The global mass and average rate of Rubisco

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Photosynthetic carbon assimilation enables the storage of energy in the living world and produces most of the biomass in the biosphere. Rubisco (D-ribulose 1,5-bisphosphate carboxylase/oxygenase), is responsible for the vast majority of global carbon fixation, and has been previously claimed to be the most abundant protein on Earth. Here, we provide an updated and rigorous estimate for the total mass of Rubisco on Earth, concluding it is ≈0.5 Gt, which is more than an order of magnitude higher than previous estimates. We find that >90% of Rubisco enzymes are found in the ≈2×10^{14} m^2 of leaves of terrestrial plants, and that the mass fraction of Rubisco in leaves is ≈2% of the total mass of leaves which we estimate at ≈30 Gt dry weight. We use our estimate for the total mass of Rubisco to derive the effective time-averaged catalytic rate of Rubisco, and find that it is ≈0.03 s^{-1} on land and ≈0.4 s^{-1} in the ocean. Compared to the maximal catalytic rate observed *in vitro*, the effective rate in the wild is ≈100-fold slower on land and ≈10-fold slower in the ocean. This analysis helps sharpen our appreciation of the large difference between lab and wild environments, and implies a more than 10-fold increase in widely cited previous estimates of the global amount of the so-called "most abundant protein on earth".

Introduction

The assimilation of atmospheric carbon by the joint activity of the photosynthetic machinery and the Calvin-Benson carbon fixation cycle are a key component that controls the global carbon cycle, and is responsible for the production of the vast majority of the organic carbon present in the biosphere (Overmann and Garcia-Pichel 2006; Raven 2009). The fixation of atmospheric CO_2 in the Calvin-Benson cycle is enabled by to the activity of the Rubisco enzyme, and as such it has a pivotal role in the global carbon cycle. Almost 40 years ago Ellis stated that the then recently discovered Rubisco is the most abundant protein on Earth (Ellis 1979). This statement was based on only a single paragraph of a much longer paper detailing its role in primary productivity, based on carbon fixation in terrestrial environments, and the turnover number of the Rubisco enzyme measured in the lab. The brief analysis made by Ellis was instrumental in emphasizing the important role of Rubisco in the environment, as well as the power of back-of-the-envelope calculations as a tool to estimate the abundance of proteins in the biosphere. However, it is not clear how robust the estimate actually is. To demonstrate the uncertainty surrounding the estimate of the total mass of Rubisco, we note that Ellis arrived at about 0.04 gigatons (Gt=10^{15} g) of protein. This can be compared to collagen, which is the most abundant protein in the human body, accounting for ≈30% of the ≈10 kg of total protein mass in an average human (BNID 111209). Collagen is found not only in humans but also in livestock. Taking into account also collagen present in livestock we get a global mass of collagen of about ≈0.07 Gt, higher than the total weight reported for Rubisco. In addition, we note that the original estimate by Ellis did not take into account marine carbon fixation, which supports a similar flux to terrestrial carbon fixation (Field 1998)

The aim of this current work is to use an independent methodology to construct a rigorous estimate for the total mass of Rubisco globally. We find that the global mass of Rubisco is ≈0.5 Gt, more than an order of magnitude higher than the previous estimate by Ellis. We use this independent estimate to probe the average rate of Rubisco globally, and find that in terrestrial environments the average rate of Rubisco is ≈1% of the characteristic k_{cat}.

Results

To estimate the total mass of Rubisco proteins, we estimate separately the total mass of terrestrial and marine Rubisco (Figure 1). For terrestrial Rubisco, we use a two step approach. We first estimate the global dry mass of leaves. We then estimate a characteristic mass fraction of Rubisco out of the dry mass of leaves. By multiplying these two components, we arrive at an estimate for the total mass of Rubisco as shown in Figure 1.

