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Estimates of global cyanobacterial biomass and its distribution

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With 7 tables in the text

Abstract: We estimated global cyanobacterial biomass in the main reservoirs of cyanobacteria on Earth: marine and freshwater plankton, arid land soil crusts, and endoliths. Estimates were based on typical population density values as measured during our research, or as obtained from literature surveys, which were then coupled with data on global geographical area coverage. Among the marine plankton, the global biomass of *Prochlorococcus* reaches 120 x 10^{12} grams of carbon (g C), and that of *Synechoccus* some 43 x 10^{12} g C. This makes *Prochlorococcus* and *Synechococcus*, in that order, the most abundant cyanobacteria on Earth. Tropical marine blooms of *Trichodesmium* account for an additional 10 x 10^{12} g C worldwide. In terrestrial environments, the mass of cyanobacteria in arid land soil crusts is estimated to reach 54 x 10^{12} g C and that of arid land endolithic communities an additional 14 x 10^{12} g C. The global biomass of planktic cyanobacteria in lakes is estimated to be around 3 x 10^{12} g C. Our conservative estimates, which did not include some potentially significant biomass reservoirs such as polar and subarctic areas, topsoils in subhumid climates, and shallow marine and freshwater benthos, indicate that the total global cyanobacterial biomass is in the order of 3 x 10^{14} g C, surpassing a thousand million metric tons (10^{15} g) of wet biomass.

Key words: Cyanobacteria, global biomass, plankton, benthos, freshwater, marine, terrestrial environments, arid land soils, abundance, quantification, population density, geography.

Introduction

There have been considerable efforts to establish and describe the importance of cyanobacteria, and even their dominance, in a large variety of habitats including marine and freshwater plankton and benthos, as well as terrestrial settings.

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However, most studies have offered only qualitative accounts of biomass and diversity, or, if quantitative assessments were presented, they were usually restricted to a geographically constrained site. The study of local cyanobacterial populations is obviously relevant to the local ecology, and may have economic and public health implications. Furthermore, intergrative studies on data obtained from a variety of sites can lead to the discovery of widely applicable, general patterns. The interpretation of a particular set of results, as well as the intergrative efforts, are facilitated when carried out within a general or global framework. Perhaps the most immediate question that arises when seeking to construct such a global framework is the extent and distribution of the global cyanobacterial biomass. How much cyanobacterial mass is out there? And how is that biomass distributed among different environments? Here we present initial attempts to determine the magnitude of the global cyanobacterial biomass and the size of significant global reservoirs.Even if rough, quantitative answers to this apparently simple question should, in fact, help in interpreting data, predicting environmental consequences of human activities, and guiding future research efforts.

Results and Discussion

The global biomass attributable to a certain habitat, organism or group of organisms, can be arrived at simply as a product of the average or typical population density and the extent of their distribution. For cyanobacterial habitats, typical areal population densities, expressed in a unified way such as chlorophyll *a* (chl *a*) concentration per unit area, vary within 3 orders of magnitude. Typical values for consideration span the range from 5 x 10^{-3} g m^{-2} in oligotrophic oceanic waters, 10^{-1} g m^{-2} in desert soils (see below), 2–8 x 10^{-1} g m^{-2} in aquatic blooms, and 0.25 –5 g m^{-2} in microbial mats. The areal extent of such habitats, however, varies within a much larger range. Oligotrophic oceanic waters cover an approximate 4 x 10^{14} m^2, whereas the global extent of microbial mats is probably restricted to approximately 10^8 m^2. This implies that in order to identify the cyanobacterial components likely to contribute significantly to global biomass one should consider first those with large distributional areas, rather than those that attain large population densities. Following that rule, we identified the cosmopolitan marine planktic cyanobacteria and terrestrial cyanobacteria from arid lands as potentially making up the largest cyanobacterial biomass reservoirs. We also considered freshwater plankton. These components are treated separately in the following discussion.

