

Global nutrient limitation in terrestrial vegetation

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[1] Most vegetation is limited in productivity by nutrient availability, but the magnitude of limitation globally is not known. Nutrient limitation is directly relevant not only to ecology and agriculture, but also to the global carbon cycle by regulating how much atmospheric CO₂ the terrestrial biosphere can sequester. We attempt to identify total nutrient limitation in terrestrial plant productivity globally using ecophysiological theory and new developments in remote sensing for evapotranspiration and plant productivity. Our map of nutrient limitation qualitatively reproduces known regional nutrient gradients (e.g., across Amazonia), highlights differences in nutrient addition to croplands (e.g., between “developed” and “developing” countries), identifies the role of nutrients on the distribution of major biomes (e.g., tree line migration in boreal North America), and compares similarly to a ground-based test along the Long Substrate Age Gradient in Hawaii, U.S.A. (e.g., foliar and soil nutrients, litter decomposition). Nonetheless, challenges in representing light and water use efficiencies, disturbance, and comparison to ground data with multiple interacting nutrients provide avenues for further progress on refining such a global map. Global average reduction in terrestrial plant productivity was within 16–28%, depending on treatment of disturbance; these values can be compared to global carbon cycle model estimates of carbon uptake reduction with nutrient cycle inclusion.

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1. Introduction

[2] Terrestrial vegetation is often limited in productivity by nutrients, particularly nitrogen (N) and/or phosphorus (P), and to some extent potassium, calcium, sulphur, magnesium, silicon and other micronutrients or trace minerals [Vitousek and Howarth, 1991]. Plant growth response to nutrient limitation or enrichment has been an active field of research in agriculture as well as ecology [Vitousek, 1984; Matson *et al.*, 1997]. Increased interest in nutrient cycling for global carbon cycle science stems from the driving question: how much atmospheric CO₂ can the terrestrial biosphere take up given increasing anthropogenic emissions [Friedlingstein *et al.*, 2006; Sitch *et al.*, 2008]?

[3] Although nutrient limitation is understood in general and in specific field and laboratory studies, the spatial distribution of nutrient limitation at the global scale is unknown [Galloway *et al.*, 2008]. It is not known how the limitations of different nutrients interact to reduce gross and net primary productivity (GPP, NPP) globally [Davidson and Howarth,

2007]. It is also unclear how nutrient limitation interacts with other limitations imposed by temperature, light, moisture, and CO₂ [Chapin *et al.*, 1986]. There is no consensus in what the reduction is in the amount of CO₂ sequestered due to nutrient limitation [Hungate *et al.*, 2003; Ostle *et al.*, 2009].

[4] Recent advances in addressing these questions come primarily in two forms: hyperspectral remote sensing and modeling. First, using airborne instruments, it has been possible to correlate canopy nutrient contents to some combination of light reflectance wavelengths at the plot level [Townsend *et al.*, 2003; Starks *et al.*, 2004; Asner and Vitousek, 2005; Ollinger and Smith, 2005; Porder *et al.*, 2005; Ollinger *et al.*, 2008; Fisher, 2009]. However, these measurements do not necessarily identify nutrient limitation, instead focusing primarily on canopy nutrient concentration. Second, land surface and terrestrial ecosystem modelers have begun developing and integrating N cycle (and to a lesser extent P cycle) representations into coupled and uncoupled land surface models [Thornton *et al.*, 2007; Wang *et al.*, 2007; Sokolov *et al.*, 2008; Xu-Ri and Prentice, 2008; Fisher *et al.*, 2010; Gerber *et al.*, 2010; Jain *et al.*, 2009; Zaehle *et al.*, 2010]. While the modeling approach encompasses much of the mechanistic processes linking nutrients (typically just N) to plant productivity and limitation, these studies have shown a wide range of modeled impacts on the global carbon cycle, reducing terrestrial carbon uptake from 7% [Zaehle *et al.*, 2010] to 64% [Thornton *et al.*, 2007]. Limitations from other nutrients have yet to be developed and integrated.

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[5] Here we present a novel approach to attempt to identify an approximation of total nutrient limitation to terrestrial plant productivity globally based on first principles and new developments in remote sensing. We start with the presupposition that in *non*nutrient limiting conditions vegetation productivity is primarily (first order) determined by CO₂, water and light/radiation (i.e., photosynthesis), as well as temperature and atmospheric water demand [Holdridge, 1947]. CO₂ is assumed to be well mixed, thus leaving water, light/radiation, temperature, and atmospheric water demand as spatially variable at relatively fine spatial resolutions (e.g., <1°). Light/radiation, temperature, and atmospheric water demand form the basis of potential evapotranspiration (PET)—that is, the amount of water that would return to the atmosphere if the surface was well watered [Monteith, 1965]; water supply reduces PET to actual evapotranspiration (AET) [Fisher et al., 2011]. AET, as an integrator of both water and energy, therefore represents to first order the upper bound of plant productivity [Rosenzweig, 1968; O'Brien, 2006]. Where there is no water and energy, there is no vegetation (in the presence of ample nutrients); increasing water and energy leads to increasing vegetation abundance, productivity and diversity [Currie, 1991; O'Brien, 1998].

