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Analysis of factors regulating ecosystem development on Mauna Loa using the Century model

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Abstract. We used the Century model to evaluate environmental controls over ecosystem development during the first 3500 y of primary succession on pahoehoe (i.e., relatively smooth, solid) lava flows of wet, windward Mauna Loa, Hawaii. The Century model is a generalized ecosystem model that simulates carbon, nitrogen and phosphorus dynamics for plant-soil systems. Preliminary results indicated the need to modify the model to include the effects of soil C accumulation on soil water storage and drainage. The modified model was parameterized to simulate observed values of aboveground productivity, biomass and soil element pools on a 3400-y-old site at 700 m elevation. Testing the model parameters at 1660 m elevation indicated that N inputs were lower and soil water drainage rates were slower at the higher elevation. We applied the modified and fully parameterized model to simulate ecosystem attributes during primary succession at five elevations, and conducted single-factor experiments with the model to identify the specific influences of variations in temperature, nutrient inputs, and rainfall on modeled ecosystem characteristics.

Simulated aboveground productivity (ANPP), net N and P mineralization, and biomass element pools all increased through time at each elevation, and all declined with increasing elevation at each point in time. After 3500 y of succession none of these attributes had reached a stable asymptote, but asymptotes were approached more quickly, and succession was therefore faster, at lower than at higher elevations. Simulated soil organic matter (SOM) pools increased with elevation, despite that plant productivity declined. These results, and similar comparisons among rainfall regimes, suggest that SOM pools were more sensitive to factors controlling decay than production rates.

Within elevations and temperature regimes, nutrient availability was the most important factor controlling simulated rates of plant productivity, biomass, and detritus accumulation during ecosystem development. Through time, SOM accumulations alleviated nutrient limitations to plants, but simulated productivity remained highly dependent upon externally supplied nutrients even after 20,000 y. Rainfall had two main effects on nutrient availability within the model: (1) it increased rates of leaching, and thus depleted nutrient supplies; and (2) it exacerbated soil flooding and thereby decreased nutrient turnover rates. High rainfall on windward Mauna Loa maintains oligotrophic conditions through time despite continuous N and P inputs.

Introduction

Ecosystem attributes are controlled by many interacting factors, making their controls difficult to interpret unambiguously from field observations. Three approaches used to address this problem, observations along natural environmental gradients, experimental manipulations, and modeling, all provide insights into ecosystem-environment interactions, but each has limitations. Two or more factors inevitably vary along any environmental gradient, not all factors are subject to clean experimental manipulation, and ecosystem models necessarily simplify complex systems, making true validation difficult. In combination, however, these three approaches provide the best means available of identifying and quantifying the mechanisms by which environmental variables influence ecosystem characteristics, processes, and development.

We have investigated environmental controls over ecosystem attributes during primary succession on windward Mauna Loa, Hawaii, using both observational and experimental approaches (Vitousek et al. 1992, 1994; Raich et al. 1996, 1997; Russell & Vitousek 1997; Russell et al. 1998). Windward Mauna Loa provides a useful setting for this work because the principal variables that control ecosystem characteristics, including climate, organisms, relief, parent material, and time (Jenny 1941, 1980) can all be maintained relatively constant, or can be investigated individually via careful site selection (Vitousek et al. 1995a; Aplet et al. 1998). Our research and that of others (Atkinson 1970; Eggler 1971; Mueller-Dombois 1967, 1987; Balakrishnan & Mueller-Dombois 1983; Drake & Mueller-Dombois 1993; Kitayama et al. 1995; Stemmermann 1983; Cordell et al. 1998) provide an extensive picture of how Mauna Loa’s biota and ecosystems vary along age, elevational, and climatic gradients. Understanding why specific ecosystem properties vary as they do along these gradients has proven to be more difficult.

Our objective was to investigate, within a modeling framework, environmental controls over ecosystem properties during primary succession along an elevational gradient on windward Mauna Loa, Hawaii. We sought to tease apart the specific effects of individual variables on ecosystem development, and to identify those factors most responsible for affecting individual processes such as productivity, biomass accumulation, and elemental cycling rates. We addressed these issues using a process-level ecosystem model, Century. Century was originally developed for application to established North American grasslands (Parton et al. 1987, 1988; Burke et al. 1991), but has since been expanded for potential application to all the major terrestrial ecosystem types (Metherell et al. 1993; Parton et al. 1994; Schimel et al. 1996, 1997).

Study site

Mauna Loa lies on the Island of Hawaii in the middle of the Pacific Ocean at 19°32′ N and 155°35′ W. The surface lava flows of this active volcano have been mapped and dated and range to $>$10,000 y old, but 90% of the surface area of windward Mauna Loa is $<$4000 y old (Lockwood 1995). Individual flows can extend from above the treeline to sea level, and are juxtaposed against flows of different ages that have the same dominant plant species. All lavas of Mauna Loa are mineralogically similar (Clague & Dalyrymple 1987; Wright & Helz 1987) and slopes are uniformly gentle. In this study we consider pahoehoe lava flows only. Pahoehoe is a solid lava with an undulating surface interspersed with cracks and tumuli, and having a smooth or ropy-textured surface.

Within the rainy belt of windward Mauna Loa climatic conditions vary along well-defined gradients. Mean annual temperatures decline linearly from 23.6 C at Hilo (10 m elevation) to 13.1 C at 1660 m elevation (Juvik & Nullet 1994). Annual rainfall increases from 3560 mm at Hilo to a peak of nearly 6000 mm at 700 m elevation and then declines (Table 1). Cloudwater deposition augments precipitation at higher elevations (Juvik & Nullet 1993). Any given location on windward Mauna Loa can therefore be defined in terms of its climate and age, and how these factors vary from location to location is well documented. These same factors serve as driving variables within Century. Hence, a broad range of environmental conditions that have real-life analogs on windward Mauna Loa can be investigated with the model, and extensive field studies have been conducted that provide data to test model predictions. Potentially important factors such as mineralogy of the parent material and biota are relatively uniform spatially, and are not further considered herein.

Methods

Throughout this study we used Century agroecosystem version 4.0 in the forest mode (Metherell et al. 1993). The Century model is a generalized ecosystem model that simulates carbon, nitrogen and phosphorus dynamics

Table 1. Major climatic variables along an elevational gradient on windward Mauna Loa, Hawaii. Data are from Juvik and Nullet (1994) unless otherwise noted.

Elevation (m)	Rainfall (mm/y)	Cloudwater[a] (mm/y)	Temperature (C)	Evapotranspiration (mm/y)
10	3560	0	23.6	1680[d]
290	4150[b]	0	21.7[c]	1180[e]
700	5750	0	19.3	880
1130	4320	620	15.5	920
1660	2620	1320	13.1	1130

[a] Cloudwater deposition is estimated from Juvik and Nullet's (1993) model, based on measurements collected from an adjacent slope on Mauna Kea.

[b] Based on weather station #88.1, elevation 342 m, State of Hawaii (1970).

[c] Estimated from linear temperature-elevation relationship derived from Juvik and Nullet (1994).

[d] Based on pan evaporation at weather station #87.0, elevation 10 m, State of Hawaii (1970).

[e] Based on pan evaporation at weather station #89.5, elevation 274 m, State of Hawaii (1970).

for plant-soil systems (Parton et al. 1993; Parton et al. 1996). The model simulates plant growth, soil water and temperature, nutrient cycling and soil organic matter dynamics for grassland, agricultural, forest and savanna systems, and has been used extensively to simulate the impact of climatic and land use changes on natural and managed systems. The model uses a monthly time step, while the major input variables include: (1) monthly precipitation and monthly average maximum and minimum air temperature, (2) soil texture, (3) lignin, nitrogen, and phosphorus content of plant material and (4) soil and atmospheric N inputs. The soil organic matter model simulates the dynamics of carbon and soil nutrients for the different soil pools (Parton et al. 1987, 1988, 1994; Schimel et al. 1994). The forest model has been tested for tropical, boreal and temperate systems and used to simulate forest system responses to different natural disturbances and management practices (Sanford et al. 1991; Kelly et al. 1997; Peng et al. 1998).

Our work involved four principal tasks. First, we utilized field-derived data to parameterize Century to simulate the first 3500 y of ecosystem development at 700 m elevation on windward Mauna Loa, comparing the output with observations from a 3400-y-old flow. This required modifying the model for application to primary succession on pahoehoe lava flows. We then tested the parameter values derived from this 700-m calibration by predicting ecosystem properties after 3400 y of succession at 1660 m elevation, changing only the climate data used to drive the model. This allowed us to identify two elevation-specific parameters. With this complete parameter set, we simulated ecosystem development during the first 3500 y of primary succession at 10, 290, 700, 1130, and 1660 m elevations, based on their different climates (Table 1). Finally, to determine the specific effects of individual environmental variables on ecosystem attributes, we evaluated the sensitivity of the model to variations in rainfall, temperature, and nutrient input rates.

