FVSBGC: a hybrid of the physiological model STAND-BGC and the forest vegetation simulator

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Abstract: The physiological model STAND-BGC was linked to the forest vegetation simulator (FVS) as a system extension. With the linked model, an FVS user can invoke STAND-BGC to obtain tree- and stand-level physiological output in addition to standard FVS mensurational output. An FVS user may choose to have increments in diameter, height, crown ratio, and mortality from STAND-BGC replace those generated by FVS. This option essentially replaces the empirical growth engine of FVS with the physiological engine from STAND-BGC. Physiological and mensurational outputs were generated for an existing, fully stocked, *Pinus contorta* Dougl. ex Loud. stand, with and without thinning, using the hybrid model. The STAND-BGC engine produced results similar to FVS for the unthinned stand but predicted more rapid tree growth than FVS following thinning. Simulations for a newly regenerated stand using the linked model allowed assessment of the predicted effects of grass competition and drought on stand production. Comparisons of model predictions to remeasured permanent plot data showed the empirical and process growth engines had similar precision, but that STAND-BGC substantially overpredicted growth, while FVS slightly underpredicted growth. The need for model calibration and opportunities for more sophisticated communication between models is discussed.

Résumé : Le modèle physiologique STAND-BGC a été joint au Simulateur de végétation forestière (SVF) en tant qu'extension du système. A l'aide du modèle auxiliaire, un utilisateur du SVF peut faire appel à STAND-BGC pour obtenir des résultats physiologiques à l'échelle du peuplement et de l'arbre en plus des résultats dendrométriques standard de SVF. Un utilisateur de SVF peut choisir d'utiliser les accroissements en diamètre, hauteur, proportion de cime et mortalité produits par STAND-BGC à la place de ceux générés par SVF. Dans les faits, cette option substitue le moteur de croissance empirique de SVF par le moteur physiologique de STAND-BGC. Des résultats physiologiques et dendrométriques ont été générés à l'aide du modèle hybride pour un peuplement dense existant de *Pinus contorta* Dougl. ex Loud., avec et sans éclaircie. Le moteur de STAND-BGC a produit des résultats comparables à ceux de SVF pour le peuplement non éclairci mais a prédit une croissance plus rapide que celle prédite par SVF suite à l'éclaircie. Des simulations effectuées à l'aide du modèle auxiliaire pour un peuplement récemment régénéré ont permis d'évaluer les effets prévus de la compétition herbacée et de la sécheresse sur la production du peuplement. Une comparaison des prédictions du modèle avec les données de placettes permanentes remesurées a montré que les moteurs empiriques et de processus ont une précision similaire. Toutefois, STAND-BGC surestime substantiellement la croissance alors que SVF la sous-estime légèrement. La nécessité de calibrer le modèle et de développer des liens plus sophistiqués entre les modèles est abordée.

[Traduit par la Rédaction]

Introduction

The shift in perception of a forest as a commodities production system to a life-support system seems nearly institutionalized. As a consequence, there has been significant interest focused on developing and evaluating process-based, or physiological, models for inclusion in the analytic toolbox available to forest managers and analysts (Johnsen et al. 2001; Landsberg and Gower 1997). For "ecosystem management" to be more than fancy packaging, traditional mensurational information from empirical models must be supplemented with some suite of ecosystem process attributes (Kimmins et al. 1999). For example, appropriate physiological models could permit exploration of the effects of proposed silvicultural treatments on stand-level water, carbon, and nutrient cycles (e.g., Amatya and Skaggs 2001). Such output could in turn be used to generate mechanistic indexes of forest health that could augment the pattern-dominated indices currently in use. Because physiological models are generally climate driven, such indices would be climate sensitive and, thus, would support the calculation of climate-dependent risk factors for alternative scenarios. Generally, such models could be useful in assessing weather and climate effects on vegetation dynamics and could provide climate-sensitive physiological variables useful in enhancing linkages to forest pest models.

While a variety of physiological models have been developed (see Johnsen et al. (2001) and Makela et al. (2000) for reviews), their use by forest managers and analysts has been limited. One factor contributing to this lack of use is availability of data needed to drive them. Typically, the units of

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management, trees and stands, are contained in forest inventory databases. Because of historical factors, these databases contain tree, stand, and site attributes suitable for initializing and driving biometrical (or empirical) growth and yield models developed specifically for such databases. Physiological models generally have not been built with an inventory processing function in mind, and thus, the initialization and driving variables are often unavailable in a land manager's existing inventory database. Another factor is suitability. Even if a physiological model could be initialized and driven by variables in a forest inventory, the output is often not suitable for the sorts of postprocessing that occurs in forest planning. Updated tree lists are a minimum, and stand or stock tables are common. Also, process models are not usually built with the ability to simulate the variety of silvicultural prescriptions needed for forest management analysis and planning. Finally, physiological models often operate at finer resolutions in time and space than most biometrical growth and yield models currently in use. The models thus do not mesh easily with the coarser resolutions inherent in most forest-management models. Recent advances in simplifying the representation of physiological processes necessary for forest-management applications may solve this last constraint (Landsberg and Waring 1997).

In the work reported on here, the STAND-BGC physiological model (Milner and Coble 1995) was linked to the forest vegetation simulator (FVS) (Wykoff et al. 1982) in an attempt to address many of these shortcomings. The approach follows the advice given in Makela et al. (2000) that process and empirical elements be represented at the same hierarchical level and is similar in nature to the hybrid model linking the biometrical model PTAEDA and the physiological model MAESTRO (Baldwin et al. 1998). Extensive ecophysiological research underlies much of the parameterization of the STAND-BGC model, so that potential users of the model are not required to establish values for most of the various process coefficients (although a number of them are user definable). Furthermore, being linked to FVS, STAND-BGC is initialized from standard forest inventory records. Moreover, silvicultural treatments, as well as tree regeneration and (or) shrub cover establishment, may be simulated within FVS before tree information is passed to STAND-BGC. The linkage of the two models thus provides the user with the benefits of both types of models

In this paper we briefly describe the two models, present the linkage details, and offer some simulations to illustrate the hybrid model's capabilities. Specifically, we compare FVS and STAND-BGC model predictions for a lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stand and then illustrate how the hybrid model could be used to assess the implications of climate variation, thinning, and grass control on forest growth. Finally, we compare each model's predictions of volume growth to that calculated from 27 remeasured permanent plots.

The models

Comparative inputs and outputs for the two models are given in Tables 1 and 2. STAND-BGC operates with SI units, while FVS inputs and outputs are entirely in English units. Detailed descriptions for FVS are presented in Wykoff et al. (1982), so the presentation here is quite short. The description of STAND-BGC is more detailed as that model has not yet received peer review.

Stand-BGC

STAND-BGC (Milner and Coble 1995) is one of the several derivatives of the stand-level physiological model FOREST-BGC (Running and Coughlan 1988). STAND-BGC is an individual-entity, distance-independent model. The term "entity" is used because STAND-BGC grows shrubs and grass in addition to trees. Shrubs and grasses are described as per unit area entities, while trees have unique dimensions.

