 1961, Usoltsev and Koltunova 2001). Furthermore, stem production tends to decrease with stand age, because foliage biomass reaches more or less a stable level, i.e. age-dependent reduction of apparent photosynthetic efficiency of foliage (Assmann 1961). These facts indicate that understorey biomass production is indirectly associated with stem production and/or foliage biomass. Considering these relationships,

understorey biomass production was estimated using the following equation;

$$\ln(ZPU) = f(\ln PF, \ln ZPS). \quad (2)$$

The method of using block dummy variables (Draper and Smith 1966) enabled comparisons of not only the regression (1) but also the net production data from the regions. All regions were encoded by block dummy variables. The productivity level of the broad-leaf forest sub-zone of the Middle European province (Region A; Table 1) was defined as zero (Table 2). Then, a partially recursive equation was constructed using the following general format;

$$\ln ZP_i = f(X_0, \dots, X_6, \ln PF, \ln ZPS). \quad (3)$$

Results and Discussion

Fitness of the equation (3) was described in Table 2, and showed that the model explained 78-99 % of the variance in the dependent variables. For each region, the recursive line-up of the equation (3) was tabulated in the following sequence: ZPS , ZPB , ZPR and ZPU (Tables 3, 4). There were relatively large differences between the estimated and original values of productivity derived from some sample plots, e.g. the productivity for two regions (A and B) seemed to have been overestimated, while those of the three regions (C, F and G) were underestimated (Tables 1, 4). Despite such a discrepancy and the restricted data set of sample plots, the time trend of estimated net production rates for each component (Table 4) indicated regional gradients of productivity for each of the larch forests. For example, the total stand productivity derived after 100 years, differed greatly among the three regions of Siberian taiga; 2.9, 3.4 and

Table 2. Scheme of coding of regional allocation of larch primary productivity by block dummy variables

Region ¹⁾	Dummy variables						
	X_0	X_1	X_2	X_3	X_4	\bar{O}_5	\bar{O}_6
A	0	0	0	0	0	0	0
B	0	1	0	0	0	0	0
C	0	0	1	0	0	0	0
D	0	0	0	1	0	0	0
E	0	0	0	0	1	0	0
F	0	0	0	0	0	1	0
G	0	0	0	0	0	0	1

- 1) A: Middle-European province/Broad-leaved forest subzone, B: Scandinavian-Russian province/Southern taiga zone, C: Transvolga-Krasnoyarsk/Forest-steppe subzone, D: Siberia/Mountain forest-tundra, E: Siberia/Middle taiga subzone, F: Far East/Southern taiga subzone (China), G: Japanese Islands/broad-leaved forest subzone

Table 3. Characteristics of the equations (3)

Dependent variables	Constants and explanatory variables of the equations									R^2	SE
	a_0	$a_1 X_1$	$a_2 X_2$	$a_3 X_3$	$a_4 X_4$	$a_5 X_5$	$a_6 X_6$	$a_7 (\ln PF)$	$a_8 (\ln ZPS)$		
$\ln(ZPS)$, $\text{ton} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	0.3371	-0.1177	0.142	-0.2544	-1.4461	-0.014	0.2309	0.9068	-	0.953	0.375
$\ln(ZPB)$, $\text{ton} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	-2.809	2.3365	2.0931	0.3197	1.1616	0.3109	2.5988	-	0.7731	0.988	0.274
$\ln(ZPR)$, $\text{ton} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	-1.3724	-1.3724	1.6458	0.850	0.1056	1.7993	1.338	0.6358	-	0.88	0.629
$\ln(ZPU / ZPS)$	-0.6909	-0.6743	-1.0504	1.1609	0.7041	0.9985	-0.5491	-0.836	-	0.781	1.409

13.8 $\text{ton} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ in the forest-tundra (region D), the middle taiga (region E) and the forest-steppe (region C), respectively. However, when the data of two marginal regions (C and D) were excluded, the stand productivity tended to increase from the middle taiga in Siberia (region E) toward west (regions A and B) or east (regions F and G). This regional trend suggests that net production rates for larch forests are primarily dependent on, not only temperature, but also precipitation regimes (e.g. Roy *et al.* 2001). Namely, the estimates of stand total (ZPt) and aboveground total (ZPa) net production rates are likely to be positively correlated with the continentality index (IC) by Khromov (1957). Continentality index is a common idea of expressing temperature difference related to latitude (Conrad 1946, Tuhkanen 1984). In this study, these relationships were approximated by the following power-form equations;

$$\ln ZPt = 7.445 - 1.343 \ln IC \quad (R^2 = 0.661), \quad (4)$$

$$\ln ZPa = 8.661 - 1.728 \ln IC \quad (R^2 = 0.716). \quad (5)$$

The analysis also indicated that the estimated productivity from larch forests was relatively large (ZPt

= 14 $\text{ton} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$, Table 4) in the forest-steppe subzone (region C) where soil moisture was essentially low. In this region, trees generally develop a root system characterized by a larger proportion of absorptive and thin (less than 1mm in diameter) roots. For instance, the proportion of such thin roots consisted of about 70% of total root biomass for pine trees growing on dry steppe conditions in the Turgai Depression (Usoltsev 1988). For larch trees, the allocation of annual net production may also be affected by soil moisture conditions, since growth of the larch species has been rather sensitive to water stress (Berg and Chapin 1994, Lai *et al.* 2000).

