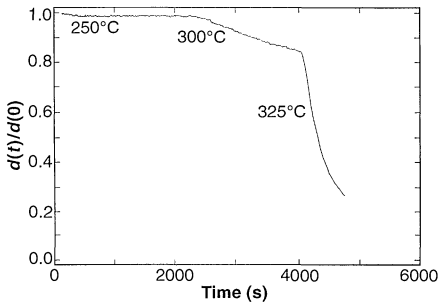

Fig. 4. Decay of the normalized SHG coefficient $d(t)/d(0) = [I(t)/I(0)]^{1/2}$ as a function of time for **PI-1**. This experiment was done on the same sample studied in Fig. 3 after the 1000-hour decay experiment shown in that experiment was completed.

probably results from the stronger coupling of the orientational motion of the NLO-chromophore in both **PI-1** and **PI-2** to the polymer backbone than occurs for the side-chain system **PI-3**. Rearrangement of the chromophores in **PI-1** and **PI-2** thus requires correlated motion of a substantial region of the polyimide backbone.

A poled **PI-1** sample was maintained at 225°C for 1000 hours while monitoring the orientational decay (Fig. 3). After a decrease of ~7% during the first 10 hours, no further measurable change occurred over a period of 1000 hours. Similar long-term stability, also shown in Fig. 3, was observed for **PI-2** held at 170°C. For the side-chain system containing a flexible tether group (**PI-3**), this kind of orientational stability was only observed for temperatures up to 100°C. Figure 4 shows the impressive short-term stability of **PI-1**. Here the polyimide is ramped up in temperature every 2000 s. At 300°C, the polymer loses only ~15% of its nonlinearity over this time increment, which is typical of device processing times.

This class of polymers can meet the severe operating and processing temperature requirements for application of these polymers in integrated optoelectronic devices. With recent advances in identifying chromophores with large optical nonlinearities (*16*) and in improving chromophore thermal stability (*5*), it should now be possible to produce thermally stable NLO polymer systems with large electrooptic coefficients.

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Plant Growth-Rate Dependence of Detrital Carbon Storage in Ecosystems

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Detrital carbon accumulation accounts for most of an ecosystem's capacity to store organic carbon because the carbon contained as plant detritus exceeds that stored in living plants by about threefold. A comparative analysis of the mass and turnover of detrital carbon in ecosystems demonstrates that these properties are strongly related to the turnover rate of the dominant primary producers and are poorly related to ecosystem primary production. These results contribute to an understanding of the factors that control carbon storage in ecosystems and the role of carbon storage in the global carbon budget.

The assessment of factors that control C storage in ecosystems (*1–3*) is essential for determining the role of vegetation in the global C budget (*4, 5*). Carbon storage in ecosystems is accounted for mostly by the detrital C mass, which amounts to about threefold that accounted for in living plant tissues (*3, 4*). Hence, knowledge of the factors that control the size and turnover of the detrital C pool in ecosystems should help elucidate the processes that control C sinks in the global C budget (*5*).

In this report we use a broad-scale comparison from published values to show that even though detrital C flux is strongly controlled by ecosystem primary production, neither one is strongly related to the mass and turnover of the detrital C pool. We then demonstrate that plant turnover rate explains a major fraction of the variance in detrital C mass and turnover among ecosystems. We compiled data from reports on aboveground biomass and primary production and the mass and production of detrital C (*6*) from a broad range of ecosystems (*7–11*).

Carbon flux into the detrital pool was strongly and linearly related to primary production (Fig. 1). This linear relation applied both to individual ecosystem types and to all the types grouped together (*12*). On average ~56% of primary production enters the detrital pool, and, with the exception of grasslands, more productive ecosystems yield a correspondingly higher C flow into the detrital pool. Our results support the general findings that litterfall rates are higher in more productive forests (*13*) and that phytoplanktonic primary production is positively correlated to phytoplankton sedimentation rates (*14*).

Detrital C mass was poorly related to both primary production and C flux into the detrital pool (Fig. 2), both of them explaining only ~10% of the variation in detrital C mass among ecosystems. The C mass of the detrital pool varied by about three orders of magnitude for similar values of C flux into this pool (Fig. 2B). The differences in detrital C mass among ecosystems were instead strongly correlated to the plant turnover rate (Fig. 3A); the tendency toward reduced detrital C mass with increasing plant growth rate accounted for 53% of the variance in detrital C mass.

