A multi-species, process based vegetation simulation module to simulate successional forest regrowth after forest disturbance in daily time step hydrological transport models[1]

J.D. MacDonald, J.R. Kiniry, G. Putz, and E.E. Prepas

Abstract: To simulate the effects of tree harvest on boreal forest catchment hydrology, the vegetation growth model within the soil and water assessment tool (SWAT) must reproduce the successional stages of forest reestablishment. The agricultural land management alternatives with numerical assessment criteria (ALMANAC), a multi-species growth model, was modified to simulate vegetation regeneration on forest sites after harvest (ALMANAC$_{BF}$). The model uses similar principles of vegetation growth as the current vegetation model in SWAT, and input requirements are consistent with typical forest inventory databases. This article describes the algorithms integrated into the ALMANAC$_{BF}$ model to simulate successional stages in forest growth, provides initial estimates of parameters required to simulate multi-species forest succession, and presents examples of the type of variability in vegetation growth scenarios that these algorithms can reproduce. The model structure and modelling approach shows promise as a tool for foresters to evaluate how patterns and timing of forest management activities influence forest watershed hydrology.

Key words: SWAT, ALMANAC, boreal forest, forest growth model, evapotranspiration, watershed hydrology.

Résumé : Dans le but de simuler les effets de la récolte forestière (OU la coupe d'arbres) sur l'hydrologie d'un bassin hydrologique de la forêt boréale, le modèle de croissance de la végétation dans le SWAT (Soil and Water Assessment Tool – Outil d'évaluation du sol et de l'eau) doit reproduire les stades successifs de régénération des forêts. Le modèle de croissance à plusieurs espèces appelé ALMANAC (Agricultural Land Management Alternatives with Numerical Assessment Criteria) a été modifié afin de simuler la régénération de la végétation sur les sites forestiers après la récolte (ALMANAC$_{BF}$). Le modèle utilise des principes de croissance de végétation similaires à ceux du modèle de végétation du SWAT et les entrées requises correspondent aux bases de données typiques des inventaires forestiers. Le présent article décrit les algorithmes intégrés dans ALMANAC$_{BF}$ pour simuler les stades successifs de la régénération des forêts, fournit des estimations préliminaires des paramètres requis pour simuler la succession de plusieurs espèces forestières et présente des exemples du type de variabilité des scénarios de croissance de la végétation que ces algorithmes peuvent reproduire. La structure du modèle et l'approche de modélisation semblent des outils prometteurs pour les experts-forestiers qui désirent évaluer la manière dont les patrons et le moment des activités de gestion forestière influencent l'hydrologie des bassins versants en forêt.

Mots-clés : SWAT, ALMANAC, forêt boréale, modèle de croissance forestière, évapotranspiration, hydrologie des bassins versants.

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Introduction

Basin-scale hydrologic and water quality simulation models can be useful tools for foresters. In particular, the ability to simulate changes to streamflow and water quality in the years following harvesting is of great value in the forest management planning process. The United States Department of Agriculture soil and water assessment tool (SWAT) (Arnold et al. 1998) has strong potential to simulate basin-scale forest hydrology (King and Balogh 2001; Miller et al. 2002; Putz et al. 2003; McKeown et al. 2004). However, the complexities of forest growth during the first 50 years following harvesting require a more representative vegetation growth model than is currently available in SWAT to effectively simulate forest disturbance and recovery (Watson et al. 2005; Wattenbach et al. 2005).

The vegetation canopy defines the plant surface area from which evapotranspiration (ET) occurs (Monteith 1965; Allen et al. 1989). The canopy moderates radiation reaching the soil surface and deposits residue on the soil surface that influences soil temperature. It also acts as a reservoir for moisture, similar to the soil (Wattenbach et al. 2005). Paired catchment studies demonstrate the importance of vegetation type on watershed water balance. Streamflow often changes when vegetation changes; coniferous species have the greatest influence followed by deciduous species, shrubs, and grasses (Bosch and Hewlett 1982; Brown et al. 2005). Modification of vegetation can have an impact on streamflow for 5 to 25 years in temperate and tropical environments (Brown et al. 2005). Forest transformations from coniferous to deciduous species and afforestation can have permanent impacts on catchment water balance (Sahin and Hall 1996; Farley et al. 2005; Wattenbach et al. 2007). Nutrient use, cycling and partitioning into different vegetation tissues varies with tree and plant species (Decatanzaro and Kimmins 1985; Wang et al. 1995). Consequently differences in nutrient export also can be expected with both afforestation and deforestation (Wang et al. 2007).

Much of the impact of changes in vegetation type can be related to the timing of the development of the canopy of different plant types throughout the growing season. Areas with annual plants have bare soils prior to seedling emergence and after leaf senescence. Similarly, areas with deciduous perennial plants can have bare soil conditions from early autumn to early spring. In a coniferous forest, a canopy remains throughout the year. Consequently, to simulate watershed hydrological responses to disturbance, forest regrowth simulations must provide a representative estimate of the successional changes in the vegetative canopy annually and over the lifetime of the forest. The vegetation growth model in SWAT was originally developed for agricultural crops. Hence, SWAT contains the essentials to model hydrology and nutrient transport for annual crop production or perennial grass production. It estimates the parameters required for hydrological calculations (leaf area and plant height) and also provides a reasonable estimate of biomass production, as well as partitioning of nutrients into the different components of the biomass throughout the annual growth cycle. A portion of the biomass is returned to the soil surface on an annual basis, which impacts both ET and nutrient cycling.

To manage the forest landscape it is divided into landscape units referred to as stands (Aldred 1981). A stand is a distinct area of forest with a canopy consisting of one tree species of similar age and productivity (i.e., similar height and wood volume) or a consistent combination of tree species each with a specific age class and productivity. Forest stand boundaries are defined by historic disturbance events, climatic cycles, and the inherent heterogeneity of abiotic and biotic factors resulting in distinct landscape polygons (Waring and Running 1998) that vary in plant and tree species, as well as productivity.

Like the agricultural crop growth model within SWAT, a forest growth model must simulate parameters required to calculate ET (leaf area and plant height). It must simulate biomass production and the partitioning of nutrients into the different components of the biomass throughout the annual growth cycle and the life of the forest. This task is more complex for forests because stands can consist of multiple species in the tree overstorey and an herbaceous understorey. After a forest disturbance (e.g., harvesting), the stand transforms over time from initial herbaceous vegetation through a successional process to an eventual mature tree canopy.

Many stand-level forest growth and yield models exist, such as FORECAST, TRIPLEX, the mixedwood growth model and FOREST–BGC (Running and Coughlin 1988; Titus 1998; Kimmins et al. 1999; Peng et al. 2002). These models are management tools developed to understand how integrated forest management practices and environmental change will influence stand growth, yield, and ecosystem function over long time periods (Peng et al. 2002; Welham et al. 2002). These models require large data sets for representation of each individual forest stand. They typically only simulate pure stands and they function on monthly or yearly time steps. Assembling the data sets required to make these models function on a watershed scale for hundreds of forest stands is difficult, particularly for remote areas like the boreal forest. Consequently, the modeller is left with the choice to either develop simplified data sets and thereby reduce the accuracy of the model, or develop representative simplified models.

The agricultural land management alternatives with numerical assessment criteria (ALMANAC) model (Kiniry et al. 1992) is a field-scale agricultural vegetation model that can simulate competition growth among a wide range of plant species. It uses simple algorithms to partition light among competing species. The ALMANAC model simulates the growth of mixed canopies, an essential feature of the mixed forests of the western Canadian Boreal Plain. The ALMANAC model uses the same soil and weather information as SWAT and the soil parameters are compatible with Canadian and US government soil survey databases. Furthermore, ALMANAC simulates plant growth processes in the same manner as the current SWAT plant growth model, but with more detail. It uses a daily time step and already has some parameters developed to simulate tree growth (Kiniry 1998; Saleh et al. 2004).

In the work described here, ALMANAC was modified (renamed ALMANAC$_{BF}$) to simulate forest growth on the Boreal Plain. In modifying ALMANAC, we adapted its multi-year simulation algorithms to describe the succes-

sional stages of forest vegetation reestablishment after disturbance. Growth and yield models often focus on simulating the growth to maturity of economically viable crop species. We outline a conceptual approach to model basin-scale forest growth using a fixed successional trajectory and describe how a basin-scale forest growth model could be linked with typical forestry geographical database information. We describe the algorithms that were integrated into ALMANAC$_{BF}$, demonstrate the different features of the model, and provide initial parameters developed from forest inventory data.

Model development: Linking to forestry

A successional trajectory approach to basin-scale forest vegetation modelling

Mature forest stands differ in their species composition and in rate of growth (productivity). Depending on the species composition, site productivity and a variety of abiotic and biotic factors, different sites may take very different paths to regenerate the mature forest after a disturbance. A part of the challenge of adapting SWAT to model forest vegetation regrowth is defining the successional species progression of a specific area on the landscape. However, in the management of forest lands, foresters routinely make quantitative predictions of how a forest will regenerate, to provide yield estimates and to plan silvicultural strategies. We have translated the empirical approach used by foresters for predicting growth and yield into a deterministic model in ALMANAC$_{BF}$.

