Temperature drives global patterns in forest biomass distribution in leaves, stems, and roots

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Whether the fraction of total forest biomass distributed in roots, stems, or leaves varies systematically across geographic gradients remains unknown despite its importance for understanding forest ecology and modeling global carbon cycles. It has been hypothesized that plants should maintain proportionally more biomass in the organ that acquires the most limiting resource. Accordingly, we hypothesize greater biomass distribution in roots and less in stems and foliage in increasingly arid climates and in colder environments at high latitudes. Such a strategy would increase uptake of soil water in dry conditions and of soil nutrients in cold soils, where they are at low supply and are less mobile. We use a large global biomass dataset (>6,200 forests from 61 countries, across a 40 °C gradient in mean annual temperature) to address these questions. Climate metrics involving temperature were better predictors of biomass partitioning than those involving moisture availability, because, surprisingly, fractional distribution of biomass to roots or foliage was unrelated to aridity. In contrast, in increasingly cold climates, the proportion of total forest biomass in roots was greater and in foliage was smaller for both angiosperm and gymnosperm forests. These findings support hypotheses about adaptive strategies of forest trees to temperature and provide biogeographically explicit relationships to improve ecosystem and earth system models. They also will allow, for the first time to our knowledge, representations of root carbon pools that consider biogeographic differences, which are useful for quantifying whole-ecosystem carbon stocks and cycles and for assessing the impact of climate change on forest carbon dynamics.

allocation | biomass fraction | root:shoot | allometry | biogeography

After acquisition via photosynthesis (gross primary production), new plant carbon (C) is respired, transferred to mycorrhizal symbionts, exuded, or converted into new biomass (net primary production). The new biomass can be foliage, stems (including boles, branches, and bark), roots, or reproductive parts. The proportional allocation of new C to these four plant biomass pools, when combined with their turnover rates, results in the proportional distribution of standing biomass among these pools. Such processes can be influenced by plant size, resource supply, and/or climate (1–10). Although simple in concept, our understanding of these processes and our ability to quantify and predict them remain surprisingly rudimentary (3–13).

The general lack of knowledge about C partitioning is important for a number of reasons, including its implications for the accuracy of global C cycle modeling and accounting. A recent study (11) concluded

> different carbon partitioning schemes resulted in large variations in estimates of global woody carbon flux and storage, indicating that stand-level controls on carbon partitioning are not yet accurately represented in ecosystem models.

Uncertainty about C partitioning in relation to biogeography and environmental effects is a particularly critical knowledge gap, because the direct and indirect influence of temperature or moisture availability on biomass partitioning could be important to growth, nutrient cycling, productivity, ecosystem fluxes, and other key plant and ecosystem processes (5, 7–10, 12). Additionally, uncertainty about belowground C allocation and biomass dynamics represents a major information gap that hampers efforts to estimate belowground C pools at continental to global scales (cf. 13 and 14).

Some of the limited evidence available supports the hypothesis that under low temperatures both selection and phenotypic plasticity should promote a relatively greater fraction of forest biomass in roots (5, 7, 8, 12, 15–18), as a result of adaptation to low nutrient supply (7, 19–22) driven by low nutrient cycling rates and limited soil solution movement. Cold environments also are often periodically dry and exhibit low plant production (19–26). Belowground resource limitations obviously also rise with increasing shortage of rainfall relative to evaporative demand, which can influence biomass distribution as well (4, 5, 17). Uncertainties include whether there are differences across climate gradients in the fraction of gross primary production respired vs. converted into new biomass; how new biomass is partitioned to foliage, stems, and roots; what the turnover rates are for these different tissues; and what are the consequences of the biomass distribution in foliage, stem, and root. In this study we focus on the last uncertainty—biomass distributions in standing pools—which is a direct consequence of new biomass allocation and subsequent turnover rate. Following optimal partitioning theory (1–4), we posit that the fraction of total forest biomass in roots should increase and in foliage should decrease when belowground resources are scarce.

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Significance

Do forests in cold or dry climate zones distribute more resources in roots to enhance uptake of water and nutrients, which are scarce in such climates? Despite its importance to forest ecology and global carbon cycle modeling, this question is unanswered at present. To answer this question, we compiled and analyzed a large dataset (>6,200 forests, 61 countries) and determined that the proportion of total forest biomass in roots is greater and in foliage is smaller in increasingly cold climates. Surprisingly, allocation to roots or foliage was unrelated to aridity. These findings allow, for the first time to our knowledge, biogeographically explicit mapping of global root carbon pools, which will be useful for assessing climate change impacts on forest carbon dynamics and sequestration.

