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Application of a forest gap model for prediction of browsing effects on riparian forest succession

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Abstract

Selective browsing by white-tailed deer (*Odocoileus virginianus*) severely impacts seedling dynamics within riparian forests on the Patuxent Research Refuge, MD. To evaluate the long-term implications of browsing for forest dynamics, field studies of seedling recruitment, seedling growth, and photosynthetic performance are used to adapt a forest gap model (ZELIG) for simulating browsing interactions with tree species life history characteristics. Primary alterations to the model include addition of small seedling demography, soil saturation effects, shade adaption of tree photosynthesis, and browsing algorithms. Simulated stands were subjected to browsing as a function of total seedling density. If a stand is browsed, then seedling species are browsed selectively based on deer feeding preferences. Model output without browsing impacts closely matches current riparian forest composition. Simulated browsing depresses total forest basal area during mid-succession by reducing regeneration and growth of early successional yellow poplar (*Liriodendron tulipifera*), allowing late successional American beech (*Fagus grandifolia*) to gain earlier dominance. Greater browsing intensities increase the impact on basal area and displace overall forest composition further from control conditions. Control and browsing simulations converge toward an American beech dominated forest in late succession. Thus browsing interacts with tree species life history strategies to alter the rate of succession, but not the long-term trajectory of succession. Further advances in simulating the impacts of deer browsing will benefit from incorporating landscape-scale deer population dynamics and spatially explicit distributions of forest trees.

Keywords: Forest simulation model; Browsing; Riparian forest; Succession; Vegetation composition

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1. Introduction

Browsing of woody seedlings and saplings by white-tailed deer (*Odocoileus virginianus*) has long been a topic for research in the Eastern United States (Webb et al., 1956; Hough, 1949; Ross et al., 1970; Anderson and Loucks, 1979; Tilghman, 1989; Stromayer and Warren, 1997; Liang and

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Seagle, in press). While many studies have focused on the potential for browsing to negatively impact forest regeneration (Liang and Seagle, in press), it is particularly difficult for empirical studies to forecast the impact of browsing on forest succession (Seagle and Liang, 1997) because of the long time scale involved, the interaction of browsing with tree species life histories, and the concurrent effects of other types of disturbance. Evaluation of these long-term interactions has gained further significance for forest management and restoration because deer densities have reached historically high levels, with some local populations at unprecedented levels (McCabe and McCabe, 1984).

Individual-based forest gap models (Botkin et al., 1972; Shugart and West, 1977) are a potential tool for addressing deer browsing impacts on forest succession because of their focus on individual tree growth and species-specific life history parameters (Jorritsma et al., 1999; Kienast et al., 1999). Gap models have been adapted to many different forest ecosystems (Botkin et al., 1972; Shugart and West, 1977; Phipps, 1979; Shugart, 1984; Kellomaki and Vaisanen, 1991). All of these models: (1) simulate the birth, growth, and death of individual trees within a small, homogenous forest gap; and (2) use light, stratified vertically through the forest canopy, as the primary resource for which individual stems compete. In contrast, the disturbance types and regimes of these models vary greatly and are often specific to the forest ecosystem being simulated. Adaptability to novel forest disturbances and applications has proven to be a valuable attribute of gap models that is facilitated by their 'bottom-up' structure (Huston et al., 1988). Beyond forest community dynamics, these models have been used to address a variety of problems at the ecosystem level (Pastor and Post, 1986; Friend et al., 1993), and also to address the spatio-temporal pattern of forest dynamics at the landscape scale (Urban et al., 1991; Weishampel et al., 1992).

Few forest gap models emphasize small seedling demography as a major aspect of forest succession, even though high vulnerability to stress in the seedling stage can differentiate among population growth rates (Leishman et al., 1992). Most gap models 'regenerate' seedlings at approximately 2.5 cm diameter at breast height (DBH), although Busing and Clebsch (1987) used 1.3 cm as the initial tree DBH in a model of Southern Appalachian spruce-fir forests. While deer browsing is certainly capable of impacting young trees of this size, much smaller seedlings are also commonly browsed by deer. Because of height constraints, browsing impacts smaller seedlings and saplings more than larger trees (Gill and Marks, 1991 De Steven, 1991b) and thus inclusion of very small size classes is imperative. This fact has led to incorporation of small seedling dynamics in other forest models simulating the effects of deer browsing (Jorritsma et al., 1999; Kienast et al., 1999). In addition, competition from herbaceous cover causes greater constraints on light and mineral nutrient limitations for the tree seedlings (Gill and Marks, 1991) than for later growth stages. Physical factors, such as soil moisture, may also have stronger impacts on seedlings (De Steven, 1991a) than later growth stages when the root system is better developed. Given the variability, sensitivity, and vulnerability of the seedling stage, small seedling dynamics is too often an overlooked aspect of forest models that is important for studying many types of environmental impacts. However, because of their vulnerability to such a wide variety of environmental constraints, tree species of different life history strategies often exhibit significant plasticity in growth, physiology, and morphology of the seedling stage (Loach, 1967; Jurik et al., 1988; Poage and Peart, 1993; Shure and Wilson, 1993; Wayne and Bazzaz, 1993), potentially making simulation of small seedling growth difficult to verify against field data.

Recently, the JABOWA-FORET genre of gap models has been compared with SORTIE, a gap model originally designed to simulate forests along the oak–northern hardwoods transition of eastern North America (Pacala et al., 1996). Extensive field data is used to parameterize SORTIE and structure submodels of tree population processes (Pacala et al., 1993; Canham et al., 1994; Ribbens et al., 1994; Kobe et al., 1995;

Pacala et al., 1995; Deutschman et al., 1999). Incorporation of seedling demography is one contrast between SORTIE (Pacala et al., 1996) and the JABOWA-FORET (Shugart, 1984; Botkin, 1993) gap models. Other aspects of most JABOWA-FORET models that have been altered for SORTIE include: (1) differentiating radial growth as a function of light availability for tree shade-tolerance classes; (2) use of a single growth-dependent mortality function for all species; (3) lack of field-verified dispersal functions; and (4) a single direction source of radiant energy (Pacala et al., 1996). All but the last of these characteristics relate to the utility of generalized tree characteristics (JABOWA-FORET), compared with species-specific traits based on empirical relationships (SORTIE). While comparisons of the FORET-JABOWA and SORTIE approaches point out progress in forest modeling strategies, it is not our purpose to compare the utility of these approaches. Rather, we consider these two philosophies reasonably complementary. Based on availability of data, we employ the ease of implementation afforded by the FORET-JABOWA paradigm to gain initial insight into the importance of deer browsing as a driving variable for forest dynamics. If browsing proves to be a significant factor in long-term forest dynamics, investing in the extensive empirical studies necessary to parameterize and apply a model based on SORTIE could be warranted.