Model development

Century was designed for application to sites with mineral soils, which are lacking at our sites. At their initiation pahoehoe flows are sterile and free of organic materials, and the potential rooting zone of plants is limited to cracks in the basaltic lava. Through time, organic materials generated by colonizing organisms builds up, creating an organic soil that blankets the lava. The Lithic Tropofolists that develop (Sato et al. 1973) are Histosols overlying pahoehoe lava bedrock; they have no discernible sand, silt, or clay. Soil texture and depth are used by Century to estimate soil water-holding characteristics, and thereby influence calculated soil water storage, evapotranspiration, water leaching, and runoff. We modified Century to predict total soil water-holding capacity from soil organic carbon (SOC) accumulation, based on data from >300 gravimetric soil moisture determinations made under a variety of moisture conditions (e.g., Raich 1998). Soil textural attributes are also used by Century to predict nutrient leaching and SOC turnover rates. Within this study texture did not vary among locations or through time, and we parameterized the model such that the influences of soil texture on simulated processes were constant among all model runs.

Lacking soils, newly formed pahoehoe sites also lack soil P, but through time P becomes available to organisms via weathering of the parent material. Century version 4.0 predicts the relative rate of parent material weathering from abiotic conditions only. Working on Mauna Loa, Cochran and Berner (1996) found that vascular plant communities increased pahoehoe weathering rates by at least an order of magnitude over rates found beneath lichen-covered or barren lavas during the first 3000–5000 y of ecosystem development. We therefore incorporated an algorithm that increased rates of P weathering in response to forest growth, by applying an existing function that predicts relative nutrient availability from fine root biomass (Metherell et al. 1993). The effect of this modification was to decrease P weathering rates during early primary succession.

One key feature of Mauna Loa’s pahoehoe flows is their tendency to become very poorly drained through time (e.g., Balakrishnan & Mueller-Dombois 1983; Hodges et al. 1986). Whereas young pahoehoe lava flows are well drained, old flows are swampy. In Century, the rate of soil water drainage from a site is controlled by a single parameter, *drain*. Whenever we assumed free soil water drainage throughout succession, Century consistently underestimated long-term SOC accumulation rates despite correctly simulating detritus production rates. We believe that developing root systems and accumulating detritus plug the cracks through which water flows, impeding water drainage from older sites.

We simulated this phenomenon by modifying the soil water drainage rate in response to changes in SOC accumulation (Figure 1(A)). As SOC builds up, drainage is impeded and soils become saturated more frequently, generating anaerobic conditions that slow rates of SOC decomposition. A minimum drainage rate of 0.75 led to a simulated SOC pool of 6860 g m^{-2} after 3400 y at 700 m elevation (Figure 1(B)), in comparison with the observed value of 6990 ± 890 g m^{-2} (Raich et al. 1997). Other physical and chemical conditions could play a role in slowing decomposition (e.g., pH – Motavalli et al. 1995). However, modifying Century's drainage function improved the model's predictions of soil C storage substantially, and reflects appropriately the development of wetland soils on these sites. Because anaerobic conditions strongly affect SOC decomposition rates, simulated SOC accumulation was very sensitive to the minimum drainage rate used (Figure 1(B)). Simulated rates of NPP, in contrast, were affected little (Figure 1(B)).

Model parameterization

The parameters that control material fluxes within Century are defined and described by Metherell et al. (1993). For this work, we modified parameters within the fix.100, site.100, and tree.100 files. Our work focused initially on the determination of parameter values that would generate quantitatively acceptable predictions of soil element pools, plant productivity, and biomass on a 3400-y-old flow at 700 m elevation, based principally on data from Raich et al. (1997).

Initial values of the state variables within the model were set to zero (or nearly so) to approximate the conditions of cooled lava, except that the initial parent P pool was set at 9999 g/m^2 to represent a large weatherable pool of lava. The potential ranges in elemental compositions of live biomass components were based on the ranges observed in field studies (Vitousek et al. 1988, 1992; Raich et al. 1997; Russell et al. 1998). Belowground C allocation was set at 40%, consistent with previous forest calibrations of Century (range 0.33–0.44, Metherell et al. 1993). The model was run for 3500 years with four time steps per month, using the stochastic weather generator of Century applied to the appropriate monthly climate data (State of Hawaii 1970; Juvik & Nullet 1994).

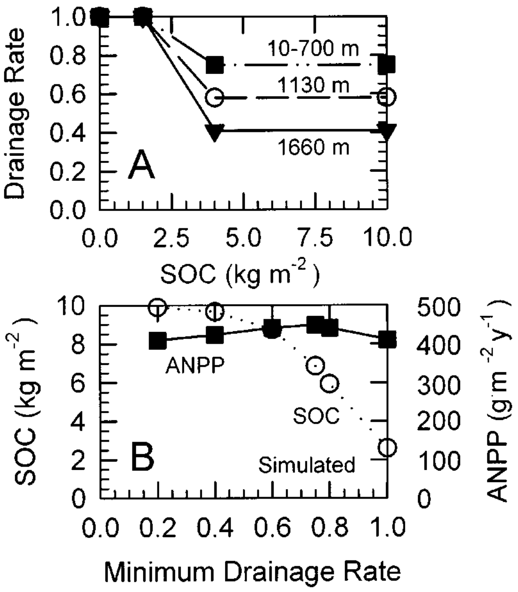

Figure 1. (A) The modeled relationship between soil organic C (SOC) accumulation and water drainage rate. The drainage rate defines the proportion of excess water that leaves the site each month, and therefore how much remains to fill soil pore volume. (B) Simulated SOC accumulation and aboveground net primary productivity (ANPP) after 3400 y at 700 m elevation, shown in response to variations in the minimum drainage rate. A drainage rate of 1.0 represents a well-drained site. Each point represents the mean of 13 individual simulation years.

As with any long-term simulation, nutrient availability within Century is controlled by the balance between nutrient inputs and outputs, and these rarely are known precisely. We first adjusted the N input rate until aboveground net primary productivity (ANPP) matched that observed. The N input rate that provided the best overall predictions of N accumulation after 3400 y of succession at 700 m elevation was 0.6 g m^{-2} y^{-1}. This is consistent with rates of accumulation on a young flow at 290 m elevation (Raich et al. 1997) and is slightly higher than the estimated total N input rate of 0.42–0.55 g $m^{-}2$ y^{-1} in a somewhat drier site at 1100 m elevation (Vitousek et al. 1987; Vitousek & Walker 1989; but see Heath & Heubert 1999). The parameter defining the maximum rate of P weathering was then adjusted until N and P became simultaneously limiting production, as found on a young pahoehoe flow at 1130 m (Raich et al. 1996). The potential rate determined by this calibration was 0.06 g m^{-2} y^{-1}, which compares well with observed P release rates of 0.005–0.5 g m^{-2} y^{-1} reported by Newman (1995).

Having established nutrient input rates that led simulated ANPP after 3400 y to be the same as that observed by Raich et al. (1997), we changed the mortality rate of tree boles until aboveground biomass also matched the observed value. Finally, we altered the parameters that control carbon-element ratios of the different SOM fractions, until simulated soil C:N matched that observed in a 3400-y-old site at 700 m elevation (Raich et al. 1997).

Given these tunings, we were able to reproduce most measured ecosystem properties after 3400 y of succession at 700 m elevation within the errors of the field measurements. Simulated ANPP averaged 458 gC m^{-2} y^{-1} in comparison with the observed value (Raich et al. 1997) of 428 g m^{-2} y^{-1}; aboveground biomass was simulated to be 6060 g/m^2 in comparison with the observed value of 5910 g/m^2; SOC accumulation was simulated to be 6860 g/m^2 in comparison with the observed 6990±890 g/m^2; total soil organic N was simulated to be 409 g/m^2 in comparison with the observed 418±42 g/m^2; and total soil P was simulated to be 15.8 g/m^2 in comparison with the observed 15.2±4.7 g/m^2.

Century overestimated biomass nutrient pools somewhat. After 3400 y aboveground plant N was simulated to average 47.7 g/m^2 and aboveground plant P was simulated to average 3.7 g/m^2: the observed values (Raich et al. 1997) were 42.4 gN/m^2 and 2.7 gP/m^2. Reducing nutrient input rates within the model led to lower simulated rates of production rather than to reduced N pools in biomass. Refinement of nutrient allocation dynamics within Century might improve these predictions. Century did not accurately simulate well accumulation of surface litter or, as a result, N and P pools in surface litter. The observed litter standing crop at 700 m elevation was 1810±330 gC m^{-2}, most of which was dead *Dicranopteris linearis* fronds (Russell et al. 1998). The simulated surface litter standing crop was 700 g m^{-2}. These results suggest that factors not currently incorporated within Century may be important in controlling litter decomposition in these sites.

