

A test of the maximum power hypothesis along an elevational gradient in the Luquillo Mountains of Puerto Rico

Nancy L. Harris, Charles A. S. Hall and Ariel E. Lugo

The maximum power principle predicts that maximum transformation of available energy into useful work occurs when a system operates at an intermediate rate and efficiency. This relation is apparent in everyday situations as we shift gears to keep near the middle of each gear range when we accelerate an automobile, or operate chain saws and other machines at a load about half their stalling rate. We tested the validity of the maximum power principle in a complex natural system by quantifying patterns of photosynthesis and respiration – an ecosystem's energy currency – along an elevation gradient in a subtropical forest of Puerto Rico. This mountain system was a useful proxy for testing the hypothesis over broader climatic gradients elsewhere. Our results indicate that metabolic rates (defined as gross primary productivity) decrease up the gradient, efficiency (defined as the ratio of net to gross primary productivity) increases up this gradient, and power (defined as net primary productivity, or the amount of useful energy produced within a given ecosystem per unit time) is maximum near the midpoint of the gradient where rate and efficiency are intermediate. These observations are non-trivially consistent with the maximum power principle and support a scalable, energy-based definition of evolutionary fitness. Given a set of environmental forcing functions in a given location, those individuals (or populations or ecosystems) that optimize the trade-off between metabolic rate and efficiency to achieve maximum power will be most fit. As environmental conditions change over the long term, this rate vs efficiency optimum will shift and those that are able to achieve maximum power in the new environment will be favored over those that are maximizing power for the old environment. We think that this net energy-as-fitness view allows for a richer series of possibilities for testing the consequences of natural selection.

N. L. Harris (nharris@winrock.org) and C. A. S. Hall, Dept of Environmental and Forest Biology, State Univ. of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, USA. Present address of NLH: Ecosystem Services Unit, Winrock International, 2121 Crystal Drive, Suite 500, Arlington, VA 22202, USA. – A. E. Lugo, International Inst. of Tropical Forestry/USDA Forest Service, 1201 Ceiba Street, Jardín Botánico Sur, Río Piedras, PR 00926, USA.

According to the first law of thermodynamics, energy entering a system can be used to do work (including storage) or lost as heat. Basic Darwinian principles suggest that individuals (or species, or perhaps other units of selection) have been selected over time to capture in some optimal way the energy that is available to them and use it to propel their genes into the future, although exactly what this optimality is or how it might work is not always clear or agreed upon. Howard T. Odum, perhaps the world's preeminent systems ecologist at the time of his death in 2002, hypothesized that because there is usually an inherent trade-off between the rate and the efficiency of a given work process, there should be natural selection for intermediate rates of work. Efficiency is maximized at low rates when heat

loss is minimized, while rapid processes use energy quickly but inefficiently. Maximum useful work per unit time, or power output, is therefore achieved at intermediate rates and efficiencies (Odum and Pinkerton 1955, Hall et al. 1992, Hall 1995, 2004) (Fig. 1).

The inverse relation between rate and efficiency can be shown clearly with simple physical machines such as Atwood's machine (two baskets with a connecting rope over a pulley). Different weights can be added to the first, upper basket to deliver products in the second basket to a higher physical location. Excessive loading of the first basket causes the rapid delivery of products in the second basket to a higher location, but most of the energy used to run the system is converted into useless heat as the first basket hits

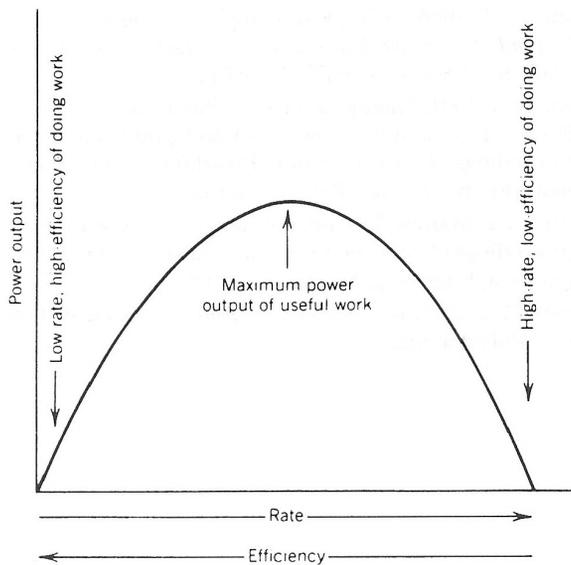


Figure 1. The trade-off between rate and efficiency in the production of power [reproduced from Hall (1995), based largely on Odum and Pinkerton (1955).]

the ground. Likewise, loading the first basket with barely more weight than the second generates a very efficient but slow work system. Maximum power, or maximum execution of useful work (i.e. lifting products to the higher level vs just producing heat), occurs when the second basket that is being lifted contains about half the weight of the first basket that is being loaded. This relation is also apparent in practical, everyday situations as we shift to keep near the middle of each gear range when we accelerate an automobile or bicycle, or operate chain saws and other machines at a load about half their stalling rate.

According to the maximum power hypothesis, evolution should also optimize the rate vs efficiency tradeoff because there would not be selection for too rapid and hence inefficient rates or for slow rates when competitors are present. This rate-efficiency tradeoff has been demonstrated for many simplified systems such as semi-natural experimental streams (Warren 1971) and fossil fuel-powered electricity-generating plants (Gilliland 1982), but its applicability to a complex natural system has not been quantified explicitly.

For a natural ecosystem, we define power – the rate of useful work – as net primary productivity (NPP). The photosynthetic transformation of carbon dioxide (CO_2) to biomass carbon over time provides the ultimate source of useful energy available to both plants themselves and to higher trophic levels. NPP represents the difference between the total rate of carbon fixed by plants through photosynthesis (gross primary productivity, or GPP) and the rate of carbon respired by plants for their own metabolic function (autotrophic respiration, or R_A). This respiration is both a necessary maintenance cost for life and an

unavoidable response to temperature, long understood in biology and chemistry as the van't Hoff, Arrhenius or Q_{10} relation. In natural ecosystems, as in physics, we define efficiency as the ratio of useful output to total inputs, or in this case, useful carbon output (NPP) to total carbon inputs (GPP), where easily measured CO_2 exchanges are a stoichiometric for measuring energy capture and use. In most ecosystems not limited by water or nutrients, the main climatic drivers that control GPP and NPP are solar energy (which drives photosynthesis) and temperature (which drives respiration).