Marine picoplankton

Virtually all of the ocean surface waters contain significant populations of planktic, unicellular cyanobacteria, belonging to the photosynthetic picoplankton. Given the shear size of their distribution area, even very gross estimates indicate

Table 1. Estimates of the global population of picoplanktic cyanobacteria of the marine *Synechococcus* group. Total extent of the oceanic realms according to SCHLESINGER (1977). Extent for *Synechococcus* obtained by exclusion of Southernmost Southern Ocean, North Polar Ocean and Bering Sea (respective areas according to KNAUR Welt Atlas). Average areal cell densities based on the reviews of LI (1998) and PARTENSKY et al. (1999).

Oceanic Realm	Total Extent $[10^{12}\ m^2]$	Extent of distribution $[10^{12}\ m^2]$	Areal cell density $[10^{11}$ cells per $m^{-2}]$	Total cells $[10^{25}$ cells$]$
Open ocean	326	300	5	15.0
Coastal Zone	36	30	20	6.0
Upwelling	0.4	0.3	20	0.6
Global	362.4	330.3	–	21.6

a global wet biomass on the order of a billion metric tons (GARCIA-PICHEL 2000). Two types of phylogenetically related, but physiologically distinct, cyanobacterial picoplankters are known:

Prochlorococcus (CHISHOLM et al. 1988) and "marine *Synechococcus*" (WATERBURY et al. 1979). The phycoerythrin-containing marine *Synechococcus* have a geographically wide distribution that includes eutrophic, mesotrophic, and oligotrophic waters in coastal, marginal, and open ocean regions, with the single exception of polar waters. This equals an area of some 300 x 10^{12} m^2. A wealth of data from distribution/abundance studies has been gathered since their discovery in the late 70's. Summaries by LI (1998) and by PARTENSKY et al. (1999) indicate that cell densities of marine *Synechococcus* typically vary within one order of magnitude, averaging aound 10^6 cells per liter or 10^{11} cells under each square meter. The distribution of the tiny, weakly fluorescent, divynil-chl *a* containing *Prochlorococcus* is somewhat more restricted than that of *Synechococcus:* it is absent from coastal and otherwise meso- and eutrophic waters, as well as from polar and subpolar open ocean waters, virtually disappearing beyong 50 °N, 50 °S (PARTENSKY et al. 1999). It is, however, dominant in terms of cell numbers and biomass in oligotrophic regions (BLANCHOT et al. 2001). The geographical area occupied by *Prochlorococcus* is estimated here to cover about 225 x 10^{12} m^2. Cell abundance typically reaches or exceeds 10^8 cells per liter or 10^{13} cells per m^2 through much of its geographical range. An estimate of the size of the global population of picoplantic cyanobacteria on the basis of geographical distribution and typical cell abundance is presented in Tables 1 and 2. Cell abundance data are vertically integrated through the photic zone, and whenever possible, are seasonally average. Because *Synechococcus* cells contain an average 250 femtograms of carbon (fg C) per cell and the much smaller *Prochlorococus* average only 53 fg C per cell (CAMPBELL et al. 1994), cell numbers can easily be translated into biomass estimates. The global biomass of *Prochlorococcus* thus reaches 120 x 10^{12} g C, and that of *Synechococcus* 43 x 10^{12} g C. This large figure surely makes

Table 2. Estimates of the global population of picoplanktic cyanobacteria of the marine *Prochlorococcus* group. Total extent of the oceanic realms according to SCHLESINGER (1977). Extent for *Prochlorococcus* based on oceanic area within 50° N and 50° S. Average areal cell densities based on the review of PARTENSKY et al. (1999) and the surveys of ZUBKOV et al. (2000) and BLANCHOT et al. (2001).

Oceanic Realm	Total Extent [10^{12} m^2]	Extent of distribution [10^{12} m^2]	Areal cell density [10^{11} cells per m^{-2}]	Total cells [10^{25} cells]
Open ocean	326	222	150	330
Coastal Zone	36	0	–	–
Upwelling	0.4	0	–	–
Global	362.4	222	–	330

Prochlorococcus and *Synechococcus,* in that order, the most abundant cyanobacteria on Earth. It is perhaps one of the paradoxes in cyanobacterial biology that these genera have been known only for several decades. In the case of the marine *Synechococcus,* it is even more paradoxical that, in spite of their monophyletic origin, well-delimited ecological origin, physiology, and biochemistry, no taxon has yet been created to separate them from other phenotypically, ecologically, and phylogenetically unrelated cyanobacteria. The only feature in common with these other genera is their coccobacilloid morphology.

