



Modeling the interacting effects of browsing and shading on mountain forest tree regeneration (*Picea abies*)

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Abstract

Although ungulate herbivory influences forest dynamics over a variety of spatial and temporal scales, relatively few models have been developed for investigating browsing effects on tree regeneration processes. We describe a new, mechanistic model (HUNGER) that modifies a well-established mathematical formulation for plant nutrient transport and conversion processes to simulate sapling response to ungulate browsing and light availability. The HUNGER model simulates primary production, height and diameter growth, dry matter allocation, and population dynamics of tree saplings at the scale of small (e.g. 0.001 ha) regeneration patches.

The model was applied to *Picea abies* saplings in mountain forests of eastern Switzerland after calibration based on data for sapling height growth, radial growth, and biomass components under varying light conditions. Independent data were used to test the ability of the model to represent sapling responses to browsing. The model slightly over-predicted sapling height, while no significant differences were found between simulated and observed basal diameter, total biomass or leaf biomass. Model experiments were conducted to explore the interactive effects of winter browsing intensity and relative light availability upon sapling net growth. Simulated shading effects were gradual until approximately 40% relative light availability (if browsing pressure was low) or 60% relative light availability (if browsing pressure was high). Below these values, the model simulates sharp declines in net growth rate. Model results suggest nonlinear responses to browsing and light availability, and the existence of light intensity thresholds for forest regeneration that should be relevant for management activities affecting deer density and crown cover.

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1. Introduction

In recent decades, numerous computer simulation models have been developed for investigating forest growth and yield dynamics, stand development, and long-term forest succession (e.g. Botkin et al., 1972;

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Pacala et al., 1993; Robinson and Ek, 2003). Most such models focus on tree growth processes, often representing mortality and especially regeneration with relatively unsophisticated formulations (Bugmann, 2001). Yet “bottom-up” factors influencing tree establishment and sapling growth, including mammalian herbivory, snow damage or the availability of suitable microsites for seed germination, may affect forest dynamics over a variety of spatial and temporal scales. The effects of browsing ungulates on forest regeneration are significant on a worldwide basis and interact strongly with other influences including the understory growing environment, disturbance regimes, and historical land-use patterns (Gill, 1992; Weisberg and Bugmann, 2003).

Current models of long-term forest dynamics that consider herbivore effects have represented browsing responses using simple empirical formulations (e.g. Bugmann, 1996; Jorritsma et al., 1999; Kienast et al., 1999). Browsing intensity may act as a filter upon the probability of tree regeneration (Bugmann, 1996), entire saplings may be consumed whenever browsing occurs (Jorritsma et al., 1999), or empirically derived functions are used to model browsing intensity effects upon height growth (Kienast et al., 1999; Seagle and Liang, 2001) or rate of sapling mortality (Weisberg and Coughenour, 2003). Although such approaches have the advantage of simplicity and ease of parameterization, they have the disadvantage of not permitting modeling of the plant-herbivore system beyond the bounds within which the empirical relationships were derived.

Many modeling approaches do not account for the historical dimension of sapling response to browsing. Such responses may be conditioned by the legacy of past browsing events and changing growth environments, as manifested in current plant nutritional status. Experimental studies have convincingly demonstrated that sapling response to clipping is strongly conditioned by the availability of stored nitrogen (e.g. Millard et al., 2001). The influence of carbon status is less clear, with numerous studies showing a decline of carbohydrate reserves associated with regrowth following clipping, but also an inability of plants to utilize all of their carbohydrate reserves, suggesting an opportunity cost to carbon storage in response to herbivory (reviewed in Chapin et al., 1990, pp. 436–437).

Sapling responses to browsing likely depend upon many interacting environmental influences including

shading, temperature, and availability of water and nutrients (Edenius et al., 1995; Bugmann and Weisberg, 2003; Weisberg and Bugmann, 2003). Since sapling morphology and carbon reserve dynamics depend on the interaction between past growing conditions (especially light availability) and browsing history, it is difficult to come up with simple empirical functions for sapling responses to either factor (browsing and light) independent of the other. Therefore, it seems important to represent the interaction between browsing and light in a more explicit manner, which might include some of the processes by which sapling growth and nutrient allocation respond to herbivory. Such an approach would facilitate the exploration of key physiological and morphological interactions during regrowth following browsing.

Berninger et al. (2000) utilized a modified transport resistance approach (Thornley, 1972) to model the growth responses of a tropical leguminous tree to silvicultural pruning, a process in many ways similar to ungulate browsing. The transport resistance approach simulates dry matter partitioning among plant organs mechanistically as material flows between sources and sinks of carbon and nitrogen (Thornley, 1991). This approach is at the core of the mathematical model described in this paper. Our objective was to develop a process-based model of sapling growth and allocation that simulates the outcome of ungulate browsing as an emergent property of underlying sapling responses. Such a model should be useful both for its practical applications in forestry, and for developing a predictive understanding of how ungulate browsing influences forest regeneration under different growing conditions. In this paper, we describe the model, its calibration and testing for two mesic mountain forests in Switzerland, and discuss emergent findings concerning the interactive effects of winter browsing intensity and relative light availability upon the ability of saplings to grow beyond the reach of browsing ungulates.

2. Methods

2.1. Model description

HUNGER (Herbivory by UNGulates and its Effects on forest Regeneration) simulates primary production, dry matter allocation including height and diameter

growth, and population dynamics of tree saplings in response to browsing intensity, shading, and climate. The model is mechanistic with regard to partitioning of carbon and nitrogen among shoot and root tissues, a critical process for simulating realistic responses to browsing events. In HUNGER as in the real world, sapling responses depend upon the past history of growth and carbon allocation as reflected in current sapling morphology (i.e. shoot:root ratio, crown shape) and availability of reserve and substrate carbon. HUNGER simulates transport of carbon and nitrogen between shoot and root systems, and conversion of carbon between substrate, reserve, and structural forms. Water uptake and transpiration are not explicitly represented in the model, and an assumption is made (not unreasonable for our mesic study area in the Northern Swiss Alps) that water availability is not limiting for tree growth. Partitioning of carbon and nitrogen is based on a transport resistance approach (Thornley, 1972, 1991), but modified so as to include reserve carbohydrate pools (i.e. plant starches) as in Berninger et al. (2000) and Levy et al. (2000). As in Levy et al. (2000) meristems are not simulated explicitly. Following Berninger et al. (2000), the transport resistance approach is used to represent transport of nitrogen and carbon between aboveground and belowground tissues, but not between separate components of aboveground and belowground parts (e.g. leaf, branch, stem), which are instead represented using empirical functions of light availability.

Our modeling approach differs from previous, similar efforts in several respects. Unlike earlier approaches that consider only quantities of biomass in various plant compartments (Thornley, 1972; McMurtrie and Wolf, 1983; Levy et al., 2000; Berninger et al., 2000), sapling height and diameter are tracked as independent variables. Sapling morphology is represented in the sense of vertically explicit accounting of shoot tissues, and variable branch lengths for different height layers within the sapling crown. Morphological plasticity of saplings in shaded environments is included using empirical adjustments for allometric coefficients according to relative light availability. Simulated saplings also adjust to shade in that lower branches self-prune if they experience a long-term carbon deficit. Plant responses to environmental variability (temperature, nitrogen, potentially soil moisture) are included. Finally, the HUNGER model includes browsing as a key pro-

cess influencing sapling growth and morphology. This is similar to the use of a similar model by Berninger et al. (2000) to predict the response of a tropical tree species (*Gliricidia sepium*) to alternative green pruning regimes.

The model describes sapling growth and survival to beyond the reach of ungulate browsing at the scale of small (e.g. 0.001 ha) regeneration patches. Although the dynamics of multiple age cohorts and species of tree saplings may be represented simultaneously, the model is an individual-based plant model. In this paper, we report only on how the model represents growth and dry matter allocation at the level of individual *Picea abies* saplings. We used *P. abies* as our model species not because it is a preferred browse species in the study area (it is of relatively low palatability), but because (1) it is the dominant tree species in much of the northern Swiss Alps and (2) its physiological characteristics (i.e. model parameters) are relatively well known in the literature.