The purpose of our simulations is to examine browsing impacts on succession and disturbance for an Eastern North American riparian hardwood forest on the Patuxent Research Refuge, a US Geological Service facility located in eastern Maryland. Empirical studies have clearly established that deer browsing alters seedling demography for this forest (Liang and Seagle, in press); however, the longer term consequences of browsing for forest species composition and forest ecosystem properties has not been evaluated. Specifically, we ask: (1) Can browsing of forest seedlings have long-term impacts on forest ecosystem properties (e.g. basal area) and forest vegetation composition?; (2) If browsing is a significant factor for forest stand dynamics, how does browsing intensity affect the rate and trajectory of forest succession?; and (3) Are browsing impacts interpretable in terms of their interaction with tree species life history strategies?

2. Methods

2.1. Study site

Vegetation surveys and field experiments for model calibration and verification were conducted at the Patuxent Research Refuge (PRR), located in the Patuxent River watershed in Prince George's and Anne Arundel Counties, Maryland (39°43′ N and 76°47′ W). The riparian hardwood forest portion of PRR is uneven-aged second growth situated along the Patuxent River. This forest has been maintained as a natural area for 60 years and sustains a high diversity of woody and herbaceous species (Hotchkiss and Stewart, 1947). Importance values based on relative density, frequency, and basal area indicate that the forest is dominated by yellow poplar (*Liriodendron tulipifera*) and American beech (*Fagus grandifolia*) (Liang, 1996). Codominance by poplar, which is an early-successional, shade-intolerant species, derives from the species' longevity and large size at maturity. American beech is a classical late-successional species, whose seedlings are shade-tolerant and whose mature individuals are also canopy dominants. Having these two contrasting life histories as codominants suggests that the forest is in a transitional state, thus providing an opportunity to study disturbance effects at a crucial period of forest succession.

Direct human disturbances have been minimized in the forest, but indirect impacts are prominent. For example, flooding intensity has been greatly reduced by upstream water management. Nonetheless, rainfall regularly saturates the poorly drained soil, and can influence seedling germination and survival. White-tailed deer (*O. virginianus*) were re-introduced to PRR in the 1940s and, in response to low hunting pressure and surrounding land use changes, deer population growth has resulted in intensive browsing of the understory vegetation and decreased regeneration of overstory tree species (Liang and Seagle, in press).

2.2. Field studies

Thirty-three circular, 16 m radius, sampling plots were randomly established in the PRR riparian forest in May, 1992. Forest vegetation was sampled in four strata: seedling (<1 m), sapling (1–2 m), subcanopy (2–5 m), and canopy (>5 m). Diameter at breast height was measured for all shrub, subcanopy, and canopy individuals in each plot. For the seedling stratum, basal diameter and height were measured for all tree seedlings in five 2×2 m subplots randomly located within each plot. Total basal area, total biomass, and relative species dominance were calculated and used for model verification.

Because of their dominance and potential impact on local seedling regeneration, ten mature American beech and ten mature yellow poplar trees were selected as center points for 11×11 m experimental study plots (Liang and Seagle, in press). Half of the plots (five beech and five poplar) were randomly selected and enclosed with a chainlink fence of 2.4 m height. Each plot was divided into quarters. In each of two randomly chosen quarters, two 2×2 m subplots were randomly placed. From 1992 to 1994, the basal diameter of each tree seedling and sapling (DBH <2 cm; height <1 m) in each subplot was measured annually (August), and each was marked with an aluminum tag. Seedling demographic data (Liang, 1996; Liang and Seagle, in press) were used for model construction and calibration. Regression analysis (Fig. 1) was used to quantify relationships between: (1) mean annual mortality rate [$1-$(number of survivors in year $t+1$/number of seedlings in year t)] and basal diameter; (2) 3-year mortality (1992–1994) of species [$1-$(number of survivors in 1994/number of seedlings in 1992)] and species shade-tolerance rank; and (3) 3-year mortality of species [$1-$(number of survivors in 1994/number of seedlings in 1992)] and seed weight (data from Latham, 1992; De Steven, 1991a). These relationships were used in construction of the seedling mortality algorithm (see Section 2.3). Species-specific mean annual growth rate, calculated as the slope from regression of basal diameter increment over time (1992–1994), was calculated from field data for model verification.

In mid-July (1993 and 1994), the month of mean maximum temperatures, photosynthetic rates of seedlings of the five most common tree species (American beech, yellow poplar, sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and green ash (*Fraxinus pennsylvanica*)) were measured in the field. Healthy seedlings with adequate leaf size (>7 cm^2) and under 50 cm in height were chosen in each exclosure or control plot. Leaf photosynthesis for each species was measured (LI-COR 6200 portable photosynthesis analyzer) across a light gradient created by variable screening of two 150 W cold beam floodlights. Photosynthetic response curves were constructed for each species to estimate photosynthetic parameters including initial slope, light saturation point, and maximum rate of photosynthesis. These values were then used in model parameterization.

2.3. Model modifications

The ZELIG model simulates secondary succession in a homogeneous plot that approximates the gap size created by the death of a dominant canopy tree. Although capable of simulating interactions among plots, such as seed dispersal and shading, we use the model for single plots because information is not available to parameterize seed dispersal algorithms. ZELIG tracks the birth (initial size equals 2.5 cm DBH), growth, and mortality of each individual tree on an annual time step. Primary environmental filters that regulate tree growth include soil moisture (drought only), soil fertility, available light, and growing degree days. The model simulates temporal and vertical variation in light within the forest canopy based on tree heights, which are a function of basal area. The profile of leaf area index through the canopy at 1-m intervals is tallied to calibrate light extinction and thus light available for photosynthesis at height intervals throughout the canopy. Although the parabolic growing-degree-day function of ZELIG has been criticized (Schenk, 1996), we have not altered this algorithm because the study site is located near latitudinal center of the range for one co-dominant species (American beech); co-dominant yellow poplar, although somewhat north of

