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Linking Tree Population Dynamics and Forest Ecosystem Processes

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SUMMARY

A new, empirically based, spatially explicit model (SORTIE) predicts that tree population dynamics in forests of southern New England are (1) nonequilibrial, (2) strongly dependent on species composition immediately following disturbance, and (3) highly spatially aggregated. The population dynamics predicted by SORTIE are the result of a clear set of physiological, morphological. and life-history traits of the individual tree species. However, those traits generally do not depend on or determine the species effects on productivity, hydrology, or nutrient cycling. As a result, idiosyncratic differences among tree species in traits such as litter quality predispose these forests to strong linkages between the relative abundance of tree species and spatial and temporal variation in forest ecosystem processes. It is clear that energetics and biogeochemistry place constraints on forest ecosystem processes, and that the rates of many ecosystem processes are strongly influenced by physical, environmental factors. However, in the absence of evidence of stronger control of tree population dynamics by ecosystem processes and physical factors, we conclude that the spatial and temporal dynamics of productivity, nutrient cycling.

and hydrology in these forests will be largely driven by the interactions between microbes, plants, and animals—often acting in extremely local neighborhoods—that determine tree population dynamics. Thus, ecosystem dynamics in these forests should be characterized by the same nonequilibrial, spatially aggregated dynamics exhibited by tree population dynamics.

INTRODUCTION

Models of forest ecosystem dynamics can be divided into two general classes: models that ignore the dynamics of component species and that seek the mechanisms regulating ecosystem processes in physiology, biogeochemistry, and energetics (e.g., Parton et al., 1988; Raich et al., 1991; Rastetter et al., 1991); and models of the population dynamics of major forest species, in which ecosystem dynamics are both driven by and potentially exert feedbacks on changes in species composition (e.g. Shugart, 1984; Pastor and Post, 1986). Inherent in this second approach is the assumption that ecosystem dynamics represent the aggregate outcome of the plant–plant and plant–animal interactions—often acting on extremely small spatial scales in local neighborhoods—that govern community composition. Our goal in this chapter is to outline a series of results from a new, spatially explicit model of tree population dynamics (SORTIE, Pacala et al., 1993). We will describe the basic structure of the model and the empirical data used to parameterize the model for the transition oak–northern hardwood forests of central New England, and then outline the model's basic predictions about tree population dynamics. We will then summarize our ongoing studies of the effects of different tree species on productivity, hydrology, and nitrogen (N) cycling within these forests, and suggest potential forms of feedbacks between these processes and tree population dynamics. Our basic theme is that many aspects of forest ecosystem dynamics can best be viewed as the aggregation of interspecific differences in individual plant and animal effects on ecosystem processes (also see Turner and O'Neill, Ch. 19; Schimel et al., Ch. 20), and that the mechanisms that underlie many of the spatial and temporal dynamics studied by ecosystem scientists are best sought at the population and community level.

THE SORTIE MODEL

The basic structure of SORTIE is conceptually very simple (Pacala et al., 1993): tree population dynamics are described by four submodels that predict (1) recruitment of new seedlings as a function of the spatial distribution of adults; (2) growth of seedlings, saplings, and mature trees as a function of local resource availability (i.e., light in the version of the model used for this chapter); (3) mortality as a function of growth rate; and (4) local resource availability as a function of the distribution of plants in the forest. The recruitment submodel predicts the spatial distribution and density of new seedlings of each tree species from empirical relationships between the densities of new seedlings and the distribution of adults (or adult females for dioecious species such as *Fraxinus americana*) (E. Ribbens, J.A. Silander, and S.W. Pacala, unpublished). The growth submodel predicts the diameter and height growth of individuals from empirical relationships between growth and local (individual plant) measurements of light availability (Pacala et al., 1993). The rationale for the mortality submodel is derived from our observations that mortality, particularly for seedlings and saplings, is a predictable function of recent growth history (R.K. Kobe, S.W. Pacala, J.A. Silander, and C.D. Canham, unpublished). The mortality submodel was parameterized using measurements of average diameter growth for the previous 5 years in both live and recently dead saplings. The resource (light) submodel predicts the seasonal average light level experienced by each individual seedling, sapling, and adult tree as a function of (1) the distribution of neighbors that are taller than the target plant (including their specific location, size, and crown geometry); (2) empirically derived, species-specific light extinction coefficients; and (3) solar geometry at the latitude of the study sites (Canham et al., 1994).