Elevation gradients provide useful proxies for studying climatic variation over larger geographic regions, as orographic uplift of air causes the formation of moisture, temperature and solar radiation gradients over relatively short distances. As a result, lowland areas of the wet tropics are relatively warm, moist and sunny while mountaintops are cool, wet and cloudy. Species composition and forest structure change with elevation in response to these climatic gradients. For example, on tropical mountains, plant species richness and diversity have been shown repeatedly to decrease toward higher elevations (Grubb 1977, Vazquez and Givnish 1998) and reductions in canopy height and increases in tree density are common (Valazquez Rosas et al. 2002). The Luquillo Experimental Forest (LEF), a subtropical forest (*sensu* Holdridge 1967) located in the Luquillo Mountains of northeastern Puerto Rico, is an ideal location in which to study environmental gradients and the associated variability in primary productivity and other ecosystem properties due to its relatively natural state, its elevation rise of >1100 m, its history of long-term data acquisition due in part to the establishment of a Long Term Ecological Research (LTER) site there, its easy access to investigators, its meteorological and other instrumentation and its long-term administration by the U.S. Forest Service. Therefore, this mountain system presents an excellent natural research laboratory in which to test broad hypotheses of ecosystem response to environmental gradients.

We hypothesized that in the lowlands of the Luquillo Mountains (which represent one end of the climatic gradient), plant metabolic rates (GPP) should be high due to abundant sunlight and leaf surface area, but since much of the carbon fixed in photosynthesis is lost as autotrophic respiration due to warm temperatures, ecosystem efficiency (NPP/GPP) should be low. For the mountain peaks (which represent the other end of the climatic gradient), we hypothesized that GPP should be low due to reduced sunlight and leaf surface area, but that ecosystem efficiency should be high due to cooler temperatures and saturated soils that limit autotrophic respiration. Along the elevation/climatic gradient, maximum power (NPP, or $\text{GPP} - R_A$) should occur at mid-elevations where both gross metabolic rates and ecosystem efficiency are intermediate relative to lower and higher elevations. Therefore, our three hypotheses related to maximum power are: 1) rates are maximum

at low elevations; 2) efficiency follows a trend opposite to rate; and 3) maximum power occurs at intermediate rates and efficiencies (Odum and Pinkerton 1955).

Methods

We tested our hypothesis using empirically-based simulations that incorporate a series of ecosystem-level field physiological measurements along with meteorological data and other data on community structure.

Field measurements

We measured rates of CO₂ exchange at major vegetation-atmosphere surfaces (leaves, tree boles, soil surfaces) at various forest sites ranging in elevation from near sea level to over 1000 m. At locations where the canopy was inaccessible, tall trees were rigged to climb using a modified arborists' technique in which a slingshot was used to shoot a line over an upper branch of each tree. After each tree was rigged, a climbing rope and mechanical ascenders were used to access the canopy. Once in the canopy, we measured in situ leaf photosynthetic response to various controlled light levels and leaf dark respiration rates in a total of 130 leaves using a portable infrared gas analyzer (LI-6400). The LI-6400 was supported in the tree canopy using a system of ropes and pulleys. Leaf temperature was controlled at 30°C when generating leaf light response curves so that relationships between respiration rate and nitrogen content could be investigated. Leaf respiratory response to various leaf temperatures was then measured separately to derive a Q₁₀ value. Both early- and late-successional species were measured and were chosen based on importance values summarized in Brown et al. (1983). Species measured included *Dacryodes excelsa*, *Manilkara bidentata*, *Cyrilla racemiflora*, *Micropholis garciniifolia*, *Prestoea montana* and *Cecropia schreberiana*. Leaves were sampled at different heights, but we categorized each as an 'upper canopy' or 'lower canopy' leaf (n≥2 for each leaf type per species per site). We used the measurement system's LED light source to generate a light response curve (including dark respiration rates) for each leaf sampled. The rate of leaf photosynthesis (or dark respiration) was logged after the combined coefficient of variation for all parameters fell <1%. The number of individual leaf light response curves generated at each elevation site ranged from 4 to 24, depending on the number of focus tree species present at each site. Leaves were harvested after measurement and the area of each leaf was calculated using a leaf area meter (LI-3000). Dry mass of leaves (without petioles) was determined after oven drying at 50°C for 2 d. Dried leaves were ground in a mill and nitrogen content was determined for each leaf using an elemental analyzer (LECO CNS 2000) at the International Inst. of Tropical Forestry (IITF) in Río Piedras, PR.

Soil respiration (including the layer of leaf litter above the soil) was measured at 56 individual soil surfaces along the elevation gradient using the soil chamber attachment of the LI-6400 (LI-6400-09). We used the machine's automated program that draws the CO₂ concentration down in the chamber to below ambient levels (measured at the soil surface), allows the concentration to rise to above ambient levels, and logs the CO₂ flux based on the measured CO₂ buildup curve within the chamber over time. Soil respiration measurements were collected twice, once during the relatively rainy season (July) and once during the relatively dry season (January). On the first sampling date, the LI-6400 sampling system was tested against a static flux system (see methods in Silver et al. 2005) at two sites. The two measurement techniques yielded statistically similar soil respiration values at both sites.

We also measured stem respiration (as CO₂ efflux per unit surface area) in eight to ten trees of each focus species (n=64 trees) by mounting the soil chamber of the LI-6400 system horizontally onto stem collars constructed from PVC pipe and secured to tree stems with silicone caulk (Xu et al. 2000). Additional details and results from the stem respiration component of this work are summarized in Harris et al. (2008).

