# Effects of climate, disturbance, and species on forest biomass across Russia[1]

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**Abstract:** We used detailed forest inventory data from 43 forests ($3.5 \times 10^3 - 115.2 \times 10^3$ stands each) and meteorological data from 30 weather stations located in proximity to these forests to assess the effects of disturbance and climate on biomass accumulation patterns across the forest zone of Russia. Chronosequences of biomass accumulation following disturbance were developed for each of the two to five dominant tree species in each forest using stand survey data collected by forest inventories in different regions of Russia between 1986 and 2003. These chronosequences represent changes in average live biomass of forest stands between age 10 and 210 years at 10-year intervals. The correlation of attributes of biomass accumulation (i.e., maximum biomass, biomass at age 40, and maximum biomass increment) with climatic and disturbance attributes was significant but weak (adjusted $R^2$ = 0.20–0.37). The effect of the most influential disturbance attributes (percent clear-cut and percent old forest) was as strong or stronger than the effect of climatic attributes (30-year averages of the sum of positive daily temperatures and climate moisture index). The effect of tree species was significant, but weaker than the effects of climate or disturbance. Combining climate, disturbance, and species attributes generally improved the models (adjusted $R^2$ = 0.37–0.53). The patterns of biomass change observed in chronosequences are influenced by the tendency of harvesting to target more productive forest stands of commercially valuable species, creating a disparity in productivity among the age cohorts. The apparent link between disturbance attributes of forests and biomass accumulation patterns in forest stands may be used to improve broad-scale modeling of changes in forest biomass with remotely sensed data.

**Résumé :** Les auteurs ont utilisé des données détaillées d'inventaire forestier provenant de 43 forêts ($3,5 \times 10^3 - 115,2 \times 10^3$ peuplements chacune) et des données météorologiques provenant de 30 stations météorologiques situées à proximité de ces forêts pour évaluer les effets des perturbations et du climat sur les patrons d'accumulation de biomasse dans l'ensemble du territoire forestier de la Russie. Des chronoséquences d'accumulation de biomasse à la suite de perturbations ont été développées pour chacune des deux à cinq espèces dominantes dans chacune des forêts à l'aide de données d'inventaire de peuplements collectées lors d'inventaires forestiers dans différentes régions de la Russie entre 1986 et 2003. Ces chronoséquences représentent les changements dans la biomasse vivante moyenne des peuplements forestiers âgés de 10 à 210 ans à intervalle de 10 ans. La corrélation des attributs de l'accumulation de biomasse (c.-à-d. la biomasse maximum, la biomasse à 40 ans et l'accroissement maximum de biomasse) avec les attributs du climat et des perturbations était significative mais faible ($R^2$ ajusté = 0,20–0,37). L'effet des attributs de la perturbation qui a le plus d'influence (les pourcentages de coupe à blanc et de forêt ancienne) était aussi sinon plus important que l'effet des attributs du climat (moyenne de 30 ans de la somme des températures quotidiennes positives et indice d'humidité du climat). L'effet de l'espèce d'arbre était significatif mais plus faible que les effets du climat ou des perturbations. Les modèles étaient généralement améliorés ($R^2$ ajusté = 0,37–0,53) en combinant les attributs du climat, des perturbations et de l'espèce. Les patrons de changement dans la biomasse observés dans les chronoséquences sont influencés par la tendance à récolter les peuplements les plus productifs avec des essences commerciales de grande valeur, créant ainsi une disparité dans la productivité parmi les cohortes d'âge. Le lien apparent entre les attributs des perturbations dans les forêts et les patrons d'accumulation de biomasse dans les peuplements forestiers pourrait être utilisé pour améliorer la modélisation à grande échelle des changements dans la biomasse de la forêt à partir de données obtenues par télédétection.

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## Introduction

The boreal forest is one of the most extensive biomes on Earth and plays a major role in the global climate system as a potential sink or source of atmospheric carbon and through effects on albedo and energy partitioning (e.g., Foley et al. 1994; Pielke and Vidale 1995). A single country, Russia, holds 22% of global forest resources or half of the global area of boreal forest (FAO 2001) and remains a major source of uncertainty in global estimates of forest cover and carbon balance. Analyses based on atmospheric inversion models indicate that high latitudes were a modest sink of carbon during the 1980s and early 1990s (e.g., Bousquet et al. 1999; Dargaville et al. 2000) and that most of the sink was in Eurasia (Schimel et al. 2001). These results are consistent with analyses based on forest inventory data, which suggest that Russia was responsible for a carbon sink of 0.1–0.4 Pg C·year$^{-1}$ in the early to mid-1990s (Liski and Kauppi 2000; Myneni et al. 2001; Goodale et al. 2002; Zhou et al. 2003; Shvidenko and Nilsson 2003). The uncertainty of these estimates is large, and the future role of these forests depends on a complex interaction of natural forces and human activities. The ratification of the Kyoto Protocol by Russia in October 2004 created renewed impetus to reduce the uncertainty of the role of Russian forests in carbon exchange with the atmosphere, to create transparent methods for monitoring terrestrial carbon stores and flux, and to inform the decision-making process for managing carbon in forest ecosystems as part of the overall national forest management strategy (Strakhov et al. 2003).

The current pattern of forest vegetation and its role in carbon cycling has resulted from the combined effects of anthropogenic and natural disturbances over a range of time scales. In addition, the effects of disturbance on carbon stores and flux depend strongly on the spatial and temporal scales of the assessment, and different processes may need to be considered depending on the scale (e.g., Harmon 2001). In many parts of the world, the legacy of land use and forest management is a major driving force that determines the transition of forest stands, landscapes, and regions from carbon sinks to sources and back (Kurz and Apps 1999; Houghton et al. 1999, 2000; Janisch and Harmon 2002; Law et al. 2004). For example, historical changes in land use were identified as the dominant factor governing the rate of carbon accumulation in the eastern United States, with tree growth enhancement contributing far less than previously reported (Caspersen et al. 2000). While the importance of land use in defining the carbon cycling processes of terrestrial ecosystems is widely accepted, there remains large uncertainty as to the relative roles of land use, climate, and fertilization by $CO_2$ and nitrogen (Schimel et al. 2001).

Climate broadly defines the distribution of vegetation types, species, and plant productivity across continents and large geographic regions. Across much of Northern Eurasia, short growing seasons and cold temperatures limit growth and regeneration of many plant species, and future warming may change species composition and carbon balance in the ecosystems that occupy this region. The net effect of these changes is, however, difficult to project. For example, increases in fire frequency and soil warming have the potential to quickly release large amounts of carbon (McGuire et al.

2004; Goulden et al. 1998; Kasischke and Bruhweiler 2002), and these responses may more than offset increases in carbon storage that might arise from increased productivity and the slow expansion of boreal forest into tundra regions. Between 1940 and 2000 the warming trend in Northern Eurasia was among the highest in the world (0.17 °C per decade; Bulygina et al. 2003), and in Siberia it was especially high (1.0 °C per decade; Folland et al. 2001). Observed changes include a decrease in the diurnal temperature range (Easterling et al. 1997) and a greater frequency of extreme events (Gruza et al. 1999). Quantitative predictions of the potential impact of climate change on the boreal forest zone require an understanding of the relationships between climatic factors and biomass accumulation across the region.

A major impediment to understanding terrestrial carbon exchange is the lack of field measurements that cover the full range of natural variability of vegetation attributes. Data from experimental plots are sparse (Bazilevich 1993; Scurlock et al. 1999) and tend to be biased towards more productive sites and economically important species (Clark et al. 2001; Gower et al. 2001). Forest inventories can provide an additional source of field data, and regional summaries of these data have been widely used for broad-scale assessments of forest biomass (e.g., Goodale et al. 2002; Shvidenko and Nilsson 2003). To facilitate the use of these data for calculating live biomass, a set of conversion factors has been developed from an extensive database collected from ecological plots (Alexeyev and Birdsey 1998). In addition, a method for estimating regional stocks of coarse woody debris (CWD) was elaborated and tested in several regions of Russia (Treyfeld and Krankina 2001; Krankina et al. 2002). Regularly published summaries of forest inventory data (e.g., Filimonov et al. 1995) aggregate the primary data from individual forest stands to province- and country-wide totals by combining the field data collected over several decades and adjusting the results for changes (areas harvested, burned, planted) reported by the forest management enterprises. The coarse spatial resolution of aggregated data and the lack of detailed information on forest ages and tree species diminishes the utility of these data for examining the spatial patterns of biomass accumulation, whereas the use of inventory data for research purposes in their primary form (without aggregation) has been limited in Russia (and elsewhere) because access to these data is often restricted.

