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The transition zones (ecotone) between boreal forests and peatlands: Modelling water table along a transition zone between upland black spruce forest and poor forested fen in central Saskatchewan

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ABSTRACT

Close association between hydrology and ecosystem productivity in boreal transition zones requires that modelling ecosystem productivity in these zones be based on accurate modelling of water table dynamics. We hypothesize that these dynamics are driven by transfers of water through surface and lateral boundaries of transition zones, and that lateral transfers can be calculated from hydraulic gradients with external water tables at upper and lower boundaries. In this study we implement these hypotheses in the *ecosys* model to simulate water table dynamics along a boreal transition zone (ecotone) in central Saskatchewan, Canada, extending from upland black spruce forest down to a poor forested fen. Simulated water table depths were compared to measured values at upper, middle and lower ecotone positions during the dry year 2003 when peat was dried, the very wet year 2004 when peat was rewetted, and the hydrologically average year 2005 when peat remained wet. These hypotheses enabled *ecosys* to simulate declines in water table depth with declines in elevation along the ecotone that matched well those observed during each of the three years. Observed:expected plots of modelled vs. measured water table depths at all positions indicated reasonable goodness of fit with slopes (with respect to 1:1 line) and R^2 of 0.92 and 0.53 in 2003–2005 period, 0.90 and 0.28 in 2003, 0.81 and 0.51 in 2004, 0.97 and 0.46 in 2005, confirming that our hypotheses enabled changes in water table depths along boreal transition zones to be properly modelled during successively dry, wet and normal years.

1. Introduction

Boreal forests, found through most of Canada, Russia and Scandinavia, play an important role in global carbon (C) cycling, being the second largest terrestrial biome on Earth with 1/3 of the total forest C, 1/3 of the total forest area, and roughly 1/4 of the total soil C (Pan et al., 2011; Gates, 1993). In vast boreal regions soil drainage governing water table (WT) is a main determinant of soil C storage (Rapalee et al., 1998), and extensive peatlands have developed on waterlogged areas (Bauer et al., 2009). Consequently, forested peatlands and wetlands occupy a substantial part of boreal landscapes with a global area of roughly 2.5×10^8 ha (Gorham, 1991; Lugo et al., 1990). Many boreal forests adjacent to peatlands are also poorly drained (Bond-Lamberty and Gower, 2007), with black spruce/bryophyte plant communities (Turetsky, 2003; O'Neill, 2000) and poorly understood hydrological controls on C sequestration (Zoltai and Martikainen, 1996). These forests often have characteristics of transitional ecosystems with declining productivities caused by shallower WT and associated increases in peat depth towards peatlands, and gradients in bryophyte community structure (Bhatti et al., 2006; Hartshorn et al., 2003).

Even though lowering of WT has been reported to cause annual basal area increments of black spruce to more than double (Lieffers and Macdonald, 1990) and annual tree ring widths to increase by several times (Dang and Lieffers, 1989), little is known about how WT affects productivity gradients along the boreal forest – peatland transitional ecosystems. Thus, the main question of this study is whether we properly understand and model the WT dynamics through the complex soil and topographic gradients along these ecosystems, which is a prerequisite to understanding and modelling their productivity gradients in subsequent studies. Before addressing the main question though, we review the emerging knowledge of their significance.

1.1. Boreal ecotone between upland forest and peatlands

The limited research conducted so far in these ecotone ecosystems was mostly caused by uncertainty in considering them

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as forests or peatlands with their distinct tree components and thin organic layers towards the forest margins, and their markedly declining productivities and deep peat towards the peatland margins. The transitional nature of these ecosystems has been recognized since the beginning of the XX century in Scandinavia (Korpela and Rainikainen, 1996a,b) as in different national peatland classifications they were described as "mire margin forests", "forested mires", "moist forests" or "swamps" (Locky et al., 2005). Recently, Bauer et al. (2009) described boreal transition zones in Canada as "peat margin swamps", based on the "swamp" definition in Canadian System of Wetland Classification stating that "swamp is a wetland influenced by minerotrophic groundwater and dominated by tall woody vegetation" (Warner and Rubec, 1997). Furthermore, Bauer et al. (2009) discriminated between "dry" and "wet" parts of the peat margin swamps, respectively towards their forest and peatland margins.

Even though these transitional ecosystems could be classified as peatlands with organic layers often >40 cm deep, they do not fit comfortably into "swamp" or another recognized wetland category (National Wetlands Working Group, 1997) with their hybrid nature of conduits for fluxes of material and energy between different systems (Ewel et al., 2001). Instead, we refer them as transition zones with pronounced gradients of productivity, peat-mineral soil profiles and WT depths that exist between rarely flooded (unlike many swamps), extremely productive forest margins (often more productive than adjacent upland forests) and well-waterlogged peatland margins (Webster et al., 2008a,b; Bhatti et al., 2006; Hartshorn et al., 2003). We also refer them as ecotone ecosystems with associated gradients in bryophyte community structure from brown and feather mosses to *Sphagnum* mosses (Yarrow and Marín, 2007).

Geographical importance of boreal transition zones, as common landscape mosaics of peat-upland complexes, can be inferred from the fact that black spruce, their main tree component, is one of the most widely distributed forest types in boreal North America (Longton, 1992), with roughly ~75% of black spruce sites growing on organic layers >40 cm (Halliwell and Apps, 1997), and peatlands covering ~20% of boreal North American landscape (Zoltai et al., 1988). The very few recent pioneering studies in these ecotone ecosystems revealed mainly four types of transition between boreal forests and peatlands in North America, i.e. forest–rich (minerotrophic) fen, forest–poor (acidic) fen, forest–bog, bog–forest, as described in greater detail by Bhatti et al. (2006) and Hartshorn et al. (2003). Forest–rich fen, forest–poor fen and forest–bog transition zones usually follow the main topographic gradient between upland black spruce (*Picea mariana*) or mixed black spruce – tamarack (*Larix lariciana*) stands and lowland forested or open fens and continental bogs. Bog–forest transition zones usually connect raised bogs of mixed stunted conifers at upper topographic locations with black spruce or Sitka spruce (*Picea sitchensis*) stands at lower topographic locations, following the gradient from organic to mineral soils overlain by *Sphagnum* and other peat-forming mosses and ericaceous shrubs.