Model description

Once all field measurements were complete, we developed a computer simulation model to scale field measurements up to the landscape level. The model combines data collected in the field on individual trees (and associated soils) with abiotic and biotic drivers derived from spatial extrapolations of ground measurements to produce spatially- and temporally-explicit estimates of gross primary productivity (GPP), autotrophic respiration (R_A) and net primary productivity (NPP). Key features of the model are as follow.

1) The model was based on geographical extrapolation of measured data for all important forcing functions such as solar radiation, temperature, leaf area index, foliar nitrogen concentration, and tree species composition. Site-specific meteorological and ecological data were used as the basis for spatial extrapolations and were drawn largely from both field data and the Luquillo Long-Term Ecological Research (LTER) database (<<http://luq.lternet.edu>>). Relationships between forcing functions and response variables (photosynthesis, respiration) were also measured directly.

2) Solar radiation and air temperature were simulated using a spatial model developed for the study site (Wooster 1989, Everham 1991, Marley 1998) that was calibrated with historical climate data (Briscoe 1966, Odum et al. 1970, García-Martinó et al. 1996) and validated using independent long-term datasets from the Luquillo LTER database. A validated sub-model of cloud cover (Wu et al.

2006) reduced incoming solar radiation based on spatial and temporal considerations.

3) Foliar nitrogen per unit leaf area was calculated for leaves at the top of the canopy as a function of elevation based on a regression analysis of our field measurements and verified with an independent dataset (Medina et al. 1981). The distribution of leaf nitrogen per unit leaf area among leaves in the canopy was modeled to decrease exponentially with cumulative relative leaf area index from the top of the canopy (Hirose and Werger 1987, Anten et al. 1995) using nitrogen values from field measurements for calibration. Field data were then used to relate leaf photosynthetic capacity (A_{\max}) to leaf nitrogen concentration.

4) Leaf area index was simulated based on a linear regression between leaf area index and elevation, derived from data collected at different elevations in the LEF (Brown et al. 1983, Weaver and Murphy 1990). Tree species composition at a particular location was simulated based on data from the Luquillo LTER database (Barone et al. 2008, summarized in Harris et al. 2008). The species distribution of leaves through the vertical canopy profile at a given location was modeled based on pre-defined rules such that, for example, *C. schreberiana* (a pioneer species) inhabited only upper canopy levels that receive abundant sunlight while *P. montana* inhabited the understory at low elevations but all canopy levels at mid- and high elevations.

5) Because the light response of photosynthesis is nonlinear, we modeled solar radiation absorbed by shaded and sunlit leaves separately to avoid the overestimation of canopy assimilation obtained when mean irradiance is used. We assumed a spherical leaf angle distribution (i.e. leaves are distributed over all angles) and approximated direct and diffuse radiation absorbed by leaves at different canopy depths using exponential profiles (Goudriaan and van Laar 1994). Shaded leaves received diffuse radiation only, while sunlit leaves received both diffuse and direct beam radiation. Radiation attenuation through the canopy was dependent upon the sun's angle of incidence (incident at a fixed solar elevation at a given time) relative to the distribution of foliage angles (distributed over all angles).

6) In each canopy layer, net photosynthesis and respiration were calculated based on simulated irradiance, area-based leaf nitrogen concentration, light-saturated photosynthetic rate and light compensation point. Field measurements of leaf dark respiration were corrected for temperature in the model using empirically-derived Q_{10} temperature response functions. Numerical integration of leaf metabolic rates from each layer yielded total canopy photosynthesis and respiration.

7) Field measurements of woody stem respiration for different tree species were combined with data on stand structure at different elevations (diameter at breast height, canopy height, stem density, species composition) to estimate landscape-level rates of stem respiration (Harris et al. 2008). As for leaf respiration, field measurements of stem respiration were corrected for temperature in the model

using an empirically-derived Q_{10} temperature response function.

8) In the model, soil respiration rates at a given location were related only to elevation and not to soil temperature, as soil temperatures did not change appreciably within a single chamber to warrant a reliable estimation of the Q_{10} value and, unlike the leaf chamber, the soil chamber of the LI-6400 does not allow for temperature control. Root respiration, the portion of total soil respiration associated with plant productivity, was assumed to be 29% of measured soil respiration, based on results from Silver et al. (2005).

Model assumptions include no water limitation (annual precipitation across the elevation gradient ranges from approximately 2000 to over 4000 mm yr⁻¹) and a forest that is composed only of the tree species measured (or others that were the physiological equivalent). Model output is in the form of season- and elevation-dependent graphs and digital maps (30-m resolution) produced in a geographic information system (GIS). Canopy assimilation as well as leaf, branch and soil respiration rates were calculated hourly and summed to estimate daily and annual fluxes.

To avoid ambiguity about the computation of our results, we define here the terminology of gross and net primary productivity calculations (Brinson et al. 1981). Gross primary productivity (GPP) is defined as the sum of daytime net photosynthesis and night respiration of plants, corrected for the number of daytime hours and leaf area index. Net daytime productivity (P_N) is the net daytime rate of organic matter productivity, measured by the CO₂ uptake of plants during daytime hours and corrected for leaf area index. Nighttime respiration is the nighttime consumption of organic matter, measured by the production of CO₂ by plants during nighttime hours and corrected for leaf area index and surface area index of woody tissues. Net 24-h primary productivity (NPP) is defined as the difference between gross primary productivity (GPP) and 24-h plant respiration (R_{T24}). R_{T24} is equal to $R_L + R_W + R_R$, where R_L is leaf, R_W is wood and stem, and R_R is root respiration.

Results

The rate of GPP decreased, and efficiency increased, from the bottom to the top of the elevation gradient, with maximum NPP occurring at intermediate elevations. Thus each of the maximum power hypotheses were supported by our analysis.

