

CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecological Monographs, 82(3), 2012, pp. 277–296
© 2012 by the Ecological Society of America

Precipitation, soils, NPP, and biodiversity: resurrection of Albrecht's curve

MICHAEL A. HUSTON¹

*Department of Biology, Texas State University, San Marcos, Texas 78666 USA, and
School of Earth and Environment, University of Western Australia, Crawley, WA 6009 Australia*

Abstract. Climate and soils are widely recognized as major drivers of virtually all properties of ecosystems and communities. However, despite major advances in the understanding of soil formation and ecosystem dynamics, the effects of climate on soil properties are not widely appreciated. Understanding the effects of water availability on the rates of chemical and biological processes that affect soil formation can help clarify the global patterns of soil fertility, which affect agricultural and forest productivity, as well as biodiversity. Empirical tests of Albrecht's conceptual model of soil development and degradation using global climate and soil data sets and soil chronosequences confirm that soil total exchangeable bases (TEB), phosphorus, nitrogen, and other components of soil fertility, along with plant productivity generally decline on older soils and under wetter conditions as precipitation exceeds potential evapotranspiration. The basic pattern of soil fertility in relation to water availability is a unimodal curve, with a maximum near or below a water balance of zero (annual precipitation minus annual potential evapotranspiration). Analysis of global data by subregions reveals significant differences between temperate and tropical soil fertility distributions, as well as significant differences between continents. The low levels of soil nutrients (e.g., TEB, P, N) and plant productivity found on ancient soils or highly weathered soils in regions with high precipitation suggest that the positive effects of low productivity on plant diversity that have been observed at local and regional scales may also occur at the global scale.

Key words: *agricultural productivity; forest productivity; gradients; net primary productivity, NPP; plant diversity; potential evapotranspiration, PET; precipitation; soil chronosequence; soil fertility; temperate zone cf. tropics; water balance.*

INTRODUCTION

The scientific understanding of soils continues to develop, from a broadly synthetic chemical and climatic equilibrium perspective (e.g., Jenny 1941, 1980, Sanchez 1976, Greenland and Hayes 1981, Brady and Weil 2002) toward a more complex understanding, incorporating microheterogeneity in chemical processes (e.g., Chadwick and Chorover 2001, Stewart et al. 2001), topographic and vegetation effects (Garten et al. 1994, Gessler et al. 2000, Quideau et al. 2003, Vitousek et al. 2003), and the complex effects of changing climate over long time periods (Cline 1961, Chadwick et al. 1999, Richter and Markewitz 2001). Unfortunately, this

understanding has not been fully disseminated across all of the sciences that need this information, including ecology, evolutionary biology, anthropology, medicine, and economics, where soil properties and their implications are often ignored or misinterpreted (see however, Hyams 1952, Meggers 1971, Huston 1993, 2005, Weischet and Caviedes 1994, Vitousek et al. 2004).

Recent advances in the understanding of soil properties in relation to the interaction of climate and soil parent materials have resulted from systematic application of quantitative methods on well-characterized volcanic soils (Chadwick et al. 1999, 2003, Chadwick and Chorover 2001, Stewart et al. 2001, Vitousek et al. 2003, Porder and Chadwick 2009), as well as analysis of data from long-term soil experiments (Rasmussen et al. 1998, Richter 2007, Richter et al. 2007, 2011, Rice et al. 2009). Many of these recent results confirm the basic conclusions of soil scientists who were working in the

Manuscript received 25 October 2011; revised 25 January 2012; accepted 27 March 2012. Corresponding Editor: J. B. Yavitt.

¹ E-mail: hustonma@txstate.edu

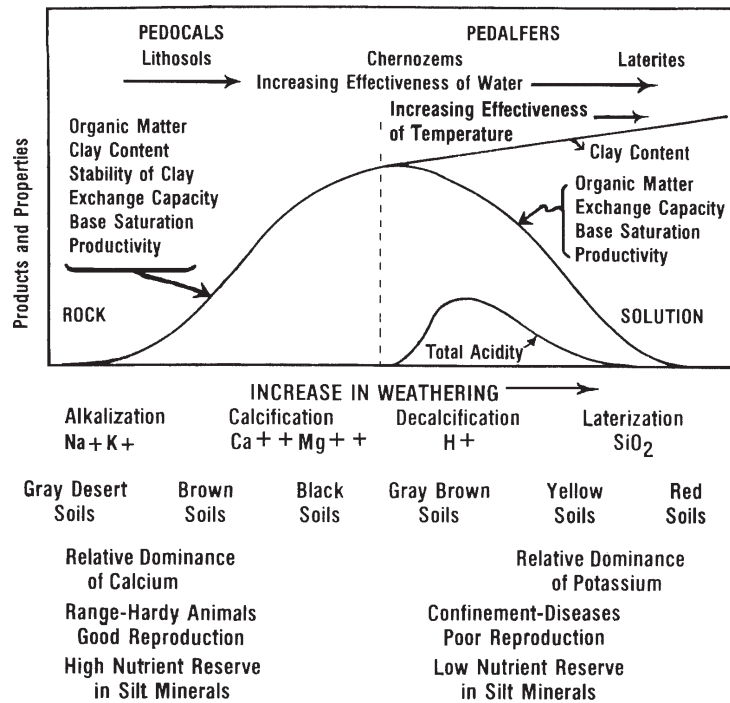


FIG. 1. Albrecht's "Diagrammatic sketch of products and properties of soils as related to increase in weathering" (Albrecht 1940a), indicating general soil types, dominant cations, and implications for animal husbandry. "As a theoretical curve of increasing weathering of rock, soil construction follows the rising curve of clay production until precipitation exceeds evapotranspiration to give soil destruction, or a falling curve of the soil's productivity" (Albrecht 1957: Fig. 6). The figure is reprinted with the permission of the University of Missouri.

midwestern United States over 70 years ago (e.g., Jenny and Leonard 1934, Albrecht 1940a), and whose generalizations about climate effects on pedogenic processes presage the conclusions of the most recent research.

William Albrecht (1888–1974), who spent most of his career at the University of Missouri, was an early soil scientist who made a major effort to synthesize and publicize knowledge about the causes and consequences of variation in soil fertility, within both academia and applied agriculture. Albrecht published prolifically in the scientific literature, as well as in newsletters, stockman's bulletins, and short-lived, highly specialized agricultural periodicals. Much of Albrecht's work emphasized the importance of soil nutrient content for the growth and health of plants, livestock, and humans (Albrecht 1940a, b, 1942, 1944, 1947a, b, 1955, 1957, 1958), and he documented declines in crop nutrient content due to new cultivars and soil nutrient depletion (Albrecht 1957), as well as health problems in livestock and humans related to nutrient deficiencies (Albrecht 1942, 1947a, b, 1957, 1958). Albrecht helped pioneer the experimental use of plant and animal growth rates as assays of soil fertility (Albrecht and Smith 1941). Not all of his conclusions have stood up well under modern scrutiny (Kopittke and Menzies 2007), but some of his explanations of soil processes provide useful generalizations that could be of great value to disciplines where

lack of understanding of basic soil processes has led to major misconceptions and misinterpretations.

In my opinion, one of Albrecht's most important contributions was a simple graph that illustrated the effect of precipitation on pedogenic processes and soil properties. Descriptions of the physical, chemical, and biological soil processes underlying this graph are found in every soil textbook, yet few present or summarize them in such an integrated synthetic form as did Albrecht (Fig. 1). In spite of Albrecht's prominence in the first half of the twentieth century, his work is rarely cited today, and his remarkable graph has apparently never been reproduced in a soil textbook. I believe that this graphical synthesis of fundamental soil processes is sufficiently valuable that it deserves fuller development and much wider recognition, not only in soil science but in all disciplines that are impacted by soil processes, which include virtually all areas of human activity. The validity of Albrecht's synthesis has been repeatedly confirmed by modern soil scientists, even though it has never been cited in a soil science paper.

Although Albrecht was clearly aware of the early work of his younger colleague, Hans Jenny (e.g., Albrecht and Jenny 1931, Jenny and Leonard 1934), the fact that Albrecht articulated and publicized these important generalizations (Albrecht 1940a, 1944,

1947*a, b*, 1957), suggests they could appropriately be called “Albrecht’s curve” or perhaps “Albrecht’s rule.”

Albrecht’s curve (Fig. 1) is a generalization that describes the net result of multiple processes that change in importance along a precipitation gradient, with a critical inflection point where precipitation equals potential evapotranspiration (i.e., the annual water balance is zero). The curve illustrates the increase in important soil properties (e.g., clay content, exchange capacity, base saturation, organic matter) during soil development, which is accelerated by water availability under dry conditions, followed by a decrease in many of the same properties as continued soil weathering leads to changes in clay properties and loss of nutrients by leaching, both of which are accelerated under wet and warm conditions. The high point of the curve, indicating the highest levels of favorable soil properties, occurs where precipitation and potential evapotranspiration are approximately equal and soil fertility is high, such as along the 95th meridian, running through the central prairie region of North America, one of the most productive agricultural regions of the world.

The major soil properties that are indicated as increasing along the curve, with a maximum at the center, are organic matter, clay content (particularly 2:1 clays with high cation exchange capacity), clay stability, exchange capacity, and base saturation, along with plant productivity. After reaching maximum levels near the center of the curve (a water balance of zero) all of these properties decline with increasing precipitation, except for clay. Clay content follows a different trajectory, rising with increasing water availability along with the other soil properties on the ascending side of the curve, but then continuing to increase (primarily as 1:1 clays with low cation exchange capacity) with increasing precipitation at a slower rate all the way to the wettest conditions. The acidic red clay soils of the southeastern United States illustrate this late, low-fertility stage of soil development, as do the clay oxisols and ultisols of the lowland tropics. In addition to chemical and physical soil properties, Albrecht also indicated where major soil types and different dominant ions in the soil solution occur along the weathering gradient, as well as some implications for animal husbandry.

Albrecht (1957: Fig. 6) describes the curve as “theoretical,” in recognition of the fact that the shape of the curve will vary depending on the relative conditions of temperature, precipitation, and soil parent material across any precipitation gradient along which soil is sampled. While the effects of many sources of heterogeneity and not all relevant soil processes are addressed, Albrecht’s curve nonetheless provides a reasonable summary of the effect of climatic conditions on important soil properties related to fertility and plant productivity.

Albrecht (1957) includes supporting data from Jenny and Leonard (1934: Fig 9) on HCl-soluble bases (Ca^{2+} , Mg^{2+} , K^+ , and Na^+ , the sum of which is called “total exchangeable bases” or TEB), as well as “Saturation

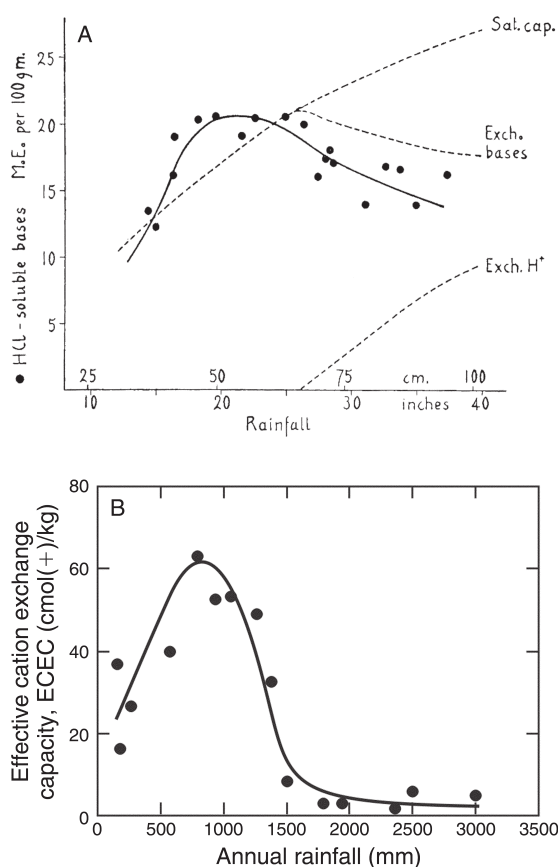


FIG. 2. (A) Relation between exchangeable cations and annual rainfall (1 inch = 2.54 cm) along the 11°C annual temperature isotherm spanning a precipitation gradient from eastern Colorado to western Missouri (USA). The solid circles represent the total HCl-soluble bases (equivalent to “total exchangeable bases” or TEB) of the 0–7 inch surface sample set assembled into county averages, and the dashed lines refer to the 0–10 inch surface samples from a series of soil profiles, illustrating the increase in acidity (H^+) as the base cations are depleted by leaching. Fig. 2A is reprinted with permission of the Soil Science Society of American from the original (Jenny and Leonard 1934: Fig. 9). Abbreviations are: Sat. cap., saturation capacity; Exch., exchangeable, and M.E., milliequivalents (meq; $\text{mg}/\text{atomic wt} \times \text{valence} = \text{mmol} \times \text{valence}$). (B) Effective cation exchange capacity (ECEC) of volcanic soils in Hawaii along a strong precipitation gradient. ECEC is generally equivalent to TEB. Fig. 2B is modified from and reprinted with permission from Chadwick et al. (2003: Fig. 7).