Trichodesmium

Tropical and subtropical populations of dinitrogen-fixing oscillatorian cyanobacteria of the genus *Trichodesmium* have been known for over a century. Surveys by LOHMAN (1920) in the subtropical Atlantic called attention to the large oligotrophic expanses where *Trichodesmium* is found: the subtropical Gyre, the Caribbean, and the Gulf of Mexico. The distribution of *Trichodesmium* encompasses a circumplanetary belt through Pacific, Indian, and Atlantic Oceans, interrupted only by coastal waters and land. The belt is roughly constrained between 25 °N and 25 °S (CAPONE et al. 1997). We estimate this belt to cover some 150 x 10^{12} m^2, or roughly between 40 and 50% of each of the world's three largest oceans. Excellent data sets exist from the Pacific Gyre (Station ALOHA, near the Hawaiian Archipelago; LETELIER & KARL 1996) from which the seasonally-averaged, photic zone-integrated *Trichodesmium* can be easily calculated: 20 x 10^5 trichomes under each m^2 of ocean surface. An alternative estimate can be derived from the Atlantic Ocean from the original LOHMAN survey (shown in CAPONE & CARPENTER 1999). This is most probably an underestimation, since only bundles were counted. Yet, upon integration over the typical 100-m deep euphotic zone, one still obtains the large number of 8 x 10^5 trichomes m^{-2}. Thus, a figure of approximately 14 x 10^5 trichomes m^2 is probably a sensible, if conservative, estimate to typify *Trichodesmium* areal abundance. With a measured carbon content of 50 ng C per trichome (LETELIER & KARL 1996) and the distributional area indicated above, the global biomass of *Trichodesmium* likely reaches at least 10 x 10^{12} g C.

Edaphic cyanobacteria in arid soils

Cyanobacteria are often common or dominant in topsoils where higher plant growth is restricted. There, they typically initiate and support the formation of biological soil crusts. Such soil crusts form in cold and hot deserts, as well as in temporarily disturbed areas of temperate regions. They contain large populations of phototrophs, either on the soil surface or immediately below it (1 to several mm deep), despite the slow growth rates imposed by the lack of water. These often cryptic communities have been described from all semi-arid and arid regions of the globe, although most reports have been from North America, the Middle East and Australia. Recent reviews have addressed ecological, floristic, and biogeochemical aspects of biological soil crusts (EVANS AND JOHANSEN 1999, BELNAP & LANGE 2001, GARCIA-PICHEL 2003). Due to the large global expanses of arid lands (over 30% of the total land surface), soil crust cyanobacteria are likely to attain global populations of significance. Gauging the magnitude of soil crust cyanobacteria is not as straightforward as in the case of planktic forms, because most published studies have been qualitative and floristic, and data on biomass levels are scarce. Also, cell counts in the soil matrix are methodologically hard to achieve. For this estimate, we assessed the population size of soil crust cyanobacteria from measurements of areal chl *a* content, either from the literature or from a review of our own unpublished data. A survey of areal chl *a* concentrations in soil crusts from a variety of arid and semi-arid locales in North America, Asia, Africa, Australia, Europe and the Middle East is presented in Table 3. The data are limited to crusts dominated by cyanobacteria, excluding those where lichens (other than cyanolichens) or mosses add a significant component to the phototrophic biomass. Chl *a* in individual samples (and independent determination) ranged from 5 to 200 mg m^{-2}, for this estimate, we used an average chl *a* concentration for each site. Inspection of the data reveals two interesting aspects. First, average areal chl *a* concentrations in soil crusts are consistently high among different sites. The standard deviations for each site are also high, indicating a marked patchiness at spatial scale sampled (usually on the order of square centimeters). Secondly, there is a tendency for arid climate sites to harbor somewhat smaller population densities than those in semiarid-sites. The mean areal chl *a* content for semiarid sites attributable to cyanobacteria (from Table 3) is 99 mg m^{-2}, with a standard deviation of 73, whereas for arid sites the mean is 47 mg m^{-2}, with a standard deviation of 46. This corresponds to 4.46 and 1.92 g C m^{-2}, respectively. It is thus reasonable to distinguish between arid and semiarid settings for our large-scale calculations. A further caveat is the determination of what percentage of arid and semiarid lands is actually covered by biological