2.1.1. Basic structure

Each modeled regeneration patch may include multiple tree species, and each tree species may include multiple age cohorts. Age cohorts are initiated when a regeneration event occurs, and persist within the model until either all members have died or the height of the cohort has exceeded a user-defined height threshold where saplings are beyond the reach of ungulate herbivores. In this paper, we report results for the dynamics of only a single cohort of one species. Growth and allocation processes are modeled for a single “representative sapling” within each cohort, over a sub-daily (0.1 day) time step. Sapling numbers within a cohort are adjusted according to mortality functions, described below, over an annual time step. The model is implemented in Microsoft Visual Studio 6.0, and is coded in C++.

The model simulates flows between carbon pools (structural, substrate, and reserve) separately for shoot and root systems (Fig. 1). Substrate C (C_{Sub}) photosynthesized from solar radiation that is not lost to respiration may be converted to structural aboveground carbon (C_{Stx}) in the growth process, converted into starch reserves (C_{Res}), or translocated to the roots. A mass balance is similarly modeled for the plant substrate form of nitrogen (N_{Res}). Nitrogen uptake, translocation to the shoot system, and conversion to biomass in growth

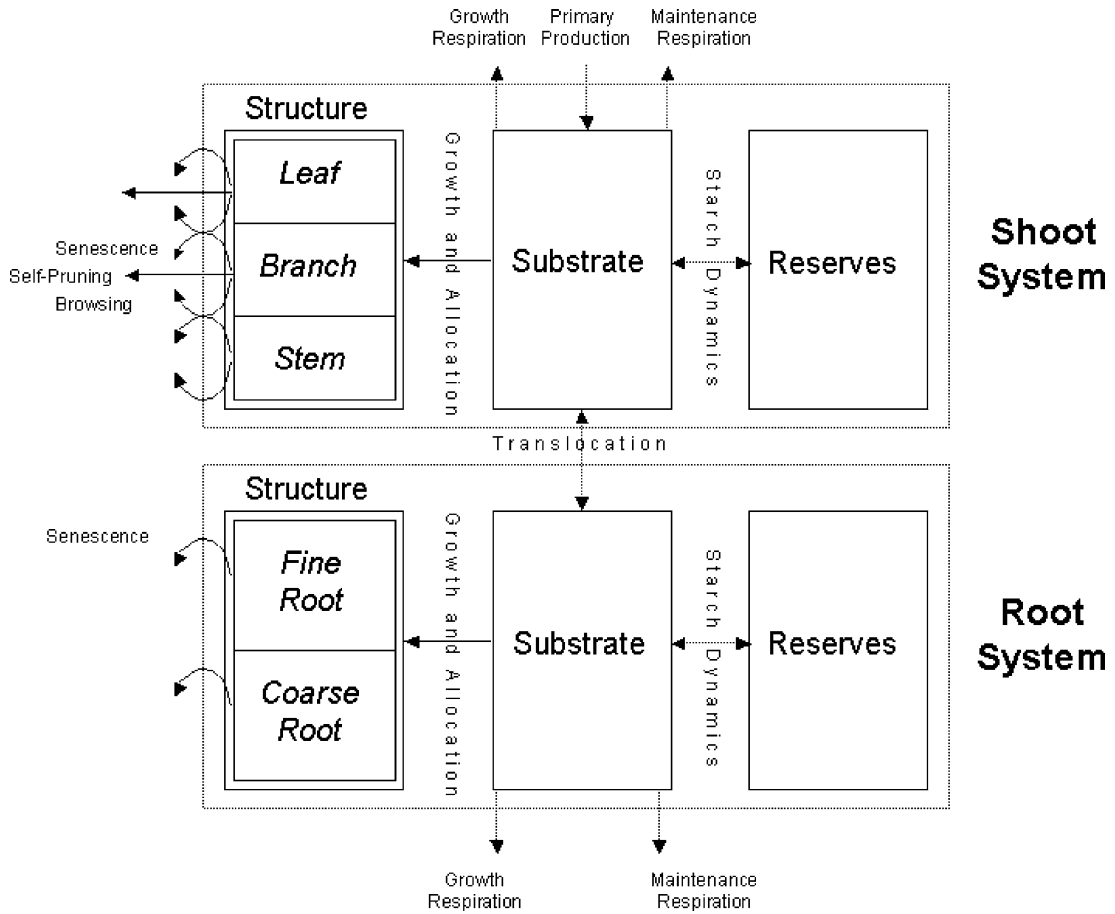


Fig. 1. Carbon flows within the model. Boxes represent pools or state variables, while arrows represent material flows between pools. Note that the leaf, branch, stem, fine root, and coarse root pools are in units of dry biomass, while the reserve, substrate, and structural pools (for both shoots and roots) include only the carbon component.

are simulated. These processes are described in greater detail below.

2.1.2. Mass balance

The mass balances (i.e. state equations) of biomass, carbon, and nitrogen within the various plant compartments can be expressed according to the following differential equations:

2.1.2.1. Shoot system.

$$\frac{dC_{Sub,s}}{dt} = P - T_c - G_{C,s} - R_{g,s} - X_s - R_{m,s} - S_{Csub,s} - H_{Csub} - Z_{Csub} \quad (1)$$

$$\frac{dC_{Res,s}}{dt} = X_s - H_{Cres} \quad (2)$$

$$\frac{dC_{Stx,s}}{dt} = G_{c,s} - S_{Cstx,s} - H_{Cstx} - Z_{Cstx} \quad (3)$$

$$\frac{dN_{Sub,s}}{dt} = -G_{N,s} - T_N - S_{Nsub,s} - H_{Nsub} - Z_{Nsub} \quad (4)$$

where all variables are defined in Table 1. The time step used to solve these equations (*dt*) is 0.1 days. Eqs. (1)–(4) refer to carbon and nitrogen quantities, while the following equations refer to dry biomasses (*B*'s) of leaves (*L* subscripts), branches (*B* subscripts) and

Table 1
Abbreviations used to describe the mass balance algorithms of the HUNGER model

Symbol	Name	Units
B_L	Leaf biomass	gDM
B_B	Branch biomass	gDM
B_S	Stem biomass	gDM
B_{FR}	Fine root biomass	gDM
B_{CR}	Coarse root biomass	gDM
$C_{Sub,i}$	Carbon substrate concentration (i = shoot, root)	gC/gDM
$C_{Res,i}$	Carbon reserve concentration (i = shoot, root)	gC/gDM
$C_{Stx,i}$	Structural carbon concentration (i = shoot, root)	gC/gDM
G_i	New biomass growth allocated to i = L, B, S, FR, CR	gC
$G_{C,i}$	Carbon growth utilization (i = shoot, root)	gC
$G_{N,i}$	Nitrogen growth utilization (i = shoot, root)	gC
H_i	Biomass loss to herbivory (i = L, B, S)	gC
H_{Cstx}	Structural carbon loss to herbivory	gC
H_{Csub}	Substrate carbon loss to herbivory	gC
H_{Cres}	Reserve carbon loss to herbivory	gC
H_{Nsub}	Substrate nitrogen loss to herbivory	gC
$N_{Sub,i}$	Nitrogen substrate concentration (i = shoot, root)	gN/gDM
P	Gross primary production	gC
$R_{g,i}$	Growth respiration (i = shoot, root)	gC
$R_{m,i}$	Maintenance respiration (i = shoot, root)	gC
$S_{Csub,i}$	Substrate carbon loss to senescence (i = shoot, root)	gC
$S_{Cstx,i}$	Structural carbon loss to senescence (i = shoot, root)	gC
T_N	Nitrogen translocation, shoot to root	gC
$S_{Nsub,i}$	Substrate nitrogen loss to senescence (i = shoot, root)	gC
S_i	Biomass loss to senescence (i = L, B, S, FR, CR)	gC
T_C	Carbon translocation flux, shoot to root	gC
T_N	Nitrogen translocation flux, shoot to root	gN
U_N	Nitrogen uptake	gN
X_i	Change in carbon reserve concentration	gC/gDM
Z_{Cstx}	Structural carbon loss to self-pruning	gC
Z_{Csub}	Substrate carbon loss to self-pruning	gC
Z_i	Biomass loss to self-pruning (i = L, B)	gC
Z_{Nsub}	Substrate nitrogen loss to self-pruning	gC