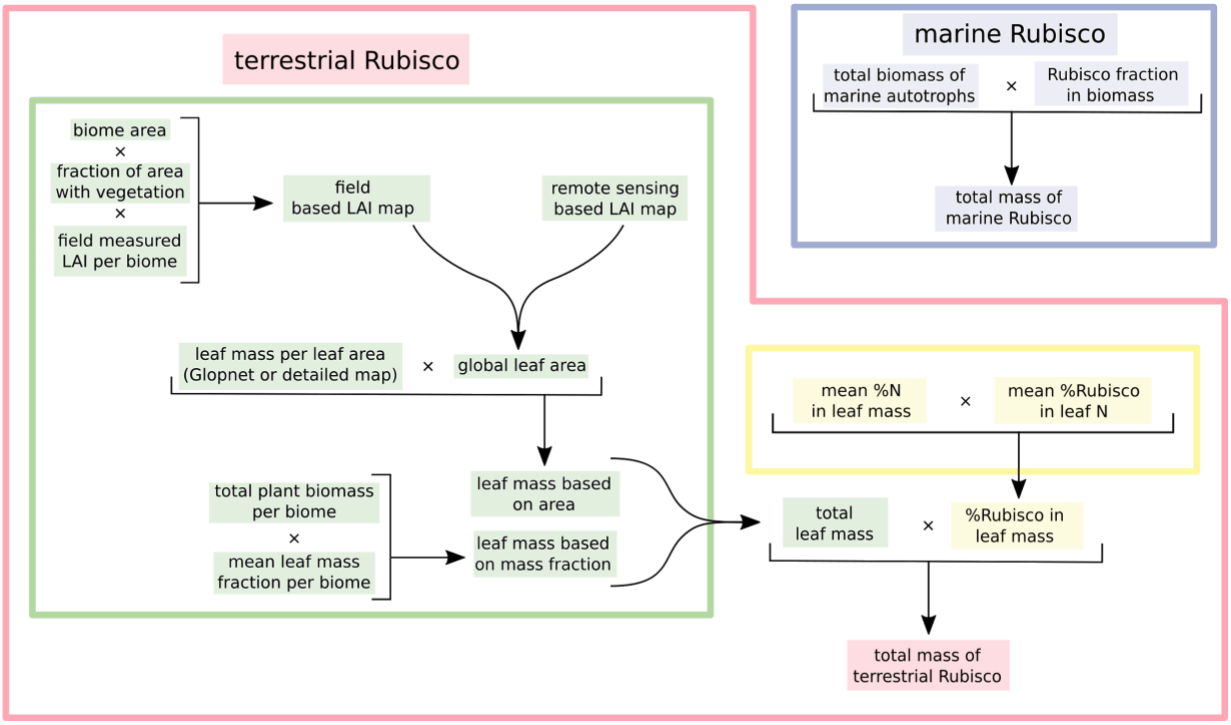

Figure 1. A schematic representation of our methodology for estimating the mass of Rubisco. Our methodology for estimating the mass of terrestrial Rubisco is composed of two parts - estimating the total mass of leaves and estimating the mean mass fraction Rubisco out of the dry leaf mass. Our methodology for estimating the mass of marine Rubisco is based on an estimate of the total biomass of marine autotrophs, as well as on reports on the fraction of Rubisco out of the dry weight of autotrophs.

Estimating the total mass of leaves globally

In order to estimate the global mass of leaves, we rely on two independent methods. The first method arises from an estimate of the total biomass of terrestrial plants (Bar-On, Phillips, and Milo 2018). This estimate of ≈450 gigatons of carbon (Gt C = 10^{15} g), translates to ≈900 Gt of dry weight, assuming ≈50% carbon content in dry weight. To convert this total plant dry weight to the total mass of leaves, we use meta-analysis of the mass fraction of different plant compartments across different biomes (Poorter et al. 2012). We use the average leaf mass fraction across biomes, weighted by the fraction of plant biomass in each biome (Erb et al. 2016). Overall, this approach yields an estimate of ≈40 Gt dry leaf weight, which is ≈4% of the total mass of plants. The second approach we use to estimate the global mass of leaves, is based, as shown in Figure 1, on first estimating the the total area of leaves on land and converting it to mass by using an estimate of the mass of leaves per unit area (LMA). To estimate the total area of leaves we rely on both field measurements (Asner, Scurlock, and A. Hicke 2003) and remote-sensing (Xiao et al. 2012) of the leaf area index (LAI) across the entire globe. LAI represents the total area of leaves per unit area. Summing across the entire surface area of land, we arrive at an estimate for the global total area of leaves of ≈2×10^{14} m^2 (see methods section for further details). This is equivalent to 200 million square kilometers or about twice the global ice-free land area. To convert the total area of leaves to mass, we rely on two separate procedures. The first relies on the a global database of plant traits (Wright et al. 2004), which measured the mass of leaves per unit area for various species of plants. We use the median mass of leaves per unit area across species of ≈100 g m^{-2}, to arrive at a total estimate of ≈20 Gt of leaves. Our second procedure relies on global maps of the mass of leaves per unit area produced in a recent study (Butler et al. 2017). In each

