B-52.4 Study on the Threshold Temperatures of Extant Forest-Vegetation Zones on Humid Tropical Mountains, and Prediction of Global Warming Effects

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Abstract The aims of this study were to investigate the altitudinal patterns of ANPP, litter decomposition rates, and carbon sequestration of tropical rainforests, and to etimate the effects of temperature on ecosystem processes under contrasting soil P supplies on Mt. Kinabalu, Borneo. ANPP (g/m2/yr) was measured as wood increment plus litterfall. Measured ANPP declined linearly with increasing altitude (ALT) and this linearlity suggested profound effects of temperature on net carbon fixation. ANPP could be explained by both ALT and PAR (annual photosynthetically active radiation,mol/m2/yr) or by ALT only, depending on the supply of soil P following: ANPP=67AT+0.15PAR–1282 (P-richer substrate); ANPP=104AT-773 (P-poorer substrate). We conclude that 1C rise in air temperature will result in the dry matter gain of 67g on P-richer substrate, and 104g on P-poorer substrate. The greater temperature dependency of ANPP on P-poorer substrate could be due to lesser demand for P to fix unit carbon under warmer conditions. Litter decomposition rates demonstrated an exponential rise against a linear increase of litterfall rates. The total amount of soil C (to saprolite or to 1 m depth when deeper) exponentially increased with increasing altitude on sedimentary rock, while the total ecosystem (AGB + soil) C was remarkably constant. Thus, when biophilic soil nutrients were not strongly limiting, the transient production-decomposition relationship could be straightforwardly transcribed to the altitudinal sequence of steady-state ecosystem structure as a function of temperature. Conversely, the ecosystem processes on ultrabasic rock appeared to be limited interactively by P and temperature, and the amount of ecosystem C decreased with increasing altitude. We suggest that warming will result in a net release of soil C as a short-term response, but in a long-term response AGB will sequester C and the net ecosystem C will eventually revert back in these rain forests if biogeochemical feedbacks do not operate between net released C and instantaneous C assimilation.

1. Introduction

The major aims of our study were to investigate the patterns of above-ground net primary productivity (ANPP) of tropical rain forests on a single mountain slope spanning from the lowland to near the forest limit, and then to functionally relate the changes of ANPP to the patterns of stand structure, soil nutrient supply, and foliar characteristics. In this study, we used altitude as a surrogate of air temperature, and attempted to discuss the effects of temperature on ecosystem processes. The adequacy of the use of mountain slopes to study effects of air temperature on ecosystem processes may be arguable considering multiple interdependent factors. However, given that the manipulation of temperature in tropical rain forests in an ecosystem context is not practical, studying the control of ecosystem processes on a single mountain can help explain the complex nature of temperature effects.

Effects of temperature may be twofold; a direct control of plant physiology and an indirect control through soil nutrient availability. The availability of soil nutrients that are supplied through mineralization of organic matter is strongly temperature dependent. Furthermore, a possible feedback between the quality of organic matter produced and the supply of the nutrients adds to the complexity. To study the interactions of temperature and nutrients, we added another variable (i.e. geological substrate) in addition to altitude. Two different geological substrates (i.e. sedimentary versus ultrabasic rock) occur at close proximity at a range of altitudes on Mount Kinabalu, Borneo. We used sedimentary substrate as sites with richer P, and ultrabasic substrate as poorer sites. Specifically, we questioned if the magnitude of altitudinal changes in ANPP and other ecosystem processes would be greater on P-richer sedimentary substrate than on P-poorer ultrabasic substrate because the temperature dependency of the processes would be greater under a relaxed nutrient limitation.

2. Materials and Methods

We established a matrix of eight study sites by choosing four elevations (700, 1700, 2700 and 3100m) each on two contrasting geological substrates (sedimentary versus ultrabasic rocks) . The sedimentary rock consists largely of sandstone and mudstone. The ultrabasic rock consists of serpentinised peridotite. Derived soils from sedimentary than from ultrabasic rocks are much richer in labile inorganic P, soluble P, and total active P. At each elevation on each substrate, we established a permanent plot of rectangular project area. In these permanent plot, we measured or analyzed litterfall, tree growth, litter decomposition rates, plant community structures including leaf area index (LAI), foliar nutrients, and the amount of carbon in soil and above-ground vegetation. ANPP was calculated as wood increment plus litterfall. Wood increment was based on the allometric equations of dry matter with tree diameter and height.