Past studies of the effects of disturbance on forest biomass focused primarily on the immediate impacts, such as the transfer of live biomass into detrital pools, transition of forest stands from old into younger age cohorts, and change in species composition from late-successional to early-successional groups (e.g., Kurz and Apps 1999; Houghton et al. 1999, 2000; Janisch and Harmon 2002). These studies often used chronosequences to calibrate the models of biomass accumulation with the age of forest stands, with the implicit assumption that except for the effects of climate (and $CO_2$ and nitrogen fertilization in some models) the patterns of biomass accumulation with stand age are constant, that is, independent of the changing disturbance regime. If the disturbance were random, this assumption would be correct; however, disturbance is not random: different forest types are not equally susceptible to natural disturbance factors and land-use practices target the most productive lands for conversion to agri-

**Fig. 1.** Schematic map of Russia with locations of forests and meteorological stations.
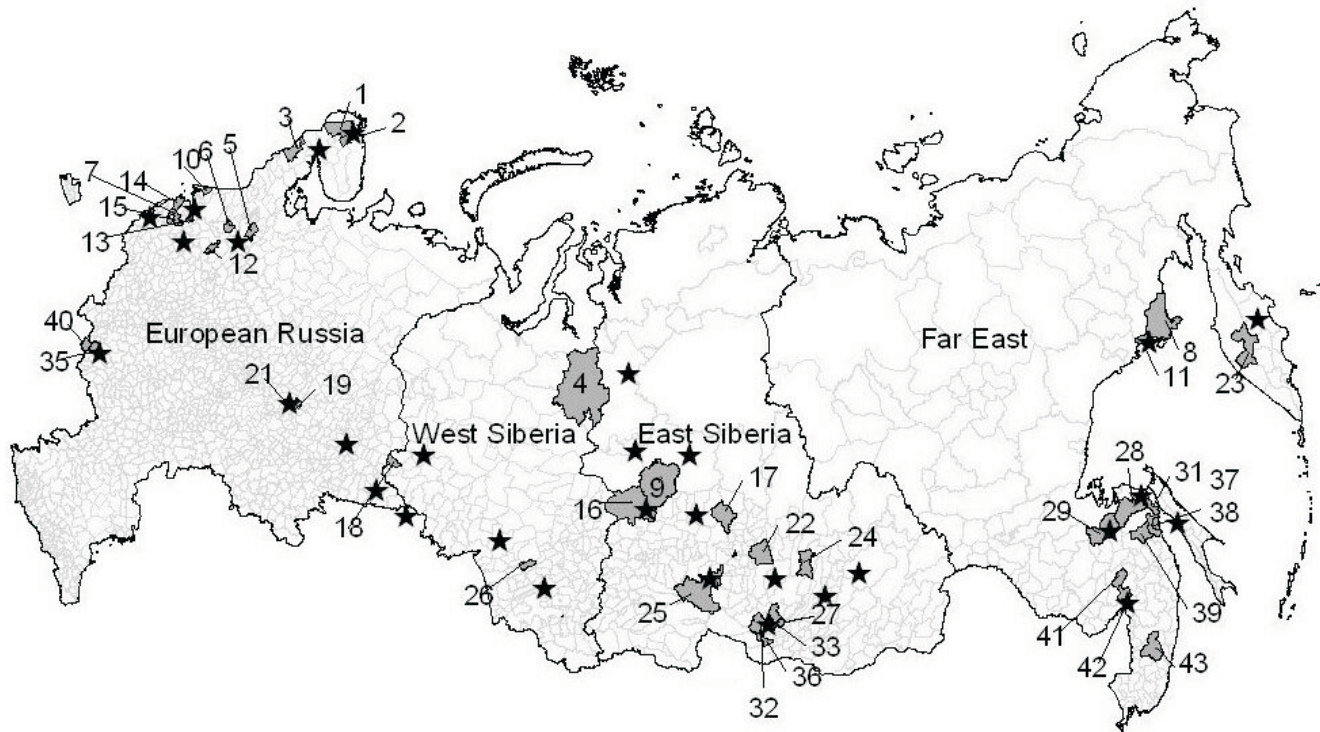


cultural use and timber harvest. The preference for harvesting productive forest stands of commercially valuable species not only selectively removes these stands from the old stand cohort, but it also increases the proportion of productive stands within the young stand cohort. In addition, forest plantations tend to produce faster growing stands with less lag time after disturbance than stands produced under natural regeneration processes. Thus, the legacy of forest disturbance and land use in forest landscapes and regions can be expected to influence the apparent patterns of biomass accumulation in forest stand chronosequences through changing the characteristics of the age cohorts of forest stands. These effects have been largely overlooked in past research.

The objective of this paper is to assess the effects of climate, disturbance regime, and dominant tree species on patterns of biomass accumulation across the forest zone of Russia. In framing this investigation the working hypothesis was that the patterns of biomass accumulation in a given location are linked primarily to the local climate and properties of tree species. We also anticipated that in locations with a long history of land use, the biomass accumulation might be depressed (relative to expectations based on climate and tree species) because of the conversion of the most productive lands to agricultural use and preferential harvest of the most productive mature forest stands for timber.

## Data and methods

To assess the effects of disturbance and climate on biomass accumulation patterns across the forest zone of Russia, two types of primary data were used: detailed forest inventory data for 43 forests and meteorological data for 30 weather

stations located in proximity to these forests (Fig. 1, Tables 1 and 2).

The forest inventory system in Russia collects consistent and detailed stand-level information on millions of hectares annually (Kukuev et al. 1997). The standard practice of carrying out a routine forest inventory is census based, whereby field crews survey each forest stand polygon (a homogeneous patch of forest vegetation), delineated from air photos and ranging in size from 0.3 to 100 ha. The inventory of a forest (i.e., forest management enterprise, or "leskhoz" in Russian) covers its entire territory, ranging in area from tens of thousands to several million hectares. Inventories are repeated at intervals ranging from 10 to >20 years; some forests have been inventoried only once. The standard set of data gathered in the field includes site productivity and drainage, tree species composition, mean height, diameter and age (rounded to the nearest 10 years for stands older than 50 years), canopy structure, wood volume, and characteristics of different types of land without tree cover (e.g., clearcuts, bogs, meadows). Over 200 different variables measured or visually estimated in the field are used to describe stand polygons, depending on the land-cover category and the management requirements for a given forest (for detailed descriptions of the Russian forest inventory system and samples of stand records, see Kukuev et al. 1997).

Forests were selected from among those inventoried between 1986 and 2003 to cover the variety of forest types, climatic conditions, and disturbance regimes within the forest zone of Russia. The area of live forest stands in each of these forests ranged from $14.7 \times 10^3$ to $3689.7 \times 10^3$ ha for a total of $23.9 \times 10^6$ ha. This represents about 3% of the total forest area of Russia (Filimonov et al. 1995). One of the larger forests (Kerbinskij) was split into two sets, and for