Ideally, the modified and fully parameterized model would quantitatively predict ecosystem attributes after 3400 years of primary succession at other elevations, based solely on the different climatic conditions present. To test this we altered only the climate drivers of Century to those characterizing 1660 m elevation and ran the model. Century substantially underestimated soil accumulation at 1660 m elevation after 3400 y; SOC by 39%, SON by 32%, and total soil P by 36%. However, decreasing the minimum drainage rate from 0.75 to 0.41 (Figure 1) improved the prediction considerably.

Century also simulated an excess of N with respect to P within the ecosystem after 3400 y. For example, simulated and observed N pools in aboveground biomass at 1660 m were 41 and 13 g/m^2, respectively, whereas simulated and observed P pools were 1.9 and 3.0 g/m^2. On old pahoehoe flows, foliar N contents are usually lower at 1660 m than at 700 m elevation (Vitousek et al. 1988, 1992; Raich et al. 1997; Russell et al. 1998), and N mineralization rates were consistently slower in soils from 1660 than from 700 m (Raich et al. 1997). Hence, the available data contradict the model's prediction of relatively high N availability at 1660 m elevation. We assumed that N inputs at 1660 m were equal to those at 700 m, but the higher elevation sites are farther from the ocean and receive less rain than do lower sites. We concluded that annual N input is an elevation-specific parameter, and adjusted its value to better simulate the conditions at 1660 m. With less empirical justification, we did a similar adjustment for soil drainage.

After altering the N input rate to 0.37 g m^{-2} y^{-1} (*cf.* 0.60 at 700 m) and the minimum drainage rate to 0.41 (*cf.* 0.75 at 700 m, Figure 1(A)), simulated ecosystem attributes after 3400 y of ecosystem development at 1660 m elevation matched quite closely those observed. Simulated ANPP averaged 261 (range 213–299) gC m^{-2} y^{-1} in comparison with observed rate (Raich et al. 1997) of 280 g m^{-2} y^{-1}. Simulated SOC, SON, and total soil P pools were 7240, 395, and 15.3 g/m^2, respectively, in comparison with observed pools of 7360±3660, 408±235, and 14.1±7.2 g/m^2. Aboveground biomass after 3400 y contained 3490 gC, 26 gN, and 2.0 gP per m^2 in the simulations, whereas vegetation in the field averaged of 3890 gC/m^2, 13 gN/m^2, and 3.0 gP/m^2. Again, improving nutrient allocation dynamics within Century might improve the model's predictions of plant nutrient pools.

Applying the model

Having established a complete set of model parameters, we first used Century to simulate ecosystem development along an elevational gradient on windward Mauna Loa. We compared the simulation outputs with observed data from four elevations, two of which were not used during model development, to evaluate the robustness of the model's predictions. We then applied the model in an experimental mode, altering temperatures, rainfall, and nutrient inputs across a range of realistic values, to determine the specific effects of these individual variables on ecosystem attributes.

Ecosystem development along age and elevational gradients

We used Century to simulate ecosystem development at five elevations, 10 m, 290 m, 700 m, 1130 m, and 1660 m, by incorporating elevation-specific climate data (Table 1) into the model. We varied only two parameters among elevations, annual N inputs and the minimum soil water drainage rate. The assigned N input and minimum drainage rates at 1130 m elevation were 0.485 gN m^{-2} y^{-1} and 0.58 (no units), respectively, these being the averages of the 700- and 1660-m elevations. Below 700 m they were assumed equal to their values at 700 m (i.e., 0.6 gN m^{-2} y^{-1} and 0.75, respectively). All model runs included stochastic weather.

Modeled trends at five elevations

Simulated aboveground net primary productivity (ANPP), net N mineralization, net P mineralization, and biomass element pools all increased through time at each elevation (Figure 2), as expected during primary succession (e.g., Crocker & Major 1955; Leisman 1957; Olson 1958; Odum 1969; Van Cleve et al. 1993). Soil and biomass element pools continued to increase throughout the simulations, particularly at higher elevations (Figure 2). Simulated productivity, plant biomass, and nutrient mineralization rates also declined with increasing elevation throughout the first 3500 y (Figure 2). The one exception to this trend was P, in that both net P mineralization and biomass P were slightly lower at 700 m than at 1130 m elevation after 3400 y.

During the first few decades of primary succession, simulated soil element pools increased in parallel with plant productivity and hence were higher at lower elevations, but this pattern changed quickly. After 2000 y there was more SOC at 1130 m than at any other elevation, and SOC pools were the smallest at 10 m, where productivity but also rates of decomposition were greatest (Figure 2). Total soil N and P accumulations mirrored those of carbon (Figure 2).

Comparisons with observations

These simulation results provided the first real opportunity to compare model predictions with field data not used to parameterize the model, including data from young lava flows at 290, 1130, and 1660 m elevations as reported by Raich et al. (1997). Although true validation of our model may be impossible (Oreskes et al. 1994), we did test the predictions made by Century against observed patterns to identify the model's strengths and weaknesses.

Pattern #1. Aboveground plant productivity (ANPP) declined linearly with increasing elevation (Raich et al. 1997). Observed and simulated trends were the same (Figure 3(A)).

Pattern #2. Aboveground plant biomass increased with flow age and generally declined with increasing elevation (Aplet et al. 1998). Again,

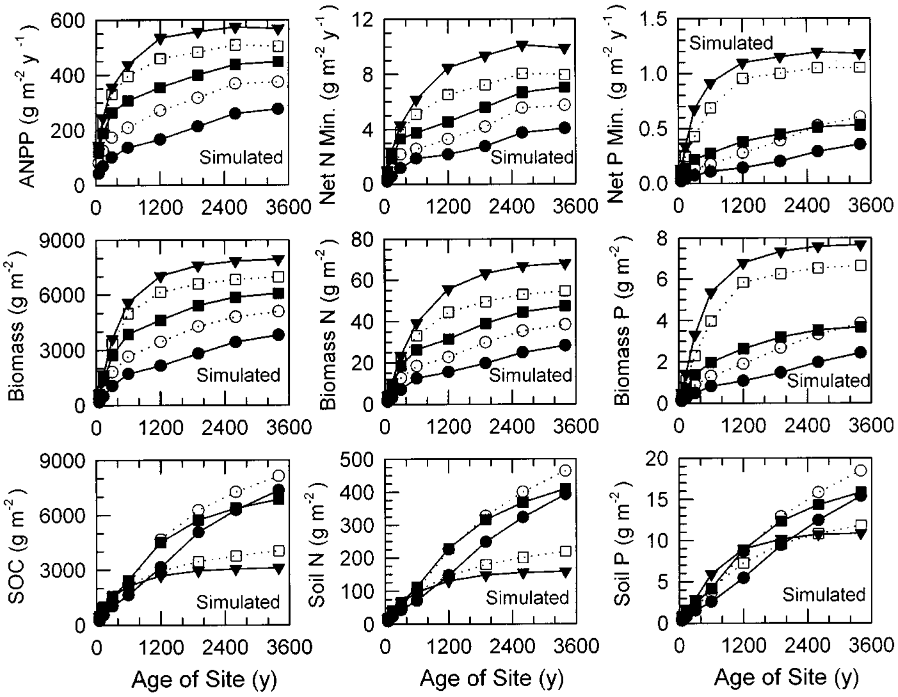

Figure 2. Simulated ecosystem attributes during the first 3500 y of primary succession at five elevations on windward Mauna Loa, Hawaii. Key to elevations: ▼—▼, 10 m; □···□, 290 m; ■—■, 700 m; ○···○, 1130 m; ●—●, 1660 m. Each symbol represents the mean of 11 individual simulation years.

simulated and observed (Raich et al. 1997) values were similar (Figure 3(B)). Simulated N and P pools in aboveground vegetation on old flows (Figure 3(C–D)) were less well simulated than were plant C pools, as found during the initial model calibrations. We did not simulate the stand-level dieback that influences these forests (e.g., Mueller-Dombois 1985, 1987) and diminishes biomass in post-dieback stands (e.g., Aplet et al. 1998).

Pattern #3. Soil elemental pools tended to decline with increasing elevation on young lava flows above 100 m elevation (Vitousek et al. 1992), but were similar at 700 and 1660 m elevations after 3400 y (Raich et al. 1997). Observed and simulated values of soil nutrient pools coincided very well on both young and old flows (Figure 3(E–G)), with the exception of the large soil pool observed on the young flow at 1130 m (Raich et al. 1997). Field results from that elevation were somewhat anomalous, but it was the elevation of maximum soil accumulation after 3400 y in our simulations (Figure 3(E)).

