The global root exudate carbon flux

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Abstract.
Root exudation, the export of low-molecular weight organic carbon (C) from living plant roots to soil, influences microbial activity, nutrient availability, and ecosystem feedbacks to climate change, but the magnitude of this C flux at ecosystem and global scales is largely unknown. Here, we synthesize *in situ* measurements of root exudation rates and couple those to estimates of fine root biomass to estimate global and biome-level root exudate C fluxes. We estimate a global root exudate flux of 15.2 PgC y^{-1}, or about 10% of global annual gross primary productivity. We found no differences in root mass-specific exudation rates among biomes, though total exudate fluxes are estimated to be greatest in grasslands owing to their high density of absorptive root biomass. Our synthesis highlights the global importance of root exudates in the terrestrial C cycle and identifies regions where more *in situ* measurements are needed to improve future estimates of root exudate C fluxes.

Keywords. Rhizosphere carbon flux, rhizodeposition, carbon cycle, belowground carbon allocation, soil carbon, global carbon flux

Introduction.

Root exudation – the release of low-molecular weight organic carbon (C) compounds from living plant roots into soil – mediates plant-soil interactions in a variety of ways, including facilitating plant nutrient acquisition via chemical and biological mechanisms (*e.g.* Jones and Darrah 1994; Meier et al. 2017), altering soil microbial communities (*e.g.* Shi et al. 2011), and impacting soil carbon dynamics (*e.g.* Yin et al. 2014). Root exudates mediate plant nutrient acquisition via a suite of chemical and biological mechanisms, in the process influencing the cycling of soil nutrients including phosphorus (P) and nitrogen (N). For instance, organic acids can increase plant access to inorganic P via rhizosphere acidification and phosphate mineral dissolution (Gillespie and Pope 1991; Hoffland 1992) or by displacing phosphate ions bound to mineral sorption sites (Jones and Darrah 1994; Bolan et al. 1994). Root exudates can also regulate mineralization of organic N and P by interacting with soil microbial communities. Enhanced root exudation has been correlated with the activities of enzymes involved in microbial N mineralization (Phillips et al. 2011; Meier et al. 2017) and P mineralization (Spohn et al. 2013).

Additionally, root exudation represents an important C flux to the soil that has unique effects on soil C dynamics. This is because root exudates can exert rapid effects on "stable" soil C formation and loss (more rapid than leaf or root litter which must be decomposed) (Sokol et al. 2019a). For example, chemical binding of C-based exudates onto soil minerals can result in soil C formation (Jones et al. 2003; Sokol et al. 2019b), whereas microbial activation due to fresh exudate C inputs could result in soil C loss via the "priming effect," in which fresh C inputs stimulate microbial respiration rates (Kuzyakov et al. 2000). Recent field and lab experiments have shown that the rate of root exudation dictates both the rates of soil C formation and soil C loss (Yin et al. 2014; Chari and Taylor 2022) and is thus a relevant parameter for estimating soil C stocks and fluxes. In addition to its role in belowground C dynamics, root exudation may also be important for regulating C uptake aboveground. For example, in the Duke Free-Air CO_2 Enrichment (FACE) experiment, aboveground productivity was sustained under elevated CO_2 in part due to enhanced exudation and accelerated N turnover (Phillips et al. 2011; Drake et al. 2011). In addition

to elevated CO_2, warming, drought, and N deposition have all been shown to influence root exudation rates over relatively short timescales (*e.g.*, Phillips et al. 2011; Calvo et al. 2019; Xiong et al. 2020). Due to its role in regulating C cycle dynamics and its potentially rapid response to global change, capturing the exudation rate accurately at the global scale is necessary for making C cycle projections.

Process-based C cycle models often incorporate root exudation indirectly as a fraction of net or gross primary productivity (NPP or GPP, respectively) into a dissolved or low-molecular weight C pool (*e.g.*, Abramoff et al. 2018; Tao et al. 2023). The magnitude of this flux can be estimated in different ways. A number of modeling studies have used experimental measurements to constrain the direct C flux from plants to dissolved C pools (Sulman et al. 2014; Wieder et al. 2018). At least one model (Fixation and Uptake of Nitrogen, or FUN) calculates the root exudate flux as a function of C supply and nitrogen (N) demand, allowing it to be coupled to soil C models (Brzostek et al. 2014; Sulman et al. 2017). While we have the ability to link these models to local site-specific exudation data, we currently have virtually no empirically derived ecosystem-scale estimates of exudate C fluxes with which to compare the output of C cycle models at large scales. Given the increasing recognition of the importance of exudates in the C cycle and the increasing effort to incorporate this flux into ecosystem models, it is critical that we establish an empirical benchmark for the exudate C flux.

One reason for the absence of an exudate C flux estimate is the challenge of making exudate C measurements *in situ.* Exudates are released from live fine roots belowground, rapidly assimilated by microbes, and occur at low concentrations relative to large soil C pools resulting in small signal to noise ratios. To maximize the accuracy of *in situ* root exudation measurements, researchers must isolate intact fine roots from soil and incubate them under conditions that simulate the soil environment. Since the 2010s, *in situ* collection of root exudates has most frequently been performed using the "cuvette method," which involves the incubation of a live fine root system in an open chamber filled with a glass bead matrix and nutrient solution culture (Phillips et al. 2008). Due to the challenges of accurately capturing root exudate C, relatively few *in situ* literature measurements exist compared to other major C fluxes. Here, we use a combination of these literature-derived measurements along with our own measurements

of *in situ* root exudation to estimate the global root exudate C flux and biome-level exudate fluxes. We provide a) estimates for root mass-specific exudation rates, b) estimates for area-specific exudation rates, c) estimates for exudation as a proportion of GPP, and d) an estimate of the global annual flux of root exudate C into soil. Given the paucity of exudation measurements that exist currently, our estimates will be useful for improving the accuracy of simulated exudation rates in artificial root exudate experiments, incorporating root exudation into process-based C models, and improving ecosystem C budgets.

