Carbon pools and efflux in forest soils of different successional stages

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Abstract: Soil microbial communities dominate carbon efflux from terrestrial ecosystems. Forest disturbance could affect carbon pools and efflux rates. We measured soil respiration, carbon content and moisture content in forests at La Selva Biological Station including 0 - 5 year-old successional plots, 30 - 34 year-old secondary forest and primary forest. We expected respiration to be highest in the earliest successional stage due to the recent input of dead organic matter, and then decrease as microbial activity depletes carbon pools. Successional stage did not clearly affect soil respiration, although successional age and respiration tended to be inversely related. Carbon content of soil samples from 0 - 4 cm did not vary across sites. Soil moisture increased with successional time, perhaps due to increased evapotranspiration in early successional plots. Our results suggest that carbon pools and efflux rates do not vary with forest disturbances such as those that created the range of successional stages in our study.

Key Words: AFDM, La Selva, microbial community, moisture content, primary forest, secondary forest, soil respiration, successional plots

Introduction

Decomposers are responsible for most of the carbon dioxide production in every ecosystem in the world (Begon et al. 1990). Forest disturbance may alter the balance between carbon pools and carbon flux and these effects can persist through forest succession. During the early phases of forest succession, soil respiration may increase because of increased biomass input, warmer soil temperatures and improved moisture conditions. Then, with relatively little new litter deposition, carbon content of soil tends to decline, but eventually equilibrates as succession proceeds (Sprugel 1985). This pattern has been observed in temperate systems, but may not be applicable to tropical systems if they have different patterns of decomposition in dead organic biomass. Successional dynamics in tropical systems are pertinent to much of the contemporary landscape because of a growing number of abandoned pastures. Decomposition rates in the tropics far exceed temperate rates, and annual litterfall increases with decreasing latitude, following a gradient in productivity. Even though carbon input is greater, the rapid turnover in tropical systems results in a much smaller litter layer than found in temperate forests (Waring and Schlesinger 1985).

A unique opportunity exists in the tropical wet forest in La Selva, Costa Rica to study changes in carbon flux and pools with successional time. Currently, the effects of succession on plant community composition and dynamics are being studied by maintaining 0.5 ha of 0 - 5 year old plots, where every 5 years the standing biomass of a plot is cut, but not removed. Additionally, the land use history of other areas in the preserve is well documented. We studied the effects of successional age on measures of carbon flux, carbon pools and soil water content in La Selva. We hypothesized that carbon efflux (microbial respiration) would initially increase in response to returning standing biomass to the soil, then decrease as microbial activity would cause a decline in available carbon. Following models for temperate forests, we expected soil organic matter and microbial productivity to equilibrate with increasing successional time (Sprugel 1985). We chose a broad range of successional ages to evaluate the stage at which carbon flux and pools come to equilibria.

Methods

On 13 - 14 February 2002, we sampled soil from 3 of the 5 successional plots, a nearby secondary forest (30 - 34 years old) upslope from 650 – 800 m on the Sendero Sabalo-Esquina, and primary forest between 150 – 300 m on the Camino Experimental Sur. Soils of these areas are similar, described as andic humitropept, or youthful soils of volcanic origin with a large organic-matter content and water-holding capacity (Sollins et al. 1994). The successional plots are staggered to show stages of growth at 0 – 1, 1 – 2, 2 – 3, 3 – 4 and 4 – 5 years. Every five years, the oldest growth plot is cut to become the new 0 – 1 plot. We haphazardly collected 7 soil samples from a depth of 0 – 4 cm from the 0 – 1, 2 – 3 and 4 – 5 plots as well as secondary and primary forests. Respiration rates were measured in the lab using volumetric respirometers. We obtained measurements for 4 of 7 samples. Respiration flasks containing a bottom layer of potassium hydroxide (~1.5 cm thick), middle layer of cotton (~1.5 cm thick) and a top layer of soil (~3 cm thick) were capped with a rubber stopper with an inserted graduated pipette. A control was made in the same manner with no soil allowing us to correct for variations in gas volume not due to soil respiration (mostly due to change in barometric pressure). Flasks were placed horizontally in a water bath for 10 min to equilibrate, and then changes in gas volume in each pipette were recorded every 10 min for 30 min. The change in volume after 30 min was corrected by subtracting one half the change in volume of the control (because the control contained about twice as much gas volume). Respiration rates ($\mu l \cdot g^{-1} \cdot h$) were calculated as two times the corrected change in volume divided by dry mass of soil.

Soil was dried overnight in drying ovens to determine soil moisture content. Carbon content was determined by heating samples in a muffle furnace at 450°C for 7 hours. Percent carbon was determined using the formula:

ash-free dry mass [(dry weight – AFDM)/dry mass) • 100

Soil moisture and carbon content were measured on 7 samples per successional stage.

We ran a general linear model of respiration rate versus successional age (treating each of three respiration trials with 1 sample per successional stage as a block). We analyzed percent carbon and percent soil moisture with the same model (block, in this case, representing two batches of samples processed in the ovens). In both models, successional stage was evaluated both as a categorical variable and as a continuous variable from 1 - 5 (early succession to primary forest). We also evaluated the effect of all combinations of soil moisture and carbon content on respiration rates.