Vegetation inventories based on aerial photographs for the Canadian boreal forest are used by foresters to classify forest stands by species composition (strata) and productivity class. For forest yield projections, foresters apply a fixed equation to a forest stand (a single land unit) that describes its growth trajectory based upon empirical yield curves (growth projections) for a given strata, canopy density, and site productivity class. The site productivity class identifies the rate and quantity of crop tree growth. Canopy density defines the density of crop trees on a site and strata define the species composition.

However, in the initial years after disturbance, sites are quickly invaded by grasses, forbs, and woody shrubs that can delay crop tree reestablishment (Lieffers and Stadt 1994; Beckingham and Archibald 1996; Landhäusser and Lieffers 1998). To plan the replanting and development of crop trees after harvest, foresters use silvicultural prescriptions based on ecosite classification, because competitive vegetation will influence the rate of crop tree establishment (Lieffers et al. 1996). Ecosite classification is a standardized approach to define sites according to their moisture regime (mesic to hygric) and nutrient richness (poor to rich) (Beckingham and Archibald 1996). Gradients are observed in the rate of crop tree development and the amount of competitive vegetation moving from poor and mesic sites to rich and hygric sites. Ecosite maps are also derived from vegetation inventories based on aerial photographs. Biomass production on disturbed sites is highly variable and little work has been done to quantify biomass production according to ecosite classification on the Boreal Plain. Nonetheless, some work has been done to estimate cattle grazing capacities on clear cuts on the Boreal Plain. Reported annual biomass production on these sites in the years immediately following forest harvest before a high shrub or tree canopy was established varied between 250–1000 kg ha^{-1} year^{-1} for xeric to mesic, poor sites and 3000–8000 kg ha^{-1} year^{-1} for rich sub-hygric and hygric sites (Lane et al. 2000; Willoughby 2000, 2005).

ALMANAC$_{BF}$ creates a single input file that can be applied to a landscape unit based on the stand's productivity class, canopy density, strata, and ecosite classification. When a site is harvested, the model will then proceed through a successional growth trajectory, in which vegetation characteristics will vary progressively, over time, based on the characteristics of the stand at the time of harvest.

Model development: Algorithms

The ALMANAC$_{BF}$ annual growth model

The algorithms in ALMANAC describing the annual cycle of plant growth were not modified in ALMANAC$_{BF}$. The fundamental concepts used are identical to those currently used in SWAT (Neitsch et al. 2002), but with algorithms to allow simulation of multiple plant species and competition between species. Briefly, both ALMANAC and SWAT simulate light interception using Beer's law, and a species-specific value of radiation use efficiency (RUE) to calculate daily potential biomass accumulation. Seasonal leaf area index (LAI) and plant height growth follow a sigmoid curve in response to growth degree days (GDD) (Phillips 1950). Leaf area and biomass growth are reduced when available water in the rooting zone is insufficient to meet potential ET. For this project, nutrient limitations on forest growth were ignored in the modelling, due to the complexity of representing nutrient feedback mechanisms in forested sites (Landsberg and Waring 1997).

The multiple-species competition portion of ALMANAC consists of a light partitioning model (Spitters and Aerts 1983) that divides photosynthetically active radiation (PAR) among competing species. The fraction of the total incoming light intercepted by all species (FRACTION (PAR)) is estimated with Beer's law (eq. [1]) after summing the products of extinction coefficient (k) and LAI of species "i" for "n" species:

$$[1] \qquad \text{FRACTION(PAR)} = 1 - \exp\left(\sum_{i=1}^{n} k_i \times \text{LAI}_i\right)$$

Descriptions of the key mathematical coefficients used to describe annual plant growth processes within ALMANAC$_{BF}$ are presented in Table 1, and abbreviations, acronyms, and units in the List of Symbols.

The proportion of FRACTION (PAR) that is intercepted by individual species in the canopy is a function of its light extinction coefficient, contribution to total leaf area, and current height. To simulate the effect of shading, a ratio is calculated (eq. [2]) that estimates the proportion of FRACTION (PAR) that each species intercepts based on its height relative to the height of the entire plant canopy (Kiniry et al. 1992).

Table 1. Adjustable coefficients in the crop parameters input file used in the growth equations in ALMANAC$_{BF}$.

Name	Symbol	Units	Range used	Explanation
Annual growth coefficients				
Biomass-energy ratio*	WA	Kg ha^{-1} per MJ m^{-2}	15–20	Potential biomass production rate per unit PAR[†]
Extinction coefficient	k	MJ m^{-2} per m^2 m^{-2} LAI	0.5–0.55	Radiation interception capacity[†]
Optimal growth temperature	T_o	°C	15	Define HU and temperature stress[†]
Min. growth temperature	T_m	°C	4	Define HU and temperature stress[†]
Max. vapour pressure deficit	VPTH	kPa	1.0	Water use and water stress calculations[†]
Slope of WA:vapour pressure deficit relationship	VPD2	Kg ha^{-1} per MJ m^{-2} per kPa	–6.5	Water use and water stress calculations[†]
Max. stomatal conductance	GSI	m s^{-1}	0.005–0.01	Water use and water stress calculations[†]
Leaf area decline fraction[‖]	RTO	% HU	0.99	Leaf area development with HU accumulation[†, ‡]
Leaf area decline rate[‖]	RLAD	m^2 m^{-2} (% HU)$^{-1}$	0.2–1.0	Leaf area development with HU accumulation[†, ‡]
Leaf area development curve	LAIC	m^2 m^{-2} (% HU)$^{-1}$	Fixed[¶]	Leaf area development with HU accumulation[†, ‡]
Plant population coefficients	PPL	m^2 m^{-2} (% cover)$^{-1}$	Fixed[¶]	Leaf area development with HU accumulation[†, ‡]
Leaf area	LAIMX	m^2 m^{-2}	3.0–4.5	Maxima for sigmoid curve calculations
Height	CHTMX	m	15–30	Maxima for sigmoid curve calculations
Root depth	RDMX	m	0.5	Maxima for sigmoid curve calculations
Long-term growth coefficients[§]				
Height curve*	TREE	m year^{-1}	% max at fixed years	Defines potential height at a given year[‡]
				Two points representing height at a fixed time
Leaf area development curve*	LT-LAIC	m^2 m^{-2} year^{-1}	% max at fixed year	Defines potential leaf area at a given year[‡]
				Two points representing leaf area at a fixed year
Leaf area limitation factor*	LTSNS	unitless	0.25–0.99	Defines a species tolerance to shading.
Optimum stem number coefficient*	YTS max$_{(O)}$	stems ha^{-1}	8 000–500 000	Calculate optimum stem number over time
Optimum stem number coefficient*	YTS min$_{(O)}$	stems ha^{-1}	340–7 000	Calculate optimum stem number over time
Stem number coefficient	YYTD	year	10–20	Used in calculating stem number over time
Stem number coefficient	SCM	unitless	6.72–13.54	Used in calculating stem number over time
Allometric equation coefficients (see eq. [6])	ABC	Mg ha^{-1}	From literature	Empirical coefficients used in natural logarithmic equations relating DBH to foliar and total biomass (four parameters per species)
Shade tolerance coefficient	SDTOL$_{(n)}$	unitless	0.85–1.00	Defines how species react to shading
Shade tolerance coefficient	HBFACT	unitless	0.25–0.30	Defines how species react to shading

*Coefficients refined in validation against forest inventory data.

[†]See Kiniry et al. (1992).

[‡]Sigmoid curves calculated by ALMANAC using four parameters per species.

[§]Coefficients added to create ALMANAC$_{BF}$.

[‖]Used only for annual competitive species.

[¶]Leaf area at fixed heat units or plant density.

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[2] $$RATIO_m = \frac{LAI_m \times k_m \times \exp(-\kappa_m \times LAIHF_m)}{\sum\limits_{i=1}^{n}(LAI_i \times k_i \times \exp(-\kappa_i \times LAIHF_i))}$$

where LAI and k are defined above, κ is the weighted extinction coefficient for the entire canopy above the half height of individual species, and LAIHF represents the sum of leaf area above the half height of individual species. The expression for RATIO indicates the PAR reaching an individual plant species is reduced exponentially by the extinction of light caused by the canopy above it.

Multi-year growth algorithms

Tree growth was included in the original ALMANAC model to simulate its impact on the growth of understorey perennials and annuals (Kiniry 1998). Consequently, there was no real description of a "forest" per se. The ALMANAC$_{BF}$ edition, includes (1) a general description of the trees in a forest stand, including stem number (number of trees), diameter at breast height (DBH), and foliar biomass; (2) an algorithm to account for variable productivity of individual forest sites; and (3) an algorithm that shifts the competitive advantage between the different species that are growing on the site to simulate forest successional change.