The observations that detrital C mass is relatively independent of C flux into the detrital pool (Fig. 2B), whereas it declines as plant growth rate increases (Fig. 3A) imply that the loss rate of detrital C

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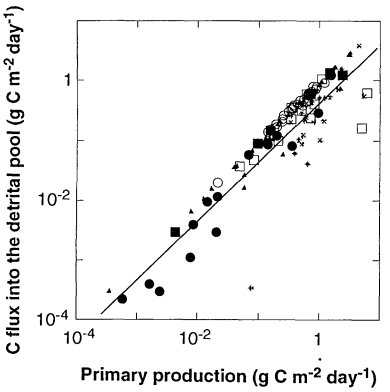

Fig. 1. The relation between C flux into the detrital pool and primary production (both in units of grams of C per square meter per day). The solid line depicts the regression equation fitted to the data. Symbols represent (*) plankton, (●) benthic microalgae, (△) macroalgal beds, (▲) freshwater macrophyte meadows, (■) seagrass meadows, (□) grasslands, and (○) forests.

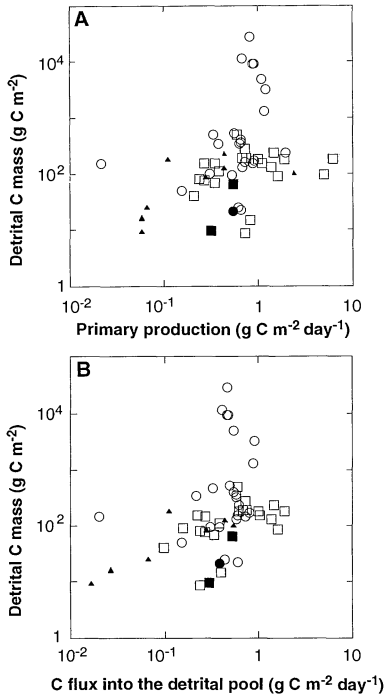

Fig. 2. The relation between detrital C mass (grams of C per square meter) and (**A**) primary production (grams of C per square meter per day), and (**B**) the C flux into the detrital pool (grams of C per square meter per day). The detrital C mass is poorly, although significantly ($P < 0.05$), correlated to the primary production ($r^2 = 0.1$, where r is the Pearson correlation coefficient) and to the C flux into the detrital pool ($r^2 = 0.13$). Symbols as in Fig. 1.

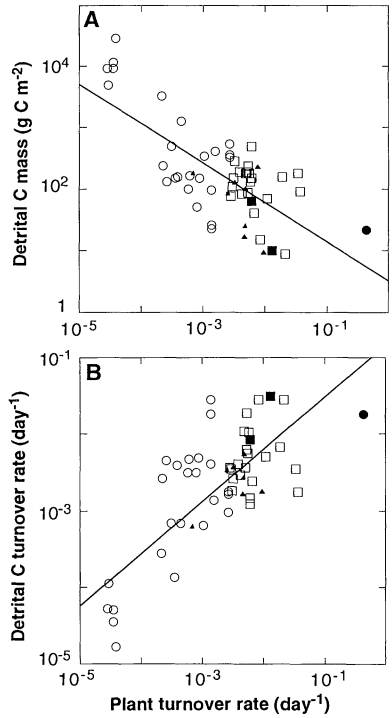

Fig. 3. (**A**) The relation between detrital C mass ($C_{detrital}$, grams of C per square meter) and plant turnover rate [PP/B, per day, where PP is primary production (grams of C per square meter per day) and B is plant biomass (grams of C)] for different ecosystems. The solid line represents the regression equation fitted to the data: $\log C_{detrital} = (0.43 \pm 0.24) - (0.67 \pm 0.08)\log PP/B$ (with $r^2 = 0.53$, $n = 53$, F test, $P < 0.00001$). (**B**) The relation between detrital C turnover rate ($TC_{detrital}$, per day) and plant turnover rate for different ecosystems. The solid line represents the regression equation fitted to the data: $\log TC_{detrital} = (-0.9 \pm 0.2) + (0.64 \pm 0.08)\log PP/B$ (with $r^2 = 0.52$, $n = 53$, F test, $P < 0.00001$). Symbols as in Fig. 1.

should increase with increasing plant growth rate. The net result of these processes is a significant tendency toward an increase in the turnover rate of the detrital C pool with increasing plant growth rate (Fig. 3B). This finding is consistent with the fast decomposition rates reported for the nutrient-rich detritus produced by fast-growing plants (*15*). Export of detrital C tends to be greater in aquatic ecosystems than in terrestrial ecosystems, but it typically represents only a small fraction of the C loss from the detrital pool (*9*, *10*); hence, export of detrital C cannot have a significant effect on the observed patterns.

Our results indicate that plant turnover rate controls the size and turnover of the detrital C pool, thereby setting the capacity of an ecosystem to store C. Hence, ecosystems dominated by slow-growing plants accumulate large, slowly decomposing detrital pools which act as C sinks both on a local and global scale (*1*, *2*). In contrast, C accumulation in the detrital pool of ecosystems dominated by fast-growing plants is much smaller. The magnitudes of primary production and the flux of C entering the detrital compartment reveal little about an ecosystem's capacity to store detrital C (Fig. 2).