STAND-BGC is initialized with an entity list containing species, height (m), diameter at breast height (cm), live crown ratio (%), and trees per hectare for tree entities and percent cover and canopy depth (m) for grass and shrub entities. A climate file containing daily minimum and maximum temperatures (°C), precipitation (mm), solar insolation ($kJ \cdot m^{-2} \cdot day^{-1}$), and relative humidity (%) must also be provided. The climate file must contain at least one full year (365 days) of records. If a simulation is for more years than is contained in the climate file, the file is rewound, and the same records are reused. A file containing soil depth and texture information must also be supplied. A default set of physiological parameters is supplied. Thirteen of these are life-form specific, while another 22 parameters are common to all life forms (Table 3). Species differences are primarily in the parameters of the equations used to define crown geometry and to estimate biomass of leaves, stems, and roots. A flow diagram for STAND-BGC is shown in Fig. 1. Like its parent, FOREST-BGC, STAND-BGC is a climate driven, carbon and water balance model that uses a "big-leaf physiology" approach in simulating growth. Stomatal conductance, net canopy photosynthesis, transpiration, and maintenance respiration are calculated on a daily time step. Growth respiration and carbon allocation occur on a yearly time step. Daily solar insolation, precipitation, and temperature drive the point estimates of physiological processes, which are scaled by canopy leaf area. Soil water potential is a major determinant of canopy net photosynthesis (PSN) through its impact on stomatal conductance. Unlike FOREST-BGC, which treats the entire stand canopy as the "big leaf", STAND-BGC simulates these processes for multiple subcanopies of each individual entity in the stand. The subcanopies for each entity are defined according to the boundaries of a vertical stratification of the general stand canopy. Solar radiation incident at the top of the stand canopy is attenuated via a Beer's law application, layer by layer, through the general canopy. A canopy structure submodel provides the vertical location and amount of leaf area for an entities subcanopy. In this way, entities compete directly for light resources. Soil water is partitioned in two layers. Entities access a volume of soil (a water bucket) depending on their leaf area. Within that volume, a set of life form and tree size based rules control access to the water in each of the layers. Small trees (height <1.3 m), grasses and shrubs have access only to the surface layer. Large trees (height >1.3 m) access either layer depending on which has the highest water potential. Entities transpire water, subcanopy by subcanopy, with a new water potential calculated for its

Table 1. Input attributes for STAND-BGC (Milner and Coble 1995) and the northern Idaho (NI) variant of FVS (Wykoff et al. 1985).

Type	STAND-BGC Attribute	Status	FVS (NI variant) Attribute	Status
Tree	DBH	Required	DBH	Required
	Height	Required	Height	Required
	Crown ratio	Required	Crown ratio	Required
	Species	Required	Species	Required
			Diameter growth	Optional
			Height growth	Optional
Grass	Percent cover	Required	na	
	Canopy depth	Required	na	
	Species	Optional	na	
Shrubs	Percent cover	Required	na	
	Canopy depth	Required	na	
	Species	Optional	na	
Site	Slope	Required	Slope	Required
	Aspect	Required	Aspect	Required
	Elevation	Required	Elevation	Required
	Soil depth	Required	Habitat type	Required
	Soil texture	Required	National Forest	Required
Climate (daily)	Precipitation	Required	na	
	T_{max}	Required	na	
	T_{min}	Required	na	
	RH	Required	na	
	Radiation	Required	na	

Note: Height is total tree height, and diameter growth is measured at breast height. DBH, diameter at breast height; T_{max}, maximum daytime temperature; T_{min}, minimum nighttime temperature; radiation, solar radiation; RH, relative humidity; na, not applicable.

water bucket following each subcanopy's transpiration. At night, all water buckets equilibrate to an overall site water balance by soil layer. Entities thus compete for soil water indirectly through their respective soil layer specific impacts on the site water balance.

At the end of each year, net carbon gain for each entity (PSN minus maintenance and growth respiration) is allocated to leaf, stem, and roots according to allocation fractions dynamically linked to soil water stress as described in Running and Gower (1991). Constant turnover ratios are applied to the leaf, stem, and root carbon pools prior to this allocation. Carbon gains or losses are converted to biomass, which in turn are used, together with the geometry appropriate to an entity, to update entity dimensions.

Two "knobs" are available for a coarse-level calibration of STAND-BGC. A precipitation multiplier may be used to adjust precipitation events. This single adjustment can have profound consequences, because STAND-BGC is strongly driven by moisture stress. A second "knob" specifies a multiplier on PSN of each entity. It can be used to adjust growth predictions to some set of observed growth data.

The forest vegetation simulator (FVS)

FVS is the generic name for the collection of individual-tree, distance-independent models used by the USDA Forest Service and many other clients. FVS is used to generate traditional growth and yield information for forest planning, as a tool for analyzing alternative silvicultural prescriptions, and provides numerous links to secondary models that model forest pests, root rot, and fire behavior. The FVS model used in this work was the northern Idaho (NI) variant.

The model uses a growth architecture approach to predict periodic height growth, diameter growth, and mortality of individual trees from tree and stand variables calculated at the start of each projection period. These variables represent tree vigor, tree growth potential, position in the stand, and overall stand density. Site quality is represented by topogeographic variables and habitat type (Pfister et al. 1978). Data used in constructing the NI variant of FVS was obtained primarily from inventory data representing climatic conditions between 1950 and 1980. Model predictions are in 10-year (DG) and 5-year (HG) time steps, in accordance with the increment data used in parameter estimation. A self-calibration utility permits users to input increment data from individual stands, thereby adjusting model predictions to reflect local tree, stand, and site conditions. With the exception of this one-time adjustment, which attenuates to the base model predictions after several growth periods, FVS simulations are not sensitive to changes in climate.

Materials and methods

Model linkage

The linkage was accomplished by making the STAND-BGC model an extension to the FVS system (Fig. 2). When the BGC extension is turned on (the shaded portion in Fig. 2), the two models run in parallel. They can share state variables at FVS cycle boundaries (every 10 years by default). In the current linkage, only simple exchanges of tree dimensions and increments are made.

STAND-BGC is invoked from within an FVS simulation via keywords entered by a user into an FVS keyword file.

Table 2. Comparative outputs from STAND-BGC and FVS describing vegetation and site attributes.

Type	STAND-BGC attribute	Resolution in Time[a]	Space[b]	FVS attribute	Resolution in Time	Space[b]
Tree	DBH	Y	W	DBH	10 years	W
	Total height	Y	W	Total height	10 years	W
	Cown ratio	Y	W	Crown ratio	10 years	W
	Crown width	Y	W	Crown width	10 years	W
	Net photosynthesis	D, Y	W, C	Volume	10 years	W
	Maintenance	D, Y	W, C	Trees per acre	10 years	W
	Transpiration	D, Y	W, C			
	Growth respiration	Y	W, C			
	Leaf C	Y	W, C			
	Root C	Y	W			
	Stem C	Y	W			
	Leaf water potential	D	W, C			
	Carbon allocation	Y	W			
	Absorbed PAR	D, Y	W, C			
Grass and shrub	% cover	Y	W	% cover	10 years	W
	Canopy depth	Y	W	Canopy depth	10 years	W
	Net photosynthesis	D, Y	W, C	Species list	10 years	W
	Maintenance	D, Y	W, C			
	Transpiration	D, Y	W, C			
	Growth respiration	Y	W, C			
	Leaf C	Y	W, C			
	Root C	Y	W			
	Stem C	Y	W			
	Leaf water potential	D	W, C			
	Carbon allocation	Y	W			
	Absorbed PAR	D, Y	W, C			
Stand	Crown competition factor	Y	S	Crown competition	10 years	S
	Basal area	Y	S	Basal area	10 years	S
	Net photosynthesis	D, Y	S, C	Volume	10 years	S
	Maintenance	D, Y	S	Stand table	10 years	S
	Transpiration	D, Y	S, C	Stock table	10 years	S
	Growth respiration	Y	S	Stand density index	10 years	S
	Leaf C	Y	S	Site index		S
	Root C	Y	S			
	Stem C	Y	S			
	Leaf water potential	D	S			
	Absorbed PAR	D, Y	S, C			
Site						
	Soil water potential	D	S			
	Soil water content	D	S			
	Outflow	D, Y	S			
	Soil temperature	D	S			

[a]D, daily; Y, yearly.
[b]W, whole tree; C, canopy layer; S, stand.

Information is passed from FVS to STAND-BGC at the start of every FVS cycle. This information includes program control variables (e.g., the FVS cycle number and current thinning status), shrub cover information (if the FVS COVER extension is invoked), and individual tree data such as species, tree record number, diameter at breast height, total height, crown ratio, and trees per acre.

Once this transfer is made, STAND-BGC grows the entities for as many years as are in a particular FVS cycle. Then program control is passed back to FVS, and the trees are grown using FVS. When both models have completed an FVS cycle, a user-controlled exchange takes place. The STAND-BGC increments for height, diameter, crown ratio, and mortality may be used by FVS in place of its own predicted increments. Each model then calls its own report writers and produces its customary output. STAND-BGC is then reinitialized with the updated tree list from FVS, and the two models continue the simulation. This simple transfer allows the user to essentially replace the empirical growth engine in FVS with the STAND-BGC process engine.