The spatially explicit nature of the model allows us to incorporate processeses such as recruitment limitation that are ignored in models such as FORET (Shugart, 1984) and JABOWA (Botkin, 1992). It also allows us to mechanistically model neighborhood competition for light by specifically incorporating the effects of both solar geometry and tree geometry on spatial variability in gap and understory light levels. Virtually all of the parameters required for the model have been estimated from field research at Great Mountain Forest in northwestern Connecticut. The forest occupies a broad plateau at elevations of 300–500 m, and represents a transition between the oak-dominated forests of southern New England, and the northern hardwood forests of northern New England. The six most abundant species in the forest (listed in order of increasing shade tolerance) are *Quercus rubra* (red oak), *Fraxinus americana* (white ash), *Acer rubrum* (red maple), *Acer saccharum* (sugar maple), *Tsuga canadensis* (eastern hemlock), and *Fagus grandifolia* (beech).

There are three distinctive features of the population dynamics predicted by SORTIE (Fig. 9-1). First, even long-term dynamics of shade-tolerant species such as beech and hemlock are nonequilibrial. The relative abundances of shade-tolerant species drift significantly over time, in part because of stochasticity associated with seedling colonization of gaps. Our field data clearly indicate that beech is the competitive dominant in the system; however, our data also reveal a fundamental tradeoff between competitive ability and dispersal in these

