Ecological Bulletins 49: 93–104.

Coarse woody debris in the forests of the St. Petersburg region, Russia

Olga N. Krankina, Rudolf F. Treyfeld, Mark E. Harmon, Gody Spycher and Evgenii D. Povarov

Krankina, O. N., Treyfeld, R. F., Harmon, M. E., Spycher, G. and Povarov, E. D. 2001. Coarse woody debris in the forests of the St. Petersburg region, Russia. – Ecol. Bull. 49: 93–104.

The significance of coarse woody debris (CWD) for biodiversity, carbon budgeting, and nutrient cycling in forest ecosystems is widely acknowledged, however the lack of comprehensive and representative data hinders the progress in understanding dead wood dynamics in forest landscapes and regions. To assess the regional stores of CWD in the St. Petersburg region of northwestern Russia we combined data collected as part of the forest inventory with measurements in 384 sample plots and results of bulk density sampling of 128 dead trees. Forest inventory data for 7 forests with a total area of 1.1 million ha (216 000 forest stands) was processed using a system of ratio estimators derived from measurements in sample plots. The amount of CWD declined with age among young forests and reached the minimum in stands 20–30 yr old. In older forests the amount of CWD increased with age to a level ranging from 30 to 50 m^3 ha^{-1} (7.0 to 15.3 Mg ha^{-1}) depending on the dominant tree species. The store of CWD in the recently disturbed forests depended on the type of disturbance: the clearcuts stored 24 m^3 ha^{-1} (9.5 Mg ha^{-1}), while after natural disturbance the store of dead wood reached 145 m^3 ha^{-1} (57 Mg ha^{-1}). The average store of CWD in the seven selected forests ranged from 5.15 to 7.39 Mg ha^{-1} and mature and older stands contributed the largest proportion of the overall store of CWD.

O. N. Krankina (krankinao@fsl.orst.edu), M. E. Harmon and G. Spycher, Dept of Forest Science, Oregon State Univ., Corvallis OR 97331-7501, USA. – R. F. Treyfeld and E. D. Povarov, Northwestern State Forest Inventory Enterprise, Ul. Koli Tomchaka 16, St. Petersburg 196084, Russia.

In boreal forest ecosystems dead trees and associated woody detritus form a large and dynamic biomass pool, which is still poorly studied, especially compared with photosynthesis and forest growth. In past assessments of carbon stores in Russian forests, woody detritus was either ignored (Kobak 1988, Melillo et al. 1988, Isaev et al. 1993) or estimated as a constant proportion relative to live biomass (Kolchugina et al. 1992, Krankina and Dixon 1994) or calculated from growth tables using assumed density (10% less than live wood) and decomposition parameters (Alexeyev et al. 1995). These approaches were applied because of the lack of data to address the subject more adequately.

Coarse woody debris (CWD) stores are difficult to assess because they vary significantly over succession and do not necessarily parallel the dynamics of live biomass. Earlier published results of measurements on experimental plots in northwestern Russia indicate that the carbon store in CWD ranges from 1 to 39 MgC ha^{-1} depending on stand age, management status, and time since disturbance (Krankina and Harmon 1995). The largest amount of CWD is found in recently disturbed areas. Dead wood stores are minimal in young stands (10–40 yr old) regenerating after clearcut harvest and in some older second-growth stands where dead trees are salvaged (1–8 MgC ha^{-1}). Overall, in our plots CWD comprised from 2 to 98% of the total above ground biomass. Although a single live/dead wood ratio is often used in carbon budget calculations, our results suggest that this approach may substantially over- or under-estimate the CWD carbon pool depending upon the type of disturbance regime in the region (Krankina and Harmon 1995, Krankina et al. 1998). Alternative approaches are needed to improve the estimates of the role of CWD in regional carbon stores and flux.

The significance of CWD for biodiversity and for carbon and nutrient cycling is widely acknowledged (e.g., Harmon et al. 1986, Kirby and Drake 1993, Berg et al. 1994, Krankina and Harmon 1995, Krankina et al. 1999), however the lack of representative data hinders the progress in understanding dead wood dynamics in forest landscapes and regions (Alexeyev et al. 1995, Harmon et al. in press). Given the paucity of field measurements of CWD, it is critical to use existing data to the extent possible and to develop methods of estimation based on other more readily available characteristics of forest stands, such as live wood volume, tree species composition and age (Krankina et al. 1998). The goal of this study was to assess the regional stores of CWD in the St. Petersburg region of northwestern Russia and to examine the impact of forest age, tree species composition, site productivity level, and disturbance on woody detritus volume and mass. Methods and techniques for estimating CWD stores developed in this study will eventually be applied to forest inventories in other regions of the Russian Federation.

Methods

Study area

The field data for this study were collected in the St. Petersburg region of northwestern Russia located between 58° and 61°N and between 29° and 34°E. The region occupies 8.1 million ha and currently 55% of this area is covered with forests. The natural vegetation of the area belongs to southern taiga type; major dominant conifer species include Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) Karst. both growing in pure and mixed stands. After disturbance, these species are often replaced by northern hardwoods including birch *Betula pendula* Roth. and aspen *Populus tremula* L. The climate is cool maritime with cool wet summers and long cold winters. Mean temperature of July is +16–17°C, mean temperature of January is –7 to –11°C, mean monthly temperatures are negative from November until March; annual precipitation is 600–800 mm. The study area is a part of the East-European plain with elevations between 0 and 250 m a.s.l. The terrain is flat and rests on ancient sea sediments covered by a layer of moraine deposits. Soils are mostly of the podzol type on deep loamy to sandy sediments. The St. Petersburg region has a long history of forest management dating from the 18th century.

General approach

Inventory of CWD in sample plots is the prevailing approach to measurement of CWD stores in forest ecosystems (e.g. Bader et al. 1995). However, extrapolation from plot measurements to larger scales of landscapes, regions, and vegetation zones requires (in theory) the application of probability sampling techniques (e.g. Cochran 1977) across vast and often inaccessible forest areas. Fortunately, the Russian forest inventory system collects a wealth of stand level data on all forest lands including some information on CWD volume (Kukuev et al. 1997). Although these data provide only a partial measurement of CWD, it is a valuable data resource that covers a large proportion of the entire forest area of Russia and can provide a basis for regional estimates. This study takes advantage of existing data resources and integrates three different types of field data: 1) forest survey data collected by the Northwestern State Forest Inventory Enterprise in 1992–1993, 2) CWD and live tree inventory in 384 sample plots, and 3) measurements of the bulk density of CWD on 128 sample trees.