Capacity” (equivalent to cation exchange capacity or CEC), and “Exchangeable H^+ ,” which is inversely correlated with pH (Fig. 2A). Jenny and Leonard report that their samples were collected in September 1931 from loess soils in pastures and grassland along a highway paralleling the 11° isotherm from eastern Colorado to western Missouri (USA), across a rainfall gradient from <430 mm to >970 mm annual precipitation. While this pattern, based only on precipitation without consideration of evapotranspiration, is clearly

consistent with Albrecht's generalization, it is obvious that the shape of the curve, and particularly the level of precipitation at which maximum soil TEB and other properties occur, will change with different relationships between potential evapotranspiration (PET) and precipitation, as well as with different soil parent materials and mean annual temperatures.

Numerous studies of soil properties along precipitation gradients where potential evapotranspiration (PET) is either constant or controlled for, and parent material is uniform, have found results that match the predictions of Albrecht's curve (e.g., Jenny and Leonard 1934, Scott 1963, Donkin and Fey 1993, Stewart et al. 2001, Chadwick et al. 2003).

Virtually all of Albrecht's (1940a) generalizations about changes in soil properties with precipitation were confirmed by the detailed transect studies of Chadwick et al. (2003) across a strong precipitation gradient (160–3000 mm) on lava-derived soils in Hawaii (Fig. 2B). In addition to declines in all of the individual base cations and total base saturation with increasing precipitation and the total volume of water moving through the soil (Chadwick et al. 2003: Figs. 4, 8, and 9), Chadwick et al. found the predicted decline in pH (2003: Figs. 7e, 9b), the increase in clay content (non-crystalline minerals, 2003: Fig. 5b, f), the unimodal pattern of soil organic matter (2003: Fig. 5a), and a unimodal pattern of effective cation exchange capacity (Fig. 2B), which is equivalent to TEB. Although Albrecht did not explicitly include phosphorus in his diagram, it is now clear that available phosphorus also follows Albrecht's curve across precipitation gradients, while total phosphorus declines monotonically with increasing precipitation, and also with increasing soil age (Walker and Syers 1976, Porder and Chadwick 2009, Peltzer et al. 2010, Laliberté et al. 2012).

A critical question is whether the general pattern described by Albrecht's curve, and confirmed by multiple chronosequences and regional-scale studies, is also found at continental and global scales, and thus potentially relevant for explaining some of the global patterns in ecology, agriculture, human health, and economics (e.g., Huston 1993, Huston and Wolverton 2009, 2011). However, evaluating the relevance of this generalization at continental and global scales requires facing the full complexity of soils, especially in terms of different parent materials, different lengths of time since the parent material was exposed to weathering processes, and variation in climatic conditions over the history of a particular soil, which may currently be experiencing a climate very different from that which shaped it in the past.

The concept of soil in equilibrium with the local climate (e.g., Dokuchaev 1883, Marbut 1935, Jenny 1941), which may be valid for some of the regional soil gradients, must be replaced at global scales by recognition that the above-mentioned factors can create huge heterogeneity in soil properties within any climatic regime or geological province (e.g., Nikiforoff 1949,

Ruhe and Scholtes 1956, Cline 1961, Wells et al. 1987, Paton et al. 1995, Richter and Markewitz 2001, Tandarich et al. 2002, Targulian and Goryachkin 2004, 2008, Holmes et al. 2005). Consequently, we should not expect to see a neat curve of points falling along a nonlinear regression (e.g., Jenny and Leonard 1934, Donkin and Fey 1993, Chadwick et al. 2003), but rather a cloud of points with most falling below an upper boundary that represents the maximum level of a given soil property that can occur under specific climatic conditions.

The two critical predictions of Albrecht's model (1940a) are:

- 1) The major components of soil fertility (e.g., TEB, organic matter) are low where annual soil water balance is either very low (negative, i.e., dry) or very high (positive, i.e., wet), and reach a maximum near a water balance of 0, where precipitation equals evapotranspiration.
- 2) Plant productivity (net primary productivity, NPP) tracks the unimodal pattern of soil fertility along a gradient of increasing soil water balance from extremely dry to extremely wet.

METHODS

I evaluated the predictions of Albrecht's model of soil development and degradation at continental and global scales using the recent high-resolution "Harmonized Global Soil Database" (FAO 2008), in relation to 1960–1990 average global precipitation; (Hijmans et al. 2005; data *available online*).² I also used standardized global estimates of PET (potential evapotranspiration) averaged over 1986–1995 (Fisher et al. 2011b), excluding Antarctica along with all land and water south of 60° south latitude. Subtracting Fisher's global map of total annual PET (at 30' resolution in units of millimeters) from WorldClim annual precipitation (at 5' resolution in units of millimeters) created a global map of water balance (at 5' resolution in units of millimeters) with values near zero where annual precipitation and annual PET are approximately equal. Drier areas have negative values while wetter areas have positive values. Rates of soil leaching are expected to increase with larger positive water balances, causing a decline in soil properties related to fertility, such as the exchangeable base cations, the sum of which is "total exchangeable bases" or TEB. TEB is positively correlated with a large suite of soil properties that affect soil fertility, including pH, effective cation exchange capacity (ECEC), base saturation, organic-matter content, and phosphorus availability (Chadwick et al. 2003, Vitousek et al. 2004: Fig. 3, Holmes et al. 2005). In the following results and discussion, TEB will be used as an index of soil fertility, and the terms "TEB" and "soil nutrients" will be used interchangeably because of the strong positive correlations

² WorldClim.org

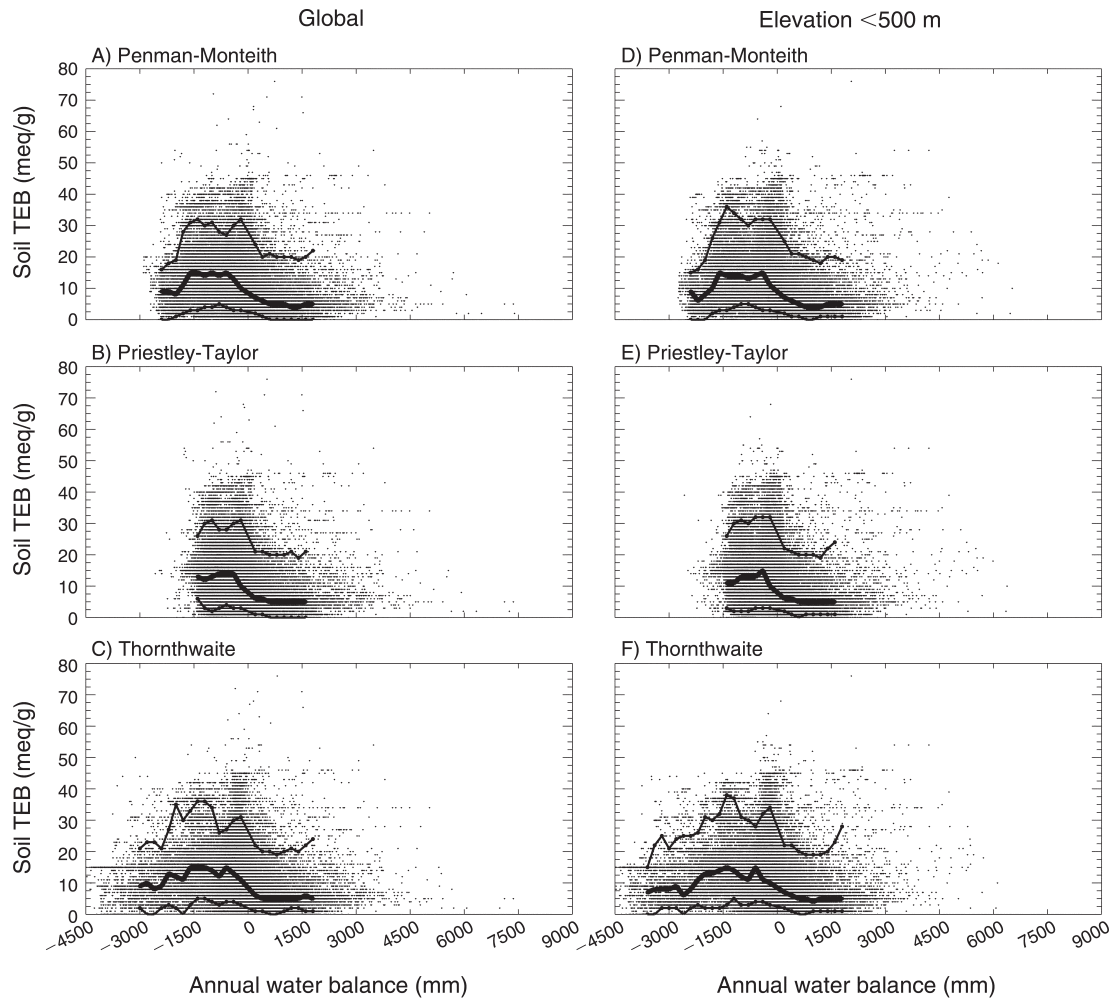


FIG. 3. Global distribution of soil “total exchangeable bases” (TEB; FAO 2008) in relation to mean annual water balance, estimated using the three major models for calculating potential evapotranspiration (PET; Fisher et al. 2011b). Panels show a random selection of 0.25% of the $5 \times 5'$ cells of land area on the earth's surface, with proportional representation corrected for latitudinal and longitudinal variation in area. The thick dark line indicates median TEB for each 200-mm increment of annual water balance. The upper thin line is the 0.9 quantile for each 200-m increment of water balance, and the lower thin line is the 0.1 quantile. Quantile estimates are based on the full data set. Right-hand panels show only TEB values for areas with elevations ≤ 500 m.

of TEB with other soil nutrients under most conditions (Stevens and Walker 1970, Walker and Syers 1976, Peltzer et al. 2010). Water balance was evaluated using PET estimates from Fisher et al. (2011b) based on the Thornthwaite (Thornthwaite 1948, Thornthwaite and Mather 1955, Mather 1978), Penman-Monteith (Penman 1948, Monteith 1965), and Priestley and Taylor (1972) models, which all showed qualitatively similar patterns.

The relationship between water balance and soil fertility was evaluated by pairing, for every $5 \times 5'$ cell of land surface, the value of TEB from the FAO soil database with the estimated value for water balance for that cell, to create simple untransformed scatterplots for the entire global land surface (Fig. 3), and various tropical, temperate, and regional subdivisions of the

continents (Fig. 4). The global land surface (excluding Antarctica) contains $\sim 2.3 \times 10^6$ cells at $5 \times 5'$ resolution. For clarity of visualization, the panels in Fig. 3 show only a 0.25% random subset of these data values, although the quantile lines are based on the full data set.