Methods.

Data collection. We collected data from 40 studies measuring root exudation *in situ* including 128 sets of measurements (Fig. 1). Thirty-three studies were derived from a literature review and 7 studies were original, unpublished measurements by the authors. The literature review was restricted to studies of *in situ* (*i.e.* we excluded hydroponic studies and greenhouse experiments) total organic C exudation measurements from mature trees, shrubs, or grasses (*i.e.*, we excluded seedlings) using the cuvette method (Phillips et al. 2008). We used the search terms “in situ” “root exudation” and “cuvette method” on Google Scholar and additionally searched citations of Phillips et al. (2008) (the original description of the cuvette method).

We collected exudation rate data from each study in units of root exudate C per unit time per root biomass, root surface area, or root length. For each study, we determined the study-average exudation rate and the species-average exudation rate if multiple species were measured in a single study. When calculating the species-average rate, a small number of species with low sample sizes had a disproportionate influence on our calculations (*e.g.*, 4 species from the same study exceeded all other values in the dataset and exceeded the mean exudation rate by 4 s.d.), so we used the study-average exudation rate data for our scaling and analyses. Exudation rates are most commonly reported on a root biomass basis, which facilitates their inclusion into ecosystem C budgets. For studies reporting root exudation on a root surface area or root length basis, we converted these measurements to a root biomass

basis using conversion factors derived from Jackson et al. (1997). Root exudation per unit root biomass per unit time (ug C g^{-1} h^{-1}) is henceforth referred to as the specific exudation rate (SER).

Scaling. We took a biome-level approach to scaling root-mass based exudation rates, which first required assigning each study in our SER dataset to one of 10 terrestrial biomes with fine root biomass data in Jackson et al. (1997) (Table 1) based on vegetation type and environmental characteristics. Of these 10 biomes, 6 are represented in the SER dataset. We then scaled the SER to a soil area basis using biome-level live fine root biomass (FRB) per soil surface area (kg m^{-2}) estimates from Jackson et al. (1997). In this scaling, we made the assumption that *in situ* root exudation measurements are made from absorptive fine root biomass (AFRB). We estimated the proportion of total FRB that is AFRB for each biome (Table 1) from McCormack et al. (2015). To scale the root exudate carbon flux from an hourly basis to a yearly basis, we assumed exudation rates during the non-growing season are 76% of the growing season root exudation rate based on the studies in our data set that included growing season and non-growing season measurements (n = 10). We estimated the length of the growing season based on the biome (Table 1; Churkina et al. 2005; Piao et al. 2007). Thus, the root exudate C flux per soil surface area per year (henceforth F_{ex} in units of kg C m^{-2} y^{-1}) is calculated as follows for each data point:

Equation 1: $F_{ex} = \text{SER} \times P_{AFRB} \times \text{FRB} \times [\text{GS} + R_{NGS}(L_{yr} - \text{GS})]$

Where SER is the specific root exudation rate (expressed on a per-root-mass basis), P_{AFRB} is the proportion of FRB in absorptive roots (as opposed to transport roots) (McCormack et al. 2015), GS is the length of the growing season, R_{NGS} is the ratio of the exudation rate between non-growing season and growing season measurements, and L_{yr} is the length of the year (Fig. 2).

To determine per-biome average GPP we corrected per-biome NPP model estimates (Kicklighter et al. 1999) by an NPP:GPP factor of 0.46 (± 0.008 SE) (Collalti and Prentice 2019). We then divided F_{ex} by the GPP of the appropriate biome to determine the proportion of GPP as root exudate C (P_{ex}). Uncertainties for FRB, P_{AFRB}, and NPP varied by biome and can be found in Table S2.

To determine the global exudate C flux, we scaled exudate C fluxes across land surface areas of each biome from Jackson et al. (1997). The 11 land area biomes differ slightly from the 10 FRB biomes presented in Jackson et al. (1997). Of the land area biomes, 5 overlap with FRB biomes from which we have SER measurements (temperate evergreen forest, temperate deciduous forest, temperate grassland, tropical seasonal forest, tropical rainforest), 4 overlap with FRB biomes without SER data (boreal forest, savanna, desert, tundra), and 2 do not overlap with FRB biomes (woodland/shrubland (which includes but does not overlap completely with the Mediterranean biome) and cultivated) (Table 1). For the 5 matching biomes, we scaled the median biome F_{ex} by the global land surface area of the biome. For the 4 biomes that are not represented in our exudation dataset, we scaled the median SER of all biomes by the biome AFRB, biome GS, and biome global land surface area. For the two biomes that do not have FRB data, we scaled the median F_{ex} of all biomes by that biome's global land surface area. Two other scaling methods, which yielded similar results, are detailed in the supplement. We estimated the global root exudate flux (G_{ex}) by summing the fluxes across the entire land surface area of each biome (Table 1, Fig. 2). To determine the proportion of global GPP, we divided G_{ex} by a global GPP estimate from Badgley et al. 2019. All terms used in scaling to the global flux may be found in Table 1.

Environmental data. We collected latitude and longitude information from each study in our dataset. We matched these coordinates to gridded global precipitation (Markus et al. 2022), temperature (Rohde and Hausfather 2020), and soil respiration (Stell et al. 2021) datasets to determine mean annual precipitation (MAP), mean annual temperature (MAT), and soil heterotrophic respiration (Rh) at each site. We analyzed relationships between SER and latitude, MAP, MAT, Rh, and mycorrhizal type (*e.g.*, plant associations with arbuscular vs ectomycorrhizal fungi) for both study-average and species-average data. We found that relationships between the species-average SER with latitude and MAT were due to several studies that sampled a high number of species at low replication (as explained above). We did not find these relationships with the study-average SER, which were less susceptible to anomalous values. As a

result, only the study-average data are presented in the main text of this manuscript, and species-average relationships can be found in Fig. S1.