We selected seven forests in the St. Petersburg region with a total area of 1.1 million ha to represent the variation in natural conditions and management history within the region (Fig. 1, Table 1). The survey data for these forests were acquired in the process of a detailed forest inventory that is performed every ten years in St. Petersburg region. Field crews from the Northwestern Forest Inventory Enterprise surveyed each forest stand polygon (a homogeneous patch of forest vegetation) delineated from air photos (Anon. 1995). A standard set of data gathered in the field included site characteristics, tree species composition, mean height, diameter and age, canopy structure, wood volume, and characteristics of different types of land without tree cover (e.g., clearcuts, bogs, meadows). Over 300 different parameters measured or visually estimated in the field were used to describe forest stands depending on land category and management requirements at a given forest (Kukuev et al. 1997). This included visual estimates of dead wood volume made separately for logs and snags in every forest stand where these volumes exceeded 10 m^3 ha^{-1}. CWD volume is estimated as part of regular forest inventory for purposes of forest health maintenance and for assessing the resources for potential wood salvage. Consequently, wood at advanced stages of decay was excluded from volume estimates and the total volume of woody debris was potentially underestimated.

The primary forest inventory data described above were processed and corrected with a system of ratio estimators

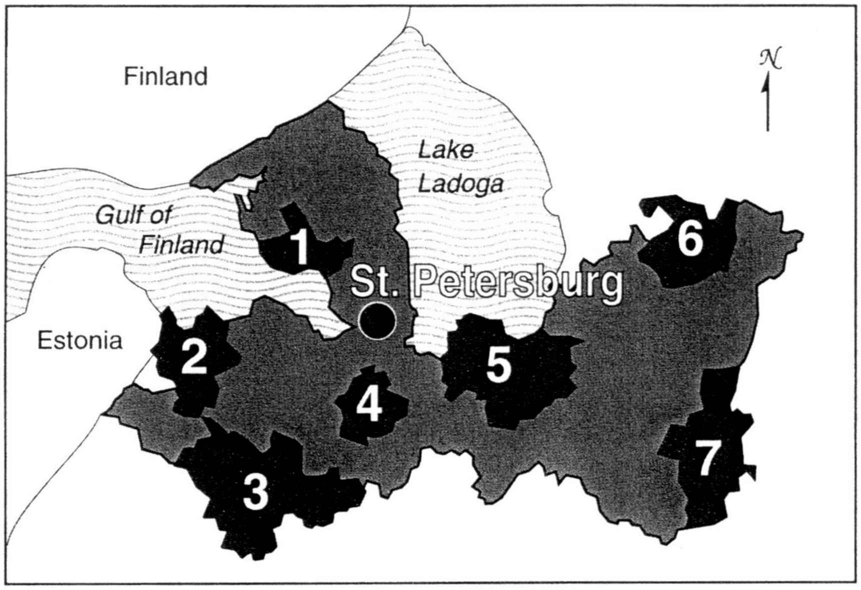

Fig. 1. St. Petersburg region and forests where CWD stores were computed from the stand–level inventory database: Roschinskii (1), Kingisseppskii (2), Luzhskii (3), Lisinskii (4), Volkhovskii (5), Podporozhskii (6), Podborovskii (7).

derived from measurements in sample plots. All stands in the database were divided into two categories depending on whether or not the visually estimated CWD volume was available. For stands where CWD volume was reported, it was corrected for the under-reported part. For forest stands where CWD was not reported in forest inventory database, the growing stock of live trees was used as a basis (i.e., auxiliary variable) for estimating CWD volume. Stand age group and dominant tree species were used to determine the selection of the appropriate ratio estimator. All volume measurements were then converted to biomass using the mean bulk density of CWD for a given forest category and woody debris type (logs or snags). Finally, we used statistical analysis to assess the effect of forest age, dominant tree species, and other factors on the amount of CWD in forest stands.

Sample plots

Two different types of sample plots were used in this study to represent the major dominant tree species of the area and different successional stages (recently disturbed forests and young to old-growth forest stands). Type I plots were measured by authors in 1993, 1994, and 1998 and range 0.1–1.0 ha in size. These 128 sample plots included several sets of old permanent plots and temporary plots set up for this study in forest stand categories that were under-represented among the available permanent plots. In the inventory of dead wood we used a decay class system which included 5 decay classes and covered all the stages of wood decomposition from nearly sound wood (decay class 1) to the most advanced stages of decomposition when CWD material is soft and friable (decay class 5). The visual characteristics of decomposition classes (e.g., extent of bark loss) varied by species (Krankina et al. 1999). Within each plot the end diameters and lengths of each piece of dead wood >10 cm in diameter and >1 m in length was recorded. All forms of CWD were inventoried including snags (standing dead), logs (dead and downed), and stumps (cut by harvest). Species and decay class of each piece were also noted. The mass of each piece was calculated by multiplying the computed volume by the average bulk density of CWD for a given species and decay class. A detailed description of the decay class system, CWD inventory methods, and results from 1993–96 sampling of bulk density were published elsewhere (Krankina and Harmon 1994, 1995, Harmon and Sexton 1996, Krankina et al. 1999).

Type II plots were set up by the Northwestern Forest Inventory Enterprise in 1994–1996 in all 7 selected forests as part of the regional forest monitoring program (Alexeyev et al. 1998). This provided an additional 256 plots where live and dead wood was measured. However, in this case the inventory procedures were based of Forest Inventory Guidelines (Anon. 1995) which excluded pieces in advanced stages of decay and the distribution of inventoried pieces by decay classes was not determined. The volume of CWD measured in Type II plots was corrected using the results of CWD inventories in Type I plots: first, ratios of total volume of logs and snags to volume of logs and snags in the early stages of decomposition (decay classes 1, 2, and 50% of class 3) were calculated in each Type I plot, then these ratios were averaged for young and for older stands separately (Table 2), and finally, the average values of ratios were applied to volumes of logs and snags, respectively, measured in Type II plots to correct them for the under-reported volume of CWD.

Table 1. Selected forests and the St. Petersburg Region.