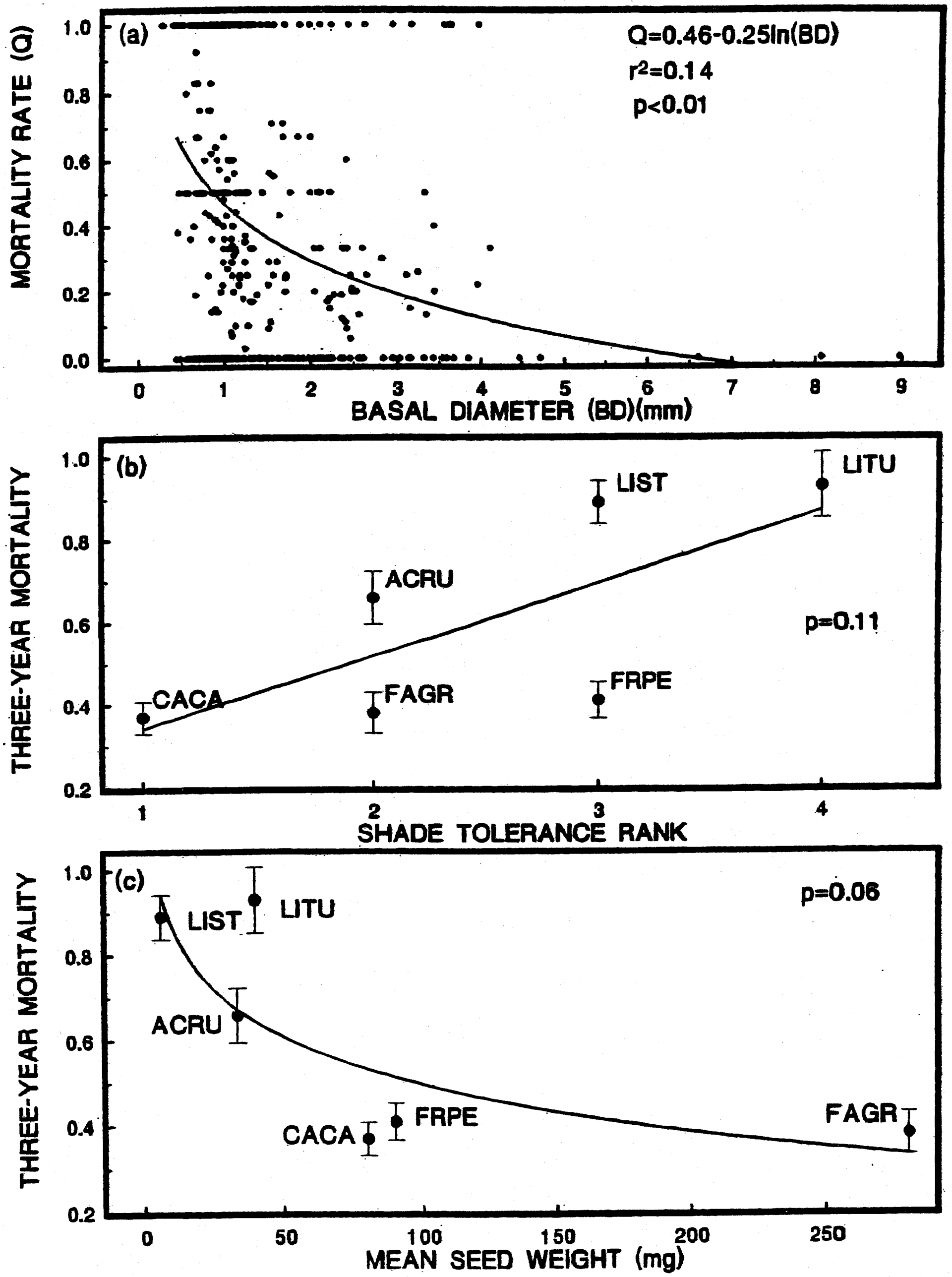

Fig. 1. Regression curves for annual seeding mortality rate (pooled over all species) on basal diameter (a), 3-year mortality on species shade-tolerance rank (b), and 3-year mortality on mean seed weight (c). Species used in the analyses include red maple (ACRU, *Acer rubrum*), ironwood (CACA, *Carpinus caroliniana*), American beech (FAGR, *Fagus grandifolia*), green ash (FRPE, *Fraxinus pennsylvanica*), sweetgum (LIST, *Liquidambar styraciflua*), and yellow poplar (LITU, *Liriodendron tulipifera*). Data for mean seed weight are from Latham (1992), De Steven (1991a).

the center of its range, is impacted most heavily by light availability; and all model simulations are run under the same climate/weather scenario so that any biases are consistent in evaluating browsing impacts. Within the basic structure of the ZELIG model, our modifications focused on: (1) incorporation of small (<2.5 cm DBH, <1.35 m height) seedling growth and population dynamics; (2) developing photosynthesis curves to reflect shade adaptation and differential responses of species to light; and (3) simulating soil water saturation and deer browsing impacts on seedling survival and growth.

2.3.1. Seedling basal diameter and height growth

To simulate growth of small seedlings, we developed a seedling growth function by modifying the tree growth function of Botkin et al. (1972). Species-specific seedling basal diameter growth is simulated in response to light availability, based on the allometric equations developed by Gottschalk (1985):

$$\delta \mathrm{BD} = (G^{*}\mathrm{BD}\{1-[(b^{*}\mathrm{BD}^{2})/X/D_{\max}{}^{*}H_{\max}]\}^{*}X^{2}) /[b^{*}\mathrm{BD}^{2*}(2X+d)] \tag{1}$$

where BD is basal diameter of the seedling, G is a species-specific growth factor, $D_{\max}$ is the maximum DBH of the species, $H_{\max}$ is the maximum height of the species, a, b, c, and d are constants specified for each shade-tolerance rank (Table 1); and $X=\mathrm{BD}(bc-ad)+d$. The constants (a–d) are specific for each shade-tolerance rank (Gottschalk, 1985). New seedlings enter the model annually from seed or as root sprouts with an initial size of 0.1 cm BD.

Height growth of small seedlings is also calculated using the allometric equations of Gottschalk (1985):

$$\mathrm{SDLHT} = (b^{*}\mathrm{BD})/[\mathrm{BD}(bc-ad)+d] \tag{2}$$

where SDLHT is seedling height (m). Height for seedlings <2.0 cm BD is a direct function of basal diameter. When seedlings reach 2 cm in basal diameter or 1.37 m in height, they recruit as saplings in ZELIG and are subject to the original model processes.