[6] The AET–productivity relationship, until recently, could not be tested with global observations. However, recent developments in remote sensing have led to a suite of remote sensing–based AET data sets that compare relatively favorably to one another and to validation ground data [Jiménez et al., 2011; Mueller et al., 2011; Vinukollu et al., 2011]. Vegetation productivity has long been linked to remote sensing–based indices of greenness (e.g., normalized difference vegetation index or NDVI, and enhanced vegetation index or EVI), though derived products of GPP, NPP, leaf area index (LAI) and fraction of absorbed photosynthetically active radiation (fAPAR), as well as fluorescence, are also available [Myneni et al., 1995; Huete et al., 2002; Turner et al., 2006; Frankenberg et al., 2011].

[7] Second-order variation in plant productivity may be due to four controls [Schulze, 2006]: (i) nutrient limitation, (ii) disturbance, (iii) water use efficiency (WUE; typically, GPP/AET), and (iv) light use efficiency (LUE; typically, GPP/fAPAR). These differences, including the climate controls, operate on disparate spatial and temporal scales. Spatially, characteristics associated with individual plants, such as WUE and LUE are not uniformly distributed throughout a landscape on the order of a 1° pixel, for example. Bulk biome types tend to display coarse commonalities of individual plant characteristics, e.g., plant functional types such as trees versus grasses [Bonan et al., 2002], so analyses of the first-order controls or the remaining second-order controls must be done with reference to biomes. Disturbance and nutrient limitation may show variation on small spatial scales (e.g., gap dynamics) [Vitousek et al., 2009], but may also manifest at larger spatial scales (e.g., mass deforestation for disturbance; geologic formation for nutrient limitation) [Walker and Syers, 1976]. Temporally, the second-order productivity controls vary tremendously. WUE and LUE covary with productivity much more when water and light are limiting; however, they vary with productivity much less when water and light are not limiting, with productivity being controlled more by the other

variables such as temperature and nutrients [Churkina and Running, 1998; Nemani et al., 2003]. Large shifts in large-scale ecosystem nutrient status change much more slowly, except in cases of disturbance [Walker and Syers, 1976; Vitousek and Farrington, 1997; Vitousek, 2004].

[8] CO₂, water, light, temperature, nutrients, disturbance, LUE and WUE all interact to control plant productivity. Global data on all of these factors except nutrients are available, though to varying degrees of reliability, which allows us to make a first attempt at identifying the global distribution of nutrient limitation. First, we may assume that CO₂ is nonlimiting and well mixed. Second, water, light and temperature combine to AET, which is globally available. Third, Hurtt et al. [2006, 2011] have developed a global map of land/vegetation disturbance (e.g., deforestation), which is widely used in land surface modeling. Fourth, periods of minimal effect of WUE and LUE variability may be observed over long time periods, so that it may be possible to identify observed productivity given available water, AET or fAPAR approaching theoretical maximum productivity during some parts of the year or during some years. Finally, plant productivity may be derived from remotely sensed products such as NDVI, EVI, GPP, or NPP. We acknowledge that each variable is not fully independent from one another, that data for each control contain large uncertainties, and that the assumptions minimizing WUE and LUE over long time periods may not necessarily be observed over our record everywhere. Therefore, the map of nutrient limitation that we present here must be interpreted with these caveats, and as a product to be built on and refined with further advances in global observations of the controls on plant productivity.

2. Methods

[9] First we aimed to determine the maximum possible productivity (we refer to NDVI here for simplicity, though we used other productivity indicators in the analysis) given the maximum available AET. We used a 19 year (1984–2002) record of remote sensing–based, globally gridded 0.5° AET calculated using the method described in Fisher et al. [2008], driven with monthly net radiation data from the NASA/GEWEX Surface Radiation Budget (SRB) Release-3.0 data set (for a previous version, see Stackhouse et al. [2001]), air temperature and water vapor pressure from the Climate Research Unit (CRU) high-resolution globally gridded data sets [New et al., 2002], and NDVI data from the Global Inventory Modeling and Mapping Studies (GIMMS) data set [Pinzon et al., 2005; Tucker et al., 2005]. An earlier version of this AET product had a reported error of 16 mm·month⁻¹, explaining 90% of the variation in measured AET at 36 FLUXNET sites [Fisher et al., 2008, 2009]. Because the analysis is based on satellite observations, nonstationary effects (e.g., CO₂ fertilization, warming) are included in the 19 year time period. We used 11 additional AET products included from Jiménez et al. [2011] for comparison; we also used MODIS products for NDVI, EVI, LAI, GPP, NPP, and fAPAR for a shorter record comparison (for strengths and weaknesses in each of these products see cited references). We removed pixels adjacent to water bodies to avoid mixed pixel contamination.