Two different types of NPP (net primary productivity) data are available to test Albrecht's model. First is the productivity of agricultural crops, which is collected globally at the country level by FAO (1999) for several crop types, including root and tuber crops and cereal grains (data *available online*).³ (These data are also recompiled and *available online* from the World Resources institute).⁴

³ <http://faostat3.fao.org/home/index.html>

⁴ www.wri.org

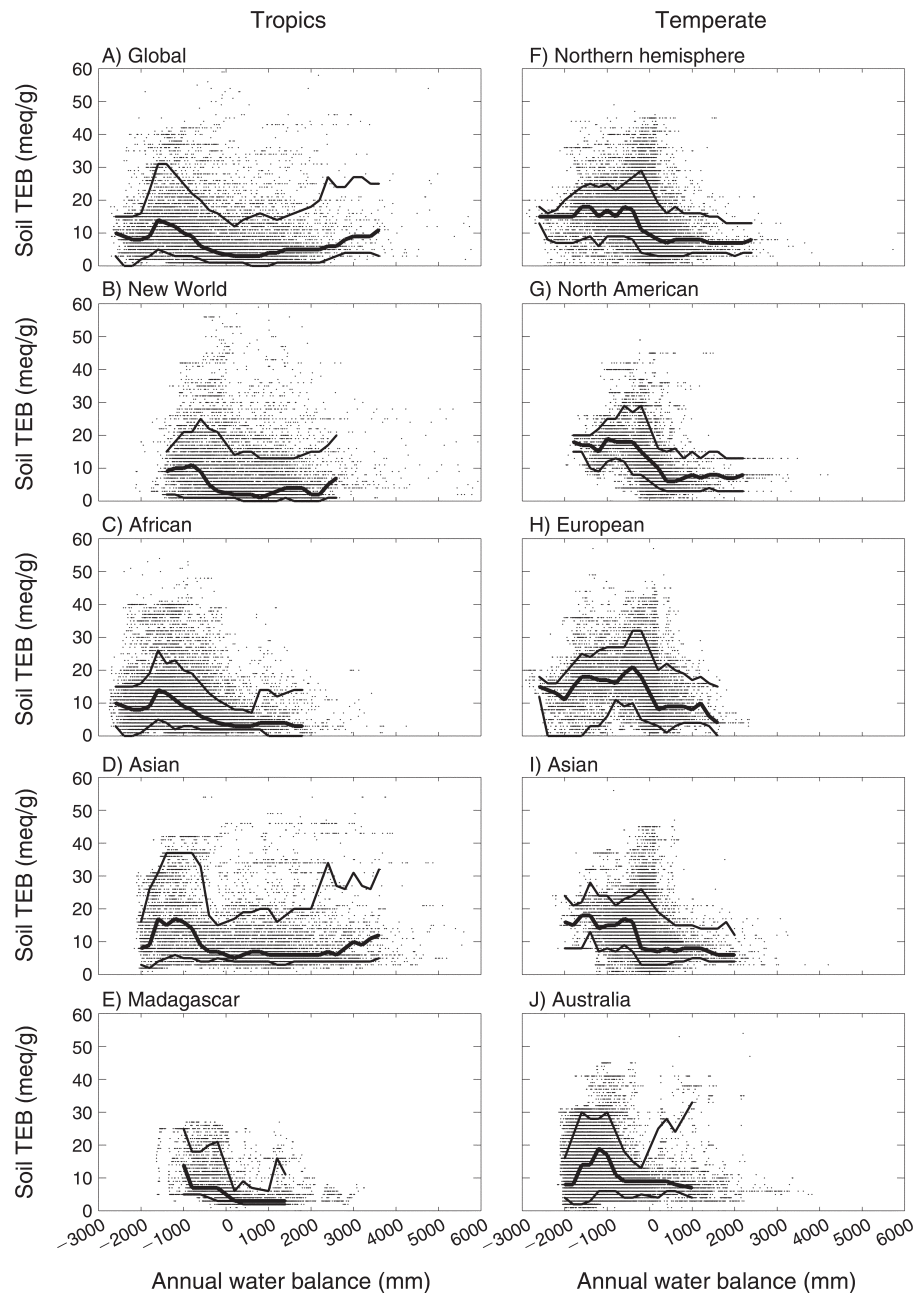


FIG. 4. Tropical and temperate regional distributions of soil total exchangeable bases (TEB; FAO 2008) in relation to mean annual water balance, calculated as annual precipitation (mm) minus potential evaporation (mm) estimated using the Penman-Monteith model (Fisher et al. 2011b). Lines indicating median (thick line), and 0.9 and 0.1 quantiles (thin lines) are calculated using all data values for each region. Data for all elevations are shown in all graphs.

The second is the productivity of natural ecosystems, for which multiple independent studies have been compiled into several global data sets (e.g., Lieth 1975, Cannell 1982, Scurlock et al. 1999, 2002, Clark et al. 2001a, b, Olson et al. 2001a, b, Scurlock and Olson 2002). For all sample sites

and areas in both of these NPP data types, TEB and water-balance values were extracted from the global soil and climate data sets, calculating median values at the country level for agricultural data, and mean values for a small region around the study plots for natural ecosystems.

RESULTS

The global values of total exchangeable bases (TEB) in Fig. 3, plotted against water balance based on the three primary models for potential evapotranspiration (PET) as calculated by Fisher et al. (2011b), represent the effects of many different factors with complex interactions in addition to the soil \times climate interactions underlying Albrecht's "theoretical curve." Many of these complicating factors, such as the presence of ancient highly weathered soils, currently dry soils that were formed under wet climatic conditions, or soils formed from nutrient-poor parent materials, cause observed soil fertility to be substantially *lower* than that predicted by the current water balance alone. Other factors, such as extremely young soils or soils recently formed from nutrient-rich parent materials such as volcanic ash, can cause soil fertility to be *higher* than would be predicted by the current water balance alone.

These factors help explain why the distribution of soil nutrient values in Fig. 3 has such high variability that it looks like a solid cloud rather than a simple curved line of points, such as those from transect studies (Fig. 2). In data such as these, where the value of the predicted response of a dependent variable (i.e., soil TEB) to an independent variable (i.e., water balance) is affected by multiple unknown or unmeasured factors, a statistical method called *quantile regression* can help describe the shape of different portions of the data distribution, characterized as quantiles (Koenker and Bassett 1978, Koenker and Hallock 2000, Cade et al. 1999, Cade and Guo 2000, Cade and Noon 2003). Thus, the points in the upper 10%, or above the 90th quantile, represent those locations where the unknown factors have had a minor effect on the response to the hypothesized causal factor, in this case the effect of water balance on soil fertility. Similarly, the shape of the line below which the lowest 10% of the values of the dependent variable fall describes the distribution of locations where soil fertility is most negatively affected by the set of unknown processes.

The highest values of soil TEB across the gradient of water balance form an upper boundary (e.g., the 0.9 quantile) that closely resembles Albrecht's curve, that is, a unimodal curve with a maximum near a water balance of zero. The asymmetric upper boundary departs from the symmetric "normal" curve used by Albrecht because the wettest places on earth, as estimated by the difference between mean precipitation and the Penman-Monteith (Fig. 3A, D) or Priestley-Taylor (Fig. 3B, E) estimates of PET, have a positive water balance of greater magnitude than the most negative water balances (caused by high PET) in dry areas. The water balance estimates based on the Thornthwaite model are more symmetrical around zero (Fig. 3C, F) because the Thornthwaite model predicts much higher PET under hot conditions (Fisher et al. 2011). Over a relatively small proportion of the earth's surface, current precipitation greatly exceeds current PET. The quantile lines in the panels of Fig. 3, formed from unsmoothed values,

show the 0.1 and 0.9 quantiles, as well as the median value (equivalent to the 50th quantile) of all the data points, with each dot along the line representing the 0.1, 0.5, or 0.9 quantile of all values within a 100-mm segment of the range of values of annual water balance.

The global median values of TEB form a curve that plateaus between roughly -1500 and -500 mm for water balance based on all three PET models, so the highest value on the median curve clearly does not occur at a water balance of zero, but rather under somewhat drier conditions. However, for the maximum TEB values there tends to be a peak in the 90th-quantile line slightly drier than a water balance of zero, as well as a peak around -1500 mm. This double peak most likely occurs because there are large areas of Earth's surface with a water balance in these ranges. Unlike in an experiment, or sampling along a transect, integrating over irregular geographical areas allows large regions to dominate the results. Visually, the upper boundary of the most dense portion of the cloud of points has a maximum near a water balance of zero and a decline toward drier or wetter conditions.

Another interesting feature of Fig. 3 is that, in spite of the general decline in maximum soil TEB with increasingly positive water balances, both the 50th and 90th quantile lines show an increase in TEB with increasing water balance above approximately 1500 mm. While this seems to suggest the counterintuitive conclusion that increased leaching of water through the soil increases soil TEB, rather than decreasing it as predicted by Albrecht (1940a) and observed in many regional-scale studies, there is likely a simple explanation for this phenomenon that reflects the complexity of soil-forming processes on a dynamic planet. Many of the highest rainfall areas on Earth are in mountain ranges that intercept moisture-laden air coming off the oceans and extract large amounts of precipitation as a result of uplift and adiabatic cooling. Such high mountain regions tend to be geologically young, with freshly exposed rocks uplifted by faulting, or volcanic ashes and lavas spread over mountain slopes and valleys. In these cases, water balance and soil parent material are not independent, nor are they likely to be in the equilibrium envisioned by Albrecht's curve because fresh parent material is continually replacing the nutrients lost by leaching under high rainfall conditions. It is particularly telling that the minimum soil TEB increases from 0 to 3 or 4 above a water balance of ~ 2500 mm, suggesting that these high levels of "excess" precipitation occur in regions with young soils where there has not yet been sufficient time for significant nutrient loss due to weathering and leaching. Nonetheless, the similarity of the patterns with all elevations included (Fig. 3, left-hand panels) and only elevations below 500 m (Fig. 3, right-hand panels), suggests that the effect of high elevation sites on the overall global pattern is relatively minor.

Fig. 3 also illustrates the major differences among the three methods of evaluating PET (see also Fisher et al. 2011b). The most notable difference is that the

Thornthwaite method (Fig. 3C) generates the highest rates of PET (negative water balance values) and the Priestley-Taylor method (Fig. 3B) the lowest. The Penman-Monteith method (Fig. 3A) generates intermediate values and also has a more plausible distribution of values with regard to global vegetation patterns (Fisher et al. 2011b). However, all of these methods were originally designed and tested primarily for agricultural crops, and each method has differing assumptions and data requirements that may be more appropriate in different climate-vegetation combinations. It may just be a coincidence that the oldest and simplest method, that of Thornthwaite and Mather (Fig. 3C, F), produces a pattern that most closely resembles Albrecht's curve. Fisher et al. (2011: Fig. 4c) found that the Thornthwaite model tended to overpredict PET at low values (<500 mm) and at high values (>2000 mm) in comparison with Penman-Monteith. The relative performance of the three models varied between continents and within continents even though their total global averages were very similar (Fisher et al. 2011b: Figs. 1 and 2).

While the overall global patterns of PET vs. water balance are consistent with the predictions of Albrecht's model, analyses of TEB-water balance relationships by subregions of the earth's surface, e.g., continents, or tropical vs. temperate, reveal significant geographical differences while still conforming to the general pattern (Fig. 4). The most striking result from the latitudinal analysis is the fact that the highest TEB values in the tropics are found under dramatically drier conditions (Fig. 4A) than in the temperate zone (Fig. 4F), with the difference equivalent to between 1000 and 1500 mm less available water. This analysis makes it clear that the broad "plateau" of high TEB between -1500 mm and 0 shown by all three PET methods at the global scale in Fig. 3, is actually composed of two separate modes, one tropical and one temperate, as suggested by the plateau and peaks of the quantile lines in Fig. 3.

Important regional differences revealed by these analyses include (1) the extremely negative water balances and low TEB values of the African tropics (Fig. 4C) where the long-term climate record of alternating wet and dry periods is well documented; (2) the extremely low minimum (e.g., 0.10 quantile) TEB over a broad range of water-balance conditions in South America (Fig. 4B) where the Amazon Basin is geologically stable and receives very high rainfall; (3) the virtual absence of extremely low TEB values, as well as a high median TEB, in the Asian tropics (Fig. 4D, 0.10 and 0.5 quantile lines) where high geological activity is associated with the Pacific "Ring of Fire"; and (4) the near absence of low TEB values under conditions of strongly negative water balances in the temperate zone, most notably in North America and Asia (Fig. 4G, 1; 0.10 quantile line below 0 water balance), where continuing geological activity provides a supply of nutrient-rich parent material for soil development in dry areas. Note that the positive slope of the 0.90

quantile line above a water balance of zero in the global pattern (Fig. 4A), which is caused by sites that have both high precipitation and high TEB, is primarily a consequence of sites in the Asian tropics (Fig. 4D), where a large proportion of the land area has high precipitation and high rates of volcanism.

In addition to various soil properties, of which the global estimates address only TEB, Albrecht's curve was also intended to predict productivity, which is plant growth, or what we now call "net primary productivity" (NPP). Albrecht's simple prediction was that productivity should follow the same curve as the soil properties. However, there are sound reasons to expect that the pattern of NPP should not follow the same pattern as soil fertility along the water-balance gradient because plant growth can be limited by many different factors (e.g., Sprengel 1839, Liebig 1840, Sanchez 1976, Howarth 1988, Chadwick et al. 1999, Vitousek 2004, Elser et al. 2007). Thus, in spite of potentially high soil fertility where it is dry, the lack of water should strongly reduce plant growth rates (NPP) under these conditions. Consequently, in the absence of irrigation or riparian water sources, maximum NPP should increase from very low levels under conditions of strongly negative climatic water balance to a maximum level near a water balance of zero, where both TEB and water availability are high. NPP is predicted to decrease above a climatic water balance of zero as increased weathering and leaching leads to reduced soil fertility and limitation of growth by low soil-nutrient content in spite of high water availability. The obvious exceptions to this generalization are wherever geological activity results in high soil-nutrient content where water availability is also high, which occurs most commonly in montane areas, but may also be found in fertile alluvium that is constantly replenished by deposition in regions with reliable river flow, as in the Nile valley.