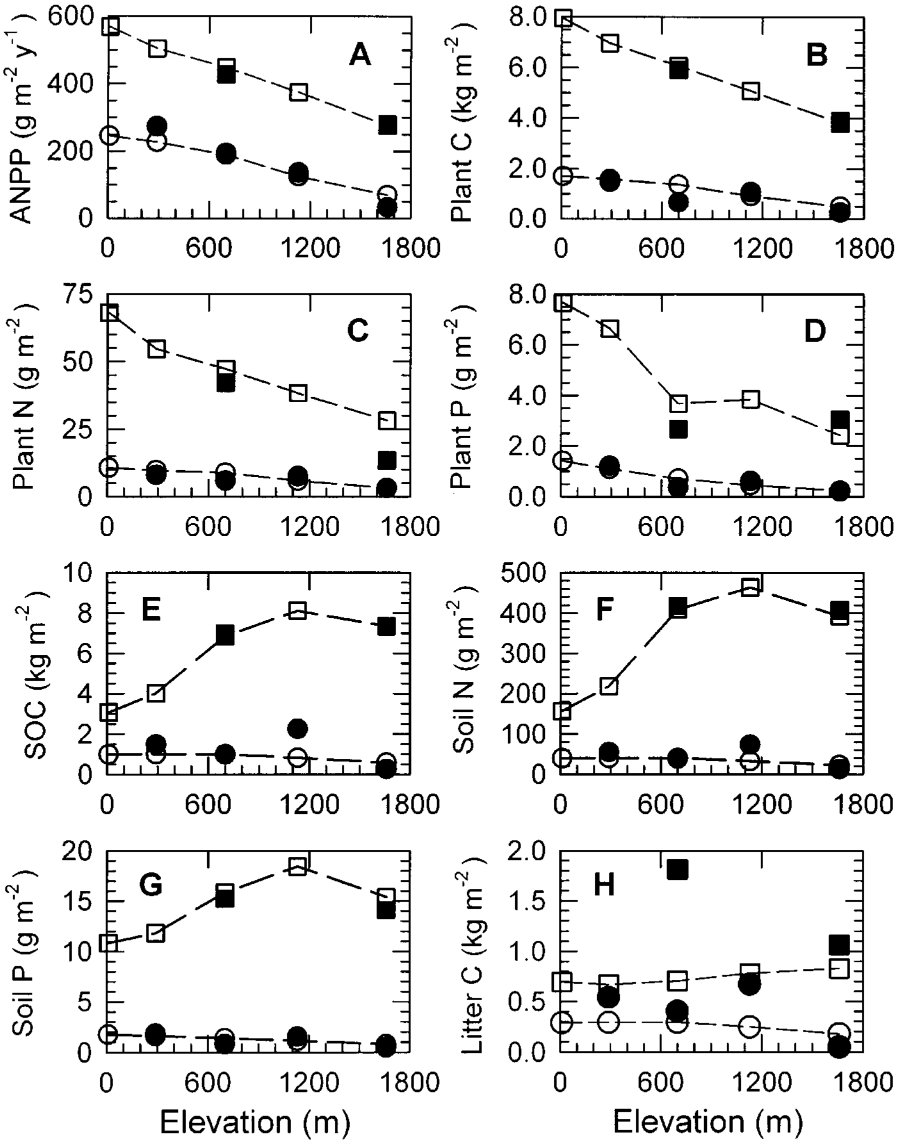

Figure 3. Observed and simulated ecosystem attributes after ca. 136 y and 3400 y of ecosystem development on windward Mauna Loa, Hawaii. Key: solid symbols are observed data from Raich et al. (1997); open symbols are mean values simulated by Century; circles are young sites; squares are old sites.

As during model parameterization, Century underestimated surface litter accumulations in the old site at 700 m elevation (Figure 3(H)) and biomass N at the highest elevation (Figure 3(C)). Century also tended to overestimate foliar nutrient concentrations (data not shown). Nevertheless, with these exceptions, Century simulated reasonably well the major trends in soil element pools, aboveground production, and aboveground biomass that were observed on windward Mauna Loa (Figure 3). This suggests that the mechanistic underpinnings of the model were sufficiently valid that we may explore additional aspects of ecosystem development along Mauna Loa's windward flank.

Simulated ecosystem attributes

Greater productivity at lower elevations (Figure 3) allowed for more rapid detritus accumulation early, but slower decomposition rates at higher elevations (Figure 4(A)) generated larger accumulations of detritus over the long term (Figure 3). Simulated soil C accumulation rates were highly variable from year to year, but averaged <5 g m^{-2} y^{-1} after the first 300 y at all elevations (Figure 4(B)). Total (plant plus detritus) C sequestration rates were fastest (20–50 g m^{-2} y^{-1}) during the first 20–70 y and thereafter declined, averaging <5 g m^{-2} y^{-1} after 2400 y (Figure 4(C)). Simulated soil C:N (Figure 4(D)) declined from 31–35 to values of 16–20 after 3400 y. Observed soil C:N ranged from 21 to 31 in four 110- to 136-y-old sites and from 17 to 18 in two 3400-y-old sites (Raich et al. 1997).

Modeled total N accumulation rates paralleled very closely those of C (*cf*. Figures 4(C) & 4(E)). After 3400 y, on-site N accumulation ranged from 14% of the cumulative input at 10 m elevation to 37% of the input at 1660 m. Most of the N was lost through gaseous emissions (34–54%) and leaching (29–38%) (e.g., Figure 4(F)), but at 1660 m on-site accumulation was the single greatest N sink. The efficiency of N capture, i.e., the proportion of the incoming N that was retained on-site, declined through time at all elevations. Hence, the more mature ecosystems were the leakiest, as predicted by Vitousek and Reiners (1975). Raich et al. (1997) found a tight correlation between ANPP and nutrient uptake and ANPP, regardless of site age or elevation. Consistent with this, Century predicted that ANPP increases with increasing N and P requirement (uptake + retranslocation) (Figure 4(G–H)).

These simulated patterns of ecosystem attributes along age and elevational gradients (Figures 2–4) describe our current understanding of ecosystem development on windward Mauna Loa's pahoehoe lava flows. They do not yet explain why ecosystem properties vary as they do with elevation. Temperatures, nutrient supply, and rainfall all vary with elevation, on Mauna Loa and elsewhere (e.g., Grubb 1977; Kitayama et al. 1998; Waide et al. 1998).

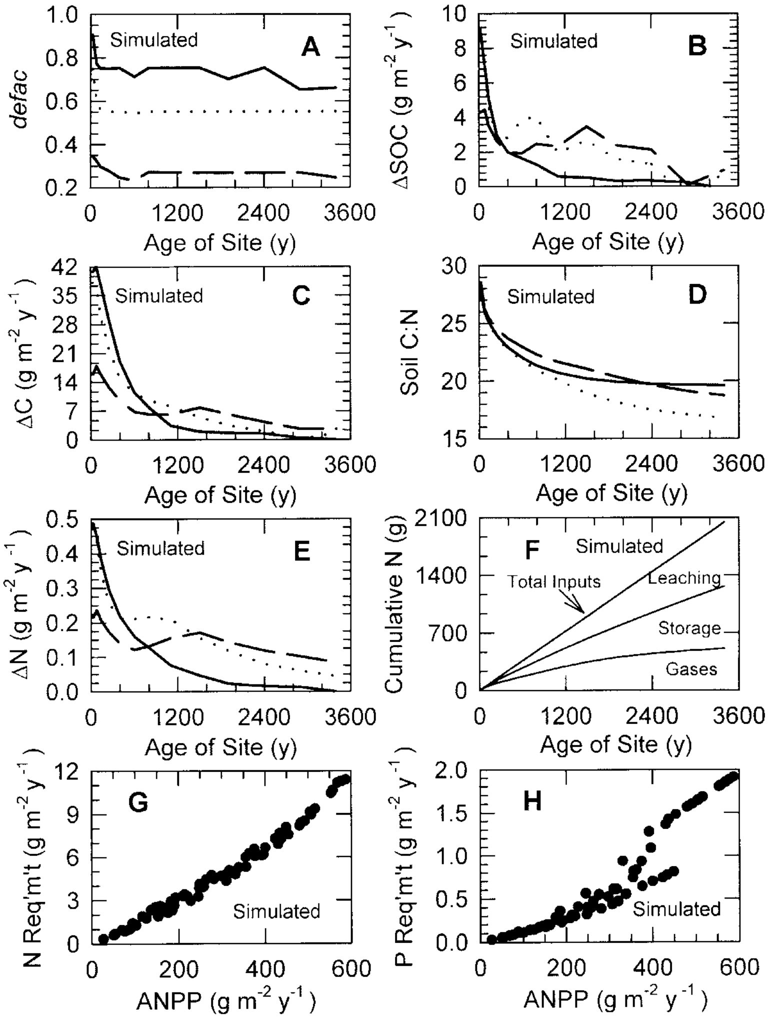

Figure 4. Simulated ecosystem dynamics during the first 3500 y of primary succession on the windward slopes of Mauna Loa, Hawaii. (A)–(E) are mean data from three elevations: 10 m (solid lines), 700 m (dotted lines), and 1660 m (dashed lines). (A) The physical decomposition rate parameter *defac* (no units), which acts as a multiplier on all decomposition processes within Century. (B) Average simulated rates of soil organic C accumulation. (C) Average simulated rates of total system C accumulation, including all live and dead materials. (D) Simulated mean soil C:N. (E) Mean simulated rates of total organic N accumulation, including all live and dead materials. (F) Simulated N budget at 700 m elevation. The top line shows cumulative N inputs; the areas below that reflect leaching losses, on-site N accumulation, and losses of N-containing gases, respectively. (G) & (H) Simulated relationships between aboveground productivity (ANPP) and nutrient requirement (i.e., uptake + retranslocation) in Century. Shown are mean values from five elevations at 13 time periods spanning 30–3400 y.