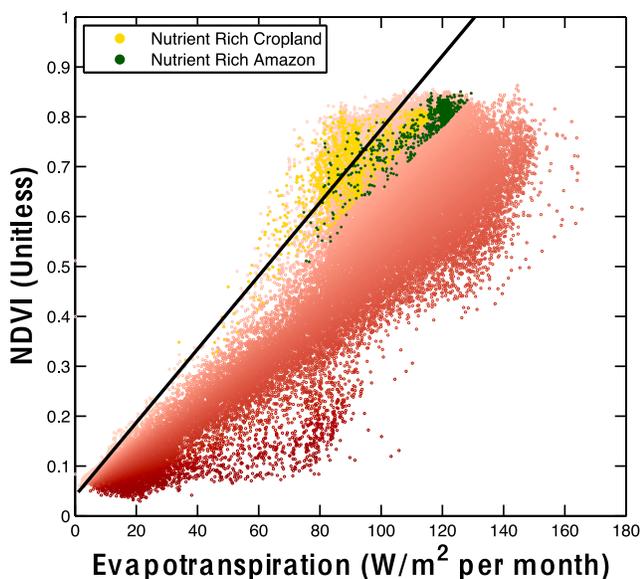


Figure 1. Paired annual maximum terrestrial monthly NDVI (e.g., productivity) and actual evapotranspiration averaged over 19 years at 0.5° globally. The pixels are colored by equal intervals away from the upper bound line, indicating increasing nutrient limitation farther from the line.

[10] NDVI temporally lags AET so that a given month with high amounts of water and energy, for example, could be followed by a greening in the next month [Running and Nemani, 1988; Szilagyi, 2002]. We searched each pixel in a given year for its maximum NDVI and AET, even if the two did not occur in the same month (time ordered for AET first), though they must be from the same year (we ran a test case for December max AET driving January max NDVI, and likewise for up to 6 months in either direction, but found negligible changes over the 19 year period analysis), and paired them. We used the maximum NDVI and AET for a given pixel over the 19 year time span to minimize the impact of limitation due to WUE and LUE. Any given year may have anomalously high or low AET and/or NDVI due to weather, disturbance or other global phenomena (e.g., volcanic eruptions), but one would not expect natural nutrient status to vary so sharply from year to year, making a long-term record of AET and NDVI necessary to account for interannual variation. We ran a Monte Carlo simulation, including all the nutrient limitation calculations across all available years, then randomly selected years 1000 times with replacement, calculating the global average of nutrient limitation for each cumulative year and recording the standard deviation of that value for the Monte Carlo plot. From the plot, we determined that 8–10 cumulative years are necessary to stabilize the global average nutrient limitation (Figure S1 in the auxiliary material); hence, the analysis cannot be done on just a few years of data.¹

[11] Disturbance (e.g., land use change, fire) was based on the Land Use Harmonization (LUH) and Global Land-use Model (GLM), which span the timeframe of 1500 to 2100 [Hurt et al., 2006, 2011]. As a conservative first approach,

we allocated any pixel with less than 50% primary land class (i.e., anthropogenically unchanged) as disturbed. We also excluded any pixel that lost more than 5% of its primary land in the 30 years prior to the AET data set period (1984–2002) under the conservative assumption that full recovery from a disturbance event takes a minimum of 30 years. Finally, we designated any pixel with an annual net loss of primary land greater than 1% during the 19 year study period as disturbed. For details on the construction of the disturbance map, see Hurt et al. [2006, 2011].