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We use a large dataset based on more than 6,200 observations of forest stands in 61 countries (Tables S1–S3 and Fig. 1) to test the following hypotheses: (*i*) with increasing temperature, proportional biomass distribution (i.e., fraction of total biomass) should decrease in roots and increase in foliage; (*ii*) with increasing water shortage (estimated by an index of rainfall to evaporative demand), proportional biomass distribution should increase in roots and decrease in foliage; and (*iii*) gymnosperm and angiosperm forests should follow similar patterns. The dataset comprises data entries for individual stands including total foliage mass per hectare (M_{fol}), total stem mass per hectare (M_{stem}), total root mass per hectare (M_{root}), and, where available, total mass per hectare ($M_{tot} = M_{fol} + M_{stem} + M_{root}$). Forests were either naturally regenerated or plantations. Stands were classified as gymnosperm or angiosperm based on whichever represented a greater fraction of basal area or biomass; almost all native forests were of mixed species.

The sampled forests varied widely in age (from 3–400 y) and size (with M_{tot} ranging from near zero to 300 Mg/ha). Differences in biomass (which we refer to as size) reflect differences in productivity, density, and especially the range of ages of sampled stands. Because tree-size scaling is allometric (3, 4, 7, 9), we use an allometric approach to account for size-related changes in biomass partitioning in examining broad biogeographic patterns. Forests with high biomass have larger trees on average than forests with low biomass (given that tree density typically is lower in the former), so the forest size allometry characterized herein likely has its roots at the individual tree scale, but our analyses use stand M_{tot}, not individual tree biomass. We also examine biogeographic differences in the fraction of M_{tot} in foliage (F_{fol}), stem (F_{stem}), and root (F_{root}).

The term "allocation" has been used historically to describe both the onward distribution, or flux, of newly acquired substances (usually C or biomass) to different plant functions and differences in how those pools are distributed at any point in time. To minimize confusion about these different measures. we hereafter use the term "allocation" along with "new biomass" or "new C" only to indicate the former and discuss either the proportion of biomass or the fraction of biomass distributed in foliage, stems, or roots to indicate the latter.

The sampled forests varied widely geographically and in mean annual temperature (MAT) (from −13 to 29 °C) and mean annual precipitation (MAP) (from 20–420 cm) (Tables S1 and S2 and Fig. 1). Because a number of seasonal and annual climatic factors covary, it is difficult to ascertain which are responsible for the observed patterns (*Materials and Methods* and *SI Materials and Methods*). Because MAP is strongly correlated with MAT and is not a good global measure of water availability, we used an aridity index, the ratio of MAP to annual potential evapotranspiration (MAP/PET) (27) as a measure of relative water availability. MAP/PET ranged from <0.5 in cold, high-latitude zones to >3 in temperate and tropical rainforests. The forests ranged from sea level to >4,000 m elevation, with the large majority at <1,000 m elevation. More sampled forests were from Asia and Europe than other continents, and more were boreal and temperate than tropical. Thus, inferences from these data are likely to be most reliable across the gradient from subtropical to cold boreal forests.

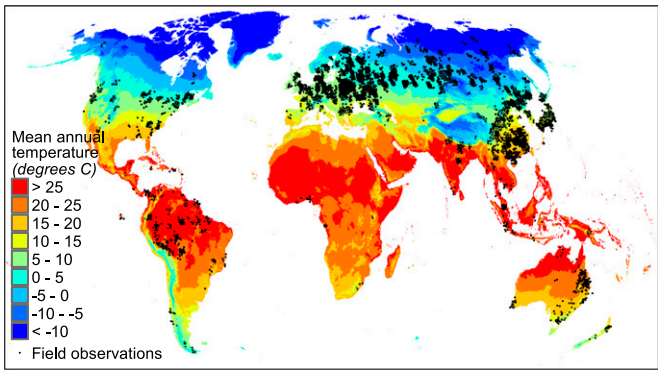

Fig. 1. Map showing location of all stands in the assembled database (see Tables S1 and S2 for additional information specific to those with root, foliage, and stem biomass data or with foliage and stem biomass data) across color-coded ranges of MAT.