Table 2. Single-factor experiments conducted with Century to evaluate controls over ecosystem properties. In each case the model was initialized to the conditions of a newly formed lava flow at 700 m elevation, a single factor was varied sequentially across a range of five levels, and the model was run for 3500 y.

Factor	Levels applied				
Annual N input rate (g m^{-2} y^{-1})	0.3	0.4	**0.6**[a]	0.9	1.2
Potential P weathering rate (mo^{-1})($\times$ 10^{-6})	3	4	**6**[a]	9	12
Mean annual temperature (C)	13.1	15.5	**19.3**[a]	21.7	23.6
Mean annual rainfall (mm)	1500	3000	4500	**6000**[a]	10000

[a] The actual or estimated value at 700 m, the baseline elevation for these simulations.

Are differences in NPP among elevations due to the direct effects of temperature on net photosynthesis rates, to indirect effects of temperature mediated through nutrient availability, or to differences in precipitation or nutrient input rate?

Single-factor effects on ecosystem development

To evaluate the specific effects of individual factors on ecosystem development, we altered single variables across a range of conditions (Table 2), one at a time, and left all other factors unchanged. We used the middle elevation, 700 m, as our baseline. We also simulated long-term ecosystem development at all five elevations by running the model for 20,000 y.

Nutrient inputs

We independently altered the total N input and potential P weathering rates from 0.5–2.0 times their baseline values (Table 2). Decreasing either N or P inputs depressed simulated NPP, plant biomass, and SOC accumulation (Figure 5). However, because N and P co-limited production in the baseline conditions, increasing the inputs of either element alone had minimal effects on productivity and C accumulations (Figure 5). Increasing inputs of both N and P, however, dramatically increased simulated productivity, biomass, and SOC accumulations (Figure 5). Nutrient stocks in biomass and detritus also increased with increasing nutrient input rates (data not shown). These model results suggest that productivity, biomass accumulation, nutrient pools in plants and detritus, and soil accumulation would all be much greater than observed if nutrient input rates were higher. They also suggest that the observed declines in productivity and plant biomass above 700 m on Mauna Loa (Figure 3) could be due to lower nutrient inputs.

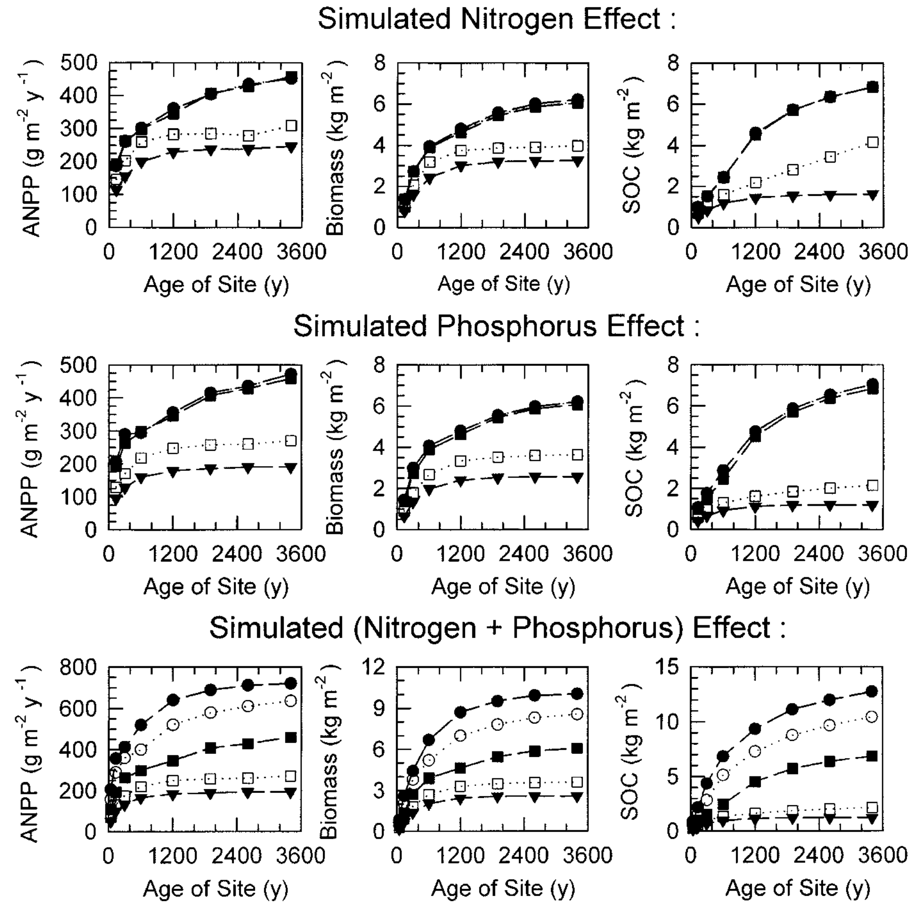

Figure 5. Simulated ecosystem attributes during the first 3500 y of primary succession on windward Mauna Loa, Hawaii, in response to different nutrient supply rates. The model was run using the parameter values and climatic conditions of 700 m elevation; only the nutrient supply rate was changed among simulations. Each symbol represents the mean of 11 individual simulation years. **Nitrogen Effect**: Total N inputs were varied from 0.5–2.0 times their calibrated value of 0.6 g m^{-2} y^{-1}. Key: ▼—▼, 0.5 × baseline; □···□, 0.67 × baseline; ■—■, 1.0 × baseline; ○···○, 1.5 × baseline; ●—●, 2.0 × baseline. **Phosphorus Effect**: Total P inputs were varied from 0.5–2.0 times their calibrated value by altering the potential P weathering rate (*pparmn(2)*) from its baseline value of 0.000006 mo^{-1}. Key: same as above for N. **Nitrogen + Phosphorus**: N and P inputs were increased simultaneously. Key: same as above.

Temperature

The effects of temperature were evaluated by changing the mean minimum and maximum temperatures within Century from those at 700 m elevation to those observed at 10, 290, 1130, and 1660 m elevations (Tables 1 & 2). If simulated differences among elevations were driven solely by temperature, predictions from this altered-temperature scenario would be the same as those from our previous elevation scenario (*cf.* Figures 2 & 6). For example, relative differences among elevations in long-term soil C and N accumulations were quite similar in the two scenarios, indicating that elevational differences in SOM accumulation were driven largely by temperature differences. Our simulations along the elevational gradient also suggested a negative correlation between elevation and NPP, net nutrient mineralization rates, and biomass element pools (Figure 2). In our simulated temperature gradient (Figure 6), these all declined as temperatures were decreased below those occurring at 700 m, suggesting their control by temperature at those elevations. However, increasing temperatures above those occurring at 700 m did not uniformly increase simulated productivity, nutrient mineralization, or plant biomass (Figure 6), all of which were predicted to increase at lower elevations (Figure 2).

In Century, temperature affects net photosynthesis directly, but it also affects plant production indirectly by affecting rates of SOM turnover and nutrient availability. Covariations between temperature and nutrient availability have made the interpretation of field results from Mauna Loa difficult (e.g., Vitousek et al. 1994; Raich et al. 1997). To disentangle temperature from nutrient-availability constraints on plant productivity, we increased the N input and P weathering rates within the model to ten times their estimated values, thereby saturating plant demands for nutrients. With no nutrient limitations, simulated plant productivity after 3400 y was 32% lower at 13.1 C (1660 m) than at 19.3 C (700 m) (Figure 6). The observed difference was 35% (Figure 3). Therefore, the observed difference in productivity between the old sites at 700 and 1660 m elevations can be explained almost entirely by direct temperature effects on modeled C assimilation rates.