[12] We calculated nutrient limitation (N.L.) from the ratio of NDVI to AET normalized to a percentage, increasing further from the upper bound in the global scatterplot of average maximum paired AET and NDVI (Figure 1):

$$N.L. = \frac{\text{paired}_{\max} \left(\frac{NDVI_x}{AET_x} \right) - \text{paired}_{\max} \left(\frac{NDVI_{\min}}{AET_{\min}} \right)}{\text{paired}_{\max} \left(\frac{NDVI_{\max}}{AET_{\max}} \right) - \text{paired}_{\max} \left(\frac{NDVI_{\min}}{AET_{\min}} \right)}$$

where the paired_{\max} is for the quotient; the x subscript is for the given pixel; and the min and max are for across the entire data set to apply consistent global normalization. We ran two cases to describe the upper bound—linear and nonlinear—for comparison. We cross checked the upper bound against large regional areas assumed to have low nutrient limitation—primarily fertilized European croplands [Smil, 1999; Galloway et al., 2008; Potter et al., 2010], but to a lesser degree the western edge of Amazonia [Aragão et al., 2009; Quesada et al., 2009a, 2009b, 2010]. Croplands, as artificial systems designed for maximum production within climatic constraints, were optimal at setting the end-member, though we included natural ecosystems also to provide greater connectivity to non-“artificial” ecosystems. We specified a y intercept of 0.04, which is the reported error of NDVI [Huete, 1988; C. J. Tucker et al., Global Inventory Modeling and Mapping Studies, 2004, <http://glcf.umiacs.umd.edu/data/gimms/>]. The color of the scatterplot points (outside of the crop and Amazonia pixels highlighted for comparison) corresponds to that of the map pixels. We chose equal intervals away from the upper bound for ease of interpretation, though the color could be based on fractional standard deviations, confidence intervals, or otherwise; the point and pixel values would remain unchanged regardless. We selected a single color gradient of red to represent the gradient of nutrient limitation (rather than multicolor, which would lead to discrete visual classification). The N.L. index is relative, and the end points 0 and 100% represent the minimum and maximum for the time period analyzed, rather than zero or complete nutrient limitation.

[13] We produced three sets of analyses: (i) one that averages the annual maximum paired monthly NDVI and AET across the full 19 year data set, producing a general climatic and vegetated state for a given pixel; (ii) one that uses only the greatest annual maximum paired monthly NDVI and AET across all years, which minimizes the contribution of WUE by using only the wettest year (the specific year resulted in being evenly and generally randomly distributed across all years); and (iii) one that removes any effect of disturbance.

[14] We performed a ground-based test of our global approach using the Hawaii Long Substrate Age Gradient, a soil chronosequence spanning six sites on the islands of Hawaii, Moloka’i and Kaua’i [Vitousek, 2004]. The sites

¹Auxiliary materials are available in the HTML. doi:10.1029/2011GB004252.