If the STAND-BGC increments are used to update the tree list in FVS, then STAND-BGC is reinitialized with exactly the tree list with which it ended the cycle. The resulting simulation is then identical to what would be produced if

Table 3. (A) Life form dependent and (B) independent parameters required for the physiological model STAND-BGC (Milner and Coble 1995).

(A) Life form dependent parameters.

Parameter description[a]	Parameter value		
	Trees	Shrubs	Grasses
Maximum leaf conductance (g_s) (m/s)	0.0016	0.0016	0.006
Minimum LWP (–MPa)	0.5	0.5	0.5
Boundary layer conductance (m/s)	0.1	0.1	0.01
Maintenance respiration coefficient: leaves (kg C/day)	0.0002	0.0004	0.0044
Maintenance respiration coefficient: stems (kg C/day)	0.0002	0.0002	0
Coarse root respiration (not currently used)	0.0002	0.0002	0.0003
Maintenance respiration coefficient: roots (kg C/day)	0.0004	0.0011	0.0044
Maximum photosynthesis rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	4	4	6
Leaf turnover (senescence) (%/year)	33	50	50
Stem turnover (senescence) (%/year)	0	20	0
Root turnover (senescence) (%/year)	40	80	50
Leaf lignin concentration (%) (not currently used)	33	18	17
Specific leaf area (m^2/kg)	25	35	25

(B) Life form independent parameters.

Parameter description[a]	Parameter value
Rain interception coefficient ($m \cdot LAI^{-1} \cdot day^{-1}$)	0.0005
Canopy light extinction coefficient (1/LAI)	–0.5
LWP at stomatal closure (–MPa)	1.65
VPD at stomatal closure (mbar)	25
Optimum temperature for photosynthesis (°C)	20
Maximum temperature for photosynthesis (°C)	45
Growth respiration coefficient: leaves (fraction/year)	0.35
Growth respiration coefficient: stems (fraction/year)	0.3
Coarse root growth respiration: fraction (not currently used)	0.3
Growth respiration coefficient: roots (fraction/year)	0.35
Leaf carbon allocation fraction in first year	0.15
Stem carbon allocation fraction in first year	0.35
Coarse root carbon allocation fraction (not used)	0.05
Root carbon allocation fraction in first year	0.5
Ratio all-sided LAI to one-sided LAI	2.3
Slope of g_s ($mm \cdot s^{-1}$) vs. PAR ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	0.01
Coefficient for maintenance respiration (s^{-1}) (Q_{10} = 2.0)	0.069
Mass fraction of C in dry matter	0.5
Maximum ratio of leaf C/(leaf C + root C)	0.66
Water stress integral fraction	0.19
Stem/coarse root allocation ratio	0.85
Fraction of total stem carbon in branches	0.25

**Note:** Life form specific parameters can be defined separately for trees, shrubs, and grasses.

[a]g_s, stomatal conductance; LAI, leaf area index; VPD, vapor pressure deficit; LWP, leaf water potential; PAR, photosynthetically active radiation; Q_{10}, respiration quotient: (change in rate of respiration for 10°C change in temperature).

STAND-BGC had no connection to FVS. The FVS output reflects the growth of trees as predicted from STAND-BGC alone. In this mode, FVS provides (*i*) a method to input entities into STAND-BGC (trees via FVS tree lists and the Establishment model, shrubs via the COVER model); (*ii*) a way to simulate silvicultural treatments (thinning and planting); (*iii*) FVS output files reflecting how FVS summarizes this growth in terms of the stand's merchantable volume, stand density index (SDI), crown competition factor (CCF),

canopy structure, etc.; and (*iv*) the opportunity to simulate insect and disease effects on a stand either before or after such a stand is simulated in STAND-BGC.

If the user does not specify use of STAND-BGC increments, then the FVS output is unaffected by STAND-BGC growth. However, STAND-BGC is still reinitialized with the FVS-grown tree list at the start of each cycle. For FVS, the resulting simulation is identical to what would be produced if FVS had no connection to STAND-BGC. For STAND-

Fig. 1. Flowchart for the STAND-BGC physiological model.
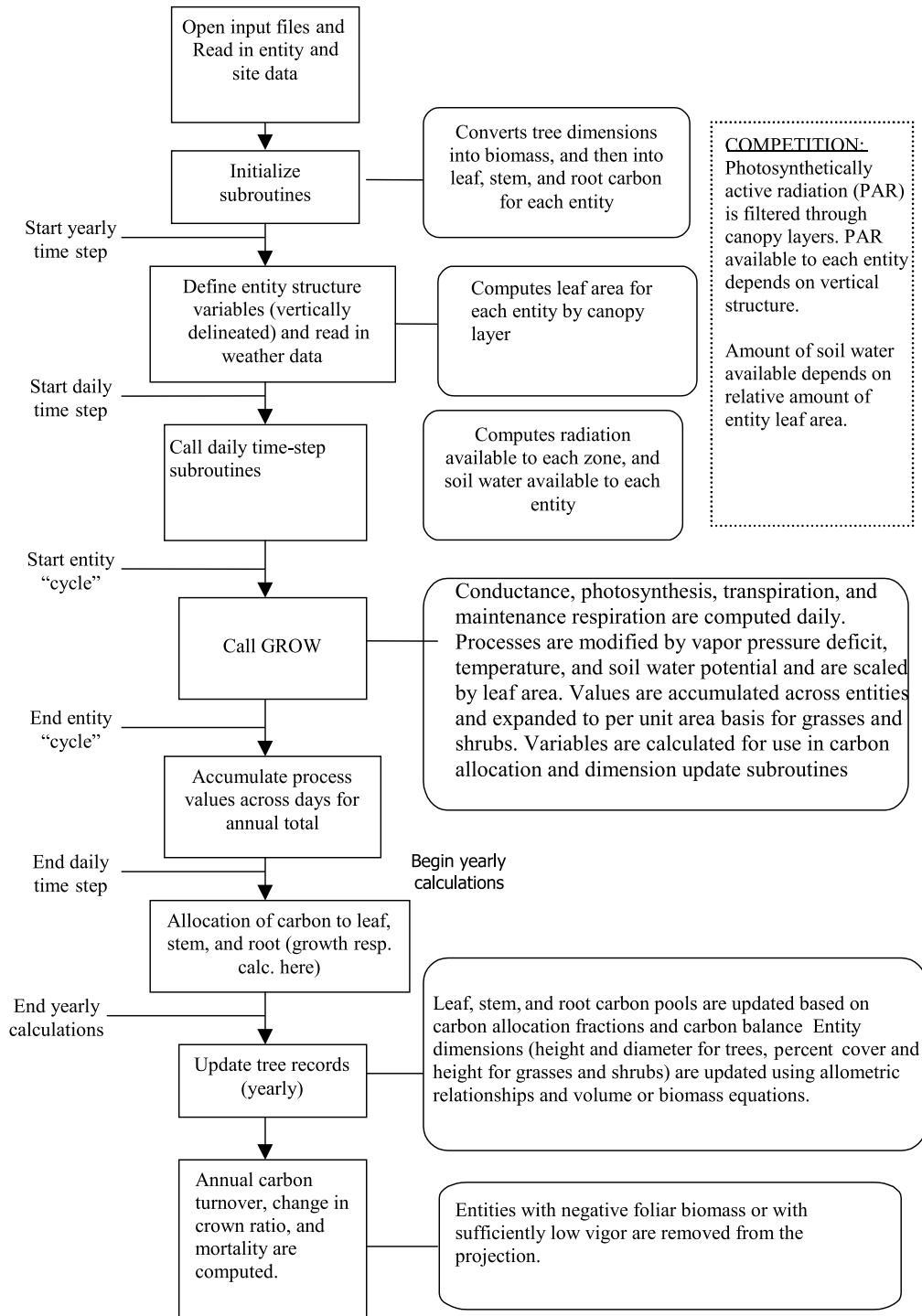
BGC, the output gives a cycle-length picture of the physiological functioning of the stand as defined by FVS, given the climate provided for that cycle.