Effects of altitude on various variables of ecosystem processes and structure were examined by linear regressions using altitude as independent variables on each substrate. When appropriate, two regressions with and without logarithmic transformations on dependent variables were compared in terms of coefficient of determination to determine if the altitudinal changes were linear or exponential. When regression coefficients were significant at $P=0.1$, differences in the slopes and intercepts of regressed lines were tested between substrates by ANOVA followed by ANCOVA.

3. Results and Discussion

Table 1 shows altitudinal changes of various measured variable on each substrate. Table 2 summarizes the results of ANOVA and ANCOVA. The estimated live above-ground biomass decreased linearly from 43.7 to 21.5 kg/m2 on sedimentary rock, and from 55.4 to 3.7 kg/m2 on ultrabasic rock. Optically measured leaf area index (LAI) decreased upslope on both substrates. The measured ANPP (g/m2/yr) decreased significantly and linearly with increasing altitude (ALT, m) following ANPP=2097-0.46*ALT (n=4, r2=0.91, P=0.04) on sedimentary, and ANPP=2064-0.58*ALT (n=4, r2=0.92, P=0.04) on ultrabasic rock. The slopes of regressed lines were not significantly different in contrast to our prediction (Table 2). The intercept was, however, significantly greater on sedimentary than on ultrabasic substrate (Table 2). The linear responses of ANPP to altitude strongly indicate the profound effects of temperature on ANPP, because the other linearly decreasing climatic factor (i.e. air pressure and associated CO2 partial pressure) cannot theoretically explain the reduction of ANPP.

Stand-level photosynthetic nutrient use efficiencies of these forests (the ratio of litterfall-mass to nutrient return) did not change with increasing altitude for N and P on sedimentary rock, but abruptly increased for P (and modestly for N) on ultrabasic rock (Table 2). Mean foliar N and P contents (area basis) of the sun leaves of abundant canopy species increased upslope on both substrates; the content was always comparable between substrates for N, but always lower on ultrabasic rock for P. Net assimilation rate (NAR) expressed as ANPP divided by LAI did not change on sedimentary rock, but linearly decreased with increasing altitude on ultrabasic rock. Hence, the reduction of ANPP could be explained by diminished LAI on sedimentary rock, and by combined effects of diminished LAI and NAR on ultrabasic rock. These foliar characteristics together with the pattern of labile soil P pools suggested that plants could adjust to maintain NAR under colder environments by increasing foliar N and P on sedimentary rock, but could not adjust due to P deficiency on ultrabasic rock.

Overall, ANPP could be expressed as a function of both air temperature (AT) and PAR (annual amount of photosynthetically active radiation), or a function of air temperature only, following:

Sedimentary; ANPP=67AT+0.15PAR-1282 (r2=0.99, P=0.09)
Ultrabasic; ANPP=104AT-773 (r2=0.92, P=0.04)

ANPP of tropical rain forests on sedimentary rock is not strongly limited by soil nutrients, and conversely limited by PAR in addition to air temperature. ANPP on ultrabasic rock is more strongly limited by P, therefore the inclusion of PAR does not improve the coefficient of determination. According to these equations, we predict that the rise of 1C air temperature will result in the dry matter gain of 67 (g/m2/yr) when P is not limiting, and of 104 (g/m2/yr) when P is limiting. The greater temperature dependency of ANPP on P-deficient substrate can be explained by the lesser demand of plants for P to fix a unit carbon under warmer condition.

Litter decomposition rates (mean standing litter biomass divided by litterfall mass) demonstrated an exponential rise against a linear increase of litterfall mass. The total amount of soil C (to saprolite or to 1 m depth when deeper) exponentially increased with increasing altitude on sedimentary rock, while the total ecosystem (AGB + soil) C was remarkably constant. The total amount of ecosystem C decreased with increasing altitude on ultrabasic rock, while soil C was remarkably constant. Thus, when biophilic soil nutrients were not strongly limiting, the transient production-decomposition relationship could be straightforwardly transcribed to the altitudinal sequence of steady-state ecosystem structure as a function of temperature. Conversely, the ecosystem processes on ultrabasic rock appeared to be limited interactively by P and temperature, and the amount of ecosystem C decreased with increasing altitude.