This study's estimation model of forest productivity, which was based on the estimated current foliage biomass, may only be applicable to deciduous tree species. As for other evergreen species, further examination is needed to modify the regression model by looking for more suitable and simple parameters instead of the current foliage biomass. Moreover, in order to discuss the geographical pattern of the productivity for larch forests, which was inferred in this report, more refined quantitative analysis is required based on climate data (e.g. temperature and precipitation) in each corresponding location.

Table 4. Time trends of calculated annual net production rates of larch stands ($\text{ton} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) on seven different regions (A-G) in Northern Eurasia

Stand age A (yrs-old)	Annual biomass growth rates of each fraction ($\text{ton} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$)						
	Needle	Stem	Branch	Above- total	Root	Under- storey	Total
	PF	ZPS	ZPB	ZPa	ZPR	ZPU	ZPt
A. Middle-European province /Broad-leaved forest subzone							
10	3.22	4.05	0.18	7.45	0.53	0.76	8.74
20	3.46	4.32	0.19	7.97	0.56	0.77	9.30
40	3.61	4.49	0.19	8.29	0.57	0.77	9.63
60	3.59	4.46	0.19	8.24	0.57	0.77	9.58
80	3.53	4.40	0.19	8.12	0.57	0.77	9.46
100	3.44	4.29	0.19	7.92	0.56	0.77	9.25
120	3.34	4.18	0.18	7.70	0.55	0.76	9.01
160	3.15	3.97	0.17	7.29	0.53	0.76	8.58
200	2.96	3.75	0.17	6.88	0.51	0.76	8.15
240	2.80	3.56	0.16	6.52	0.49	0.75	7.76
280	2.66	3.40	0.16	6.22	0.47	0.75	7.44
320	2.52	3.24	0.15	5.91	0.46	0.75	7.12
360	2.40	3.10	0.14	5.64	0.44	0.75	6.83
B. Scandinavian-Russian province /Southern taiga zone							
10	8.06	8.26	3.19	19.51	0.96	0.37	20.84
20	8.63	8.79	3.35	20.77	1.00	0.37	22.14
40	8.96	9.10	3.44	21.50	1.02	0.37	22.89
60	8.90	9.04	3.42	21.36	1.02	0.37	22.75
80	8.72	8.87	3.37	20.96	1.00	0.37	22.33
100	8.49	8.66	3.31	20.46	0.99	0.37	21.82
120	8.25	8.44	3.24	19.93	0.97	0.37	21.27
160	7.76	7.98	3.11	18.85	0.93	0.37	20.15
200	7.31	7.56	2.98	17.85	0.90	0.37	19.12
240	6.90	7.18	2.86	16.94	0.87	0.36	18.17
280	6.53	6.83	2.75	16.11	0.84	0.36	17.31
320	6.20	6.51	2.65	15.36	0.81	0.36	16.53
360	5.89	6.22	2.56	14.67	0.78	0.36	15.81

Table 4 (continued)