Results

Variation in Biomass Fractions with Size (Stand Biomass). It is well known that as trees grow larger an increasing fraction of their total biomass is held in their stemwood (3, 4, 5, 7, 9, 10). Because our dataset includes a wide range of tree sizes and stand biomass, we first examine this issue and then account for this size-scaling in subsequent analyses of biomass distribution in relation to aridity and temperature. Examining how M_{fol} and M_{root} vary in relation to M_{stem} shows that, as expected, with increasing forest biomass F_{root} and F_{fol} decrease and thus F_{stem} increases. The standardized major axis (SMA) regression slopes are <1 for the log–log bivariate relationships of M_{root} to M_{stem} (slopes = 0.89 for gymnosperm and 0.91 for angiosperm stands, $r = 0.92$ and $r = 0.90$, respectively) and of M_{fol} to M_{stem} (slopes = 0.79 for gymnosperm and 0.81 for angiosperm stands, $r = 0.55$ and $r = 0.74$, respectively). We use the SMA regression here because comparable error is distributed in both terms, and we were not predicting M_{fol} or M_{root} from M_{stem}. Because the slopes were <1 and 95% confidence intervals did not overlap with 1, the data indicate that with increasing forest biomass, F_{stem} increases and F_{root} and F_{fol} decrease. The need to account for this size-scaling allometry guides our subsequent analyses and presentation of results, in which we first illustrate relations of biomass partitioning to climate for forests grouped into size classes based on stem biomass and then use more formal models to assess how F_{fol} and F_{root} vary with forest size, phylogeny, stand origin, aridity, and temperature.

Temperature-Related Patterns of Biomass Fractions. Across all forest sizes, F_{fol} averaged 4.2% and 8.5 in angiosperms and gymnosperms, respectively, with 10% and 90% quantiles of 1% and 10% in angiosperms and 2% and 18% in gymnosperms. F_{root} averaged 20.5% and 19.2% in angiosperms and gymnosperms, respectively, with 10% and 90% quantiles of 12% and 30% in angiosperms and 13% and 26% in gymnosperms. F_{stem} represented 72–75% in angiosperm and gymnosperm forests on average.

F_{fol} generally increased with temperature, whereas F_{root} decreased with temperature. To illustrate these patterns, we display the biomass fractions in relation to MAT across forests of differing sizes (i.e., by M_{stem} classes) (Fig. 2 and Fig. S1). On average, F_{fol} increased twofold with increasing MAT ($P < 0.01$) in both gymnosperms and angiosperms in all size classes (Fig. 2). Gymnosperms and angiosperms also have decreasing F_{root} (by 10–30%) with increasing MAT ($P < 0.05$ in all but one case) (Table S4). F_{fol} in gymnosperms and F_{root} in angiosperms are particularly sensitive to MAT in small-biomass forests. Differences between gymnosperms and angiosperms narrow in larger forests. F_{stem} increased with MAT in angiosperms and decreased in gymnosperms in small-biomass forests but otherwise did not vary markedly with temperature (Fig. S1). The relations of biomass fractions to MAT in Fig. 2 are directionally consistent with those identified in the full statistical analyses that follow (Table 1, Tables S5 and S6 and Figs. 3 and 4).

Allometric Approach to Biogeographic Variation in Biomass Fractions. Fig. 2 illustrates the general trends for biomass fractions in relation to MAT using fractions derived from three individually measured variables (foliage, stem, and root biomass) and simple linear regressions that did not account for other sources of variation. Hence, we also analyzed M_{fol} and M_{root} in relation to multiple factors and interactions across a continuous gradient of

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forest size. To account for how biomass fractions vary with forest size (biomass), we used an allometric approach that assesses the relation of M_{fol} and M_{root} to climate metrics at a standardized M_{stem}, by including M_{stem} in the model as a covariate. Thus, positive relations of M_{fol} or M_{root} with a climate metric indicate that an increasing biomass fraction is found in foliage or roots, respectively, and negative relations indicate the opposite. We use M_{stem} as the covariate rather than M_{tot}, because M_{stem} is a good indicator of forest size and, unlike M_{tot}, is independent of M_{fol} and M_{root}. However, the results are similar whether M_{tot} or M_{stem} is used as the covariate.

Surprisingly, the aridity index was not a significant ($P > 0.15$) predictor in models that related M_{root} and M_{fol} to the combination of MAT, the aridity index, phylogeny, stand origin, and M_{stem}. This result refuted our aridity hypothesis. Moreover, there was no interaction between the aridity index and MAT ($P > 0.40$) for either variable, indicating that response of M_{root} and M_{fol} to MAT was not dependent on moisture availability. Hence the aridity index was not included in Figs. 2–4 and was dropped from further analyses.