The predictions of Albrecht's curve for both soil properties and plant productivity would be expected to be poor in any locations where soil properties are not in equilibrium with the local climatic conditions, for the various reasons discussed previously. It is also important to recognize that large spatial scale (e.g., $5 \times 5'$ cells) estimates of water balance do not reflect local concentrations of water associated with streams, rivers, and springs. These are the local areas where agriculture is usually practiced in arid regions. Consequently, in restricted areas crop production rates or natural ecosystem NPP can be much higher than predicted by regional water balance.

The two different types of NPP data, country-level crop productivity from FAO (1999), and plot-level NPP of natural ecosystems from recent compilations of the National Academy of Sciences International Biological Program and other data (Olson et al. 2001a, b) show similar patterns and suggest an important refinement to Albrecht's model. At the global scale, the FAO crop data show a monotonic increase (0.90 quantile line) in

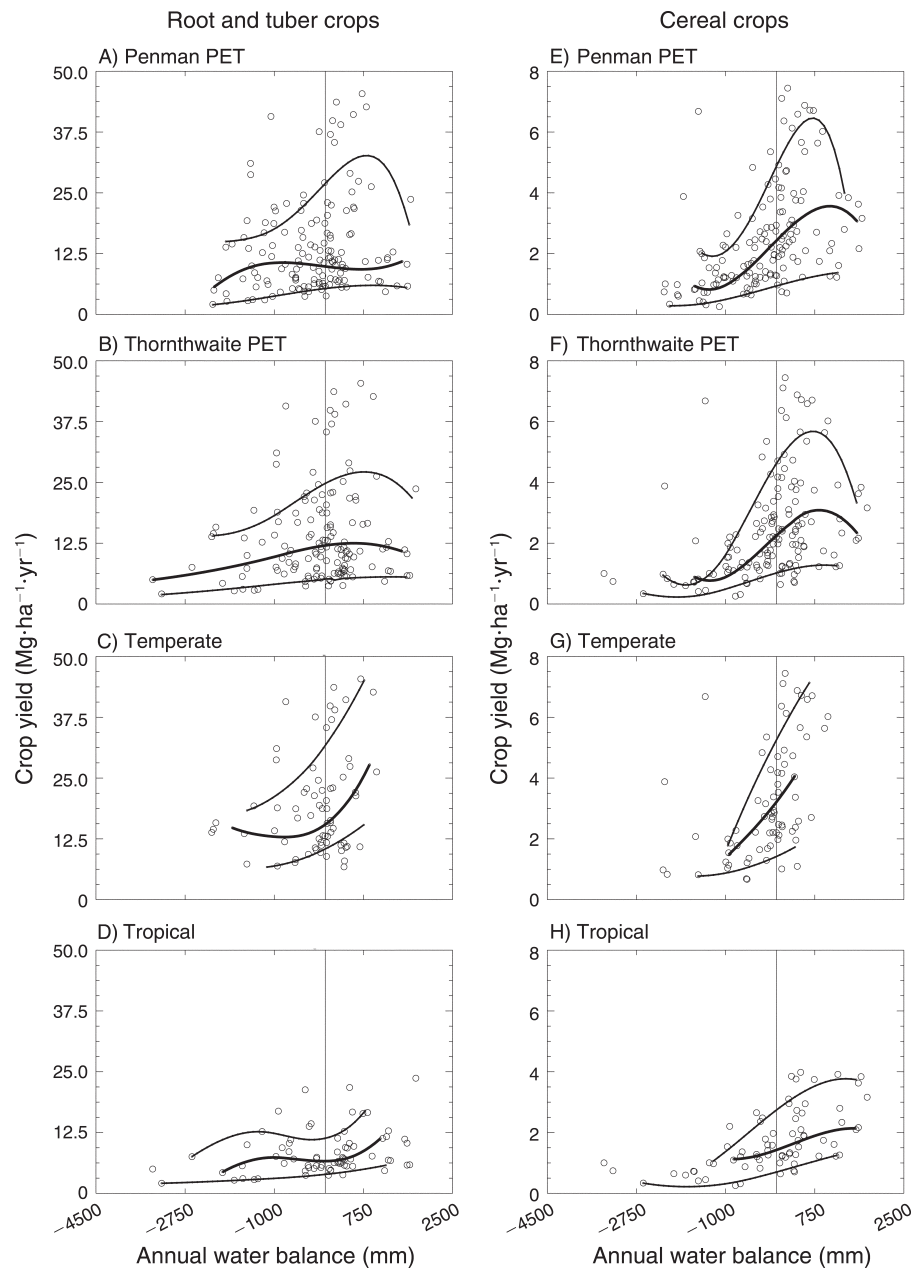


FIG. 5. Relationship of country-level mean crop yields to median annual water balance for each country for (A, B) root and tuber crops, and (E, F) cereal crops, with water balance calculated using either (A, E) the Penman-Monteith model or (B, F) the Thornthwaite model. The separate (C, G) temperate and (D, H) tropical graphs show annual water balance based on the Thornthwaite model. Crop yields are from FAO (1999). Quantile lines are as in Fig. 3. The thin vertical line indicates zero water balance. Five temperate countries were excluded from the quantile analysis because they have water sources (rivers and/or irrigation) that are independent of local climate. Outliers, from highest to lowest values, are Israel, Australia, and Jordan for roots and tubers; Egypt and Saudi Arabia for cereal crops.

annual yield from the driest conditions (mean annual water balance of -2000 mm based on Penman-Monteith) to a maximum around $+750$ mm annual water balance for both root and tuber crops (Fig. 5A, B) and cereal crops (Fig. 5E, F). From the maximum, yields for

both crop types decline sharply with increasing wetness, but do not reach the low levels of the driest sites. However, when the crop productivity data are separated into temperate (Fig. 5C, G) and tropical (Fig. 5D, H) groups, it becomes clear that the low crop productivity

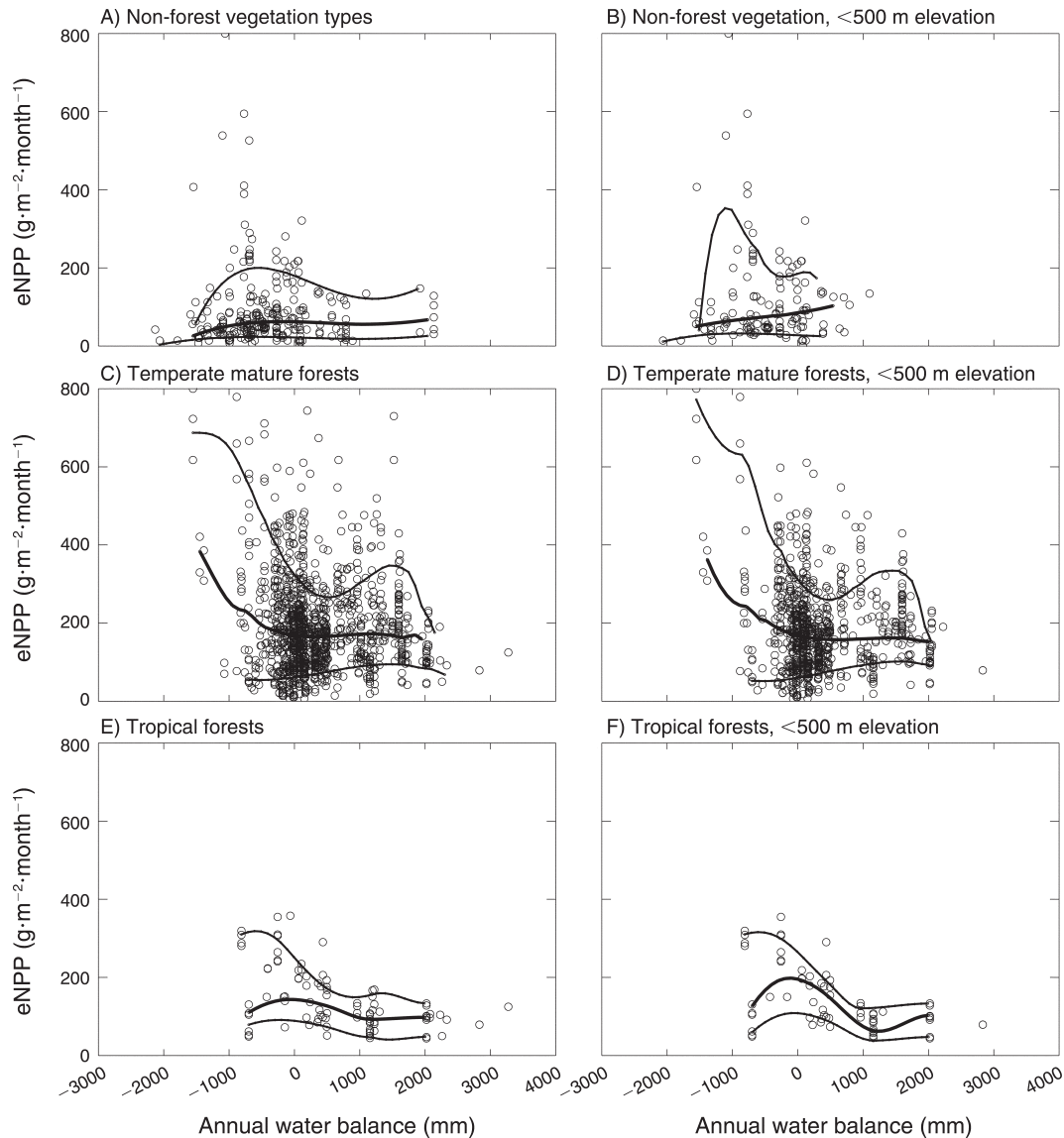


FIG. 6. Productivity of natural ecosystems, calculated as monthly average growth during the growing season only, called “eNPP,” based on Global Primary Productivity Data Initiative data sets A and B (Olson et al. 2001*a, b*) in relation to mean annual water balance in the region where each site is located: (A, B) non-forest natural vegetation (grasslands, deserts, savannas, shrublands, tundra); (C, D) temperate forests; (E, F) tropical forests. Values in the right-hand panels (B, D, F) are limited to sites below 500 m elevation. Quantile regression lines show values for eNPP across variation in mean annual water balance. The thin lines are the 0.9 and 0.1 quantiles, calculated for the same data segments as the thick median (0.5 quantile) line.

above a water balance of 750 mm seen in the global analysis is strictly a tropical phenomenon, since there are few temperate countries with median water balance that high. In addition, the median and maximum crop yields in the temperate zone are approximately double those in the tropics, for both crop types. These agricultural production patterns are exactly what would be predicted based on the difference between the water-balance conditions at which soil TEB is highest between the tropics and temperate zone (Fig. 4A–D vs. F–I). In the

tropics the areas with highest soil TEB are too dry for productive agriculture, and optimal water-balance conditions occur where soils have lower TEB.

The productivity pattern for natural herbaceous ecosystems, using mean monthly NPP during the growing season ($\text{g dry matter} \cdot \text{m}^{-2} \cdot \text{month}^{-1}$, called “eNPP” [meaning ecologically or evolutionarily relevant or effective; Huston and Wolverton 2009]), is similar to that of the agricultural crops, but appears to reach a maximum under drier conditions, around -750 mm,

rather than the +750 mm of the agricultural crops (Fig. 5). The highest rates of eNPP for both herbaceous vegetation types (Fig. 6A, B) and temperate forests (Fig. 6C, D) occur under surprisingly dry conditions. The sample sites in these dry regions are most likely in wetter topographic positions such as stream and river valleys where local water availability is not accurately represented by annual climatic water balance. Among the highest productivity sites, the maximum eNPP declines with increasingly wetter conditions, as indicated by the negative slope of the 90th quantile in Fig. 6A–F, including the tropical forest sites (Fig. 6E, F), where maximum eNPP is much lower.

It is clear that the three primary methods for estimating PET make substantially different predictions about the rates and distribution of PET over Earth's surface (Fisher et al. 2011b: Fig. 1) as well as about the relationship between water balance and soil properties (Fig. 3), and water balance and crop yields (Fig. 5). The Thornthwaite model is the oldest and simplest and is based only on temperature. The Priestley-Taylor model is based on radiation, and requires more parameters, while the Penman-Monteith model uses both temperature and radiation and requires numerous difficult-to-estimate parameters. Unfortunately, there are no reliable measurements (of either PET or the parameters required by the models) with which to test the models over a broad range of conditions. Until there are accepted standard ground-based measurements of PET covering an adequate sample of the global land area, it will be impossible to confirm which model is most accurate, or to develop a better model.