Table 3. Standing stock of edaphic cyanobacteria in soil crusts from arid lands

Location	Climate	Annual Precipitation [mm]	Chlorophyll *a* [mg m^{-2}] Average	Chlorophyll *a* [mg m^{-2}] SD or Range	Ref.	Abundance[a] [%]	Cyanobacterial Biomass Density [mg m^{-2}] carbon	Cyanobacterial Biomass Density [mg m^{-2}] dry weight
Bardena Blanca, N. Spain	semiarid	450	39	25	1	90 %	1755	3510
Serengeti, E. Africa	semiarid	400	58	44	1	90 %	2592	5185
Lake Mere, Australia	semiarid	310	89	70	1	90 %	4005	8010
S. E. Utah, USA (light)	semiarid	225	22	22	1	90 %	990	1980
S. E. Utah, USA (dark)	semiarid	225	101	27	1	90 %	4545	9090
S. E. Utah, USA (cyanolichens)	semiarid	225	111	110	1	90 %	4995	9990
San Nicolas, Is., California, USA	semiarid	370	151	98	1	90 %	6795	13590
China NW (Inner Mongolia)	semiarid	300	97	82	1	90 %	4365	8730
Escalante, Utah, USA	semiarid	270	41	50	1	90 %	1861	3722
Holloman, New Mexico, USA	semiarid	292	33	49	1	90 %	1467	2935
Jornada, New Mexico, USA	semiarid	257	273	157	1	90 %	12285	24570
Mongolia (Transect)	arid-semiarid	50–350	22	16	1	90 %	990	1980
Mongolia (Transect)	arid-semiarid	50–350	175	42	1	90 %	7875	15750
Joshua Tree, CA, USA	arid	103	56	44	1	90 %	2520	5040
Lake Mead, NV, USA	arid	100	22	21	1	90 %	990	1980
Mojave Desert Survey, USA	arid	64–110	16	20	1	90 %	720	1440
Lower Sonoran, Desert, Arizona	arid	252	20	13	1	90 %	900	1800
River Ille banks, Kazahkstan	arid		12	–	2	90 %	540	1080
Dead Sea Valley(Transect)	arid		40	0–16	3	100 %	2000	4000
Central Australia	arid		150	169–130	4	100 %	7500	15000
Negev Desert	arid		34	17–51	5	90 %	1530	3060
Tunisia	arid		102	–	3	30 %	1530	3060

References: **1** – This work; **2 –** TSIJIMURA et al. 2000; **3** – DOR & DANIN 1996; **4** – LANGE 2001; **5** – KIDRON 1995.
a: % of Chl *a* attributable to cyanobacteria. Directly given in publication or estimated from accounts of taxonomic composition **b:** calculated from Chl *a*, using abundance and the following ratios: Chl ***a*** to dry weight = 1/100, Organic Carbon to dry weight = 1/2, dry wt to wet weight = 1/5

Table 4. Estimates of the global carbon biomass of edaphic cyanobacteria from aridland crusts. Areal extents are according to MIDDLETON & THOMAS (1997). Typical population densities are averages from Table 3.