Forest name	Total forest area, thousand ha	Total number of forest stands, thousand	Percent clearcut area	Percent area of burned or dead forest	Percent area dominated by conifers	Percent area of mature and older forest	Percent area of high productivity forests	Percent area with visual estimates of CWD
Kingisseppskii	117.5	25.1	1.1	0.2	72	24	31	4.4
Lisinskii[1]	73.8	17.0	1.2	0.2	54	24	53	8.4
Luzhskii[1]	178.2	37.1	1.3	1.1	63	38	51	8.0
Podborovskii[1]	146.5	22.3	0.3	0.04	75	32	33	8.8
Podporozhskii	212.8	26.7	0.5	0.1	64	42	39	13.5
Roschinskii[1]	198.7	65.4	0.6	0.2	86	17	47	9.0
Volkhovskii[1]	156.2	22.3	1.2	0.1	50	36	37	8.5
St. Petersburg Region	4577.1	not available	0.8	0.1	69	24	not available	not available

[1] Forests used in the analysis of changes in CWD stores with age of forest stands.

Calculation procedures

Plot measurements were grouped by dominant tree species and age of live trees; plots in recently disturbed forest stands including clearcuts and windthrow areas were examined separately. Plots dominated by Scots pine or Norway spruce were further aggregated into a conifer group. This is distinct from the hardwood group where birch or aspen are the dominant species. Three age groups were defined according to the system adopted by the Russian forest inventory: 1) young forests for ages ≤ 40 yr in conifers and ≤20 yr in hardwoods; 2) middle-age forests for ages 41–80 yr in conifers and 21–60 yr in hardwoods, 3) mature and old forests >81 yr in conifers and >61 yr in hardwoods.

To calculate ratio estimators, the measured volumes of logs and snags in each plot were compared with the visual estimates reported in the forest inventory database. The visual estimates of log and snag volumes were found in forest inventory database for 37 and 41 sample plots, respectively. For these plots the ratio estimator or correction factor (measured volume divided by visually estimated volume) was calculated separately for logs and snags. The correction factor averaged 3.21 ± 0.73 for logs, indicating that the volume of logs was under-reported 3-fold when the visual estimate was present in forest inventory database. For snags, the mean value of the correction factor (0.942 ± 0.15) was not significantly different from 1 implying that the volume of snags reported in forest inventory database does not require correction.

Visual estimates of log and snag volumes were missing in forest inventory database for 347 and 343 plots, respectively. For these plots the measured volumes of logs and snags were used to calculate the ratio of CWD (log or snag) volume to live wood volume. These estimator ratios were averaged by species and age groups (Table 3) and applied to live wood volume in the forest inventory database to estimate the volume of CWD in those forest stands where the volume of logs or snags or both was not reported. For young forests the ratio varied widely and this precluded the calculation of a meaningful estimator ratio. We attributed this to the fact that dead wood found in young forest stands had been generated when the previous generation of trees was killed by disturbance. Consequently, the amount of CWD did not correlate with the current volume of young trees in plots. For young forests, the mean volumes of logs and snags per unit area were used to substitute for the missing values in the inventory database (Table 3).

Different methods of calculating CWD volume were used for forest lands without live tree cover. For burned and dead stands the volume of snags and logs reported in the forest inventory database was used without correction. When the CWD volume estimates were missing for burned and dead forests they were assumed to equal 90% of the average growing stock volume for the region or 150

Table 2. Ratios of total volume of CWD in sample plots to volume inventoried in Type II plots based on Forest Inventory Guidelines (Anon. 1995) (decay classes 1, 2, and 50% of class 3).

Debris type	Age group	Number of plots	Ratio (mean ± SE)
Logs	Young	20	3.65 ± 0.68
	Middle-age and older	89	1.83 ± 0.14
Snags	Young	11	1.46 ± 0.15
	Middle-age and older	88	1.08 ± 0.02

m^3 ha^{-1}. Detailed calculation procedures are on file at the Northwestern Forest Inventory Enterprise.

The average bulk density of logs and snags was calculated for all plots of Type I by dividing the total mass of logs and snags in plot by their respective volumes. Mean values of CWD density were computed separately for conifer and hardwood dominated plots in 3 age groups (Table 4). The mean density of CWD in recently disturbed forests (2 clearcuts and 4 windthrow sites) is not significantly different for logs and snags and equals 0.295 ± 0.015. To determine the mass of CWD the mean bulk densities (Table 4) were applied to volumes of CWD computed from the forest inventory database as explained above.

The data on CWD derived from the stand-level forest inventory database was grouped based on stand characteristics (dominant tree species, stand age, and site productivity class) and area-weighted averages of CWD amount and CWD/live wood volume ratio were computed for each group within each selected forest (Table 1). These forest-level averages were treated as individual observations in further statistical analysis. We applied the General Linear Model procedure (GLM) to assess the influence of the above factors on CWD volume and mass and on the CWD/live wood volume ratio (further referred to as the CWD ratio). Means were compared using ANOVA with the Tukey pairwise comparison test with $p<0.05$. The regression analysis was performed using the GLM procedure (Anon. 1985).

Results

Analysis of plot data

The average volume and mass of CWD changed over successional stages: from 186 m^3 ha^{-1} (61 Mg ha^{-1}) in recently disturbed forests, to just 2.1 m^3 ha^{-1} (0.5 Mg ha^{-1}) in young forest stands between ages 21 and 40 yr, to 55 m^3 ha^{-1} (14.6 Mg ha^{-1}) in forests older than 120 yr (Fig. 2). The CWD ratio was higher in conifer than in hardwood forests and increased with forest age in both species groups (Table 3). Among the examined forest stand categories the CWD ratio was the highest in mature and old conifer forests (15.1%) and the lowest in middle-aged hardwoods (3.7%). Regression analysis after separating Type I plots by dominant species group (conifers and hardwoods) indicates a low but statistically significant positive correlation between the CWD ratio and the age of live trees in plots older than 20 yr and without signs of recent disturbance (r^2 is 0.36 and 0.23 for conifers and hardwoods, respectively). A similar weak correlation was found between the volume of CWD and the age of forest stands older than 20 yr (r^2 is 0.35 and 0.38 for conifers and hardwoods, respectively).