**Table 1.** Forest inventory data overview (forests are sorted by latitude beginning with the highest latitude).

| Forest name (administrative region) | Inventory year | Live forest area ($10^3$ ha) | Dead forest area ($10^3$ ha) | Clear-cut area ($10^3$ ha) | No. of stand records ($10^3$) | Species analyzed |
|---|---|---|---|---|---|---|
| 1. Kol'skij (Murmansk[a]) | 1999 | 623.2 | 1.6 | 5.1 | 25.8 | Pine, spruce, birch |
| 2. Murmanskij (Murmansk[a]) | 2000 | 354.3 | 0.2 | 0.5 | 18.9 | Pine, spruce, birch |
| 3. Pyaozerskij (Karelia[b]) | 1998 | 198.7 | 0.02 | 8.3 | 10.8 | Pine, spruce, birch |
| 4. Krasnosel'kup (Khanty-Mansi[c]) | 1998–1999 | 3689.7 | 3.3 | 1.9 | 115.2 | Pine, spruce, larch, siberian pine, birch |
| 5. Pudozhskij (Leningrad[a][d]) | 1998–1999 | 669.7 | 0.4 | 19.1 | 41.9 | Pine, spruce, birch |
| 6. Podporozhskii (Leningrad[a][d]) | 1992 | 201.3 | 0.3 | 2.1 | 25.3 | Pine, spruce, birch, aspen |
| 7. Roschinskij (Leningrad[a][d]) | 1992 | 175.1 | 0.9 | 2.1 | 56.9 | Pine, spruce, birch, aspen |
| 8. Olskij (Magadan[a]) | 2002 | 1545.9 | 51.7 | 1.5 | 10.8 | Larch |
| 9. Severo-Yenisejskij (Krasnoyarsk[e]) | 1995 | 112.6 | 0.5 | 0 | 3.7 | Pine, spruce, fir, siberian pine, birch, aspen |
| 10. Volkhovskii (Leningrad[a])[4] | 1992 | 143.3 | 0.2 | 3.4 | 20.5 | Pine, spruce, birch, aspen |
| 11. Magadanskij (Magadan[a]) | 1986 | 144.3 | 14.8 | 14.8 | 6.6 | Larch, birch |
| 12. Podborovskii (Leningrad[a][d]) | 1992 | 137.9 | 0.1 | 1.3 | 21.2 | Pine, spruce, birch, aspen |
| 13. Lisinskii (Leningrad[a][d]) | 1992 | 65.3 | 0.2 | 1.5 | 15.4 | Pine, spruce, birch, aspen |
| 14. Kingisseppski (Leningrad[a][d]) | 1992 | 127.4 | 0.5 | 3.0 | 25.6 | Pine, spruce, birch, aspen |
| 15. Luzhskii (Leningrad[a][d]) | 1992 | 89.5 | 3.3 | 3.9 | 20.5 | Pine, spruce, birch, aspen |
| 16. Nizhne-Yenisejskij (Krasnoyarsk[e]) | 1995 | 200.8 | 0.02 | 0 | 4.1 | Pine, spruce, larch, siberian pine, birch |
| 17. Kodinskii (Krasnoyarsk[e]) | 2003 | 891.9 | 4.5 | 6.0 | 26.4 | Pine, spruce, fir, larch, birch, aspen |
| 18. Tjumenskij (Tjumen'[a]) | 1998 | 83.0 | 1.7 | 0.9 | 17.0 | Pine, spruce, birch, aspen |
| 19. Wotkinsk (Udmurtia[b]) | 1997 | 50.8 | 0.05 | 3.0 | 11.6 | Pine, spruce, fir, birch, aspen |
| 20. Igirminskij (Irkutsk[a]) | 1998 | 681.0 | na | na | 29.4 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 21. Izhevskij (Udmurtia[b]) | 1997 | 77.1 | 0.03 | 3.0 | 18.5 | Pine, spruce, fir, larch, birch, aspen |
| 22. Shestakovskij (Irkutsk[a]) | 1997 | 1282.2 | 43.3 | 6.8 | 43.8 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 23. Bystritskii (Kamchatka[a]) | 1995–1996 | 1225.1 | 4.7 | 3.2 | 13.3 | Spruce, larch, birch |
| 24. Ul'kanskij (Irkutsk[a]) | 1996 | 647.3 | 13.3 | 5.7 | 18.1 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 25. Nizhne-Udinsk (Irkutsk[a]) | 1996 | 2549.1 | na | na | 48.7 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 26. Ordynskii (Novosibirsk[a]) | 1999 | 25.9 | 0 | 0.4 | 7.2 | Pine, birch, aspen |
| 27. Ust'-ordynski (Irkutsk[a]) | 1987 | 305.2 | 102.0 | 27.7 | 13.4 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 28. Tahtinskij (Khabarovsk[e]) | 1997 | 411.7 | 1.5 | 4.4 | 12.4 | Spruce, larch, birch, aspen |
| 29. Kerbinskij-East (Khabarovsk[e]) | 1996–1997 | 847.8 | 6.3 | 1.4 | 23.9 | Spruce, fir, larch, birch, aspen |
| 30. Kerbinskij-West (Khabarovsk[e]) | 1996–1997 | 372.7 | 0.3 | 0.01 | 5.6 | Spruce, larch |
| 31. Lasarevskij (Khabarovsk[e]) | 1994 | 343.3 | 24.8 | 8.3 | 11.0 | Spruce, larch, birch |
| 32. Usol'skij (Krasnoyarsk[e]) | 2000 | 88.4 | 4.1 | 1.5 | 3.5 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 33. Goloustovskij (Irkutsk[a]) | 2001 | 198.3 | 4.6 | 0.3 | 14.2 | Pine, spruce, larch, siberian pine, birch, aspen |
| 34. Angarskij (Irkutsk[a]) | 1996 | 91.7 | 13.4 | 0.6 | 13.4 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 35. L'govskij (Kursk[a]) | 2000 | 14.7 | 0 | 0.2 | 4.6 | Pine, birch, aspen |
| 36. Sludyanskij (Irkutsk[a]) | 1997 | 284.7 | 4.4 | 0.03 | 12.1 | Pine, spruce, fir, larch, siberian pine, birch, aspen |
| 37. Kizinskij (Khabarovsk[e]) | 1996 | 186.9 | 3.7 | 2.2 | 7.9 | Spruce, fir, larch, birch |
| 38. De-Kastrinski (Khabarovsk[e]) | 1994 | 383.4 | 17.7 | 11.8 | 16.0 | Spruce, fir, larch, birch, aspen |
| 39. Bystrinskij (Khabarovsk[e]) | 1996–1997 | 551.6 | 4.8 | 9.8 | 22.9 | Spruce, fir, larch, birch, aspen |
| 40. Ryl'skij (Kursk[a]) | 2000 | 31.3 | 0 | 0.4 | 8.7 | Pine, spruce, birch, aspen |
| 41. Bolonskij (Khabarovsk[e]) | 1995 | 309.2 | 1.8 | 3.5 | 10.7 | Spruce, larch, birch, aspen |
| 42. Litovskij (Khabarovsk[e]) | 1997 | 245.7 | 0.7 | 0.3 | 10.3 | Spruce, larch, birch, aspen |
| 43. Khorskij (Khabarovsk[e]) | 1999–2000 | 475.0 | 0.4 | 0.05 | 17.7 | Spruce, fir, larch, siberian pine, birch, aspen |

[a]Oblast (administrative region).
[b]Republic of (state within the Russian Federation).
[c]Autonomous region.
[d]Leningrad region was not renamed when the name of the regional center was changed to St. Petersburg in 1991.
[e]Kray (territory).

one forest (Olskij) the data from two consecutive inventories (1986 and 2002) were used. Within each forest we obtained stand-level databases, each containing records for 3500 – 115 200 forest stands, for a total of 923 000 stands (Table 1). For each forest stand we retrieved records of the stand area, the dominant tree species (tree species with the greatest stem volume), the volume of live stem wood over bark, and the age of trees. For stands where trees were clear-cut or killed by natural agents, only stand areas were recorded.