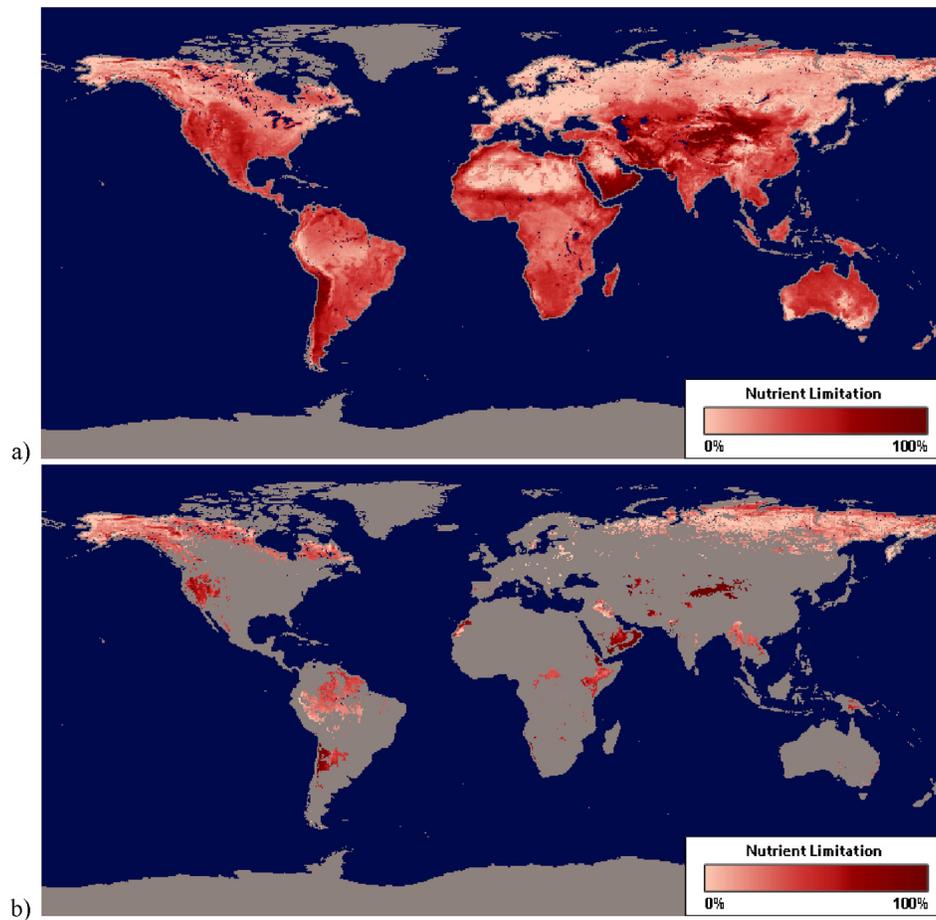


Figure 2. (a) Map of remote sensing–based nutrient limitation and disturbance at 0.5° ; (b) remaining undisturbed pixels for comparison without any effect of disturbance. Nutrient limitation is defined as the percentage productivity (or greenness or other proxy) less than what would otherwise be dictated by climatic constraints.

have soils ranging in age from 300 to 4,100,000 years old. Each site has been minimally disturbed by human activities. AET was calculated at each site using in situ meteorological data from the Global Surface Summary of Day data set (available at <http://www.ncdc.noaa.gov/oa/climate/climatedata.html>), 1° net radiation from NASA/GEWEX Surface Radiation Budget 3.0 assumed to be relatively homogeneous across the closely located islands, and 250 m MODIS NDVI data for the period of 2002 to 2007. We compared our AET–NDVI nutrient limitation approach against in situ measurements of soil and foliar nutrient concentrations as well as litterfall decomposition rates, which are considered indicative of nutrient limitation.

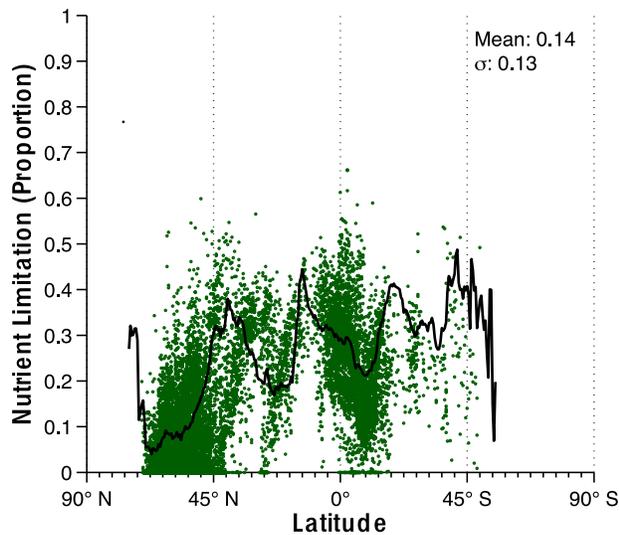
3. Results

[15] The majority of the land surface exhibits some degree of nutrient limitation (Figure 2a). Some known large-scale nutrient gradients (see section 4 for references therein) may be observed: a gradual change in limitation across Amazonia; the relative nutrient depletion of savanna and grassland ecosystems compared with the rain forests in Africa; and, agricultural hot spots in Australia, Europe, and the major

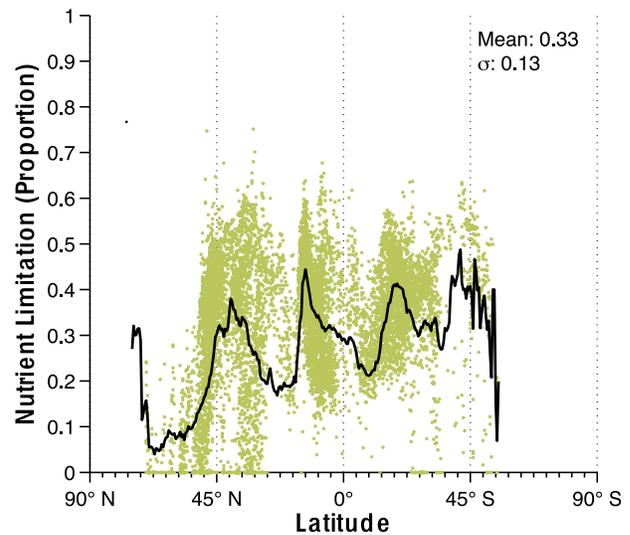
Indian and Pakistani agricultural regions along the Indus River and in northwestern India (Punjab, Haryana regions). Desert areas appear to span the spectrum of nutrient limitation (e.g., nonlimited in the Sahara, but very limited in the Gobi), but this apparent pattern is more likely an artifact of very low NDVI and AET causing anomalous values from random noise (and, of course, are water limited more than anything else); we chose not to mask out the barren areas (Figure S2) for full disclosure. The impact of WUE was largely minimal at the global scale, affecting mostly savanna regions (Figures S3a and S3b).