Field data

Light response curves generated from field data of leaf CO₂ exchange for each species using a nonlinear mixed model (Peek et al. 2002) are shown in Fig. 2. Rates of

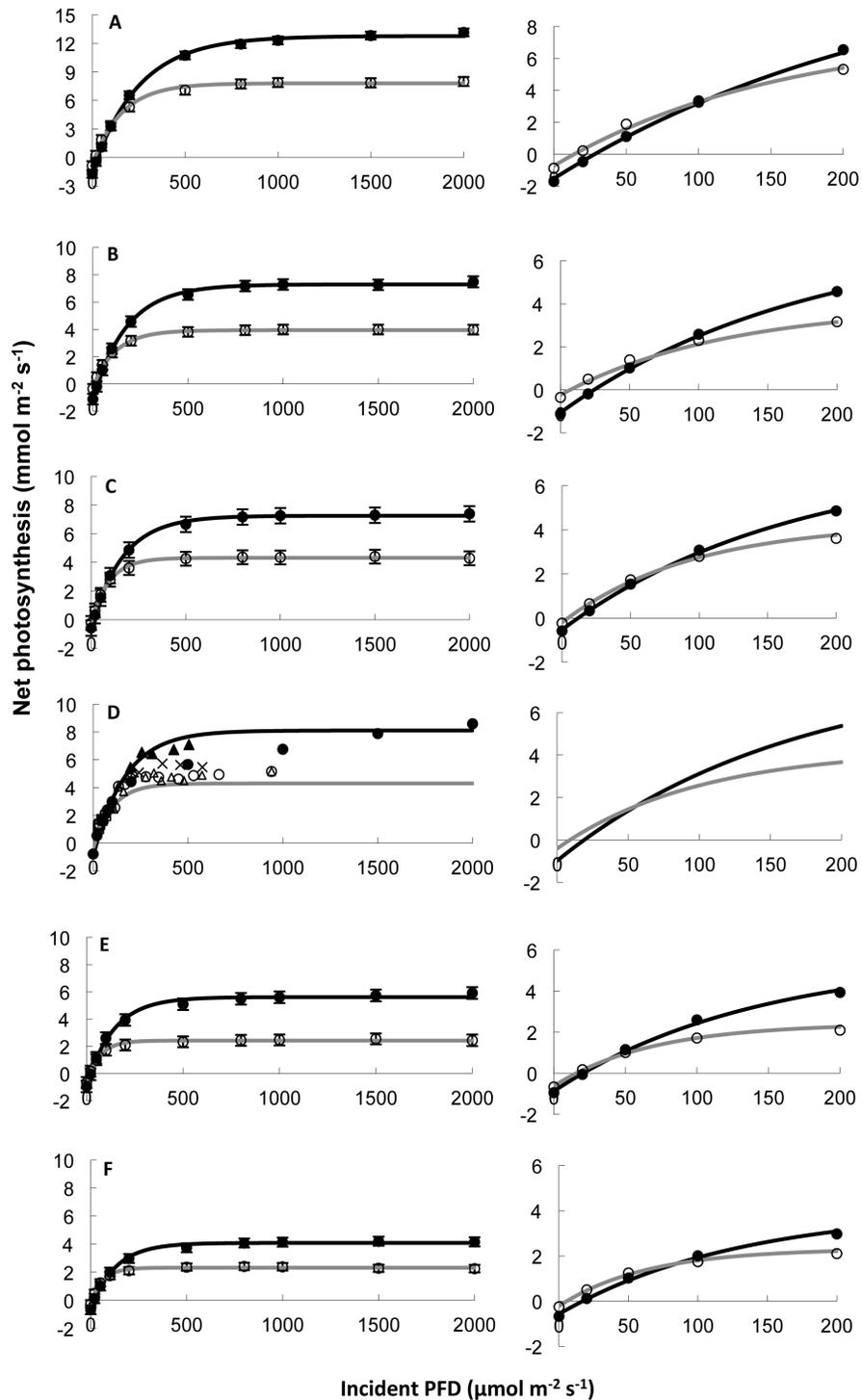


Figure 2. Mean (± 1 SE) net photosynthetic CO₂ assimilation against incident photosynthetic photon flux for upper (closed circles) and lower (open circles) canopy leaves of six tree species in the Luquillo Experimental Forest, Puerto Rico. Also shown are fitted curves from parameter estimates obtained from a nonlinear mixed model (Peek et al. 2002). Figures in the right-hand panel are expanded to show photosynthetic differences at low light levels. (A) *Cecropia schreberiana*; (B) *Dacryodes excelsa*; (C) *Manilkara bidentata*; (D) *Cyrilla racemiflora*; (E) *Micropholis garciniiifolia*; (F) *Prestoea montana*. Closed circles in (D) represent a light response curve generated using controlled irradiance for an upper canopy leaf, while other points represent photosynthesis measured in seven different leaves of different trees at ambient light levels.

light-saturated photosynthesis (A_{\max}) were significantly higher ($p < 0.0001$) in upper canopy leaves relative to lower canopy leaves, and photosynthesis saturated at higher light levels. Among different species, A_{\max} values were highest for the early successional species *C. schreberiana* and lowest for palm species *P. montana*, while rates for the four late-successional species occupying different elevational ranges (*M. bidentata*, *D. excelsa*, *C. racemiflora* and *M. garciniiifolia*) were relatively similar. Leaf photosynthetic response to ambient vs controlled irradiance was similar (Fig. 2D). Species with high A_{\max} values such as *C. schreberiana* generally had high leaf respiration rates and lower estimated apparent quantum efficiencies than species with low A_{\max} values. Conversely, the species with the lowest A_{\max} value (*P. montana*) had low respiration rates and used light more efficiently at low irradiances as reflected in a high apparent quantum efficiency. Thus at a physiological level, we found a tradeoff between rate and efficiency. Leaf mass per unit area increased with elevation (Fig. 3B), which resulted in nitrogen content per unit leaf area increasing with elevation (Fig. 3C) and nitrogen content per unit leaf mass decreasing with elevation (Fig. 3A). A_{\max} and dark respiration rates (measured at constant temperature) were significantly correlated with area-based leaf nitrogen content in virtually all species measured (Fig. 4). The measured Q_{10} value for leaf respiration response to temperature was 1.76. Estimated variation in relative tree species composition with elevation (Fig. 5) was based on data collected by Barone et al. (2008).