location in the map we multiply our estimate for the total leaf area by the local mass of leaves per unit area. When integrating across the entire globe, we arrive at an estimate of ≈20 Gt. This value also includes crops which are a relatively small fraction (≈2%) of the biomass of plants because of their high turnover rate relative to trees (Bar-On, Phillips, and Milo 2018). The relatively modest difference between the leaf mass fraction method (40 Gt) and the leaf area method (20 Gt) for estimating the global mass of leaves, even though they are based on independent datasets, each with its own assumptions and caveats, suggests a relative robustness of our estimate. As a best estimate for the total mass of leaves, we use the average mass from both approaches (highlighted in green in Figure 1), which is ≈30 Gt.

Estimating the mass fraction of Rubisco proteins out of leaf dry mass

Next, we estimate the average fraction of Rubisco out of the total leaf mass (highlighted in yellow in Figure 1). We rely on a recent meta-analysis which characterised several physiological parameters across a wide variety of plant species (Onoda et al. 2017). Specifically, we use the concentration of nitrogen in leaves, along with a measure of the fraction of leaf nitrogen that is in Rubisco. By multiplying these two numbers, we get an estimate for the fraction of the leaf mass that is nitrogen in Rubisco. As nitrogen accounts for ≈1/6 of the total mass of Rubisco (Milo and Phillips 2015), we can estimate the total fraction of Rubisco out of the leaf dry mass. We limit our analysis to woody plant species as they account for most of the biomass on earth. The fraction of Rubisco out of the dry weight of leaves in woody plants is log-normally distributed with a median fraction of ≈2% (Figure 2). Combining our estimate for the global mass of leaves with our estimate for the mass fraction of Rubisco in leaves, we estimate that the total mass of terrestrial Rubiscos is ≈0.5 Gt.

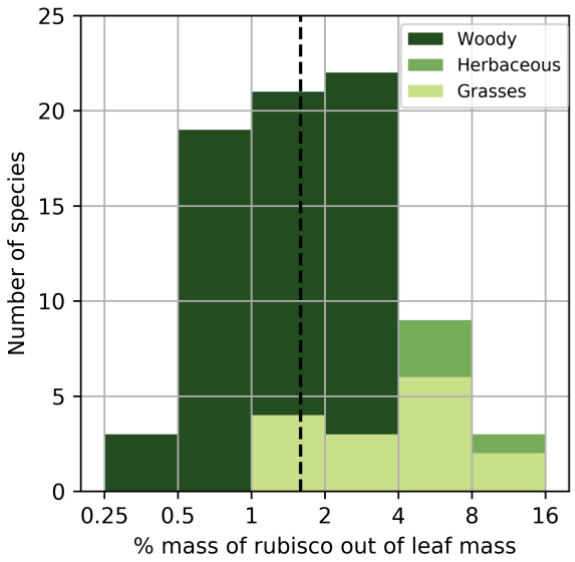

Figure 2. The distribution of the fraction of Rubisco out of the dry mass of leaves. Each color denotes a different category of plant growth form, with blue values representing woody plant, the orange values representing herbaceous plants, and the green values representing grasses. The vertical red line marks the average fraction used for the analysis.

Estimating the mass of marine Rubisco proteins

About half of global net primary productivity occurs in the oceans (Field et al. 1998). Therefore, one might expect the global mass of Rubisco proteins in the marine environment to be significant. We estimate the total mass of Rubisco proteins in the marine environment by combining an estimate for the total biomass of marine autotrophs with estimates on the Rubisco content of marine autotrophs (highlighted in blue in Figure 1). We recently estimated the total marine autotrophic biomass at ≈1 Gt C (Bar-On, Phillips, and Milo 2018). Assuming carbon is ≈50% of the dry biomass, we estimate the total biomass of marine autotrophs at ≈2 Gt. Microalgae usually have protein content of ≈50% of dry mass (Bleakley and Hayes 2017), so we estimate ≈1 Gt of proteins in marine autotrophs. We next estimate the mass fraction of Rubisco proteins out of the dry mass of marine autotrophs. We rely on several reports (Raven 1991; Losh, Young, and Morel 2013; Zorz et al. 2015) which reported values of 1-12% for different species of microalgae and cyanobacteria. We use the geometric mean of all the reported measurements of ≈4% as our best estimate of the characteristic mass fraction of Rubisco proteins out of the dry mass fraction of marine autotrophs. Multiplying our estimate of 1 Gt proteins in marine autotrophs with our estimate that Rubisco accounts for ≈4% of the total cellular protein, we estimate the total mass of marine Rubisco proteins at ≈0.04 Gt, which is less than 10% of the total mass of Rubisco.