2.3.2. Seedling mortality

Our field studies indicated that seedling recruitment fluctuates both spatially and temporally, and also varies among tree species at PRR. In addition, seedling mortality of the five dominant species is species-specific, depends on seedling size and seedling shade tolerance, and is related to mean seed weight (Fig. 1). Based on our field data, species-specific small seedling mortality (SNOGRO) is best described by:

$$\mathrm{SNOGRO} = [A - S_i \ln(\mathrm{BD})]\mathrm{SW}_i \tag{3}$$

where A is a constant fitted during model calibration, S_i is species shade-tolerance rank for species i, and SW_i is the rank of seed weight for species i. S is a qualitative scaling of shade tolerance from one (tolerant) to four (intolerant) that is based on previous characterizations for the species found in this forest and our interpretations of species life history information (Burns and Honkola, 1990). Seed weight ranks (large = 1, medium = 2, small = 3) are used because seed weight data were not available for all PRR species either from our empirical data or from published sources. While a rather coarse estimate of the influence of seed size on early seedling success, this parameter does differentiate the positive nutritional effects of large seed size among broad species groups. Notably, however, most species had the same seed size rank and results were not sensitive to this parameter. In application, SNOGRO represents the annual probability of seedling mortality and ranges from 0.0 to 1.0; seedlings in a simulation die when SNOGRO is larger than a computer-generated uniform random number on the interval (0, 1). Preliminary model runs indicated that SNOGRO overestimated mortality because the function itself was derived solely from seedling data collected under full forest canopies (Fig. 1). Thus, we recalibrated the SNOGRO function based on field observations of stem density, reducing the community (all species combined) probability of seedling mortality by approximately 20%.

2.3.3. Light growth function

In ZELIG, the growth of different species in response to available light is relativized by their shade tolerance. Relativization precludes species-

Table 1
Model parameters for the 19 tree species used in the riparian hardwood simulations[a]

Species	S	B	W	D	SW	Light Growth			Basal diameter growth				ECP	
						C_1	C_2	C_3	a	b	c	d	K	C
Acer rubrum L.	2	4	3	2	3	1.34	3.44	0.06	2.29	31.95	0.023	0.082	0.02	0.00032
Carpinus caroliniana Walt.	1	1	3	2	2	1.01	4.62	0.05	3.00	32.00	0.030	0.090	0.01	0.00030
Carya glabra (Mill.) Sweet	3	3	1	3	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Cornus florida L.	1	4	1	3	2	1.01	4.62	0.05	3.00	32.00	0.030	0.090	0.01	0.00030
Diospyros virginiana L.	4	4	3	2	1	2.50	1.78	0.08	0.75	10.46	0.009	0.062	0.07	0.00036
Fagus grandifolia Ehrh.	2	1	2	2	1	1.34	3.44	0.06	2.29	31.95	0.023	0.082	0.02	0.00032
Fraxinus pennsylvanica Marsh.	3	2	4	1	2	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Ilex opaca Ait.	1	1	2	2	2	1.01	4.62	0.05	3.00	32.00	0.030	0.090	0.01	0.00030
Liquidambar styraciflua L.	3	4	3	3	3	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Liriodendron tulipifera L.	4	4	2	2	3	2.50	1.78	0.08	0.75	10.46	0.009	0.062	0.07	0.00036
Nyssa sylvatica Marsh.	2	4	4	2	2	1.34	3.44	0.06	2.29	31.95	0.023	0.082	0.02	0.00032
Pinus virginana Mill.	4	1	1	3	3	2.50	1.78	0.08	0.75	10.46	0.009	0.062	0.07	0.00036
Platanus occidentalis (Jacq.)	4	4	4	1	3	2.50	1.78	0.08	0.75	10.46	0.009	0.062	0.07	0.00036
Quercus alba L.	3	2	1	3	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Quercus bicolor Willd.	3	2	4	2	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Quercus lyrata Walt.	3	2	5	1	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Quercus michauxii Nutt.	3	2	4	1	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Quercus palustris Muenchh.	3	2	4	1	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034
Quercus rubra L.	3	2	2	2	1	1.71	2.52	0.07	1.44	16.96	0.016	0.072	0.04	0.00034

[a] Shade tolerances (S) (Seagle and Liang, 1997) range from 1 = most tolerant to 4 = least tolerant. Browsing preferences (B) (Seagle and Liang, 1997) range from 1 = least preferred to 4 = most preferred. Soil saturation tolerances (W) (Sabine, 1992) range from 1 = least tolerant to 4 = most tolerant. Drought sensitivity categories (D) range from 1 = least tolerant to 3 = most tolerant. Seed weight (SW) rankings include 1 = large, 2 = medium, and 3 = small. Parameters for the light growth function (C_1, C_2, and C_3), basal diameter growth (a, b, c, and d), and ecological compensation point (ECP) (K and C) are not species-specific, but reflect the different shade-tolerance categories.

specific relationships between growth and light availability but provides distinct light responses for species groups that can be used to decrement optimal growth for each simulated stem. However, light responses for species or species groups may not be distinct at all light levels. Seedling photosynthesis data from our study area indicate that even tree species with very different shade tolerances display shade adaptation. For example, several species, ranging from highly shade intolerant yellow poplar to shade tolerant American beech, displayed similar initial slopes in their response to light availability (Table 2). Maximum photosynthesis rates varied for these species, with the highest rate being found for yellow poplar. We thus modified the parameters of the tree growth function (Botkin, 1993) and calibrated this function (Loach, 1967) to reflect: (1) shade adaptation to low light environments (similar growth responses under low light) by species of all shade tolerances, and (2) different magnitudes of photosynthesis for each shade-tolerance class. The resulting light–growth relationships (Fig. 2) were used to modify tree potential growth.

Table 2

Mean maximum photosynthesis rates ($P_{\max}$) and initial slopes (AQy) of species-specific photosynthesis curves for seedlings of five tree species found in the Patuxent Research Refuge riparian forest understory.

Species	$P_{\max}$ (micromoles/m^2/s)	AQy
Acer rubrum	3.77 (0.53)	0.106 (0.103)^a
Liquidambar styraciflua	4.11 (0.53)	0.275 (0.103)^a
Liriodendron tulipifera	5.25 (0.33)	0.112 (0.065)^a
Fagus grandifolia	4.13 (0.28)	0.125 (0.055)^a
Fraxinus pennsylvanica	3.32 (0.32)	0.230 (0.062)^a
Platanus occidentalis	NA	NA

Standard errors for each mean are in parentheses. All measurements were made on seedlings in the field. For each variable, significant ($P<0.05$) differences are indicated by different letter superscripts.

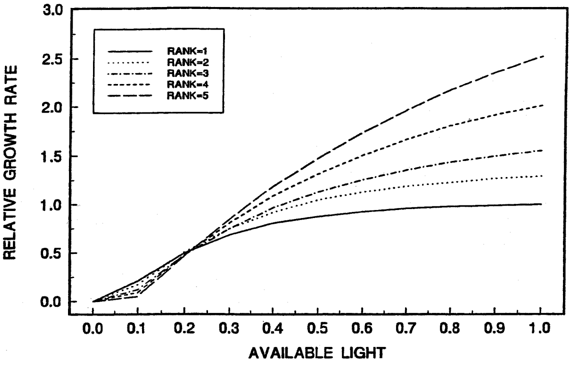

Fig. 2. Relative growth for tree species of different shade-tolerance ranks (1 = most tolerant, 5 = least tolerant) in response to available light. The differentiation of light–growth response among species is small in the low light condition and large in the high light condition.