This linkage of the two models thus allows users familiar with FVS output to see how a climate-driven process model projects stand growth.
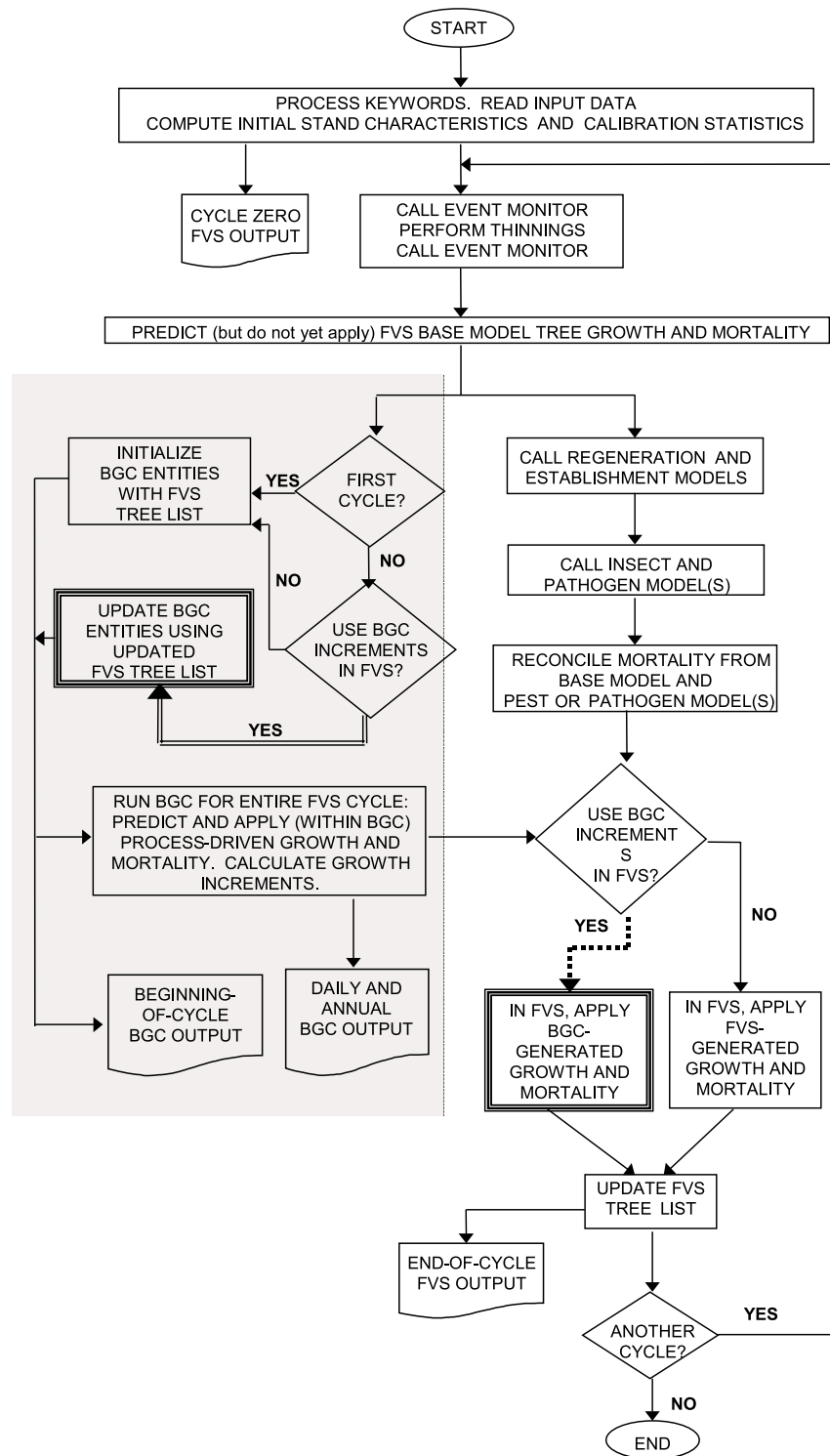
Simulations

Existing stand

Data from a permanent, fixed-area plot, 0.04 ha (0.1 acre) in size, was used to initialize the simulation. The plot is in a pure lodgepole pine stand located in western Montana near Missoula. Summary statistics include the following: quadratic mean diameter at breast height, 18.8 cm (7.4 in.); density, 746 trees/ha (302 trees/acre); top height (mean height of largest 100 trees/ha by diameter), 13.7 m (45 ft); basal area, 20.7 m²/ha (90 ft²/acre); slope, 15%; aspect, NE; elevation, 1158 m (3800 ft); and grass cover, 30%. The habitat type is *Pseudotsuga menziesii/Physocarpus malvaceus* (Pfister et al. 1977). A 30-year daily climate file was created

Fig. 2. Flowchart showing how STAND-BGC (shaded area) operates as an extension to FVS. STAND-BGC cycles are at daily and yearly time steps. FVS cycles have a 10-year time step. Growth increments from FVS may be replaced with those from STAND-BGC to effectively change growth engines. If STAND-BGC increments are not passed to FVS, the models run in parallel, with STAND-BGC producing estimates of physiological processes for each year of an FVS cycle.

by extrapolating 30-year data from a nearby valley bottom weather station using the model MTCLIM (Hungerford et al. 1989).

The stand was projected 30 years into the future, with and without thinning. The thinning treatment (simulated by FVS) removed 50% of the trees per acre for each diameter class.

Fig. 3. Simulated trends in soil water potential for the surface (*a*) and subsurface (*b*) soil layers for a lodgepole pine stand with and without thinning. The development of water stress closely follows the pattern of (*c*) precipitation (PPT) for the specified climate.
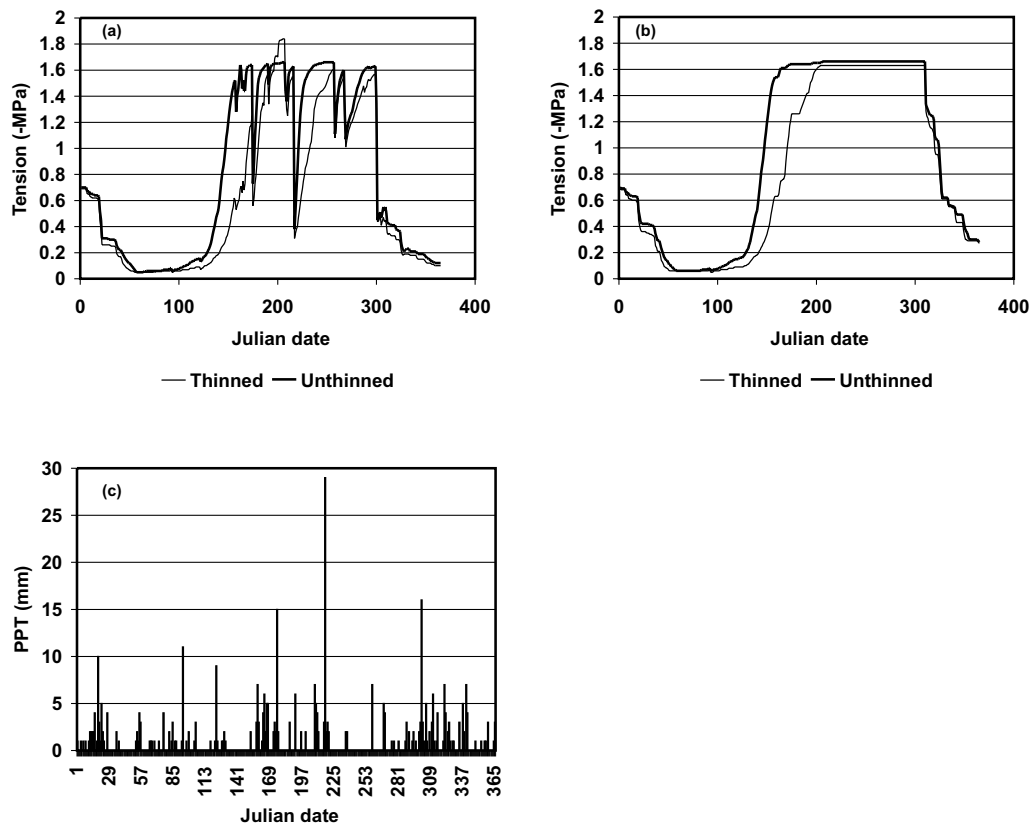
The regeneration establishment model (Ferguson and Crookston 1991) in FVS was invoked. One pair of simulations was done wherein increments were not shared by FVS and STAND-BGC, and one pair where STAND-BGC increments were passed to FVS. STAND-BGC was calibrated to FVS by adjusting the PSN multiplier "knob" in STAND-BGC until the top height of STAND-BGC grown trees was approximately equal to the top height of FVS grown trees at the end of 30 years. Top height is defined here as the mean height of the largest 100 trees/ha (40 trees/acre) by diameter. A multiplier on PSN of 0.9 resulted in roughly equivalent height growth of the top height trees.