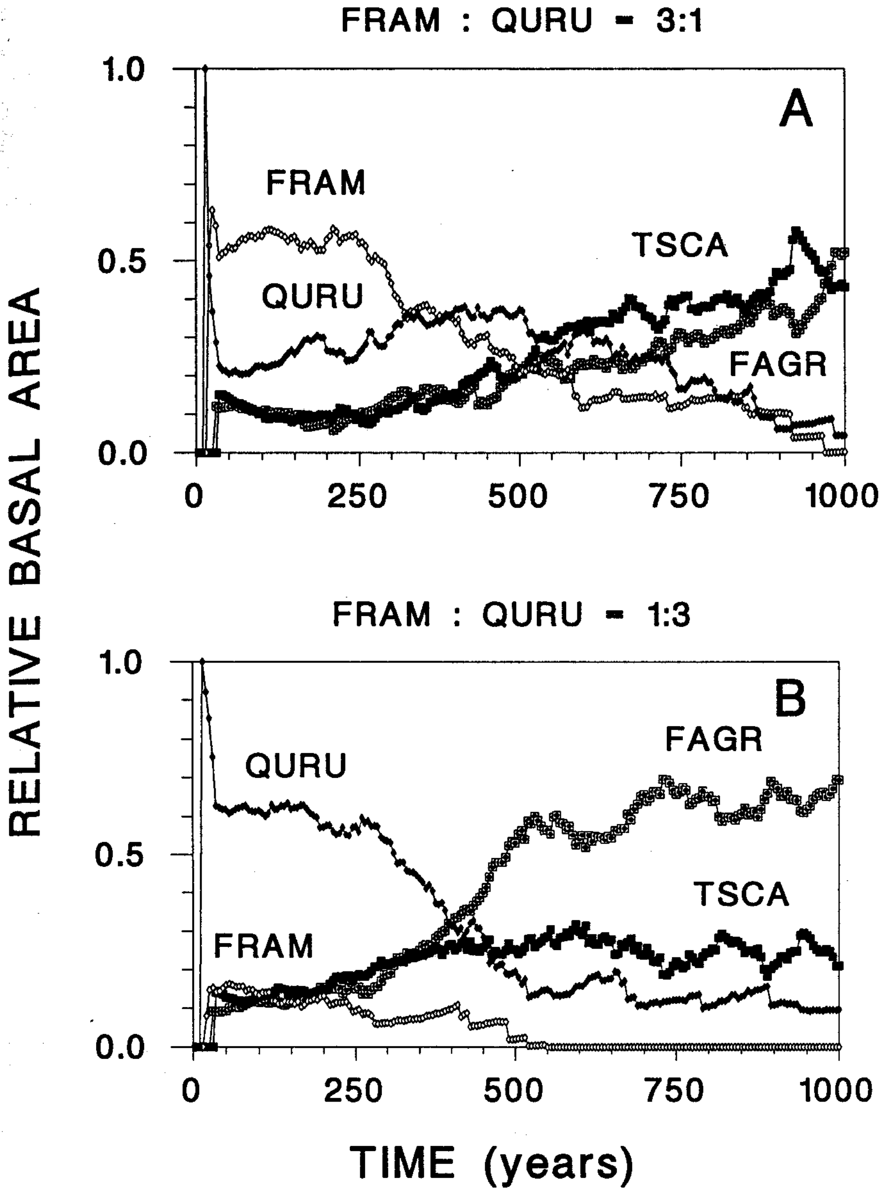

Figure 9-1. SORTIE simulations of changes in relative basal area over time in a 1-ha stand, using only four species for simplification. FRAM (◇) = *Fraxinus americana*; QURU (◆) = *Quercus rubra*; FAGR (▣) = *Fagus grandifolia*; and TSCA (■) = *Tsuga canadensis*. Species-specific parameter values used in the simulation are given in Pacala et al. (1993). The simulations begin by randomly distributing 100 seedlings each of TSCA and FAGR (the two most shade-tolerant species in the system) within the hectare. The initial seedling abundances of FRAM and QURU were varied from 300 FRAM : 100 QURU in Fig. 9-1A to 100 FRAM : 300 QURU in Fig. 9-1B.

species. Analytical models indicate that such tradeoffs can act as powerful mechanisms for species coexistence (S.W. Pacala and D. Tilman, unpublished).

Second, the spatial distributions of species within stands become highly aggregated during succession, again because of the relatively limited effective dispersal distances of all six of these species (i.e., mean dispersal distances of < 20 m; E. Ribbens, J.A. Silander, and S.W. Pacala, unpublished). Striking patchiness in the distribution of tree species develops even in the absence of any physical, environmental heterogeneity within the stand. Patches of a given late successional species tend to be only slowly invaded by other shade-tolerant species because locally produced seeds and seedlings are generally much more numerous than seedlings of the invading species, and the competitive differences among the shade-tolerant species are fairly small.

Third, long-term successional dynamics are strongly affected by the initial abundances of species following disturbance (Fig. 9-1). As expected from a large body of research on forest succession, the relative abundances of different early successional tree species during the first several hundred years following catastrophic disturbance are strongly influenced by the relative abundances of both advance regeneration (i.e., juveniles that survive the disturbance) and seedlings established immediately following the disturbance (whether from seed banks or seed dispersal) (Canham and Marks, 1985). SORTIE also predicts that differences in the abundances of early successional species have effects well beyond the time when the species are displaced from the stand. In the example in Fig. 9-1, a high initial abundance of northern red oak led to an approximately 250-year period of strong dominance by that species, with exclusion of the other early successional species (white ash) within approximately 500 years. However, as the abundance of red oak declined, the abundance of beech increased dramatically (Fig. 9-1). In contrast, the simulation with a comparable density of initial white ash seedlings did not result in comparable levels of dominance by white ash, and as white ash declined, there was a transient increase in red oak abundance, followed by eventual codominance by both beech and hemlock (Fig. 9-1). These long-term, persistent effects of initial conditions following disturbance appear to reflect differences in the competitive interactions between specific pairs of shade-tolerant and -intolerant species in the system.

The current version of SORTIE describes the dynamics of tree species, without explicit consideration of other plant growth forms. However, an understory plant species also appears to have a profound effect on stand structure and succession in these forests. Hayscented fern (*Dennstaedtia punctilobula*) often forms dense, vegetatively spreading layers of foliage 30–50 cm tall in the understory of northeastern forests. There has been widespread concern about its ability to inhibit regeneration of commercially important tree species in the Allegheny Plateau of Pennsylvania (Horsley, 1986). In stands at

Great Mountain Forest, hayscented fern cover is directly proportional to incident, understory light levels: in areas of the understory that receive relatively high light levels, hayscented fern cover is also high (Hill and Pacala, 1992). As a result, the fern effectively eliminates many of the light gaps that are normally exploited by newly emerging tree seedlings (Hill and Pacala, 1992). When this simple effect is incorporated in SORTIE, the model predicts two fundamental changes in forest dynamics: first, succession is accelerated, because only the most shade-tolerant species can successfully penetrate the dense fern layer; and second, total tree biomass is significantly reduced (by as much as 40%) because the sparse understory is much slower to fill gaps formed when canopy trees die (J. Hill, unpublished).