Estimating the effective rate of terrestrial and marine Rubisco

Our approach for estimating the total mass of rubisco is not based on the rate of Rubisco, in contrast to the method used by Ellis. Therefore, we can use our estimate for the total mass of Rubisco to estimate the average effective rate of carbon fixation by Rubisco. In this section, we calculate the effective rate of both terrestrial and marine Rubisco. The methodology we use is similar to recent efforts to quantify *in-vivo* rates of enzymes (Davidi et al. 2016). Namely, we estimate the total flux (reactions per unit time) that is supported by the combined action of all Rubisco proteins in a given environment (terrestrial or marine). We then divide the total flux by an estimate the total number of Rubisco active sites which we derive from our estimates of the total mass of Rubisco. By dividing the total flux by the number of proteins that support this flux, we get an estimate for the average catalytic rate of a single Rubisco enzyme.

For the terrestrial environment, gross primary productivity (GPP), which includes all carbon fixation including that amount which will be respired by the organism, is estimated at ≈120 Gt C yr^{-1} (Beer et al. 2010). This value represents the total flux of carbon fixed on land each year and though the exact value is still debated, it is estimated to be accurate to better than 2 fold (Welp et al. 2011), which for the purposes of our analysis is accurate enough. We use the terrestrial GPP as a measure of the total flux that is supported by the combined action of all terrestrial Rubisco proteins. In order to calculate the effective rate of an average Rubisco, which is measured in reactions per second, we convert the estimate of terrestrial GPP to units of molecules of CO_2 fixed per second. As each CO_2 molecule contains one carbon atom, which has a molecular weight of 12 Da, we can express the the global GPP flux in units of carbon atoms fixed per second. As each year has $\approx 3\times10^7$ seconds, the total flux of terrestrial carbon fixation is $\approx 2\times10^{32}$ carbon atoms (and thus CO_2 molecules) per second as derived in Figure 3B.

We convert our estimate for the total mass of terrestrial Rubisco proteins to an estimate of the total number of Rubisco active sites by using the molecular weight of a Rubisco active site, which is ≈70 kDa (one large and one small subunit in type I Rubisco; (Ma et al. 2009). We calculate that the total number of Rubisco active sites is $\approx 5\times10^{33}$ (or about 10^{33} Rubisco L8S8 octamers). Dividing the total rate of all Rubisco enzymes by the total number of Rubisco enzymes, we calculate that the average catalytic rate of a single Rubisco is ≈0.04 s^{-1} as depicted in Figure 3C.

For the marine environment, gross primary productivity (GPP) is estimated at ≈80 Gt C yr^{-1} (del Giorgio and Duarte 2002). As with the terrestrial environment, we convert the GPP into units of reactions per second, and arrive at an estimate of ≈1.3×10^{32} carbon atoms (and thus CO_2 molecules) per second. Our estimate for the total mass of marine Rubisco is ≈0.04 Gt, which correspond to 4×10^{32} marine Rubisco active sites. Dividing the total rate of all marine Rubisco enzymes by the total number of Rubisco active site, we calculate that the average catalytic rate of a single Rubisco in the marine environment is ≈0.4 s^{-1} about an order of magnitude higher than Rubisco in the terrestrial environment.

