This dissertation describes work I conducted in collaboration with many others to examine the response of cloud forest ecosystems to global change and the role that photosynthetic pathways play in the carbon cycle. In the second chapter, my co-authors (Pru Foster and Stephen Schneider) and I examine the potential impacts of climate change on tropical montane cloud forests. These forests are critically endangered ecosystems that provide a range of ecosystem services, from serving as watersheds to regulating seasonal water releases. They are also very rich in endemic species, perhaps in response to the unique microclimates resulting from frequent cloud contact. We predict changes in cloud formation heights in a doubled-CO$_2$ world, with attendant impacts on these unique ecosystems. In the third chapter, I describe a global distribution of C$_3$ and C$_4$ plants I developed for use in carbon cycle studies. Because of their distinct morphology and biochemistry, C$_4$ plants respond very differently to light, temperature, and carbon dioxide than do C$_3$ plants. A better understanding of the terrestrial carbon cycle using forward and inverse modeling techniques therefore requires knowledge of the spatial and temporal extent of both photosynthetic types. The global distribution I developed combines new remote sensing products with physiological modeling. With this approach, I have simulated the carbon fluxes associated with each photosynthetic type using the SiB2 land surface model. This distribution predicts the areal coverage of C$_4$ vegetation to be 18 million km$^2$ (~10% of the land surface), and C$_4$ gross primary productivity to be 20% of global productivity. The fourth chapter concerns work at the regional scale, where I have used isotopic techniques to estimate the C$_4$/C$_3$ mixture of a tallgrass prairie site in Oklahoma. The photosynthetic mixture is required for understanding the physiological controls on carbon, water and energy fluxes measured at the site with an eddy covariance system. Results suggest seasonal changes in this mixture: in
the cooler and wetter spring, C$_3$ grasses and forbs predominate (~60% of ecosystem nighttime respiration), while the hotter and drier summer favors the growth of C$_4$ grasses (50-80% of ecosystem nighttime respiration). However, measurements of photosynthesis early in the growing season suggest higher C$_4$ percentages than the nighttime respiration approach. This disagreement between the two approaches might result from a disequilibrium between the isotopic composition of photosynthesis and respiration. This new disequilibrium, if confirmed by further measurements, would have implications for global budgeting techniques that use carbon isotopes in CO$_2$ to partition the net sink between oceans and land. I have also developed the use of the oxygen isotope composition of CO$_2$ as a new and independent constraint on C$_3$/C$_4$ contributions to net carbon exchanges.

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KEYWORDS: C4, CARBON CYCLE, CARBON DIOXIDE, GRASSLAND, ISOTOPE, PHOTOSYNTHESIS, PRAIRIE

2


Remote sensing is an important means of examining net CO$_2$ exchange between terrestrial ecosystems and the atmosphere and the effects of elevated [CO$_2$] on plant productivity at multiple spatial and temporal scales. In particular, indices derived from narrow-waveband reflectance that are sensitive to dynamic physiological attributes may reveal periods of photosynthetic downregulation and may improve plant productivity models. Here we examined the relationship between photosynthesis, photoprotective xanthophyll cycle pigments, and the Photochemical Reflectance Index (PRI) for mature woody Mediterranean plants under two conditions: natural drought and exposure to atmospheric CO$_2$ enrichment. We also examined plants under severe water stress to test and compare the effects of physiology and structure on PRI, the Normalized Difference Vegetation Index (NDVI), and the Water Band Index (WBI). PRI varied primarily with leaf physiology, and NDVI primarily with stand structure. WBI was affected by both attributes and, unlike PRI, did not scale well from leaves to whole stands. PRI was well linked to photoprotective xanthophyll cycle pigments and electron transport. Both PRI and these pigments varied with seasonal changes in midday photosynthesis, demonstrating that the xanthophyll cycle is an important form of photoprotection for evergreen Mediterranean species undergoing photosynthetic downregulation. By contrast, NDVI was not sensitive to physiological changes but was well correlated with green canopy cover. These results suggest that the "big-leaf hypothesis" (which states that canopies can be characterized by a single reference leaf) cannot be applied to all physiological indices. Furthermore, in agreement with the "functional convergence hypothesis" (which states that plant physiology and structure change to match CO$_2$ fixation capacity), our results indicate a coordinated regulation of photosystem two activity and carbon uptake. However, they also demonstrate that this relationship may be disrupted during early leaf development and with elevated [CO$_2$]. Overall, these studies support the use of hyperspectral indices to monitor plant physiology at the leaf, canopy and stand scales. However, confounding of structural and physiological signals is significant and will make it difficult to separate the mixed influences on these indices. To better understand these influences large-scale manipulative experiments and canopy radiative-transfer models that incorporate physiological parameters are needed.