2.3.4. Ecological compensation point

In our initial model simulations, we found that light levels beneath the simulated canopy were too restrictive to small seedling growth. In ZELIG, the light compensation point of a leaf is used to determined the minimum height of a tree crown (Urban, 1990). This physiological constraint fails to include other energetic costs, such as those of supporting tissues and leaf maintenance costs. Consequently, the leaf profile of the forest simulated by the ZELIG model seems skewed downward, depressing light availability in the lower understory. To modify light availability in the understory and allow existence of a reasonable number and diversity of seedlings, we use an ecological compensation point (Givnish, 1989), or 'whole-plant' economic approach, to derive the size-dependent compensation point. Based on Givnish (1989), the ecological compensation point (ECP) for different species in the model is calculated as:

$$\mathrm{ECP} = [206.35 * \mathrm{e}^{(K_i * H)}]C_i \qquad (4)$$

where H is tree height, and K_i and C_i are species-specific constants calibrated to produce realistic forest canopy profiles (Hedman and Binkley, 1988). ECP is relativized to full sunlight.

2.3.5. Soil moisture function

Drought, but not soil saturation, limits relative growth of tree species in the original ZELIG. Because of the prominence of soil saturation at

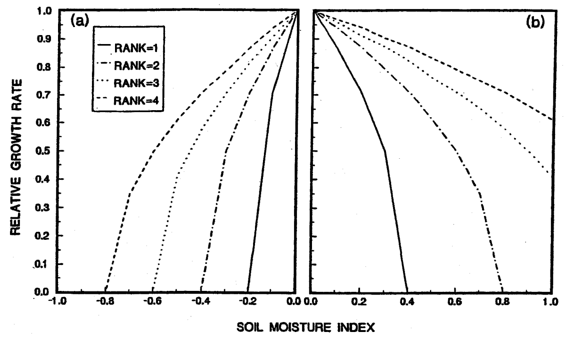

Fig. 3. Relative growth of tree species having different soil moisture tolerance ranks (1 = most tolerant, 4 = least tolerant) in response to proportion of drought days (a) and soil saturation days (b) during the growing season. Species ranks were derived from Sabine (1992).

PRR, we reconstructed the relative growth response to the soil moisture index to incorporate the effect of soil saturation on growth (Fig. 3). In essence, tree relative growth rates can be decreased by prolonged soil saturation as well as by periods of drought (Mitsch, 1988). Species ranks for these two tolerances (Table 1) were derived from published sources and are independent. Responses of tree species to soil saturation are based on the number of days during the growing season that soil water exceeds soil field capacity (Botkin et al., 1972). For both drought and soil saturation, the soil moisture index and species-specific tolerance ranks (Table 1 and Fig. 3) were used to decrease optimal tree growth rates and thus increase the likelihood of mortality.

2.3.6. Deer browsing

Deer browsing is an important biotic filter in the PRR riparian forest that decreases growth rates of seedlings and sprouts (Liang and Seagle, in press). At the community or stand level, deer browsing within this forest is clearly density-dependent, with stands having greater numbers of stems being browsed preferentially (Liang and Seagle, in press). Nonetheless, within a forest stand, deer also display clear preferences for certain species, while avoiding others (Liang and Seagle, in press). We thus simulated browsing as a sequential two-step foraging decision: (1) whether a simulated plot will be browsed is dependent on stem density; and (2) if a simulated plot is subjected to browsing, species within the plot are browsed selectively. The probability of a plot being browsed (BPROB) is:

$$\mathrm{BPROB} = 1/[1 + e^{(2.67 - \mathrm{BMOD}*\mathrm{TDEN})}] \qquad (5)$$

where TDEN is the total density (stems/m^2) of seedlings less than 2 cm DBH in the plot. Thus, the likelihood of a plot being browsed is directly dependent on the availability of seedlings within the plot. The effect of TDEN on the probability of a plot being browsed was calibrated from an empirical relationship between stem density and browsing intensity at PRR (Liang and Seagle, in press). BMOD is used to index different deer densities (higher values effect higher deer densities) and assumes a static deer population for each simulation scenario. Long-term studies for this area have not been carried out to equate specific browsing intensities with different deer population sizes, and thus this variable is not linked to specific deer densities. Nonetheless, varying BMOD does modify the relationship between TDEN and BPROB to simulate potential impacts of different deer population sizes. In our formulation of BPROB, very high deer densities (high BMOD) can reduce seedling densities (low TDEN) to the extent that simulated plots are unlikely to be browsed, reflecting overbrowsing and subsequent avoidance of browse-depleted areas. While this interaction seems realistic, we have not simulated direct feedback from resource availability to deer population size or simulation of spatial pattern in food availability. Thus, we have limited our simulations to values of BMOD that do not deplete seedlings to the point that browsing ceases, emphasizing the impacts of selective browsing.

If a simulated plot is browsed, then browsing intensity on specific seedling species is described by:

$$\mathrm{BF}_i = \mathrm{RDEN}_i^{(1/P_i)} \qquad (6)$$

where BF_i, the species-specific browsing factor, is a function of species relative density (RDEN_i) and species-specific browsing preference rank (P_i, ranging from 1 = least preferred to 4 = most preferred) of species i (Table 1). These browsing preference ranks were derived from the general literature and adjusted specifically for PRR using field observations of browsing (Liang, 1996). Thus, common species that are most preferred will be browsed most intensively. Values for BF are inversely related to browsing and range from 0 (severe browsing) to 1 (no browsing impact). Because browsing usually does not directly kill seedlings, BF is used as a growth modifier in the seedling growth algorithm. Thus, browsing can slow a seedling's growth and increase its probability of dying. This approach contrasts with that used by Jorritsma et al. (1999), who included herbivore biomass, along with availability and quality of forage, to simulate browsing likelihood and intensity. In addition, Jorritsma et al. (1999) assumed that browsing consumed entire seedlings, while our approach assumes that browsing only slows growth and thus increases the probability of seedling death.

2.4. Model simulations

Forest plots were simulated independently of each other, with each simulation starting from bare ground on fixed-size, 800 m^2 plots. The 800 m^2 plot size approximates the minimum gap size in eastern temperate forests (Shugart, 1984). Field vegetation was also sampled on permanent plots of this size. Simulated forest composition and total basal area (averages of ten replicate simulations) were compared with empirical data from PRR (Liang, 1996) for verification of the model's capability to simulate riparian vegetation. This comparison was made using 300-year control model runs (no browsing) because: (1) disturbance history dictates that 300 years would be about the maximum age of any stands within the PRR riparian forest, and (2) browsing is a recent addition to this ecosystem in comparison with the ages of dominant trees. In addition, seedling basal diameter increments were compared with field data (Liang, 1996) to assess simulated seedling growth.