Regenerated stand

A set of simulations was made for a naturally regenerated stand. The establishment model in FVS was used to start the new stand from bare ground. All site and climatic characteristics were identical to those for the existing stand simulations. For the simulations using STAND-BGC increments, runs were made with and without 30% grass cover. For the simulation with grass cover, an additional run was made where precipitation was reduced by 20% to simulate a drier climate. All simulations were for 30 years. STAND-BGC was calibrated to FVS as before, using the PSN multiplier. In this case, PSN was reduced by 30%.

Validation

Data from 27 permanent plots were used in an initial evaluation of FVSBGC. The plots were established in 1984–

1985 in mixed-size-class, mixed-species stands on industrial lands in western Montana to monitor responses to partial cutting. Ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western larch (*Larix occidentalis* Nutt.), and lodgepole pine were the dominant species. The last remeasurement was in 1996. These data were previously used in evaluating the FVS model (NI variant) (Schwalm and Milner 2002).

For STAND-BGC, daily climate files for each plot location were created by extrapolating 1984 data from nearby valley bottom weather stations using the MTCLIM model (Hungerford et al. 1989) and the physical site descriptions of each location. Soil depth and texture information was not available, so a mean sandy–loam soil 1 m deep was specified. Understory vegetation (percent cover and height) was used as recorded in 1984.

For FVS, inputs were as described in Schwalm and Milner (2002). Neither FVS nor STAND-BGC was calibrated to the local conditions. Each model used its own mortality equations. All STAND-BGC parameters were the defaults, as listed in Table 3.

FVSBGC was run three times for each plot: once using the FVS growth engine, once using the STAND-BGC engine, and once for zero years for the 1996 tree lists. The latter run was so that the same height–diameter curves and volume equations were used to summarize the observed 1996 data. For each tree surviving the 12-year period, observed and predicted volume growth for each model was obtained by calculating the difference between beginning and

Fig. 4. (*a*) Simulated 30-year stand-level trends in tree and grass leaf area index (LAI) for the unthinned stand. (*b*) Simulated 30-year stand-level trends in net primary production (NPP), maintenance respiration (MRESP) and growth respiration (GRESP). (*c*) Annual precipitation for the simulation period.
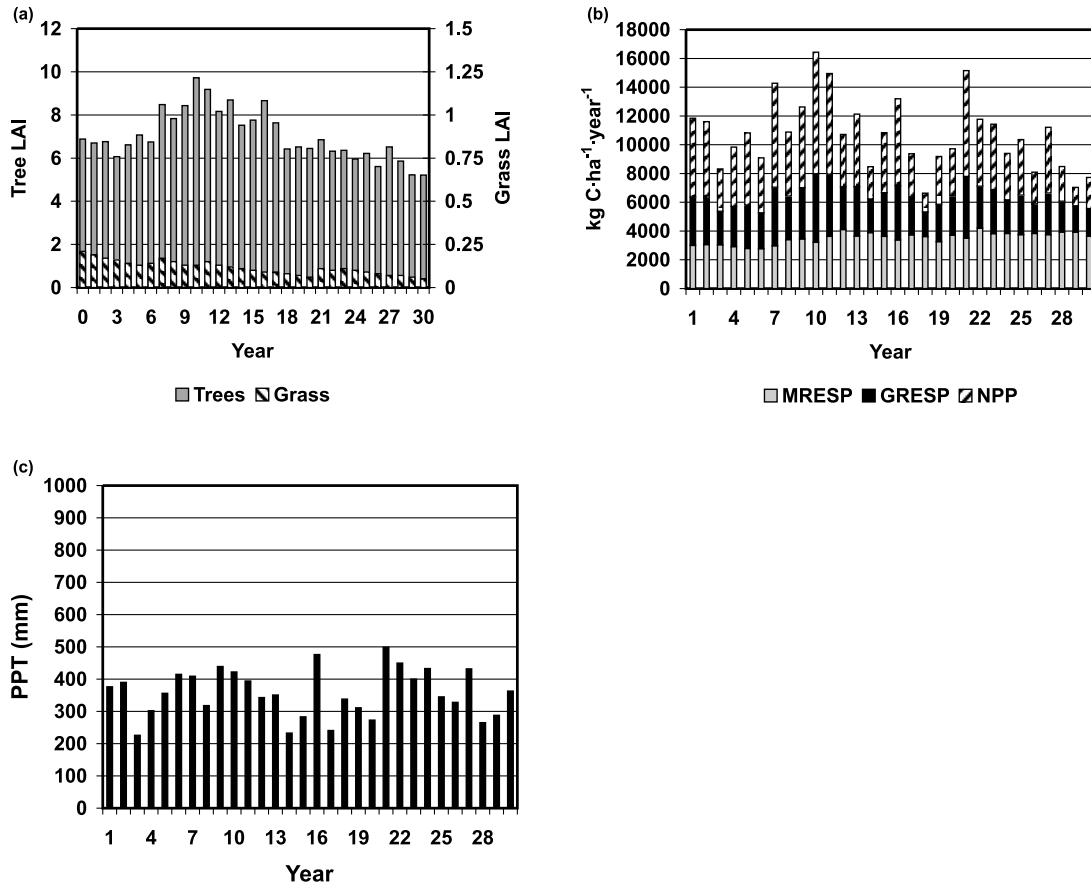

Results

Existing stand simulations

STAND-BGC stand and tree level outputs are illustrated in Figs. 3–6. Data in the figures are from the simulation where STAND-BGC increments are used in FVS. Identical results would be obtained by running STAND-BGC as a stand-alone model.

In Fig. 3, trends in soil water potential for the thinned and unthinned stand during a single year are shown. Thinning delays the onset of water stress in both soil layers. The surface layer is far more sensitive to daily precipitation events than is the subsurface layer and can develop more negative water potentials. Thirty-year trends in stand level all-sided leaf area index (LAI) and carbon budgets are shown in Fig. 4. While the LAI is sensitive to annual variation in climatic conditions, the general level is fairly constant (Fig. 4*a*). From a hydrologic equilibrium standpoint (Nemani and Running 1989), the stand was fully occupying

the site at the start of the simulation. An increase in LAI would increase water stress, reducing NPP, which would cause reductions in LAI resulting from constant leaf turnover rates. The relative proportions of carbon fixed going to maintenance and growth respiration (MRESP and GRESP) and to net primary production (NPP) are shown in Fig. 4*b*. In a year with high precipitation, nearly 50% of the carbon fixed by the canopy ends up in new plant tissues. In very droughty years, NPP is less than 25% of the total. When the stand is thinned, STAND-BGC simulates a rapid response in leaf area (Fig. 5*a*). Within 10 years, tree LAI has recovered to prethinning levels. LAI of grass also increases following thinning. Because of an increase in resources (primarily water), a greater proportion of carbon fixed by the canopy is available for plant growth (Fig. 5*b*). Even in the driest years, NPP amounts to at least one-third of the total. Using the ratio of net canopy photosynthesis and maintenance respiration as an index of stand vigor one can see that thinning increases stand vigor (Fig. 5*c*) and that the increased vigor is maintained throughout the 30-year projection. At some point in the future, stand vigor should begin to decrease again. However, the heavy thinning to 10.4 m²/ha of basal area (45 ft²/acre) produced a lightly stocked stand with such vigorous individuals that canopy production remains high relative to maintenance respiration costs throughout the simulation period.

end-of-period volumes. Because trees had been subsampled for height, some "observed" heights were just products of height–diameter equation. To focus on real growth, only measured trees were used in the model comparisons. This resulted in only 85 of 300 surviving trees being included in the final data set.