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KEYWORDS: CARBON DIOXIDE, CHAPARRAL, NORMALIZED DIFFERENCE VEGETATION INDEX (NDVI), PHOTOCHEMICAL REFLECTANCE INDEX (PRI), PIGMENT, REMOTE SENSING, STRESS, WATER, WATER BAND INDEX (WBI)

3


Rates of carbon (C) cycling in soils are an important component in the equation of forest carbon balance yet at present they are poorly quantified. This research focuses on quantifying rates of soil C cycling at three temperate forests in the eastern United States along a latitudinal gradient from Maine to Tennessee. Measurements of C and radiocarbon ($^{14}$C) stocks and fluxes are our principal measurement tools.
Total soil C stocks (to 80 cm depth) decrease along the gradient and are 14.6, 8.4 and 4.9 kg C m⁻² at Howland ME, Harvard Forest MA, and Walker Branch TN, respectively. Much of this trend is due to decreasing C stocks in the organic (O) horizons. Howland and Harvard Forest both have large humified C stocks in the O horizon with long turnover times (15-50 years), while at Walker Branch this humified component is largely absent and turnover times are much shorter (7-15 years). On timescales of human interest, significant C accumulation in these soils will happen only in the O and A horizons, which have large C stocks that cycle on decadal and centennial timescales. The deeper mineral horizons, despite their large stocks, have long turnover times (200-2000 years) and can store C effectively only over millennia. Soils of northern sites such as Howland and Harvard Forest have greater C storage potential than the southern site of Walker Branch. Currently, well-drained soils account for an uptake of 5-50 g C m⁻² yr⁻¹ or 1-25% of the measured net ecosystem C uptake at each of the sites. Measurements of the ¹⁴C in respired CO₂ from incubations of soil organic matter combined with C and ¹³C mass balance allow partitioning of soil respiration into heterotrophic and autotrophic sources. Heterotrophic respiration contributed from 44-84% of total soil respiration for well-drained soils at Howland and Harvard Forest in 1999. The average age of heterotrophic respiration at all three sites is 8-9 years. The amount of total soil respiration from C fixed >1-2 years ago decreases along the latitudinal gradient and is 55, 42 and 33% at the Howland, Harvard Forest, and Walker Branch, sites respectively for 1998.

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**KEYWORDS:** CARBON, CARBON CYCLE, FORESTS, ISOTOPE, RESPIRATION, SOIL