In each forest the records for live forest stands were grouped by dominant tree species and 10-year age-classes, and the average wood volume ($m^3 \cdot ha^{-1}$) was calculated for each grouping. These values were converted to tree biomass ($Mg \cdot ha^{-1}$) using a set of conversion factors differentiated by tree species, vegetation zone, and geographic region, with separate sets of factors for the Europe–Ural (Western) part of Russia and for the regions east of the Ural Mountains (Siberia and the Far East). These conversion factors were derived from an extensive compilation of biomass measurements made in re-

**Table 2.** Meteorological data overview: stations sorted by latitude beginning with the highest latitude.

| Station No. | Station name | Lat. (°N) | Long. (°E) | Annual sum of temp. >0 °C (°C) | Annual precip. (mm) | Climate moisture index | Forest No. from Table 1 |
|---|---|---|---|---|---|---|---|
| 22113 | Murmansk | 69.0 | 33.1 | 1362.6 | 477.0 | 27.7 | 1, 2 |
| 22217 | Kandalaksa | 67.1 | 32.4 | 1528.8 | 522.7 | 28.4 | 3 |
| 23472 | Turuhansk | 65.8 | 87.9 | 1419.5 | 562.5 | 31.0 | 4 |
| 22820 | Petrozavodsk | 61.8 | 34.4 | 2025.9 | 595.7 | 29.2 | 6 |
| 23891 | Bajkit | 61.7 | 96.4 | 1599.3 | 515.7 | 19.3 | 9 |
| 23884 | Bor | 61.6 | 90.2 | 1759.3 | 601.6 | 27.5 | 16 |
| 22837 | Vytegra | 61.0 | 36.5 | 2149.7 | 673.3 | 32.9 | 5, 12 |
| 26063 | Sankt-Peterburg (Leningrad) | 60.0 | 30.3 | 2545.0 | 640.0 | 29.0 | 7, 10, 13, 14, 15 |
| 25913 | Magadan | 59.5 | 150.7 | 1222.7 | 534.5 | 38.4 | 8, 11 |
| 26188 | Vereb'e | 58.7 | 32.7 | 2313.0 | 732.4 | 34.0 | 10 |
| 29263 | Enisejsk | 58.5 | 92.2 | 2021.8 | 474.5 | 10.2 | 9, 16 |
| 29282 | Boguchany | 58.4 | 97.5 | 2054.9 | 465.6 | –5.0 | 17 |
| 28275 | Tobol'sk | 58.2 | 68.2 | 2199.1 | 455.4 | 8.9 | 18 |
| 26406 | Liepaja | 57.8 | 28.3 | 2708.8 | 693.4 | 33.1 | 15 |
| 28411 | Igevsk | 56.9 | 53.3 | 2419.8 | 519.6 | 11.3 | 19, 21 |
| 28440 | Ekaterinburg | 56.8 | 60.6 | 2275.8 | 498.3 | 10.8 | 18 |
| 32389 | Kluci | 56.3 | 160.8 | 1689.8 | 634.8 | 28.0 | 23 |
| 28661 | Kurgan | 55.4 | 65.4 | 2564.1 | 382.4 | –8.1 | 18 |
| 29612 | Barabinsk | 55.3 | 83.7 | 2314.9 | 432.1 | –7.4 | 26 |
| 29698 | Nizne-Udinsk | 54.9 | 99.0 | 2029.4 | 397.5 | –2.6 | 25 |
| 30521 | Zigalovo | 54.8 | 105.2 | 1888.2 | 343.3 | –10.2 | 20, 22, 24, |
| 30555 | Troiskij Priisk | 54.6 | 113.1 | 1179.1 | 413.8 | 9.9 | 24 |
| 30636 | Barguzin | 53.6 | 109.6 | 2098.1 | 365.5 | –6.9 | 24 |
| 29838 | Barnaul | 53.4 | 160.8 | 2545.4 | 531.7 | –6.5 | 26 |
| 31369 | Nikolaevsk-na-Amure | 53.2 | 140.7 | 1924.3 | 639.0 | 29.2 | 28, 31 |
| 31416 | Im.Poliny Osipenko | 52.4 | 136.5 | 2187.8 | 475.9 | 2.7 | 29, 30, 39 |
| 30710 | Irkutsk | 52.3 | 104.3 | 2178.3 | 473.4 | 2.5 | 27, 32, 33, 34, 36 |
| 34009 | Kursk | 51.8 | 36.2 | 2889.0 | 642.7 | 16.0 | 35, 40 |
| 32061 | Aleks.-Sahalinskij | 50.9 | 142.2 | 2013.7 | 635.6 | 33.4 | 37, 38 |
| 31735 | Khabarovsk | 48.5 | 135.1 | 2856.2 | 668.6 | 24.4 | 41, 42, 43 |

search plots (Alexeyev and Birdsey 1998). The biomass estimate included the entire biomass of live trees (above ground and below ground), but did not include other biomass components (understory vegetation, litter, coarse woody debris).

We used the "species" designation accepted by the Russian forest inventory in which several species of the same genus are sometimes grouped together, while other major species are reported separately, as follows:

| | |
|---|---|
| Pine | *Pinus sylvestris* L. |
| Spruce | *Picea* spp. |
| Fir | *Abies* spp. |
| Larch | *Larix* spp. |
| Siberian pine | *Pinus siberica* Du Tour |
| | *Pinus koraiensis* Siebold & Zucc. |
| Aspen | *Populus tremula* L. |

The average biomass values in the 10-year age-classes form a set of chronosequences of biomass change with forest stand age for the major dominant tree species in each forest. We eliminated from this data set biomass averages based on less than three stand records, fragmented chronosequences,

and species that occurred in fewer than 10 forests. The final forest inventory data set included 205 chronosequences for seven dominant tree species (a sample of chronosequences is shown in Fig. 2).

From each chronosequence we derived three attributes that we expected to be linked to climate and disturbance regime: maximum biomass (Mg·ha$^{-1}$), which is the highest point on each chronosequence; biomass at stand age 40 years (Mg·ha$^{-1}$) which reflects biomass accumulation following disturbance; and maximum biomass increment (Mg·ha$^{-1}$·year$^{-1}$) calculated for the 10-year interval, where the change in biomass is the greatest in a given chronosequence. To characterize the patterns of biomass change in older stands we also calculated the percent decline of biomass after reaching the maximum by subtracting maximum biomass from the average value of biomass in all stands with ages greater than the stand age corresponding to maximum biomass and expressing this difference in percentage of maximum biomass. For those chronosequences where no clear maximum was found in ages up to 210 years (e.g., pine chronosequence in Kodinskij forest, Fig. 2), we calculated percent change in average biomass for ages >120 years compared to the average value for ages 100, 110, and 120 years. The percent biomass change in old forest stands (%BCOF) was negative for chronosequences where

**Fig. 2.** Sample of chronosequences of biomass accumulation with age of forest stands (indicating the range of values, variation in patterns, and chronosequence lengths); other 196 chronosequences not shown.
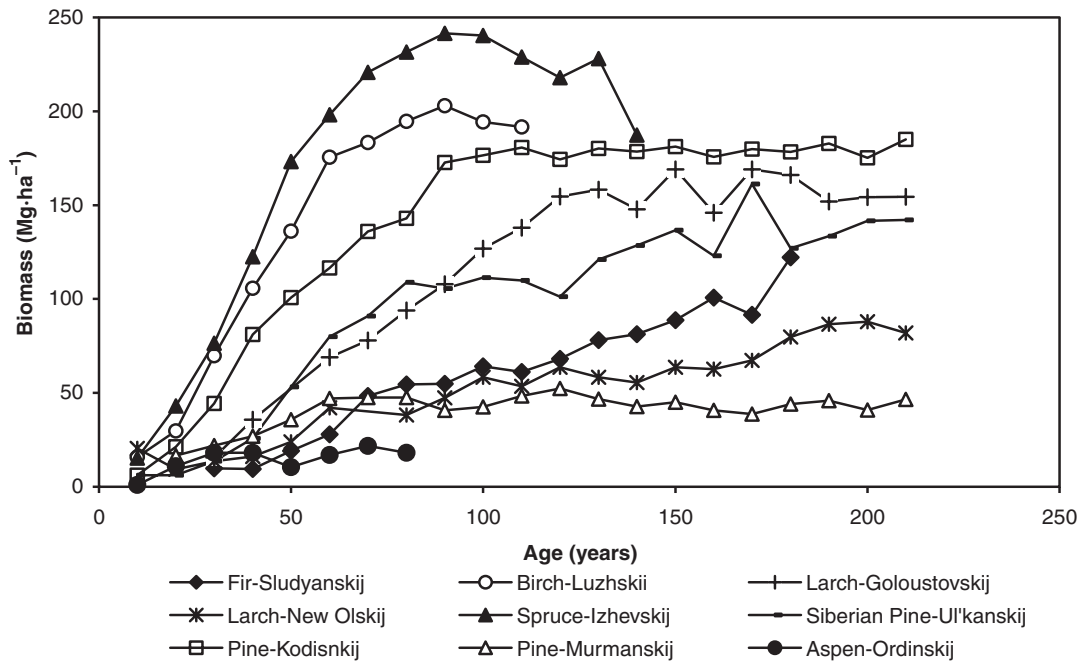


biomass declined after reaching maximum and positive for chronosequences where biomass increased continuously beyond the age of 120 years.