Statistical analysis. We used ANOVA models to analyze differences in SER, F_{ex}, and P_{ex} between different biomes. We used Tukey's Honest Significant Difference test to determine which biomes were different from each other. We used separate linear models to assess relationships between SER and each environmental predictor variable. All stats were done with the "stats" package. Significance was assessed at an alpha value of P = 0.05.

Results.

Specific root exudation rate. The median SER across all biomes was 67.4 ug C g^{-1} h^{-1} (IQR = 17.8 – 107.6 ug C g^{-1} h^{-1}). The mean SER is inflated due to non-normally distributed data; thus, we choose to report median SER here, which is likely closer to the true value (this is also true for all subsequent calculations). We did not find any statistically significant effects of biome type on SER (Fig. 3a). We found the species-average SER was greater in arbuscular mycorrhizal plant species than ectomycorrhizal plant species, but this difference was non-significant (P = 0.06) and disappeared when latitude was included as a covariate (P > 0.2). Study-average SER was greater in studies with only AM species than studies with only EM species, independent of latitude (P = 0.046 Fig. S2). We did not observe any effects of MAP, MAT, latitude, or soil heterotrophic respiration on the study-average SER (Fig. S1).

Area-based root exudate C flux. We determined the root exudate C flux on a m^{-2} basis by scaling SER by AFRB. The median F_{ex} was 0.079 kg C m^{-2} y^{-1} (IQR = 0.018 – 0.171 kg C m^{-2} y^{-1}). F_{ex} was significantly higher in temperate grasslands than temperate forests and Mediterranean biomes ($P \leq 0.040$, Fig. 3b).

Proportion of C allocated to exudates. We derived biome-level GPP estimates to determine the proportion of GPP as root exudates (*i.e.*, $P_{ex} = F_{ex}/\text{GPP}$) within each biome. For the six biomes for which we could calculate P_{ex}, the median P_{ex} was 5.5% (IQR = 1.6% – 12.6%) and the median proportion of NPP was 12.0% (IQR = 3.5% – 27.4%). We found a significant effect of biome type on P_{ex}, with temperate grasslands having higher P_{ex} than all other biome types ($P < 0.002$, Fig. 3c).

We also compared our derived F_{ex} to existing literature measurements of total belowground carbon allocation (TBCA) by mass balance for six field sites representing each biome in our SER dataset (Table 2). TBCA includes C allocated to root respiration, root production, rhizodeposition/exudation, and mycorrhizal allocation (Carol Adair et al. 2009). In theory, F_{ex} should be some non-trivial proportion of TBCA, but should not exceed TBCA. Indeed, F_{ex} ranged from 6% of TBCA (temperate coniferous forest) to 60% (temperate grassland) depending on the site.

Global root exudate C flux. We scaled median biome-level data by land surface area measurements to determine the global root exudate C flux (Table 1). The median global root exudate C flux (G_{ex}) was 15.2 Pg C y^{-1}. We also scaled the first and third quartiles to obtain a range of 8.1 – 22.8 Pg C y^{-1}. This flux represents 10.4% (range = 5.5% – 15.5%) of global annual GPP (147 Pg C y^{-1}) (Badgley et al. 2019). While measurements in temperate forests account for 73% of the studies in our dataset, globally temperate forests only contribute 2.8% of the root exudate C flux. On the other hand, grasslands constitute only 3 measurements (< 8% of the dataset), but grasslands (temperate and savanna) represent 45% of the estimated global exudate C flux (Fig. 4).

Sensitivity analysis. We varied each factor involved in our flux estimate independently to determine the sensitivity of the scaled estimate to each factor (Table S3). Per Equation 1, F_{ex} is equally dependent on SER, FRB, and P_{AFRB}. Of these three factors, P_{AFRB} is the one that carries the most uncertainty, so an improved estimate of P_{AFRB} is most likely to affect our flux estimates. Varying P_{AFRB} by the range presented in McCormack et al. (2015) resulted in an uncertainty around the median F_{ex} of over ±70%. F_{ex}

is also dependent, to a lesser degree, on GS and R_{NGS}. However, varying these terms affected the median F_{ex} by less than ±10%.

Discussion.

Our primary goal in this meta-analysis was to derive the most accurate and robust estimate of the annual global root exudate C flux possible given current data availability. Our analysis suggests a considerable global exudate flux of 15.2 PgC y^{-1} comprising 10.4% of global GPP. Before this study, the magnitude and importance of the root exudate C flux was largely unknown. At 10.4% of global annual GPP, the global root exudation flux (G_{ex}) matches remarkably well with measurements from growth chamber experiments reporting 4 – 18% of photosynthetically fixed C released as root exudates (Barber and Martin 1976; Dror and Klein 2022). The amount of C released as exudates is likely to affect soil microbial activity, soil nutrient availability, and soil C dynamics, all of which affect feedbacks to plants and ecosystems at the global scale – and the results of this study suggest that this amount is considerable. Thus, we impress the importance of continued measurements of root exudation, studies which investigate the effects of root exudates on soil C dynamics, and incorporation of the root exudate C flux into models.