DISCUSSION

Refining Albrecht's curve

The pattern predicted by Albrecht's curve, based upon the principles of pedogenesis and the relatively small amount of data available in the 1930s, appears at both global and regional scales using data extracted from gridded global data sets of soil and climate properties (Figs. 3 and 4), and geographically distributed data sets of plant productivity (Figs. 5 and 6). Not surprisingly, however, these empirical results reveal patterns that differ substantially from Albrecht's original symmetrical "theoretical" curve (Fig. 1). The primary differences are that, except for estimates based on the Thornthwaite model, the decline in total exchangeable bases (TEB) in soil is truncated at moderately dry conditions, and that the curve for maximum plant net primary productivity (NPP) does not follow the curve for maximum soil TEB, but rather is shifted to wetter conditions. The first difference is a consequence of different potential evapotranspiration (PET) algorithms, and the second difference is not surprising given the reasonable assumption that plant growth is potentially limited by different resources under different conditions (Sprengel 1839, Liebig 1840, Vitousek 2004, Elser et al. 2007). Consequently, under

negative water-balance conditions, even though TEB is potentially high, low water availability limits plant growth, which increases with increasing water availability to a maximum near (or wetter than) a water balance of zero. Under increasingly wet conditions, plant growth becomes limited by soil nutrients (estimated using TEB in our examples) and declines to meet the same curve as the decline in TEB as water availability and nutrient leaching rates increase.

It is striking that the highest soil TEB levels in the tropics are found under conditions about 1000 mm drier than in the temperate zone. This is most likely a consequence of shifting climatic patterns, so that soils that are currently experiencing a water balance of near zero have been much wetter at times in the past. In the temperate zone the maximum levels of soil TEB are reached near a water balance of zero, suggesting that these younger soils do reflect an equilibrium with their current water regime, while the maximum rates of plant productivity, at least for crops, are apparently reached under somewhat wetter conditions. For plant productivity we can propose a revision to Albrecht's theoretical curve that includes the effect of interacting limiting resources (water and soil nutrients) on plant growth.

The revised versions of Albrecht's curve in Fig. 7 are based on the patterns of TEB and NPP in relation to an annual water balance calculated using both the Penman-Monteith and the Thornthwaite models of PET (Fig. 3 A, C). The curve based on water balance estimated using the Thornthwaite model (Fig. 7B) is more similar to Albrecht's symmetrical "theoretical" curve than the curve based on Penman-Monteith (Fig. 7A). The shapes of the TEB distribution and the plant responses differ between the two estimates of water balance, as well as between the temperate zone (Fig. 7C) and the tropics (Fig. 7D). Consequently, the revised Albrecht's curves differ depending on the PET model used and the geological and climatic history of the region in which the data are collected.

The functional relationships between soil water balance and soil properties underlying Albrecht's original "theoretical" curve are still valid, but variation in soil age, both chronological and pedogenic, along with the effects of long periods of time and climate regimes that alternate between wet and dry, inevitably shift the peak of maximum soil TEB to drier conditions. Throughout much of the tropics, as well as in other parts of the world, a long history of fluctuating climatic conditions has caused many older soils to reach a low nutrient state typical for wet conditions or very old soils, even though the current climatic conditions may be quite dry.

It will be difficult to develop more regionally precise versions of Albrecht's curve until we have much better data on variation in soil water (based on annual and monthly water-balance data, as well as measurements of soil water availability and leaching rates, e.g., Chadwick et al. 2003), along with better global data on soil properties and plant productivity (e.g., Clark et al. 2001a, Huston and Wolverton 2009, 2011). It should be reiterated that

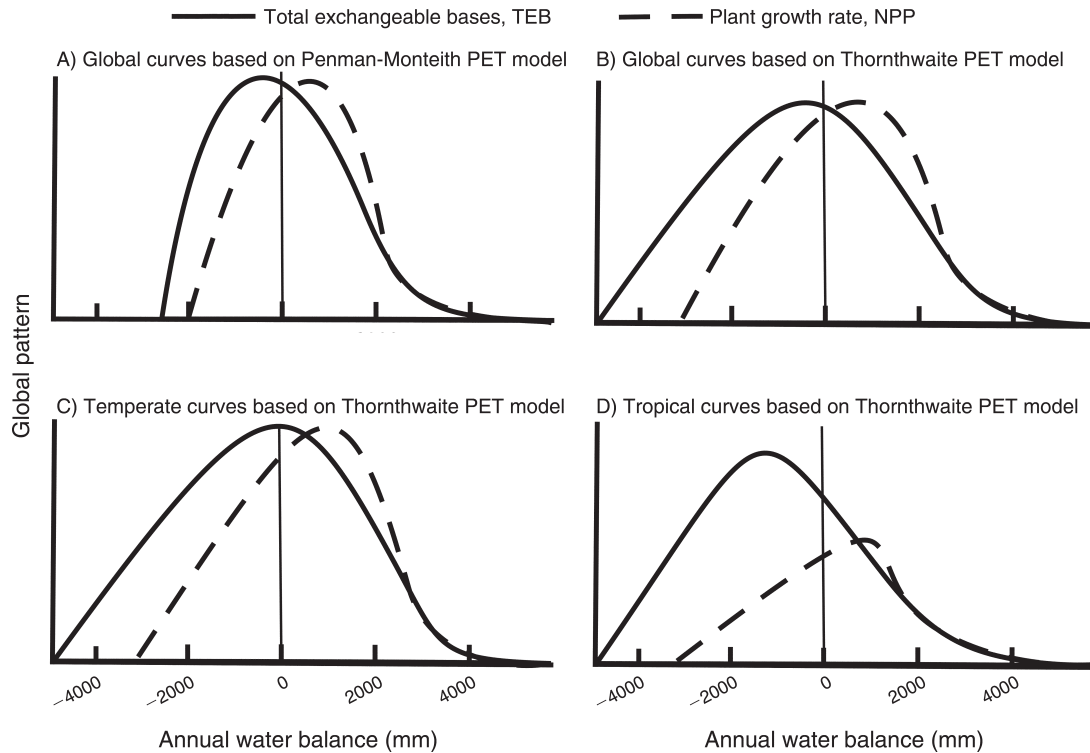


FIG. 7. Revised versions of Albrecht's curve, based on (A) Penman-Monteith and (B) Thornthwaite models of potential evapotranspiration (PET) at the global scale, showing the response of net primary productivity (NPP; dashed curve) to the transition between water limitation, where annual water balance is negative, to limitation by soil nutrients, represented by total exchangeable bases (TEB; solid curve) where the annual water balance is positive. The global TEB curves approximate the patterns shown in Fig. 3A and C, while the plant response curves are based on Fig. 5 and Fig. 6. The (C) temperate and (D) tropical curves are based on the Thornthwaite PET model and approximate the TEB patterns shown in Fig. 4A and F, while the plant response curves are based on Fig. 5.

Albrecht included organic matter, clay content, and clay stability, in addition to exchange capacity and base saturation (analogous to TEB), as following the general pattern of his curve. Predictive models based on soil water balance would need to be calibrated separately for different soil properties and for regions with different geological and climatic histories, and it will be interesting to see and understand how the various relationships differ from Albrecht's simple generalization.

Jenny and Leonard (1934) published data on multiple additional factors that varied predictably along the precipitation gradient they surveyed, including (1) depth of carbonate zone, (2) nitrogen content, (3) inorganic colloid content, and (4) soil pH. Similarly, Donkin and Fey (1993) found significant negative relationships between water balance and a variety of soil chemical properties in their transect across humid subtropical eastern South Africa, as well as somewhat different responses in soils from different parent materials. Research on soil chronosequences (e.g., Stevens and Walker 1970, Walker and Syers 1976, Walker et al. 1981, Wardle et al. 2004, Peltzer et al. 2010) demonstrates that the properties of very old soils in any climate converge

with those predicted by Albrecht's curve to occur on soils developed under high-rainfall conditions. A better understanding of the distribution of all of these soil properties, including soil carbon, in relation to annual water balance and soil age will provide a much stronger foundation for predicting local, regional, and global patterns of plant growth in agricultural and natural ecosystems, and will likely be valuable for biodiversity studies, conservation, carbon sequestration, and economic development.

Implications of regional differences in soil fertility and water balance

While the general pattern of a unimodal distribution of maximum soil TEB in relation to annual water balance appears at all spatial scales and in all regions of the earth examined (Figs. 3 and 4), there are clearly major differences between some of the regions (Fig. 4). The most dramatic regional difference at the global scale is the shift in the position of the "mode" of maximum soil TEB between the tropics and the temperate zone. In the tropics (Fig. 4A–D) the bulk of land area with high levels of TEB has a strongly negative annual water balance (between -1500 mm and -1000 mm). In

contrast, in the temperate zone (Fig. 4F–I) the greatest areas of land with high TEB values occur near or slightly below an annual water balance of zero.

Although the precise position of the mode of maximum TEB is difficult to determine, it is evident that most of the high TEB values are found under much drier conditions in the tropics than in the temperate zone (either north or south). There are several potential explanations for this. One possibility is that many tropical soils are on average older than temperate soils, either chronologically and/or in terms of soil weathering and degradation processes, which occur more rapidly under warm than under cold conditions, assuming sufficient water is available. Only under continuously dry conditions or with continual replenishment by material with high nutrient content can high soil fertility be maintained over time in the tropics. It is also obvious that the temperate zone has been glaciated more recently, more extensively, and more frequently than the tropics. Thus, the younger temperate soils have a pattern more similar to Albrecht's idealized curve, while the older, more-weathered tropical soils show the effects of a longer, warmer and/or wetter and more complex history of soil development, leading to greater depletion of soil nutrients under all but continually dry conditions. Active volcanoes and young mountains in the tropics should have soil TEB distributions in relation to water balance that are more similar to those in the temperate zone (e.g., Chadwick et al. 1999, 2003).

Overall, the temperate zone has a much larger proportion of its land mass with conditions of both high soil TEB and favorable soil moisture conditions (approximately 0 ± 500 mm) than does the tropics, where on average current conditions are drier and soil fertility (e.g., TEB) lower (Fig. 4A vs. 4F; see also Huston and Wolverton 2009, 2011). This is likely to be part of the explanation for the persistent low productivity of agriculture in the tropics (Fig. 6E–H; see also Grigg 1985, Huston 1993, Weischet and Caviedes 1993) and is relevant to understanding the differences in biodiversity between the tropics and the temperate zone (Huston 1979, 1993, 1994).

While the general temperate–tropical differences in water balance and soil TEB also appear at the smaller scale of the continents, there are striking differences between the continents (see Richter and Babbar 1991) that are likely to have important implications for agriculture, economics, and biodiversity. Most notably, Africa stands out as being substantially drier than either the New World or Asian tropics (Fig. 4B, C, and D), and as having a much smaller proportion of its total land mass with both high TEB and favorable water-balance conditions. In Africa most of the high TEB soils occur under very dry conditions. However, it must be noted that the most productive agricultural regions of the world have TEB levels between 6 and 12. Substantially higher TEB levels may provide relatively little benefit for

agriculture, particularly under the dry conditions where sodium (Na) is often the dominant cation.

It is also noteworthy that the Asian tropics have virtually no land area with TEB values below 4 (Fig. 4D), which contrasts most strongly with the New World tropics (Fig. 4B), which have extensive areas of extremely low TEB soils in the Amazon basin and elsewhere, as well as with the African tropics (Fig. 4C). The striking properties of the Asian tropics, with no extremely poor soils, and substantial areas of high TEB soils across a wide range of favorable water-balance conditions, are due primarily to its position on the Pacific Plate boundary, where recent volcanism and mountain building has created extensive areas of rich, young soils. In addition, the very small land-to-ocean ratio caused by the many small islands and archipelagoes results in abundant rainfall over most of the land surface. This would be expected to lead to high productivity in natural and agricultural ecosystems, as well as to large body sizes and/or high population densities in animals, including humans (Huston and Wolverton 2011).

In the temperate zone there are also differences among the three major continental regions (Fig. 4G, I), although they all show the basic temperate-zone pattern of the mode of maximum TEB at or slightly below a water balance of zero. North America (Fig. 4G), and to a lesser extent Asia (Fig. 4I), show a dramatic absence of low TEB levels under the driest conditions, with minimum TEB values >10 near -2000 mm, dropping linearly to a TEB of 1 near an annual water balance of zero (0.10 quantile lines in Fig. 4G and I). This is most likely due to the high geological activity in the arid western part of North America, and to the young soils of the arid interior portions of the geologically active Tibetan and Himalayan plateaus in temperate Asia. Temperate Europe, including the Mediterranean, Near Eastern regions, and North Africa has a substantially larger proportion of arid lands.