Forest stand description

The first change that was made to ALMANAC was the addition of a sigmoid curve to describe maximum annual leaf area and increase in plant height over the life of the forest. We then incorporated a site-specific input parameter (SFTLAI) that shifts the position on the multi-year leaf area development curve to modify the potential LAI in year 1 after disturbance. The long-term sigmoid curve is mathematically the same as annual sigmoid curves in ALMANAC (Kiniry et al. 1992), with the exception that the time scale is expressed in years rather than degree days. Sigmoid curves generated by ALMANAC are forced through the origin and two selected points using eq. [3]:

[3] $$F = \frac{X}{X + \exp(y1 - y2 \times X)}$$

where the fraction (F) is a function of a time dependent factor (X). The model generates the equation from two pairs of input values of F and X. For example, annual leaf area input consists of two values indicating percentage total leaf area (F) at two corresponding values of GDD (X). Parameters y1 and y2 are generated by a curve fit within the model to these two input points (Kiniry et al. 1992).

To calculate stem number (the number of trees), we developed an attenuated exponential decay curve that was fit to Alberta Phase 3 Forest Inventory data for each tree species (eq. [4]).

[4] $$STMX_i = (YTSmax_i - YTSmin_i) \times \left[\left(0.02(Y - YYTD_i)\right)^2 \times \exp\left(\frac{Y - YYTD_i}{SCM_i}\right) \right] + YTSmin_i$$

where for species "i", $STMX_i$ is the maximum number of stems per hectare in a given year, $YTS\,max_i$ and $YTS\,min_i$ are the maximum and minimum number of stems per hectare reported in forest inventory yield tables, respectively, Y is the year after stand establishment, $YYTD_i$ is the initial year of stem number decline and SCM_i is a species-specific crop parameter that defines the steepness of the exponential decrease in stem number after stand establishment. The $STMX_i$ is constant until canopy closure (year $YYTD_i$) and then decreases exponentially. In ALMANAC$_{BF}$, the user specifies the values for YTS max, YTS min, and YYTD for a species and ensures that $Y \geq YYTD$. On this basis, the model calculates standard decreases in stem number with stand maturity.

Average diameter at breast height for a tree species (DBH$_i$) is back calculated for species "i" in the forest stand using species-specific allometric equations (Ter-Mikaelian and Korzukhin 1997) (eq. [5]):

[5] $$DBH_i = \left(\frac{AVBT_i}{ABC1_i}\right)^{ABC2_i}$$

where for species "i", $AVBT_i$ is the average biomass per tree expressed as biomass per hectare/STMA$_i$, STMA$_i$ is the number of trees (stems) per hectare, and ABC1$_i$ and ABC2$_i$ are coefficients relating biomass to DBH$_i$. Foliar biomass (FOL in eq. [6] is then calculated using an additional allometric equation based upon the simulated DBH$_i$.

Net annual above ground biomass production (NPP) for a specific species "i" is calculated by subtracting losses of annual FOL$_i$ and annual stem loss from gross annual production (GPP) for species "i" (eq. [6]).

[6] $$NPP_i = GPP_i - FOL_i$$
$$- \left((STMLYA_i - STMA_i) \times AVBT_i \right)$$

where STMLYA$_i$ is stem number for species "i" from the previous year, and STMA$_i$ and AVBT$_i$ are as defined above.

Height growth follows a sigmoid curve, but is limited by the RATIO of intercepted PAR for each individual species. In this manner, height is synchronized with biomass. The model selects the dominant shading species (i.e., the species that receives the largest fraction of PAR due to its height and occupation in the canopy). For this species, height growth is not limited. The dominant shading species is identified using eq. [7]:

[7] $$HTMOD_{MAX}$$
$$= \MAX_{i=1\ to\ n}\left[HTMOD_i = RATIO_i \times \frac{LAIMAX_i}{LAIPC_i} \right]$$

where HTMOD$_i$ is the RATIO of PAR intercepted by species 1 to n and normalized by the ratio of the maximum potential LAI of the species (LAIMAX$_i$) at 100% cover to the

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LAI at the percent cover defined by the user in the input file ($LAIPC_i$).

It is important to assure that the height increment is reduced proportional to the PAR-RATIO, and not due to the relative proportion that the species occupies in the canopy, as defined by the input chosen for the site. Therefore, daily height increments of all other species are reduced by the RATIO of PAR received by each species normalized by the ratio of $LAIMAX_i$ to $LAIPC_i$ (eq. [8]):

$$[8] \quad HTINCRA_i = HTINCRP_i \left(\frac{HTMOD_i}{HTMOD_{MAX} \times SDTOL_i} \right)^{HBFACT_i}$$

where $HTINCRA_i$ is the actual daily height increment for species "i" corrected for the effect of shading, $HTINCRP_i$ is the potential height increment calculated as a function of the ideal sigmoid height growth curve, $HTMOD_i$ and $HTMOD_{MAX}$ are defined as above, and $SDTOL_i$ and $HBFACT_i$ are species-specific plant parameters that define how individual species react to shading. The factor $SDTOL_i$ allows species "i" to tolerate a certain amount of shading without reducing height growth to account for species that maintain investment in height growth (Perry 1994) when shaded to the detriment of diameter growth. As $SDTOL_i$ decreases, species "i" will tolerate a certain amount of shading without reducing height growth. The factor $HBFACT_i$ accounts for variable allocations of biomass to diameter growth because certain species will invest less biomass in height growth and more in diameter and leaf area growth (Pothier and Prévost 2002; King 2005).

Variable site productivity

Generally, as the productivity of a forest site decreases, the stem number increases, while DBH, height, and wood volume (consequently biomass) decrease. These empirical observations are incorporated into typical yield tables that indicate variable productivity (Plonski 1974). To simulate variable site productivity, we used a similar approach to that used in the TRIPLEX model (Bossel 1996; Peng et al. 2002). $ALMANAC_{BF}$ calculates stem number directly from site-specific input data. The DBH is back calculated from simulated biomass, and foliar biomass is calculated from species-specific allometric equations based on the simulated DBH. As stem number increases, the DBH decreases proportionally. Consequently, since allometric equations are exponential relationships between DBH and foliar biomass, the foliar biomass of individual trees decreases exponentially. We assume that as foliar biomass decreases, LAI is reduced proportionally.

The model calculates foliar biomass for a given site productivity class. In parallel, the model calculates an optimum foliar biomass based on the "optimum" stem number (optimum stem number is a species-specific parameter). The actual LAI (LAIPCA) for species "i" that is used to calculate species growth is then estimated with eq. [9]:

$$[9] \quad LAIPCA_i = LAIPC_i \left(\frac{BFOLSI_i}{BFOLSIO_i} \right)$$

where the maximum potential LAIPC for species "i" at a given percent cover is reduced by the ratio of foliar biomass at the site ($BFOLSI_i$) to the optimum foliar biomass ($BFOLSIO_i$) at a good site with lower stem density and higher DBH trees. Using this simple approach, productivity is reduced proportionally to allometric differences in trees at different stand densities.

Successional changes in species domination

Finally, we incorporated an algorithm that describes successional transitions from one plant type to another during forest growth after disturbance. The transitions are based on shading in the understorey. As the height and leaf area of the upper canopy increases, the area available to shorter species with adequate light to grow becomes limited, and therefore their frequency of occurrence will decrease (Lieffers and Stadt 1994). As canopy height increases, annual potential LAI for shorter members of the vegetation cover is limited by a species-specific factor ($LAILIM_m$) according to eq. [10]:

$$[10] \quad LAILIM_m = \left[\frac{(HT_m \times LAIP_m)}{\sum_{i=1}^{n}(HT_i \times LAIP_i)} \right]^{LTSNS_m}$$

where $LTSNS_m$ is a species-specific factor that defines how a species reacts to shading, HT_m and HT_i are the heights of species "m" and "i", respectively, and $LAIP_m$ and $LAIP_i$ are the maximum leaf areas attained by species "m" and "i" in the previous year, respectively. The factor $LAILIM_m$ defines the maximum potential leaf area that species "m" can reach under a given canopy.

Parameter summary

To adapt $ALMANAC_{BF}$ to forest growth, we incorporated a total of 19 parameters under seven categories (Table 1). Most parameters can be found in current scientific literature or were derived from yield tables, with some parameters like the sigmoid growth curves, fit to forest inventory data. The $ALMANAC_{BF}$ input file was modified to include YTS max and YTS min and SFTLAI, the factor that modifies potential LAI in year 1 after disturbance (harvesting). The input for the sigmoid curve is the current year and the factor SFTLAI is added to the current year. Consequently a SFTLAI factor of 3 will result in the potential leaf area in year 1 after disturbance being equivalent to year 4 on the standard curve.

Material and methods

Site description

The $ALMANAC_{BF}$ model was developed to address the complexities of Boreal Plain forests. A comprehensive description of this region of the Boreal Plain is provided in Smith et al. (2003). Briefly, the annual precipitation is 300 to 625 mm per year. The relief is flat to gently sloping. Upland soils are predominantly deep, silty clay luvisols, formed on calcareous deposits with some occurrence of courser textured, more acidic brunisols on glacio-fluvial and glacio-alluvial deposits. Shallow aquifers exist due to impermeable layers in glacial deposits resulting in occurrences of organic soils and gleysols.