The abbreviations L, B, S, FR and CR refer to leaf, branch, stem, fine root and coarse root, respectively. The unit expressions gC, gN, and gDM refer to grams of carbon, grams of nitrogen, and grams of dry matter, respectively.

stems (S subscripts):

$$\frac{dB_L}{dt} = \sum_{h=1}^{N_h} (G_{L,h} - S_{L,h} - H_{L,h} - Z_{L,h}) \quad (5)$$

$$\frac{dB_B}{dt} = \sum_{h=1}^{N_h} (G_{B,h} - S_{B,h} - H_{B,h} - Z_{B,h}) \quad (6)$$

$$\frac{dB_S}{dt} = \sum_{h=1}^{N_h} (G_{S,h} - S_{S,h} - H_{S,h}) \quad (7)$$

where changes in biomass are iterated over height layers (h) through the number of height layers in each representative sapling (N_h), G_i is the new biomass growth allocated to i = leaves, branches and stems, S_i

the biomass loss to senescence, H_i the biomass loss to browsing, and Z_i the biomass loss to self-pruning.

2.1.2.2. Root system. Eqs. (8)–(11) for carbon and nitrogen balance of roots are analogous to Eqs. (1)–(4) for the shoot system:

$$\frac{dC_{\text{Sub},r}}{dt} = T_c - G_{C,r} - R_{g,r} - X_r - R_{m,r} - S_{C_{\text{Sub},r}} \quad (8)$$

$$\frac{dC_{\text{Res},r}}{dt} = X_r \quad (9)$$

$$\frac{dC_{\text{Stx},r}}{dt} = G_{C,r} - S_{C_{\text{Stx},r}} \quad (10)$$

$$\frac{dN_{\text{Sub},r}}{dt} = U_N + T_N - G_{N,r} - S_{N_{\text{Sub},r}} \quad (11)$$

Eqs. (12) and (13) for biomass increments of fine roots (subscript FR) and coarse roots (subscript CR) are analogous to Eqs. (5)–(7) for the shoot system, except that roots are neither partitioned into height layers nor directly reduced by ungulate herbivory:

$$\frac{dB_{\text{FR}}}{dt} = G_{\text{FR}} - S_{\text{FR}} \quad (12)$$

$$\frac{dB_{\text{CR}}}{dt} = G_{\text{CR}} - S_{\text{CR}} \quad (13)$$

2.1.3. Gross primary production

Gross primary production (P) is estimated separately for, and then summed over each height layer of each representative sapling, using an approach similar to that of Landsberg and Waring (1997):

$$P = \sum_{h=1}^{N_h} E_P I_h \quad (14)$$

where E_P is the radiation conversion efficiency and I_h the quantity of photosynthetically active radiation (PAR) intercepted (MJ) in height layer h . Intercepted PAR is calculated using Beer's law (Monsi and Saeki, 1953) and simple geometric relationships, assuming a cylindrical crown shape, as in Berninger et al. (2000):

$$I_h = \text{In}_h \pi \text{Bl}_h^2 (1 - e^{-k_{\text{Ext}} \text{Lb}_h (k_{\text{SLA}} \pi \text{Bl}_h^2)^{-1}}) \quad (15)$$

where Bl_h is the branch length (m), k_{Ext} the light extinction coefficient, k_{SLA} the specific leaf area, Lb_h the leaf biomass (g), and In_h the irradiance (MJ m^{-2}) incident upon height layer h . The light incident upon each

layer (In_h) is iteratively reduced by light absorption in each of the layers above.

Radiation conversion efficiency (E_P) is the product of a species-specific optimal efficiency (k_P) and a parabolic temperature-dependent modifier function. The model structure also contains modifiers on P for soil moisture and nitrogen effects, but these have not been used in the present study. No information is available on soil nitrogen in the study area, and hydrological processes are not yet implemented in the model. However, the study area is quite mesic at all seasons, and it is reasonable to assume that water limitations on P are not important.

2.1.4. Respiration

In a widely used formulation (Le Roux et al., 2001), maintenance respiration (R_m) per unit structural carbon mass (C_{stx}) is an exponential function of temperature (T):

$$R_m = k_{zr} e^{k_{tr} T} C_{\text{stx}} \quad (16)$$

where k_{zr} is the maintenance respiration rate at 0°C and k_{tr} a temperature coefficient (assumed constant at 0.0693, analogous to a Q_{10} coefficient of 2). Growth respiration (R_g) is calculated as a constant fraction (k_{gr}) of structural carbon allocated to growth (G_c):

$$R_g = k_{gr} G_c \quad (17)$$

2.1.5. Growth

As in Levy et al. (2000) and the original Thornley (1972) model, utilization rates of carbon (G_C) and nitrogen (G_N) in structural growth are given by

$$G_C = k_{fC} u W s \quad (18)$$

$$G_N = k_{fN} u W s \quad (19)$$

where k_{fC} and k_{fN} are the fractions of carbon and nitrogen, respectively, in structural matter. Relative growth rate (u) is directly proportional to the product of carbon and nitrogen substrate concentrations, following the Michaelis–Menten formulation:

$$u = \begin{cases} \frac{k_{\text{umx}} C_{\text{sub}} N_{\text{sub}}}{k_u + C_{\text{sub}} N_{\text{sub}}} & C_{\text{sub}} \geq k_{\text{CTh}}, N_{\text{sub}} \geq k_{\text{NTh}} \\ 0 & \text{else} \end{cases} \quad (20)$$

where C_{sub} and N_{sub} are substrate carbon and nitrogen concentrations, respectively, k_{umx} and k_{u} are Michaelis–Menten coefficients, and k_{CTh} and k_{NTh} are threshold carbon and nitrogen substrate concentrations below which growth cannot occur. The same equations are used to calculate structural growth of shoots and roots, except that the parameter values for k_{umx} , k_{u} , k_{CTh} , and k_{NTh} may differ.

2.1.6. Dry matter allocation

Carbon partitioning between shoot and root systems is an emergent outcome of the transport and conversion processes modeled, following the general approach originally outlined in Thornley (1972). However, the modeling of dry matter allocation within these systems is based on empirical functions derived from harvested saplings (see below). Allocation to fine versus coarse components of root tissue is modeled using an empirical allometric coefficient (k_{FCr}). For shoots, the proportion of new structural carbon allocated to stem tissue is represented as an empirical function of relative light availability, such that an increased proportion is allocated to stem tissue under conditions of higher light. This pattern allows saplings growing in the shade to develop characteristic growth forms with a high ratio of crown diameter to tree height, and long lateral branches near the top of the sapling (i.e. an “umbrella” or flat-topped appearance, which was also observed in the sampled saplings). Such morphological plasticity leading to plate-shaped crowns has been widely observed for saplings of a variety of tree species, particularly for late-successional species growing in deep shade (e.g. King, 1994; Messier and Nikinmaa, 2000), and has been reported for *P. abies* (Greis and Kellomäki, 1981). Our approach, however, does not allow for asymmetric crown growth responses to local differences in light availability, as can be modeled using more detailed representations of the crown growth process (e.g. Moravie et al., 1997; Robert, 2003). New carbon allocated to stem tissue is converted to biomass and distributed uniformly among the stem components of the various height layers.