The proportion of snags ranged from 0 to 100% of the total volume of CWD in sample plots, however, a low proportion of snags (< 40%) occurred most frequently in all species × age groupings (Fig. 3). Young stands commonly had a low proportion of snags, but a very high proportion

Table 3. Parameters for estimating CWD volume in forest stands with no CWD reported in the forest inventory database: volume of dead wood in young forests and CWD/live wood volume ratio in middle aged and older forests (mean ± SE).

Species group	Age group	Number of plots	Parameter	Logs	Snags
All	Young	42	CWD volume, m^3 ha^{-1}	8.8 ± 4.8	1.9 ± 0.6
Conifers	Middle age	168	CWD/live wood ratio, %	6.7 ± 0.9	4.4 ± 1.1
	Mature and old	97		12.1 ± 1.6	3.0 ± 0.4
Hardwoods	Middle age	19	CWD/live wood ratio, %	2.5 ± 0.9	1.2 ± 0.3
	Mature and old	16		5.7 ± 2.0	4.0 ± 1.4

Table 4. Mean bulk density of CWD (± SE).

Debris type	Species group	Age group	Number of plots	Mean bulk density of CWD, Mg m^{-3}
Logs	All	Disturbed	6	0.296 ± 0.016
		Young	26	0.185 ± 0.016
	Conifers	Middle age	43	0.246 ± 0.006
		Mature and old	31	0.237 ± 0.008
	Hardwoods	Middle age	5	0.110 ± 0.035
		Mature and old	14	0.274 ± 0.026
Snags	All	Disturbed	5	0.293 ± 0.012
		Young	12	0.280 ± 0.025
	Conifers	Middle age	43	0.327 ± 0.006
		Mature and old	28	0.319 ± 0.008
	Hardwoods	Middle age	6	0.333 ± 0.027
		Mature and old	10	0.345 ± 0.019

of snags also occurred among the younger forests more frequently than in other age groups. On average, the volume of logs in plots was greater than the volume of snags (Table 3).

The distribution of CWD material by decay classes varied with forest age. In younger forests most of the CWD volume and mass belonged to decay classes 3–5, while in older forests most of the CWD material was in decay classes 1 and 2 (Fig. 4). In forests older than 80 yr the largest proportion of CWD is concentrated in decay class 2, while decay classes 1 and 2 play approximately equal role between ages 21 and 80. The mass of CWD in all decay classes is greater in the older forests than in younger ones.

The bulk density of CWD material found in log form was consistently lower than the bulk density of snags in all forest stand categories except disturbed stands, where most of the inventoried CWD was produced simultaneously and thus displayed similar bulk density (Table 4). The bulk density of logs was especially low in young and middle aged hardwood forests. In both of these categories the lack of new CWD material and the advanced decomposition of CWD left from the previous generation of trees probably explains the low bulk density of logs.

Analysis of regional stores of CWD

The visual estimates of CWD were reported in the forest inventory database only for a small fraction of the total forest area – between 4.4 and 13.5% in the studied forests

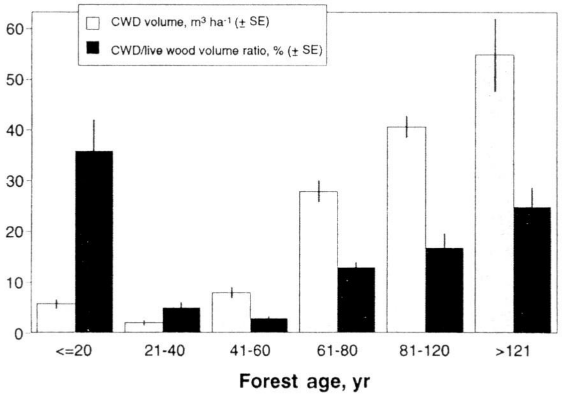

Fig. 2. Changes of CWD volume and CWD/live wood volume ratio with the age of forest stands in sample plots.

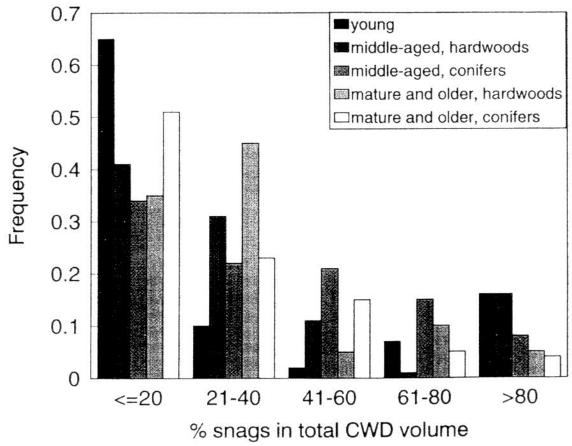

Fig. 3. Proportion of snags in total CWD volume (frequency of occurrence among sample plots).

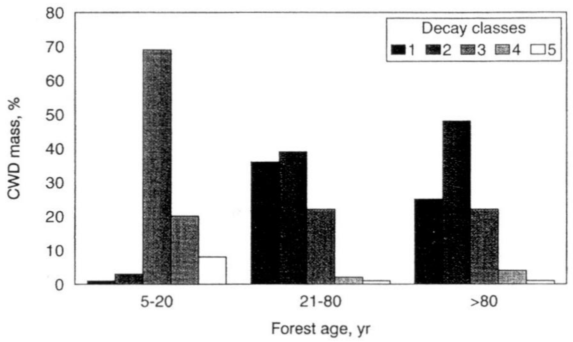

Fig. 4. The distribution of CWD mass in sample plots by decay classes (from nearly sound wood in decay class 1 to the most advanced stages of decomposition in decay class 5).

(Table 1). However, these estimates represent the sites with the highest concentrations of dead wood and taking them into account was quite important for calculating landscape-level stores: estimates based on CWD reported in the forest inventory database made up 12–29% of the total CWD volume (the remainder was calculated based on the volume, species and age of live trees). The fraction of forest area where CWD volumes were estimated in the field varied with species and age of forest stands (Fig. 5). It ranged from 1% in forests between ages 20 and 40; to over 25% in aspen stands age 80 and older. The volume of CWD was visually estimated on 14% of clearcut areas and on 54% of the area of dead forests.