Of most interest, and supporting our temperature hypothesis, M_{root} and M_{fol} each varied in relation to MAT (Table 1) after accounting for M_{stem}, with forests in increasingly cold environments having a proportionally greater F_{root} and a lesser F_{fol} (Tables S5 and S6 and Figs. 3 and 4). For both angiosperms and gymnosperms standardized for M_{stem}, M_{root} decreased with MAT, and M_{fol} increased with MAT (as indicated by the direction of the parameter estimates and the significance, $P < 0.0001$, of MAT as a main effect in the model) (Table 1, Tables S5 and S6, and Figs. 3 and 4). The full models that included phylogenetic group and stand origin as well as M_{stem} and MAT showed significant main effects of all four factors ($P < 0.05$) (Table 1), except for stand origin for M_{root}. As expected, M_{root} and M_{fol} both varied significantly with M_{stem} (Table 1). Of more interest, the parameter estimates (Tables S5 and S6) indicate that the F_{root} and F_{fol} decreased with increasing M_{stem} (consistent with results using the SMA regression). On average, when standardized for MAT and M_{stem}, gymnosperm forests tended to have more M_{fol} and less M_{root} than angiosperm forests, and plantations had more M_{fol} than natural stands.

Although responses to MAT generally were consistent for gymnosperm and angiosperm forests and for forests of differing origins and sizes, the specifics differed in some cases (Table 1 and Figs. 3 and 4). For example, the increase in M_{fol} (standardized for M_{stem}) with increasing MAT was more pronounced in gymnosperms than in angiosperms (Fig. 3), and in small-biomass forests the shifts in relation to MAT were least pronounced for foliage in angiosperms (Fig. 3) and for roots in gymnosperms (Fig. 4).

Although the trends in Figs. 2–4 are generally similar whether based on the biomass fractions (Fig. 2) or on the allometric relations of M_{fol} and M_{root} to M_{stem} (Figs. 3 and 4), there are differences in the strength and shape of relations with MAT. These differences arise largely because the allometric analyses account for other factors and interactions and, by using logarithms, also allow nonlinearities, whereas the simple regressions are linear by default. Also, as expected, the total variance explained in the full allometric models was much higher than in the simple regressions of biomass fraction to MAT by size classes; this variance also may contribute to the steeper responses of biomass fractions in Figs. 3 and 4 than in Fig. 2. Because the allometric analyses account directly for stand size and other factors (e.g., origin) and for interactions and allow nonlinearities, the relationships described by the allometric models (Table 1 and Figs. 3 and 4) are likely a better characterization of the biomass distributions than the simple regressions of the fractions themselves (Fig. 2).

It would be informative to know if the cross-taxa biomass partitioning patterns also are observed within closely related taxa, because some of the shifts noted for gymnosperm and angiosperm forests pooled could result from compositional shifts with MAT. If so, we might see biogeographic patterns in biomass fractions across all taxa but not within genera or species. However, when we examine patterns for stands of specific genera, the results are largely consistent with those for the pooled data. Of the seven genera with >90 stands with M_{root} data, all six boreal or cold temperate genera had significant main or interactive effects of MAT, in all cases with greater M_{root} in colder environments at standardized M_{stem} (Table S7). The warm-temperate genus had no response to MAT. For the 11 genera with >100 stands with both M_{fol} and M_{stem} data, results also are largely consistent with patterns across all data. The relation of M_{fol} with MAT was positive in seven of the eight boreal and/or cold temperate genera (−1 °C < MAT < 9 °C) and was not significant in the other (main effect, Table S8). For two of the three warm-temperate or subtropical genera (13 °C < MAT < 21 °C), there was a negative relation of M_{fol} with MAT. Thus, the cold-temperate and boreal genera tended to show temperature-dependent biomass fraction patterns similar to the overall data, with genera from warmer climates being much less consistent in this respect. However, sample sizes (number of genera) for warm-climate genera are small.