The portion of shoot growth biomass not allocated to stem is partitioned to leaves and branches in a multi-step process. First, this quantity is divided among height layers such that the relative amount of branch and leaf biomass allocated to the upper third of the shoot varies according to an empirical function of light

availability. This, in combination with self-pruning, further enables morphological plasticity of saplings in dense shade. Second, for each height layer the model checks whether there is the expected proportion of leaf biomass relative to the branch biomass present. This expected proportion varies according to an empirical function of light (k_{LFBf}), consistent with the observation from destructively sampled saplings that *P. abies* saplings in greater shade have a greater ratio of leaf to branch biomass. The proportion of leaf to branch biomass might differ from k_{LFBf} due to senescence or browsing, which reduce leaf and branch tissues at different rates. If there is too little leaf, the plant first allocates sufficient biomass to leaves so that the expected allometric relationship (k_{LFBf}) is achieved, before allocating the remaining biomass.

2.1.7. Height and diameter growth

In order for tree form to be represented, stem biomass growth must be converted into volume increment and then partitioned into height and diameter components. Unlike many forest succession models that assume a constant allometric relationship between tree height and diameter regardless of growing environment, the HUNGER model allows height and diameter to vary independently. The increment of wet stem volume (dV_{w}) is calculated from the increment of dry stem volume (dV_{d}) as

$$dV_{\text{w}} = \frac{A_{\text{ST}} dV_{\text{d}}}{k_{\text{WD}} \left(1 - \frac{k_{\text{Vsk}}}{100} \right)} \quad (21)$$

where A_{ST} is the allocation of biomass to the stem, k_{WD} a wood density parameter, and k_{Vsk} a parameter describing volumetric wood shrinkage from green to oven-dry volume (% units). Assuming that the new stem volume increment takes the geometric form of a cone, wet volume increment is converted into an index of tree-volume increment (V_{x}):

$$V_{\text{x}} = dV_{\text{w}} \frac{12}{\pi} = \Delta D^2 H \quad (22)$$

The differentiation of $D^2 H$ yields

$$\Delta(D^2 H) = 2DH \Delta D + D^2 \Delta H = V_{\text{x}} \quad (23)$$

Given this relationship, diameter (D) and height (H) increments are then calculated independently as a func-

tion of relative light availability, following Lindner et al. (1997):

$$dD = \frac{V_x}{2HD + fH D^2} \quad (24)$$

$$dH = \frac{fH V_x}{2HD + fH D^2} \quad (25)$$

given that

$$fH = k_{Sm} + k_{EI} \left(\frac{1}{L_{rel}} - 1 \right) \quad (26)$$

where fH is a coefficient describing the relative proportion of volume increment that is converted to height growth, L_{rel} the relative light availability (proportion of extraterrestrial photosynthetically active radiation) incident upon the tree regeneration layer, and k_{sm} and k_{EI} are curve-fitting parameters for the effect of shading (hence, competition) on relative allocation to height growth, as in Lindner et al. (1997).

2.1.8. Carbon reserve dynamics

Starch breakdown (reserve unloading) and synthesis (reserve loading) follow the approach of Berninger et al. (2000):

$$X = \frac{(C_{sub} - k_{CThr})W^{0.2}}{k_{rs}} \quad (27)$$

reserve unloading, $C_{sub} \leq k_{CThr}$

$$X = \left(1 - \left(\frac{C_{Res}}{k_{Rmax}} \right)^3 \right) \frac{(C_{sub} - k_{CThr})W^{0.2}}{k_{rs}} \quad (28)$$

reserve loading, $C_{sub} > k_{CThr}$

where X is the change in reserve concentration (negative if unloading, positive if loading), C_{Res} the reserve carbon concentration (gC/gDM), W the dry biomass of the shoot or root system, k_{rs} the conversion resistance between substrate and reserve carbon, k_{Rmax} the maximal concentration of reserve carbohydrates in the shoot or root, and k_{CThr} is the threshold reserve concentration that determines if reserves are mobilized or accumulated. Reserve carbon is mobilized when substrate carbon concentrations are lower than k_{CThr} . When substrate concentrations are high, more starch is accumulated. As the reserves approach their maximal

allowable concentration, the rate of starch accumulation decreases asymptotically until k_{Rmax} is reached. The rate of conversion in either direction is increased by greater structural biomass. The same equations are used to calculate carbon reserve dynamics of shoots and roots, except that all parameter values are permitted to differ.

2.1.9. Translocation

Following Berninger et al. (2000) and Thornley (1997), we use a modified transport resistance approach to simulate transport of carbon and nitrogen substrate between shoot and root:

$$T_C = \left(\frac{1}{W_s^{0.2}} + \frac{1}{W_r^{0.2}} \right)^{-1} (C_{sub,s} - C_{sub,r})k_{TC}k_{tt} \quad (29)$$

$$T_N = \left(\frac{1}{W_s^{0.2}} + \frac{1}{W_r^{0.2}} \right)^{-1} (N_{sub,s} - N_{sub,r})k_{TN}k_{tt} \quad (30)$$

where T_C is the transport rate of carbon from shoot to root (note that a negative value would lead to carbon flow in the reverse direction), T_N the transport rate of nitrogen from shoot to root, W_s and W_r are the dry biomasses of shoots and roots, respectively, $C_{sub,s}$ and $C_{sub,r}$ are the carbon substrate concentrations in shoots and roots, respectively, $N_{sub,s}$ and $N_{sub,r}$ are the nitrogen substrate concentrations in shoots and roots, respectively, k_{TC} and k_{TN} are transport conductance coefficients for carbon and nitrogen, respectively, and k_{tt} is a temperature coefficient.

The rate of transport between shoot and root is therefore directly proportional to the difference of concentrations between shoot and root substrate pools, and inversely proportional to the reciprocal of plant structural mass. The direction of flow is determined by which plant tissue type (shoot or root) has greater substrate concentration. It was necessary to add the temperature modifier of translocation rate because we are modeling plant growth and allocation processes year-round in a temperate system where winter temperatures can be limiting for transport processes.

2.1.10. Nitrogen uptake

In the absence of soil nitrogen data to develop a more complex model (e.g. Berninger et al., 2000), we represented the nitrogen uptake to the roots (U_N), following

Thornley (1997) as

$$U_N = \left(\frac{k_N W_{FR}}{1 + \left(\frac{N_{sub,r}}{k_{JN}} \right)} \right) k_{TN} \quad (31)$$

where W_{FR} is the dry biomass of fine roots, k_N a nitrogen uptake efficiency parameter, k_{JN} a parameter providing for inhibition of N uptake when root nitrogen concentration is high, and k_{TN} a temperature coefficient where nitrogen uptake may be reduced at cold temperatures.

2.1.11. Senescence, self-pruning, and browsing

Simulated saplings can lose biomass in three distinct ways, through senescence, self-pruning, and browsing. The senescence rate (S_i) of a given biomass compartment i (i.e. plant organ: stem, branch, leaf, fine root, coarse root) is simply a fixed proportional loss:

$$S_i = k_{si} W_i \quad (32)$$

where k_{si} is a proportional loss parameter. In the case of leaves, k_{si} can vary by month of the year; for other tissue types, k_{si} is a constant.

Losses of substrate carbon and nitrogen are assumed to be directly proportional to losses of structural biomass, although a fixed proportion of retranslocation prior to senescence is assumed:

$$S_{Csub,j} = (1 - k_{CRT}) C_{sub,s} \frac{S_j}{W_j} \quad (33)$$

$$S_{Nsub,j} = (1 - k_{NRT}) N_{sub,s} \frac{S_j}{W_j} \quad (34)$$

where $S_{Csub,j}$ and $S_{Nsub,j}$ are senescence rates for carbon and nitrogen substrates, respectively, in plant tissue type j (shoot or root), k_{CRT} and k_{NRT} are retranslocation coefficients for carbon and nitrogen, W_j the dry biomass of shoot or root tissue, and S_j the total amount of structural biomass lost through senescence from shoot or root tissue. It is assumed that no reserve carbon is lost during senescence.