The mean stores of CWD varied with forest age and the pattern was different among tree species (Fig. 6a, b). The amount of CWD declined with age in young forests and reached the minimum in stands 20–30 yr old. In older forests the amount of CWD increased to a level ranging from 30 to 50 m^3 ha^{-1} (7.0 to 15.3 Mg ha^{-1}) depending on the dominant tree species. The small number of stands older than 110 yr among hardwoods and older than 140 yr among conifers precluded the analysis of CWD stores beyond these ages. The variation of average CWD volume and mass in species × age groupings was moderate among the examined forests. The standard error of means was within 12% of the mean values with the exception of mature and older aspen forests where the standard error of the means reached 20%. The differences in CWD stores among forests of the same age but with different dominant species were statistically significant in many cases (Fig. 6).

The store of CWD in recently disturbed forests depended on the type of disturbance: clearcuts stored 24 m^3 ha^{-1} (9.5 Mg ha^{-1}), while stands affected by natural disturbance stored 145 m^3 ha^{-1} (57 Mg ha^{-1}). In spite of this high per-ha store, the contribution of disturbed forests to the landscape–level store of CWD is relatively small (1–10%, Table 5). The largest fraction of the overall dead wood store in the forest landscape usually comes from mature and older forest stands, which have lower stores per unit area, but are more extensive than recently disturbed areas.

The CWD ratio followed a pattern of change with forest age similar to the absolute amount of CWD (Figs 6, 7). However, for the CWD ratio the decline continued longer and the differences between species were better expressed among young stands (the ratio was lower among hardwoods than among conifers). After age 80 the species curves converged and the average ratio gradually increased from 0.14 at age 80 to 0.17 at age 120 and older (Fig. 7). The CWD ratio could not be calculated for many stands younger than 20 yr because their live wood volume was not reported in the forest inventory database (the volume of live wood is only reported when it exceeds 40 m^3 ha^{-1}). No significant effect of site productivity on CWD ratio was evident in middle-aged, mature, and older forests, but in young forest stands the ratio was higher on sites with lower productivity (Fig. 8).

We found a high positive correlation between forest age and the average amount of CWD (both volume and mass) following the period of CWD decline in the early stages of

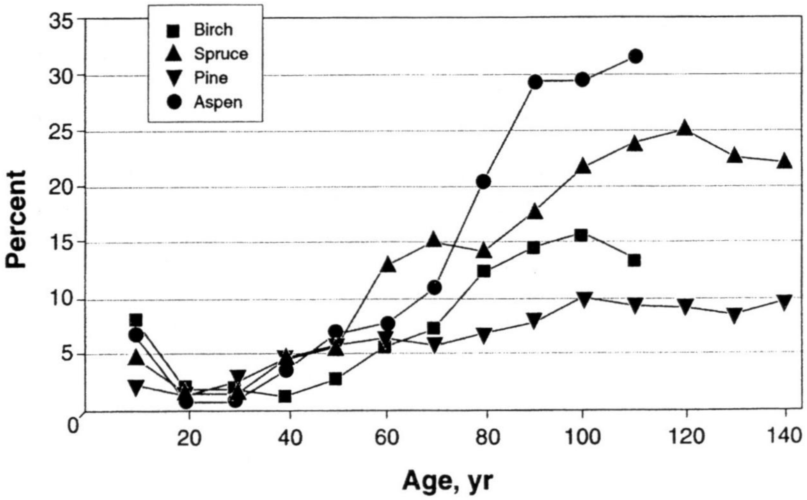

Fig. 5. Percent of total forest area where visual field estimates of CWD volume are reported in forest inventory database.

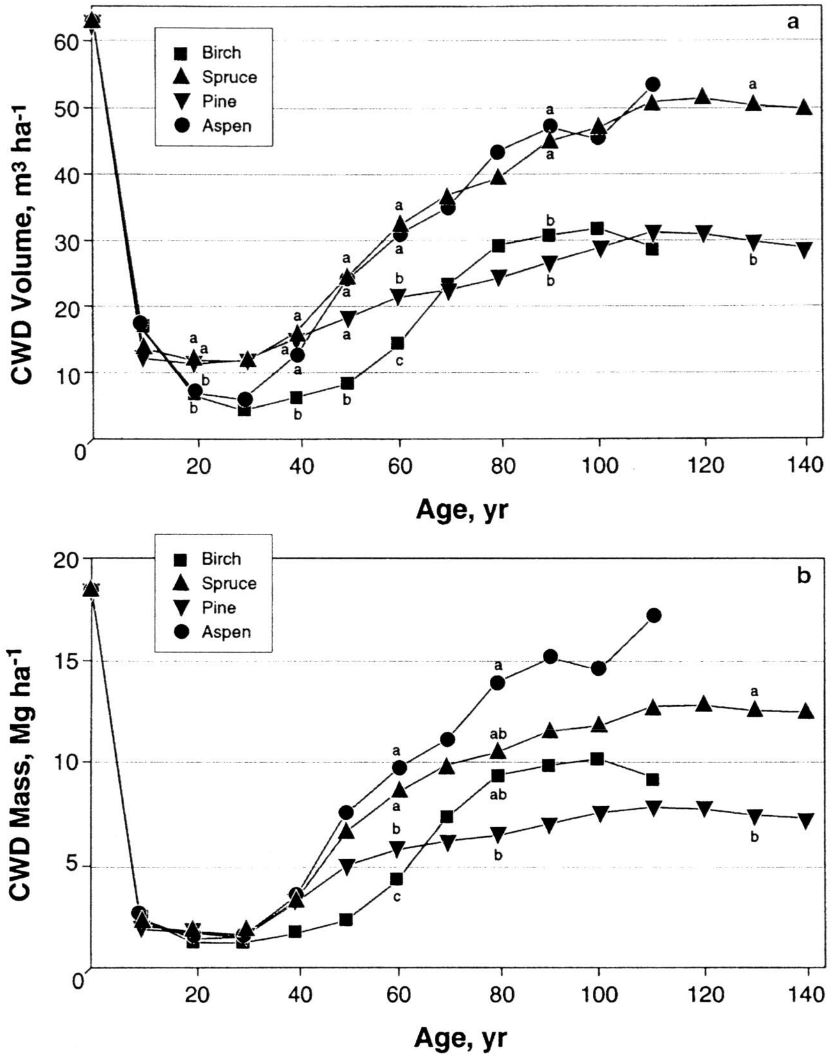

Fig. 6. Changes of CWD volume a) and mass b) with the age of forest stands. Data points for a given age marked by the same letter are not significantly different (ANOVA with the Tukey pairwise mean comparison test, $p<0.05$ (Anon. 1985)).

stand development (Table 6). The correlation between CWD ratio and age was weaker particularly in aspen. However, the positive and statistically significant slope values indicate that for the examined age interval (50–130 yr in conifers and 50–100 yr in hardwoods) the rate of CWD accumulation exceeds the rate of accumulation of live wood.