Aside from biomass aggradation following disturbance, we expected to find other effects of the disturbance regime, including depressed maximum biomass in heavily logged forests and increased growth in young stands because of active reforestation in these forests. To characterize the disturbance regime in each forest we calculated from the inventory data the percentage of the total forest area that was reported as clearcut and the percentage of the total forest area reported as dead stands (%clear-cut and %dead). These two attributes reflect the cumulative effects of disturbance over a period of time preceding the inventory because the forest area reported as clear-cut and dead includes all stands where forest cover has not yet regenerated sufficiently after the most recent disturbance to meet the inventory definition of forest (0.3 of maximum stocking density, which is equivalent to 40% crown cover). The dead stand category includes stands of predominantly dead trees killed by a variety of agents or combinations of them, including fire, insects, droughts, wind, floods, and air pollution. Fire is the most important cause of stand-replacing disturbance in Russia: on actively monitored forest lands (about 60% of the total forest area) between 51% and 72% of forest dieback is attributed to fire, and on forest lands that are not monitored regularly the role of fire is even greater (Krankina et al. 1994). Thus, percent dead forest stand area in a forest reflects primarily the fire history in years preceding inventory. To represent the longer-term impact of forest disturbance, we calculated the percentage of forest area where stand age is ≥120 years (%old).

We used long-term averages of local meteorological data to characterize the climate in each forest. Because the meteorological network is sparse, a single station was used for most forests; for some forests averages from two or three of the closest stations were used (Table 2). The data for each of

30 meteorological stations included daily temperature (maximum, minimum, and mean) and daily precipitation for all years between 1961 and 1990. Thirty-year mean daily values of all four variables were calculated, and these data were used to compute the following derived climatic variables:

(1) sum $t > 0$ (annual mean sum of positive daily mean temperatures, °C)
(2) growing season $t$ (annual mean sum of daily mean temperatures for days with minimum $t > 0$ °C)
(3) sum $t > 5$ (annual mean sum of daily mean temperatures >5 °C)
(4) precipitation (annual mean sum of daily precipitation, mm)
(5) growing season precipitation (sum of daily precipitation for days with minimum $t > 0$, mm)

We also calculated the climate moisture index (CMI), which is mean annual precipitation minus potential evapotranspiration, with units of centimetres per year. The "simplified Penman-Monteith" method of Hogg (1997) was used to estimate potential evapotranspiration because it requires data that were readily available to us: mean daily maximum and minimum temperatures for each month, monthly precipitation, and elevation. The average elevation above sea level for each forest was calculated from USGS elevation and topography data sets (GTOPO30 2003).

We explored between 40 and 50 regression models describing the plausible relationship between each of three dependent variables (maximum biomass, biomass at age 40, and maximum increment) and various combinations of climatic variables, disturbance characteristics, and their interactions with each other and with tree species. Models were compared and selected for further analysis using Akaike's information criterion (AIC), with small sample size adjustment (Burnham and Anderson 2002). For selected models (Table 3) the $R^2$ (adjusted for the number of parameters in the model) was calculated using the SAS version 8.2 general linear models

**Table 3.** Comparison of models based on climate, species, disturbance characteristics, and their combination for dependent variables maximum forest biomass, biomass at age 40, and maximum biomass increment, for all dominant tree species combined.

| Model | Independent variables[a] | AICC | Adj. $R^2$ | RMSE |
|---|---|---|---|---|
| **Maximum forest biomass (43.3–245.2 Mg·ha⁻¹)** | | | | |
| 1 | sum t > 0 [+; 47.9]; (sum $t$ > 0)$^2$ [–; 39.5] | 1855.7 | 0.26 | 34.1 |
| 2 | sum $t$ > 0 [+ 24.2]; (sum $t$ > 0)$^2$ [–; 26.7]; CMI; CMI × (sum $t$ > 0) | 1857.9 | 0.26 | 34.1 |
| 3 | sum $t$ > 0 [+; 28.3]; (sum $t$ > 0)$^2$ [–; 29.2]; CMI; species [3.2]; CMI × (sum $t$ > 0) × species [3.7][b] | 1857.2 | 0.34 | 32.7 |
| 4 | %clear-cut [+; 44.3]; (%clear-cut)$^2$[–; 30.9] | 1688.9 | 0.21 | 33.6 |
| 5 | %clear-cut [+; 37.1]; (%clear-cut)$^2$ [–; 20.0]; %old; %clear-cut × %old [–; 25.4]; | 1660.1 | 0.34 | 33.1 |
| 6 | %clear-cut [+; 43.0]; (%clear-cut)$^2$ [–; 23.5]; %old; species [2.3][a]; %clear-cut × %old [–; 30.8] | 1660.3 | 0.38 | 32.4 |
| 7 | sum $t$ > 0 [+; 31.8]; (sum $t$ > 0)$^2$ [–; 29.5]; %clear-cut [+; 20.8]; (%clear-cut)$^2$ [–; 7.4]; %old; species [2.7][b]; %clear-cut × %old [–; 26.5]; | 1634.8 | 0.48 | 29.8 |
| **Biomass at age 40 (8.8–126.1 Mg·ha⁻¹)** | | | | |
| 8 | sum $t$ > 0 [+; 15.0]; (sum $t$ > 0)$^2$ [–; 10.9]; CMI [+ 12.0]; | 1693.0 | 0.20 | 25.5 |
| 9 | sum $t$ > 0 [+ 16.5]; (sum $t$ > 0)$^2$ [–; 12.4]; CMI [+; 9.0]; species [3.5][b] | 1686.3 | 0.25 | 24.6 |
| 10 | %clear-cut [+; 90.9]; (%clear-cut)$^2$[–; 62.3] | 1508.6 | 0.37 | 23.0 |
| 11 | %clear-cut [+; 92.9]; (%clear-cut)$^2$[–; 65.4]; species [3.5][b] | 1501.9 | 0.42 | 22.1 |
| 12 | %clear-cut [+; 72.7]; (%clear-cut)$^2$ [–; 56.8]; %old; species [4.5][b]; %clear-cut × %old [–; 18.8] | 1467.9 | 0.53 | 19.8 |
| **Maximum biomass increment (0.96–7.01 Mg·ha⁻¹·year⁻¹)** | | | | |
| 13 | sum $t$ > 0 [+; 21.4]; (sum $t$ > 0)$^2$ [–; 16.3]; CMI; | 1351.2 | 0.20 | 0.95 |
| 14 | sum $t$ > 0 [+; 30.3]; (sum $t$ > 0)$^2$ [–; 22.6]; CMI [+; 5.0]; species [4.9][b]; CMI × (sum $t$ > 0) × species [3.0][b] | 1345.8 | 0.28 | 0.90 |
| 15 | %clear-cut [+; 45.3]; (%clear-cut)$^2$[–; 30.7] | 1226.4 | 0.22 | 0.96 |
| 16 | %clear-cut [+; 36.3]; (%clear-cut)$^2$ [–; 30.0]; %old; species [3.7][a]; %clear-cut × %old [–; 4.8] | 1217.3 | 0.21 | 0.95 |
| 17 | sum $t$ > 0 [+; 7.6]; (sum $t$ > 0)$^2$[–; 5.1]; %clear-cut [+; 23.0]; (%clear-cut)$^2$ [–; 16.2]; %old; species [4.1][b]; %clear-cut × %old | 1203.5 | 0.37 | 0.86 |

**Note:** All models are statistically significant (($P$ >$F$) < 0.01). AICC, Akaike's information criterion corrected; CMI, climate moisture index; RMSE, root mean square error.

[a]Slope sign (+ for positive; – for negative) and $F$ values from type III tests of fixed effects for ($P$ <$F$) < 0.05.

[b]Slope sign varies by species.

procedure (SAS Institute Inc. 1999). The same procedure was used to assess the effect of independent variables within the model with type III test of fixed effects ($F$ value).