At the smaller scale of large islands and island continents, Madagascar (Fig. 4E) and much larger Australia (both temperate and tropical, Fig. 4J) both have a dry-shifted tropical-type distribution of TEB in relation to water balance, in spite of the fact that more than half of Australia is in the temperate zone. The soils in Madagascar have substantially lower TEB levels than those in Australia, although neither island has much land area with extremely low TEB levels.

Implications of Albrecht's curve for global patterns of NPP and biodiversity

For the past two centuries, ecologists have interpreted global vegetation patterns in relation to climatic variables, particularly precipitation, which is presumed to have a positive effect on plant growth (NPP) with a linear or asymptotic response of growth to increasing precipitation (e.g., Lieth 1972, 1975). While it is obvious that there are major differences in vegetation structure,

NPP, and species diversity between desert and forest regions that can be reasonably attributed to increased water availability, most ecologists, plant physiologists, and ecosystem modelers have long assumed that both species diversity and plant growth rates increase monotonically with increasing precipitation (Lieth 1972, Currie 1991, Currie and Fritz 1993, Currie et al. 2004, O'Brien 1993, 1998, O'Brien et al. 1998, Hawkins et al. 2003, Gillman and Wright 2010). Tropical rainforests have been considered to have both the highest productivity and highest species diversity of all terrestrial ecosystems, as well as the highest rainfall. The consensus has been that plant and animal diversity increases with increasing precipitation and warmer temperatures, and that high productivity is the cause of the increased diversity.

However, two of the most detailed early studies of tropical forest structure and diversity (Holdridge et al. 1971, Hall and Swaine 1976) both found that, while tree species richness increased with increasing precipitation, richness was negatively correlated with soil fertility, i.e., the highest species diversity occurred on sites with the lowest soil nutrient levels. Both studies also found that two measures related to forest productivity, maximum tree height (m) and total basal area (m²/ha), increased from the driest sites (which also had the highest soil nutrient content), to a maximum at intermediate levels of precipitation, and then declined with further increase in precipitation (and decreasing soil nutrient levels), matching the prediction of Albrecht's curve. Thus, it is not surprising that a recent analysis of plant productivity data that included tropical sites (Schoor 2003) found a decline in forest NPP with increasing rainfall, which was attributed to "negative effects of water in excess of biological demand" (Schoor 2003:1169). Schoor concluded that current global vegetation models may be substantially over-predicting NPP in the tropics.

The patterns of soil fertility and plant productivity in relation to annual water balance described by Albrecht's curve provide a simple mechanism to explain the decline in plant growth rates (NPP) under high rainfall conditions. However, Albrecht's curve also has major implications for understanding patterns of biodiversity, which were not an issue during Albrecht's career. As confirmed by the large-scale empirical tests of Albrecht's curve presented here, both soil fertility and plant productivity decrease with increasing precipitation, specifically the amount of water moving through the soil profile. This means that, although species diversity usually increases with increasing precipitation, it is actually increasing as both soil fertility and plant productivity decrease (Holdridge et al. 1971, Hall and Swaine 1976, 1981, Huston 1980, Swaine 1996).

The ubiquitous effects of the processes described by Albrecht are clearly illustrated by a type of soil gradient that does not involve variation in precipitation, but rather soil age. Soil chronosequences are formed by geological processes that repeatedly create new sub-

strates for soil formation out of the same basic materials under the same climatic conditions (Stevens and Walker 1970, Wardle et al. 2004, Peltzer et al. 2010). Examples include lava flows of different ages, or sand dunes that are continuously formed as sea level drops or sediment builds beaches. These processes create series of soils of increasing age, with the youngest soils at the current site where fresh material is accumulating (e.g., lava flows or active sand dunes), and the oldest soils furthest away from the site of soil initiation. Over the past century, many different soil chronosequences have been studied by soil scientists and ecologists (Major 1951, Dickson and Crocker 1953/1954, Olson 1958, Jenny et al. 1969, Stevens and Walker 1970, Walker and Syers 1976, Walker et al. 1981, Wardle et al. 2008, Peltzer et al. 2010, Walker et al. 2010).

The patterns of soil development and ecological changes along most chronosequences are very similar to those described by Albrecht's curve, with time rather than precipitation on the *x*-axis, because the fundamental mechanisms causing both types of patterns are identical. The critical factor along both chronosequences and precipitation gradients is the mineral dissolution and leaching caused by water moving through the soil. In the case of chronosequences over short distances where there is no variation in precipitation, the effects of water accumulate over time, with greater volumes of water having moved through the old soil profiles than through the younger soil profiles. Along precipitation gradients, which ideally have a uniform, even-aged parent material (e.g., Jenny and Leonard 1934), the volume of water moving through the soil profiles varies with effective precipitation (precipitation minus evapotranspiration) operating over the same time period across the gradient. While pedogenic processes occur much more slowly in dry environments than in wet environments, the inevitable accumulation of these changes over time creates patterns of soil properties that are very similar to those seen along gradients of precipitation or water balance, even for chronosequences in dry environments (e.g., Laliberté et al. 2012).

Recent international efforts to sample or resample multiple chronosequences using standardized methods (Wardle et al. 2004, 2008, 2012, Fukami and Wardle 2005, Walker et al. 2010, Gundale et al. 2011) reveal clear patterns of species diversity along soil chronosequences. Most soil chronosequences have a unimodal pattern of both soil nutrient content and plant biomass across the age gradient, with both plant biomass and the availability of critical soil components such as nitrogen and organic matter increasing during primary succession, reaching a maximum, and subsequently declining on the oldest soils. This decline in soil fertility and plant productivity has been called "ecosystem retrogression" (Clements 1916, Tansley 1920, 1935, Jenny et al. 1969, Peltzer et al. 2010), in contrast with the "progressive" stages of plant succession in which biomass increases over time. The soil processes involved in these temporal

stages are directly analogous to the “constructive” and “destructive” phases of soil development along a gradient of soil weathering rates described by Albrecht (1940a). The pattern of species diversity along most of the documented chronosequences shows a rapid increase in both total biomass and tree species richness during the initial primary-succession phase, with high biomass (presumably indicating high productivity) and high tree species richness found in intermediate-aged soils, followed by a decline in both biomass and tree species on the oldest soils (Wardle et al. 2008:Fig. 1). While the oldest soils on many chronosequences are apparently too infertile to support much tree growth, with a consequent drop in tree species richness, all of the chronosequences where total vascular plant species richness was sampled found an increase in total richness over time, with the oldest, most infertile soils often having the highest species richness (Wardle et al. 2008:Fig. 2, Laliberté et al. 2012).

In contrast to many of the findings along soil chronosequences, most contemporary ecological and evolutionary theories of species diversity propose that species diversity is highest where plant productivity is highest (e.g., Currie and Paquin 1987, Currie 1991, O'Brien 1993, 1998, O'Brien et al. 1998, Francis and Currie 2003, Hawkins et al. 2003, Brown et al. 2004, Currie et al. 2004, Field et al. 2005, Krefl and Jetz 2007, Gillman and Wright 2010) and assume that the high-diversity tropical rain forests have high NPP. However, these theories have failed to take into consideration the negative effects on plant growth and productivity of low soil fertility caused by nutrient leaching under high rainfall conditions.

In addition to calling into question the NPP predictions of global vegetation models (Potter et al. 1993, Field et al. 1998, Cramer et al. 1999, Potter 1999, Roy et al. 2001, Saugier et al. 2001, Running et al. 2004), the soil fertility and NPP patterns documented along soil chronosequences and precipitation gradients, as predicted by Albrecht's curve, demonstrate that the actual effects of plant productivity on plant diversity are the opposite of the assumptions of most current ecological hypotheses about the causes of high species diversity. The ecological theories that predict that species diversity is highest where plant productivity is highest are simply wrong. Species diversity, particularly of plants, is usually low where productivity is high, and is highest in locations where productivity is moderately low (Grime 1973a, b, 1979, Huston 1979, 1980, 1994). A recent reanalysis of ground-based measurements of net primary productivity in forests (Huston and Wolverton 2009, 2011) confirms that the growth rates of tropical forests ($\text{g dry mass}\cdot\text{m}^{-2}\cdot\text{month}^{-1}$) during the growing season, is substantially lower than in the temperate zone, suggesting that the global-scale latitudinal gradient of species diversity has the same relationship to soil fertility and NPP as the patterns of plant diversity observed along many soil chronosequences, as well as along small-scale

topographic soil gradients (e.g., Weaver and Fitzpatrick 1934, Tomanek and Albertson 1957, Barnes et al. 1983, Laughlin et al. 2007).

The global pattern of soil fertility in relation to water balance has a wide range of implications. At the coarse scale of latitudinal patterns, the increase in both temperature and precipitation from the poles toward the equator produces a general latitudinal gradient of soil fertility, with higher average fertility in the cooler, drier temperate zone and lower average fertility in the warm, wet tropics (Huston 1993, 1994, Huston and Wolverton 2009). This latitudinal fertility gradient (with local and regional variations; see Fig. 4) produces a general latitudinal gradient of plant productivity and animal body size, both on land and in the oceans, with productivity and animal body size being lower in the tropics (Huston 1994, Huston and Wolverton 2011).

The global applicability of Albrecht's curve provides a new framework for understanding the regulation of species diversity by clarifying that precipitation and plant productivity tend to be positively correlated below a water balance of zero and negatively correlated above a water balance of zero. In the context of the global patterns of soil fertility and plant productivity demonstrated here, the theories of species diversity that predict diversity increases with increasing productivity would predict that diversity should be low in wet tropical rainforests and high in productive temperate forests, which is the opposite of what we observe.

However, there are two closely related theories, based on competitive exclusion among plants, that predict diversity should be low where plant growth rates are high (and competitive exclusion occurs rapidly) and highest where plant growth rates are low (and reduced competition allows greater coexistence under nonequilibrium conditions). The “humped-back model” (Grime 1973a, b, 1979) and the “dynamic equilibrium model” (Huston 1979, 1994, Huston and DeAngelis 1994) predict that plant diversity should be low where productivity is high and highest where productivity is low, but still sufficient for survival of most species. Because both high and low precipitation (specifically strongly negative or positive water balances) are generally associated with low productivity, it is clear that low plant productivity and high plant diversity can potentially occur under two contrasting sets of climatic conditions. Superimposed on the pattern of plant productivity across the full global gradient of water-balance conditions, these models predict that highest plant diversity should occur in low-productivity wet systems and also in low-productivity semiarid systems (Fig. 8). Plant diversity should be lowest under the optimal combination of water and nutrient conditions near a water balance of zero.

This bimodal distribution of maximum species diversity (Fig. 8) is similar to the bimodal pattern of species richness predicted by Austin and Smith (1989: Fig. 6) along a resource gradient from low “deficient stressed”

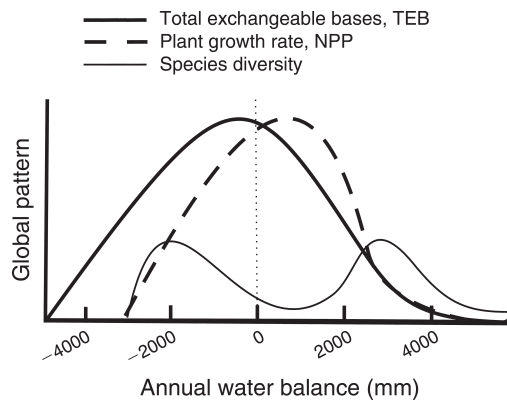


FIG. 8. Predicted bimodal global pattern of species richness (thin line) across the global gradient of TEB (heavy line) and plant productivity (dashed line) as eNPP ($\text{g dry mass} \cdot \text{m}^{-2} \cdot \text{month}^{-1}$) in relation to water balance calculated as precipitation minus potential evapotranspiration (based on Albrecht [1957]). Species diversity is predicted to be lowest where eNPP is high and highest where eNPP is low due to either limitation by water (negative “water deficiency” end of x -axis) or by soil nutrients (positive “water excess” end of x -axis). Values near the bottom of the y -axis are low; values near the top are high. All three are relative scales with different units appropriate for the three properties being graphed.

resource conditions to high “toxic stressed” conditions, in that species richness is low under the optimal conditions near the center of the gradient. However, in the gradient of water availability underlying Albrecht’s curve, water does not reach toxic levels, but rather causes a shift in the type of resource that limits plant growth from water under dry conditions to soil nutrients under very wet conditions.