The global proportion of GPP that we estimate as root exudation (10.4%) differs from the median proportion of GPP in all the studies in our dataset (5.5%) – a difference that underscores the importance of grasslands to the global root exudate carbon flux. Grassland observations make up only a small proportion of our dataset (3 out of 40 studies), but together temperate grasslands and savannas represent 20% of the global land surface area (Jackson et al. 1997) and 45% of G_{ex}. Grasslands contribute much more to G_{ex} than their surface area would suggest because they have a much higher proportion of absorptive fine root biomass (P_{AFRB}), where exudation primarily occurs, than forest ecosystems. The SER in grasslands is not significantly higher than other biomes, but because grasslands have both high FRB and P_{AFRB}, the F_{ex} is much higher in grasslands at 46% of GPP (compared to the overall median of 5.5%) (Fig. 3). Additionally, our TBCA comparison showed that exudation could be around 60% of TBCA at

the grassland site, compared to 6-16% at other sites. While these numbers appear high, grasses invest most of their productivity belowground (Sun et al. 2021) and do not allocate C to build transport roots (McCormack et al. 2015), so grasses may be able to expend more C on absorptive root exudation. This is also consistent with stable isotope experiments which show most grassland belowground C export is associated with heavy fraction soil (where exudates accumulate) rather than light fraction soil (where root litter accumulates) (Fossum et al. 2022). However, we do caution that field-collected exudation data is extremely rare for grasslands (3 studies), so our estimates for this particularly important biome are based on relatively little current information (Fig 4).

Our estimate for the global exudate C flux (15.2 PgC y^{-1}) is similar in magnitude to the estimate of 13.1 PgC y^{-1} allocated to mycorrhizal fungi derived by Hawkins et al. (2023). Hawkins' results suggest that ectomycorrhizal plants allocate a greater proportion of their productivity to mycorrhizae than arbuscular mycorrhizal plants. Interestingly, our results provide some evidence that arbuscular mycorrhizal species may allocate more C to exudation than ectomycorrhizal species (Fig. S2), which suggests a potential trade-off between exudation and mycorrhizal C allocation. Arbuscular mycorrhizal associated plants may be more incentivized to allocate C to exudation as their mycorrhizae do not provide them with a robust organic nutrient acquisition mechanism (Read 1991; Phillips et al. 2013). However, we note that we did not find differences in exudation across arbuscular and ectomycorrhizal species in temperate forests where these species most commonly co-occur, so this difference may be better ascribed to an environmental or phylogenetic pattern. Finally, it's important to note that exudation measured via the cuvette method (all of the studies in this meta-analysis) can also include fungal exudates (Kaiser et al. 2015), so these two flux estimates could partially overlap.

From a methods perspective, our results suggest that the cuvette method is robust for approximating root exudation rates. The agreement of our results with TBCA measured by mass balance suggests that the cuvette method captures the root exudate C flux to an accurate order of magnitude. Had the estimates of F_{ex} exceeded TBCA, further refinements to the method may have been warranted.

Nonetheless, some important considerations about field-collected exudate C data remain. Below, we discuss potential applications of the exudate fluxes we present here and suggest future approaches aimed at improving the quality of root exudate data for future flux estimates.

Using the estimates from this paper. The estimates provided in this paper have a variety of potential applications for guiding future empirical research and constraining parameters for future modeling efforts. Artificial root exudate (ARE) experiments: In ARE experiments, artificial exudate solutions are used to simulate the effects of root exudation on soil biological and physicochemical properties. One limitation of ARE experiments is that it is challenging to *a priori* simulate an accurate root exudation rate, so the responses observed in ARE experiments may not always be applicable in nature. Here, we provide estimates that researchers working in a variety of biomes can use to set the rate of root exudation in their experiments. For example, researchers could apply the F_{ex} value presented here for their biome of interest and scale this value by the surface area of their incubation chamber and length of the experiment to know how much total artificial exudate C should be added.

Processed-based models: In process-based C cycle models, there is often a low-molecular weight carbon (LMWC) or dissolved organic carbon (DOC) pool (*e.g.,* Abramoff et al. 2018; Tao et al. 2023). Carbon can reach these pools either directly from plant input (*i.e.,* root exudation) or via microbial transformation of non-LMWC/DOC plant inputs. Since P_{ex} is a function of GPP and models typically incorporate total C input to soil as some function of productivity, or GPP, modelers can use P_{ex} to describe the proportion of plant input that moves directly to the LMWC/DOC pool without being microbially processed. We anticipate this flux may be larger than currently parameterized in processed-based models. For example, Wieder et al. (2018) incorporates exudation as 2% of NPP, or ~1% of GPP compared to our median P_{ex} estimates of 12% NPP and 5.5% GPP.

Ecosystem C fluxes: Ecosystem scientists and practitioners can use the estimates presented in this paper to constrain their estimates of root exudation without taking belowground measurements. For example, at field sites with remote monitoring of GPP from a flux tower, scientists can use our P_{ex} estimates to

303 determine an approximation of the C flux into soil as root exudates without on-site belowground field
304 work. By comparing this estimate to TBCA as measured by mass balance (Palmroth et al. 2006; Carol
305 Adair et al. 2009), researchers can approximate the proportion of C allocated belowground to
306 exudation/rhizodeposition compared to fine root production.
307
308 *Data interpretation.* We encourage readers to consider several caveats when interpreting these data. First,
309 we stress that the SER was not different between biomes, and that differences in the exudation rate only
310 emerged at the soil area level, due to high FRB and P_{AFRB} in grasslands. Thus, our results do not show, for
311 example, that grass roots exude more C than tree roots on a per-root basis. Rather, the enhanced F_{ex} in
312 grasslands is simply due to high absorptive fine root biomass. In fact, a key finding of our analysis is that
313 there were no differences in SER across biome types, but this could simply be because a large majority of
314 our data came from temperate forests. We call for more observations in non-temperate forest biomes to
315 increase the statistical power of future analyses.
316 Additionally, we suggest that the estimates proposed in this paper are more likely to be
317 overestimates than underestimates due to the way root exudation is measured. Commonly, root exudation
318 rates are measured as the net release of C by a mass of fine root tissue into a cuvette over some incubation
319 period (Phillips et al. 2008). Because exudates are measured from live fine roots, the cuvette incubation is
320 inherently an open system and is thus prone to C contamination from outside sources, even though
321 measurements are typically standardized with rootless "control" incubations. The consequence of this is
322 that studies with a low sample size are particularly prone to the influence of a contaminated measurement.
323 For this reason, we decided to focus on study-average rather than species-average data in this manuscript
324 because presenting species-average data contained a high number of species with low sample sizes (*i.e.*,
325 giving more weight to data with less replication). Biomes with a smaller number of studies in our dataset
326 may be more likely to have a higher SER due to the same effect. This is also why we focused primarily on
327 median rather than mean estimates.