1.2. Modelling water table dynamics in forest and peatlands

As productivities of peatlands and many forest ecosystems are strongly affected by changes in WT depths, proper modelling of WT dynamics is a prerequisite for reliable estimates of ecosystem productivity and C balance (Grant et al., 2012; Ju et al., 2006). A number of ecosystem models have been developed and applied for forest and peatland ecosystems in recent decades, with different complexity of their hydrological modules (Dimitrov et al., 2011; Ju et al., 2006). Many earlier ecosystem models either do not simulate WT dynamics (Kucharik et al., 2000; Garnier et al., 1997; Haxeltine and Prentice, 1996; Sellers et al., 1996) or require WT as an input to simulate ecosystem productivity and respiration (St-Hilaire et al., 2010; Frolking et al., 2002). Other models simulate WT from balancing simple (1D) hydrological schemes (Kennedy and Price, 2004; Potter et al., 1993; Oostindie and Bronswijk, 1992; Bronswijk, 1988), thereby omitting lateral water fluxes. Recent complex ecohydrological models, such as *ecosys* (Grant et al., 2012; Dimitrov et al., 2010a), BEPS (Sonnentag et al., 2008; Chen et al., 2005, 2007), InTEC (Ju et al., 2006), ORCHIDEE (Krinner et al., 2005), LPJ (Sitch et al., 2003; Prentice et al., 2000), simulate both vertical and lateral water fluxes, and thereby are capable of modelling hillslope WT dynamics based on spatial (3D) hydrological schemes.

1.3. Rationale of modelling water table dynamics along boreal transition zones

In this study we use the model *ecosys*, which couples hydrological to biogeochemical and ecosphysiological mechanisms in ecosystems, in order to simulate dynamically changes in C and energy fluxes through the soil–vegetation–atmosphere continuum by linking WT depth to productivity through O_2 effects on nutrient cycling driven by microbial redox reactions and root uptake (Grant et al., 2012; Dimitrov et al., 2010c, 2011). *Ecosys* has already simulated successfully forest and peatland hydrology at a site scale in the course of the year by simulating near-surface soil water contents (θ) in boreal black spruce site (Grant, 2004) and WT and θ at various depths in northern fens (Grant et al., 2012) and bogs (Dimitrov et al., 2010a). These earlier studies in peatlands demonstrated that seasonal changes in WT at a coupled hummock-hollow terrain could be simulated from water exchanges across the model surface boundary (precipitation vs. evapotranspiration) and lateral subsurface boundaries (discharge vs. recharge), as the lower subsurface boundary is assumed zero for wetlands.

The main objective of this study is to model and better understand the ecotone hydrology. To accomplish this objective, we extended our previous modelling work from a site to a landscape scale by modelling daily and seasonal changes in WT along a transect representing the boreal transition zone between a black spruce upland forest and a lowland poor fen. Unlike the site-scale WT in bogs that are largely independent from watershed hydrology or in fens that are usually focal water-gathering positions for the surrounding watersheds, the WT along transition zones are strongly dependant on watershed hydrology through complex hydraulic gradients acting at their forest and peatland margins (Bauer et al., 2009). Therefore, lateral subsurface boundary conditions need to be well defined in the model to simulate properly WT dynamics along boreal transition zones. Lateral water exchanges in *ecosys* were governed by the depth of and distance to an assumed external WT (WT_{ext}) through recharging/discharging water in/out of the site soil profile when WT at lateral subsurface boundaries moved below/above WT_{ext}. Subsurface water in *ecosys* flows down topographic gradients within the saturated zone of the model transect. Thereby, watershed hydraulic gradients can be created in *ecosys* by allowing the elevations of WT_{ext} at different lateral subsurface boundaries to vary with their topographic positions. We hypothesize that these different WT_{ext} elevations, which may be set from hydrological characteristics of the watershed independently of the model, together with surface boundary conditions can simulate and explain seasonal and interannual variability of WT at the different landscape topographic positions with different organic–mineral soil profiles, during alternating hydrologically diverse years.

2. Methods

2.1. Model overview, simulating water table dynamics in context of simulated hydrology

Ecosys has been applied to various ecosystems (in North America and world-wide), such as forests (Grant et al., 2007a,b, 2009; Grant, 2004), grasslands (Grant and Flanagan, 2007), tundra (Grant et al., 2011), crops (Grant et al., 1999, 2004) and peatlands (Grant et al., 2012; Dimitrov et al., 2010a,b,c, 2011). Attached Supplementary material summarizes algorithms and equations for modelling hydrology and WT, heat, gas and solute fluxes, gross primary productivity (GPP), autotrophic respiration (R_a), plant water relations, heterotrophic respiration (R_h) and nutrient transformations, solved from hourly changes in atmospheric boundary conditions, i.e. incoming shortwave radiation, air temperature, relative humidity, wind speed and precipitation (rain, snow), provided as model input to drive *ecosys*. Here we consider only the key *ecosys* algorithms and equations for hydrology and WT, provided in the text below and referred with their original numbers in the Supplementary material; those for hydrological effects on soil O_2 availability, nutrient transformations and uptake, and ecosystem productivity modelled along the ecotone are considered in a related study (submitted manuscript ECOMOD-13-538).