Analysis of variance of the CWD mass within species (4) × age group (3) × productivity level (3) classes showed that these factors and their interactions explain 95% of the total variance. Forest age was the most significant factor, followed by productivity level and species.

Among the seven selected forests the average store of CWD ranged from 5.15 to 7.39 Mg ha^{-1} (Table 5). If we take the store of CWD in mature and older forests as a conservative estimate of the potential maximum store of CWD, then the current stores are 2.5–4.6 Mg ha^{-1} lower and represent 55–75% of this maximum.

Discussion

Accurate estimation of dead wood amount and distribution across large areas is important for understanding and managing CWD for a variety of goals, including carbon sequestration and biodiversity. Because past research and existing forest inventories focus primarily on live trees, there is little data available to support large-scale estimates (Harmon et al. 2001). Our experience shows that the Russian Forest Inventory Data combined with results of targeted field measurements can be effectively used to study the regional stores of CWD. This approach offers a cost-effective alternative to implementation of a probability sampling system (e.g. Cohran 1977), which is desirable but may be practically impossible, particularly on vast forest lands of Russia. The estimator ratios were derived from CWD measurements in plots that were mostly set up for various purposes unrelated to the present CWD study.

Table 5. CWD stores in selected forests: average mass of CWD in Mg ha^{-1} and percent of total CWD store in the forest contributed by different categories of forest lands.

Forest name	Disturbed forest (clearcuts and dead) Mg ha^{-1} (%)	Young Mg ha^{-1} (%)	Middle-aged Mg ha^{-1} (%)	Mature and older Mg ha^{-1} (%)	Average for all forest lands Mg ha^{-1}
Kingisseppskii	17.3 (4)	1.7 (14)	5.9 (39)	9.3 (43)	5.15
Lisinskii	14.7 (3)	2.4 (15)	8.5 (45)	10.0 (37)	6.5
Luzhskii	30.7 (10)	2.0 (9)	6.3 (25)	10.3 (58)	6.99
Podborovskii	14.8 (1)	2.1 (16)	6.2 (26)	10.3 (57)	5.77
Podporozhskii	15.5 (1)	2.2 (12)	7.0 (21)	10.2 (66)	6.61
Roschinskii	25.5 (3)	2.0 (5)	7.9 (69)	9.9 (23)	7.39
Volkhovskii	11.7 (2)	2.1 (13)	6.3 (23)	11.1 (62)	6.46

Therefore the location of most plots (over 70% of the total) was random with respect to the goal of this study.

The prevalence of logs over snags in sample plots and the wide range of variation in the proportion of snags (Fig. 3) suggests that it is difficult to estimate the total CWD store from field studies where CWD measurements are limited to snags. Unfortunately, it is standard in many forest inventory systems to include only standing dead trees in routine measurements on sample plots (Anon. 1995). Proposed new guidelines for including CWD measurements into forest inventory process in Russia will help to correct this problem. A significant difference in wood density between logs and snags (Table 3) also indicates the importance of inventorying these two types of CWD separately.

The relatively low proportion of snags in most plots may reflect the transitory nature of this biomass component. The proportion of snags can increase temporarily after a period of increased tree mortality, but with time the snags fall over. In the St. Petersburg region the trees that die standing fall over in ca 10 yr, while the retention of CWD material in the log pool is much longer (Krankina and Harmon 1995). In addition, an unknown proportion of tree mortality transfers wood directly into the log pool without the intermediate snag stage. A relatively high proportion of snag-dominated CWD measurements among younger stands (Fig. 3) reflects the different types of stand-replacing disturbances that initiated these young forests: fires produce large amounts of snags, while windthrows and harvesting mostly generate downed material. Although clearcutting is sometimes viewed as a proxy for wildfire disturbance, the type of CWD material it generates is quite different. The high frequency of field measurements where the proportion of snags is small was observed worldwide (Harmon et al. 2001), but in the St. Petersburg region the overall prevalence of logs appears to be particularly high. The humid maritime climate in St. Petersburg region and widespread poor drainage conditions may contribute to the development of butt rots in dead trees causing them to fall.

The results derived from the forest inventory database demonstrate patterns of successional dynamics of CWD

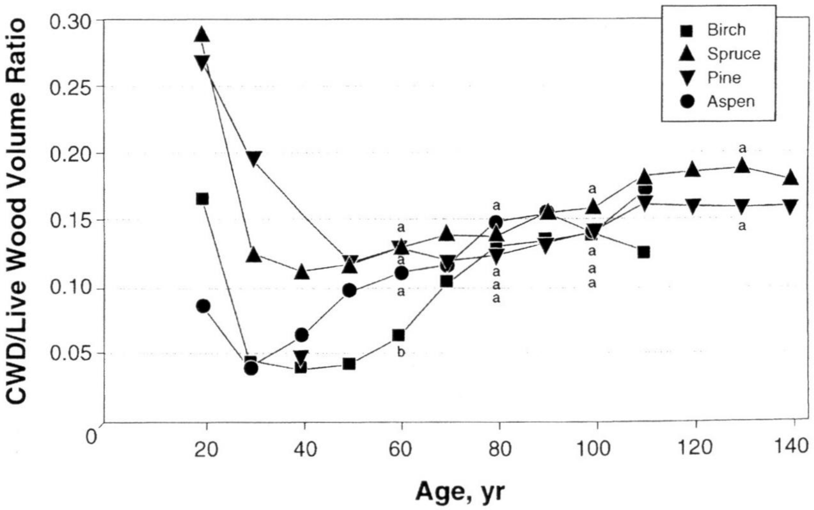

Fig. 7. Changes of CWD ratio with the age of forest stands. Data points for a given age marked by the same letter are not significantly different (ANOVA with the Tukey pairwise mean comparison test, $p<0.05$ (Anon. 1985)).