This is a fundamentally different mechanism than that represented by the normal curve typically used to describe the “niches” of plants or animals. One-dimensional niche axes span a range from “too little” to “too much” of the condition or resource of interest, e.g., temperature, water, nutrient concentrations, prey size, and so forth. In contrast, Albrecht’s curve is caused by a transition in the relative rates of different processes that cause the accumulation or loss of specific soil properties. The critical transition in soil process rates occurs around a water balance of zero, above which increased nutrient dissolution and leaching leads to a decrease in the concentration of some soil components (e.g., TEB), and an increase in others (e.g., 1:1 clays, acidity). Likewise, along the same gradient of water balance, the limiting factor for plant growth (NPP) shifts from water to nutrients as conditions become wetter, and also shifts from one soil nutrient to another as conditions become wetter and/or soils become older (e.g., Laliberté 2012).

This approach to understanding the regulation of plant diversity clarifies that all high-diversity systems have a fundamental commonality, regardless of whether they occur under wet or dry conditions. Low plant

growth rates (i.e., mean monthly NPP) are the unifying link between the high-diversity semiarid Mediterranean climate shrublands (e.g., the Cape of South Africa and southwestern Australia) and high-diversity lowland tropical rainforests on poor soils, most notably in South America and Africa. The same unimodal relationship of maximum species diversity to productivity is found across all spatial scales wherever there are strong gradients in essential resources and plant productivity, from hillsides, to regions, to the entire globe.

Water balance and soil fertility are relevant not only to the biodiversity of natural ecosystems, but to the productivity of agriculture and forestry. The global latitudinal gradient of soil fertility, which is consistent with Albrecht’s curve, is likely to be the major factor underlying the persistent failure of most tropical agriculture to achieve the productivity levels of agriculture in the temperate zone (Fig. 5C, D, G, H); see also Huston 1993, 1994, 2005, Weisheit and Caviedes 1994). The global patterns of soil fertility and plant productivity suggest a strategy for land use in which intensive cultivation is restricted to the most fertile and productive soils, and less productive soils are used with decreasing intensity in order to maximize their capability to provide non-food ecosystem services such as carbon sequestration, hydrologic function, and biodiversity preservation (Huston 1993, 1994, 2005, Huston and Marland 2003).

This same variation in soil fertility has major implications for optimizing cost-benefit ratios in land-use and conservation decisions. Since biodiversity tends to be high where soil fertility and productivity are relatively low, the monetary value, at least in terms of agricultural opportunity cost, of low-fertility lands with high conservation value should be quite low. This is reflected in the fact that most of the public and private lands that have been set aside as parks and preserves, both within the United States and globally, are lands with low agricultural value (Huston 1993, 1994). Because there are important regional variations in the average global patterns of soil fertility, it should not be surprising that the cost of protecting lowland forests in Southeast Asia is much higher than in either South America or Africa (Fisher et al. 2011a [see, however, Edwards et al. 2011, Ruslandi et al. 2011]). The soils in Southeast Asia are much more fertile (Fig. 4D) than those in South America and Africa (Fig. 4B, C), and the human population density is at least 10 times greater than in South America or Africa (Nye and Greenland 1960).

There are few issues in ecology and evolution that are not affected by the abundance, sizes, and health of organisms, all of which are strongly influenced by food availability, and thus by soil fertility and plant productivity. Likewise, agricultural economics and the health and density of human populations are also directly affected by soil fertility and plant productivity. Improving the human condition while conserving the critical functions and diversity of the biosphere requires a sound understanding of the spatial distribution of

Earth's renewable resources, particularly soils and plant productivity. A broader recognition of the underlying processes and implications of Albrecht's curve would be a major step toward achieving sustainable management of Earth's natural resources.

ACKNOWLEDGMENTS

The data used in these analyses were collected by thousands of individual scientists and compiled by publicly funded consortia and dedicated individuals, to whom we all owe a great debt of gratitude. I especially thank Freddy Nachtergaele of the FAO Soil Resources and Land Classification Unit for his long-term support of my use of FAO soil data, and Josh Fisher, of the NASA JPL Water and Carbon Cycles Group, for his generous support in my use of his PET model output. I also thank Peter Henrys and Brian Cade for advice regarding quantile regression, and absolve them of any responsibility for errors I may have committed. I am grateful to my colleagues at the University of Western Australia, Martin Fey, Ian Abbott, Lyn Abbott, Etienne Laliberté, and Hans Lambers, for many stimulating discussions during the development of this paper, as well as to Dan Richter and an anonymous reviewer for helpful criticisms. My work was supported by NSF OPUS Grant 0918927 and a Developmental Leave Grant from Texas State University.

LITERATURE CITED

- Albrecht, W. A. 1940a. Land classification in relation to the soil and its development. Pages 44–53 in *Proceedings of the First National Conference on Land Classification*. Agricultural Experiment Station, College of Agriculture, University of Missouri, Columbia, Missouri, USA.
- Albrecht, W. A. 1940b. Animals recognize good soil treatment. *In* *Better Crops with Plant Food* [magazine]. Reprinted as EE-9, American Potash Institute, Washington, D.C., USA.
- Albrecht, W. A. 1942. Sound horses are bred on fertile soils. *Percheron News*, July 1942. 15:20–21, 41.
- Albrecht, W. A. 1944. Soil fertility and national nutrition. *Journal of the American Society of Farm Managers and Rural Appraisers*, April 1944.
- Albrecht, W. A. 1947a. Our teeth and our soils. *Annals of Dentistry* 6:199–213.
- Albrecht, W. A. 1947b. Soil fertility as a pattern of possible deficiencies. *Journal of the American Academy of Applied Nutrition* 1:7–27.
- Albrecht, W. A. 1955. Why your cattle break through the fence. *Western Livestock Journal* 33:35–38.
- Albrecht, W. A. 1957. Soil fertility and biotic geography. *Geographical Review* 47:86–105.
- Albrecht, W. A. 1958. Soil fertility and animal health (originally serialized in the *Aberdeen Angus Journal*, 1956–1957). Fred Haines Printing Company, Webster City, Iowa, USA. Reprinted in 1975, 2005 as Volume 2 of *The Albrecht Papers* by Acres USA, Austin, Texas, USA.
- Albrecht, W. A., and H. Jenny. 1931. Available soil calcium in relation to “damping off of soy bean seedlings”. *Botanical Gazette* 92:0263–0278.
- Albrecht, W. A., and G. E. Smith. 1941. Biological assays of soil fertility. *Proceedings of the Soil Science Society of America* 6:252–258.
- Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83:35–47.
- Barnes, P. W., L. L. Tiezen, and D. J. Ode. 1983. Distribution, production, and diversity of C₃- and C₄-dominated communities in a mixed prairie. *Canadian Journal of Botany* 61:741–751.
- Brady, N. C., and R. R. Weil. 2002. *The nature and properties of soils*. Thirteenth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Towards a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Cade, B. S., and Q. F. Guo. 2000. Estimating effects of constraints on plant performance with regression quantiles. *Oikos* 91:245–254.
- Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment* 1:412–420.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311–323.
- Cannell, M. R. G. 1982. *World forest biomass and primary production data*. Academic Press, London, UK.
- Chadwick, O. A., and J. Chorover. 2001. The chemistry of pedogenic thresholds. *Geoderma* 100:321–353.
- Chadwick, O. A., L. A. Derry, P. M. Vitousek, B. J. Huebert, and L. O. Hedin. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* 397:491–497.
- Chadwick, O. A., R. T. Gavenda, E. F. Kelly, K. Ziegler, C. G. Olson, W. C. Elliott, and D. M. Hendricks. 2003. The impact of climate on the biogeochemical functioning of volcanic soils. *Chemical Geology* 202:195–223.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, and J. Ni. 2001a. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11:356–370.
- Clark, D. A., S. Brown, D. W. Kicklighter, J. Q. Chambers, J. R. Thomlinson, J. Ni, and E. A. Holland. 2001b. Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications* 11:371–384.
- Clements, F. E. 1916. *Plant succession*. Publication 242. Carnegie Institute of Washington, Washington, D.C., USA.
- Cline, M. G. 1961. The changing model of soil. *Soil Science Society of America Proceedings* 25:442–446.
- Cramer, W., D. W. Kicklighter, A. Bondeau, B. Moore III, G. Churkina, B. Nemry, A. Ruimy, A. L. Schloss, and the participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology* 5:1–15.
- Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. *American Naturalist* 137:27–49.
- Currie, D. J., and J. T. Fritz. 1993. Global patterns of animal abundance and species energy use. *Oikos* 67:56–68.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. F. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121–1134.
- Currie, D. J., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329:326–327.
- Dickson, B. A., and R. L. Crocker. 1953/1954. A chronosequence of soils and vegetation near Mt. Shasta, California, I, II, and III. *Soil Science* 4:123–142, 143–143; 5:173–191.
- Dokuchaev, V. V. 1883. Russian chernozem. *In* *Selected works of V.V. Dokuchaev*, Moscow. 1948. Volume 1, pages 14–419. Israel Program for Scientific Translations, Jerusalem, Israel.
- Donkin, M. J., and M. V. Fey. 1993. Relationships between soil properties and climatic indexes in Southern Natal. *Geoderma* 59:197–212.
- Edwards, D. P., B. Fisher, X. Giam, and D. S. Wilcove. 2011. Underestimating the costs of conservation in Southeast Asia. *Frontiers in Ecology and the Environment* 9:544–545.
- Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwa-

- ter, marine, and terrestrial ecosystems. *Ecology Letters* 10:1135–1142.
- FAO [Food and Agriculture Organisation of the United Nations]. 1999. FAOSTAT. Online statistical service. FAO, Rome, Italy.
- FAO [Food and Agriculture Organisation of the United Nations]. 2008. Harmonized world soil database, version 1.0. FAO Land and Water Digital Media Series 34. FAO/IIASA/ISRIC/JRC-EU/Academia Sinica, Rome, Italy. www.fao.org/nr/land/soils/harmonized-world-soil-database/en
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240.
- Field, R., E. M. O'Brien, and R. J. Whittaker. 2005. Global models for predicting woody plant richness from climate: development and evaluation. *Ecology* 86:2263–2277.
- Fisher, B., D. P. Edwards, X. Giam, and D. S. Wilcove. 2011a. The high costs of conserving Southeast Asia's lowland rainforests. *Frontiers in Ecology and the Environment* 9:329–334.
- Fisher, J. B., R. J. Whittaker, and Y. Malhi. 2011b. ET come home: potential evapotranspiration in geographical ecology. *Global Ecology and Biogeography* 20:1–18.
- Francis, A. P., and D. J. Currie. 2003. A globally consistent richness–climate relationship for angiosperms. *American Naturalist* 161:523–536.
- Fukami, T., and D. A. Wardle. 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society B* 272:2105–2115.
- Garten, C. T., M. A. Huston, and C. A. Thoms. 1994. Topographic variation of soil nitrogen dynamics at Walker Branch Watershed, Tennessee. *Forest Science* 40:497–512.
- Gessler, P. E., O. A. Chadwick, F. Chamran, L. Althouse, and K. Holmes. 2000. Modeling soil–landscape and ecosystem properties using terrain attributes. *Soil Science Society of America Journal* 64:2046–2056.
- Gillman, L. N., and S. D. Wright. 2010. Mega mistakes in meta-analysis: devil in the detail. *Ecology* 91:2550–2552.
- Greenland, D. J., and M. H. B. Hayes, editors. 1981. The chemistry of soil processes. John Wiley, Chichester, UK.
- Grigg, D. 1985. The world food problem, 1950–1980. Oxford University Press, Oxford, UK.
- Grime, J. P. 1973a. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Grime, J. P. 1973b. Control of species density in herbaceous vegetation. *Journal of Environmental Management* 1:151–167.
- Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, New York, New York, USA.
- Gundale, M. J., A. Fajardo, R. W. Lucas, M. C. Nilsson, and D. A. Wardle. 2011. Resource heterogeneity does not explain the diversity–productivity relationship across a boreal island fertility gradient. *Ecography* 34:887–896.
- Hall, J. B., and M. D. Swaine. 1976. Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology* 64:913–951.
- Hall, J. B., and M. D. Swaine. 1981. Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation in Ghana. W. Junk, The Hague, The Netherlands.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J. F. Guegan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, and J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. Tosi. 1971. Forest environments in tropical life zones: a pilot study. Pergamon, New York, New York, USA.
- Holmes, K. W., P. C. Kyriakidis, O. A. Chadwick, J. V. Soares, and D. A. Roberts. 2005. Multi-scale variability in tropical soil nutrients following land-cover change. *Biogeochemistry* 74:173–203.
- Howarth, R. W. 1988. Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecology and Systematics* 19:89–110.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81–101.
- Huston, M. A. 1980. Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* 7:147–157.
- Huston, M. A. 1993. Biological diversity, soils, and economics. *Science* 262:1676–1680.
- Huston, M. A. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge, UK.
- Huston, M. A. 2005. The three phases of land-use change: Implications for biodiversity. *Ecological Applications* 15:1864–1878.
- Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist* 144:954–977.
- Huston, M. A., and G. Marland. 2003. Carbon management and biodiversity. *Journal of Environmental Management* 67:77–86.
- Huston, M. A., and S. Wolverton. 2009. The global distribution of net primary production: resolving the paradox. *Ecological Monographs* 79:343–377.
- Huston, M. A., and S. Wolverton. 2011. Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. *Ecological Monographs* 81:349–405.
- Hyams, E. S. 1952. Soil and civilization. Thames and Hudson, London, UK.
- Jenny, H. 1941. Factors of soil formation. McGraw-Hill, New York, New York, USA.
- Jenny, H. 1980. The soil resource: origin and behavior. Springer-Verlag, New York, New York, USA.
- Jenny, H., R. J. Arkley, and A. M. Schultz. 1969. The pygmy forest ecosystem and its dune associates of the Mendocino coast. *Madroño* 20:60–74.
- Jenny, H., and C. D. Leonard. 1934. Functional relationships between soil properties and rainfall. *Soil Science* 38:363–381.
- Koenker, R., and G. Bassett. 1978. Regression quantiles. *Econometrica* 46:33–50.
- Koenker, R., and K. Hallock. 2000. Quantile regression: an introduction. www.econ.uiuc.edu/~roger/research/intro/rq3.pdf
- Kopittke, P. M., and N. W. Menzies. 2007. A review of the use of the basic cation saturation ratio and the “ideal” soil. *Soil Science Society of America Journal* 71:259–265.
- Kreft, H., and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA* 104:5925–5930.
- Laliberté, E., B. L. Turner, T. Costes, S. J. Pearse, K.-H. Wyrwoll, G. Zemunik, and H. Lambers. 2012. Experimental assessment of nutrient limitation along a 2-million-year dune chronosequence in the south-western Australia biodiversity hotspot. *Journal of Ecology* 100:631–642.
- Laughlin, D. C., S. R. Abella, W. W. Covington, and J. B. Grace. 2007. Species richness and soil properties in *Pinus ponderosa* forests: a structural equation modeling analysis. *Journal of Vegetation Science* 18:231–242.
- Liebig, J. 1840. Organic chemistry in its application to agriculture and physiology. Taylor and Walton, London, UK.
- Lieth, H. 1972. Modeling the primary productivity of the world. *Nature and Resources* 8:5–10.
- Lieth, H. 1975. Modeling the primary productivity of the world. Pages 237–263 in H. Lieth and R. H. Whittaker, editors.