The model also represents self-pruning, where saplings tend to lose their lower branches under shaded conditions. Self-pruning was widely observed in *P. abies* saplings sampled under field conditions. Saplings grown in full sun (relative light availability from 0.67 to 0.83) had live crown ratios that were on average 14%

greater than those growing under more shaded conditions (relative light availability from 0.10 to 0.25). Self-pruning is simulated by tallying, for each height layer in the representative sapling of each cohort, the number of growing seasons for which maintenance respiration has exceeded gross primary production (i.e. a carbon deficit). When the carbon deficit tally exceeds a species-specific threshold (k_{Prune}), all branch and leaf biomass is removed from that height layer. Losses of substrate carbon (Z_{Csub}) and nitrogen (Z_{Nsub}) from the self-pruned height layers are calculated as for normal senescence (Eqs. (32)–(34)).

Browsing is simulated as a stochastic process. A model input, the species-specific proportion of saplings undergoing browsing in a given year or month, is treated in the model as the probability of the representative sapling for a given cohort being browsed during that time period. Whether browsing occurs in any time step is determined using a $U(0, 1)$ random variate.

Two forms of browsing are modeled: top-down and lateral. Top-down browsing can be treated either as a fixed height increment removed (cm) each time browsing occurs, or as a removal of current annual growth (or if browsing occurs in winter, the previous season's annual growth). In either case, the structural dry mass of completely browsed height layers, and a proportional quantity of structural dry mass of partially browsed height layers, are decremented from leaf, branch and stem tissues, and from the pool of shoot structural carbon. Shoot substrate carbon (H_{Csub}), substrate nitrogen (H_{Nsub}), and reserve carbon (H_{Cres}) are decremented proportionally to the level of biomass removed, without retranslocation.

Lateral browsing is simulated as a stochastic process independent of top-down browsing, and both types of browsing may be simulated simultaneously. In lateral browsing, a height layer to be browsed is randomly selected with a uniform probability. A user-input, fixed branch length increment (cm) is removed each time step when browsing occurs. Losses of structural dry mass, carbon, and nitrogen pools occur analogously as for top-down browsing, except that no stem biomass is removed (only leaves and branches are laterally browsed).

2.1.12. Phenology

Phenology is represented quite generally in the model, by using mean daily temperature to define be-

ginning and ending dates for the growing season. Growing degree-days are accumulated as temperature exceeds a critical threshold (k_{TDD}), and the growing season begins once a critical number of growing degree-days (k_{iDD}) has been reached. The growing season ends either when the number of growing degree-days has exceeded a critical threshold (k_{fDD}) or when mean daily temperature has fallen below the minimum temperature for plant growth (k_{TMN}). Growth and dry matter allocation occur only during the growing season; other plant processes (e.g. production, respiration, translocation, carbon reserve dynamics) can occur all year but are regulated by temperature. Although simple, this representation of phenology allows the model to capture qualitative differences in growing season effects between sites and weather years. More complex, realistic approaches (reviewed in Kramer, 1994) might be useful for capturing seasonally varying browsing responses, but would require additional data to parameterize.

2.1.13. Sapling population dynamics

Eqs. (1)–(34) refer to the growth dynamics of individual saplings, each representing the dynamics of an entire age cohort. Each cohort is composed of identical individuals. The growth dynamics of individual saplings are linked to the population dynamics of tree regeneration patches through the influence of the annual height growth rate on sapling mortality. As for most forest gap models (reviewed in Bugmann, 2001), our model assumes that low growth rates are indicative of environmental stress, which in turn causes tree mortality. Modeled sapling mortality occurs annually, at the beginning of each growing season. Stress mortality (M_S) occurs according to a species-specific probability each year during which the number of slow-growth years exceeds a species-specific threshold. The number of slow-growth years is incremented each year height growth falls below a threshold value, and is reset to 0 each year height growth exceeds that value.

Additional modeled sources of mortality include a stochastic mortality component (M_Z), as well as a browsing-related probability of mortality (M_B) related to a user-defined input function of mortality probability according to the proportion of sapling biomass consumed. The former allows for sapling mortality due to processes not represented by the model, while the latter allows browsing to kill saplings through mechanisms other than stress associated with growth reduction. At

an annual time step, sapling numbers within a cohort (N_C) are therefore modeled as

$$\frac{dN_c}{dt_m} = N_C - (M_{B,c} + M_{Z,c} + M_{S,c}) \quad (35)$$

At the level of an age cohort, there is by definition no recruitment of new saplings. Recruitment of overall sapling numbers of a given species occurs during the establishment of new cohorts, and is not described here, since the current work describes growth and mortality of individual cohorts within a single species.

2.2. Model calibration and testing

The model was calibrated using field data for *P. abies* growth and biomass components from the Werdenberg region of eastern Switzerland, in Canton St. Gallen. The particular site (9.3816 E longitude, 47.1918 N latitude) is located on a north-facing slope at an altitude of approximately 1100 m. Climate is typical for the Northern Alps, with strong oceanic influences and an interpolated mean annual precipitation of 2000 mm (Spreafico and Weingartner, 1992). The geology is loosely structured diamictite below very clayey soils, with acidic pH values. Forest composition is conifer-dominated with a fairly even representation of Norway spruce (*P. abies*) and European silver fir (*Abies alba*) in the upper canopy, and broad-leaved tree species (mainly *Fagus sylvatica*) in the subcanopy. Twenty-one *P. abies* saplings were harvested from this site, excluding root systems. Saplings were selected to cover a wide range of height classes (12–113 cm) and light environments (9–83% canopy light transmittance).

The light environment experienced by each sapling was sampled by taking a single hemispherical photograph at approximately 5–30 cm above sapling height, using a digital camera (Nikon Coolpix 990 camera with an FC-E8 fisheye lens, focal length 8.2 mm) set on a self-leveling mount, oriented to magnetic north. Photographs were taken on an overcast day with even lighting conditions. Key parameters of the light regime were estimated from image analysis of the photographs (as in Canham et al., 1994), using the Gap Light Analyzer software (GLA; Frazer et al., 1999). Relative light availability was estimated for each sapling as the ratio of total light transmitted to the extraterrestrial radiation

above canopy height. We used ArcView GIS software and a 25-m resolution digital elevation model to calculate a “topographic mask” that the GLA software used to account for topographic shading effects of nearby ridgelines.

Sapling height and basal diameters were measured prior to harvest, using a metric ruler and dial caliper with 0.1 mm precision. Following harvest, saplings were oven-dried to constant weight, at a temperature of 105 °C for at least a 24-h period. Needles were removed and weighed. Stems and branches were sliced prior to drying into 10-cm vertical sections, and then weighed separately within each section. After weighing, the bottom-most section was sliced into thin discs. Each disc was sanded using sandpaper of progressively finer grit until tracheids were clearly visible under magnification. Tree rings were then counted along 2 radii, independently by two dendrochronologists. The oldest ring count, representing the earliest year of woody growth at the position of the root collar, was used to indicate sapling age.

Model calibration runs “grew” the Werdenberg saplings from 2 years of age (initial height and diameter of 5 and 0.015 cm, respectively) until the year of harvest, using historical weather data extrapolated to the Werdenberg sample site, shade conditions (relative light availability) particular to each sapling, and modeled solar radiation given site-specific latitude, slope aspect, and slope steepness of the site. Comparisons were made between sapling dimensions and biomass at the end of the simulation with these values at the time of harvest (for both cases, September 2001). Only two of the harvested saplings (one having grown under dense shade, the other under full sunlight) were used to calibrate the model, by manually adjusting uncertain parameters (cf. Table 2) until there was reasonable (i.e. within approximately 10%) agreement between observed and simulated sapling height, diameter, leaf biomass, branch biomass, stem biomass, and total biomass. We conducted statistical testing of model outputs for the remaining 19 saplings, which varied in their light environment and age at the time of sampling. Paired *t*-tests and linear regression models were used to compare the distributions of simulated and observed values. Distributions of biomass data were strongly right-skewed, and therefore the logarithmic transformation was applied prior to statistical comparison of observed versus simulated data sets.