Fig. 5. (*a*) Simulated 30-year stand-level trends in tree and grass leaf area index (LAI) for the thinned stand. (*b*) Simulated 30-year stand-level trends in net primary production (NPP), maintenance respiration (MRESP), and growth respiration (GRESP). (*c*) Ratio of net canopy photosynthesis (PSN) and MRESP as an indicator of stand vigor.
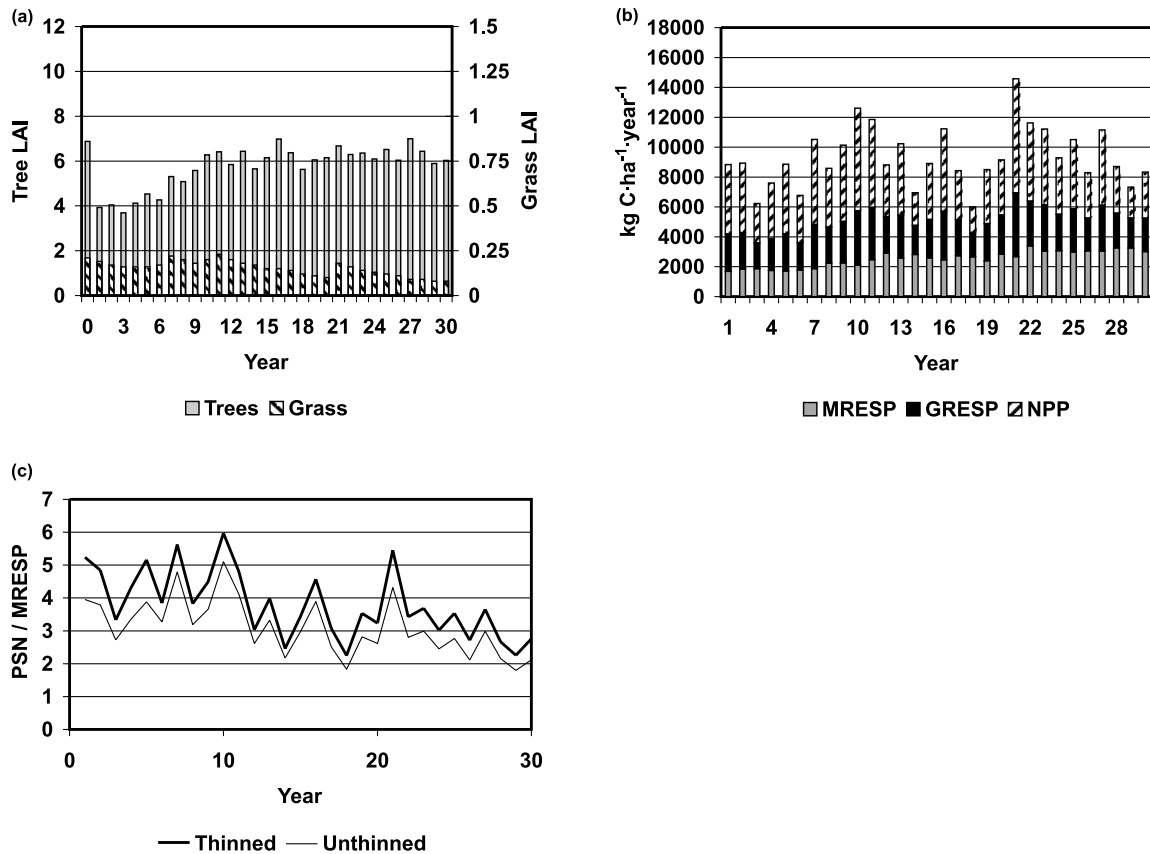
Trends in the carbon budgets for trees in dominant versus suppressed crown classes, in the nonthinned condition, show dramatic differences (Figs. 6*a* and 6*b*). Suppressed trees have small crowns and struggle to allocate enough photosynthate to leaves to overcome respiration costs and turnover. Drought conditions further aggravate the situation, to the point where even when climatic conditions improve, the tree cannot recover. The vigor index (PSN/MRESP) for the suppressed tree is in steady decline, while that for the dominant tree varies from year to year but maintains a high level (Fig. 6*c*). Mortality of individuals in STAND-BGC is modeled as a function of this declining vigor.
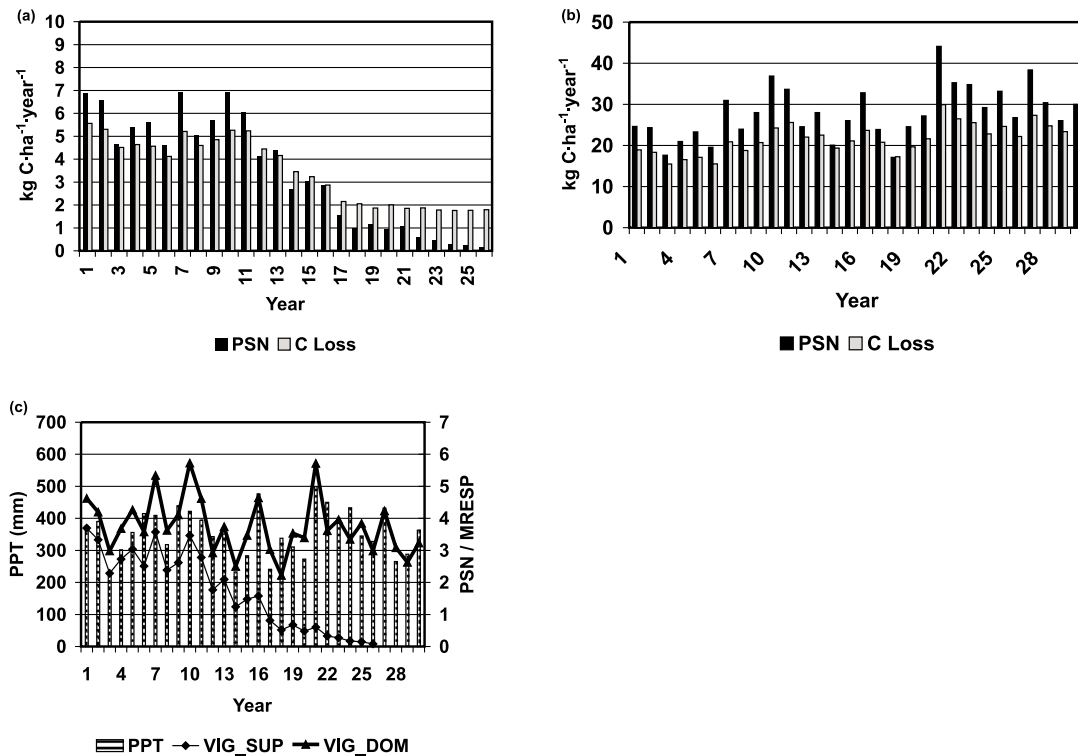
For the nonthinned condition, the growth and yield consequences of swapping growth engines was minimal. For the 30-year simulation, trends in volume per acre and trees per acre were nearly identical (Figs. 7*a* and 7*b*). However, following thinning, the two models showed quite different responses. When STAND-BGC increments were used, the simulation showed a much more rapid response in volume per acre than when the FVS increments were used (Fig. 7*c*). This reflects the rapid LAI response seen in Fig. 5*a*. Generally, STAND-BGC growth increments probably reflect potential responses, while those from FVS are means and reflect data containing impediments not represented in STAND-BGC. The two models showed similar trends in trees per acre through the first two decades following thinning, primarily because tree numbers were heavily influ-

enced by new trees added by the FVS establishment model (Fig. 7*d*). In the third decade, STAND-BGC predicted higher mortality rates, primarily among small trees. Differences in mortality may be because STAND-BGC removes entire tree records upon simulated death, while FVS just reduces the trees per acre representation of a tree record. A single plot has relatively few tree records so the death of one tree has a large impact. Alternatively, in STAND-BGC, death depends on where on the declining vigor trajectory mortality is invoked. A change in this somewhat arbitrary specification would result in quite different mortality rates. More sophisticated model linkages could perhaps make use of each model's approach.