Model simulations of 600 years were used to assess the impact of browsing on forest succession. In addition to control simulations ($BMOD = 0$), forest responses to different degrees of browsing were simulated using three values for BMOD (2, 4, and 8). For each browsing simulation, browsing effects were initiated in year 100 to simulate the introduction of browsing into an established forest. To quantify the impact of browsing on the forest ecosystem, stand basal areas were compared for control and each browsing scenario. Impacts on vegetation composition were assessed by calculating the annual displacement of browsed vegetation composition from the control. Displacement was calculated using the chord distance metric (Ludwig and Reynolds, 1988) and was applied to the basal area of all 19 tree species to provide an overall measure of difference. Specific effects of browsing on forest composition were examined by plotting the annual proportion of basal area represented by the dominant tree species (yellow poplar and American beech) under control and browsed conditions.

3. Results

3.1. Model verification

Three-hundred-year simulations of the PRR riparian forest without deer browsing resulted in a cumulative forest basal area of approximately 40 m^2/ha (Fig. 4). Empirical measurements collected from the study site revealed a mean basal area of 41 m^2/ha (Liang, 1996; Fig. 4), with single plots ranging from 21.3 to 76.5 m^2/ha (Liang, 1996). Thus, our model very accurately simulates total forest basal area. In terms of species composition, our simulations suggest that forest basal area is heavily dominated by yellow poplar, with a basal area of approximately 22 m^2/ha (55% of total basal area) at year 300. Field measurements confirm that the PRR forest is dominated by yellow poplar (Fig. 4), although the proportion is lower at 40%. American beech represents another 7 m^2/ha (17.5%) of the simulated forest basal area, and also has the second largest proportion of basal area (15.9%) in our field data (Fig. 4). Our simulations apparently overestimate the basal area of oak (*Quercus* spp.) slightly. The greatest underestimations were for green ash and sweetgum. Clearly the model simulates forest composition highly similar to the existing PRR riparian forest, especially given the uncertainty of stand ages within PRR and the high variation in stand ages as suggested by the range in empirical plot total basal areas. To examine the robustness of our simulated forest composition, we also compared model output with independent field data from a forest at the Smithsonian Environmental Research Center (SERC), MD. SERC, located on the coastal plain (38°53′ N, 76°33′ W), has geography, species composition, and land-use history similar to the PRR riparian forests (Parker et al., 1989), and has not been disturbed for the past 80 years. Without calibrating the model specifically for SERC, exact replication of the field data is unexpected. Nonetheless, there is again strong agreement in dominance by yellow poplar and a significant American beech component. The higher basal area of oak at SERC agrees with our simulations. Because the SERC data were collected on a somewhat drier alluvial terrace (Liang, 1996), the absence of green ash and greater prevalence of oak is reasonable.

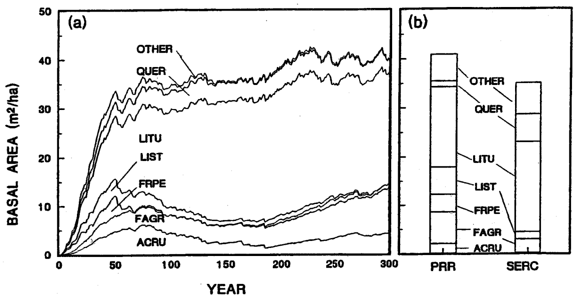

Fig. 4. Species-level basal areas for a 300-year simulation without deer browsing (a), and observed species basal areas from field samples taken at the Patuxent Research Refuge (PRR) and Smithsonian Environmental Research Center (SERC) forests (b). Species included in these graphs are red maple (ACRU, *Acer rubrum*), ironwood (CACA, *Carpinus caroliniana*), American beech (FAGR, *Fagus grandifolia*), green ash (FRPE, *Fraxinus pennsylvanica*), sweetgum (LIST, *Liquidambar styraciflua*), and yellow poplar (LITU, *Liriodendron tulipifera*). Oak (*Quercus*) species are represented collectively as QUER.

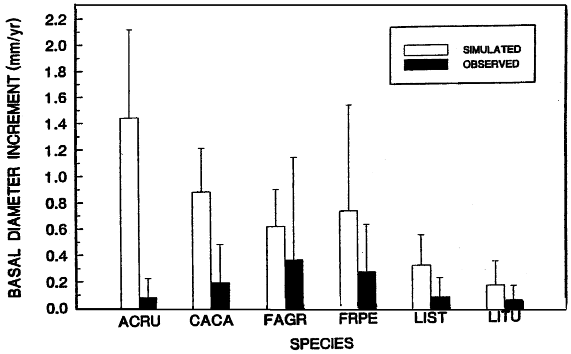

Fig. 5. Comparison of observed and simulated seedling basal area increment (± 1 S.D.) of six major tree species. Observed data are from 1992 to 1994 in the Patuxent Research Reserve riparian forest. Simulated basal diameters are for seedlings growing between 61 and 100 years of the simulation with available light less than 10% of full sunlight and with basal diameter less than 0.3 cm.

To evaluate simulated seedling growth, we compared 3 years of field data on seedling basal diameter increment collected within unbrowsed exclosure plots under mature trees to simulated growth of small (≤ 0.3 cm) seedlings under low light conditions (i.e. less than 10% of full sunlight) (Fig. 5). Several trends are clear from this comparison. First, our simulations overestimate seedling growth in general. Thus, our simulations err in the same way for all species. This overestimation of mean seedling growth rate is particularly noticeable for red maple and ironwood (*Carpinus carolinensis*). Second, despite overestimating mean growth rate, model predictions were generally within one standard deviation of field observations for American beech, green ash, sweetgum, and yellow poplar. These four species are clearly more dominant than red maple or ironwood within this forest (Fig. 4). Thus, the higher simulated growth rates for ironwood and red maple do not strongly impact overall forest composition and basal area dynamics.

3.2. Browsing impacts

With the addition of browsing at year 100, simulated riparian forest basal area diverges from unbrowsed control conditions (Fig. 6a). This divergence begins earliest for the most intensive browsing scenario (BMOD = 8), but is notable for all browsing scenarios by year 200.