Discussion

Temperature and Aridity as Drivers of Biomass Fractions. Biomass partitioning varied with MAT, in support of our hypothesis, but evidence for the role of water shortage as a driver of partitioning was surprisingly weak. This finding is largely consistent with some (8, 17), but not all (4), of the prior studies based on more limited data and with a recent synthesis of small individual plants (5). Why forests should show more responsiveness of partitioning to temperature than water availability is not clear, because the

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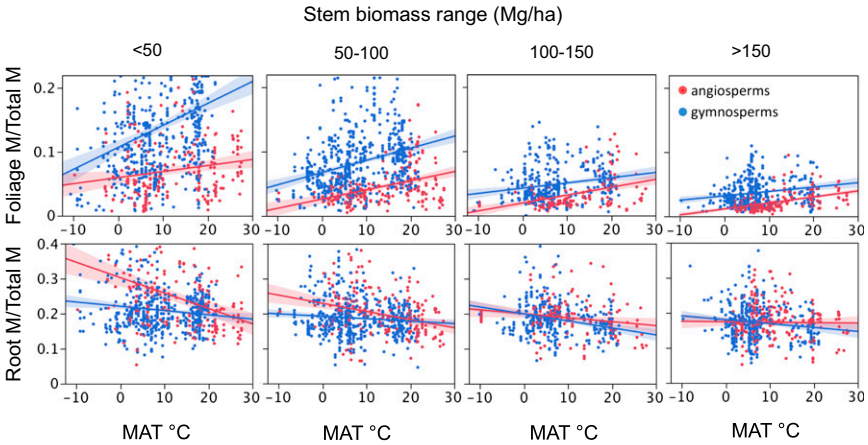

Fig. 2. F_{fol} (Foliage M/Total M) and F_{root} (Root M/Total M) in relation to MAT for angiosperm and gymnosperm forests in four forest M_{stem} classes (<50, 50–100, 100–150, and >150 Mg/ha). The linear regression and the 95% confidence interval for the fit are shown also. See Table S4 for fits of these relationships and Fig. S1 for data for F_{stem}. Some extreme high-value points are not visible because of the cut-offs of the *y* axis; however those data points represent <1% of all points, and they were included in the regression fits shown.

Table 1. Summary of analyses of phylogeny (gymnosperm, angiosperm), stand origin (natural, planted), MAT, and log_{10}stem biomass effects on foliage and root biomass (log_{10} values)

	Foliage biomass, Mg/ha			Root biomass, Mg/ha		
Source	Sum of squares	F ratio	Prob > F	Sum of squares	F ratio	Prob > F
Phylogeny	57.1	790.7	<0.0001	0.3	10.6	0.0012
Origin	5.7	79.3	<0.0001	0.0	0.1	0.7304
MAT	15.4	213.0	<0.0001	0.8	28.9	<0.0001
$Log_{10}M_{stem}$	116.2	1,607.9	<0.0001	136.9	5,039.0	<0.0001
Phylogeny*origin	0.6	8.1	0.0045	0.0	0.0	0.9110
Phylogeny*MAT	3.1	42.4	<0.0001	0.2	6.3	0.0120
Phylogeny*$log_{10}M_{stem}$	0.9	12.1	0.0005	0.4	13.0	0.0003
Origin*MAT	0.7	10.4	0.0013	0.0	0.9	0.3333
Origin* $log_{10}M_{stem}$	3.0	41.9	<0.0001	0.1	4.6	0.0325
MAT* $log_{10}M_{stem}$	0.8	11.5	0.0007	0.1	3.1	0.0768
Phylogeny*origin*MAT	1.3	17.9	<0.0001	0.4	13.2	0.0003
Phylogeny*origin* $log_{10}M_{stem}$	0.2	2.4	0.1211	0.2	6.1	0.0138
Phylogeny*MAT* $log_{10}M_{stem}$	1.0	13.9	0.0002	0.5	17.9	<0.0001
Origin*MAT* $log_{10}M_{stem}$	0.2	2.2	0.1388	0.1	1.9	0.1698

Whole model for M_{fol}, $R^2 = 0.54$, $P < 0.0001$, $n = 6{,}276$; for M_{root}, $R^2 = 0.83$, $P < 0.0001$, $n = 3{,}043$. Degrees of freedom = 1 for all independent variables and interactions. Parameter estimates and coefficients are presented in Tables S5 and S6.

simplest version of optimal partitioning theory suggests greater biomass would be distributed to roots in both cold and dry climates. Perhaps fluctuations in water availability over timescales shorter than a plant's ability to shift its allocation strategy limit the efficacy of a single partitioning strategy (28). For example, in one long-term field study, partitioning to roots was lower in low than in high water availability conditions (28), perhaps because with a greater water supply other soil resources (nutrients) became more limiting. In contrast, although temperatures fluctuate seasonally in most cold environments, high-latitude or high-altitude habitats are consistently colder, on average, than low-latitude or low-altitude ones at any time during the year. If low temperatures do correspond with low availability of soil resources, this correspondence would apply consistently across time.