Simulated WT depth is calculated at the top of the saturated zone in each landscape position, below which air-filled porosity is zero through the rest of the soil profile. This WT depth arises from influxes vs. effluxes of water in vertical and lateral directions within the landscape and through surface and subsurface landscape boundaries of one-, two- or three-dimensions (Grant et al., 2012) and is calculated as follows:

$$d_{WT} = d_l - t_l\left(1 - \frac{\theta_{g,l}}{\theta^*_{g,l}}\right) \tag{D8b}$$

where d_{WT} (m) is WT depth below the soil surface, d_l (m) is the depth to the bottom of soil layer l immediately above the uppermost saturated layer in the simulated soil profile, t_l (m) is the thickness of soil layer l, $\theta_{g.l}$ ($m^3\,m^{-3}$) is the current air-filled porosity of soil layer l calculated as a difference between its total porosity and its water and ice contents, and $\theta^*_{g.l}$ ($m^3\,m^{-3}$) is the air-filled porosity of soil layer l at its air-entry water potential. In this way, $d_{WT} \to d_l - t_l$, i.e. the top of layer l, when $\theta_{g,l} \to 0$, and $d_{WT} \to d_l$, i.e. the bottom of layer l, when $\theta_{g,l} \to \theta^*_{g,l}$. When $\theta_{g,l} = 0$, d_{WT} moves into layer $l-1$ and when $\theta_{g,l} > \theta^*_{g,l}$, d_{WT} moves into layer $l+1$. Since WT is usually referred as either WT depth below the soil surface, or WT elevation above an arbitrary datum in soil (Ingram, 1983), the terminology such as WT increase/decrease may have an opposite meaning in each of these cases. To reconcile that we use hereafter negative values for WT depth indicating below soil surface. Thus, changes of WT depths and WT elevations follow the same direction to/from the soil surface/arbitrary datum.

Surface boundary influxes of water are given by precipitation provided as model input. Precipitation enters *ecosys* soil profile either as rain or after simulated snow melt calculated in the snowpack from the general heat flux equation [D13]. Surface boundary effluxes of water are calculated from transpiration [Eq. B1] and evaporation [Eq. D6], driven by energy balances for canopy, snow, surface litter and soil surfaces, and coupled with subsurface water transfers through roots [Eq. B5] and through snowpack, surface litter and soil [Eq. D7]. Surface influxes and effluxes drive water runoff along the landscape surface according to kinematic wave theory [Eqs. D1–D5], and vertical and lateral subsurface water fluxes [Eq. D7] within and among the landscape soil profiles, according to soil hydraulic properties [Eq. D9] and boundary conditions [Eqs. D7, D10]. Subsurface water fluxes are calculated between both micropore and macropore fractions of adjacent soil cells (which lined in parallel to the landscape surface constitute soil layers) in x (east-west), y (north-south) and z (vertical) directions. Micropore fluxes in each direction are driven by soil water potential gradients (matric, osmotic, gravimetric) between source and target cells, constrained by their hydraulic conductivities:

$$Q_{w,i} = K'_i \Delta_i \Psi s, \quad i = x, y, z \tag{D7}$$

where Q_w ($m^3\,m^{-2}\,h^{-1}$) are soil water fluxes, $\Delta\psi_s$ (MPa) are soil water potential differences and K' ($m\,MPa^{-1}\,h^{-1}$) are hydraulic conductances in x, y and z directions. Depending on saturation status of source and target cells, micropore fluxes are calculated from either 3D Richard's or Green–Ampt equations. Macropore fluxes, especially important for the upper peat, are calculated from a 3D Hagen–Poisseuille equation (Dimitrov et al., 2010a).

Hydraulic conductances K' between source and target cells are calculated as geometric means from their hydraulic conductivities, in each direction respectively:

$$K'_i = \frac{2K_{S,i}K_{T,i}}{K_{S,i}L_{T,i} + K_{T,i}L_{S,i}}, \quad i = x, y, z \tag{D9}$$

where K_S and K_T ($m^2\,MPa^{-1}\,h^{-1}$) are hydraulic conductivities, and L_S and L_T (m) are lengths of source and target cells, respectively, in x, y and z directions. For each cell, K is calculated from θ by Green and Corey $K-\theta$ functions with soil-specific saturated K (K_s) that may differ in horizontal and vertical directions, and ψ_s is calculated from Brooks and Corey water retention curves defined by input values of ψ_s and θ at field capacity and wilting point. Thus, changes of θ in each grid cell result from summation of all incoming and outgoing water fluxes, as follows:

$$\frac{\Delta\theta_{S,i}}{\Delta t} = \frac{\left(\sum_i \Delta Q_{w,i} + \Delta Q_f\right)}{L_{S,i}}, \quad i = x, y, z \tag{D8a}$$

where $\Delta\theta_S$ ($m^3\,m^{-3}$) is the water content difference, Δt (h) is the time step, ΔQ_w ($m^3\,m^{-2}\,h^{-1}$) are differences between incoming and outgoing water fluxes, Q_f ($m^3\,m^{-2}\,h^{-1}$) is the freeze-thaw flux, and L_S (m) are cell spatial dimensions in x, y and z directions. Changes of θ determine changes of θ_{air}, hence simulated WT dynamics [Eq. D8b] as described above.