These tests do not represent an independent validation of the model, since allometric relationships from all 21 saplings evaluated were used in model development. However, comparisons of observed versus simulated data for the Werdenberg saplings provide an indication as to the predictive ability of the model to represent sapling growth and dry matter allocation under unbrowsed conditions, for this particular site and application.

2.3. Model validation

A second site used for model testing was sampled at Schwanden, Canton Glarus, Switzerland, an area of similar climatic regime and vegetation composition as the Werdenberg site. Data from this site were not used for model calibration or development, and so allowed an independent validation of how well the model represents sapling responses to variable browsing, under conditions of high light. The Schwanden site is one of four long-term study sites used to assess regeneration following a high-severity windstorm in 1990 that caused extensive blow-down throughout central Europe (Schönenberger, 2002a). Among other variables, sapling height and occurrence of browsing (and other disturbances) were monitored in multiple years from 1992 to 2000 (Schönenberger, 2002b).

Simulated sapling height growth was compared to that of measured *Picea* saplings at the Schwanden site. Sapling growth was simulated for the 1994–2000 time period according to the observed incidence of browsing (lateral and terminal). Browsing was assumed to occur only during the 6 winter months, and to consume the previous year’s annual growth (terminal browsing) or 10 cm of branch length (lateral browsing). Light availability was assumed to be 90% (open conditions following windstorm).

Simulated outputs were compared with observed data for *P. abies* sapling height in the year 2000, seven years after planting. The data sets were compared graphically by plotting observed (*y*) versus predicted (*y-hat*) data directly, with the line of perfect fit (*y = y-hat*) marked, as recommended by Mayer and Butler (1993). Simulation results were also evaluated statistically against observed data using paired *t*-tests, linear regression analysis, and the modeling efficiency (EF) statistic (Mayer and Butler, 1993). The EF statistic is identical to the commonly used R^2 statistic, but repre-

Table 2
Key parameters of the HUNGER model

Symbol	Name	Equation	Units	Value	Source
k_{EXT}	Light extinction coefficient	(15)	Unitless	0.50	1
k_{SLA}	Specific leaf area	(15)	g m^{-2}	217	2
k_P	Optimal radiation conversion efficiency	–	gC/MJ (PAR)	1.74	3*
k_{ZR}	Maintenance respiration rate (0°C)	(16)	gC/gDM	$2\text{E}-4$ (Lf), $5\text{E}-5$ (St), $1\text{E}-4$ (Rt)	4*
k_{tr}	Respiration temperature coefficient	(16)	Unitless	0.0693	5
k_{gr}	Growth respiration coefficient	(17)	Unitless	0.23	6
k_{fc}	Fraction of carbon in dry matter	(18)	Proportion	0.48	7
k_{fn}	Fraction of nitrogen in dry matter	(19)	Proportion	0.03	7
k_{umx}	Maximum relative growth rate	(20)	day^{-1}	0.030 (Sh), 0.022 (Rt)	8*
k_u	Michaelis–Menten coefficient	(20)	day^{-1}	0.002 (Sh), 0.002 (Rt)	Fit
k_{CTh}	Carbon substrate threshold for growth	(20)	gC/gDM	0.01 (Sh), 0.02 (Rt)	Fit
k_{NTh}	Nitrogen substrate threshold for growth	(20)	gN/gDM	0.01 (Sh), 0.001 (Rt)	Fit
k_{FRCR}	Root allocation to fine roots	–	Proportion	0.50	Guess
k_{LBr}	Leaf fraction in leaf + branch biomass	–	Proportion	0.50–0.65 (light-dependent)	Data
k_{WD}	Wood density	(21)	g cm^{-3}	0.68 (St), 0.61 (Br)	Data
k_{Vsk}	Volumetric wood shrinkage (green – oven-dry)	(21)	Percent	22.64	Data
k_{Sm}	Shading coefficient for height growth allocation	(25)	Unitless	54.27	Data
k_{E1}	Shading coefficient for height growth allocation	(25)	Unitless	–2.63	Data
k_{rs}	Conversion resistance for reserve carbon	(28)	Unitless	2.00	Guess
k_{Rmax}	Maximum reserve concentration	(28)	gC/gDM	0.10 (Sh), 0.12 (Rt)	Fit
k_{CThr}	Threshold concentration for reserve mobilization	(28)	gC/gDM	0.016 (Sh), 0.018 (Rt)	Fit
k_{TC}	Transport conductance coefficient for carbon	(29)	Unitless	18.	Fit
k_{TN}	Transport conductance coefficient for nitrogen	(20)	Unitless	4.	Fit
k_N	Nitrogen uptake efficiency parameter	(30)	gN/gDM	0.008	8*
k_{Si}	Senescence coefficient	(31)	Proportion/day	$2.7\text{E}-4$ (Lf), $1\text{E}-5$ (Br), 0 (St), 0.001 (FR), $1\text{E}-5$ (CR)	9 (Lf), Guess, 10 (FR), Guess
k_{CRT}	Carbon retranslocation coefficient	(32)	Proportion	0.40	Guess
k_{NRT}	Nitrogen retranslocation coefficient	(33)	Proportion	0.50	Guess
k_{Prune}	Carbon deficit threshold for self-pruning	–	Years	1	Guess
k_{TDD}	Development threshold for plant growth	–	$^\circ\text{C}$	4.5	11*
k_{iDD}	Degree day threshold for onset of growth	–	$^\circ\text{days}$	20	Fit
k_{fDD}	Degree day threshold for cessation of growth	–	$^\circ\text{days}$	1600	Fit
k_{TMN}	Temperature to end growing season	–	$^\circ\text{C}$	3.5	Fit

Sources: (1) Waring et al. (1998), (2) Oleksyn et al. (1998), (3) Landsberg and Waring (1997), (4) Roberntz and Stockfors (1998), (5) Jones (1992), (6) Penning de Vries (1975), (7) Dewar (1993), (8) Millard and Proe (1993) for *P. sitchensis*; (9) Slovik (1996), (10) Majdi (2001), (11) Jones (1992); An asterisk following a reference under the Source column indicates that the starting value used was from the source indicated, but that the parameter value was then calibrated further (but in no case exceeding 20% deviation from the original value). The word “Fit” in the Source column indicates that no reliable data were available for the parameter, which was fit through a manual calibration process. The word “Guess” indicates that no reliable data were available for the parameter, which was kept constant through the calibration process. The word “Data” indicates that data collected for this study were utilized to fit model parameters. Certain parameters have different values for different plant parts considered, where plant parts are abbreviated Lf = leaf, Br = branch, St = stem, Sh = shoot, Rt = root, FR = fine root, CR = coarse root.

sents the proportion of variation explained by the line of perfect fit, and not a fitted regression line.

2.4. Simulation experiments

To illustrate the potential utility of the model for describing the interactive effects of browsing and light availability on tree regeneration potential, results from a single, comprehensive simulation experiment are reported. Winter browsing of current annual growth was simulated according to varying levels of browsing intensity (annual probability of a representative sapling being browsed) and light availability (proportion of extraterrestrial photosynthetically active radiation reaching the sapling layer). Both treatments were varied from 0.0 to 1.0, using increments of 0.1 units. Browsing probability was distributed evenly across the six winter months (November–April). All browsing of current annual growth was assumed to be top-down; no additional lateral shoot browsing was simulated. Only a single age cohort of saplings was simulated, with no subsequent recruitment of new individuals. Response variables of interest are (1) the number of years required for the sapling cohort to reach an “escape height” of 150 cm and (2) the proportion of saplings surviving after a 40-year simulation period.