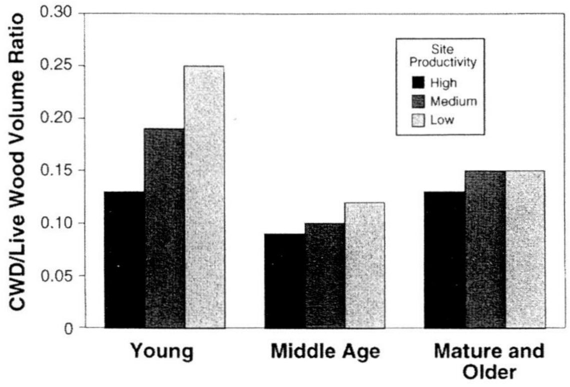

Fig. 8. CWD ratio in forests of different productivity levels and age groups.

similar to those previously projected by models and observed in plots (Krankina and Harmon 1994, 1995, Krankina et al. 1999). Additional data allowed us to make comparisons among the major dominant tree species and to examine the effects of site productivity. The diverging levels of CWD mass among mature forests of different species (Fig. 6) correspond to the relative abundance of high-productivity stands: for pine, birch, spruce, and aspen the average fraction of high-productivity stands in the mature and older age-group is 16.7, 43.7, 60.3, and 92.3%, respectively. This is a reflection of both the differences in ecological characteristics among the four species (pine and birch are more tolerant to poor site conditions than spruce and aspen) and in their management. The removal of more productive mature conifers by timber harvest increases the relative abundance of low-productivity forests in older age classes. At the same time, there is relatively little demand for hardwoods, especially aspen, and therefore the distribution of mature hardwoods is less affected by past timber harvest. Relatively high stores of CWD in mature spruce and aspen stands are probably associated with the higher productivity level for these types. In addition, aspen is prone to mortality caused by heart-rot fungi, especially in older forests.

Differences in forest stand productivity and disturbance history appear to override the influence of decomposition rates on CWD stores. Because conifers decompose slower than hardwoods (Krankina and Harmon 1995) one would expect the stores of CWD to be generally higher in conifer forests, however, our results do not support this assumption. Furthermore, the differences among the individual dominant species show the importance of taking tree species (or at least genus) into account in regional assessments of dead wood stores. Classification of forests into conifers and hardwoods in our study area would have obscured the differences related to species and led to the conclusion that there are no significant differences in CWD dynamics between conifer and hardwood forests.

While the general pattern of successional change is quite consistent with earlier reports, the rate of change in CWD stores during the early stages of forest stand development is in apparent contradiction with the rates of CWD decomposition measured in the region. The exponential rate constants, which include both mass and volume losses equal 3.3% for pine, 3.4% for spruce, and 4.4% for birch (Krankina and Harmon 1995). These rates suggest that CWD material will lose 50% of its mass in 15–21 yr, while the loss of mass in young forests appears to occur much faster (Fig. 6 and Table 5). Obviously, the kinds of disturbance that produced the young stands

Table 6. Regression analysis of CWD volume, mass, and CWD/live wood volume ratio over forest age in the selected forests in the St. Petersburg region. Each observation is the mean value of dependent variable in forest stands of a given age and dominant tree species within a selected forest.

Dependent variable	Species	Range of independent variable (age)	Number of observations	Intercept (SE)	Slope (SE)	r^2	F (Pr>F)
CWD volume	Pine	30–140	60	9.97 (1.32)	1.65 (0.14)	0.69	131 (0.0001)
	Spruce	30–140	60	6.64 (2.11)	3.67 (0.23)	0.82	257 (0.0001)
	Birch	30–110	45	–7.65 (4.0)	3.89 (0.35)	0.74	125 (0.0001)
	Aspen	30–110	43	–7.81 (4.77)	5.85 (0.65)	0.66	80 (0.0001)
CWD mass	Pine	30–140	60	2.33 (0.43)	0.45 (0.05)	0.62	94 (0.0001)
	Spruce	30–140	60	1.60 (0.67)	0.95 (0.07)	0.75	173 (0.0001)
	Birch	30–110	45	–2.77 (0.86)	1.30 (0.12)	0.75	127 (0.0001)
	Aspen	30–110	43	–2.74 (1.57)	1.94 (0.22)	0.66	81 (0.0001)
CWD ratio	Pine	50–130	45	0.085 (0.007)	0.006 (0.001)	0.63	72 (0.0001)
	Spruce	50–130	45	0.074 (0.010)	0.009 (0.001)	0.62	71 (0.0001)
	Birch	50–100	30	–0.045 (0.003)	0.020 (0.003)	0.65	53 (0.0001)
	Aspen	50–100	29	0.044 (0.035)	0.011 (0.005)	0.19	6 (0.0184)

present in the region do not necessarily correspond to those included in the "disturbed" category at the time of the last forest inventory. In the seven forests examined the store of CWD in recently disturbed forests averaged 18.6 Mg ha^{-1} and declined to 1.3–1.8 Mg ha^{-1} (10–14 times) in young forests (20 yr old, Fig. 6), while the exponential decomposition model would project 6.6–8.7 Mg ha^{-1} of CWD. One possible explanation of this inconsistency is the change in decomposition rate over time (Harmon et al. 2000). The observed loss of mass implies a decomposition rate of ca 10% which is similar to the rate that was measured using the new decomposition vector (or remeasurement) method in all birch logs and in pine logs during the middle (fast) stage of decomposition (Harmon et al. 2000). Other factors could contribute to the decline of CWD following disturbance, including wood salvage after natural disturbance events and fragmentation of CWD in the process of soil preparation for plantations. Additional research is needed to examine how each of these factors contributes to the drop in CWD store following stand-replacing disturbance.

The average stores of CWD correlate closely with the age of forest stands of a given tree species (Table 6), thus the age class composition of forests within the major dominant tree species in the region can serve as a basis for estimating the regional stores of CWD. However, the analysis of our plot data shows that at the individual stand level this correlation is weak and projections of CWD stores in a forest stand will have large errors. In forest regions where the natural disturbance regime is largely replaced by timber harvest (as in the St. Petersburg region) the contribution of disturbed forests to overall CWD stores is fairly low (Table 5) and the abundance of CWD material is associated mostly with the presence of older forest stands.