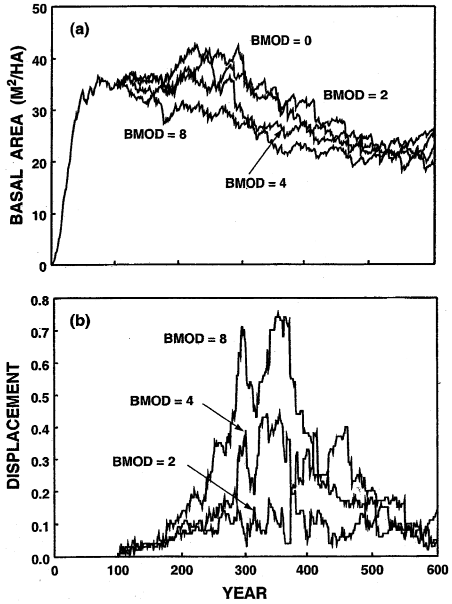

Fig. 6. Total basal area dynamics (a) of the Patuxent Research Refuge (PRR) riparian forest simulated under control conditions (BMOD = 0, no deer browsing) and under three successively higher intensities of deer browsing (BMOD = 2, 4, 8). Displacement of browsed PRR riparian forest composition from control conditions (b) for the same browsing intensity simulations shown in (a). Displacement was calculated using the chord distance metric (Ludwig and Reynolds, 1988) and has a maximum value of 1.4.

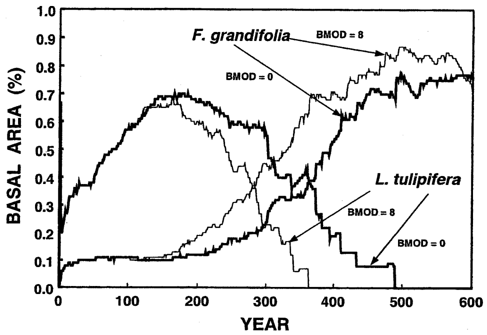

Fig. 7. Time traces of the proportion of total forest basal area comprised of American beech (*Fagus grandifolia*) and yellow poplar (*Liriodendron tulipifera*) for control (no browsing, BMOD = 0) and heavily browsed (BMOD = 8) simulations for the Patuxent Research Refuge riparian forest.

Despite temporal variation in the amount of divergence, greater browsing intensity clearly causes a greater decline in forest basal area. An exception is for the least intensive browsing scenario (BMOD = 2), which actually results in higher basal area than the control from years 350–450. Basal areas for browsed simulations generally remain lower than the control until approximately year 450, when browsing simulation basal areas begin to converge with the control (Fig. 6a).

Stand displacement, a measure of general vegetation composition difference, also displays temporally dynamic variation (Fig. 6b). Nonetheless, when browsing intensity is increased, vegetation composition is displaced further from the control (Fig. 6b). As with basal area effects, displacement begins soon after browsing is implemented at year 100 in the simulations, becomes notable by year 250, generally peaks from year 250 to 450, and then declines toward the end of the simulations.

Under the conditions that browsing was introduced to the simulations, both total stand basal area dynamics and composition displacement suggest that deer browsing has its greatest impact during mid-succession. Under control conditions, between years 250 and 450 forest domination by early successional, long-lived yellow poplar declines precipitously, and poplar is replaced by late-successional American beech (Fig. 7). Because both of these species are large canopy dominants at maturity, the gradual decline of yellow poplar is a consequence of: (1) the long lifespan of mature yellow poplar trees, (2) the inability of yellow poplar to regenerate vigorously in a shaded environment, and (3) the shade tolerance of American beech seedlings. The decline in total forest basal area from approximately year 300 onward (Fig. 6a) results from the smaller maximum size of individual American beech trees as they gain canopy dominance in the simulated forest. Deer browsing interacts with this natural succession of tree life history strategies by speeding the decline of yellow poplar, thus releasing advanced regeneration of American beech into canopy dominance (Fig. 7). This differential effect on the two species results from a strong difference in browsing preference for yellow poplar and American beech (Table 1).

4. Discussion

Based on our seedling photosynthetic data and other empirical studies (Loach, 1967; Jurik et al., 1988), it is evident that tree seedlings can generally adapt to a shaded environment regardless of generalized life history type. Based on this concept, we reduced the differential growth response of species under low light conditions. By doing this we were able to promote higher seedling diversity beneath a closed forest canopy and reproduce our field observations of 'shade-intolerant' seedlings coexisting with those of 'shade-tolerant' species beneath a closed canopy. This coexistence is a central theme in gap dynamics and forest succession theory, and helps account for biodiversity in both tropical and temperate forests (Runckle, 1982; Nunez-Farfan and Dirzo, 1988). This coexistence, however, does not imply that all species have the same growth responses to light competition, only that these responses tend to converge at lower light levels (Fig. 2). Species having a greater degree of shade tolerance remain clearly at a competitive advantage over longer successional time periods. This results in the eventual dominance of the PRR riparian forest by American beech.

Multiple factors have been demonstrated to influence seed reproduction (Koenig et al., 1994) and the emergence and growth of seedlings (De Steven, 1991a; Latham, 1992), and it is difficult to quantify the interaction of these factors. Thus, it is possible that our simulations do not reflect the entire range of potential constraints on seedling growth in the field. Perhaps the most apparent reason is lack of control over seedling history, which affects below-ground resources available for growth. Delineating the multiple local factors that can impact seedling growth needs detailed experiments of multiple factors and their interactions (for example, Latham, 1992), and our simulations of seedling growth indicate that further such studies are needed for tree seedlings in the PRR riparian forest to more accurately simulate species-specific growth rates. Despite this need, our simulated seedling growth rates were largely within a single standard deviation of empirical measures, with all simulated rates being high. If our simulated rates introduce bias into our simulations, it is toward greater basal area of red maple and ironwood. Neither of these species displayed a strong tendency toward basal area dominance in our simulations or in our field data. Thus, we conclude that seedling growth rate is not the primary factor determining basal area for these species in our model, and our results concerning browsing impacts on forest composition and basal area are not regulated by seedling growth rates.

Our simulations indicate the potential for distinct impacts of deer browsing on riparian forest succession patterns but not on final forest composition. In contrast, both Kienast et al. (1999), Jorritsma et al. (1999) found browsing to alter long-term forest composition in European forests. Our reduction of forest basal area by browsing results from selective browsing of yellow poplar and reduced recruitment of poplar into the forest canopy during early stand succession. Because of its large size at maturity, the loss of dominant yellow poplar trees depresses overall stand basal area. Such 'structural' effects were also noted in simulations of forest browsing in Switzerland (Kienast et al., 1999). Low browsing preference for American beech should confer some resistance of late-successional PRR forests to browsing. Previous studies have examined the ability of forests to resist or buffer disturbance (Holling, 1973; Denslow, 1985), and further applications of our simulation model may be useful for determining the temporal dynamics of forest resistance to deer browsing or the 'risk' of forest damage by deer browsing (Kienast et al., 1999).