LINKAGES BETWEEN TREE POPULATION DYNAMICS AND ECOSYSTEM PROCESSES

Productivity and Carbon Cycling

We now turn to the issue of the linkages between these features of tree population dynamics and forest ecosystem processes. During the initial phases of secondary succession, the process of self-thinning results in predictable changes in stand structure and productivity that appear to be largely independent of the precise composition of a stand (e.g., Mohler et al., 1978; Bormann and Likens, 1981). However, there are well-known differences among tree species in (1) total biomass for trees of similar stem diameter or crown volume (e.g., Fig. 9-2A); (2) the relative allocation of that biomass to different structures (i.e., roots, stems, leaves, and seeds) (e.g., Tritton and Hornbeck, 1982); and (3) the chemical constituents of the biomass that determine the fate of the organic matter (including both the risks of death of the tissue, particularly due to herbivores, and the rate of eventual decomposition) (Melillo et al., 1982; McClaugherty et al., 1985; Melillo et al., 1989). Models that have linked forest stand dynamics with productivity and decomposition clearly indicate that the long-term dynamics of carbon allocation, storage, and decomposition in forests are sensitive to changes in forest species composition (e.g., Pastor and Post, 1986). We suggest that as the realism of the population dynamics of these models is improved, the dynamics of productivity, decomposition, and carbon storage in forests will be found to be even more sensitive to the kinds of nonequilibrial, spatially heterogeneous dynamics exhibited by SORTIE.

Hydrology

It has long been appreciated that streamflow can be strongly affected by the structure and composition of vegetation within the watershed (e.g., Kittredge,

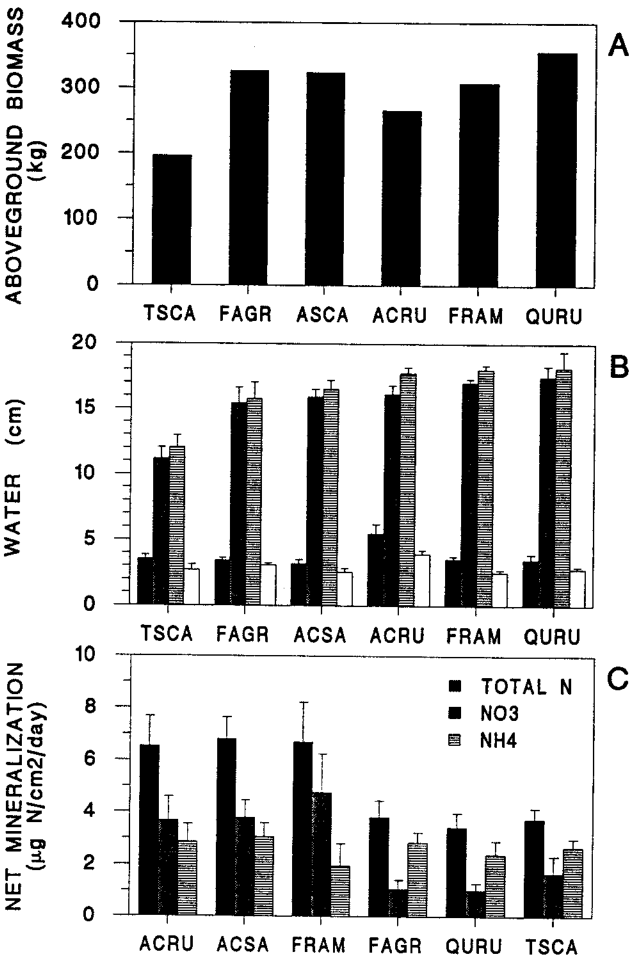

Figure 9-2. (A) Aboveground biomass (kg) of 25-cm DBH trees of the six dominant species at Great Mountain Forest. Biomass estimates were calculated from dimension analysis equations given in Tritton and Hornbeck (1982). (B) Effects of the six dominant canopy tree species on growing season water budgets (1991). Data (means and standard errors) are from six replicate trees of each species within a 3-ha area. Solid bars are initial soil water content (in cm) in the top 15 cm of soil at the start of the growing season. Cross-hatched bars represent total growing season precipitation in rainfall collectors placed beneath the tree crowns (at 1 m above the soil surface). Clear bars represent the soil water content at the end of the growing season, and horizontally hatched bars represent the surface soil water losses estimated by mass balance. (C) Midsummer net N mineralization rates (means and standard errors) in the surface soil beneath the crowns of the six dominant tree species. Mineralization was estimated from 28-day incubations of *in situ* cores of the top 15 cm of forest floor plus mineral soil beneath six replicate trees of each of the species in each of two stands. Solid bars show total net N mineralization; cross-hatched bars give net nitrification rates, and horizontally hatched bars show net ammonification rates.

1948; Swank and Douglass, 1974; Swank et al., 1988). We have documented the effects of the major tree species at Great Mountain Forest on surface soil water budgets, primarily to test for interspecific differences in the effects of canopy trees on soil water availability for seedlings and saplings (Fig. 9-2B). While we did not find evidence of significant differences among the species in their ability to deplete surface soil moisture content during the growing season, there were significant differences among the species in interception losses due to evaporation from foliage (Fig. 9-2B). The relative differences in interception losses during the growing season from hemlock (TSCA) crowns vs. the five deciduous species would be amplified even more during the dormant season due to hemlock's evergreen foliage (Swank et al., 1988). Physiological differences among species in transpiration rates may further amplify the effects of tree population dynamics on hydrologic yield from watersheds (Swank et al., 1988). Hence, as forest composition changes (due to combinations of directional, successional trends and the more unpredictable drift and fluctuations predicted by the model), the hydrology of the watershed could change markedly.