328 Finally, we note that in scaling SER to F_{ex} (and then to P_{ex} and G_{ex} subsequently) we relied on
329 estimates of several other parameters including FRB, P_{AFRB}, GS, and P_{NGS}. Of these parameters, FRB was
330 well constrained by Jackson et al. 1997 and GS and P_{NGS} had relatively smaller effects on F_{ex} (Table S3).
331 P_{AFRB} estimates, on the other hand, are the most uncertain (McCormack et al. 2015) and also carry equal
332 weight as SER and FRB in determining F_{ex}. Thus, we suggest our estimate is susceptible to change as
333 P_{AFRB} estimates are honed and encourage researchers to make P_{AFRB} measurements when collecting root
334 trait data.
335
336 *Future measurements*. We urge researchers to continue taking *in situ* measurements of root exudation.
337 Below, we outline several areas scientists can target in the future.
338 Improve measurement quality: Several steps can be taken to improve the quality of SER measurements.
339 First, we strongly encourage researchers to prepare blank incubations and filter their samples when using
340 the cuvette method. As a quality control method, researchers can look for a correlation between the total
341 root exudate C and the root mass or root surface area. If there is no relationship, and specifically if low
342 mass roots are generating high amounts of exudates, this is an indication that C contamination could be
343 exceeding acceptable levels. C contamination could come from many sources, including both the
344 environment and materials used in exudate collection. We urge researchers to be rigorous in checking for
345 potential contamination before publishing measurements.
346 Collect exudates in under-represented biomes: Measurements of root exudation in temperate forests are
347 over-represented in our dataset. From our current dataset, we are unable to determine if there are biome-
348 level differences in the SER, largely due to substantial differences in data availability between biomes
349 (Fig. 3a, Fig. 4). We encourage researchers to target biomes that have an overrepresentation in the global
350 root exudate flux relative to an underrepresentation in the proportion of the dataset (Fig. 4). These include
351 grasslands, tropical rainforests, agroecosystems, and all biomes in the global south. Improving data from
352 these biomes should be the highest priority for constraining future global exudate C flux estimates.

353 Agroecosystems merit special consideration as agricultural practices such as fertilization could have
354 unique effects on exudation not observed in natural ecosystems.
355 Collect exudates seasonally, including outside the growing season: Exudation measurements are rarely
356 taken outside of the plants' dominant growing season, but these measurements are vital to determining the
357 exudate C flux on annual timescales. Additionally, plants in different biomes exhibit reduced C
358 assimilation during the non-growing season for different reasons. Since the plant response to the non-
359 growing season is different between biomes where the non-growing season is driven by low precipitation
360 vs. those driven by cold temperatures, unique estimates for the non-growing season rate in all biomes will
361 be important for constraining the global exudate C flux.
362 Consider the effects of global change: Global environmental change affects numerous plant and soil
363 processes, and a number of experimental measurements suggest drivers such as warming, drought, or
364 elevated CO_2 will affect the root exudation rate as well (*e.g.*, Phillips et al. 2011; Xiong et al. 2020; Brunn
365 et al. 2022). If the estimates made in this paper are applied to climate change scenarios or experiments,
366 estimates of root exudation would scale with GPP responses to climate change (*e.g.*, increase under eCO_2
367 or decrease under drought). However, experiments suggest global change effects on exudation rates are
368 not conserved in this manner – eCO_2 has been found to decrease SER on numerous occasions (Dong et al.
369 2021), and drought to increase it (Calvo et al. 2019). We encourage scientists to continue measuring SER
370 responses to climate change, and specifically to do so *in situ* in large-scale global change experiments
371 with multiple drivers of change to help constrain these estimates.
372 Consider exudation in the context of root traits: Plants exhibit a suite of root traits, many related to
373 nutrient or water acquisition, that can vary based on their individual physiology or environment. Most
374 measured root traits are morphological (*e.g.*, specific root length, root tissue density, root diameter) or
375 related to growth (*e.g.*, fine root biomass, production, turnover) (*e.g.*, Kong et al. 2019; Chen et al. 2021).
376 Because exudation can be a plant strategy for acquiring both inorganic and organic soil nutrients (*e.g.*,
377 Jones and Darrah 1994; Meier et al. 2017), we suggest researchers measuring root exudation incorporate

it as a root trait in analyses of the root economic spectrum. Plants may trade off belowground C investment to exudation as opposed to structural C investment in root system expansion depending on their environment. Establishing relationships between exudation and other root traits may improve our ability to predict exudation rates and fluxes.