Our browsing preference ranks for the tree species represent our best estimate from multiple literature sources, but it is feasible that these ranks could vary both locally and geographically and influence simulated browsing impacts. Much of the browsing-induced displacement of forest composition from control conditions results from greater browsing preference for shade-intolerant yellow poplar. The dynamics of yellow poplar (and American beech) within the PRR riparian forest highlight the importance of considering browsing interaction with the life histories of locally dominant tree species. For example, application of our model to upland forests (mixed oak and oak-pine types) at PRR would likely reveal distinctly different impacts of browsing. Because of the similarity in browsing preferences of most oaks, the long-term impact of browsing in mixed oak forests on basal area and composition might be much more subtle. Thus, the characterization of local parameters for browsing effects, species composition, and tree life history characteristics cannot be over-emphasized.

Our simulated impacts of browsing on the PRR riparian forest clearly indicate the potential importance of browsing for forest dynamics. Recognition and quantification of such impacts within a forest food web have multiple implications. First, such results provide a long-term framework for managing deer populations and browsing impacts. Second, some previous assessments suggest that long-term forest dynamics from gap models are not sensitive to parameterization of regeneration (Leemans, 1991; Botkin and Nisbet, 1992). These assessments did not include species-specific loss of regeneration to a selective biotic agent such as deer. In contrast, our simulations suggest that selective browsing of seedlings and saplings can alter the dynamics of forest succession, even if final forest composition is not affected. While forest gap models are a useful tool for simulating global change (Vance, 1996), our results suggest that biotic factors that create long-term, gradual changes in forest community composition or ecosystem-level characteristics such as forest standing biomass should be factored into analyses of global change impacts. Separating biotic and abiotic effects on changing forest composition will be difficult when both manifest themselves gradually over long time frames. To complicate this interaction further, browsing can effect changes in ecosystem processes indirectly by altering forest species composition and thus decomposition substrates (Pastor et al., 1988 McInnes et al., 1992). We do not expect white-tailed deer browsing-induced changes in forest composition within the PRR riparian forest to result in dramatic decomposition and nutrient cycling changes because the tree species are too similar in chemical characteristics. However, not all forests currently experiencing severe deer browsing are composed of chemically similar species. Finally, from the ecological perspective of understanding interactions between a generalist browser and the vegetative community on which it feeds, our results promote many questions. For example, can browsing influence the spatial pattern of tree species within the forest? Addressing such questions of ‘within community’ dynamics will require the greater detail inherent in the SORTIE paradigm for gap models, such as spatially explicit tree locations and species-specific seed dispersal parameters. Nonetheless, parameterization of SORTIE to assess potential browsing impacts in multiple forests of varying composition and under various local growing conditions seems unrealistic at this point. This would be a feasible goal within the JABOWA-FORET paradigm. While we would expect a SORTIE-based model to produce similar long-term browsing impacts as demonstrated by our model, this complementarity of applications for SORTIE and JABOWA-FORET approaches to forest modeling is an asset to both science and management.

Our implementation of deer browsing does not explicitly consider deer population dynamics or deer population age structure. This conceptual approach is similar to that used by Kienast et al. (1999), who based browsing intensities on empirical measurements but did not specifically implement a deer population model in simulating long-term browsing impacts. In contrast, Jorritsma et al. (1999) simulated browsing as a function of forage palatability and potential deer intake, with intake based on a general model of browser biomass. None of these individual-based forest-modeling approaches have incorporated the spatial distribution of forests within the landscape and subsequent effects of forest patch distribution on browsing intensity. For the PRR site, we do not believe that integration of a deer population model is appropriate in conjunction with a forest gap model, largely because of landscape-level effects on deer population size and spatial distributions. Other than lack of hunting and predators, the primary reason that deer populations have reached problematic densities is because of the juxtaposition of agricultural, forest, and often suburban habitats (McCabe and McCabe, 1984).

This is certainly the case for PRR, which is situated within the Baltimore–Washington metropolitan area. Feedback from forest browse availability in a gap model to deer population growth/decline would be quite meaningless because, although deer use the forest for cover and browsing, population sizes are dictated by availability of food from agricultural areas, lawns, etc. Thus, our simulations are meant to explore the implications of different deer densities for forest ecosystems embedded in landscapes that support different deer population sizes. Our results indicate significant long-term impacts.

Within our browsing algorithm structure, patchy utilization of the forest for browsing is implicit because browsing is less likely to occur in forest stands having low seedling densities. This implementation of density-dependent browsing at the stand level, followed by selective browsing of the seedling community within forest stands reflects our empirical analysis of how deer interact with the PRR forest (Liang and Seagle, in press). Thus, deer foraging may ultimately be viewed as a three-level foraging hierarchy, where deer populations using forest habitats are determined by the production and distribution of food at the landscape scale, resulting deer densities interact with forest regeneration dynamics to pattern forest patch use and, finally, selective within-patch browsing can influence forest composition dynamics. Integration of landscape-scale deer population models with advanced forest succession simulators, such as SORTIE, will bridge these multiple scales and extend our insight to the impacts demonstrated here.

5. Conclusion

Our simulations demonstrate the potential for deer browsing to increase the rate of forest succession by decreasing regeneration of the early successional dominant yellow poplar. Nonetheless, whether browsed or unbrowsed, the trajectory of riparian forest succession at PRR is toward American beech domination. This long-term importance of tree species life history traits, relative to disturbance by an overabundant browser, suggests an interesting choice for forest management and conservation at PRR. Should conservation of the ‘endpoint’ of succession, or the mechanism of getting to that endpoint, be the goal of management? Given the potential rapid effect of browsing on the balance between yellow poplar and American beech, the current dominance of forest basal area by poplar, and the low regeneration rate of poplar (Liang and Seagle, in press), this forest is poised for an accelerated rate of succession. Differentiating such biotic-induced changes in forest composition from climatic effects, both of which are gradual and highly interactive with species life history characteristics, is an important challenge for joint empirical and modeling studies.

By conceptually basing many of our model modifications on site-specific field data but implementing them in a format that allows ready modification among study sites, our model reflects a philosophical blend of JABOWA-FORET generality and SORTIE specificity. The potential for deer browsing to impact forest basal area and mid-successional species composition demonstrated by our model suggests that the intensive site-specific parameterization of the SORTIE approach could useful for examining interactions of browsing with seedling demography. Nonetheless, we feel that linking individual-based forest models with a landscape-scale deer population model will be needed to truly generate any feedback between deer population size and forest browse availability.

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