Table 2. Summary of observed (O) mature (average age 90 years) forest stand characteristics of the Boreal Plain from Millar Western permanent and temporary sampling plot data, sorted by strata (species) and productivity class, as defined by the Alberta Vegetation Inventory with ALMANAC$_{BF}$ simulated (S) values reported at age 90 years.

Stand characteristics	TPR[†]		Aw	Aw-Pl	Aw-Sw/Sb	Pl	Pl-Dec	Sb	Sw	SwSb-Dec
			Strata*							
Total biomass (Mg ha^{-1})	U	O			60			74	76	
		S			79			51	72	
	F	O	90	50	270	90	43	57	110	110
		S	92	110	120	100	115	66	100	120
	M	O	95	130	110	120	135	66	110	130
		S	102	130	130	130	145	68	110	120
	G	O	120	150	110	145	130	110	120	83
Foliar biomass (Mg ha^{-1})	U	S	120	160	140	160	160	72	115	130
		O			6.9			9.2	8.8	
	F	S			3.0			8.2	13	
		O	4.0	3.1	10	9.7	8.1	6.1	11	9.8
	M	S	1.6	3.6	7.2	5.2	4.9	9.0	15	12
		O	4.1	7.2	6.3	8.6	7.9	8.4	8.4	9.5
	G	S	1.7	4.4	7.4	6.1	5.8	9.2	14	11
		O	4.1	9.0	5.4	9.3	9.7	13	11	6.6
	U	S	1.9	5.8	7.0	6.5	6.0	9.6	14	10
		O			11			8.5	9.0	
Height (m)	U	S			13			5.8	7.7	
		O	14	17	19	11	5.8	11	11	14
	F	S	13	13	13	11	12	7.9	13	13
		O	15	18	15	15	20	9.0	14	15
	M	S	15	16	15	15	15	8.4	14	14
		O	16	18	17	18	18	11	17	14
	G	S	19	20	17	19	19	10	14	17
DBH (cm)	U	O			11			9.7	27	
		S			13			6.4	11	
	F	O	22	19	37	11	3.5	11	14	14
		S	22	15	22	12	15	9.9	16	17
	M	O	21	23	22	16	23	11	20	18
		S	25	19	25	17	18	10	18	20
	G	O	20	22	20	20	24	14	22	16
		S	29	24	27	22	22	11	19	23
	n		124	23	51	178	31	94	48	26

Note: *n*, number of sample sites.

*Aw, deciduous species, dominantly trembling aspen. Pl, lodgepole pine. Sb, black spruce. Sw, white spruce, Dec, mixed Aw, balsam poplar, and white birch.

[†]Productivity classes (TPR) are U, unproductive; F, fair; M, medium; and G, good.

The forest structure is complex and mixed forest stands are very common. Dry upland stands are typically rapidly growing, consisting of pure lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), pure trembling aspen (*Populus tremuloides* Michx.), and mixed trembling aspen–lodgepole pine. Richer moist sites have pure white spruce (*Picea glauca* (Moench) Voss), pure deciduous (trembling aspen and balsam poplar (*Populus balsamifera* L.), and mixed spruce – deciduous stands – fir (*Abies* sp.). Wetlands and sites with organic soils are predominantly slow growing pure black spruce (*Picea mariana* (Mill.) BSP) and mixed black spruce – deciduous – Larch (*Larix* sp.) stands (Beckingham and Archibald 1996).

Data sources for model simulations

Most of the input data were obtained from existing public sources, for example measurements for the Whitecourt, Alberta weather station from 1984 to 2001 (Environment Canada 2007). However, climate data for 2001 to 2004 were obtained from a meteorological station located 40 km northwest of Whitecourt, maintained by the Forest Watershed and Riparian Disturbance (FORWARD) project in the Millar Western Forest Products Ltd. forest management agreement (FMA) area. Data consisted of daily precipitation, maximum and minimum temperature, solar radiation, wind speed, and relative humidity.

The Agricultural Region of Alberta Soil Inventory Database (AGRASID 2001) provided soil parameters required for model simulations. These data consisted of saturated hydraulic conductivity, bulk density, and water holding characteristics for each horizon of each soil series observed in Alberta. For all simulations in this article, one soil type was used, a common orthic gray luvisol, with silty loam texture (Hubalta series), the dominant soil series in the Millar Western FMA area.

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Temporary and permanent sample plot data

Forest data were obtained for the area surrounding the FORWARD research watersheds (Smith et al. 2003; Prepas et al. 2006). Temporary (TSP) and permanent sample plot (PSP) data were collected in the FMA area between 1996 and 2004 and consisted of 853 individual plots covering stand ages from 5 years after disturbance to old growth stands as old as 180 years. Detailed descriptions of TSP and PSP vegetation data and detailed methodology on forest plot measurements are available elsewhere (The Forestry Corp. 1998; Millar Western Forest Products 2004). Briefly, each tree in a 100 m^2 (TSP) or 400 m^2 (PSP) plot was classified according to species, height, height to live crown, DBH, crown class (position in the canopy ranked by height whether, dominant, co-dominant, intermediate, or suppressed), crown development, age (dominant trees were cored), lean, and tree quality.

The Alberta Vegetation Inventory (AVI) (Alberta Environmental Protection 1996) was used to differentiate the forested landscape into individual forest stands throughout the FMA area. The forest stands were differentiated into eight individual strata based on the dominant species in the dominant storey. Information obtained from the AVI for data analysis and modelling was strata, site productivity class, and ecosite classification. Additional information was provided by Millar Western regarding forest stands that had been harvested since the development of the forest inventory. Stand age for each polygon within the geographic information system database was taken from the AVI and supplemented with harvest data. All information was received from Millar Western in the form of a geographically referenced database that had each attribute required to set up model input files associated with each polygon within the FMA area.

We summarized the detailed individual tree measurements based on crown class only using the trees that were present in actual forest canopies (i.e., dominant, co-dominant, and intermediate trees). Contributions of suppressed trees to total and foliar biomass were insignificant (<10%). Total and foliar biomass was calculated using allometric equations (Ter-Mikaelian and Korzukhin 1997). Biomass per hectare was calculated as the stem number per hectare of each crown class times the average biomass from the average crown class DBH. The height and DBH of each tree species in the plot was weighted based on number of stems and the average height per canopy class. Individual plot data were summarized based on stand strata from AVI polygons and age class defined by 10-year intervals.

Results

Characteristics of Boreal Plain forest stands

The TSP and PSP data provided a general overview of the characteristics of the forests of this region. Eight strata could be clearly defined, four of which represented mixed stands (Table 2). In general, late juvenile and mature forest strata that had not entered into the old growth stage (stands from 55 to 125 years of age) increased in total biomass, total height, and DBH in the following order: black spruce (Sb), deciduous species (mainly trembling aspen (Aw)), white spruce (Sw), SwSb–Dec (Dec refers to mixed Aw, balsam

poplar and white birch (*Betula papyrifera* Marsh.)), Aw–SwSb, Aw–lodgepole pine (Pl), Pl–Dec, Pl. Mixed stands were generally more productive than pure stands of the dominant species occurring in a mixture. Foliar biomass increased in the following order: Aw, Aw–SwSb, Aw–Pl, Pl–Dec, SwSb–Dec, Sb, Pl, Sw. This demonstrates a gradient with increased deciduous plants in mixed forests representing the lower biomass to leaf area ratio of deciduous foliage. Overall productive sites (Good sites) were 35%, 35%, 25%, and 17% greater in biomass, height, foliar biomass, and DBH, respectively, than fair sites and 92%, 80%, 16%, and 70% greater in biomass, height, foliar biomass, and DBH, respectively, than unproductive sites.

Model parameterization

ALMANAC$_{BF}$ was developed so that the characteristics of the simulated trees could be compared to data that are collected by forestry companies in their TSP and PSP sampling programs. To refine the growth parameters for trees in the model, we worked with a subset of the TSP and PSP data. Selecting only pure stands of Aw ($n = 51$), Pl ($n = 55$), Sb ($n = 60$), and Sw ($n = 42$) and summarizing the TSP and PSP data by age class, we created a chronosequence of height and biomass.

We refined the biomass energy ratio (WA), leaf area development curve (LAIC), maximum height (CHTMX), and the initial and final stem numbers (YTS max$_{(O)}$ and YTS min$_{(O)}$) (Table 1) iteratively until we had the best fit to the observed data, judged by a linear regression with the highest r^2 for total biomass, foliar biomass, height, and DBH (Table 3). In previous work (MacDonald et al. 2005), we refined coefficients related to seasonal parameters (height partitioning coefficients, seasonal heat unit relationships). We retained these parameters and a standard set of physiological parameters (Table 1) throughout all simulations.