## Results

Forest inventory data were well distributed across forest regions and vegetation zones within Russia (Fig. 1) and covered a wide range of climatic conditions (Table 2). The dominant tree species were well distributed across the range of temperature (Fig. 3) and moisture regimes. The assembled chronosequences indicated a wide range of growth rates and biomass accumulation patterns (Fig. 2). Maximum biomass ranged from less than 46 Mg·ha⁻¹ in the birch stands of Kolskij, Magadanskij, and Murmanskij forests, where sum $t$ > 0 is 1200–1400 °C, to more than 240 Mg·ha⁻¹ in the spruce and fir stands of Izhevskij, Wotkinskij, and Rylskij forests (sum $t$ > 0 was >2400 °C). Maximum increment in biomass followed a similar pattern, with the lowest values found in the colder climates and the highest in the warmest (Fig. 4). Interestingly, the spruce chronosequences were among those with both the lowest and the highest values of maximum biomass increment (0.96 Mg·ha⁻¹year⁻¹ in the Murmanskij forest and 5.68 Mg·ha⁻¹·year⁻¹ in the Rylskij forest), thus indicating the ability of spruce to dominate forest stands under a wide range of conditions, even in environments that are quite unfavorable for its growth. The variation in all three characteristics of biomass accumulation (maximum biomass,

biomass at age 40, and maximum increment) also increased with increasing sum of temperatures (Fig. 4).

The smallest values of biomass at age 40 (<10 Mg·ha⁻¹) were found in stands of spruce (Tyumenskij forest), fir (Sludyanslij forest), and Siberian pine (Goloustovskij forest). These are late-successional species that are known to grow slowly at an early age. The largest values of biomass at age 40 were in the aspen stands of the Izhevskij and Wotkinskij forests (126 Mg·ha⁻¹) at approximately the same temperatures (sum $t$ > 0 = 2429 °C) as forests with the lowest biomass at age 40 (2178–2346 °C, Fig. 4). The locations with the smallest biomass at age 40 had a considerably drier climate (CMI = 2.5 to 3.9) than the locations with the largest biomass (CMI = 11.3).

The total number of tested models was large, and only the best-performing models are shown in Table 3. The sum $t$ > 0 and its squared term were statistically significant in all of the best climatic models for all three dependent variables. However, the increase of variance with temperature (which could not be eliminated by logarithmic transformation) suggests that the data may not have fully met the model assumption of constant variance, thus potentially weakening the robustness of our model intercomparisons. Adding CMI to the model improved the prediction of biomass at age 40 and maximum biomass increment (AICC was reduced by >2; Table 3). Including species (and CMI × sum $t$ > 0 × species interaction for maximum biomass and maximum biomass increment) further increased correlation and reduced the error terms. An example of the effect of species is the

**Fig. 3.** Distribution of examined chronosequences for different tree species across the range of the annual sum of positive temperatures.
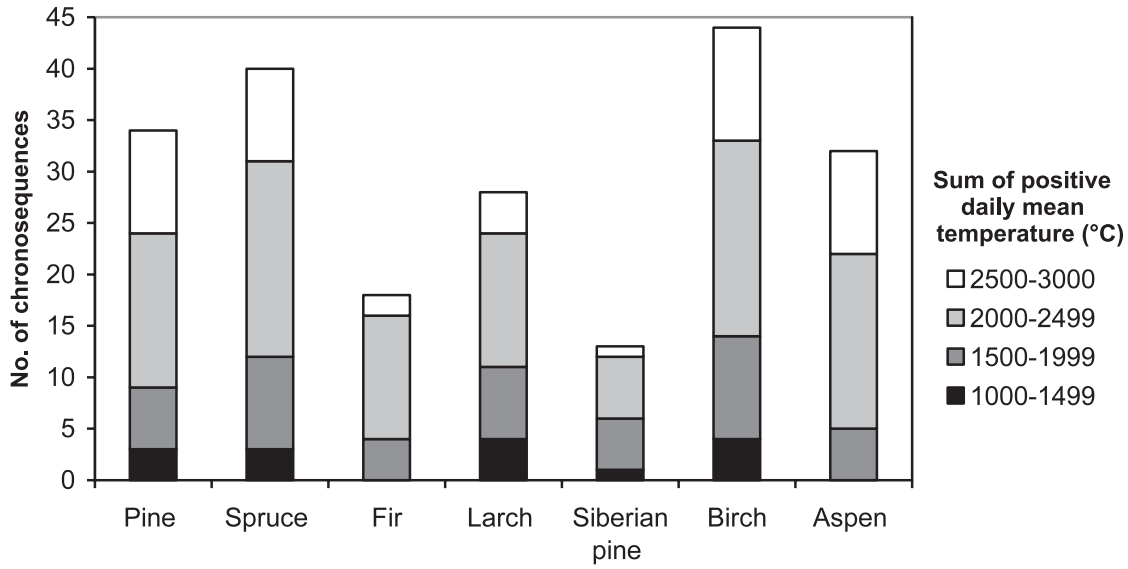


**Fig. 4.** Scatterplots of selected dependent variables (maximum forest biomass, biomass at age 40, and maximum biomass increment) over percentage of clearcuts in the total forest area and sum of positive temperatures.
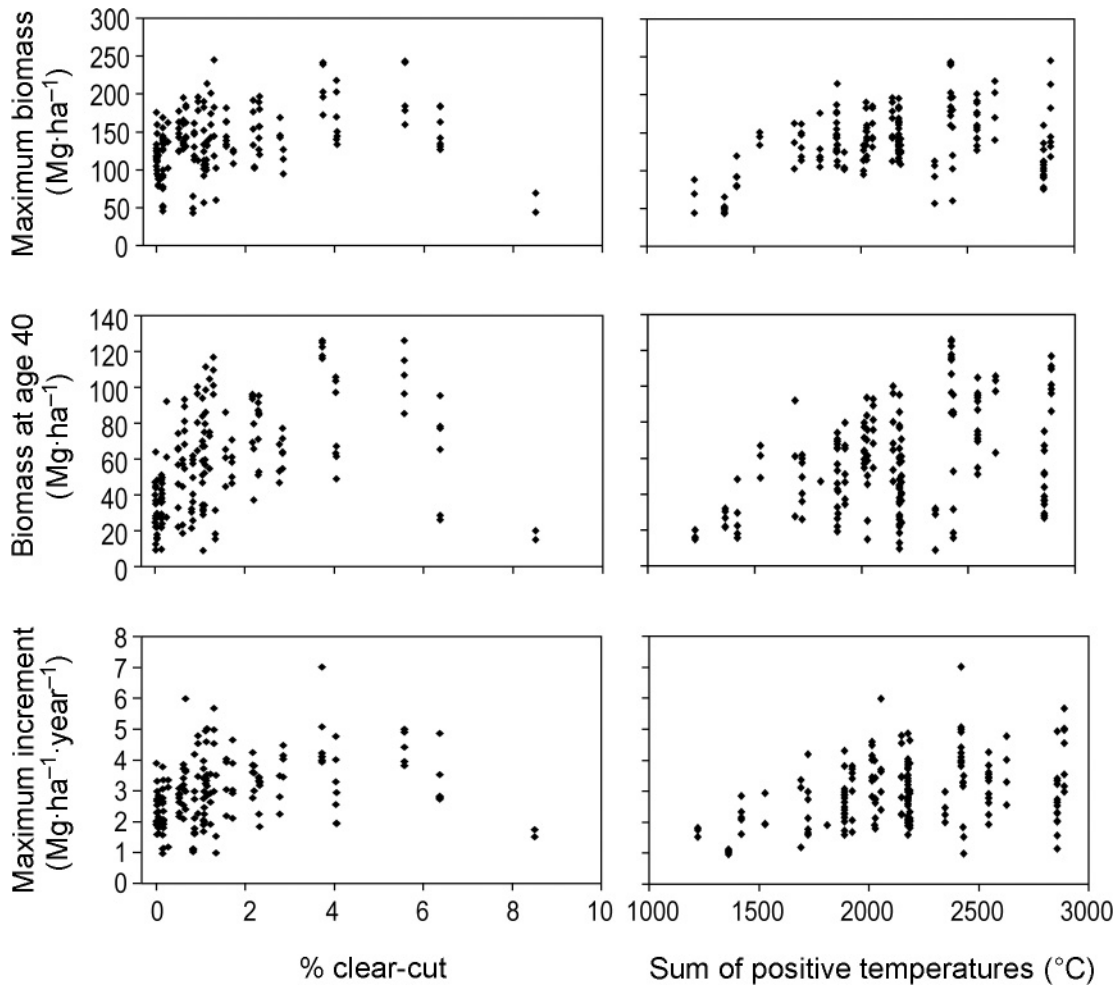
**Table 4.** Comparison of models based on climate, disturbance characteristics, and their combination for dependent variables maximum forest biomass, biomass at age 40, and maximum biomass increment of individual dominant tree species.