Low elevation species *D. excelsa* and *M. bidentata* had higher measured rates of stem respiration per unit bole surface area than species occupying higher elevations (Harris et al. 2008), and the measured Q_{10} value for stem respiration vs temperature was 1.49. Soil respiration rates were also highest at low elevations and decreased significantly along the elevation gradient (Fig. 6). Soil temperatures did not vary appreciably within a single chamber to allow a reliable estimation of Q_{10} .

Empirical model

Ecosystem rates and efficiencies, estimated for the 13 sites where leaf photosynthesis and respiration were measured in the forest, are given in Fig. 7. Rates (total carbon fixed per unit time, or GPP) were highest in the lowlands (Fig. 7A) while ecosystem efficiency (NPP/GPP) was highest at the mountaintops (Fig. 7B). Maximum power (NPP) occurred at mid-elevations where both rate and efficiency were intermediate (Fig. 7C). All three components of the maximum power hypothesis – rate, efficiency, and power – are supported by the measured data.

Although only one point was available at the lowest elevation (15 m) due to extensive urban and suburban development across most of the lowlands (Fig. 7), this point is not necessary to show that there is a tradeoff between

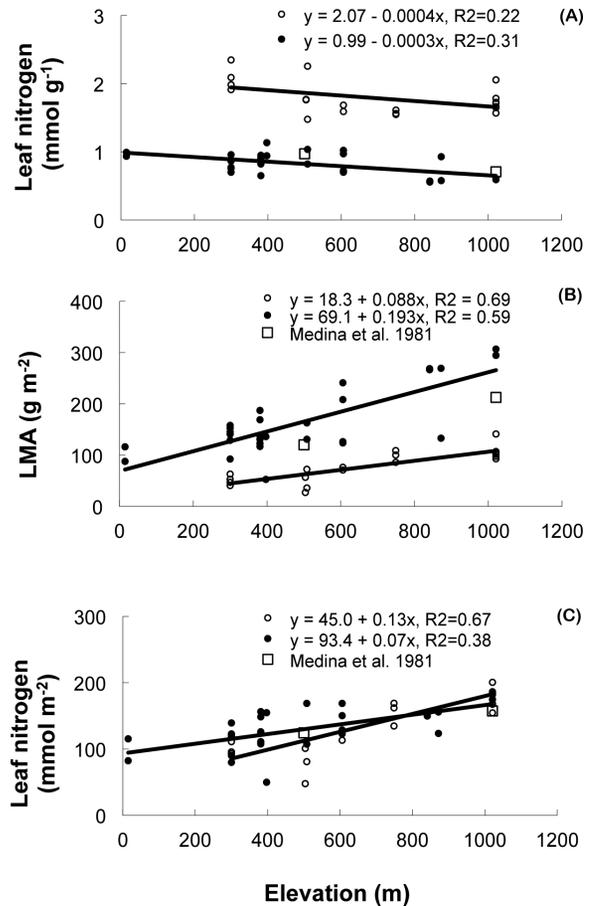


Figure 3. Elevational trends in leaf structural properties of upper canopy leaves of *Cecropia schreberiana* (open circles) and *Dacryodes excelsa*, *Manilkara bidentata* and *Micropholis garciniiifolia* (closed circles) along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. Also shown are data from Medina et al. (1981) collected in the same forest. All regressions are significant at $\alpha = 0.05$. (A) Leaf nitrogen per unit leaf mass; (B) leaf mass per unit leaf area; and (C) leaf nitrogen per unit leaf area.

rate and efficiency, the idea behind maximum power. Furthermore, our spatial model of forest productivity, based on measured data and also as scaled over the forest landscape, shows that both GPP and R_A decline with increasing elevation, while NPP is maximum at intermediate elevations (Fig. 8). GPP ranged from 38 Mg C ha⁻¹ yr⁻¹ at low elevations to 11 Mg C ha⁻¹ yr⁻¹ at high elevations, with a forest-wide mean of 29 Mg C ha⁻¹ yr⁻¹ (Fig. 8A). Total autotrophic respiration (R_A) also decreased along the elevation gradient from 27 Mg C ha⁻¹ yr⁻¹ at the lowest elevations to 4 Mg C ha⁻¹ yr⁻¹ at high elevations (Fig. 8B) and varied slightly over the year in response to changing temperatures, with simulated rates of autotrophic respiration 5% lower on average in the cooler, drier months (December–April) than in the warmer, wetter months (May–