3. Results

3.1. Model behavior

The basic model on which the HUNGER approach is based (Thornley, 1972) was designed to simulate balanced exponential growth. Such growth implies that extensive variables (e.g. mass variables such as biomass) increase exponentially, while intensive variables (e.g. substrate and reserve concentrations, shoot:root ratios) remain constant or, in the case of our seasonally varying model, fluctuate seasonally around a stationary mean. Some of the many modifications we have made, including self-pruning and separation of certain physiological processes into different height layers, might be expected to interfere with this anticipated behavior (i.e. balanced exponential growth).

However, given the behavior of the simulated Werdenberg saplings, it appears that the model still approximates balanced exponential growth in the absence of

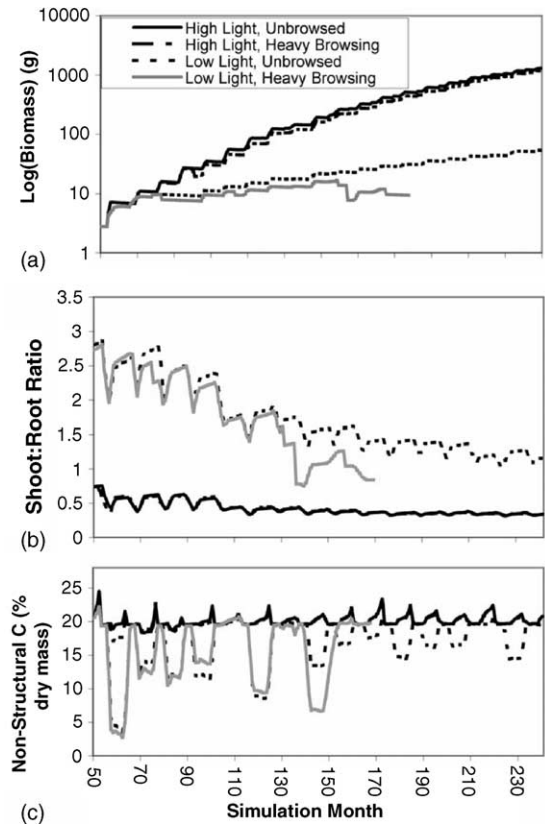


Fig. 2. Examples of model behavior for high and low light (relative light intensities of 0.8 and 0.2, respectively), and for unbrowsed and heavily browsed (browsing intensity of 0.6) saplings. Simulation runs are for 20 years. Note that the low light, heavily browsed sapling dies at approximately month 170. Output variables are (a) total biomass (logarithmic scale, g); (b) shoot:root ratio; and (c) total non-structural carbon in roots (% dry mass).

browsing (Fig. 2). Total biomass increases according to a roughly exponential function under high light, regardless of browsing level (Fig. 2a; note the logarithmic scale). Under high light, saplings recover from browsing effects on biomass. Under low light, saplings suffer biomass loss and eventually mortality. Similarly, saplings in high light are able to maintain a relatively constant, low shoot:root ratio (Fig. 2b). Saplings in low light are not able to maintain a constant shoot:root ratio when browsed, since root reserves are insufficient. Under high light, browsing has very little effect on root carbon reserves (Fig. 2c). Under low light, however, root carbon reserves are taxed regularly on a seasonal basis. Simulated seasonal variations of non-structural carbon

in roots are similar to those observed for other conifer species such as *Pinus sylvestris*, where root carbohydrate reserves are highest in early spring, decrease over the course of the growing season, increase rapidly upon dormancy in the autumn, and then increase steadily over the course of the winter (Oleksyn et al., 2000; reviewed in Chapin et al., 1990). When moderate browsing occurs, very low levels of total non-structural root carbon are reached, and the sapling cannot recover.

3.2. Model testing

For the Werdenberg study area, 21 destructively sampled *P. abies* saplings showed no signs of browsing damage, but varied greatly with respect to their light environment. While two of these saplings were used to calibrate the model in the sense of fine-tuning uncertain parameters, the remaining 19 provide a test of the model's ability to represent sapling growth under varying light conditions. The model over-predicted fi-

nal height by approximately 10 cm ($p=0.03$; Fig. 3a), while no significant differences were found between simulated and observed basal diameter, total biomass, or leaf biomass ($p=0.80, 0.34, 0.36$, respectively; Fig. 3b–d). Model outputs do not suggest a bias, with the possible exception of leaf biomass, which is significantly underestimated for one simulated sapling (Fig. 3d). The coefficient of determination between simulated and observed values ranges from 0.44 to 0.67 (Fig. 3).

The data set from the Schwanden experiment (Schönenberger, 2002b) provides an opportunity to validate the ability of the model to predict height growth responses of *P. abies* saplings having experienced variable (and known) browsing intensities, but grown under conditions of nearly full light. The fit to these data is reasonably good (Fig. 4), considering the many processes influencing sapling growth at this site which are not included in the model (e.g. varying substrate quality and level of competition from the herbaceous

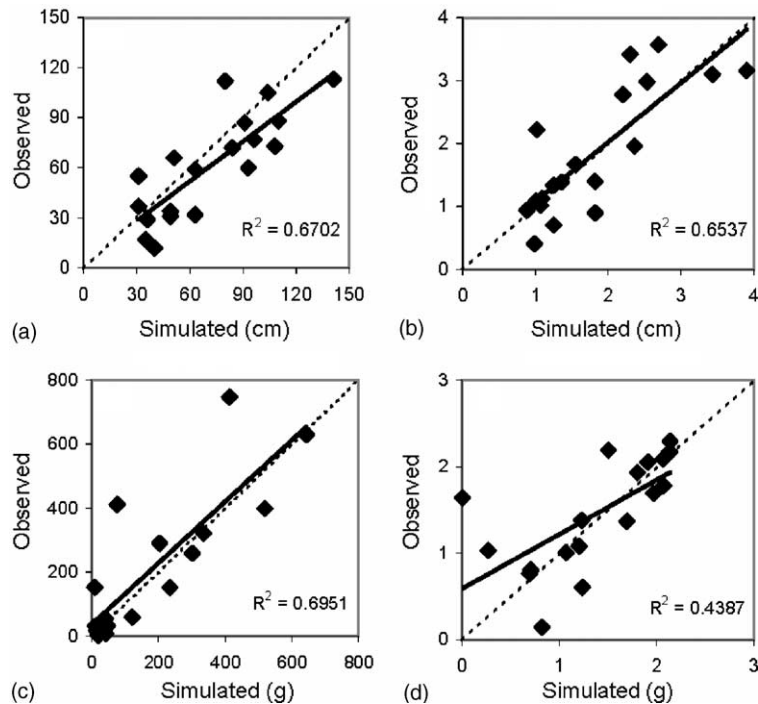


Fig. 3. Model testing for the Werdenberg site, where unbrowsed *P. abies* saplings were sampled under widely varying light conditions. Output variables, at the level of individual saplings, are (a) height (cm); (b) basal diameter (cm); (c) total biomass (g); and (d) leaf biomass (g). Shown are plots of simulated vs. observed values, with the diagonal line representing the line of perfect fit ($y=x$). Also shown is the regression line for observed vs. simulated data.

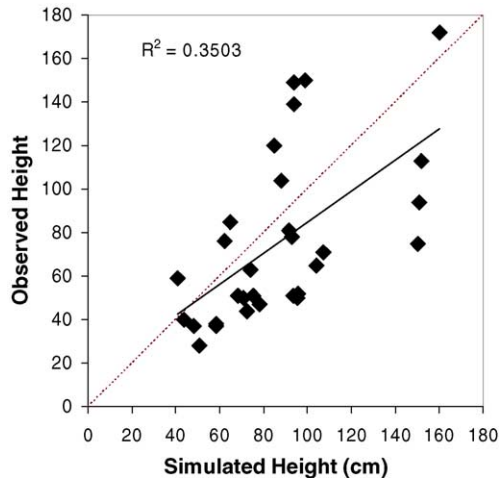


Fig. 4. Model validation for the Schwanden site, where *P. abies* saplings with known browsing histories were grown under similar, full light conditions. The output variable is sapling height in the year 2000. Shown is a plot of simulated vs. observed values, with the diagonal line representing the line of perfect fit ($y=x$). Also shown is the regression line for observed vs. simulated sapling height.

and shrubby understory). There is no significant model bias ($F_{2,30}=0.44$; $p=0.65$). There is only a marginally significant difference (paired $t_{29}=2.05$; $p=0.058$) between the means of observed and simulated sapling heights (75.67 ± 13.8 and 87.31 ± 11.4 , respectively), consistent with the earlier finding (from the Werdenberg data set) that the model over-predicts sapling height by approximately 10 cm. While there is a great deal of “noise” (Fig. 4), as evidenced by a low EF statistic (EF = 0.198), the model seems to predict sapling responses to browsing in a qualitatively correct way even at the level of individual tree saplings.