Nitrogen Cycling

The dominant tree species at Great Mountain Forest also clearly differ in their effects on N cycling. Net N mineralization rates at any given location within a forest vary more than twofold as a function of the identity of the canopy tree directly overhead (Fig. 9-2C). These differences occur even within a spatial scale of <10 m between adjacent trees (Finzi et al., 1993). Net ammonification rates were uniform across all six species; however, the six species can be divided into two functional groups on the basis of differences in apparent nitrification (Fig. 9-2C). The three species with high net nitrification (sugar maple, red maple, and white ash) are all known for the production of high-quality leaf litter relative to the other three species (beech, hemlock, and red oak). These effects on rates of N mineralization persist even after the canopy tree dies and forms a gap (data not presented). Although there has been a great deal of concern over the potential for nitrate export from forests and contamination of water supplies because of excess deposition of N from anthropogenic sources (e.g., Aber et al., 1989), our results suggest that changes in the relative abundance of species within a stand may also play a major role in determining the potential for nitrate export. It is worth noting that of the three major late successional tree species in this system (beech, hemlock, and sugar maple), the two species with low rates of apparent nitrification (beech and hemlock) are both threatened with reductions in relative abundance due to the spread of introduced pests or pathogens [i.e., beech bark disease (*Nectria coccinea*) and both the hemlock wooly adelgid (*Adelges tsugae*) and the hemlock looper (*Lambdina athasaria*)]. Thus, these two introduced pests may dramatically increase the potential for nitrate export and contamination of groundwater, by indirectly causing an increase in sugar maple abundance, the remaining late successional species within the forests.

These differences in local rates of N mineralization within stands clearly have the potential to feedback upon the population dynamics of the component species by altering the relative growth of seedlings and saplings. For example, of the three late successional species in these forests, sugar maple saplings show stronger responses to soil N availability than do beech and hemlock saplings (unpublished data). This suggests that the high litter quality and N cycling rates of sugar maple trees may act as an autocatalytic feedback loop that promotes persistence of the species in these forests (see also Wedin, Ch. 24). We also have preliminary evidence that these differences in N cycling rates may have an indirect effect on tree regeneration that is mediated by herbivores. In particular, tissue N concentrations of saplings in the forest understory appear to vary not only as a function of the identity of the seedling (presumably due to inherent interspecific differences in N metabolism), but also as a function of the identity of the canopy trees overhead (presumably as a result of the effects of canopy trees on local N availability in the soil and luxury consumption of N by seedlings in deep shade) (C. Tripler and C. Canham, unpublished). These differences in tissue N concentration appear to affect the risk of browsing of the seedlings by white-tailed deer (*Odocoileus virginianus*) (C. Tripler and C. Canham, unpublished).

SYNTHESIS

In summary, SORTIE predicts that tree population dynamics in these forests are (1) nonequilibrial, (2) strongly dependent on initial conditions following disturbance; and (3) spatially aggregated, with relatively little linkage over distances greater than even 25 m. The population dynamics predicted by SORTIE are the result of a clear set of species-specific physiological, morphological, and life-history traits (Pacala et al., 1993). However, those traits generally do not depend on or determine patterns of carbon allocation and storage by a species, or the species' effects on hydrology and N cycling. As a result, idiosyncratic differences among species in traits such as litter quality predispose these forests to strong linkages between the relative abundance of tree species and spatial and temporal variation in forest ecosystem processes. Moreover, although the list of tree species present in a given environment may be generally predictable, SORTIE indicates that the absolute abundances of species at a site, and the changes in relative abundance during secondary succession, may vary immensely due to historical effects, particularly the distribution and abundance of colonists following disturbance. There is no question that energetics and biogeochemistry place constraints on forest ecosystem processes, and that the rates of many ecosystem processes are strongly affected by physical, environmental factors. However, in the absence of evidence of stronger control of tree population dynamics by ecosystem processes and physical factors, we conclude that the spatial and temporal dynamics of productivity, nutrient cycling, and hydrology in these forests will be largely driven by the interactions between microbes, plants, and animals—often acting in extremely local neighborhoods—that determine tree population dynamics. Thus, ecosystem dynamics in these forests should track the nonequilibrial, spatially aggregated dynamics exhibited by tree populations.

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