- Primary productivity of the biosphere. Springer-Verlag, Berlin, Germany.
- Major, J. 1951. A functional, factorial approach to plant ecology. *Ecology* 32:392–412.
- Marbut, C. F. 1935. Soils of the United States. United States Department of Agriculture, Washington, D.C., USA.
- Mather, J. R. 1978. The climatic water balance in environmental analysis. D.C. Heath and Company, Lexington, Massachusetts, USA.
- Meggers, B. J. 1971. Amazonia: man and culture in a counterfeit paradise. Aldine-Atherton, Chicago, Illinois, USA.
- Monteith, J. L. 1965. Evaporation and environment. Pages 205–233 in *Symposium of the Society for Experimental Biology*. Cambridge University Press, Cambridge, UK.
- Nikiforoff, C. C. 1949. Weathering and soil evolution. *Soil Science* 67:219–230.
- Nye, P. H., and D. J. Greenland. 1960. The soil under shifting cultivation. Technical Communication number 51. Commonwealth Bureau of Soils, Harpenden, UK.
- O'Brien, E. M. 1993. Climatic gradients in woody plant species richness: towards an explanation based on an analysis of Southern Africa's woody flora. *Journal of Biogeography* 20:181–198.
- O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography* 25:379–398.
- O'Brien, E. M., R. J. Whittaker, and R. Field. 1998. Climate and woody plant diversity in Southern Africa: relationships at species, genus and family levels. *Ecography* 21:495–501.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette* 119:125–170.
- Olson, R. J., K. R. Johnson, D. L. Zheng, and J. M. O. Scurlock. 2001a. Global and regional ecosystem modeling: databases of model drivers and validation measurements. ORNL/TM-2001/196. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.
- Olson, R. J., J. M. O. Scurlock, S. D. Prince, D. L. Zhang, and K. R. Johnson. 2001b. NPP multi-biome: global primary production data initiative products. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Paton, T. R., G. S. Humphreys, and P. B. Mitchell. 1995. Soils: a new global view. Yale University Press, New Haven, Connecticut, USA.
- Peltzer, D. A., et al. 2010. Understanding ecosystem retrogression. *Ecological Monographs* 80:509–529.
- Penman, H. L. 1948. Natural evaporation from open water, bare soil, and grass. *Proceedings of the Royal Society of London A* 193:120–146.
- Porder, S., and O. A. Chadwick. 2009. Climate and soil-age constraints on nutrient uplift and retention by plants. *Ecology* 90:623–636.
- Potter, C. S. 1999. Terrestrial biomass and the effects of deforestation on the global carbon cycle. *BioScience* 49:769–778.
- Potter, C. S., J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney, and S. A. Klooster. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. *Global Biogeochemical Cycles* 7:811–841.
- Priestley, C. H. B., and R. J. Taylor. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review* 100:81–92.
- Quideau, S. A., R. C. Graham, X. Feng, and O. A. Chadwick. 2003. Natural isotopic distribution in soil surface horizons differentiated by vegetation. *Soil Science Society of America Journal* 67:1544–1550.
- Rasmussen, P. E., K. W. T. Goulding, J. R. Brown, P. R. Grace, H. H. Janzen, and M. Korschens. 1998. Long-term agroecosystem experiments: assessing agricultural sustainability and global change. *Science* 282:893–896.
- Rice, C. W., P. M. Bertsch, J. Bouma, J. W. Harden, J. L. Hatfield, J. D. Jastrow, W. A. Jury, and J. Ruiz. 2009. *Frontiers in soil science research*. National Academies Press, Washington, D.C., USA.
- Richter, D., Jr., and D. Markewitz, editor. 2001. *Understanding soil change*. Cambridge University Press, Cambridge, UK.
- Richter, D. D., et al. 2011. Human-soil relations are changing rapidly: proposals from SSSA's cross-divisional Soil Change Working Group. *Soil Science Society of America Journal* 75:2079–2084.
- Richter, D. D., Jr., and L. I. Babbar. 1991. Soil diversity in the tropics. *Advances in Ecological Research* 21:316–389.
- Richter, D. D., Jr., M. Hofmockel, M. A. Callahan, D. S. Powlson, and P. Smith. 2007. Long-term soil experiments: Keys to managing Earth's rapidly changing ecosystems. *Soil Science Society of America Journal* 71:266–279.
- Richter, D. deB., 2007. Humanity's transformation of Earth's soil: pedology's new frontier. *Soil Science* 172:957–967.
- Roy, J., B. Saugier, and H. A. Mooney, editors. 2001. *Terrestrial global productivity: past, present, and future*. Academic Press, San Diego, California, USA.
- Ruhe, R. V., and W. H. Scholtes. 1956. Age and development of soil landscapes in relation to climate and vegetational changes in Iowa. *Soil Science Society of America Proceedings* 20:264–273.
- Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto. 2004. A continuous satellite-derived measure of global primary production. *BioScience* 54:547–560.
- Ruslandi, O. Venter, and F. E. Putz. 2011. Overestimating conservation costs in Southeast Asia. *Frontiers in Ecology and the Environment* 9:542–544.
- Sanchez, P. A. 1976. *Properties and management of soils in the tropics*. John Wiley and Sons, New York, New York, USA.
- Saugier, B., J. Roy, and H. A. Mooney. 2001. Estimations of global terrestrial productivity: Converging toward a single number? Pages 543–557 in J. Roy, B. Saugier, and H. A. Mooney, editors. *Terrestrial global productivity*. Academic Press, San Diego, California, USA.
- Schuur, E. A. G. 2003. Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology* 84:1165–1170.
- Scott, R. M. 1963. Exchangeable bases of mature, well-drained granitic soils in relation to rainfall in East Africa. *Journal of Soil Science* 13:1–9.
- Scurlock, J. M. O., W. Cramer, R. J. Olson, W. J. Parton, and S. D. Prince. 1999. Terrestrial NPP: toward a consistent data set for global model evaluation. *Ecological Applications* 9:913–919.
- Scurlock, J. M. O., K. Johnson, and R. J. Olson. 2002. Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology* 8:736–753.
- Scurlock, J. M. O., and R. J. Olson. 2002. Terrestrial net primary productivity: a brief history and new worldwide database. *Environmental Reviews (NRC-CNRC)* 10:91–110.
- Spengel, C. P. 1839. *Die Lehre vom Dünger oder Beschreibung aller bei der Landwirtschaft gebräuchlicher vegetabilischer, animalischer und mineralischer Düngermaterialien, nebst Erklärung ihrer Wirkungsart*. Muller, Leipzig, Germany.
- Stevens, P. R., and T. W. Walker. 1970. The chronosequence concept and soil formation. *Quarterly Review of Biology* 45:333–350.
- Stewart, B. W., R. C. Capo, and O. A. Chadwick. 2001. Effects of rainfall on weathering rate, base cation provenance, and Sr isotope composition of Hawaiian soils. *Geochimica et Cosmochimica Acta* 65:1087–1099.

- Swaine, M. D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* 84:419–428.
- Tandarich, J. P., R. G. Darmoody, L. R. Follmer, and D. L. Johnson. 2002. Historical development of soil and weathering profile concepts from Europe to the United States of America. *Soil Science Society of America Journal* 66:335–346.
- Tansley, A. G. 1920. The classification of vegetation and the concept of development. *Journal of Ecology* 8:118–144.
- Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:284–307.
- Targulian, V. O., and S. V. Goryachkin. 2004. Soil memory: types of records, carriers, hierarchy, and diversity. *Revista Mexicana de Ciencias Geológicas* 21:1–8.
- Targulian, V. O., and S. V. Goryachkin, editors. 2008. Soil memory: soil as a memory of biosphere–geosphere–anthroposphere interactions. Institute of Geography, Russian Academy of Sciences, Moscow, Russia.
- Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. *Geographical Review* 38:55–94.
- Thornthwaite, C. W., and J. R. Mather. 1955. The water balance. *Publications in Climatology* 8:1–104.
- Tomanek, G. W., and F. W. Albertson. 1957. Variations in cover, composition, production, and roots of vegetation on two prairies in western Kansas. *Ecological Monographs* 27:267–281.
- Vitousek, P. M. 2004. Nutrient cycling and limitation: Hawaii as a model system. Princeton University Press, Princeton, New Jersey, USA.
- Vitousek, P., O. Chadwick, P. Matson, S. Allison, L. Derry, L. Kettley, A. Luers, E. Mecking, V. Monastera, and S. Porder. 2003. Erosion and the rejuvenation of weathering-derived nutrient supply in an old tropical landscape. *Ecosystems* 6:762–772.
- Vitousek, P. M., T. N. Ladefoged, P. V. Kirch, A. S. Hartshorn, M. W. Graves, S. C. Hotchkiss, S. Tuljapurkar, and O. A. Chadwick. 2004. Soils, agriculture, and society in precontact Hawaii. *Science* 304:1665–1669.
- Walker, J., C. H. Thompson, I. F. Fergus, and B. R. Tunstall. 1981. Plant succession and soil development in coastal sand dunes of subtropical eastern Australia. Pages 107–131 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concepts and applications*. Springer-Verlag, New York, New York, USA.
- Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology* 98:725–736.
- Walker, T. W., and J. K. Syers. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19.
- Wardle, D. A., R. D. Bardgett, L. R. Walker, D. A. Peltzer, and A. Lagerstrom. 2008. The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences. *Oikos* 117:93–103.
- Wardle, D. A., M. Jonsson, S. Bansal, R. D. Bardgett, M. J. Gundale, and D. B. Metcalfe. 2012. Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. *Journal of Ecology* 100:16–30.
- Wardle, D. A., L. R. Walker, and R. D. Bardgett. 2004. Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* 305:509–513.
- Weaver, J. E., and T. J. Fitzpatrick. 1934. The prairie. *Ecological Monographs* 4:109–295.
- Weischet, W., and C. N. Caviedes. 1994. The persisting ecological constraints of tropical agriculture. John Wiley and Sons, New York, New York, USA.
- Wells, C. G., L. D. McFadden, J. C. Dohrenwend, and B. D. Turrin. 1987. Influences of late Quaternary climatic changes on geomorphic and pedogenic processes on a desert piedmont, eastern Mojave Desert, California. *Quaternary Research* 27:130–146.

SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.8vq1j>