Conclusion. This study represents the first effort to estimate the root exudate C flux at the biome and global scales. Our results suggest that root exudation is a considerable C flux into soils (roughly 10.4% of global GPP), that grasslands represent a relatively high exudate C flux due to their high fine root biomass, and that root exudation rates do not vary strongly across latitude or global gradients of temperature, precipitation, or soil heterotrophic respiration. We found some evidence that mycorrhizal associations impact root-specific exudation rates but note that studies where arbuscular and ectomycorrhizal plants co-occur showed no differences in exudation rates. Importantly, our analyses also indicate that measurements of this flux are data poor outside of temperate forests. Thus, we call for more measurements of root exudation in grasslands, tropical rainforests, and agroecosystems. Given the magnitude of the exudate C flux that our analysis suggests, we call for its continued and increasingly detailed incorporation into ecosystem C budgets and process based models.

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Data availability. The data analyzed in this study is publicly available at the following web address: [public web address to be supplied following acceptance of manuscript]

Tables & Figures

Biome	**Median SER** (ug C g^{-1} h^{-1})	**FRB** (kg m^{-2})	P_{AFRB}	**GS** (d)	**Land surface area** (10^6 km^2)	**Total flux** (PgC y^{-1})
Mediterranean	119.2	0.28	0.33	365	NA[1]	NA[1]
Temperate coniferous forest	12.5	0.50	0.33	150	5.0	0.1
Temperate deciduous forest	47.4	0.44	0.33	125	7.0	0.4
Boreal forest	67.4*	0.23	0.33	130	12.0	0.5
Temperate grassland	69.9	0.95	0.81	100	9.0	3.5
Savanna	67.4*	0.51	0.81	210	15.0	3.3
Tropical deciduous forest/seasonal forest	134.8	0.28	0.33	365	7.5	0.8
Tropical evergreen forest/rainforest	180.5	0.33	0.33	365	17.0	2.9
Woodland/shrubland	NA[+]	NA[+]	NA[+]	NA[+]	8.5	0.7
Desert	67.4*	0.13	0.81	200	18.0	1.0
Tundra	67.4*	0.34	0.81	55	8.0	1.0
Cultivated	NA[+]	NA[+]	NA[+]	NA[+]	14.0	1.1
Total (G_{ex})						**15.2**

Table 1. Parameters used in determining the global root exudate carbon flux. *scaled using cross-biome median SER, [+]scaled using cross-biome median F_{ex}, [1]land surface area is included in woodland/shrubland. SER = specific exudation rate; FRB = fine root biomass; P_{AFRB} = proportion absorptive fine root biomass; GS = growing season.

Site	Biome	TBCA (se)	F_{ex} of biome (se)	Projected proportion of TBCA (se)
Cehegín, Spain[a]	Mediterranean	0.774 (0.035)	0.096 (0.013)	0.12 (0.02)
Duke FACE, NC, USA[b]	Temperate coniferous forest	1.191 (0.083)	0.073 (0.033)	0.06 (0.03)
ORNL FACE, TN, USA[b]	Temperate deciduous forest	0.782 (0.044)	0.086 (0.023)	0.11 (0.03)
BioCON, MN, USA[c]	Temperate grassland	0.682 (0.019)	0.385 (0.078)	0.6 (0.1)
Kaupulehu dry forest preserve, HI, USA[d]	Tropical deciduous forest	0.97	0.109 (0.095)	0.11 (0.10)
La Selva, CR[e]	Tropical evergreen forest	1.03 (0.20)	0.169 (0.029)	0.16 (0.04)

Table 2. Comparison between mass-balance TBCA (total belowground carbon allocation) and root exudate C flux (F_{ex}) (both in kg C m^{-2} y^{-1}) in six field sites from biomes represented in this meta-analysis. Sources for TBCA are a) Almagro et al. (2010), b) Palmroth et al. (2006), c) Carol Adair et al. (2009), d) Litton et al. (2008), e) Raich et al. (2014). TBCA = total belowground carbon allocation; F_{ex} = root exudate C flux per soil area.

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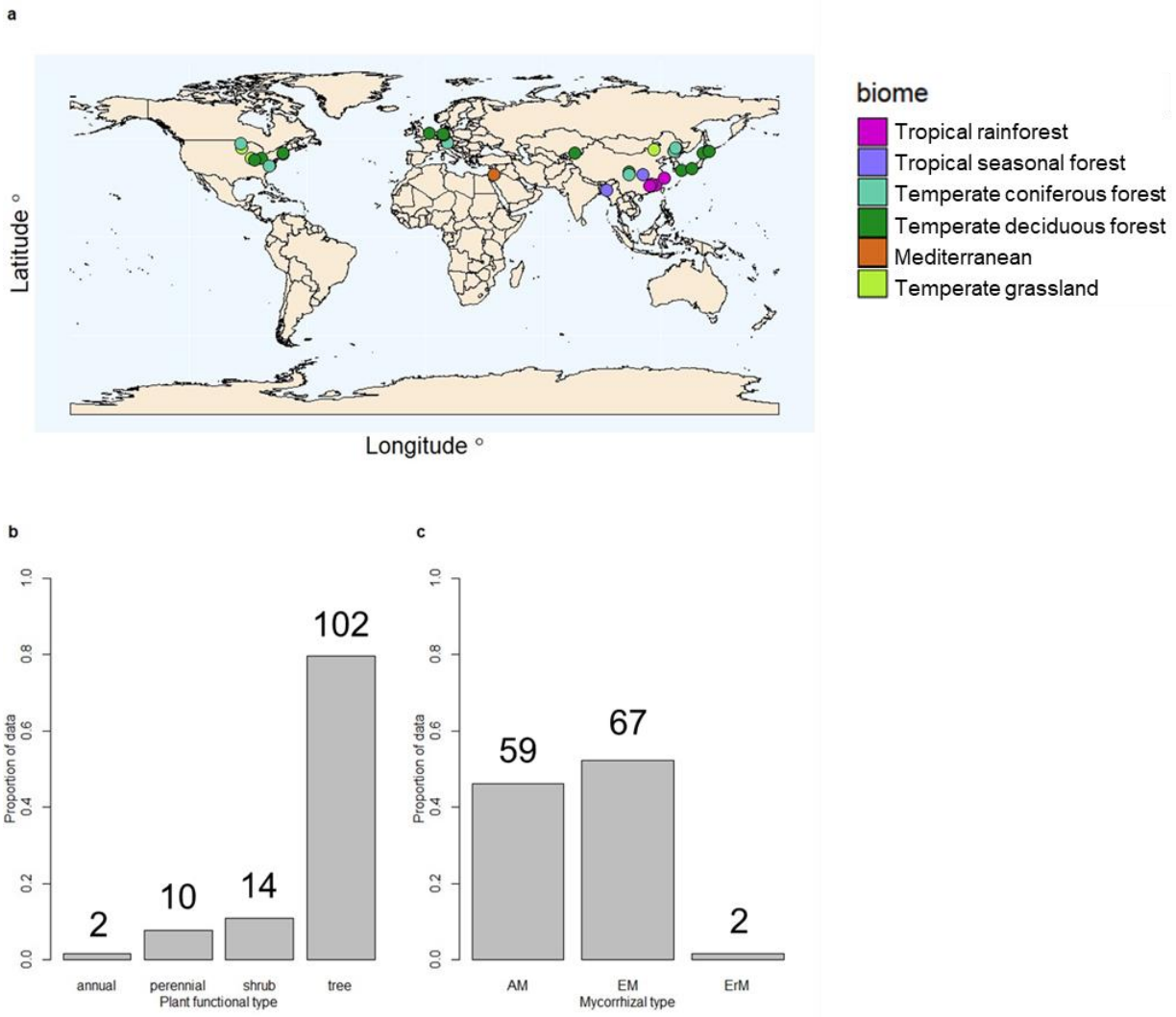