[16] The relative patterns generally remained constant when using the full range of productivity products from MODIS compared against MODIS NDVI (Figure S4). The patterns with EVI, GPP, and NPP were more pronounced, with low nutrient limitation sites being even less limited and high nutrient limitation sites being even more limited than with NDVI. This move away from moderate nutrient limitation was particularly pronounced with LAI. Nutrient limitation was reduced with fAPAR. The nonlinear upper bound case also produced similar patterns, but with less nutrient limitation (Figure S5). The patterns were consistent with different AET products as well, with the interquartile range

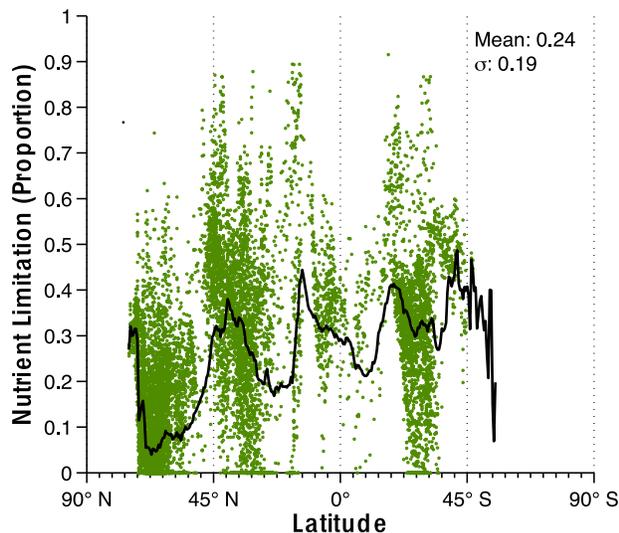
a) Forest



b) Savanna and Grassland



c) Shrubland



d) Cropland

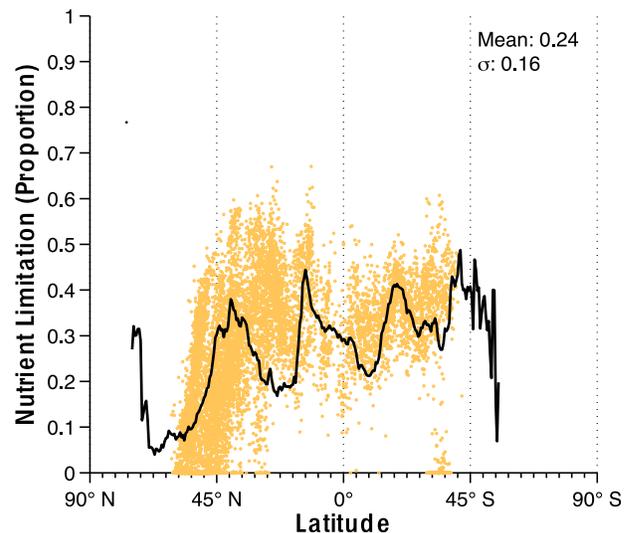


Figure 3. Nutrient limitation by relevant bulk IGBP biome averaged latitudinally for (a) forest, (b) savanna and grassland, (c) shrubland, and (d) cropland. The black line is the mean for all biomes combined. Nutrient limitation is defined as the proportion of productivity (or greenness or other proxy) less than what would otherwise be dictated by climatic constraints.

in nutrient limitation based on the suite of AET data sets spanning 10–30% of the ensemble mean averaged latitudinally (Figure S6).

[17] Figure 2a shows a combination of nutrient limitation and disturbance; we make no attempt to link disturbance to nutrient limitation, rather focusing on separating the two where possible. However, removal of any disturbed pixels by our conservative interpretation of the *Hurt et al.* [2006, 2011] disturbance model resulted in very little vegetation left untouched (Figure 2b). We provide some less conservative definitions of disturbance in the auxiliary material (Figures S7a–S7c). Still, the global mean of maximum NDVI was 0.61 when all disturbance-classed pixels are removed (i.e., nutrient limitation only), an increase from

0.54 when all pixels are included (i.e., nutrient limitation + disturbance). These values were much less than the global mean NDVI if nutrient limitation is removed; i.e., all pixels are forced to the upper bound of the AET-NDVI scatterplot. In this case, global mean NDVI was 0.71 with disturbance-classed pixels removed, and 0.69 with all pixels included. Nutrient limitation therefore represents a reduction in global mean NDVI within a range of 16.3% (nutrient limitation only) to 27.8% (nutrient limitation + disturbance).