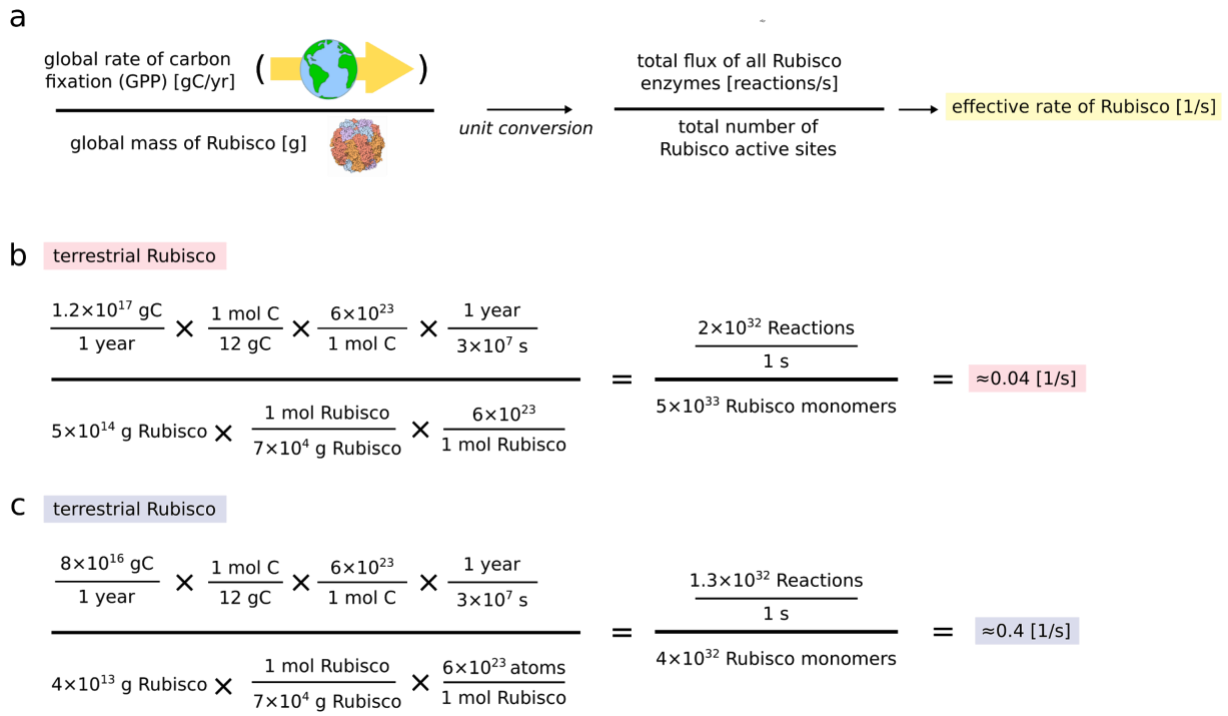

Figure 3. Estimating the effective rate of an average Rubisco. We use estimates for the total annual rate of carbon fixation - the gross primary productivity - in the terrestrial and marine environments, in conjunction with our estimates for the total mass of Rubisco in those environments. We convert the units of the total rate of carbon fixation to reactions per second using the fact that each reaction of rubisco fixes one carbon atom, which weighs 12 Da. We also convert our estimates for the total mass of Rubisco into the number of active sites by dividing the total mass by the molecular weight of an active site. By dividing the total amount of reactions all the active sites are performing each second by the total number of active sites, we get an estimate for the average rate of a single active site. In B and C we demonstrate the calculation for terrestrial and marine Rubisco, respectively.

Discussion

Our work provides a new methodology for estimating the total mass of Rubisco globally. Whereas Ellis used the catalytic rate of Rubisco *in vitro* in the lab to estimate the total amount of Rubisco, we rely on mass fractions out of the total autotrophic biomass. We estimate that the total mass of Rubisco enzymes is ≈0.5 Gt in the terrestrial environment, and ≈0.04 Gt in the marine environment. Our estimate is more than an order of magnitude higher than the current estimate of ≈0.04 Gt (Ellis 1979). Relying on measured mass fractions allows for much better constraints on the parameters used to estimate the total mass of Rubisco, hence leading to the large difference from previous values. Our estimate also is in line with the claim that

Rubisco is the most abundant enzyme in the world, even though a comprehensive comparison of the mass of Rubisco with the mass of other ubiquitous proteins is required for establishing such claim.

One additional benefit of our methodology is that because it is not based on the catalytic rate of Rubisco, we can use our estimate to infer the effective time averaged rate of Rubisco. We find that the effective rates of terrestrial and marine Rubisco are ≈0.04 and 0.4 s^{-1}, respectively. How does this rate compare with the maximal catalytic rate of Rubisco in plants? The characteristic k_{cat} of C3 plants, which dominate plant biomass, is ≈3 s^{-1} (Galmés et al. 2005; Galmés et al. 2014). Thus, the effective catalytic rate of Rubisco in wild terrestrial environments is ≈1% of its maximal rate. The characteristic k_{cat} of marine autotrophs is not significantly different than C3 plants, even though cyanobacterial Rubisco is usually faster (Shih et al. 2016; Young et al. 2016). As such, the effective catalytic rate of Rubisco in the marine environment is ≈10% of its maximal rate. The apparent inefficiency of Rubisco, especially in the terrestrial environment, is striking and requires explanation. There are many possible explanations for the lower effective catalytic rate of Rubisco. The rate of Rubisco might be limited from different abiotic factors such as the availability of solar radiation (e.g. during night, in cloudy conditions and when leaves are shaded in the canopy), the concentration of CO_2 Rubisco enzymes are exposed to, water supply, nutrient supply, temperature, etc. It could also be caused by *in vivo* factors such as photorespiration, the regeneration of RuBP, activation state of Rubisco, etc. This is only a very partial list that should be quantitatively explored further in the future.