Mechanisms Underlying Temperature Gradients in Biomass Distribution. What processes drive the differences in root and foliage partitioning with temperature documented in the current study? Differences in proportional biomass distribution to roots, foliage, and stems, by definition, must be caused by differences in the proportion of new C allocated to different tissue types, by differences in turnover rates of different tissue types, or by the two processes in combination. Because stem wood has a much lower turnover rate than roots or foliage, biogeographic variations in the turnover rates of foliage and roots is much more likely to contribute to the observed biogeographic patterns of biomass distribution.

Our findings indicate that trees and forests in cold climates have lower F_{fol} and also probably allocate a smaller proportion of new biomass to foliage, because, given what is known about turnover rates, such allocation patterns likely are necessary for the observed distribution patterns to occur. Whether the proportional allocation of new biomass to foliage, stems, or roots varies with temperature is highly uncertain (but see ref. 5 for juveniles in laboratory experiments), but more is known about turnover rates. Both across and within species, evergreen gymnosperms have markedly lower foliage turnover in colder environments (29–32). Thus, the likely explanation for the observed lower F_{fol} in evergreen conifers in cold than in warmer habitats is a lower allocation of new biomass to foliage. Because angiosperms in cold climates are almost all deciduous, and thus all foliage turns over annually, angiosperm forests probably also allocate less new biomass to foliage and have a low F_{fol} in cold climates. Thus, trees and forests in colder climates likely have lower allocation to foliage as well as lower F_{fol} in their standing pools.

Root biomass data are notoriously variable because of differences in sampling methods, challenges caused by spatial heterogeneity in soil and root biomass, and different components measured. Thus, the results presented herein and elsewhere include considerable uncertainty. Nonetheless, root turnover also has been reported to be lower in colder, higher-latitude or higher-altitude environments, based on either a small number of specific contrasts (33) or on syntheses across vegetation types (7) or forests (34). Theory also suggests that root turnover rates should be lower in low-productivity ecosystems (33). Thus, data and theory both indicate that root turnover, like foliage turnover, is probably slower on average in colder environments. Therefore the greater F_{root} in colder climates likely results at least in part from lower root turnover rates, although greater allocation of new biomass to roots in cold climates could contribute also.

Examining how conditions vary among the sampled sites could help explain the observed biogeographic variation in F_{fol}, F_{stem}, and F_{root}. Among stands in this compilation, MAT varies linearly ($r > 0.85$) with the absolute value of latitude, MAP varies curvilinearly ($r > 0.75$) with both MAT and absolute value of latitude, and the aridity index (MAP/PET) varies weakly with either absolute latitude or MAT. Further, the mean temperature of the warmest quarter of the year and the total precipitation of this same quarter were linearly related with MAT and MAP, respectively, and were similarly correlated with latitude. Hence, for this dataset, the low-to-high latitude gradient represents a climate gradient in which temperatures and precipitation (both growing season and annual) decrease and in which there is a weak trend for precipitation to be less than PET; thus, higher latitudes are colder and on average are slightly drier in a relative sense. The greater F_{root} in colder and drier forest ecosystems observed in our analyses is consistent with independent data

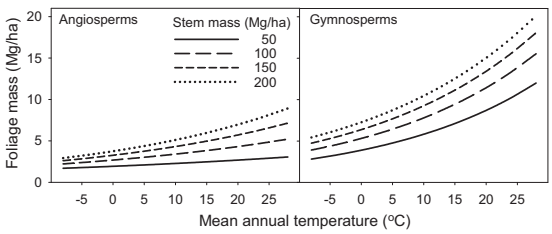

Fig. 3. Illustration of foliage mass (M_{fol}) in relation to mean annual temperature (MAT) for angiosperm and gymnosperm forests. Fits are from Table S5 for M_{fol} vs. MAT (°C) at four stem masses (50, 100, 150, and 200 Mg/ha). Full statistics are provided in Table 1 and Table S5.