[18] We provide descriptive plots of nutrient limitation by biome type and across latitudinal bands (Figures 3a–3d). We combined relevant land cover classes from the International Geosphere-Biosphere Programme (IGBP) into four bulk classes: forest, savanna and grassland, shrubland, and

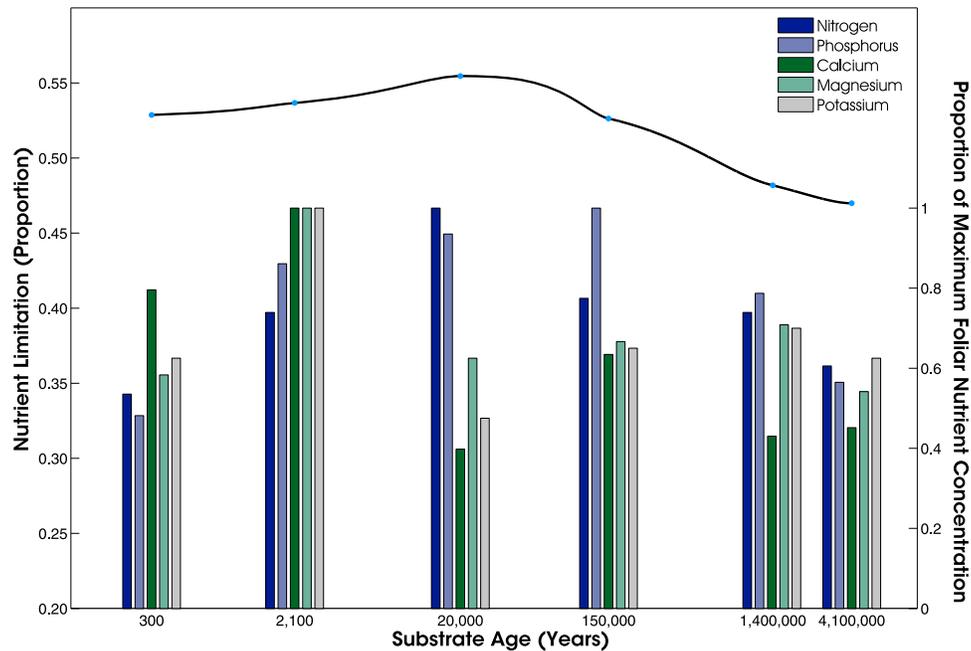


Figure 4. Remote sensing-based nutrient limitation compared against in situ foliar nutrient concentrations at the Hawaii Long Substrate Age Gradient chronosequence. Nutrient limitation is defined as the proportion of productivity (or greenness or other proxy) less than what would otherwise be dictated by climatic constraints.

cropland. The range in nutrient limitation in northern hemisphere forests was greater than that for tropical forests, though in general tropical forests were more nutrient limited than boreal forests; nutrient limitation in northern hemisphere forests tended to be greater in North America than in Eurasia. Savannas, grasslands and shrublands tended to be more nutrient limited than forests particularly around the tropics (e.g., Congo basin versus Sahel). Croplands were generally less nutrient limited than nonforests across the same latitudinal band, with a sharp drop in nutrient limitation for croplands north of 45°N (e.g., Europe) and around 30°S (e.g., Australia).

[19] For the Hawaii Long Substrate Age Gradient chronosequence, our estimation of nutrient limitation generally followed the pattern of ground-based foliar nutrient concentrations (Figure 4). The youngest site was somewhat nutrient limited, and nutrient limitation decreased as the sites aged, but increased again past a midage level until the oldest sites, which were the most nutrient limited. This follows the theory that young soils have P and other rock mineral-based nutrients, but little N (biologically based, apart from deposition), except for from N-fixers so are somewhat nutrient limited; midage soils have P and have had time build up N so are least nutrient limited, and old soils are most nutrient limited, having lost P to irreversible leaching and the gradual loss of N because N-fixers are no longer prevalent [Walker and Syers, 1976; Vitousek and Farrington, 1997; Vitousek, 2004].

[20] Foliar nutrient concentrations were similarly correlated with our approach regardless of whether or not the correlation was with N alone ($r^2 = 0.53$), P alone ($r^2 = 0.46$), N + P ($r^2 =$

0.51) or N + P + cations ($r^2 = 0.51$) with all nutrients weighted equally. We also compared our approach to soil nutrient concentrations, which revealed a high correlation with N + P + cations ($r^2 = 0.85$) (Figure S8), and with litter decomposition rate ($r^2 = 0.59$) (Figure S9).