Regenerated stand simulations

Volume per acre production, using FVS increments, was bracketed by those using STAND-BGC increments with (lower production) and without (higher production) a grass component (Fig. 8*a*). The FVS and STAND-BGC growth engines produced reasonably similar volume per acre values when a grass component was included. This is partly due to the calibration of STAND-BGC, but also because FVS increments are based on parameters containing the competitive effects of an unknown amount of understory vegetation. When STAND-BGC increments were used, volume production increased by more than 50% when no grass was present. This increase was due primarily to differences in height and

Fig. 6. Simulated individual tree trends in carbon production (PSN) and losses (carbon losses = all respiration losses plus turnover) for (*a*) a suppressed tree and (*b*) a dominant tree. When precipitation (PPT) is low, suppressed trees lose vigor (VIG_SUP) and have difficulty responding when precipitation increases, while dominant trees are able to maintain high levels of vigor (VIG_DOM) (*c*). Tree vigor is defined as the ratio of net canopy photosynthesis (PSN) to maintenance respiration (MRESP).

Validation

Observed volume growth was regressed on the predicted growth from each model. The two growth models explained very similar amounts of the observed variation in tree volume growth; the R^2 was approximately 0.7 for each. In both cases the intercept was near zero. For FVS, the slope coefficient was 1.33, while for STAND-BGC it was 0.22. Thus, on average, the FVS model underpredicted tree volume growth by about 33% and the STAND-BGC model overestimated growth by about 80%.

Discussion

The goal of this work was to produce a hybrid biometrical–physiological model that could potentially be used in forest planning analyses where an additional suite of physiological output was desired. By essentially "serving" STAND-BGC from within FVS, this goal was achieved.

diameter growth (Figs. 8*b* and 8*d*), as mortality rates were quite similar (Fig. 8*c*). Such production differences are not uncommon in empirical studies. Finally, when using the STAND-BGC increments, the 20% reduction in precipitation resulted in a 50% drop in volume production in the stand with a grass component. Again, more sophisticated linkages could be implemented wherein multipliers derived from the process engine output could be applied to FVS functions (or parameters) to simulate responses to conditions not currently represented in FVS.

Given a climate file and a few additional soil or site characteristics, users of FVSBGC can obtain an estimate of the carbon and water balance processes presumably underlying the biometrical predictions. The user can get "slices in time" information about processes for an FVS controlled simulation or can get a STAND-BGC controlled simulation with full access to the FVS management and silvicultural options. The latter provides a means to evaluate the effects of climate and understory vegetation on stand dynamics and production, investigations not currently possible in FVS.

The validation results were encouraging. Although quite biased for the test data, STAND-BGC explained about the same amount of variation in observed, 12-year, individual-tree volume growth as did FVS. Therefore, one might speculate that the physiological output from STAND-BGC should be relatively correct, that is, useful for examining and explaining differences in growth among trees due to variation in climate and competition. A more extensive validation is currently in progress that will compare model mensurational outputs to longer term permanent plot data and compare the physiological output to published data.

The self-calibration feature in FVS, which adjusts model predictions based on measured past diameter and (or) height growth, would likely eliminate most of the bias noted for FVS in this study. Past diameter growth, for example, would contain the effects of local site and competition conditions. For STAND-BGC, some scaling or localizing was made possible by allowing the user to specify multipliers on canopy PSN and (or) annual precipitation. In this study, the value of

Fig. 7. Simulated standing volume and mortality trends for a lodgepole pine stand with no thinning (*a* and *b*) and with thinning (*c* and *d*). Curves labeled STAND-BGC are from an FVS run where diameter and height growth, change in crown ratio, and mortality estimates are from STAND-BGC. STAND-BGC was calibrated to FVS using a PSN multiplier of 0.9.
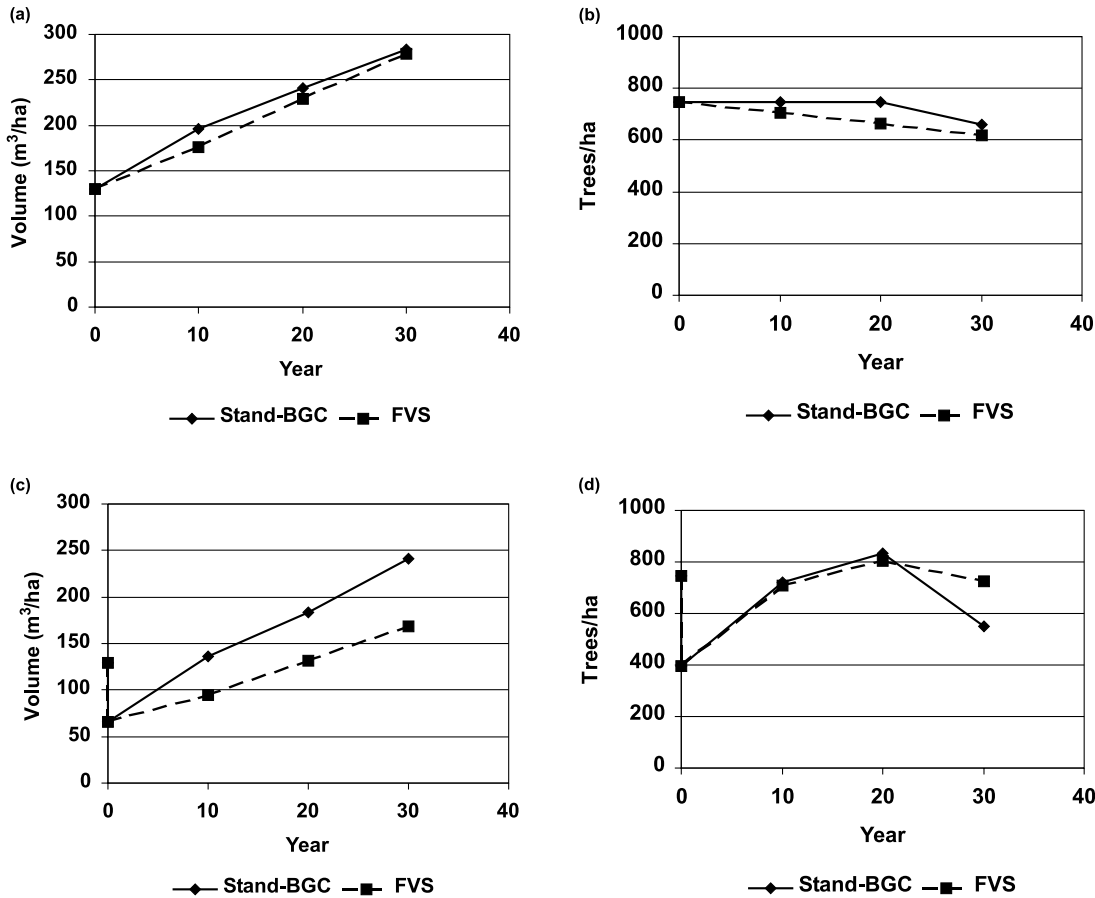

the multiplier(s) was set so that a stand attribute reflecting growth process from STAND-BGC (usually top height) was similar to that from FVS. This simple calibration could be internalized much as in FVS. However, additional validation and sensitivity analyses are needed before defensible calibration logic can be recommended.