Rainfall

We altered annual rainfall from the ca. 6 m/y received at 700 m elevation to 1.5, 3, 4.5 and 10 m/y, without altering its seasonal distribution. All of these rainfall amounts occur within Hawaii. According to Century, plant productivity, net nutrient mineralization rates, and total plant nutrient stores on windward Mauna Loa would all be greater if rainfall averaged only 1.5 m/y, and all declined with increasing rainfall (Figure 7). Rainfall averaging

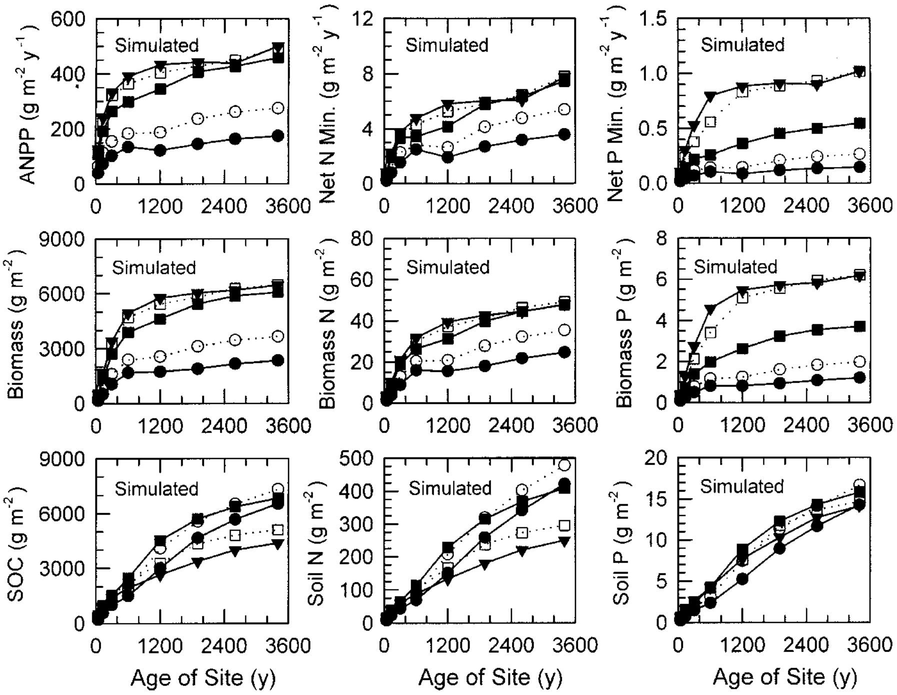

Figure 6. Simulated ecosystem attributes during the first 3500 y of primary succession on windward Mauna Loa, Hawaii, in response to different mean annual temperatures. The model was run using the parameter values and climatic conditions of 700 m elevation; only the temperatures were changed among simulations. Key: ▼—▼, 23.6 C; □···□, 21.7 C; ■—■, 19.3 C; ○···○, 15.5 C; ●—●, 13.1 C. Each symbol represents the mean of 11 individual simulation years.

6 m/y reduced plant productivity, biomass, and nutrient mineralization rates by 23–44% of their levels at 1.5 m/y of rain. Increasing rainfall to 10 m/y exacerbated these trends. The very high rainfalls received at 700 m elevation may explain the very low forest biomass observed on young sites at that elevation (Figure 3).

Within Century, rainfall amount affected ecosystem development in two main ways. First, increasing rainfall caused soils to flood more frequently, depressing rates of SOM decomposition, decreasing net N and P mineralization rates, and promoting the accumulation of soil organic C, N, and P (Figure 7). Second, greater rainfall promoted N and P leaching. In comparison with 1.5 m/y of precipitation, at 6 m/y cumulative N leaching over the first 3400 y was increased by 143% and cumulative P leaching was increased by 22%. Increasing rainfall reduced predicted gaseous losses of N, from 960 g/m^2 over the first 3400 y at 1.5 m/y of rainfall to 754 g/m2 in the 6 m/y scenario,

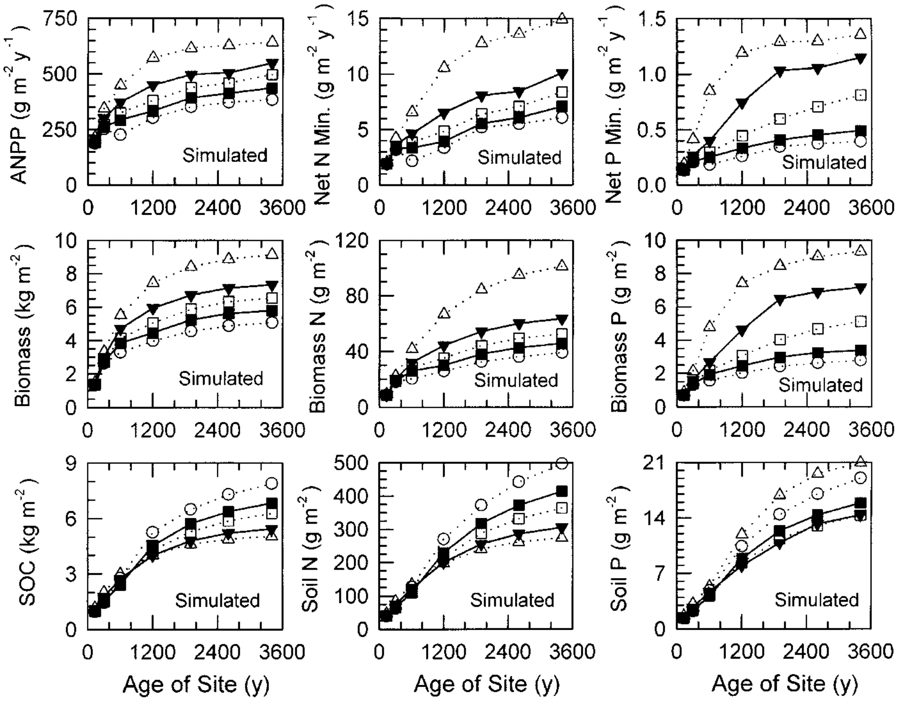

Figure 7. Simulated ecosystem attributes during the first 3500 y of primary succession on windward Mauna Loa, Hawaii, in response to different rainfall regimes. The model was run using the parameter values and climatic conditions of 700 m elevation; only the total annual precipitation was changed among simulations. Key: △ · · · △, 1.5 m/y; ▼—▼, 3 m/y; □ · · · □, 4.5 m/y; ■—■, 6 m/y; ○ · · · ○, 10 m/y. Each symbol represents the mean of 11 individual simulation years.

but over the same range N losses through leaching increased from 320 to 778 g/m^2. These effects combined to generate lower nutrient availability to plants as rainfall was increased. This model result is consistent with studies along a precipitation gradient in Hawaii (Austin & Vitousek 1998): concentrations of available soil P and N and foliar nutrient contents per unit leaf area all declined with increasing precipitation. As a result of decreased nutrient availability, simulated plant productivity was reduced (Figure 7).

Time

To determine if any of the elevational patterns that we simulated (Figure 2) would change in the longer term, we ran the model for 20,000 y at five elevations, using the elevation-specific climate data (Table 1) and parameters as drivers. The results from this exercise were similar to the 3500-y

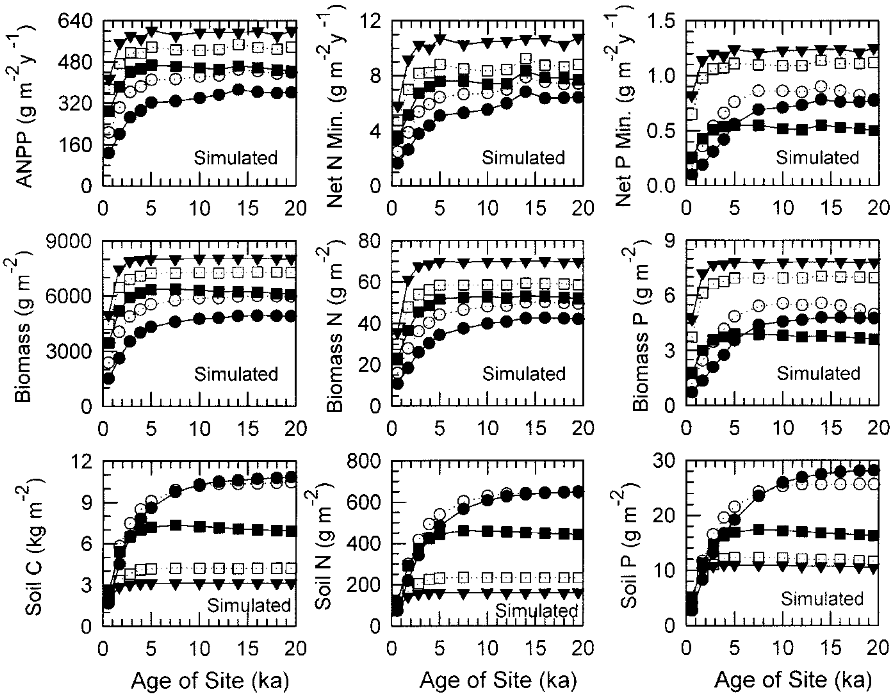

Figure 8. Simulated ecosystem attributes during the first 20,000 y of primary succession at five elevations on windward Mauna Loa, Hawaii. Elevation-specific climate and N input values were used, as in Figure 2, which shows the first 3500 y at these same elevations. Key: ▼—▼, 10 m; □ · · · □, 290 m; ■—■, 700 m; ○ · · · ○, 1130 m; ●—●, 1660 m. Each symbol represents the mean of 11 individual simulation years.

runs (*cf.* Figures 3 and 10), but also highlighted some additional points. First, productivity and soil element pools continued to increase after 3500 y, emphasizing the slow nature of ecosystem development on these sites (Figure 8). Simulated soil C, N, and P pools were still increasing after 20,000 y at our highest-elevation site. Second, high- and low-elevation sites developed into structurally different ecosystems: forest biomass declined but SOM (and total detritus) pools increased with increasing elevation (Figure 8).