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As concern over global warming intensifies, sequestration and storage of atmospheric CO₂ has become an important scientific and policy issue. Confusion persists, however, over interpretation of forest carbon (C) source-sink dynamics, in part because conclusions drawn depend on temporal and spatial scales of analysis (e.g. day-week scale vs. successional-scale), type of disturbance, and methodology (e.g. mass-based vs. flux-based). There is a need to resolve this confusion given that strategies for mitigating anthropogenic CO₂ emissions are based on estimates of forest C fluxes during various stages of succession, over which C fluxes and stores may change. Empirical study of changes in forest C stores can help to resolve this confusion by clarifying the C sources-sink dynamics of forests in space and time. To better understand the impacts of disturbance on C source-sink dynamics, changes in C stores of an evergreen-dominated forest on the Wind River Ranger District in Southwestern Washington, U.S.A., were investigated along a 500-year chronosequence of 36 stands. Principal objectives were to evaluate 1) decomposition rates (k) of logs, stumps, and below-ground coarse roots, 2) net primary productivity (NPP) of dominant tree species’ boles at the stand level, and 3) successional changes in net ecosystem productivity (NEP) for live trees and coarse woody debris (CWD), here called NEPₚ. In the case of decomposition, log and stump k values did not differ significantly within the two principal species studied, indicating substitution of log k values for stump k values in models of forest C budgets may be valid when stump decomposition data is lacking. Decomposition rates between species differed, with Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) decomposing more slowly (k = 0.013 yr⁻¹) relative to western hemlock (Tsuga heterophylla (Raf.) Sarg. (k = 0.036 yr⁻¹). This difference in k between species was observed for both above-ground stumps and logs as well as below-ground coarse roots. Given our mean k estimates and adjusting for regenerating stand age, these stands are losing C at a rate of 0.16-0.83 Mg C ha⁻¹ yr⁻¹ (assuming all CWD is P. menziesii to 0.13-1.68 Mg C ha⁻¹ yr⁻¹ (assuming all CWD is T. heterophylla) from stumps, logs, and snags. Including coarse roots increases these losses to 0.28-1.25 Mg C ha⁻¹ yr⁻¹ and 0.30-2.53 Mg C ha⁻¹ yr⁻¹, respectively. Based on these findings, if fragmentation of these decomposing C pools is ignored, and fragmented fractions have oxidized to CO₂, stands thought to be net C sinks could in reality be net C sources to the atmosphere. Net primary production in tree boles (NPPₚ) of regenerating stands (so called second-growth) ranged between 0.15-5.28 Mg C ha⁻¹ yr⁻¹. NPPₚ of 500-year old stands ranged between 1.3-3.9 Mg C ha⁻¹ yr⁻¹, similar to NPP of boles in 20-25 year old second-growth. Mean radial increment widths from old-growth stands indicated that NPPₚ of these stands (neglecting mortality) can increase, decrease, or remain relatively constant. Based on 5-year increments for the previous fifteen years, the majority of old-growth stands sampled showed small increases in radial growth over time. Timing of the transition from negative to positive of NEPₚ ranged between 0 and 57 years after disturbance and depended strongly on live-tree growth rates as well as the fate of CWD and harvested wood. Estimated maximum and minimum NEPₚ
were 3.9 Mg C ha\(^{-1}\) yr\(^{-1}\) and -14.1 Mg C ha\(^{-1}\) yr\(^{-1}\), respectively. Maximum mean C stores of 393 Mg C ha\(^{-1}\) were reached approximately 200 years after disturbance. At a rotation age of 80 years, regenerating stands stored approximately 50% as much C in woody biomass as a 500-year old primary forest, indicating conversion of older forests to plantations released C to the atmosphere. Given the high biomass of mature and old-growth stands relative to younger regenerating stands in the forest studied, landscape C stores in live wood would appear to be maximized in stands of older age classes.

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KEYWORDS: BIOMASS, CARBON CYCLE, FORESTS, GROWTH AND DEVELOPMENT, LITTER, PRODUCTIVITY, TERRESTRIAL ENVIRONMENT, TREE

5


Climate change has significant influences on the hydrologic cycle for forested areas in the southeastern United States because of the relationship between a forest's physiology and the climate condition, as well as the intensive forest cover rate in the region. A physiological and hydrological model (PnET-II) was used in this work to study the characteristics of the hydrologic cycle for forested watersheds in the southeastern United States. The model's systematic biases, including overestimation of runoff in wet seasons and underestimation of runoff in growing seasons, were summarized for 17 experimental watersheds. A new model version, called PnET-II3SL, was developed with four revisions: 1) replacing the original single-layer soil moisture scheme with a three-layer soil moisture scheme, 2) adjusting the overland (fast) flow fraction based on antecedent moisture condition and precipitation intensity, 3) introducing a factor to adjust the water use efficiency for growing seasons, and 4) parameterizing proper values for growing-degree-day drivers. PnET-II3SL exhibited substantial improvements in simulations of runoff for the 17 experimental watersheds. The validated PnET-II3SL model was then employed for all forested portions of the southeastern United States under two climate scenarios, HadCM2 and CGCM1, to attempt to evaluate future changes in water availability in two river systems (the Mississippi River and the Alabama River) contributed by forested areas. The PnET-II3SL model predicted that forested areas will produce less evapotranspiration, and thus more water availability, in these two river systems in the 21st century.

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KEYWORDS: ALABAMA RIVER BASIN, EVAPOTRANSPIRATION, FORESTS, HYDROLOGY, MISSISSIPPI RIVER BASIN, MODEL, MOISTURE, REGIONAL ANALYSIS, RIVER, RUNOFF, SOIL