Another way of phrasing the question is why we see so much Rubisco expression operating much more slowly that physically possible, when nature could have sufficed with a smaller amount of Rubisco working faster. There are several possible explanations for this conundrum, which we touch upon briefly. One line of argument is that excess Rubisco enables plants to respond fast to changing environmental conditions such as changes in illumination conditions (e.g. sun flecks). This is akin to suggested excess ribosomal pool in carbon limited bacteria (Mori et al. 2017; Korem Kohanim et al. 2018). Another possible hypothesis is that Rubisco serves for storage of nitrogen in plant tissues. In terms of elemental stoichiometry, plants have an abundant supply of carbon from the atmosphere, but are limited by the supply of other crucial elements such as nitrogen and phosphorus. Proteins have elemental stoichiometry suited for storing nitrogen when carbon is abundant, without the requirement of phosphorus, which would be required for storage in nucleic acids. Thus, plants can use protein as reservoirs of nitrogen, and Rubisco, being an abundant protein within plants, might serve this role.

Our analysis of the effective rates of Rubisco enzymes in the terrestrial and marine environment exposes a strong difference between the two environments, with marine Rubisco enzymes operating at a rate which is an order of magnitude larger than the ocean. Why are marine Rubisco enzyme much faster in the ocean? We suggest two factors which might help explain the difference. The first is CO_2 undersaturation. Most of the photosynthesizing organisms in the marine environment, cyanobacteria and eukaryotic phytoplankton, are equipped with carbon-concentration mechanisms that increase the local concentration of CO_2 in the vicinity of Rubisco, which help to reduce the limitation of CO_2 subsaturation (Mackinder et al. 2016). A second factor is self shading. Due to the microscopic size of photosynthesizing organisms in the ocean and their relatively diluted biomass densities, shading is not present in the marine environment. In the terrestrial environment, the high density of leaves per unit area, quantified in the form of the leaf area index, creates a situation in which leaves in lower parts of the canopy are shaded by leaves at the top of the canopy and

thus get a limited supply of photons, which limits the rate of carboxylation by Rubisco located in leaves lower in the canopy.

Overall, our analysis sheds light on the distribution of Rubisco in the natural environment, provides a didactic framework for evaluating the effect of different plant traits on the abundance of Rubisco. We utilize the estimate of the total mass of Rubisco to show that on average, Rubisco is operating far below its maximal rate. Further studies will uncover the relative importance of factors that contribute to limiting the rate of Rubisco, and to what extent Rubisco might play additional roles other than its catalytic function.

Methods

A full description of our analysis including the data sources and the code used to generate our results can be found in the following link:

Calculating the total area of leaves

To estimate the total area of leaves we construct two maps of the distribution of leaf area across the globe. The first map we use is the GLASS LAI product map (Xiao et al. 2012) which is based on remote-sensing. As the amount of leaves changes throughout the year due to deciduous plants, we use monthly composite maps, and calculate the annual average of the total leaf area. We chose to use the composite map with a total biomass closest to the annual mean.
As remote-sensing of LAI can get saturated at high LAI values (Liang, Li, and Wang 2012), we use as an independent source ground measured values of LAI in different biomes (Asner, Scurlock, and A. Hicke 2003). The average ground measured LAI values for each biome represent the amount of leaf area per vegetated land surface, but in many biomes (e.g. deserts) most of the land surface in not vegetated. We use a recent study which produced a global map of vegetation coverage (Song et al. 2018). For each location we multiply the fraction of land which is vegetated (either by trees or by short vegetation) by the average LAI measured in the specific biome the location resides in. Ground based measurements of LAI are likely to be overestimates of the annual mean LAI in deciduous biomes, as LAI of zero will usually not be reported. By combining remote-sensing based estimates, which likely underestimate the actual leaf area, as well as ground-based measurements, which are likely overestimates, we make our estimate of the total leaf area more robust.

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