Boundary conditions govern vertical influxes/effluxes, thereby WT in the model [Eq. D8a,b], by setting permeability of the lower subsurface boundary (usually assumed zero for wetlands) and lateral influxes/effluxes by setting distances to and depths of WT_{ext} at lateral subsurface boundaries:

$$Q_{l,i} = K_b \frac{[\psi' - \psi_{s,l} + 0.01(d_l - d_{t,i})]}{(0.5L_{b,i} + L_{t,i})}, \quad i = x, y \tag{D10}$$

where Q_l ($m^3\,m^{-2}\,h^{-1}$) are water fluxes between the boundary grid cell in which the WT is located and WT_{ext}, K_b ($m^2\,MPa^{-1}\,h^{-1}$), $\psi_{s,l}$ (MPa) and d_l (m) are respectively the lateral hydraulic conductivity, the soil water potential and the depth of the boundary grid cell in which the WT is located, ψ' (MPa) is soil water potential at saturation, $d_{t,i}$ (m) is the depth of WT_{ext}, and $L_{b,i}$ and $L_{t,i}$ (m) are respectively the horizontal dimensions of the boundary grid cell in which the WT is located, and the horizontal distances to WT_{ext} in x and y directions. The $d_{t,i}$ and $L_{t,i}$ of the WT_{ext} are set to represent watershed hydraulic gradients across simulated landscapes in northern, eastern, southern and western directions. These gradients drive recharge/discharge of water when modelled WT at each lateral subsurface boundary moves below/above its WT_{ext} [Eq. D10]. Simulated WT within the landscape soil profile thereby responds to differences in rates of surface water exchange (precipitation vs. evapotranspiration) vs. those of lateral discharge/recharge governed by WT_{ext}.

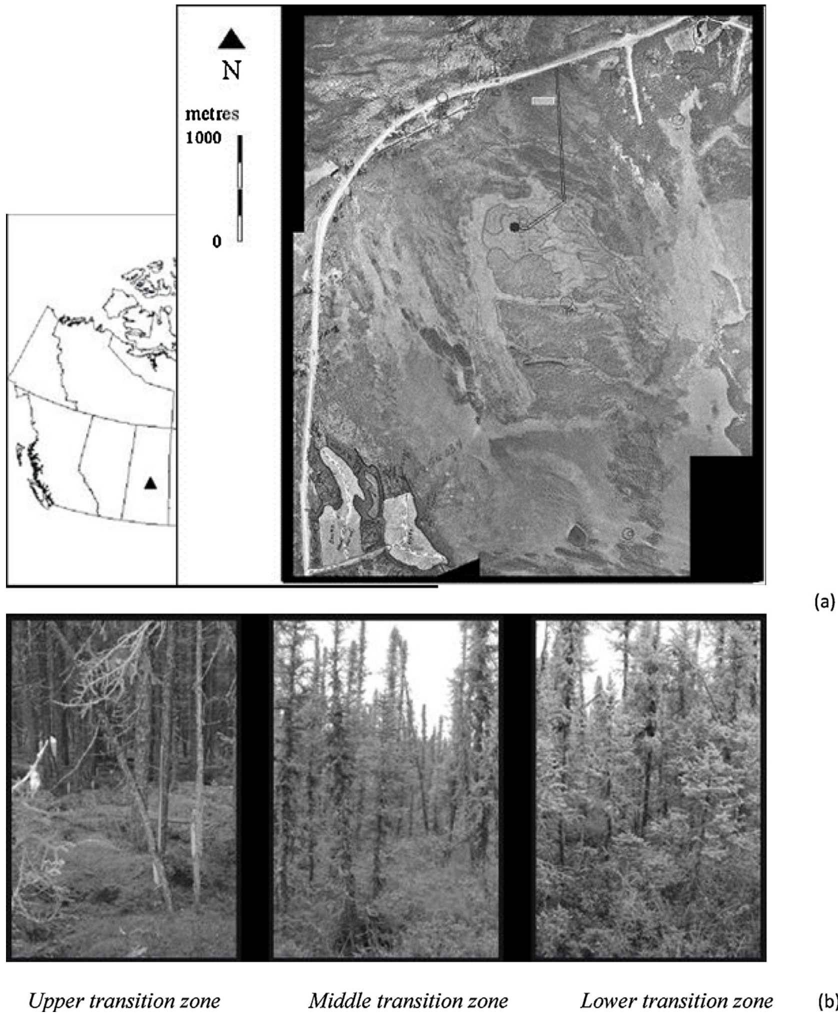


Fig. 1. Location of the study area, marked by a black triangle, in central Saskatchewan, Canada, and location of the Old Black Spruce Fen (OBSF) transition zone, marked by a light rectangle, within the local watershed area of the Old Black Spruce site (OBS), marked by a black circle (a). Declining tree biomass and height from the upper (close to the forest) down the lower (close to the peatland) positions of the OBSF transition zone (b).

Simulated WT is also affected by soil freezing/thawing, driven by simulated conductive–convective heat flux through the ground surface (soil surface, litter or snow layer, depending on exposure) solved from surface energy balance closure [Eq. D11] and the general heat flux equation [D13]. This flux, together with conductive–convective heat fluxes through the lower and lateral subsurface model boundaries, drive the 3D conductive–convective soil heat fluxes ($G_{x,y,z}$) among adjacent model cells in x, y and z directions [Eq. D12] (Dimitrov et al., 2010b; Grant et al., 1990). These fluxes drive changes in soil temperatures, and hence freezing/thawing in each cell. Freezing acts to transform soil water to ice, lowering ψ_s [Eqs. D7 and D8a] and thereby drawing more water towards the freezing zone, hence lowering simulated WT [Eq. D8b]. Conversely, thawing acts to transform soil ice to water, rising ψ_s and eventually WT. Explicit modelling of WT provides another opportunity, in addition to simulating θ at various depths, to test how well *ecosys* models ecosystem hydrology.