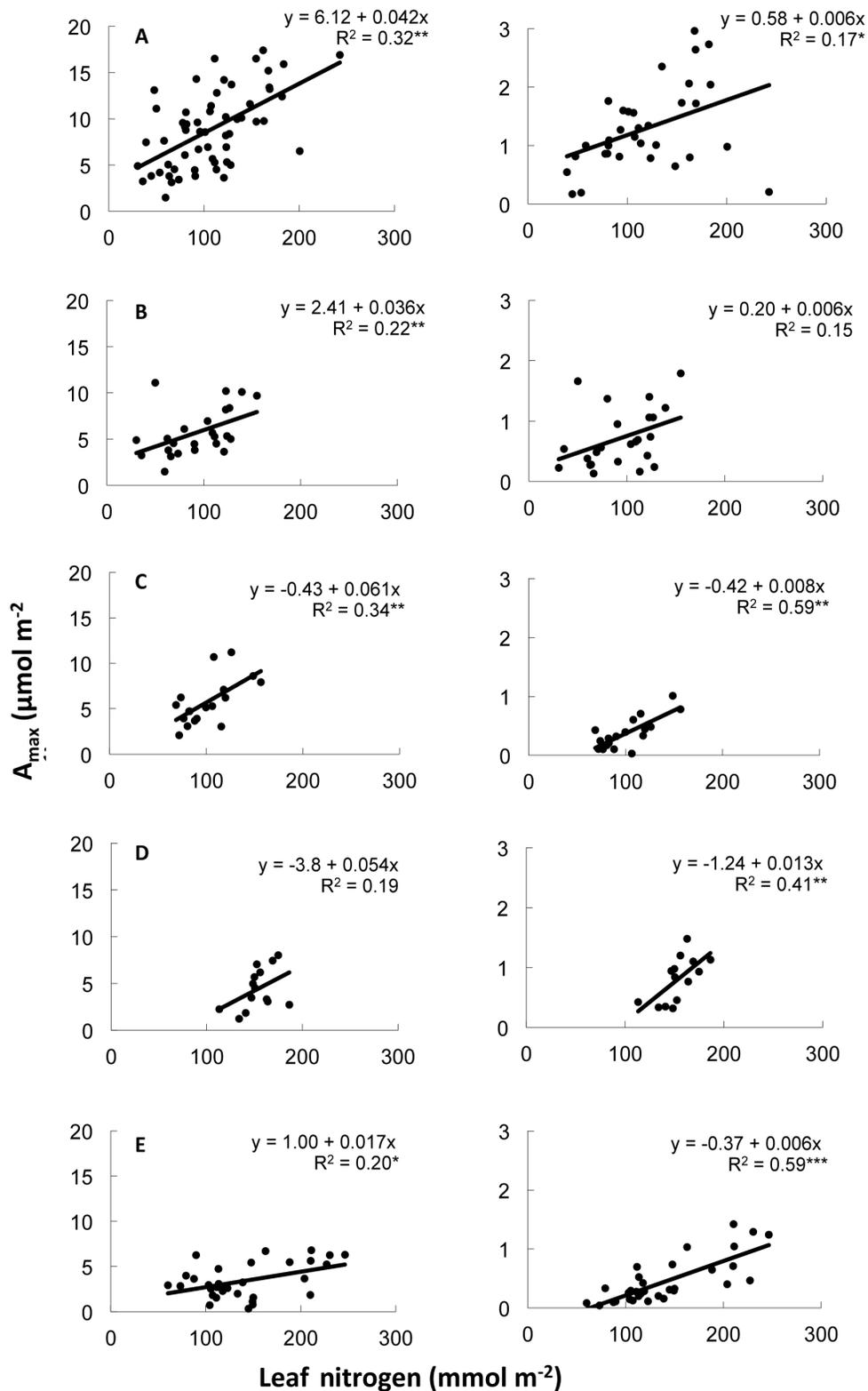


Figure 4. Relations of light-saturated photosynthesis (A_{\max}) and dark respiration (R_d) vs leaf nitrogen content for five tree species in the Luquillo Experimental Forest, Puerto Rico. Significant regressions are indicated by asterisks (* $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$). (A) *Cecropia schreberiana*; (B) *Dacryodes excelsa*; (C) *Manilkara bidentata*; (D) *Micropholis garciniifolia*; (E) *Prestoea montana*.

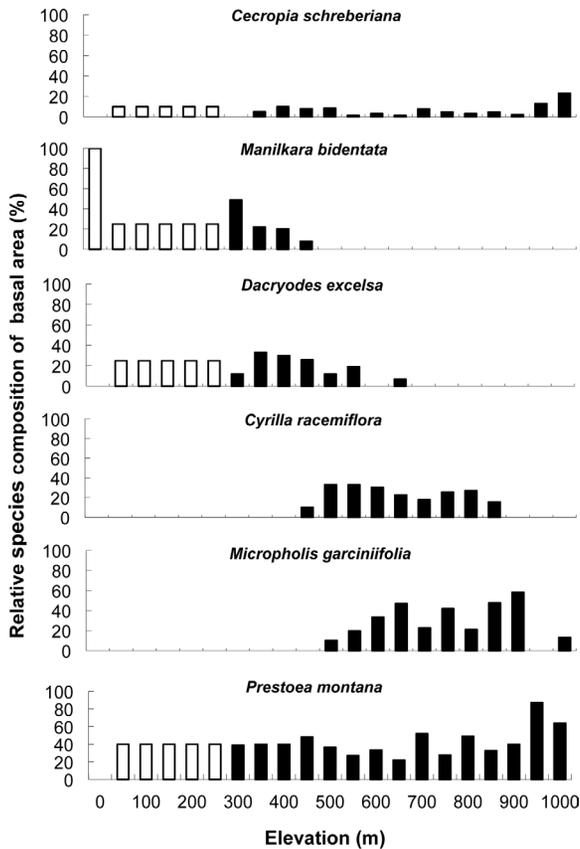


Figure 5. Estimated species distribution patterns along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. Data collected originally by Barone et al. (2008) and archived at <<http://luq.lternet.edu>>. The percentage of each species at a given elevation (y-axis) is represented on the basis of basal area, and percentages are relative among the six species modeled. Species distribution patterns below 300 m were estimated (open bars). Figure identical to Fig. 2 in Harris et al. (2008), except *Tabebuia rigida* was grouped together with *Micropholis garciniifolia* as its physiological equivalent in this analysis.

November). Annual NPP in the LEF ranged from 8 Mg C ha⁻¹ yr⁻¹ at the lowest elevations to a maximum value of 24 Mg C ha⁻¹ yr⁻¹ at the intermediate elevation of 450 m to 6.5 Mg C ha⁻¹ yr⁻¹ at the highest elevations (Fig. 8C). These values are within the ranges of the (very few) other data that are available for this forest (Odum and Jordan 1970, Weaver et al. 1986, Weaver and Murphy 1990). After we incorporated heterotrophic soil respiration into the carbon budget, the Luquillo Forest as a whole sequesters approximately 37 Mt C (134 Mt CO₂) annually, which suggests that this secondary tropical forest is an important sink for atmospheric CO₂.

Discussion

Our conclusions are based on measured data as well as model results, which when taken together add richness to the analysis and provide firm support of the maximum power principle operating across the gradients of the Luquillo Mountains. Both the plot-level data and the spatial model that evaluates NPP trends over all elevations (Fig. 8C) show a mid-elevation NPP peak, with NPP values increasing up to approximately 500 m and then declining. If there were no landscape model, and there were no rate and efficiency trends in the measured data, then our conclusion would rest solely on the trend displayed in Fig. 7C (maximum NPP at mid-elevations) in which the lowest elevation measurement point dictates the trend. However, the purpose of the model was to extend the plot-level analysis to the landscape scale by simulating the forcing functions and measured response curves that influence NPP. Increasing different input parameters (leaf area index, leaf nitrogen concentration, etc.) in the model by 10% at the low elevation site did not change values of GPP, NPP, R_A or NPP/GPP by >20%, and hence did not change our conclusion. Furthermore, the physiological data used to develop the model show clear elevational trends (Fig. 3, 6).