The slow, long-term declines in plant productivity, P mineralization, and biomass P in the simulations at 700 m elevation (Figure 8) were the result of accumulated leaching losses of P under the 6 m per year of rainfall received at that elevation. This long-term nutrient depletion is probably a consequence of our modeling P inputs from rock weathering only. Dust from central Asia was deposited on these sites during glacial times, sustaining rainforest productivity over long time periods (Chadwick et al. 1999), and virtually all lava flows greater than 3500 y old on windward Mauna Loa have received ash from local volcanic eruptions.

Discussion

Field studies on windward Mauna Loa showed that aboveground plant productivity declined with increasing elevation (Raich et al. 1997); plant biomass increased with site age and declined with increasing elevation (Aplet & Vitousek 1994; Aplet et al. 1998); nutrient uptake by vegetation declined with increasing elevation (Raich et al. 1997); soil depth increased with site age (Kitayama et al. 1995; Raich et al. 1997); and soil element pools were similar on old flows at 700 m and 1660 m elevations despite their different productivities (Raich et al. 1997). Determining why these variables change as they do along environmental gradients on Mauna Loa, based on field studies alone, has proven to be difficult. For instance, Raich et al. (1997) found that ANPP, nutrient uptake, temperature, and elevation were all highly correlated among young-flow sites. What specific factors control ecosystem attributes on windward Mauna Loa?

We initiated all our simulations on barren pahoehoe lava, free of soil, vegetation, and organic matter. Simulated plant productivity, biomass, and soil element pools approached their maximum values more quickly at lower than at higher elevations (Figures 2 & 8), as found in field studies (Raich et al. 1997), indicating that ecosystem development proceeded faster at lower elevations. However, when we provided excess nutrients within our altered-temperature scenario, all sites reached their maximum simulated productivity rates within about 200 y, indicating that the slower rates of ecosystem development at higher elevations were due to nutrient limitation, not cooler temperatures. Succession proceeded faster where nutrient availability was higher. In our simulations, lower nutrient availability at higher elevations was due both to lower rates of nutrient cycling and lower inputs of N. Precipitation inputs of nutrients have not been measured along an elevational gradient on Mauna Loa, but this prediction is directly testable.

One factor we did not consider with Century was stand-level dieback, during which entire forest canopies die over a span of years (Mueller-Dombois 1985, 1986, 1987; Hodges et al. 1986). Our predictions of live plant biomass were based on estimating the mean annual mortality rate of tree boles over 3400 y of succession, a period that includes dieback events. Our predictions represent long-term averages that include dieback events, and they are consistent with our field data (e.g., Figure 3) and with the observation that forest biomass increases with forest age and declines with increasing elevation on ’a’a (i.e., clinker-rock) lava flows (Aplet & Vitousek 1994; Aplet et al. 1998).

Soil organic matter accumulation

Soil OM, including C, N, and organic P, is the soil on pahoehoe lava sites, so factors controlling the accumulation of SOM are integral to ecosystem development in Mauna Loa. Our simulations suggest that soil accumulation on windward Mauna Loa proceeds much faster than it would if these sites were well drained (Figure 1). Diminished soil drainage through time was simulated to halve the rate of SOC decomposition at 700 m elevation, via increasing the frequency of anaerobic conditions. A secondary effect of the more rapid soil accumulation that followed soil flooding was a more rapid increase in on-site water storage. Through time, simulated water supply to plants became increasingly buffered against dry periods.

The SOM pool is controlled in part by rates of detritus production but, after 3400 y, plant productivity and SOM pools varied inversely along the simulated elevational gradient (Figure 9(A)). As temperature was increased within the model, NPP increased and SOM accumulation declined (Figure 9(B)). As rainfall was increased, NPP decreased and SOM pools increased (Figure 9(C)). Only within climatic regimes, where production varied as a function of nutrient availability (Figure 9(D)), were SOM pool size and NPP positively correlated after 3400 y. Among climatic regimes, long-term SOM pools were controlled more by their rates of loss (decomposition) than supply (production). The similarity in simulated SOM pools in our elevational and temperature scenarios (Figures 9(A & B)) suggests that temperature was the single major factor controlling elevational patterns of SOM accumulation after 3400 y. A trend of increasing soil C storage with increasing elevation on tropical mountains has been reported previously (Jenny et al. 1948; Pécrot 1959; Alexander & Pichott 1979).

Plant productivity

One objective of our study was to distinguish the effects of temperature from those of nutrient availability and rainfall, all of which varied with elevation on Mauna Loa, and all of which influenced rates of NPP (Figure 9). Rainfall declines above its maximum at about 700 m elevation (Table 1), but lowering rainfall in our simulations had the effect of stimulating productivity and nutrient mineralization rates (Figure 7). As these are opposite our observed and simulated trends (Figures 2 & 3), differences in precipitation are unlikely to explain the declines in production at higher elevations. Rather, our simulation results suggest the following.

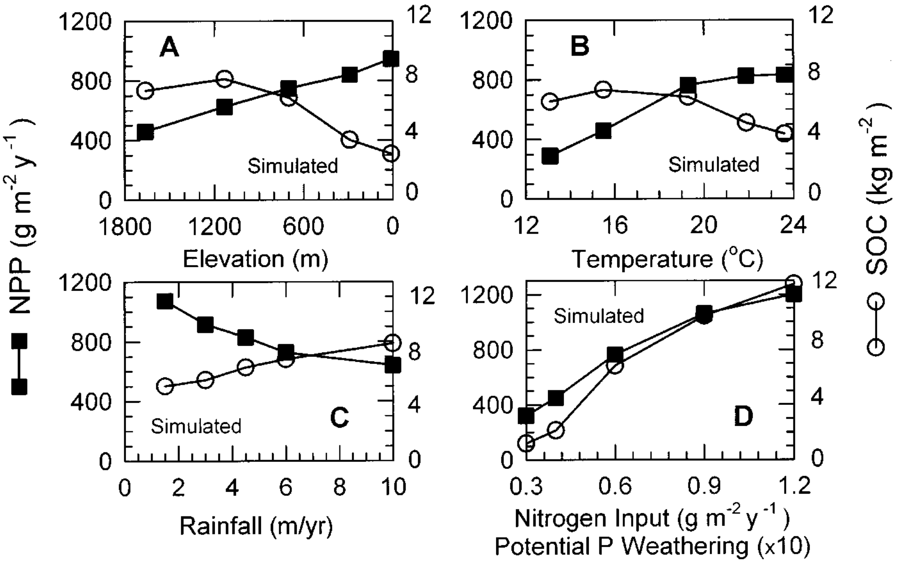

Figure 9. Simulated total net primary productivity (NPP) and soil organic carbon (SOC) pools after 3400 y of succession on windward Mauna Loa, Hawaii, in relation to environmental factors. (A) Simulated variations with elevation (Figure 2). (B) Simulated variations in response to different temperature regimes (Figure 6). (C) Simulated variations in response to different rainfall regimes (Figure 7). (D) Simulated variations in response to changing nutrient (N + P) supply (Figure 5).

Plant productivity declines with decreasing nutrient availability (e.g., Figures 5 & 9). Therefore, lower nutrient availability at higher elevations could generate lower rates of NPP. Given excess nutrients, simulated NPP varied with temperature. Therefore, cooler temperatures at higher elevations also could cause lower rates of NPP. Under nutrient limitations, declines in productivity would be associated with lower foliar nutrient concentrations, which vary in response to nutrient supply. If cooler temperatures alone controlled the decline in productivity, however, the demands of plants for nutrients would decline without a concomitant decline in nutrient availability. In our simulated elevational gradient, foliar N and P concentrations both declined with increasing elevation (Figure 10), and this model result is consistent with field observations (Vitousek et al. 1988, 1992; Raich et al. 1997; Russell et al. 1998). Both our simulations and field data support the conclusion that decreasing nutrient availability contributes to the declines in ANPP that we observed with increasing elevation on Mauna Loa. The elevational gradient on Mauna Loa appears to be both a temperature and a nutrient-availability gradient.