Variable site productivity is simulated in ALMANAC$_{BF}$ by the modification of LAI, based on allometric differences in trees of different size. By increasing stem density (Table 3) on a site, there is a corresponding reduction in site total productivity associated with LAI reduction that is proportional to the differences in DBH of the dominant trees growing on good sites relative to those growing on fair sites. Consequently, the model simulates different total gross annual biomass due to differences in LAI among sites and differences in net biomass accumulation due to differences in tree mortality: annually more, but smaller trees die on unproductive sites. In the case of the Pl stand development (Fig. 1) decreasing initial and final stem densities in simulations (fair sites compared to good sites) result in a corresponding increase of 60%, 120%, 80%, and 30% in total biomass, height, DBH, and foliar biomass, respectively, compared to observed values of 60%, 60%, and 80% increase in total biomass, height, and DBH, respectively, and a 5% decrease in foliar biomass.

Overall, the model reproduced the general trends in forest data. At a simulated age of 90 years after disturbance, averaging all species, productive sites (good sites) were 30%, 39%, 4%, and 35% greater in biomass, height, foliar biomass, and DBH, respectively, than fair sites and 90%, 80%, 7%, and 100% greater in biomass, height, foliar biomass,

Table 3. Input parameters for ALMANAC$_{BF}$ derived through optimization and used throughout simulations.

Parameter description	Source		YYTD	YTS	G	M	F	U
					Input parameters and variations			
Stand population description	Optimized with biomass, height and DBH chronosequence, TSP/PSP data	Aw	10	max	14 000	28 000	38 000	38 000
				min	500	590	700	1050
		Pl	20	max	16 000	30 000	69 000	114 000
				min	550	820	1200	2690
		Sb	20	max	56 000	100 000	120 000	200 000
				min	2300	2400	2500	5000
		Sw	20	max	16 000	20 000	24 000	200 000
				min	540	750	1080	2000
Orthic gray luvisol, Hubalta series, common Boreal Plain glacial till soil (silty loam)								
Soil input	AGRASID (2001)	Texture			% Clay			11–36
		Saturated conductivity			(mm h^{-1})			10–100
		Water holding capacity			(% volume)			8–10
		Coarse fragment			(%)			0–18
Tree input parameters	Optimized from TSP/PSP biomass ratios	Aw-SwSb			(percent cover)		70% Aw	30% Sw
		Aw-Pl			(percent cover)		80% Aw	20% Pl
		Pl-Dec			(percent cover)		50% Pl	50% Aw
Grouping of Ecosite classifications into three categories								
Ecosite category	Broad estimate from literature	Xeric			40% Annual		40% shrub	SFTLAI-0
		Mesic			70% Annual		70% shrub	SFTLAI-0
		Sub-hygric			100% Annual		100% shrub	SFTLAI-2

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Fig. 1. ALMANAC$_{BF}$ simulations of variable growth in different productivity classes of Lodgepole Pine Stands. (*a*) Stand biomass. (*b*) Stand height. (*c*) Diameter at breast height (DBH). (*d*) Foliar biomass. Comparison to observed means in TSP/PSP data from stands ranging from 55 to 125 years of age.
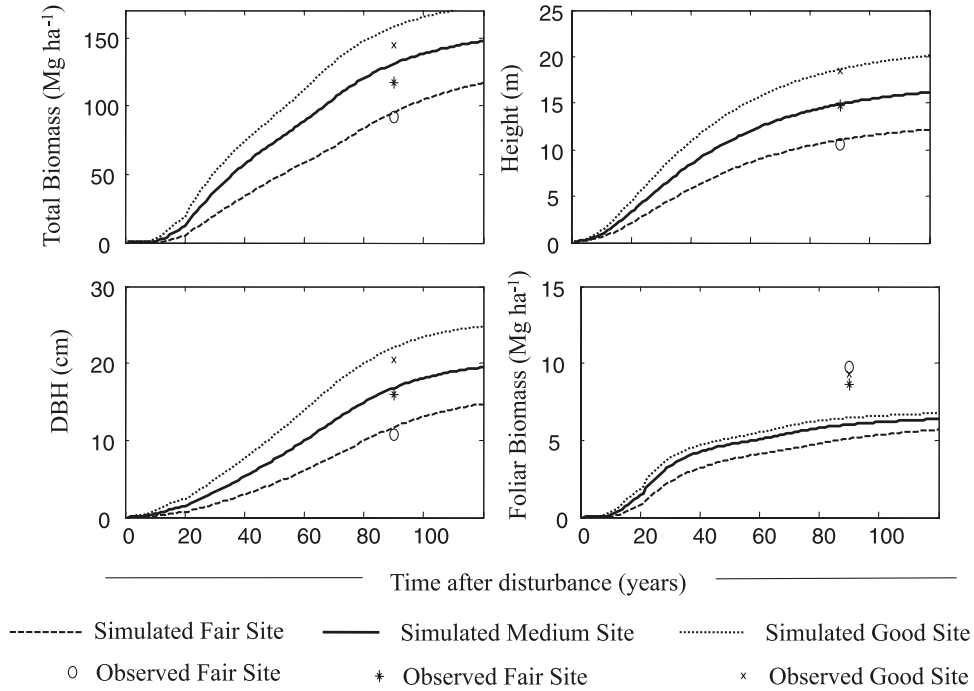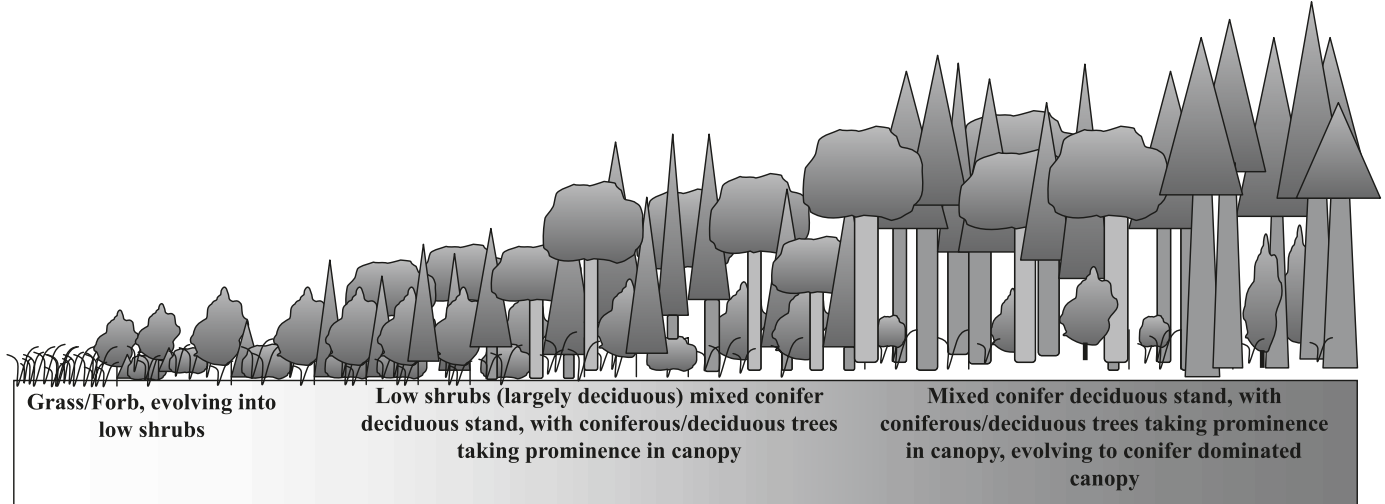

Fig. 2. Graphic representation of typical Boreal Forest succession after disturbance for a conifer-leading deciduous strata.

and DBH, respectively, than unproductive sites. Simulated stands increased in total biomass, total height, and DBH in the order: Sb, Aw, Sw, Aw–SwSb, SwSb–Dec, Pl, Aw–Pl, and Pl–Dec. As was the case in the observed data, simulated mixed stands were generally more productive than pure stands of the dominant species present in a mixture. The higher productivity of the mixed stands is a result of the non-linear (sigmoid) relationship between the percent cover in the input file, and the LAI (parameters PPL in Table 1). Consequently in mixed stands, the potential LAI for the combined species was slightly elevated relative to a pure stand. Foliar biomass increased in the order Aw, Aw–Pl,

Pl–Dec, Aw–SwSb, Pl, Sb, SwSb–Dec, and Sw, demonstrating a gradient with increased deciduous plants in mixed forests representing the lower biomass to leaf area ratio of deciduous foliage.