| Species | No. observations | Climate model[a] | | | Disturbance model[b] | | | Combined model[c] | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Adj. $R^2$ | $F$ | $P >F$ | Adj. $R^2$ | $F$ | $P >F$ | Adj. $R^2$ | $F$ | $P >F$ |
| **Maximum biomass (Mg·ha$^{-1}$)** | | | | | | | | | | |
| Pine | 30 | **0.43** | 8.5 | 0.0004 | 0.10 | 1.6 | 0.2124 | 0.42 | 3.5 | 0.0148 |
| Spruce | 40 | **0.32** | 7.1 | <0.0001 | **0.63** | 16.3 | <0.0001 | **0.67** | 11.0 | <0.0001 |
| Fir | 15 | 0.22 | 2.7 | 0.0864 | **0.85** | 19.5 | <0.0001 | **0.93** | 18.3 | <0.0001 |
| Larch | 24 | **0.68** | 19.6 | <0.0001 | **0.26** | 3.1 | 0.0402 | **0.71** | 9.3 | <0.0001 |
| Birch | 33 | **0.50** | 12.3 | <0.0001 | **0.45** | 7.2 | 0.0005 | **0.60** | 7.3 | <0.0001 |
| **Biomass at age 40 (Mg·ha$^{-1}$)** | | | | | | | | | | |
| Birch | 39 | **0.29** | 6.8 | <0.0001 | **0.56** | 13.4 | <0.0001 | **0.57** | 8.1 | <0.0001 |
| **Maximum biomass increment (Mg·ha$^{-1}$·year$^{-1}$)** | | | | | | | | | | |
| Pine | 29 | **0.64** | 17.8 | <0.0001 | 0.10 | 1.6 | 0.2133 | **0.61** | 6.4 | <0.0001 |
| Fir | 13 | **0.44** | 4.2 | 0.0405 | **0.63** | 4.6 | 0.0495 | **0.98** | 67.2 | 0.003 |
| Larch | 23 | 0.06 | 1.7 | 0.1875 | **0.56** | 8.0 | 0.0007 | **0.56** | 4.9 | 0.005 |
| Birch | 42 | **0.51** | 15.7 | <0.0001 | **0.37** | 6.3 | <0.0001 | **0.55** | 7.5 | <0.0001 |
| Aspen | 29 | 0.12 | 2.2 | 0.1157 | **0.37** | 4.7 | 0.0071 | **0.33** | 2.7 | 0.0379 |

**Note:** Species with no significant models for a given dependent variable (($P >F$) > 0.05) are not shown. Regression coefficients, $R^2$, for models with (($P >F$) < 0.05) are in bold.

[a]Independent variables are sum $t > 0$, (sum $t > 0)^2$, and CMI.

[b]Independent variables are %clear-cut, (%clear-cut)$^2$, %old, and %clear-cut × %old interaction.

[c]Independent variables are sum $t > 0$, (sum $t > 0)^2$, climate moisture index, %clear-cut, (%clear-cut)$^2$, %old, and %clear-cut × %old interaction.

higher maximum biomass of larch (160 ± 28 Mg·ha$^{-1}$) compared with that of birch, aspen, or spruce (126 ± 16, 130 ± 14, and 130 ± 22 Mg·ha$^{-1}$, respectively) in all 13 forests where these four species co-occur (all values are means ± standard deviation). Greater longevity probably contributes to greater accumulation of biomass in larch stands compared to stands of other species.

The percentage of the area in clearcuts (%clear-cut) ranged from 0% to 8.5% in the examined forests. Eleven forests, all located in East Siberia and the Far East, had less than 0.5% of their forest lands in clearcuts; however, the forests with a high proportion of clearcuts were scattered throughout the country. Percentage of dead forest stands (%dead) in the examined forests ranged from 0% to 23%. In six forests in East Siberia and the Far East the area of dead stands exceeded 4%; forests with the smallest areas of dead stands were located primarily in the western developed part of Russia, where fires are controlled and the forest stands that do get burned or killed by other agents tend to be quickly salvaged and replanted (Table 1, Fig. 1). The proportion of old stands (where the age of dominant species was ≥120 years) varied widely, from more than 50% in 8 forests located in Siberia and the Far East to less than 5% in 10 forests all located in western Russia. While geographic patterns of disturbance characteristics were evident, there were no obvious connections between them; for example, the forests with a low proportion of old stands (<20%) did not have the highest percentage of clearcuts, rather it varied between 0.1% and 5.6%.

For all three dependent variables examined, models based solely on %clear-cut and (%clear-cut)$^2$ fit the data better than models based solely on climatic variables, although for maximum biomass the adjusted $R^2$ was slightly lower in the model based on %clear-cut than in the model based on climatic variables (Table 3). Adding species improved the fit of models based on disturbance characteristics (lower AICC),

just as it did for the climate-based models. In general, the dependent variables increased with increasing %clear-cut up to 4%–6% and then declined (Fig. 4).

The interaction of %clear-cut and %old proved significant in the models for all three dependent variables. In general, the values of maximum biomass (181 ± 36 Mg·ha$^{-1}$), biomass at age 40 (95 ± 22 Mg·ha$^{-1}$), and maximum increment (3.8 ± 1.0 Mg·ha$^{-1}$·year$^{-1}$) were all significantly higher (at α = 0.05 in Tukey's studentized range test) in forests with active ongoing timber harvest (where clearcuts make up >2%) and where most of the mature stands had been harvested in the past (stands older than 120 years make up <20% of the total forest area). Forests where both %clear-cut and %old forest were high tended to have lower biomass values; however, no significant differences were found.

Other climatic and disturbance attributes had smaller effects on the dependent variables, and the models based on these other attributes did not fit the data as well as the models discussed previously. It is noteworthy that the best model for biomass at age 40, which was the best-fitting model overall, was based on disturbance characteristics only ($R^2$ = 0.53, Table 3). However, for maximum biomass and maximum increment the best models were based on a combination of climatic and disturbance characteristics (Table 3) and used a total of 13 parameters (7 for continuous independent variables and 6 for species).

Several models of maximum biomass and maximum increment for individual tree species provided higher correlation (adjusted $R^2$) than the generalized models that included all the species (Tables 3, 4); however, the models of biomass at age 40 were not significant for any of the individual species except birch. For fir, the disturbance-based models of maximum biomass and maximum increment worked particularly well (adjusted $R^2$ = 0.85 and 0.63, respectively; Table 4). In addition, models of maximum biomass for spruce,