3.3. Interactive effects of browsing and light availability on sapling height growth

The effects of browsing and light on the number of years for saplings to exceed 150-cm in height (i.e. escape browsing pressure) are nonlinear and interactive (Fig. 5). Simulated shading effects are gradual until approximately 40% relative light availability (if browsing pressure is low) or 60% relative light availability (if browsing pressure is high). Below these values, the model simulates sharp declines in net growth rate. Even though *P. abies* saplings may be relatively shade toler-

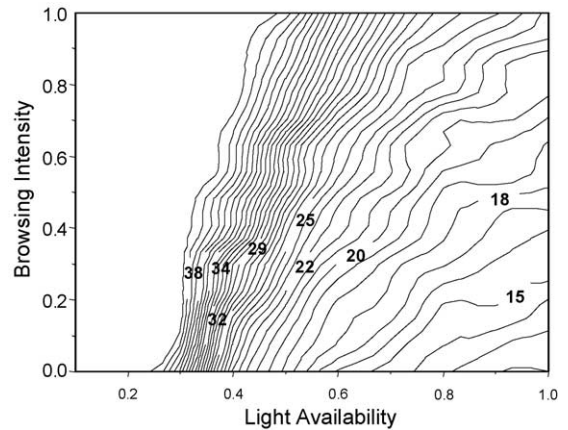


Fig. 5. Response surface for the browsing–light interaction, expressed as a contour plot. The labeled contour lines represent the number of years required for a spruce sapling to exceed 150 cm of height given the specified levels of browsing pressure and light availability. The upper limit shown is 40 years, although most of the data points shown as 40 years indicate scenarios where saplings did not grow beyond 150 cm even after 40 years. Browsing intensity ranges from 0.0 to 1.0 and refers to the annual probability of a sapling being browsed. Relative light availability similarly ranges from 0.0 to 1.0 and refers to the proportion of total photosynthetically active radiation above the overstory canopy that is available to the sapling layer.

ant and can persist multiple decades under dense overstories, there is clearly a threshold light level below which growth is dramatically reduced.

Simulated browsing effects are relatively more important at higher light intensities. This may result in part from the browsing scenario evaluated, where current annual growth is completely consumed in each browsing event. Therefore, more is browsed at higher light intensities where growth is greater. The observed relationship may have “real-world” validity if foraging deer, seeking to concentrate foraging efforts upon more palatable, younger tissues, do actually respond to reduced growth rates by browsing less on each plant.

4. Discussion

The physiologically based modeling approach of HUNGER appears suitable for realistically representing *P. abies* sapling growth rate as an emergent outcome of browsing and light regimes. The modified transport resistance approach (Thornley, 1972, 1991) underlying

the model adequately predicts biomass development of plant parts, height, and diameter growth under different conditions of light availability. Despite uncertainty concerning several model parameters, some of which are difficult if not impossible to measure, the model was able to produce realistic results for sapling biomass growth, radial growth, height growth, and dry matter partitioning. This robustness to parameter uncertainty suggests that future, detailed sensitivity analysis might lead to model simplification. In addition, several model assumptions require further analysis, including the implicit assumption of no disproportionate reduction in meristem mass due to preferential browsing of buds and small branches.

The transport resistance approach as implemented in the model is designed to describe dry matter allocation and growth (i.e. transport and conversion of plant nutrients) under balanced, equilibrational conditions (Thornley, 1997). However, as pointed out by Berninger et al. (2000), the model also seems well suited for capturing transient responses to perturbations involving biomass reduction, such as browsing or pruning. Several experimental studies have observed a decline in non-structural carbohydrate concentrations following winter pruning or defoliation of conifers (Chapin et al., 1990; Bauer et al., 2000; Li et al., 2002), and such declines have been observed to be more long-lasting in root tissues (Li et al., 2002). In addition, the ability of saplings grown in a high light environment to maintain a relatively constant shoot:root ratio despite severe herbivory (Fig. 2b) is consistent with findings of experimental clipping studies, which have shown that maintenance of basic allometric ratios remains a key priority regardless of clipping intensity (e.g. Oosterheld, 1992).

Few existing models of plant response to herbivory are designed to represent compensatory growth responses, as have been observed to occur in tree saplings particularly where browsing intensity is low (Kienast et al., 1999; Millard et al., 2001; Antonen et al., 2002). Mechanisms of compensatory growth in response to browsing pressure are not well known but might include an increased root:shoot ratio, a reduction of shaded foliage which may have represented a net carbon sink for the plant, or increased photosynthetically active radiation (PAR) available for remaining foliage (Danell and Bergstrom, 1989; Hawkes and Sullivan, 2001). The transport-resistance-based approach of HUNGER allows for a more nuanced

representation of sapling responses. Under favorable conditions, simulated browsed saplings can maintain biomass levels nearly as great as those of unbrowsed saplings (Fig. 2), suggesting that the model captures at least some of the mechanisms for compensatory growth.

The simulated interaction between browsing and light availability is consistent with results from experimental and observational studies for other coniferous tree species. *Abies balsamea* saplings subject to simulated browsing in Isle Royale National Park were less likely to recover when canopy cover was at least 60% (McLaren, 1996). Furthermore, as observed in our modeling study, the effects of light on *A. balsamea* sapling growth were comparable in magnitude to those of simulated browsing. Based on similar experimental studies, others have concluded that plants are more likely to recover from herbivory when they are growing in low-stress environments (Maschinski and Whitham, 1989; Danell et al., 1991; Oosterheld and McNaughton, 1991). Relevant stress factors may include nutrient availability, competition, or other microsite differences.

5. Conclusions

Our goal was to improve our understanding of how tree saplings respond to different browsing and light regimes, as these two factors interact to influence growth and allocation to different plant parts. To this end, we developed a physiologically based model of sapling growth and survival to beyond the reach of ungulate browsing, as a function of browsing intensity, shading and climate. In this paper, we have described testing and validation results for the growth and dry matter allocation components of the model. Results for sapling population dynamics (i.e. survivorship) followed similar patterns and maintained similar relationships with browsing intensity and relative light availability. These results, however, are of limited value (and so are not reported here) since we lacked data to parameterize the model routines addressing sapling mortality. Realistic simulation of sapling mortality responses to browsing given variable environmental conditions is hampered by a lack of long-term data sets, where survivorship of individual saplings is tracked under variable growing conditions. Such hard-to-collect,

long-term data sets are difficult to find, and funding sources for their development are limited.

Future plans for the HUNGER model include linking it with a model of forest gap dynamics (ForClim; Bugmann, 1996), and then applying the linked model to address implications of ungulate herbivory and natural disturbances for the long-term ability of Swiss “protection forests” to maintain their slope stability functions (Brang et al., 2001). Similar approaches involving hierarchical linkage of tree, stand, and landscape submodels have been developed to model forest dynamics in the northern United States (Bragg et al., 2004). In its current, standalone form the HUNGER model is also of potential use to forest and wildlife managers interested in responses of tree saplings to the interaction of browsing and growing conditions. Model results suggest non-linear responses to browsing and light availability, and the existence of thresholds that natural resource practitioners should be aware of when managing deer density and crown cover in tandem.

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