564

565 Fig. 1. a) distribution of sites in the dataset on the globe colored by biome, b) proportional distribution of
566 plant functional types in the dataset, c) proportional distribution of mycorrhizal types in the dataset. The
567 numbers in b) and c) are the number of observations of each type.

568

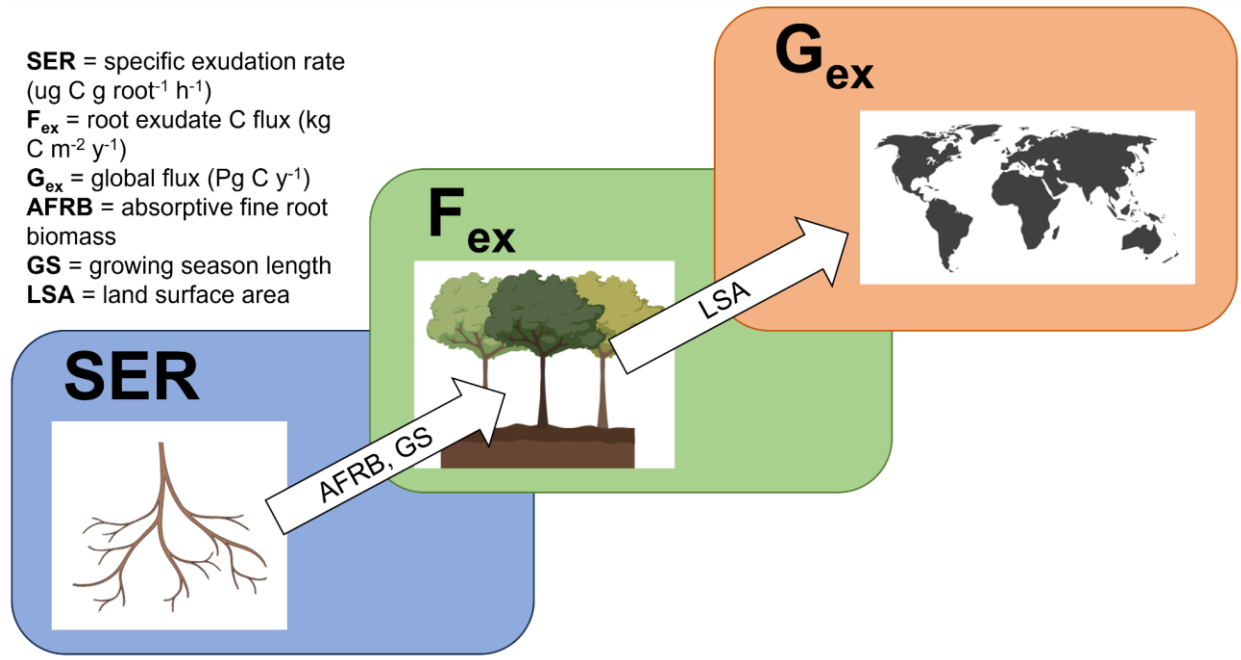

Fig. 2. Conceptual figure illustrating the scaling process described in Methods. Specific root exudation rates (expressed on a per root mass basis) were scaled spatially using estimates of absorptive fine root biomass and temporally using estimates of growing season length to get exudate C flux estimates on a per-meter ground area basis (F_{ex}). These estimates were then scaled to the entire biome using estimates of land surface area for each biome and all biomes were summed to get a global root exudate C flux estimate (G_{ex}).