**Fig. 5.** Biomass change with age in old forest stands (%BCOF; positive values indicate increase, negative values indicate decline) and the proportion of old forest (age ≥120 years old) in the total forest area.
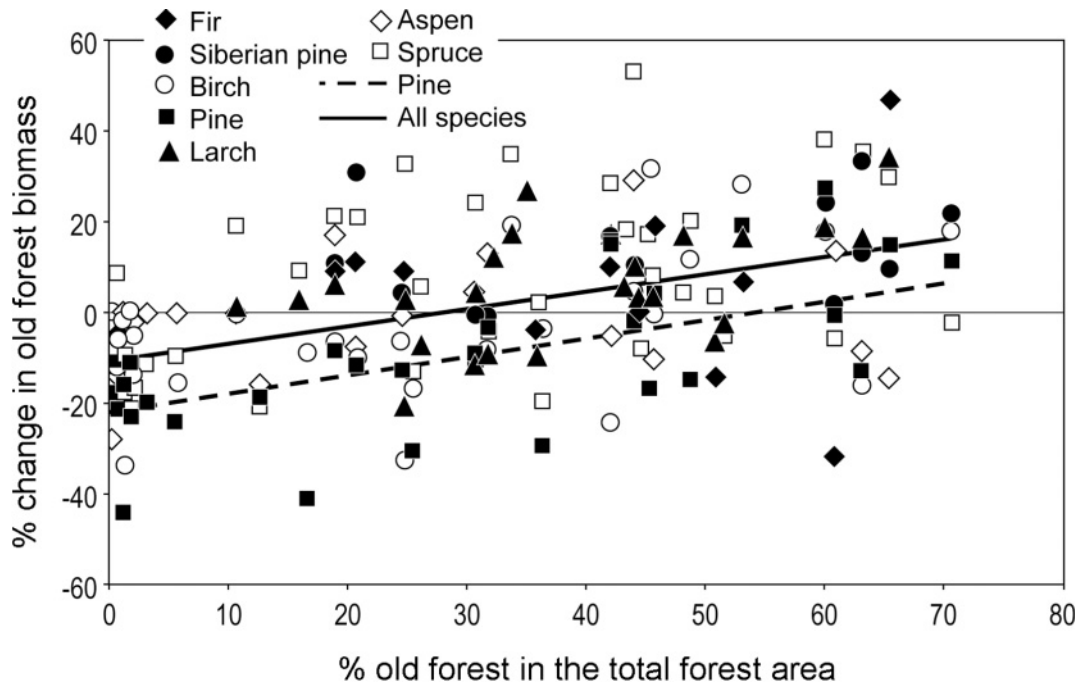


larch, and birch and models of maximum increment for pine, larch, and birch appear to work better than the models for all species combined. No significant species-specific models were found for Siberian pine, probably because of the limited number of chronosequences (Fig. 3).

Biomass declined substantially after reaching a maximum in some chronosequences, continued to fluctuate about a maximum in others, or increased continuously through age 210 in yet others (Fig. 2). The percent biomass change in older forest stands (%BCOF) was related to the proportion of older stands in the total forest area: the greater the area of old stands, the higher the increase in biomass in stands older than 120 years or the smaller the decline (Fig. 5; %BCOF: $-10.8 + 0.386$ (%old); $F = 57.2$; $(P > F) < 0.0001$; $R^2 = 0.24$). Pine stands are often the first to be harvested, and for pine the decline of biomass is on average 12% greater than for all species combined (Fig. 5; %BCOF: $-22.8 + 0.420$ (%old); $F = 17.4$; $(P > F) = 0.0003$; $R^2 = 0.38$).

## Discussion

While both climatic variables and measures of forest disturbance are linked to forest biomass accumulation, the nature of this link is different. Climate imposes a major ecophysiological constraint on photosynthesis and respiration; the balance of these processes determines plant productivity at the stand level. In addition, climate is an important factor in controlling soil nutrient availability (e.g., Reich et al. 1997). The attributes of the biomass accumulation curve selected for this analysis represent a set of important measures of stand productivity: biomass at age 40 reflects juvenile growth, maximum increment represents the peak growth rate, maximum biomass indicates the potential upper limit of biomass accumulation, and the change in biomass after reaching maxi-

mum distinguishes between continuous biomass accumulation and biomass decline in old stands. The first three of the selected attributes were expected to be linked primarily to the local climate and properties of tree species. Contrary to our expectations, however, the climatic variables explained only a fraction of the overall variance of biomass accumulation, and the prediction of juvenile growth (i.e., biomass at age 40) was particularly poor (Table 3). The poor correlation between biomass accumulation and climate underscores the challenge of projecting the future role of terrestrial vegetation in global carbon cycles under different climate change scenarios.

Properties of tree species clearly play a role in biomass accumulation in several distinct ways. Longer-lived conifer species (pine, Siberian pine, and larch) tend to reach higher maximum levels of biomass than relatively short-lived northern hardwoods (aspen and birch). Preferential harvest of pine causes a greater decline in biomass in older pine stands than in stands of other species because of the greater removal of productive stands from the old age cohort (Fig. 5). The great tolerance of pine for poor soils ranging from sandy dunes to peatlands may add to this effect by providing a large pool of stands with low biomass that are unlikely to be harvested. In favorable climatic conditions the hardwood species (aspen) tend to occupy more productive sites and produce higher levels of biomass at age 40.

The estimation of disturbance impacts on biomass stores depends greatly on the spatial scale of the analysis (Harmon 2001). At the broad scale of this analysis, fire (as measured by the proportion of dead stands in a given forest) appeared to have a limited effect on biomass accumulation, and this may be attributed to the stochastic nature of fire regimes. In contrast, timber harvesting targets mature forests and the most productive mature stands among them. The cumulative

effect of the removal of the most productive stands from the population of mature stands is to depress the average biomass in older stands (Figs. 2, 5). This effect, rather than successional processes in older forest stands, may be behind the lower estimates of carbon accumulation rates derived from inventory data relative to those measured in plots or predicted by models (e.g., Isaev et al. 1993; Law et al. 2004). The extent of the biomass decline after a maximum and the attribution of this process to natural successional stand development versus the effects of forest-use history each have important implications for projecting future patterns of carbon sources and sinks in forest ecosystems.

Timber harvest selectively transfers the more productive forest lands into younger age-classes, thus increasing the average biomass of young stands. This effect, combined with the likelihood of greater investment in artificial forest regeneration in the most productive timber-producing locations, may explain the correlation between biomass at age 40 and disturbance attributes (Fig. 4, Table 3). As these effects accumulate over time, there can be a profound impact on the inventory-based curves of forest biomass versus age across large spatial scales. Because these curves are chronosequences that represent substitution of space for time, they are subject to the influences of both "real" changes in biomass with stand age as well as the influence of "survivorship bias" that develops over time at larger scales under nonrandom disturbance regimes such as forest harvesting.

It may also be important to consider how nonrandom disturbance regimes such as forest harvesting may influence large-scale analyses of climatic effects on forest productivity and biomass. For example, the forests of warmer regions tend to be more frequently harvested, potentially leading to a greater human impact on the inventory-based chronosequences of biomass accumulation in these regions. If unrecognized, these types of effects could lead to biases in future projections of boreal forest responses to climate change, as well as assessments of the role of these forests in global carbon cycling. Such effects are difficult to assess, however, because of the complexity of interactions involving tree species, site types, climate, and disturbance regimes. In the analysis of chronosequences presented here these effects could not be fully decoupled, but they could potentially be addressed in the future through a more sophisticated simulation modeling approach.

The findings of this study can be used to improve the predictions of carbon pools and flux based on remote sensing methods. Remote sensing is an essential tool for monitoring forest cover and its role in carbon cycling, but linking remotely sensed variables with forest attributes that can predict the distribution of carbon pools and flux remains a challenge. A commonly used approach relies on remote sensing to derive leaf area index, normalized difference vegetation index, or other parameters for use in process-based simulation models (e.g., Running et al. 2000; Schimel et al. 2001; Turner et al. 2004). An alternative method predicts change in carbon stores based on detection of forest harvest with satellite imagery and regional models of successional change (Cohen et al. 1996; Krankina et al. 2004), and a research effort is underway to blend the two approaches (Law et al. 2004). To improve modeling of the role of terrestrial ecosystems in carbon cycling it is critical to identify the at-tributes of forest cover that are detectable with satellite imagery and linked to broad-scale patterns of biomass accumulation and forest productivity. The link between disturbance (especially the abundance of clearcuts and loss of old-growth forest stands) and biomass accumulation in a given forest may prove useful in modeling changes in biomass over large geographic regions. Remote sensing methods for detecting clearcuts are well developed, and the old-growth forest stands have been successfully mapped (e.g., Cohen et al. 2001; Cohen et al. 2002). In this study the highest values of biomass stores and accumulation rates were found in forests with locally abundant clearcuts where most of the old forest stands were already harvested. This holds true even on lands that were managed under the command economy of the Soviet period, and a closer link can be expected in countries with greater economic controls over timber harvest. On the other hand, large clear-cut areas and the low proportion of mature stands in several forests with low productivity (Magadanskij, Tyumenskij, and Ordynskij forests) can be attributed to extremely slow regeneration processes and diverse local factors that motivated large-scale timber harvests, including local needs for timber in remote regions.

## Acknowledgments

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