Understorey vegetation

Across the three ecozones in the Millar Western FMA area, there are approximately 50 ecosite classifications. In theoretical simulations (described in more detail below), we varied the percent cover (equivalent to the seeding rate for annual crops), as well as the factor SFTLAI, which modifies the sigmoid curve controlling potential LAI change with

Fig. 3. ALMANAC$_{BF}$ simulations of the relative proportion of occupation of leaf area index (LAI) of different species in the forest canopy (*a*)–(*c*) and actual LAI (*d*)–(*f*) under different simulated forest stand types: (*a*) and (*d*) mixed white spruce (Sw)-aspen (Aw) sub-hygric ecosite; (*b*) and (*e*) mixed Aw-lodgepole pine (Pl) mesic ecosite; (*c*) and (*f*) mixed Pl-Aw xeric ecosite.
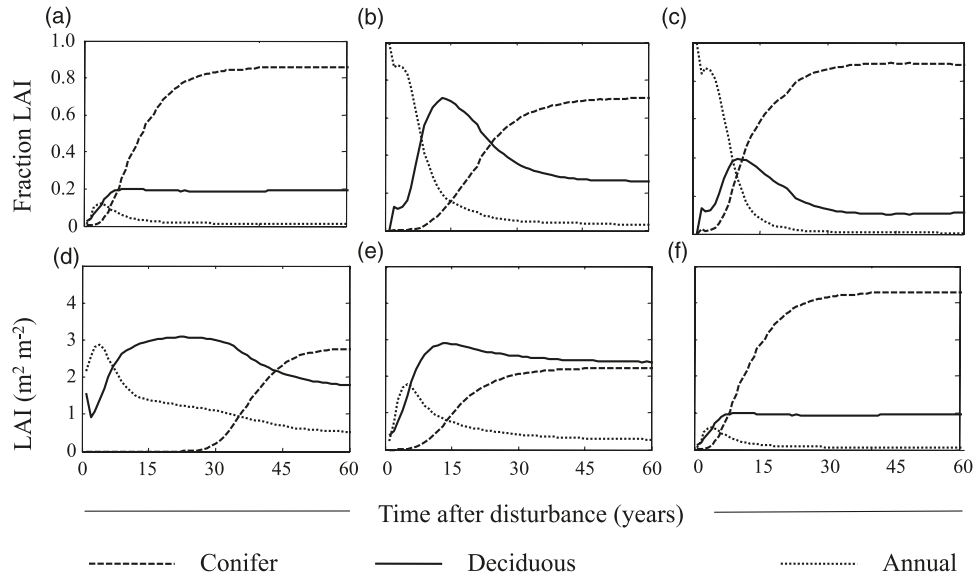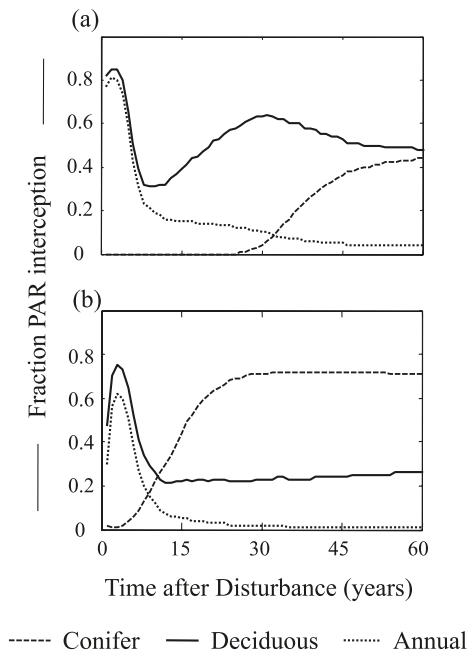

Fig. 4. ALMANAC$_{BF}$ simulations of photosynthetically active radiation (PAR) interception in: (*a*) mixed white spruce (Sw)-aspen (Aw) sub-hygric ecosite; (*b*) mixed lodgepole pine (Pl)-Aw xeric ecosite.

time (Table 3). A fixed plant growth parameter (mass carbon per unit energy input) for generic perennial grasses and forbs that have an annual growth cycle was set at 1.2 g C MJ^{-1} with a maximum potential LAI of 5.0, when fully established at 100% cover and a maximum height of 1 m. A fixed parameter for deciduous shrubs was set at 1.7 g C MJ^{-1} with a maximum potential LAI of 3.5, when fully established at 100% cover and a maximum height of 3.5 m.

Based on these input parameters, we simulated variations in annual biomass production that ranged from 0.22 to 1.5 Mg ha^{-1} in "xeric" sites compared to 3 to 3.7 Mg ha^{-1} in the simulated "sub-hygric" sites. The model does not simulate the extremes reported in the literature; however with simple modification of input parameters, the model is very capable of providing a reasonable simulation of differences in productivity.

Successional changes in forests: Leaf area index and light interception

While TSP and PSP data provide an idea of the type of stands that exist on the forest landscape, those forests have passed through a process of succession to arrive at their present forest structure. A typical growth trajectory in the boreal forest involves successional changes in plant species composition (Fig. 2). Immediately after disturbance, the vegetation covering the site is dominated by annual forbs and perennial grasses, evolving into low shrub cover. Around the time of canopy closure, we observe a deciduous–coniferous tree and shrub canopy, evolving into a young mixed deciduous–coniferous forest and eventually, a mature forest dominated by large coniferous species or staying as a deciduous overstorey. The forest strata (tree species), ecosite, and site productivity determine how the site will evolve.

In ALMANAC$_{BF}$ model simulations, the combination of the light partitioning equations (eqs. [1] and [2]) with the long-term leaf area development equation (eq. [3]) and the successional equation that limits potential leaf area based on species height and LAI in previous years (eq. [10]) describe changes in LAI over the life of the stand. Leaf area is a fundamental parameter in hydrological modelling, because it defines the area of a vegetative canopy that captures light and intercepts rainfall.

Different combinations of crop tree species (strata) growing in different ecosites (Figs. 3*a* to 3*f*) result in very differ-

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Fig. 5. ALMANAC$_{BF}$ simulations of the relative proportion of total foliar biomass of different species in the forest canopy of a forest regenerating after disturbance (a)–(c) under different forest trajectories and foliar biomass (d)–(f). Stand types include: (a) and (d) mixed white spruce (Sw)-aspen (Aw) sub-hygric ecosite; (b) and (e) mixed Aw-lodgepole pine (Pl) mesic ecosite; (c) and (f) mixed Pl-Aw xeric ecosite.
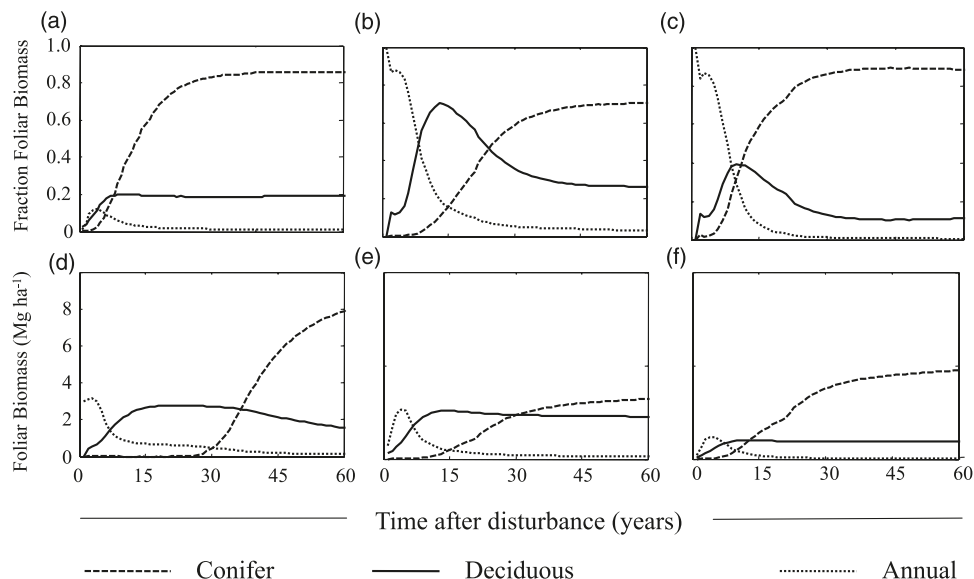
ent growth trajectories as represented by changes in LAI with time after disturbance. In the years immediately after disturbance, annual (i.e., grasses and forbs) plants dominated the canopy in all scenarios, but were reduced to 10% of the total canopy (0.3–0.5 m^2 m^{-2}) over the first 20 to 40 years. In conifer-dominated stands (Figs. 3a and 3c), deciduous species dominated the forest canopy from 5 years after disturbance to 15 or 50 years, depending on the rate of conifer growth; pine species rapidly dominating the forest canopy (20–30 years) and spruce developing slowly (40–50 years). In aspen-dominated stands (Fig. 3b), coniferous species gradually established a secondary canopy. Each simulated strata varied in the period that deciduous, conifer, and annual species dominated the forest canopy.

While the proportions of the LAI were dependent on species combinations, the absolute values of LAI were dependent on ecosite and site productivity. In the xeric-sub-mesic site, leaf area developed slowly over the first 5 to 10 years (0.17 in year 1, 1.3 in year 5, 2.3 m^2 m^{-2} in year 10), whereas it developed rapidly on the hygric site (3.7 in year 1, 4.4 in year 5, 4.4 in year 10) and rapidly reached a maximum in year 8 (Figs. 3d to 3f).