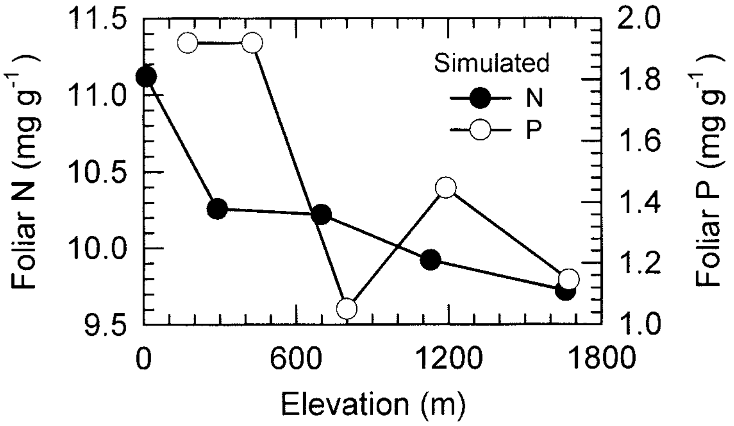

Figure 10. Simulated foliar nutrient concentrations after 3400 y of primary succession on windward Mauna Loa, Hawaii, in relation to site elevation.

Our simulations also suggest that direct temperature limitations on photosynthetic C assimilation would be more important were nutrient availability higher. We defined total N availability as the sum of net N mineralization and total N inputs, and plotted NPP as a function of N availability as simulated by our different model runs. The maximum NPP simulated at any given N supply (Figure 11) suggests that the temperature regime had virtually no effect on NPP when N availability was low (<5 g m^{-2} y^{-1}), but was wholly responsible for differences among elevations when N availability was high (>20 g m^{-2} y^{-1}). Our conclusion that temperature-mediated nutrient availability generated the elevational gradient in NPP that we observed on windward Mauna Loa is a result of low nutrient-cycling rates in those sites. Why, then, do these sites remain nutrient limited over the long term, despite annual inputs of both N and P?

Nutrient losses and the maintenance of oligotrophy

Our results suggest that the large amounts of precipitation received on windward Mauna Loa promote oligotrophy by leaching nutrients from the system and by depressing rates of nutrient mineralization (Figure 7). In both cases nutrient limitations to plant production were exacerbated, but for different reasons. By continually washing away a portion of the nutrient pool, excessive water inputs promoted the maintenance of oligotrophic conditions despite annual nutrient inputs, as proposed by Hedin et al. (1995) for Chilean watersheds. Large amounts of rainfall also increased the frequency of soil flooding, which slowed decomposition and nutrient mineralization rates. These decreased decomposition rates enhanced SOM accumulation, but there

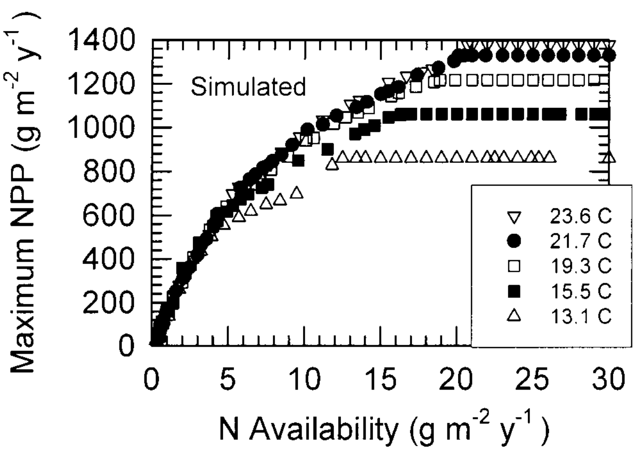

Figure 11. The maximum simulated NPP shown in relation to simulated N availability from all of our different model simulations of windward Mauna Loa. Data are grouped by mean annual temperature. In most years, NPP was lower than that shown due to limitation by a factor other than N availability.

was nevertheless a decrease in net N and P mineralization rates (Figure 7). Thus, rainfall had dual impacts: increased leaching removed nutrients from the ecosystems, whereas lower rates of soil turnover kept nutrients on-site but unavailable; both effects lowered nutrient availability to plants. These predictions are consistent with data from long-term soil chronosequences in Hawaii; foliar nutrient concentrations tended to be lower (Vitousek et al. 1995b), and tree diameters were consistently smaller (Kitayama & Mueller-Dombois 1995), on wet ($>$4 m/y of rainfall) versus mesic ($\approx$2.5 m/y of rainfall) sites.

Although we have no data on rates of nutrient leaching from these sites, our simulation results offer some predictions. Century predicts that C, N, and P leaching increases through time, but that water fluxes do not (Figure 12). This suggests that concentrations of C, N, and P in leachate waters should be greater on older flows, and thereby provides a testable hypothesis. The simulated temporal changes in nutrient leaching rates (Figure 12) are inversely proportional to rates of net biomass accumulation (Figure 4), as predicted by Vitousek and Reiners' (1975) model. However, Vitousek and Reiners (1975) observed that nitrate was the predominant form of N being leached, possibly due to the high rates of N deposition received at their site (e.g., Hedin et al. 1995). Century predicts that virtually all of the P and most of the N leached from Mauna Loa's ecosystems is in organic form (Figure 12).

Century also predicts that significant losses of nitrogenous gases occur from our sites (e.g., Figure 4(F)), primarily as a result of nitrification. Both simulated organic leaching and N-gas production rates increased with rates

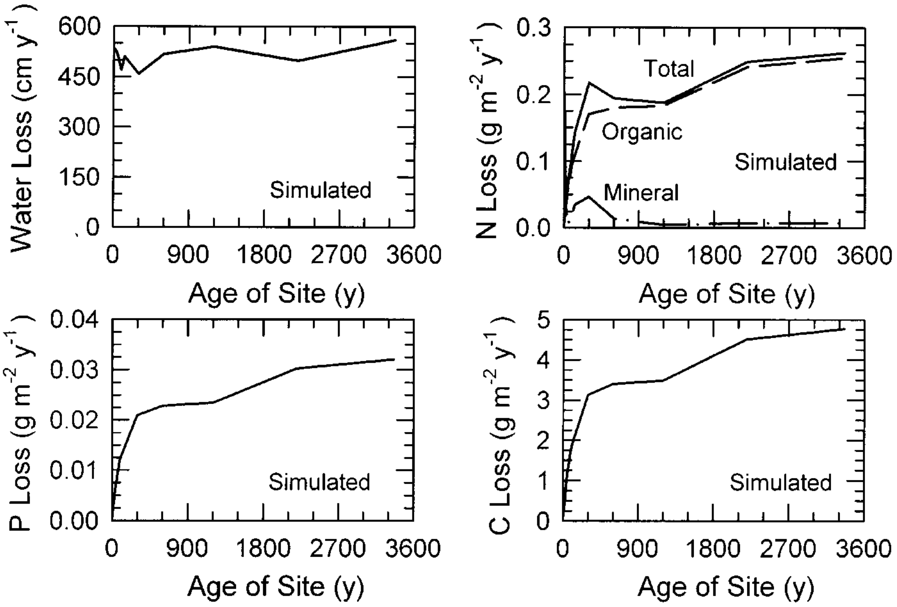

Figure 12. Simulated rates of water, nutrient, and organic carbon leaching during the first 3500 y of primary succession at 700 m elevation on windward Mauna Loa, Hawaii. For N, leaching of mineral N, organic N, and total (inorganic + organic) are shown. The leaching of inorganic P was not discernible at the scale presented; virtually all P losses were organic.

of biological activity, and therefore nutrient supplies were depleted faster as elemental cycling rates increased. Nutrient supplies were also depleted by leaching of mineral N and P from the available soil pool. However, plant and microbial immobilization of inorganic nutrients maintained low levels of mineral N and P in the soil, resulting in low simulated mineral nutrient loss rates (Figure 12). Over the long term such a process, working alone, could result in on-site nutrient accumulation, and decreasing nutrient limitation through time (Vitousek et al. 1998). According to our simulations, oligotrophy persisted in our sites despite minimal losses of mineral N and P. Simulated losses of organic nutrients caused nutrient limitations to persist over the long term (e.g., Vitousek et al. 1998). The ecosystems of windward Mauna Loa’s pahoehoe flows appear to remain nutrient limited not because nutrient input rates are low, but because they are leaky.

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