A central question generated by this study is how the two types of models should interact as a true hybrid. On the one hand, a well-designed biometrical model, when fit to adequate data, provides the most accurate way to estimate change in forest conditions similar to those represented in the data (Vanclay 1994). In such a model, like FVS, the entire complexity of growth processes is contained in the parameter estimates. Average trends should be very reliable. Unfortunately, databases are never complete, and many management questions require simulations for conditions poorly represented in the empirical data. On the other hand, the physiological model explicitly represents underlying processes; its empiricism is at a higher resolution. Assuming for the moment that the correct processes have been adequately specified and modeled, such a model is arguably more "transportable" and predictions for new conditions may be considered reasonable from first principles. However, the system complexity represented in the physiological model is quite limited compared with the complexity embedded in the

parameters of the biometrical model. Thus, one might wish to use the biometrical model to scale output from the physiological model. For example, the STAND-BGC growth engine typically causes young stands to respond quickly to release from competition from understory vegetation, which is something FVS cannot do. However, the response seems too quick and dramatic when compared with data from empirical studies. The myriad factors that mitigate a tree's response to increased site resources are poorly represented in STAND-BGC, but they are, to a large degree, represented in the FVS parameters. Thus, the information embedded in the FVS parameters should be useful in scaling or otherwise localizing the physiological model's predictions. More sophisticated feedback could be accomplished wherein model parameters are modified. For example, water-stress information from STAND-BGC running under a drought scenario could become a multiplier on the mortality function in FVS. Alternatively, predicted growth rates from FVS could become multipliers with which to scale physiological process rates (e.g., photosynthesis, allocation ratios, etc) in BGC. How, when, and where these modifiers are applied, could be controlled via an overseer program similar to the event monitor currently used in FVS to control treatments.

This study illustrates a move away from pursuing an answer to the question "which model is best" to the question of

Fig. 8. Simulated trends in standing volume (*a*), top height (*b*), trees per hectare (*c*), and basal area per hectare (*d*) for a regenerated stand. Labels on simulations are as follows: FVS, increments from FVS only; BGC_WG, increments from STAND-BGC with a grass component; BGC_NG, increments from STAND-BGC without a grass component; BGC_WG DRY, increments from STAND-BGC with a grass component and a 20% reduction in precipitation. STAND-BGC was calibrated to FVS using a PSN multiplier of 0.7.
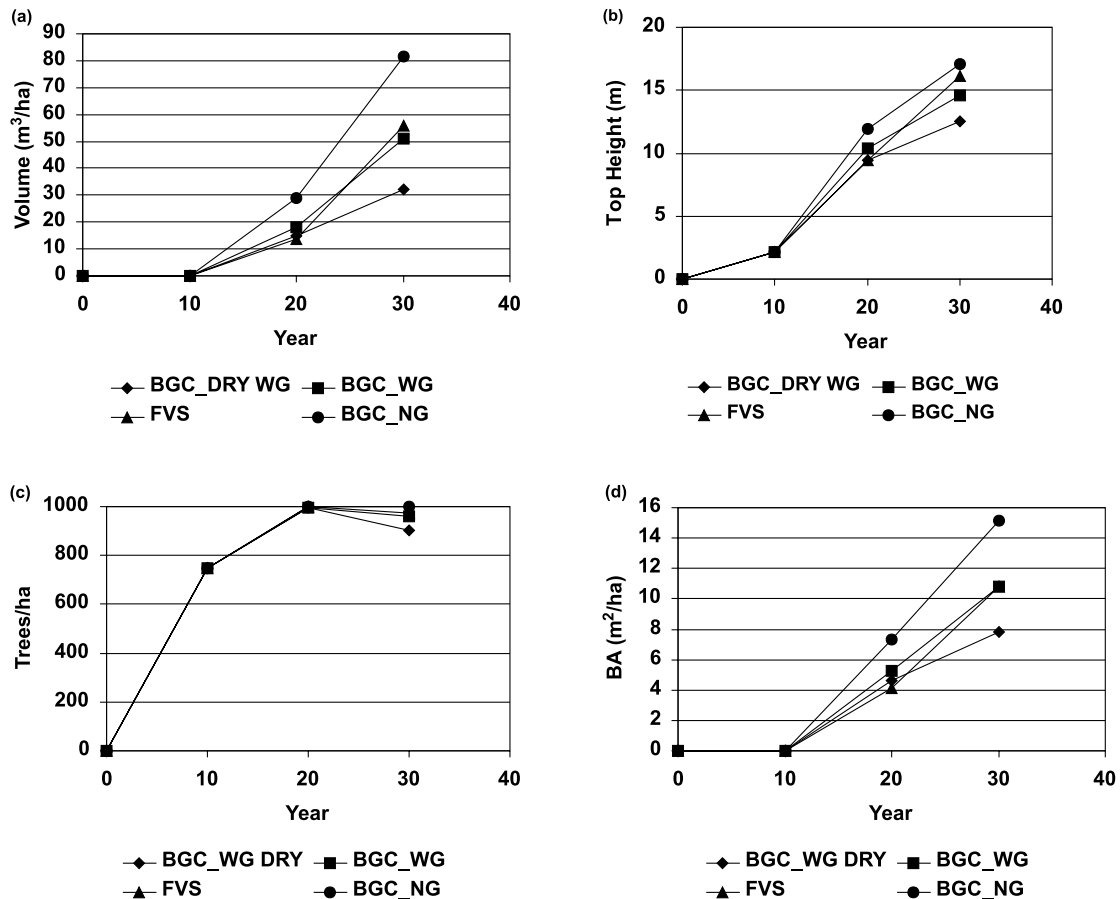
how to get the most out of the two modeling systems. Addressing this question focuses our efforts on structuring systems wherein models can "talk" to each other and away from building monolithic models that try to do everything with one modeling architecture.

References

Amatya, D.M., and Skaggs, R.W. 2001. Hydrologic modeling of a drained pine plantation on poorly drained soils. For. Sci. **47**(1): 103–114.

Baldwin, V.C., Jr., Dougherty, P.M., and Burkhart, H.E. 1998. A linked model for simulating stand development and growth processes of loblolly pine. *In* The productivity and sustainability of southern forest ecosystems in a changing environment. *Edited by* R.A. Mickler and S. Fox. Ecol. Stud. 128. pp. 305–325.

Ferguson, D.E., and Crookston, N.L. 1991. User's guide to version 2 of the regeneration establishment model: part of the prognosis model. USDA Forest Service, Intermountain Research Station, Ogden, Utah.

Hungerford, R.D., Nemani, R.R., Running, S.W., and Coughlan, J.C. 1989. MTCLIM: a mountain microclimate simulation model. USDA For. Serv. Res. Pap. INT-414.

Johnsen, K., Samuelson, L., Tesky, R., McNulty, S., and Fox, T. 2001. Process models as tools in forestry research and management. For. Sci. **47**(1): 2–8.

Kimmins, J.P., Mailly, D., and Seely, B. 1999. Modelling forest ecosystem net primary production: the hybrid simulation approach used in FORECAST. Ecol. Modell. **127**: 183–205.

Landsberg, J.J., and Gower, S.T. 1997. Applications of physiological ecology to forest management. Academic Press, San Diego, Calif.

Landsberg, J.J., and Waring, R.H. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance, and partitioning. For. Ecol. Manage. **95**: 209–228.

Makela, A., Landsberg, J.J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Agren, G.I., Olivier, C.D., and Putton, P. 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiol. **20**: 289–298.

Milner, K.S., and Coble, D.W. 1995. A mechanistic approach to predicting the growth and yield of stands with complex structures. *In* Proceedings of the Conference: Uneven-Aged Management: Opportunities, Constraints, and Methodologies, 29 Apr. 1995, Missoula, Mont. *Edited by* K.S. O'Hara. University of Montana, Missoula, Mont. MFCES Misc. Publ. 56. pp. 144–166.

Nemani, R.R., and Running, S.W. 1989. Testing a theoretical climate – soil – leaf area hydrologic equilibrium of forests using satellite data and ecosystem simulation. Agric. For. Meteorol. **44**: 245–260.

Pfister, R.D., Kovalchik, B.L., Arno, S.F., and Presby, R.C. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34.

Running, S.W., and Coughlan, J.C. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Modell. **42**: 125–154.

Running, S.W., and Gower, S.T. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications II. Dynamic carbon allocation and nitrogen budgets. Tree Physiol. **9**: 147–160.

Vanclay, J.K. 1994. Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, U.K.

Wykoff, W.R., Crookston, N.L., and Stage, A.R. 1982. User's guide to the stand prognosis model. USDA For. Serv. Tech. Rep. INT-133.