2.2. Site conditions

Our study site (53°59′54″ N, 105°6′55″ W) is the Old Black Spruce Fen (OBSF), described in detail in Bhatti et al. (2006) and located in southern BOREAS (Boreal Ecosystem-Atmosphere Study) and BERMS (Boreal Ecosystem Research and Monitoring Sites) study areas of central Saskatchewan, approximately 100 km northeast of Prince Albert (Fig. 1a). The region is a mosaic of boreal forests and some peatlands overlying Luvisolic, Brunisolic, Regosolic or Organic soils on fine sandy loams (Anderson, 1998; Acton et al., 1990).

Despite its name, OBSF is in fact a transition zone ~200 m long between upland boreal black spruce forest to the west and a poor treed fen lower in elevation by ~2.5 m to the east, with markedly declining biomass and height of black spruce trees towards the fen and well developed bryophyte cover along all its length (Fig. 1b). The site has a predominantly eastern aspect and negligible north-to-south elevation differences. The forest margin of the site is approximately 1 km from the BOREAS Southern Old Black Spruce (SOBS) flux tower site (Gower et al., 1997) and the peatland margin is near White Swan Lake. Annual and growing season precipitation and average air temperatures measured for 1994–2008 at the SOBS flux tower are stated in Table 1, with their averages for the entire period. The ecotone follows a soil gradient of deepening peat, starting from ~60 cm thickness at the forest margin and accumulating to ~160 cm at the fen margin, overlying fine sandy loams. Local hummock–hollow microtopography is negligible, with differences between hummock and hollow surfaces <5 cm towards the forest margin and <10 cm towards the fen margin, suggesting a uniform soil surface along the ecotone. WT often drops lower than

Table 1
Annual and growing season (June 1–September 30) precipitation and average air temperatures (T_{air}), measured at the Southern Old Black Spruce flux tower during 1994–2008 and their averages for the entire period.

Years	Annual precipitation (mm)	Annual average, T_{air} (°C)	Growing season precipitation (mm)	Growing season average, T_{air} (°C)
1994	436	0.4	251	13.6
1995	445	0.2	234	13.6
1996	565	−1.0	343	12.8
1997	485	2.3	258	14.5
1998	486	2.1	296	14.9
1999	438	2.6	290	13.2
2000	489	1.1	359	12.4
2001	264	2.8	142	14.5
2002	369	0.1	240	13.0
2003	313	1.1	212	14.1
2004	780	−0.2	543	11.0
2005	598	1.8	441	12.8
2006	646	2.4	488	14.2
2007	500	0.8	328	13.0
2008	414	0.2	247	13.4
1994–2008	482	1.1	312	13.4

80 cm below local (hummock) surface towards the forest margin and rises along the transition zone higher than 20 cm below local (hummock) surface towards the fen margin.

2.3. Field measurements for model running and testing

To drive *ecosys*, half-hourly continuous measurements were provided from 1994 to 2008 for incoming shortwave radiation ($W\,m^{-2}$), air temperature (°C), relative humidity (%), wind speed ($m\,s^{-1}$), and precipitation (mm), measured 2 m above the canopy at the SOBS flux tower site (fluxnet.ccrp.ec.gc.ca/MeasuredData/SK-OldBlackSpruce/Meteorology). Missing records in the model drivers were substituted by corresponding values recorded at the nearest Waskesiu Lake weather station (53°55′ N, 106°4′ W) for long time intervals (more than a few days), by values in nearby or corresponding periods for short time intervals (up to a few days), or interpolated from the adjacent values for very short time intervals (a few hours). The winter precipitation for the days with snow was calculated from positive increments of snow depth, corrected by an assumed snow bulk density of $0.11\,Mg\,m^{-3}$.

WT depths during 2003–2005 were measured daily below the hummock surface at 4 approximately equidistant topographic positions along a ~200 m long field transect at OBSF from the upland black spruce forest in the west down to the poor fen in the east. Also, at each topographic position, peat depth was measured and samples were analyzed for soil bulk density and water contents at field capacity and wilting point from fibric and deep peat, and from upper and lower mineral soil. Bhatti et al. (2006) described in detail all site measurements at OBSF.

2.4. Model experiment: simulating a boreal transition zone

To simulate the OBSF transition zone a model transect of 6 topographic positions, each with surface dimensions 48 m by 48 m, was designed to represent the site's west-to-east slope of 0.7° and north-to-south slope of 0°, according to the field bearings. These topographic positions represented from west to east the upland boreal forest, forest margin, upper mid-transition, lower mid-transition, fen margin, and lowland fen (Fig. 2a). The upland forest and lowland fen positions were used as transect boundaries so that simulated WT depth in the forest margin, upper and lower mid-transitions and fen margin were not directly affected by uncertainties of water exchanges through model boundaries at the upper and lower ends of the landscape slope.

The 4 internal topographic positions of the model transect corresponded to the 4 topographic positions of the field transect from the forest margin through upper and lower mid-transitions, to the fen margin (Bhatti et al., 2006). Elevations of the mid-point in each topographic position were calculated from the 0.7° transect slope and horizontal lengths of the positions (Fig. 2a). The WT depth at the upper mid-transition in the model (Fig. 2a), even though part of simulations, was not used in model-data comparisons due to an unexplained rise of measured WT depth at the corresponding upper mid-transition position in the field. This rise might have been caused either by unknown, local subsurface pathways of soil water or eventual device malfunction. Thus, hereafter we consider only the lower mid-transition positions in the model and in the field as representative for ecotone mid-transition.