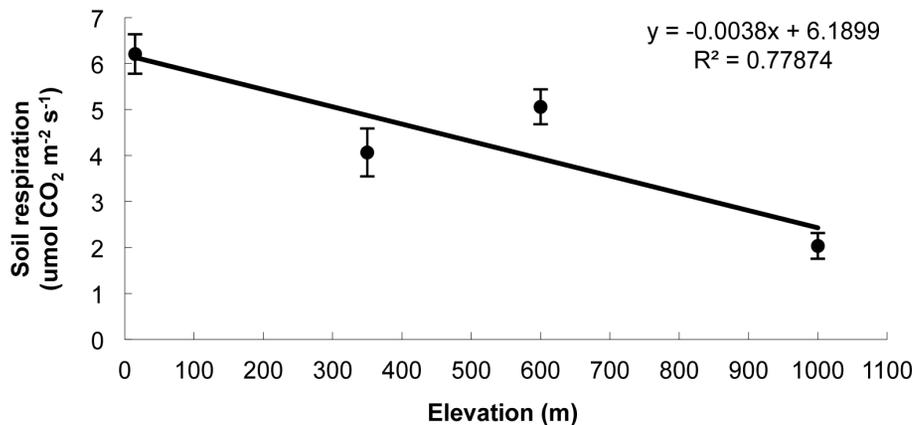


Figure 6. Soil respiration rates along an elevation gradient in the Luquillo Experimental Forest, Puerto Rico. n=10 at each elevation. Values represent the average of two sampling dates (January and July).

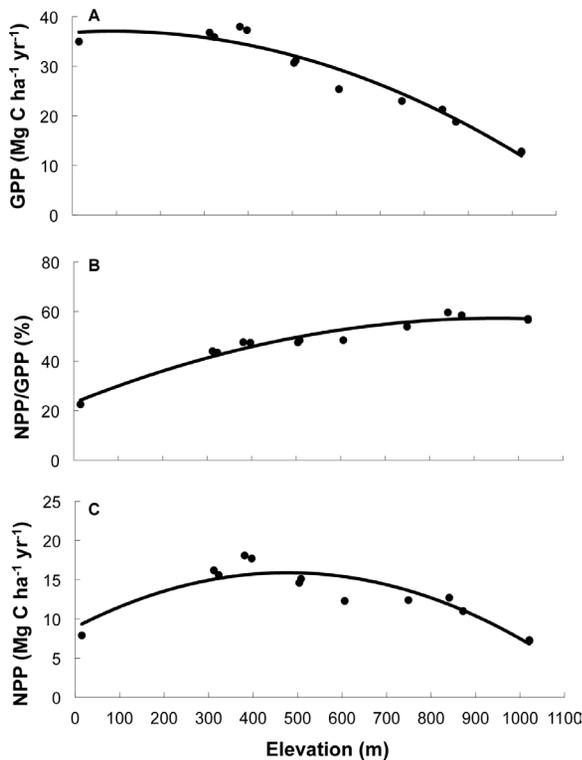


Figure 7. (A) Estimated rate of gross primary productivity (GPP) along an elevational gradient in the Luquillo Experimental Forest, Puerto Rico, (B) efficiency (NPP/GPP) along the same gradient and (C) power (NPP) along the same gradient. The points shown are the elevations of the 13 field sites at which leaf photosynthesis and respiration were measured. Also shown are 2nd-order polynomial regression lines.

Thus the trends in primary productivity across the elevation gradient are robust and support Odum's maximum power principle: maximum net primary productivity of the Luquillo forest ecosystem exists where metabolic rate and efficiency are intermediate.

Our results indicate that NPP is highest in the LEF in the middle of the elevation/climatic gradient where a suite of climatic and biotic drivers (solar insolation, temperature, rainfall, leaf area index) are optimized for ecosystem productivity. How does this conclusion fit into the context of the much larger gradient scenario of all forests worldwide? In other words, should there be maximum power at intermediate elevations on any forested mountain? Or do the environmental conditions at mid-elevations of the Luquillo Mountains just happen to be about optimal for tree growth? Given the reality of the Q_{10} response of biological material, does this location represent some kind of planetary optimum for plant productivity? We tested this hypothesis in two ways. First, we used a published review of tropical NPP values (Clark et al. 2001) to determine where our NPP estimates for the LEF fall in relation to other tropical forests. The six highest NPP estimates from

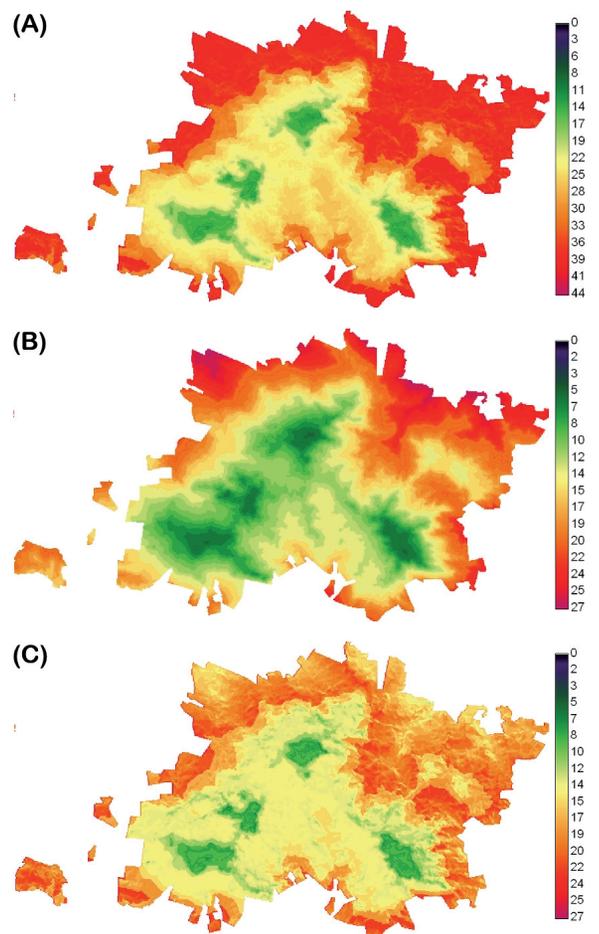


Figure 8. Simulated annual (A) gross primary productivity, (B) autotrophic respiration and (C) net primary productivity ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$) for the Luquillo Experimental Forest, Puerto Rico, extrapolated from field measurements. The green areas on each map reflect the four peaks of this mountain system.