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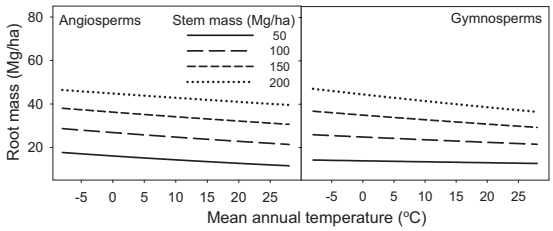

Fig. 4. Illustration of root mass (M_{root}) in relation to MAT for angiosperm and gymnosperm forests. Fits are from Table S6, for M_{root} vs. MAT (°C) at four stem masses (50, 100, 150, and 200 (Mg/ha). Full statistics are provided in Table 1 and Table S6.

indicating that both low temperatures and dry conditions likely lead to high C allocation belowground in high-latitude spruce forests (8).

Cold temperatures influence physical properties such as water viscosity and membrane permeability, which, coupled with influences on metabolic processes, typically limit both root and microbial activity (19, 22, 35). Low temperatures have negative effects on the decomposition and mineralization of organic matter, thereby reducing the supply of nitrogen and phosphorus (22, 35–37). Low-temperature suppression of nutrient movement in soils and nutrient uptake by roots also are well-known phenomena (22, 38). Thus, forests in high-latitude and high-altitude conditions face low temperatures, a modest trend toward low water availability, and low nutrient supply. All three factors restrict access to belowground resources in cold climates, as is consistent with both theory and some of the available evidence (3, 5, 7, 39). Hence, it is likely that both cold temperatures and low soil resources contribute to the observed patterns of greater F_{root} associated with low MAT.

Evaluating which aspect of climate, or its timing, is most important to fractional biomass distribution is challenging. Production and turnover of foliage, stems, and roots contribute to standing biomass distributions and occur at various times during the year. Hence, there is no simple framework for assessing how conditions during the warmest or wettest part of the year should contribute (differently than annual metrics) to the biogeographic patterns in F_{root} and F_{fol} observed in this analysis. Moreover, MAT and the temperature of the warmest quarter of the year were similarly significant predictors of biomass partitioning, but because these variables are strongly correlated with each other, analyses cannot distinguish between them. We use MAT in all presented analyses but interpret this metric as a general measure of both seasonal and annual temperature.

Given that tree density typically is lower in forests with higher biomass, the rank order of average individual tree biomass almost certainly mirrors stand biomass across the spectrum from low- to high-biomass forests in our dataset. Therefore, the direction of biomass distribution patterns quantified herein likely would apply to individual trees, as they do to forest stands. If it is advantageous (i.e., provides higher fitness) for individual trees to have higher F_{root} and lower F_{fol} in cold environments, there are at least two processes that could contribute to the observed patterns. First, the species (and their populations) that are most successful in cold climates could be those that have intrinsically greater F_{root}. In this case, inter- and intraspecific compositional differences would result in high F_{root} at low MAT. Second, individual phenotypic plasticity may shift any given genotype to a higher F_{root} in a cold climate because of a lower relative supply of belowground resources (along with cold temperature itself). It is possible, perhaps likely, that both these mechanisms (adaptive filters and phenotypic plasticity) contribute to the observed patterns. Ecologically relevant field data on both mechanisms are sparse, but we do know that species growing in low nutrient supply or at low temperatures can show greater F_{root} (3, 5), and experimental work has shown that, even in common gardens, intraspecific populations from cold origins have greater F_{root} (18).

Knowledge Gaps, Relevance to Modeling, and Future Steps. Our analyses show the outcome of allocation and turnover on the fraction of live tree biomass distributed to foliage, stems, and roots. They do not provide information about allocation or turnover per se but only about their aggregate impacts on the standing pools in the live plant components. Allocation to and turnover of plant organ components remain poorly understood mechanistically and empirically and represent major targets for future research. Differences in allocation to purposes other than plant growth, such as to mycorrhizal symbionts, also likely vary across resource gradients (40) as well as across the large climate gradients examined here, but these processes are even more poorly understood and quantified. Given current levels of ignorance concerning allocational and turnover processes and rates, our empirically based results should prove useful in providing a robust validation dataset for future measurements and models of allocation and turnover and in making new parameterization values for models. For example, our insights into the relationships of F_{root}, F_{stem}, and F_{fol} distributions with climate and stand biomass will strengthen estimates of current and future ecosystem C cycling, especially at regional to global scales (32, 41). Models generally specify new biomass allocation and turnover rate, not standing fractional distributions; however, the latter could serve to constrain allocation and turnover rate (see ref. 32 for an example), because these together should result in observed distributions. Although the central role of ecosystem C cycling in the global climate system is well recognized (42, 43), belowground C dynamics and root biomass patterns, in particular, remain areas of high uncertainty (13), and allocation schemes in land-surface models generally are inadequate (32, 41). To assist future modeling efforts, simple equations for angiosperm and gymnosperm forests predicting foliage and root biomass as a function of aboveground (or stem) biomass and MAT are illustrated and provided in Figs. S2 and S3. Knowledge that root biomass distribution responds to temperature will enhance both inventory-based C accounting and simulation modeling of total ecosystem C stocks and balance (44, 45). In particular, quantitative understanding of how biomass distribution is influenced by climatic conditions is essential for accurate assessments of the future ecosystem C dynamics under climate change (32, 45, 46). However, issues remain in reconciling the way the C pools are divided in different measurement, modeling, and monitoring efforts (47).