Our estimates of CWD stores averaged over the entire forest area (5.15–7.39 Mg ha^{-1}) agree with the results of an earlier assessment of CWD stores in the region (6.66 Mg ha^{-1}, Kobak et al. 1999). However, our analysis of changes in CWD stores with the age of forest stands calls into question the notion that CWD in the boreal zone does not accumulate as the forest grows older (e.g. Alexeyev et al. 1998).

The estimated decline in average CWD stores by 2.5–4.6 Mg ha^{-1} can be largely attributed to the long history of forest management in the St. Petersburg region. Considering that the total forest area in the region is 4577×10^3 ha, the decline in regional stores of CWD represents the net cumulative release of 5.7–10.5 million tonnes of carbon into the atmosphere. This loss of carbon occurred on existing forest lands and does not include potentially greater losses associated with land-use change. The present regional stores of CWD are probably at a very low level because timber harvesting in the region peaked during the late 1980s. In the near future the regional stores of CWD can be expected to increase as timber harvest is presently in deep decline (Kobak et al. 1999). These changes will likely improve the habitat conditions for species dependent on CWD for their survival (Kirby and Drake 1993, Samuelsson et al. 1994, McMinn and Crossley 1996, Jonsell et al. 1998, also see other papers in this volume). However, expanding thinning regimes that prevent some of the natural tree mortality may contribute to further decline in CWD pool (e.g. Alexeyev et al. 1998). Promising forest management options that could enhance the stores of CWD in the region include extending harvest rotations, retention of trees on clearcuts, and improved silvicultural treatments to boost stand productivity and stocking levels (Krankina and Harmon 1994, Franklin et al. 1997).

Acknowledgements – This work was sponsored by the National Science Foundation Long-term Studies Program (DEB-9632929) and Terrestrial Ecology Program (DEB-9652618), by USDA-CSRS-NRICGP (Contract #95-37109-2181), NASA Land Cover and Land Use Change Program (NAG5-6242), and the Federal Forest Service of the Russian Federation.

References

Alexeyev, A. S., Tietiukhin, S. V. and Sennov, S. N. 1998. Forestry as a basis for sustainable forest management. – In: Selikhovkin, A. V. (ed.), Sustainable forest management: scientific basis and concepts. – For. and Environ. Group LTD, St. Petersburg – Joensuu, pp. 89–156.

Alexeyev, V. et al. 1995. Carbon in vegetation of Russian forests: methods to estimate storage and geographical distribution. – Water Air Soil Pollut. 82: 271–282.

Anon. 1985. SAS statistics guide for personal computers. Ver. 6. – SAS Inst., Cary, NC.

Anon. 1995. Guidelines for inventory of the state forest lands of Russia. – Russian Federal For. Serv., Moscow, Russia, in Russian.

Bader, P., Jansson, S. and Jonsson, B. G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. – Biol. Conserv. 72: 1–8.

Berg, A. et al. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat association. – Conserv. Biol. 8: 718–731.

Cochran, W. G. 1977. Sampling techniques. – Wiley.

Franklin, J. F. et al. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. – In: Kohm, K. A. and Franklin, J. E. (eds), Creating a forestry for the 21st century. Island Press, pp. 111–139.

Harmon, M. E. and Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. – Publication #20, U.S. LTER Network Office, Univ. of Washington, Seattle, WA, USA.

Harmon, M. E. et al. 1986. Ecology of coarse woody debris in temperate ecosystems. – Adv. Ecol. Res. 15: 133–302.

Harmon, M. E., Krankina, O. N. and Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. – Can. J. For. Res. 30: 76–84.

Harmon, M. E. et al. 2001. Predicting broad-scale carbon stores of woody detritus from plot-level data. – In: Lai, R., Kimble, J. and Stewart, B. A. (eds), Assessment methods for soil carbon. CRC Press, New York, pp. 533–552.

Isaev, A. S. et al. 1993. Estimation of carbon pool and its annual deposition in phytomass of forest ecosystems in Russia. – Lesovedenie 5: 3–10, in Russian.

Jonsell, M., Weslien, J. and Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. – Biodiv. Conserv. 7: 749–764.

Kirby, K. J. and Drake, C. M. 1993. Dead wood matter: the ecology and conservation of saproxylic invertebrates in Britain. – English Nature Science No. 7, Peterbourough, U.K.

Kobak, K. I. 1988. Biotical components of carbon cycle. – Leningrad, Gydrometeoizdat, in Russian.

Kobak, K. I., Kukuev, Y. A. and Treyfeld, R. F. 1999. The role of forests in changing carbon content of the atmosphere (example from Leningrad region). – Lesnoye Khoziajstvo 5: 43–45, in Russian.

Kolchugina, T. P. et al. 1992. Carbon balance of forest biomes (undisturbed ecosystems) in the former Soviet Union. – In: Proc. of the IPCC Workshop, Univ. of Joensuu, Finland, pp. 52–62.

Krankina, O. N. and Dixon, R. K. 1994. Forest management options to conserve and sequester terrestrial carbon in the Russian Federation. – World Resour. Rev. 6: 88–101.

Krankina, O. N. and Harmon, M. E. 1994. The impact of intensive forest management on carbon stores in forest ecosystems. – World Resour. Rev. 6: 161–177.

Krankina, O. N. and Harmon, M. E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forest. – Water Air Soil Pollut. 82: 227–238.

Krankina, O. N. et al. 1998. The use of Russian forest inventory data for carbon budgeting and for developing carbon offset strategies. – World Resour. Rev. 10: 52–66.

Krankina, O. N., Harmon, M. E. and Griazkin, A. V. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: northwestern Russia. – Can. J. For. Res. 29: 20–32.

Kukuev, Y. A., Krankina, O. N. and Harmon, M. E. 1997. The forest inventory system in Russia. – J. For. 95: 15–20.

McMinn, J. W. and Crossley, D. A. (eds) 1996. Biodiversity and coarse woody debris in southern forests. – USDA For. Serv. Gen. Tech. Rep. SE-94.

Melillo, J. M. et al. 1988. Land-use change in the Soviet Union between 1850–1980; cause of a net release of CO_2 to the atmosphere. – Tellus 40: 116–128.

Samuelsson, J., Gustafsson, L. and Ingelög, T. 1994. Dying and dead trees: a review of their importance for biodiversity. – Swedish Environ. Prot. Agency Rep. 4306, Uppsala.