The soil profile at each topographic position in the model consisted of 20 model cells, interconnected horizontally to those in adjacent positions in soil layers, and vertically to those within each position according to the ecotone's organic–mineral soil gradient (Fig. 2b). Soil layers of the forest margin, mid-transition and fen margin in the model were parameterized with hydrological properties at the corresponding positions and depths in the field transect. Hydrological properties of soil profiles at the forest margin, mid-transition and fen margin in the model are averaged in Table 2 by depth intervals of fibric and deep peat, and upper and deep mineral soil. Soil layers of upland forest and lowland fen were parameterized identically to the corresponding soil layers of forest margin and fen margin, respectively. The soil properties required by *ecosys* but not measured at the OBSF site were assigned from literature reports for the Cumic Humic Regosol at the nearby SOBS site (Anderson, 1998) and other poor peatlands (Dimitrov et al., 2010a,b), as shown in Table 2. Simulated water, heat, gas and solute fluxes were allowed only through the western boundary at the upland forest and eastern boundary at the lowland fen as all north and south subsurface boundaries were closed, following the site's main west-to-east slope and negligible north-to-south slope.

In earlier site-scale model runs, WT_{ext} was set as a single value by which recharge/discharge was governed for a single topographic position. To simulate recharge/discharge in landscape-scale model runs with topographic positions at different elevations, we ran *ecosys* with $WT_{ext,W}$ set at 62.5 cm below the soil surface of upland forest at the western end of the landscape, and with $WT_{ext,E}$ set at 50 cm below the soil surface of lowland fen at the eastern end of the landscape. Water therefore flowed through the saturated zone of the landscape towards the fen following an elevation gradient in WT depth. The $WT_{ext,E}$ was consistent with the average fen WT depth measured in October 2003 just before the winter soil freeze started. Partially following the local landscape topography, $WT_{ext,W}$ was interpolated from $WT_{ext,E}$ and the average WT depth of 110 cm

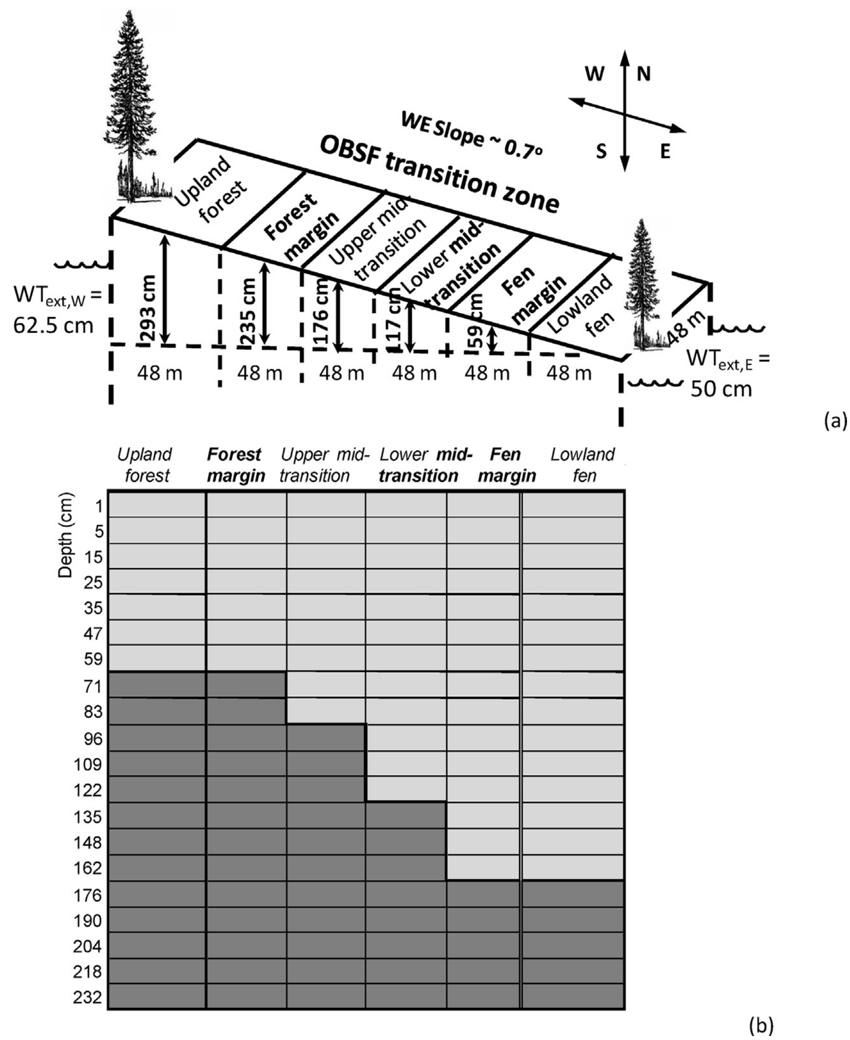


Fig. 2. *Ecosys* landscape transect, representing the Old Black Spruce Fen (OBSF) boreal transition zone (ecotone), consisting of six topographic positions, i.e. upper boundary (upland forest), upper ecotone (forest margin), middle ecotone (upper and lower mid-transition), lower ecotone (fen margin) and lower boundary (lowland fen) with local elevations between them and external water tables at western and eastern model boundaries, $WT_{ext,W}$ and $WT_{ext,E}$, used to model the watershed hydraulic gradients along the main WE slope of the landscape transect (a). *Ecosys* soil profile associated with the six topographic positions, with twenty horizontal soil layers, consisting of horizontally and vertically interconnected model cells of peat (light grey) or mineral soil (dark grey), simulating organic–mineral soil gradient along the OBSF ecotone (b).

measured in October 2003 at the nearby SOBS site (Ju et al., 2006), located higher than OBSF in the watershed (Fig. 1a). Given the elevational difference between the upland forest and the lowland fen, $WT_{ext,W}$ was higher by elevation, even though deeper with respect to the local soil surface, than $WT_{ext,E}$ (Fig. 2a) Both $WT_{ext,W}$ and $WT_{ext,E}$ were set at 1 m from the western and eastern lateral boundaries, respectively, assuming that water exchange was governed by water tables adjacent to the boundaries. The model run was initialized with biological properties of black spruce and moss (Grant, 2004; Grant et al., 2009), and spun up for 106 years repeating 7 times the 15-year available weather period from 1994 to 2008, following a year of simulated planting. This period allowed CO_2 exchange in the model to achieve stable values through successive weather sequences, as defined in Grant et al. (2012).