	Total Extent [10^{12} m^2]	Average Density [g Carbon per m^2]	% Cover	Total Biomass [10^{12} g Carbon]
Semiarid lands	23.05	4.46	40	41
Arid lands	15.69	1.92	50	15
Hyperarid lands	9.78	0	0	0
Totals	48.52	–		55

crusts as opposed to higher plant cover, rocks, and uncrusted soils. There are simply no large-scale surveys that address this issue. On the Colorado Plateau of Utah, as much as 70% cover can be achieved by crusts, as seen in remote sensing data (KARNIELI et al. 2001). For our calculations, we used an estimate of 40% crust cover in semiarid lands and 50% for arid lands, where higher plant cover is more restricted. These are admittedly subjective, but decidedly conservative, estimates, particularly given that areas without crust are already incorporated in the average data for surveys and transects in Table 3. There are no available data on hyperarid areas, possibly because edaphic algae become restricted and crusts are not well-developed. We neglected their possible contribution to the totals here. As estimate of the global biomass of edaphic cyanobacteria from arid lands is given in Table 4.

Endolithic and hypolithic cyanobacteria in arid lands

A second potentially important component of terrestrial microalgal communities in arid lands is associated with the lithic environment. Endolithic phototrophic communities have been described from sedimentary rocks (sandstone, limestone) and granite in a variety of deserts, both hot and cold. Cyanobacteria tend to dominate endolithic communities in hot deserts (BELL et al. 1986). They can make significant contributions to the total primary productivity of arid areas (BELL & SOMMERFIELD 1987). Hypolithic cyanobacteria are also common under translucent pebbles in deserts (CAMERON & BLANK 1966). A survey of available literature values for areal biomass estimates of endolithic and hypolithic environments is presented in Table 5. While this survey yielded only a very restricted data set, it demonstrates that the cyanobacterial population densities of such communities in hot arid areas vary between 0.15 and 2.3 g C m^{-2}, giving an average of 1.21 (S.D = 0.97) g C m^{-2}.

While it is obvious that bare rock makes a sizeable component of the total global area in aridlands, no data could be located on the percentage coverage by rocks and pebbles. Consultations with expert geomorphologists lead to a consen-

Table 5. Standing Stocks of Endo- or Hypolithic Cyanobacteria

Location	Lithology	Formation	Climate	Type	Biomass estimator[a] Chlorophyll a [mg m^{-2}] Average	Range	Organic Carbon [g m^{-2}] Average	Range	Ref	Abundance[b]	Average Density [mg m^{-2}] carbon	dry weight
Colorado Plateau, Arizona	Sandstone	Coconino	Semiarid	Endoliths	80				1	80%	1600	3200
Northern Province, S. Africa	Sandstone	Tshipise	Semiarid	Endoliths	29.12	0.05–71.8			2	100%	728	1456
Mojave Desert, USA; Sonoran Desert, Mexico; Negev Desert, Israel	Sandstone, Granite	Various Semiarid	Arid to	Endoliths			4.75	1.5–8	3	50%	2375	4750
S. Victoria Land	Sandstone		Polar arid	Endoliths	4	1.8–6.2			4	50%	50	100
Dry Valleys	Sandstone	Beacon	Polar arid	Endoliths			1.56	1.39–1.65	5	50%	780	1560
Niagara Falls, Canada	Limestone	Niagara Scarpmer	Continental	Endo and Epiliths	73			1.5–73		40%	730	1460
Gobi Desert, Mongolia	–	Pavement	Continental	Hypoliths			0.305	0.16–47	6	50%	152.5	305

References. **1**–BELL et al. 1986; **2**–WEBER et al. 1996; **3**–FRIEDMAND & KIBLER 1980; **4**–FRIEDMANN et al. 1980; **5**–WYNN-WILLIAMS 2000; **6**–FRIEDMANN, 1995.
a: averages are directly reported when given in original publication. Alternatively a mean value for the range provided has been calculated. **b:** % of the biomass estimator attributable to cyanobacteria. Directly given in publication or estimated from accounts of taxonomic composition. **c:** calculated from biomass estimators using abundance and the following ratios: Chl a to dry weight = 1/200, Organic Carbon to dry weight = 1/2, dry weight to wet weight = 1/5

sus figure of some 30 % for the US Southwest. Under this assumption, and using the extent of arid and semiarid lands in Table 4, our global estimate for lithophilic cyanobacteria in arid lands is 14.09 x 10^{12} g C.