Results

There was little effect of successional age on respiration rates. However, respiration rates tended to decrease with successional time (Fig. 1). Respiration rates were independent of all combinations of moisture and carbon and their interactions ($P > 0.16$) with successional age (Fig. 2). Moisture content was positively related to successional age ($F_{1,18}$ =

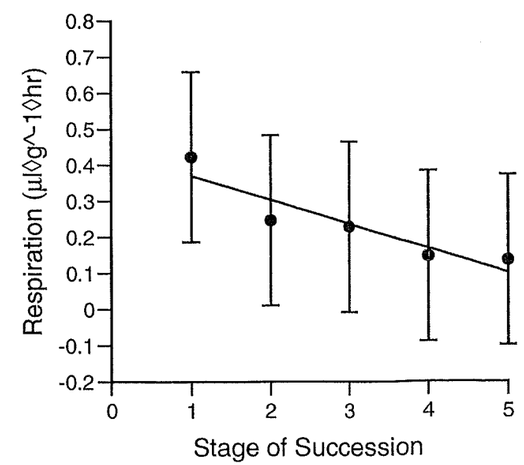

FIG. 1. Respiration rate of forest soils in different successional stages. Stage 1 = 0 to 1 year succession, 2 = 2 to 3 year succession, 3 = 4 to 5 year succession, 4 = secondary forest, 5 = primary forest.

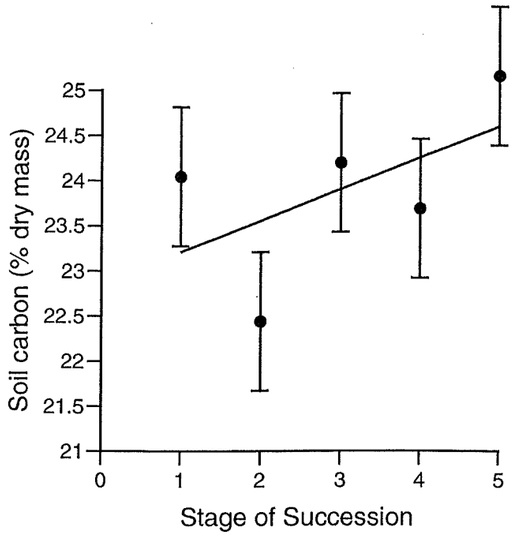

FIG. 2. Percent carbon in soils from forests at different successional stages. Stage 1 = 0 to 1 year succession, 2 = 2 to 3 year succession, 3 = 4 to 5 year succession, 4 = secondary forest, 5 = primary forest.

10.58, P = 0.003), but when the primary forest was excluded, there was little relationship ($F_{1,11}$ = 1.82, P = 0.19).

Discussion

Our hypothesis was refuted by the lack of a significant relationship between respiration rates and successional age (Fig. 1). Respiration rates may have been independent of successional time because the disturbance experienced by the successional plots was relatively minor. When biomass is cut but not removed, few nutrients leach out of the system, and standing carbon is returned to the soil. The minor disturbance may only minimally affect respiration rates, or its effects might be short-lived due to extremely rapid turnover.

However, estimates of respiration rate declined in order from early succession to primary forest. The lack of significance might have been due to small sample sizes and measurement error with the respirometers (especially because of changing barometric pressure during the measurements). Respiration rates were independent of carbon levels and soil moisture, suggesting that if respiration does vary with successional stage, it was attributable to something other than carbon or water content. Higher respiration rates in younger forests could be due to higher resource quality of litter from pioneer species, which devote fewer resources to secondary metabolites (Coley 1983). Respiration rates might also vary across successional stage if the microbial community shifts, perhaps in response to the changing food resource or changing soil temperature.

Contrary to our hypothesis, carbon content of soil did not vary across successional stages (Fig. 2). At soil depths of 0 – 4 cm, carbon levels appeared to be stable through all successional stages. This is as expected if litter input and microbial respiration do not change with successional stage. It appears that carbon content of the soil is resistant to relatively minor disturbance.

Interestingly, soil moisture content did increase with successional age. This trend is contrary to patterns in temperate forests, where early successional phases are often associated with increased moisture (Sprugel 1985). The pattern at La Selva could reflect decreased evapotranspiration in the cooler, more sheltered primary forest. The young successional plots, in contrast, had areas of low vegetation cover. However, this relationship was largely driven by the primary forest, which was located on a different terrace (Sarapiqui River) than the secondary and successional plots (Puerto Viejo River), so differences could have been due to soil type rather than successional stage.

Carbon flux could be more comprehensively measured by examining respiration rates across the entire soil community (microbes plus other detritivores). Additionally, variation in carbon pools with successional time may be occurring at depths greater than 4 cm. Analyzing samples from different soil depths could reveal patterns in microbial abundance across space and successional time.

Differences in carbon content and respiration rate may be more pronounced in systems with past intensive land use. Succession from abandoned farm and pasture land could follow a very different trajectory than the rapid succession occurring on the fertile successional plots at La Selva. Nonetheless, our results indicate that carbon pools and flux rates in tropical systems are relatively invariant across successional stages.

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