4. Discussion

[21] One issue this analysis raises is how best to compare to ground measurements of nutrient limitation? In the ecological literature there is no clear consensus on how best to describe and measure nutrient limitation [Kaspari *et al.*, 2008]. Nutrient limitation has been widely described as a function of foliar nutrient concentration or ratios [Koerselman and Meuleman, 1996; Aerts and Chapin, 1999; Tessier and Raynal, 2003; Güsewell, 2004], whereas other times nutrient limitation is described as the growth response to fertilization [Elser *et al.*, 2007; LeBauer and Treseder, 2008]. However, there are problems with nearly all approaches. There are species-specific differences in foliar nutrients, and the growth response in fertilization studies is typically measured in stem diameter growth whereas carbon could be allocated elsewhere. Typically, only N, and maybe P, are considered. Even if there were “perfect” in situ measurements of nutrient limitation, our analysis necessitates these measurements to be comparable at the pixel size of our global analysis (0.5°). However, there are a number of large-scale, regional patterns in nutrient status that may be qualitatively comparable to our results. The nutrient gradient in Amazonia as determined from extensive field studies, for example, is comparable to the gradient we observe in our results [Aragão *et al.*, 2009; Quesada *et al.*, 2009a, 2009b, 2010].

[22] Agricultural regions show some divergence in nutrient limitation between “Developed” countries such as Australia or those in Europe and “Developing” countries such as India or those in Africa; it is well known that fertilizer use is greater in Developed than Developing countries, though it may be difficult to separate management practices (e.g., irrigation, pest control, seed variety, crop type) from nutrient response [Smil, 1999; Galloway et al., 2008; Potter et al., 2010]. The same pattern can be seen at a smaller scale along the Nile River, which appears in sharp contrast as less nutrient limited relative to the surrounding desert.

[23] We found that savannas and grasslands tended to be relatively nutrient limited, which is supported by numerous studies showing that these biomes may be among the most nutrient limited ecosystems, though disturbance (fire, grazing) is interlinked with these ecosystems [Bremen and de Wit, 1983; Bustamante et al., 2006; Elser et al., 2007; Lee et al., 2010]. For example, Chen et al. [2010] showed that fire in savannas bordering both the northern and southern edges of the Congo basin led to nutrient depletion in the savannas, but subsequently led to nutrient deposition in the rain forest, which is congruent with our results.

[24] In boreal regions, work in Alaska has shown that the tree line is moving north in response to rising temperatures [Lloyd, 2005], but a similar study in northern Quebec and Canada’s Northwest Territories has shown no changes in tree line [Masek, 2001]. Timoney [1995] showed that variation in the Canadian tree line was heavily dependent on soil nutrient levels, with the tree line extending further north in places with higher nutrient availability. We found that Alaska was significantly less nutrient limited ($p < 0.001$) than the northern Canadian boreal region, suggesting that tree line mobility in these areas may be linked to nutrient limitation. In general we found that the least nutrient limited ecosystems were the boreal forests of North America, Europe and Northern Asia. It has been speculated that these forests constitute a large carbon sink, responding greater to rising CO₂ and changing temperatures than other forests, arguably linked with N deposition rates [Nadelhoffer et al., 1999; Magnani et al., 2007; Reay et al., 2008; Thomas et al., 2010].

[25] Nutrient limitation contributes to controlling numerous global ecological processes with increasing importance in terrestrial ecosystem impacts and feedbacks to climate change. Our results provide a first attempt at a global, spatially explicit and consistent, and ecophysiology-based data set of total nutrient limitation to be used in global carbon cycle studies and scrutinized with local and regional data. These results provide a new perspective on ground-based nutrient cycle research, including isotopic work [Craine et al., 2009], particularly as the contributions of individual nutrients are not explicit in our approach. Still, challenges remain in representing light and water use efficiencies, disturbance, and comparison to ground data with multiple interacting nutrients, which we identify as key avenues for further progress on refining such a global map. Nonetheless, our results provide a benchmark with which to compare results from improved methods in modeling and other remote sensing techniques. We found a global average reduction in terrestrial plant productivity due to nutrient limitation of 16–28%, depending on treatment of disturbance, which reduces the range of limitation from N alone in land surface models of 7–64% [Thornton et al., 2007; Wang et al., 2007;

Sokolov et al., 2008; Xu-Ri and Prentice, 2008; Fisher et al., 2010; Gerber et al., 2010; Jain et al., 2009; Zaehle et al., 2010]. Our comparison to the LSAG demonstrated proof of concept though not proof in totality. Logical follow-on work would connect this analysis to ongoing meta-analyses of nutrient limitation in the ecological literature [Elser et al., 2007; LeBauer and Treseder, 2008] with finer spatial resolution (e.g., Landsat, 30 m).

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