These relationships also will enhance modeling efforts to predict the consequences on ecosystem C of vegetation shifts in response to climate change, land-use practices, and invasive species. Specifically, our observation of higher F_{root} and lower F_{fol} in cold areas (i.e., high-latitude boreal forests) implies that, over the long term, warmer temperatures may decrease root biomass and increase foliage biomass in forests. However, the mechanisms and ecological consequences of such processes remain highly uncertain (5, 7, 10, 48). Is biomass distribution an adaptive response to the environmental filter imposed by cold, nutrient-poor conditions? How phenotypically plastic are new biomass allocation, tissue turnover, and biomass distribution in standing pools? If biomass distribution is adaptive, will climate change alter the selective pressures on these traits, and, if so, will resident species respond by shifts in F_{root} and F_{fol}, or would species from warmer climates have adaptive advantages because of intrinsically lower F_{root} and higher F_{fol}? We hope that future research will bring answers to these important questions quickly.

Materials and Methods

Data Compilation. We used woody plant biomass records from databases developed by Usoltsev (49) (mostly for former Soviet Union countries), Luo et al. (17), Cannell (48), and by 122 articles for >1,000 stands. See *SI Materials and Methods* for more details. The dataset consists of per stand entries on M_{fol}, M_{root}, and M_{stem} per hectare. Data usually were based on harvests of subsets of trees and the application of allometric and/or biometric scaling equations. Root data are reported only when they were measured directly in some fashion and also represent an estimate of M_{root}. Of the total of 8,565

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forest stands in the dataset, 6,276 had data for M_{fol}, M_{stem}, phylogeny, origin, and MAT (and were not removed because of fertilization, pruning, thinning, or other disturbance). A total of 3,043 stands met similar criteria for M_{root}. Bioclimatic variables (MAT, MAP) were obtained from WorldClim (www.worldclim.org/bioclim.htm). The database was structured by site, geographic location, climate (MAT, MAP), genus, species, phylogeny (angiosperm, gymnosperm), stand origin, and stand age. Stands were classified as angiosperm or gymnosperm based on the majority of the basal area or biomass. For the studied forests, MAT was strongly correlated with the absolute value of latitude (R^2 = 0.78), weakly correlated with altitude (R^2 = 0.06), and best described as a function of both latitude and altitude (R^2 = 0.84).

Data Analyses. Because of the strong allometry of biomass in the different pools in questions—i.e., because of shifts in proportional biomass distribution with tree size—we use an allometric approach in which we quantify how either root or foliage biomass per hectare ($\log_{10}$ of M_{root} or M_{fol} respectively) varies in relation to total stem biomass ($\log_{10}$ of M_{stem}) and MAT and their interaction. This approach helps partition responses to climate from the very strong signal of forest size and age. Data were transformed to normalize the distribution. For statistical reasons we focus analytically on the relations of M_{fol} or M_{root} to M_{stem} rather than to M_{tot} to minimize data contained in both the dependent and independent variable (3, 50). For consistency we present and discuss the fraction of M_{tot} in foliage ($F_{fol} = M_{fol}/M_{tot}$), stem ($F_{stem} = M_{stem}/M_{tot}$), and root ($F_{root} = M_{root}/M_{tot}$) based on observations that included all three of these components, because doing so is the only way to express all three on the same basis. To explore the role of seasonal as well as annual climate metrics, we analyzed M_{root} and M_{fol} in relation to the combination of M_{stem} and several climate metrics, including temperature, precipitation, and an index of relative water availability for both the full year and the warmest quarter (*SI Materials and Methods*).

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