Light interception was partitioned among the different species using the simple PAR partitioning model described by Kiniry et al. (1992). In general, PAR interception was proportional to LAI development (Figs. 4a to 4b). However, as tree species established their canopy over the shrub and annual species, the proportion of light allotted to the annual plant and shrub species was decreased relative to their proportion of the LAI (eq. [2]). At 50 years after disturbance, annuals maintained an LAI that is 10 to 15% of total canopy but receive only 5 to 10% of total PAR.

Biomass partitioning

The concept of RUE is used to convert PAR to biomass. Biomass is partitioned among the different species based on

the distribution of LAI (Fig. 3) and the PAR intercepted by each individual species (Fig. 4). Consequently, the proportional changes in biomass are similar to changes observed in the relative proportion of LAI and PAR interception. However, from the perspective of hydrological transport modelling, it is the distribution of biomass among different plant types that is important, because the model must provide a reasonable estimate of biomass that is returned to the forest floor in the form of litter and also nutrients that are stored in plant tissues for the long term. The use of species specific allometric equations (eq. [5]) allows an estimate of foliar tissue to be derived by back-calculating DBH from the total biomass.

Among different combinations of mixed forests (Fig. 5), foliar biomass also follows the same pattern as LAI and PAR interception with a transformation from an annual species dominated canopy, to deciduous cover to an eventual coniferous contribution. The exception in the case of foliar biomass is the disproportionately large biomass of coniferous foliage per unit leaf area relative to deciduous foliage. As a consequence, even in sites that are dominated by deciduous trees with respect to leaf area, coniferous foliage rapidly comes to occupy the largest proportion of foliar biomass.

As was the case with LAI, variability was seen in the real values of foliar biomass observed with the input associated with ecosite classification (Figs. 5d to 5f). In simulated subhygric sites, annual foliar biomass ranged from 3 to 5 Mg ha^{-1} in the first 10 years after disturbance compared to only 1 to 1.5 Mg ha^{-1} in the case of the simulated xeric site.

Changes in evapotranspiration

The ALMANAC$_{BF}$ model calculates ET using the Penman-Monteith equation and simulated water uptake exactly as does the SWAT model, assuming EPCO (the parameter defining the distribution of water uptake from soil horizons)

Fig. 6. ALMANAC$_{BF}$ simulations of cumulative annual evapotranspiration in a theoretical forest site using the Penman-Monteith equation with constant weather input data. (*a*) Year 1 after disturbance varying maximum site LAI to simulate ecosites spanning the edatopic grid, varying from rich, hygric sites (moist, nutrient rich sites) to xeric, poor sites (dry nutrient poor sites). (*b*) Sw–Aw strata at different ages during the growth trajectory. (*c*) ET in juvenile and mature forests, different strata, different site productivity.
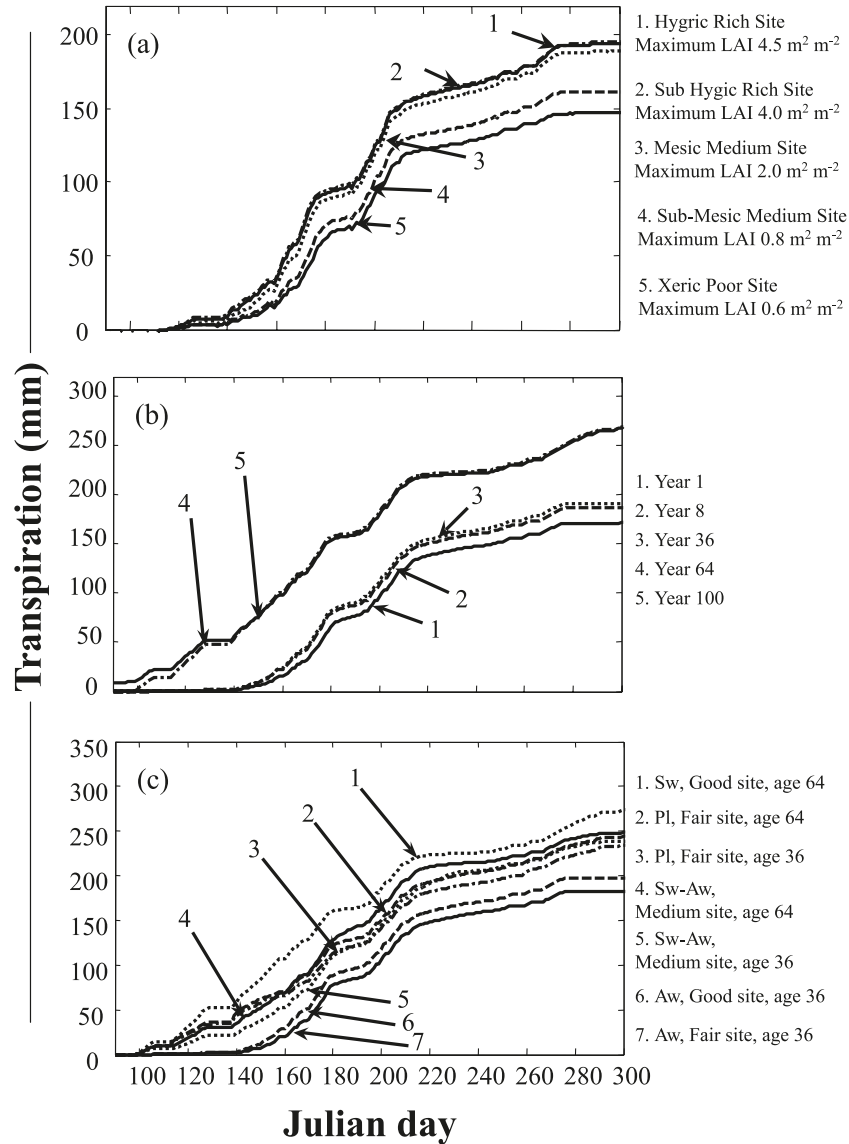
is 1.0 (Kiniry et al. 1992; Neitsch et al. 2002). As calculated by the Penmen-Monteith equation, transpiration is influenced only by plant parameters, height and LAI and is limited by plant water availability. Simulated variations in species and ecosite result in changes in transpiration that produce important variations in simulated seasonal transpiration throughout the age of the stand (Figs. 6*a* to 6*c*). The most important differences indicated by the simulations were (1) the more productive sites, with greater potential LAI, had roughly 20% greater transpiration than xeric–poor sites in the first year after disturbance (Fig. 6*a*); (2) transpiration increased by as much as 40% (Fig. 6*b*) from year 1 to a peak beginning in the middle of the growth cycle (64 years of age); (3) in the transition from juvenile stands (age 36) to mature stands (age 64) annual transpiration differed by as much as 55% among Aw, Sw, and Pl strata (Fig. 6*c*);

(4) seasonal differences among conifer, annual, and deciduous species were evident, with roughly 20% of total annual transpiration occurring in early spring in coniferous stands before deciduous and annual canopies were established (Figs. 6*b* and 6*c*); and (5) an increase in stand productivity resulted in an increase of about 14% in the annual total of transpiration (Aw fair site productivity to Aw good site productivity) (Fig. 6*c*).

Discussion and conclusions

ALMANAC$_{BF}$ is intended to provide a generic description of variability in forest growth, with very little information about individual sites. The simulations presented here were carried out using the soil, water, and nutrient subroutines in ALMANAC, but the model algorithms described in this ar-

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ticle have now been integrated into the SWAT model code. The model is in the process of being validated at the catchment scale.

Using a single set of growth parameters, the model described the general trends in the TSP and PSP data set with respect to total biomass, canopy height, foliar biomass, and DBH in both pure and mixed forest stands. In pure stands of Aw and Pl, foliar biomass was generally underestimated because, though the model is simulating a pure stand of Aw and Pl, the majority of the sites defined as Aw or Pl had up to 20% of other species. Balsam fir and Sw intermediate storeys can contribute significantly to total biomass and for accurate simulations of nutrient cycling, the role of these intermediate trees may need to be included in simulations of so called "pure stands". The biomass energy ratio of ALMANAC$_{BF}$ ranged between 1.3 in the case of Sb to a maximum of 1.7 g C MJ^{-1} for Aw. Reported biomass energy ratio values for trees have ranged from 1.5 g C MJ^{-1} (Kiniry 1998) to 1.8 g C MJ^{-1} (Landsberg and Waring 1997). Therefore, the relationships between energy and biomass accumulation used in ALMANAC$_{BF}$ were consistent with those observed in other studies. Furthermore, with minor modifications of the ALMANAC$_{BF}$ input file, a wide range of plant growth characteristics can be simulated (total biomass range of 0.25 to 3.7 Mg ha^{-1}, LAI from 0.2 to 4.5 m^2 m^{-2}) for a generic annual plants (grasses and forbs) and shrubs in the first 10 years of stand establishment, while retaining constant plant parameters. The model is capable of simulating very different scenarios of successional recovery after forest disturbance.