Stand age A (yrs-old)	Annual biomass growth rates of each fraction (ton·ha ⁻¹ ·yr ⁻¹)						
	Needle	Stem	Branch	Above- total	Root	Under- storey	Total
	PF	ZPS	ZPB	ZPa	ZPR	ZPU	ZPt
C. Transvolga-Krasnoyarsk /Forest-steppe subzone							
10	3.82	5.44	1.81	11.07	3.08	0.31	14.46
20	3.91	5.56	1.84	11.31	3.13	0.31	14.75
40	3.92	5.57	1.84	11.33	3.13	0.31	14.77
60	3.84	5.47	1.82	11.13	3.09	0.31	14.53
80	3.72	5.31	1.78	10.81	3.03	0.31	14.15
100	3.60	5.16	1.74	10.50	2.97	0.31	13.78
120	3.48	5.00	1.70	10.18	2.90	0.31	13.39
160	3.25	4.70	1.62	9.57	2.78	0.31	12.66
200	3.04	4.43	1.54	9.01	2.67	0.31	11.99
240	2.86	4.19	1.48	8.53	2.56	0.31	11.40
280	2.71	3.99	1.42	8.12	2.48	0.30	10.90
320	2.56	3.79	1.37	7.72	2.39	0.30	10.41
360	2.44	3.63	1.32	7.39	2.32	0.30	10.01
D. Siberia /Mountain forest-tundra							
10	0.50	0.58	0.05	1.13	0.38	1.66	3.17
20	0.48	0.56	0.05	1.09	0.37	1.65	3.11
40	0.46	0.54	0.05	1.05	0.36	1.65	3.06
60	0.44	0.52	0.05	1.01	0.35	1.65	3.01
80	0.42	0.49	0.05	0.96	0.34	1.62	2.92
100	0.40	0.47	0.05	0.92	0.33	1.62	2.87
120	0.39	0.46	0.05	0.90	0.33	1.62	2.85
160	0.36	0.43	0.04	0.83	0.31	1.62	2.76
200	0.33	0.40	0.04	0.77	0.29	1.62	2.68
240	0.31	0.38	0.04	0.73	0.28	1.62	2.63
280	0.30	0.36	0.04	0.70	0.28	1.58	2.56
320	0.28	0.34	0.04	0.66	0.26	1.58	2.50
360	0.26	0.32	0.03	0.61	0.25	1.58	2.44
E. Siberia /Middle taiga subzone							
10	2.13	0.65	0.14	2.92	0.46	0.35	3.73
20	2.12	0.65	0.14	2.91	0.45	0.35	3.71
40	2.08	0.64	0.14	2.86	0.45	0.35	3.66
60	2.02	0.62	0.13	2.77	0.44	0.35	3.56
80	1.94	0.60	0.13	2.67	0.43	0.35	3.45
100	1.87	0.58	0.13	2.58	0.42	0.35	3.35
120	1.80	0.56	0.12	2.48	0.41	0.35	3.24
160	1.68	0.53	0.12	2.33	0.39	0.35	3.07
200	1.57	0.50	0.11	2.18	0.38	0.35	2.91
240	1.47	0.47	0.11	2.05	0.36	0.35	2.76
280	1.39	0.44	0.10	1.93	0.35	0.34	2.62
320	1.32	0.42	0.10	1.84	0.34	0.34	2.52
360	1.25	0.40	0.09	1.74	0.32	0.34	2.40
F. Far East /Southern taiga subzone							
10	1.48	1.97	0.14	3.59	1.97	1.93	7.49
20	1.46	1.95	0.14	3.55	1.95	1.93	7.43
40	1.41	1.89	0.13	3.43	1.91	1.93	7.27
60	1.36	1.83	0.13	3.32	1.86	1.92	7.10
80	1.30	1.75	0.13	3.18	1.81	1.91	6.90
100	1.25	1.69	0.12	3.06	1.77	1.91	6.74
120	1.20	1.63	0.12	2.95	1.72	1.90	6.57
160	1.12	1.53	0.11	2.76	1.65	1.89	6.30
200	1.04	1.43	0.11	2.58	1.57	1.88	6.03
240	0.98	1.36	0.10	2.44	1.51	1.88	5.83
280	0.92	1.28	0.10	2.30	1.45	1.87	5.62
320	0.87	1.22	0.10	2.19	1.40	1.86	5.45
360	0.83	1.17	0.09	2.09	1.36	1.86	5.31

Table 4 (continued)

Stand age A (yrs-old)	Annual biomass growth rates of each fraction (ton·ha ⁻¹ yr ⁻¹)						
	Needle	Stem	Branch	Above- total	Root	Under- storey	Total
	PF	ZPS	ZPB	ZPa	ZPR	ZPU	ZPt
G. Japanese Islands /Broad-leaved forest subzone							
10	2.29	3.74	2.25	8.28	1.64	0.54	10.46
20	2.42	3.93	2.33	8.68	1.69	0.54	10.91
40	2.49	4.04	2.39	8.92	1.73	0.55	11.20
60	2.46	3.99	2.36	8.81	1.71	0.54	11.06
80	2.40	3.90	2.32	8.62	1.69	0.54	10.85
100	2.34	3.81	2.28	8.43	1.66	0.54	10.63
120	2.27	3.71	2.23	8.21	1.63	0.54	10.38
160	2.13	3.50	2.13	7.76	1.56	0.54	9.86
200	2.00	3.31	2.04	7.35	1.50	0.54	9.39
240	1.88	3.13	1.96	6.97	1.44	0.53	8.94
280	1.79	2.99	1.89	6.67	1.40	0.53	8.60
320	1.70	2.86	1.83	6.39	1.35	0.53	8.27
360	1.61	2.72	1.76	6.09	1.31	0.53	7.93

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