The relation between detrital C mass and plant turnover rate described here provides a basis to assess the response of the detrital C pool to global changes in plant turnover rate. Several lines of evidence suggest that global changes in land use and climate may be conducive to a global increase in plant turnover rate (*1*, *3*, *16*–*20*). Coastal eutrophication has been shown to cause a shift from slow-growing, thick macroalgae and seagrasses to fast-growing phytoplankton and macroalgae (*16*). Deforestation replaces slow-growing plants (that is, forests) by faster growing (that is, grasslands and agricultural crops) plants (*1*, *3*, *17*). Grasslands are expected to expand through the northeastern American territories, which are presently colonized by mixed conifer-hardwood forests, in response to an atmospheric warming of 1.5° to 4.5°C by the end of the century (*18*). The turnover rate of tropical forests has increased since the 1950s (*19*), and higher atmospheric CO_2 concentrations may lead to a further increase in plant turnover rate (*20*). Our results suggest that these trends toward a global increase in plant turnover rate could result in a net decline in ecosystem C storage from losses of soil C. This prediction is in agreement with results from simulation models that combine the effects of change in climate, atmospheric composition, and the global spread of agricultural crops and range lands (*1*).

Our prediction of the effect of global changes in plant turnover rate on the size of the detrital C pool remains, however, qualitative because our data do not represent a random sample of the different ecosystems on Earth. Furthermore, the patterns described here represent empirical relations that may be blurred by feedback effects associated with simultaneous changes in growth conditions in response to changing global temperature and atmospheric CO_2 concentration (*21*). Yet, we demonstrate that the size and turnover rate of the detrital C pool are closely related to the turnover rate of the plant community and are poorly related to ecosystem primary production. Thus, the mechanisms linking the dynamics of the detrital C pool to plant turnover rate must be investigated to improve our capacity to model C storage in ecosystems and to evaluate its role in the global C budget.

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12. The relation between C flux into the detrital pool ($FC_{detrital}$, grams of C per square meter per day) and primary production (*PP*, grams of C per square meter per day) for all the ecosystem types is described by the equation

$$\log FC_{detrital} = (-0.25 \pm 0.04) + (1.00 \pm 0.04)\log PP$$

with r^2 (r is the Pearson correlation coefficient) = 0.84, F test, $P < 0.01$, and $n = 121$. The slopes (± SE) of the log-log linear regression equations between C flux into the detrital C pool and primary production fitted to each ecosystem type are as follows: plankton, 1.54 ± 0.25 ($P < 0.0001$, $r^2 = 0.61$, $n = 24$); benthic microalgae, 1.12 ± 0.07 ($P < 0.0001$, $r^2 = 0.96$, $n = 16$); macroalgae beds, 0.97 ± 0.03 ($P < 0.0001$, $r^2 = 0.99$, $n = 13$); freshwater macrophyte meadows, 1.19 ± 0.09 ($P < 0.0001$, $r^2 = 0.93$, $n = 16$); seagrass meadows, 0.99 ± 0.05 ($P < 0.0001$, $r^2 = 0.99$, $n = 6$); grasslands, 0.50 ± 0.016 ($P < 0.01$, $r^2 = 0.42$, $n = 13$); and forests 0.98 ± 0.07 ($P < 0.0001$, $r^2 = 0.99$, $n = 33$). All of the slopes were not significantly different from 1 (null hypothesis, H_0: slope = 1, t test, $P > 0.1$), except the slope for grasslands. The relation between C flux into the detrital pool and primary production for grasslands is influenced by two reports from the African savanna (*10*), where herbivory is disproportionately higher than in the remaining grassland systems. These high levels of herbivory greatly reduce detrital C flux resulting in a nonlinear relation between C flux into the detrital pool and primary production for the grasslands in the data.
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22. Dead plant material was calculated as the sum of standing dead material, still attached to the plant, and sheded material on the floor. Most reports quantified the mass of dead plant material on the floor after samples collected from the soil surface were sieved through a mesh with a pore size of 1 mm. This procedure underestimates detrital C mass in the soil because it ignores plant material <1 mm and that buried below the soil surface. The detrital mass of planktonic and benthic microalgae represents particulate detritus alone, because it is measured as the abundance of dead cells.
23. Nongrazing cell mortality was quantified as the sum of cell sedimentation rates and lysis rates. Direct estimates of cell lysis are very scarce, and most of the compiled reports on microalgal lysis rates were derived from the following carbon budget equation: primary production = biomass increment + grazed production + exuded production + sedimentation rate + exported production by advection + lysis rate (all variables in grams of C per square meter per day).
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