2.5. Model testing: corroborating hypotheses

To test our hypotheses, simulated daily WT depths along the simulated transition zone transect were compared at the forest margin, mid-transition and fen margin with those measured during the very dry year 2003 with well drained peat after a drought that had started in 2001, the very wet and cool year 2004 with the largest annual rainfall and the 2nd lowest mean annual air temperature in 1994–2008 period, and the hydrologically average year 2005 (Table 1). To evaluate goodness of fit, observed WT depths were plotted vs. simulated ones on observed: expected (obs:exp) plots with fitted and 1:1 lines for each ecotone position during the entire 2003–2005 period and for each year along the entire transect, all plots created in Microsoft Excel. Coefficients of determination (R^2) and slopes of fitted lines indicated how many observations the model managed to explain and how well when compared to 1:1 lines. To investigate the relative impact on simulated landscape WT of uncertainty in evaluating boundary hydrolocical gradients, the obs:exp plot for the entire ecotone during 2003–2005 with $WT_{ext,W} = -62.5$ cm, interpolated for the watershed, was compared vs. a corresponding obs:exp plot with $WT_{ext,W} = -50$ cm, the average observed WT at the upper ecotone boundary during 2003–2005.

3. Results

Changes in surface water exchange under contrasting precipitation from 2003 to 2005 and lateral hydraulic gradients $WT_{ext,W}$ and $WT_{ext,E}$ in the model (Fig. 2a) caused changes in simulated WT

Table 2
Hydrological and biological soil properties used to parameterize *ecosys*, averaged for fibric and deep (hemic, sapric) peat, and upper and lower mineral soil at the upper (forest margin), middle (mid-transition) and lower (fen margin) positions of the Old Black Spruce Fen (OBSF) transition zone. $K_{s,v}$ and $K_{s,h}$ are vertical and horizontal saturated hydraulic conductivities of soil matrix, θ_{FC} and θ_{WP} are soil water contents at field capacity (−0.03 MPa) and wilting point (−1.5 MPa), C, N, P are carbon, nitrogen, phosphorus. Peat properties measured or derived from measured at the OBSF site are marked by asterisk; the rest of the peat properties and mineral soil properties are assigned from literature reports for other poor peatlands (Dimitrov et al., 2010a,b) and for Cumic Humic Regosol at the SOBS site (Anderson, 1998).

Soil properties (units)	Forest margin				Mid-transition				Fen margin			
	Fibric peat 0–25 cm	Deep peat 25–59 cm	Upper mineral 59–83 cm	Lower mineral 83–232 cm	Fibric peat 0–25 cm	Deep peat 25–122 cm	Upper mineral 122–148 cm	Lower mineral 148–232 cm	Fibric peat 0–25 cm	Deep peat 25–162 cm	Upper mineral 162–190 cm	Lower mineral 190–232 cm
Bulk density* (Mg m^{-3})	0.07	0.18	1.59	1.66	0.06	0.13	1.59	1.66	0.06	0.14	1.59	1.66
Total porosity* (m^3 m^{-3})	0.95	0.90	0.40	0.38	0.96	0.92	0.40	0.38	0.96	0.91	0.40	0.38
Macroporosity (m^3 m^{-3})	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0
$K_{s,v}$ (mm h^{-1})	7.2	7.2	48.6	1787.3	75.0	25.0	48.6	1710.0	75.0	25.0	48.6	1636.7
$K_{s,h}$ (mm h^{-1})	36.0	36.0	48.6	1787.3	375.0	125.0	48.6	1710.0	375.0	125.0	48.6	1636.7
θ_{FC}* (m^3 m^{-3})	0.10	0.40	0.20	0.03	0.10	0.40	0.20	0.03	0.10	0.40	0.20	0.02
θ_{WP}* (m^3 m^{-3})	0.05	0.20	0.05	0.01	0.05	0.20	0.05	0.01	0.05	0.20	0.05	0.01

depth [Eq. D8b] at forest margin, mid-transition and fen margin that were tested against field observations. This testing allowed us to investigate simulated deep WT along the boreal transition zone during a dry year 2003 (Fig. 3a–d), followed by WT increases with rewetting during a very wet and cool year 2004 (Fig. 4a–d), and finally shallow WT maintained after wetting during a hydrologically average year 2005 (Fig. 5a–d).

3.1. Modelling water table dynamics in a dry year preceded by a drought

When modelled WT [Eq. D8b] at the upland forest became lower than $WT_{ext,W}$, this topographic position was recharged through its western lateral boundary [Eq. D10], driving subsurface soil water movement down to forest margin, mid-transition, fen margin and lowland fen topographic positions, according to ψ_s (gravimetric and matric) gradients [Eq. D7] and K [Eq. D9a,b]. During the dry year 2003 (Table 1, Fig. 3a), recharge through the western boundary was not sufficiently rapid to maintain simulated WT at the forest margin at levels measured in the field (Fig. 3b). However, subsurface movement from the upper positions raised WT in mid-transition (Fig. 3c), fen margin (Fig. 3d), increasing discharge through the eastern lateral boundary as WT at lowland fen rose with respect to $WT_{ext,E}$. The total water recharge through the western model boundary during 2003 was 54 mm, while the total water discharge through the eastern model boundary was 110 mm, indicating that *ecosys* simulated landscape water fluxes driven by watershed hydraulic gradients down to the fen during the dry 2003.