We suggest that warming will result in a net release of soil C as a transient response because the exponential increase of decay constant K exceeds the linear increase of net carbon fixation. However, in a long-term stabilized response, the net release of carbon will be compensated by the increase of AGB and the net ecosystem C will eventually revert back in these rain forests. This scenario applies when biogeochemical feedbacks do not operate between net released C (transient release) and instantaneous C assimilation. The investigation into whether this biogeochemical feedback operates will improve the ability of prediction.

Table 1. Above-ground net primary productivity (ANPP) by components, decomposition rate of litter (k), and the amount of carbon storage.

Alt.(m)	700	1700	2700	3100	700	1700	2700	3100
Substrate		Sedimentary				Ultrabasic		
Litterfall(g/m2/yr)	1110	780	532	631	1113	628	594	164
Wood (g/m2/yr)	803	423	248	185	602	185	131	35
ANPP(g/m2/yr)	1913	1222	780	816	1715	813	725	199
K (yr-1)	1.69	1.18	1.00	0.87	1.67	0.71	0.80	0.44
Soil C(ton/ha)	61.5	93.1	151.1	262.4	94.13	85.48	84.24	66.7
Above C(ton/ha)	245.5	147.5	154.0	111.5	276.0	120.0	63.5	19.0
Ecosystem C(ton/ha)	307.0	240.6	305.1	373.9	370.1	205.5	147.7	85.7

Table 2. Summaries of linear regressions on each of the two substrates and ANCOVA between the two substrates. AGB (above-ground biomass), ANPP (above-ground net primary production), LMA (leaf mass per area), QUE ($ANPP/PAR_{absorbed}$; phtosynthetically active radiation-use efficiencies), LAI (leaf area index) and NAR (ANPP/LAI; net assimilation rate). Nutrient-use efficiencies include PUE (phosphorus-use), NUE (nitrogen-use), CaUE (Ca-use), MgUE (Mg-use), and KUE (K-use). For all cases, n=4.

		Sedimentary			Ultrabasic			ANCOVA (F)	
Indep.	Depend.	Intercept	Slope	r^2	Intercept	Slope	r^2	Slope	Intercept
Alt.	AGB	46.3	-0.00759	0.802*	68.3	-0.0214	0.981***	**16.305****	**8.313****
Alt.	ANPP	2097	-0.464	0.914**	2063	-0.578	0.921**	0.296	**3.865***
Alt.	Litterfall	1194	-0.216	0.857*	1348	-0.348	0.879*	1.431	1.142
Alt.	Litter/Δ wood	0.799	7.149E-4	0.807*	1.020	0.00125	0.992***	4.088	**17.63*****
Alt.	Ln(PUE)	8.59	8.87E-6	0.004	8.090	6.783E-4	0.855*		
Alt.	Ln(NUE)	4.602	1.027E-4	0.602	4.543	2.708E-4	0.915**		
Alt.	Ln(CaUE)	5.831	-1.554E-4	0.080	5.594	-2.347E-4	0.356		
Alt.	Ln(MgUE)	6.161	1.125E-4	0.345	6.035	2.083E-4	0.983***		
Alt.	Ln(KUE)	5.775	1.364E-4	0.639	5.895	5.146E-4	0.662		
Alt.	LMA	120.5	0.0345	0.974**	128.2	0.0512	0.849*	1.147	**8.098****
Alt.	Foliar N (area)	1.596	1.198E-4	0.468	1.382	2.397E-4	0.905**	1.261	0.079
Alt.	Foliar P (area)	25.859	0.00486	0.868*	10.397	0.00539	0.927**	0.094	**99.92*****
Alt	LAI	5.334	-8.676E-4	0.907**	6.505	-0.00138	0.792		
Alt.	QUE	0.261	-0.0486	0.998***	0.248	-5.954E-5	0.843*	0.372	**5.256***
Alt.	NAR	401	-0.0406	0.361	361	-0.071	0.949**		
Alt.	Decomp. K	1.816	-3.201E-4	0930**	1.874	-4.664E-4	0.839*	0.885	2.810
PAR	NAR	-231	0.060	0.963**	-66.7	0.030	0.225		
LAI	ANPP	-507	466	0.765	-510	377	0.943**		

*P<0.1: **P<0.05; ***P<0.01