Published simulations of forest hydrology using stand level models have typically used satellite input data (MacKay and Band 1997; Coops and Waring 2001) or measured values (Amthor et al. 2001) as sources of LAI estimates of mature forests. Such simulations focus on validating ET estimates for mature forests, rather than providing a tool that could be used to predict the impact of landscape modifications on forest hydrology. Likewise, when simplified forest growth subroutines have been integrated into existing basin-scale hydrological simulations, they have only focused on mature forests (Watson et al. 2005; Wattenbach et al. 2005) and were not developed to simulate forest regeneration. Consequently, adaptation of these forest growth models to simulate forest regeneration would still have required reworking of the model algorithms or the development of complex vegetation sequences to simulate successional reestablishment of forests.

The ALMANAC$_{BF}$ model development focused on the development of algorithms that could simulate the regrowth of forests after disturbance. This approach addressed a gap in growth and yield model approaches that tend to ignore the early years of stand establishment, focusing on simulating young stand dynamics after forest canopies have closed. Models that do not simulate the initial years after stand establishment fail to describe variability in vegetation transpiration and nutrient uptake and storage in these years. Paired catchment studies demonstrate important differences in runoff due to vegetative cover (Brown et al. 2005) and due to forest management actions (Wang et al. 2007). The majority of the impact on water quality and quantity is in the initial 10 years after harvest. It is also understood that these differences are, in part, a result of changes in runoff due to differences or changes in landscape features and infiltration characteristics (Brown et al. 2005; Wang et al. 2007). To estimate the relative importance of changes in the landscape features relative to changes associated directly with the vegetation, models must provide representative simulations of vegetation's role in watershed water balance. Important variations in factors such as total biomass in annual shrubs, foliar biomass and the seasonal dynamics of annual plants, as well as deciduous and coniferous trees and shrubs, are required to provide reasonable estimates of canopy rainfall and radiation interception, ET, and nutrient uptake.

The ALMANAC$_{BF}$ simulations of different forest strata at different stand age and site productivity resulted in important differences in simulated transpiration. Transpiration varied from 150 to 270 mm year^{-1}. These simulations have not been compared to measured data and must be treated with caution. Blanken et al. (2001) and Pomeroy et al. (1994) working on the Boreal Plain measured ET in similar forests that ranged from 1.5 to 2 times our simulated values. Pomeroy et al. (1994) noted however, that ET decreased moving from coniferous stands to mixedwood stands to regenerating stands, and to clearcuts, with a relative difference of 140% between fresh clearcuts and mature coniferous stands. This is very consistent with our simulated differences in transpiration (i.e., coniferous stands > mixedwood stands > regenerating stands > fresh clearcuts), with transpiration in the most productive mature coniferous stands 180% that observed in the least productive fresh clearcuts.

In watersheds where runoff represents 5 to 40% of annual precipitation, such as those on the Boreal Plain (Prepas et al. 2006), changes in ET of up to 20% of annual precipitation could have an important impact on catchment water balance. The variations in stand strata, ecosite, and site productivity classes that we tested in our theoretical simulations are typical of boreal forest stands occurring in the Millar Western FMA area and are important enough that they need to be included in simulations of hydrological impacts of boreal forest disturbance and recovery.

The ALMANAC$_{BF}$ model is simple and consistent with the current SWAT growth model. It was integrated directly into SWAT model code without major modifications to the hydrological model and with few extra data requirements. Beer's Law is an accepted approach for modelling forest light interception (Lieffers et al. 1996) and the simple height-weighted light partitioning approach of ALMANAC has been recognized as a reliable method of partitioning light among multiple species (Rossiter and Riha 1999; Bartelink 2000). Allometric equations and the basic concepts of yield tables are standard principles in forestry (Plonski 1974; Ter-Mikaelian and Korzukhin 1997). Also, by retaining the basic vegetation growth processes in SWAT, we have attempted to keep the model easily understandable by SWAT model users.

In the future, the GDD functions currently used in SWAT will be modified for forests, because tree growth may not function according to the GDD model that was developed for annual vegetation (Price et al. 2001). Furthermore, the sigmoid leaf area equations that do not account for canopy decline in mature forests will be replaced (Running and Coughlin 1988; Landsberg and Waring 1997). Nonetheless,

the model algorithms outlined in this article that simulate partitioning of light and biomass among species and biomass within species, as well as the simple procedures to simulate succession of a stand overtime, are promising. Furthermore, the model algorithms take advantage of all useful site-specific information that can be derived from data available at the landscape scale in foresters' geographically referenced databases.

Acknowledgements

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List of symbols

$ABC1_i$, $ABC2_i$ species-specific plant parameter. Coefficients used in allometric equations relating biomass to DBH (unitless).

$AVBT_i$ internal model-calculated coefficient. Average biomass per tree calculated as biomass per hectare over stem number per hectare (Mg tree^{-1}).

$BFOLSI_i$ foliar biomass for an individual tree at the input productivity class calculated with allometric equations (kg tree^{-1}).

$BFOLSIO_i$ foliar biomass for an individual tree at a good site at lower stem density and higher DBH trees (kg tree^{-1}).

DBH_i average breast height diameter for a tree species (m).

EPCO SWAT model parameter defining the distribution of water uptake from soil horizons (unitless).

ET evapotranspiration (mm).

FOL_i foliar biomass (Mg ha^{-1}).

FRACTION (PAR) internal model-calculated coefficient. Fraction of PAR intercepted by the complete canopy (unitless).

GDD growth degree days (°C days).

GPP gross primary productivity (Mg ha^{-1} year^{-1}).

$HBFACT_i$ species specific plant parameter. Defines how individual species react to shading to calculated height growth (unitless).

HT_i, HT_m calculated output. Height of an individual species (m).

$HTINCRA_i$ internal model-calculated coefficient. Actual daily height increment corrected for the effect of shading (m).

$HTINCRP_i$ internal model calculated coefficient. Potential height increment calculated as a function of the ideal sigmoid height growth curve (m).

$HTMOD_i$ internal model calculated coefficient. Ratio of PAR intercepted by species 1 to n, normalized by the ratio of the maximum potential LAI of the species at 100% cover to the potential LAI at the cover input by the user (unitless).

HTMODMAX internal model-calculated coefficient. Value for the maximum ratio of PAR intercepted by the dominant species in the input array (unitless)

HU heat units.

k_i, k_m species-specific plant parameter. Light extinction coefficients as defined by Beer's Law (unitless).

LAI_i, LAI_m calculated output. Leaf area index (m^2 m^{-2}).

$LAIHF_i$, $LAIHF_m$ internal model-calculated coefficient. Value of the combined leaf area index above half the height of a species within the array of modelled species (m^2 m^{-2}).

$LAILIM_i$ internal model-calculated coefficient. Factor limiting leaf area development for understorey species (unitless).

$LAIMAX_i$ species specific plant parameter. Leaf area index at 100% cover (m^2 m^{-2}).

$LAIP_i$, $LAIP_m$ internal model-calculated coefficient. Maximum annual leaf area of a species in the year previous to the current year (m^2 m^{-2}).

$LAIPC_i$ internal model calculated coefficient. Species leaf area index at the percent cover defined by the user in the input file (m^2 m^{-2}).

$LAIPCA_i$ internal model-calculated coefficient. Species actual leaf area index corrected for site productivity index (m^2 m^{-2}).

$LTSNS_m$ species-specific plant parameter. Defines how a species reacts to shading in calculating leaf area limitation in understorey (unitless).

i, m, n subscripts to designate a species in an array of species (i.e., species 1 through n).

NPP net primary productivity (Mg ha^{-1} year^{-1}).

$RATIO_i$, $RATIO_m$ internal model-calculated coefficient. Relative proportion of PAR that a species intercepts taking into account shading (unitless).

RUE_i species-specific plant parameter. Radiation use efficiency (Kg MJ^{-2}).

SCM_i species-specific plant parameter. Defines the exponential decrease in stem number after stand establishment (unitless).

$SDTOL_i$ species-specific plant parameter. Defines how individual species react to shading to calculate height growth (unitless).

SFTLAI site specific input. Shifts the multi-year leaf area development curve depending on the ecosite classification (year).

$STMA_i$ calculated output. Stem number in the current year (stems ha^{-1}).

$STMLYA_i$ internal model-calculated coefficient. Stem number from the previous year (stems ha^{-1}).

$STMX_i$ internal model-calculated coefficient. Maximum number of stems per hectare for a species (stems ha^{-1}).

VPD vapour pressure deficit. Difference between the amount of moisture in the air and how much moisture the air can hold when saturated (kPa).

Y internal model calculation. The year after stand establishment (year).

$YTS\,max_i$ site specific input. Maximum number of stems reported in yield tables that is associated with a productivity class (stems ha^{-1}).

$YTS\,min_i$ site-specific input. Minimum number of trees reported in yield tables (stems ha^{-1}).

$YYTD_i$ species-specific plant parameter. The first year that stem number begins to decline (year).

κ_i, κ_m internal model-calculated coefficients. The weighted extinction coefficient of the combined canopy above half the height of a species within the array of modelled species (unitless).