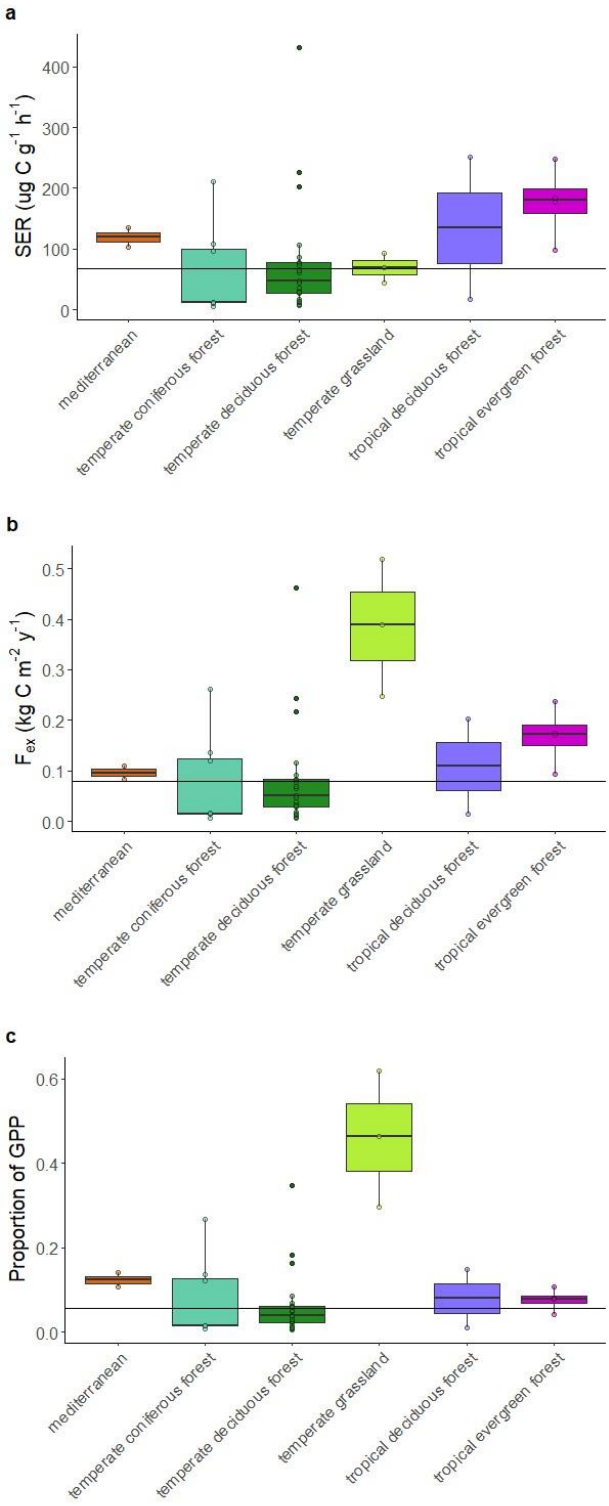

Fig. 3. Exudation rates by biome. a) mass-specific exudation rate, b) soil area specific exudate C flux, c) proportion of GPP released as root exudates. For each biome, horizontal lines represent the median and boxes represent the inter-quartile range and whiskers represent 1.5 times the interquartile range. Colored dots represent individual data points (studies) used in our analyses and corresponding black dots represent outliers. Panel-wide black horizontal lines are cross-biome medians.

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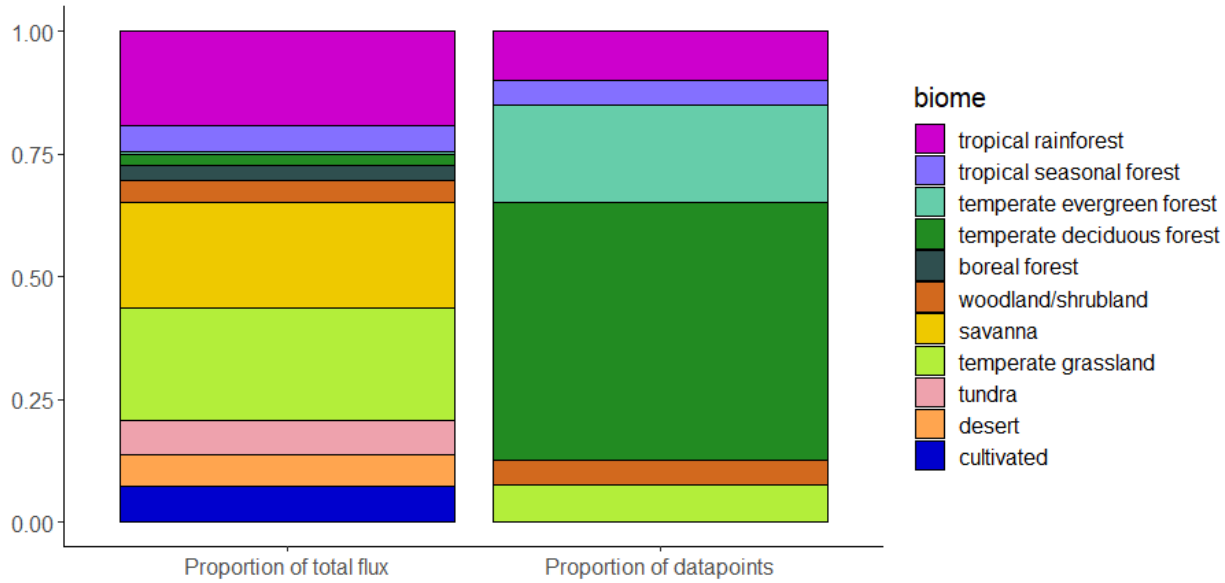

584
585 Fig. 4. The proportion of the global root exudate flux from each biome (left) and the proportion of studies
586 represented in our dataset from each biome (right). The left bar shows the proportional contribution of
587 each biome to the global root exudate flux (Table 1). The right bar shows the proportion of studies in our
588 dataset from each biome. The total number of data points for the right bar is 40.