Freshwater plankton

Cyanobacteria are well-known and important members of lake plankton under oligotrophic, mesotrophic, and eutrophic conditions. The bloom-forming species are notorious because of the public health effects associated with their presence. The literature on lake plankton biomass, as well microbial community structure is rather rich. In order to assess the global contribution of cyanobacteria to freshwater plankton biomass, we sought studies that specifically establish cyanobacterial presence in large lakes or groups of lakes. This is because most of the world's freshwater is found in large to very large lakes. In the survey presented here (Table 6), we included studies that provided both data on yearly averaged plankton community structure as well as measurementss of chl *a* concentration. The data was then integrated through the respective mixed zone to obtain cyanobacteria-specific areal biomass density estimates as well as total biomass estimates. We extrapolated values obtained from those lakes (accounting for 93 % of all the surface covered by freshwaters) to the rest of lakes that were unaccounted for (Table 7) to obtain a final global estimate of 3 x 10^{12} g C.

Other environments

Other environments exist that cover relatively large geographical areas and in which cyanobacteria play an important role as primary producers. They are, however, not amenable to analysis because of the scarcity of available data on biomass density or because of difficulties in estimating their distributional extent. Among the neglected components, one needs to include terrestrial cyanobacteria found in polar and subpolar areas (including the tundra) that cover about 15 x 10^{12} m^2, similar in magnitude to arid lands. Diverse assemblages of cyanobacteria inhabit these soils (Plichta & Luscińska 1988, Elster et al. 1999, Liengen 1999), and because of the low temperatures, biomass tends to accumulate. If cyanobacterial density in these communties equals those found in semiarid lands, their global contribution would add another 20–40 x 10^{12} g C to the global cyanobacterial biomass. This is probably the largest component we did not include and deserves further study. Soil cyanobacteria in temperate soils covered by plant litter (i.e., *Leptolynbya*-like forms), while attaining very small population densities may also add to the terrestial component of global cyanobacterial biomass due to the large areas covered. Other communities we did not include are epi- and endolithic cyanobacterial communities in temperate and tropical climates, benthic cyanobacterial assemblages in tropical shallow waters, cyanobacterial benthos/periphyton in small freshwater ponds, and ephemeral patches in temperate and tropical

Table 6. Total yearly averaged cyanobacterial biomass in large inland water bodies of different origin.

Origin Lake	Surface area[a] [10^9 m^{-2}]	Depth of Mixed Zone [m]	Average Areal Chlorophyll *a* [g m^{-2}]	Cyanobacterial abundance[b] [volume fraction]	Total cyano-. bacterial Chl *a* (10^8 g)	Reference
Tectonic						
Tanganyika	32.9	40	0.100	0.10	3.29	1,2
Baikal	31.5	40	0.160	0.05	2.52	3,4
Malawi	22.4	30	0.300	0.10	6.72	5
Balkash	18.2	10	0.120	0.50	10.92	6
Turkana	8.9	40	0.080	0.05	0.37	7
Nicaragua	8.2	8	0.400	0.80	0.26	8
Issik-Kul	6.2	60	0.030	0.20	0.37	6
Torrens	5.9	40	0.080	0.05	0.24	7
Albert	5.6	40	0.080	0.05	0.22	7
Victoria	68.0	30	0.600	0.80	326.40	9
Aral	64.1	10	0.100	0.10	6.41	10
Chad	16.6	2	0.400	0.25	16.60	11,12
Titicaca	8.0	20	0.060	0.10	0.48	13
Eyre	7.7	2	0.030	0.80	1.85	14
Other	215.2	20	0.209	0.20	119.55	(c)
Glacial						
Scandinavian	166.0	5	0.010	0.10	1.66	15,16
Canadian Shield	841.0	5	0.010	0.10	8.41	17,18,19
Saskatchewan	67.2	5	0.050	0.50	16.80	after 20
U.S.A.	79.6	20	0.100	0.10	7.97	19,21
Other	93.1	20	0.100	0.10	9.31	(d)
Flood plane	218.0	–	0.002	0.30	1.53	22