the literature review averaged 12 (low estimate) to 22 (high estimate) $\text{Mg C ha}^{-1} \text{ yr}^{-1}$. This puts the mid-elevation forest of the Luquillo Mountains among the top candidates for highest forest productivity in the tropics (mean forest-wide NPP at 500 m = 19 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$). Second, we must consider the environmental conditions at mid-elevations of the Luquillo Mountains within the larger gradient context of all forests worldwide. NPP in temperate evergreen and boreal forests is limited by reduced sunlight and temperature during the winter months, and NPP in temperate deciduous forests is limited further by reduced leaf area during the winter months. NPP in tropical dry forests is limited by water availability for most of the year. In lowland tropical wet forests (most similar to those growing at low elevations in the LEF), NPP is limited by high temperatures that drive up respiration rates and (sometimes) a dry season that limits water availability for part of the year. With a near constant air temperature of about 23°C,

approximate 12-h days throughout the year, moderate cloud cover, the absence of a pronounced dry season and three meters of rainfall per year, tropical montane forest at mid-elevations in the Luquillo Mountains may represent an optimal position in global gradient space (sensu Hall et al. 1992) for a forest ecosystem to achieve maximum power. Additional support for this hypothesis may be demonstrated by forests of the southeast United States, mostly at lower elevations, which share many of the same environmental characteristics as the mid-elevation Luquillo forest and are also highly productive ecosystems (Brown and Schroeder 2000). It should be noted, however, that maximum NPP is not necessarily equivalent to maximum standing biomass; the LEF is a hurricane-impacted forest in which disturbance, and therefore recovery through high rates of productivity, is common. Furthermore, direct comparisons between instantaneous flux measurements scaled up over time (this study) and biomass accumulation measured over decades (Odum and Jordan 1970, Weaver et al. 1986, Weaver and Murphy 1990) are not completely warranted. Flux measurements scaled up over time will always be higher than measurements of biomass accumulation, because component flux measurements reflect direct metabolism (i.e. measurements are made at the beginning of the carbon 'pipeline') while the biomass accumulation approach reflects 'end-of-pipe' carbon measurements that do not account for lost carbon through processes such as herbivory, release of gaseous carbon compounds, shedding of plant parts, and undocumented mortality.

The results of this study highlight important questions regarding natural selection and fitness. Since about 1970, ecologists, once unified around Eugene Odum's classic text (Odum 1953), more or less split into two different groups, one focused on individuals and communities and a second focused on ecosystems and energy. The first group tended to mistrust the second's emphasis on energy as an important and unifying numéraire, because they believed that present conditions of ecosystems and their species were a product of evolution where fitness was key. However, the definition of 'fitness' in modern biology, often based in terms of survival and reproduction, quickly becomes tautological (i.e. those who survive and reproduce are fit, and those who are fit survive and reproduce). Considerable recent work has shown that net energy leads to fitness by allowing more and larger surviving offspring. For example, Thomas et al. 2001 showed a direct connection between energy and reproduction in their studies of passerine bird populations in Corsica and southern France. Persistence of breeding pairs was higher in populations that matched the timing of reproduction with the timing of available food supply. As food supply and demand were progressively mismatched, the increased cost of rearing young pushed the metabolic effort of adults beyond their apparent sustainable limit, drastically reducing the persistence of adults in the breeding population. Likewise, greater net energy production in trees can be al-

located towards growth and reproductive output. For example, if the production of additional leaves higher up in the canopy results in higher carbon gains that exceed the carbon needed to cover the respiration costs of additional stem structure such that these taller plants can maximize their net energy capture, then maximum power will favor taller plants. Or, if switching the timing of photosynthesis and respiration in desert plants results in lower transpiration rates (an energy cost) and thus higher net carbon gains, then maximum power will favor this physiological adaptation in this environment. The specific characteristics favored in a given location will depend on the climatic forcing functions as well as biological interactions. For example, organisms inhabiting desert or swamp environments will develop different strategies than those of tropical forests to maximize power output. Therefore, given a set of forcing functions in a given location, those individuals (or populations or ecosystems) that optimize the trade-off between metabolic rate and efficiency to achieve maximum power will be most fit in the present environment. In terms of evolutionary game theory, those that maximize power gain the highest 'payoffs' (i.e. fitness). As environmental conditions change over the long term, the rate vs efficiency optimum will shift and the individuals, populations and/or ecosystems that are able to achieve maximum power in the new environment will be favored over those that are maximizing power for the old environment. We think that this net energy-as-fitness view is less circular, scalable across various levels of biological organization and allows for a re-synthesis of ecology and a richer series of possibilities for testing the consequences of natural selection.

In conclusion, our results of primary productivity for the Luquillo Mountains suggest that the maximum power principle applies to even very complex natural ecosystems such as (at least) this subtropical forest where maximum power is achieved at intermediate, rather than maximum, rates and efficiencies. The maximum power principle was demonstrated along an elevation gradient in Puerto Rico, but this gradient can also be viewed as a proxy for the narrow gradients that exist within a specific site or the broader climatic gradients that exist across the globe. Evolution functions around the optimization of tradeoffs to maximize net energy capture and thus fitness; maximum power may be one means of achieving this.

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