a – according to Maybeck (1995). **b** – as outlined in the references (without picoplankton), **c** – mean of all tectonic lakes (Lake Chad not considered) **d** – conditions assumed to be as in glacial lakes of U.S.A. References: **1** – SARVALA et al. 1999; **2** – HECKY & KLING 1981; **3–** BONDARENKO et al. 1996; **4** – IZMESTEVA et al. 1990; **5** – HABERYAN & MHONE 1991; **6–** ALADIN & PLOTNIKOV 1993; **7–** EVANS 1997; **8–** ERIKSON 1998; **9–** CRUL 1998; **10–** MICKLIN & WILLIAMS 1966; **11–** CARMOUZE et al. 1983; **12** – COMPÈRE & ILTIS 1983; **13–** ILTIS 1992; **14–** DE DECKER & WILLIAMS 1986; **15–** ARST et al. 1999; **16** –KUTSER et al. 1998; **17** – FEE et al. 1985; **18** – MASSON et al. 2000; **19** – NICHOLLS & HOPKINS 1993; **20–** HAMMER 1986; **21–** FREY 1963; **22–** ROGER 1996.

Table 7. Calculation of global cyanobacterial carbon biomass in inland water bodies.

Status	Surface area [10^9 m^2]	Areal cyanob. Chl *a*[a] [g m^{-2}]	Biomass[b] [10^{12} g C]
Considered in Table 6	1984.3	0.0286	2.84
Not considered in Table 6	151.1[c]	–	0.22[d]
Total	2135.4	0.0286	3.01

a – Average using all data in Table 6. **b** – Assuming a typical ratio of Chl. *a* to C-content of 1:50. **c** – extent according to MAYBECK (1995). **d** – Assuming the same population density as in areas considered in Table 6.

environments. These environments are all characterized by high population densities, and while their geographical extent is certainly much smaller than those treated above, it is not minute. These may perhaps add global contributions in the order or 1–10 x 10^{12} g C to the final tally, but finer estimates will be difficult to obtain.

Conclusions

The estimates presented here indicate that the global cyanobacterial biomass reaches at least 232 x 10^{12} g C and most likely is closer to 300 x 10^{12} g C, if the environments not included in this survey were taken into account. The latter figure implies a dry biomass by weight (phytomass) of 600 x 10^{12} g and a wet biomass of 3 x 10^{15} g. For comparison, the yearly world production of paper is 0.3 x 10^{15} g and that of corn is 0.06 x 10^{15} g. The total biomass in land plants (most of which is inactive woody tissue) amounts to 560 x 10^{15} g C (SCHLESINGER 1997). Cyanobacteria thus make up about 1/2000 of the global carbon biomass.

We regard our estimates to be a reasonable assessment despite the fact that some of our assumptions, particularly regarding percentage cover of terrestrial environments and the relative abundance of cyanobacteria among phototrophs, were admittedly subjective. However, even large errors in cover estimates would not result in order of magnitude differences in the final estimates, as the final estimates are mostly influenced by the order of magnitude of their geographical distribution and by cyanobacterial density. Estimates for marine and freshwater plankton are certainly more robust than those for terrestrial habitats. This is due in large part to the unequal size of available literature on the two topics. This fact is perhaps one of the most striking conclusions of this survey: terrestrial cyanobacteria have not been given the attention they deserve given the large size of their global population. In our survey, about 74 % of all global cyanobacterial mass is in the oceans and about 25 % is terrestrial. Inclusion of neglected habitats such as the polar regions is likely to shift this towards a more even distribution. Planktic freshwater biomass accounts only for a small percentage (around 1 %) of the global biomass. Interestingly, Lake Victoria contains about 1/2 of this biomass.

With respect to well-represented cyanobacterial genera, and based on our present data, *Prochlorococcus* represents more than 50% of the global cyanobacterial mass, while marine *Synechococcus* accounts for about 18% and *Trichodesmium* for about 4%. Important cosmopolitan soil forms in arid lands such as *Microcoleus vaginatus* and *Nostoc* sp. (GARCIA-PICHEL et al. 2001) must also contribute on the order of 5% each. *Chroococcidiopsis* sp., the most common cyanobacterium in endolithic communities, is probably in the same range. All other forms must thus contribute the remaining 13%.

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