Seasonal variation in WT was driven by changes in precipitation and thawing at each topographic position. The model captured WT rise measured at the mid-transition and the fen margin following precipitation after the spring thaw (Fig. 3a) that commenced on DOY 109 at mid-transition and on DOY 98 at fen margin (Fig. 3c and d). Both simulated and measured WT at the mid-transition and the fen margin remained high during the rainy period ∼DOY 135–200, then declined to ∼DOY 250 with increasing ET and with decreasing precipitation and discharge while simulated WT at the eastern boundary approached down to $WT_{ext,E}$ [Eq. D10]. Thereafter, simulated and measured WT at all the positions declined slowly until the end of the year with declining lateral hydraulic gradients modelled while WT at lowland fen approached further down and close to $WT_{ext,E}$ (Fig. 3a, c and d).

3.2. Modelling water table dynamics in a very wet year following a dry year

During the very wet year 2004 (Table 1, Fig. 4a), the entire peat profile was refilled (Fig. 4b–d) by the extreme precipitation through the surface boundary and subsurface water recharge through the western lateral boundary while WT at the upland forest position was still lower than $WT_{ext,W}$ after the 2001–2003 drought. Thus, simulated WT [Eq. D8b] rose at the forest margin from below 80 cm, consistent with measurements for DOY 105–118, to above 40 cm during simulated spring thaw in ∼DOY 145–160, then closely followed the measured WT for the rest of the year (Fig. 4b). Similarly to that at the forest margin, simulated WT at mid-transition and fen margin followed closely general rise in measured WT (Fig. 4c and d) with heavier precipitation (Fig. 4a) after simulated spring thaw in ∼DOY 140–160. During DOY 101–201, both measured and simulated WT rise of ∼400 mm at forest margin (Fig. 4b) was more than the water column of 360 mm, arising from 263.5 mm precipitation entering the soil with bulk density of the 40–80 cm depth interval (Table 2) minus simulated evapotranspiration losses of 159.7 mm. Thereby, precipitation alone was unable to explain the WT rise during that period and the difference of ∼40 mm (=400–360 mm)

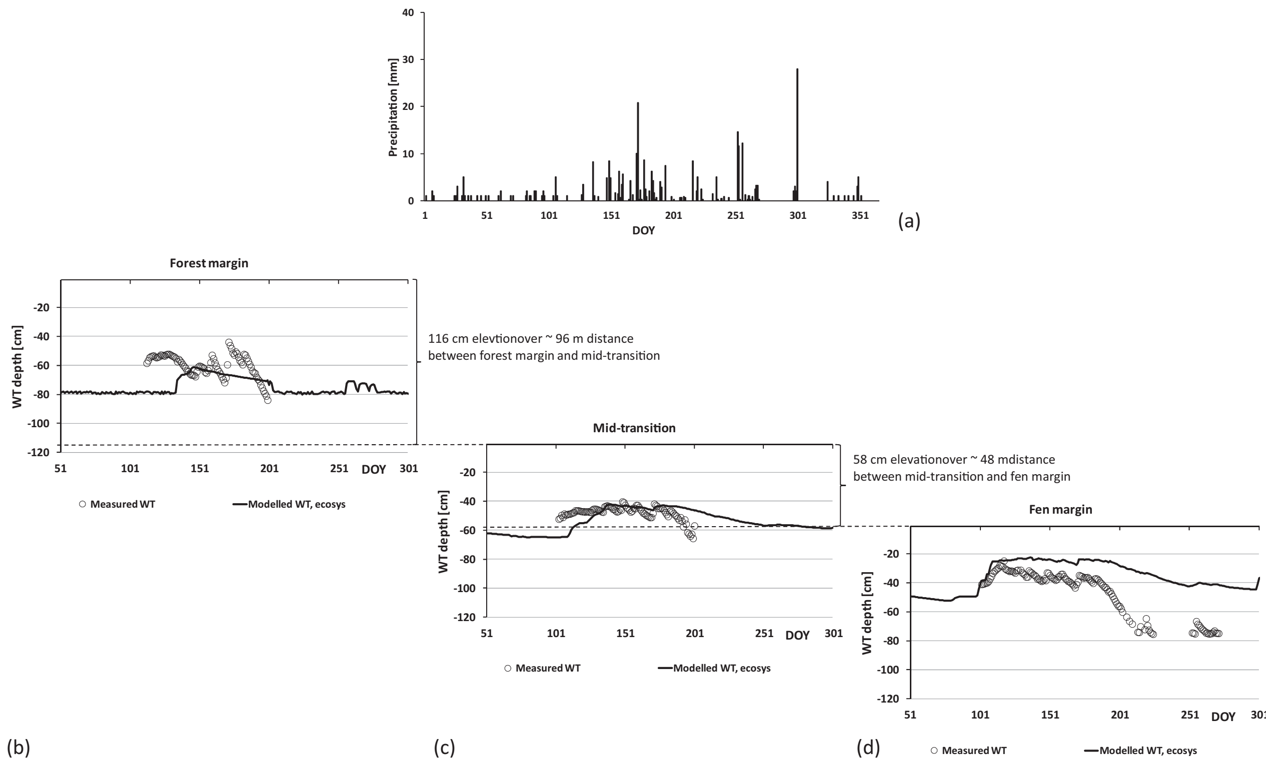


Fig. 3. Daily precipitation at Old Black Spruce Fen (OBSF) transition zone (a), modelled vs. measured daily water table (WT) at OBSF upper (forest margin) (b), middle (mid-transition) (c), and lower (fen margin) (d) positions, with terrain elevations and distances between them, during the dry year 2003; DOY is day of year.

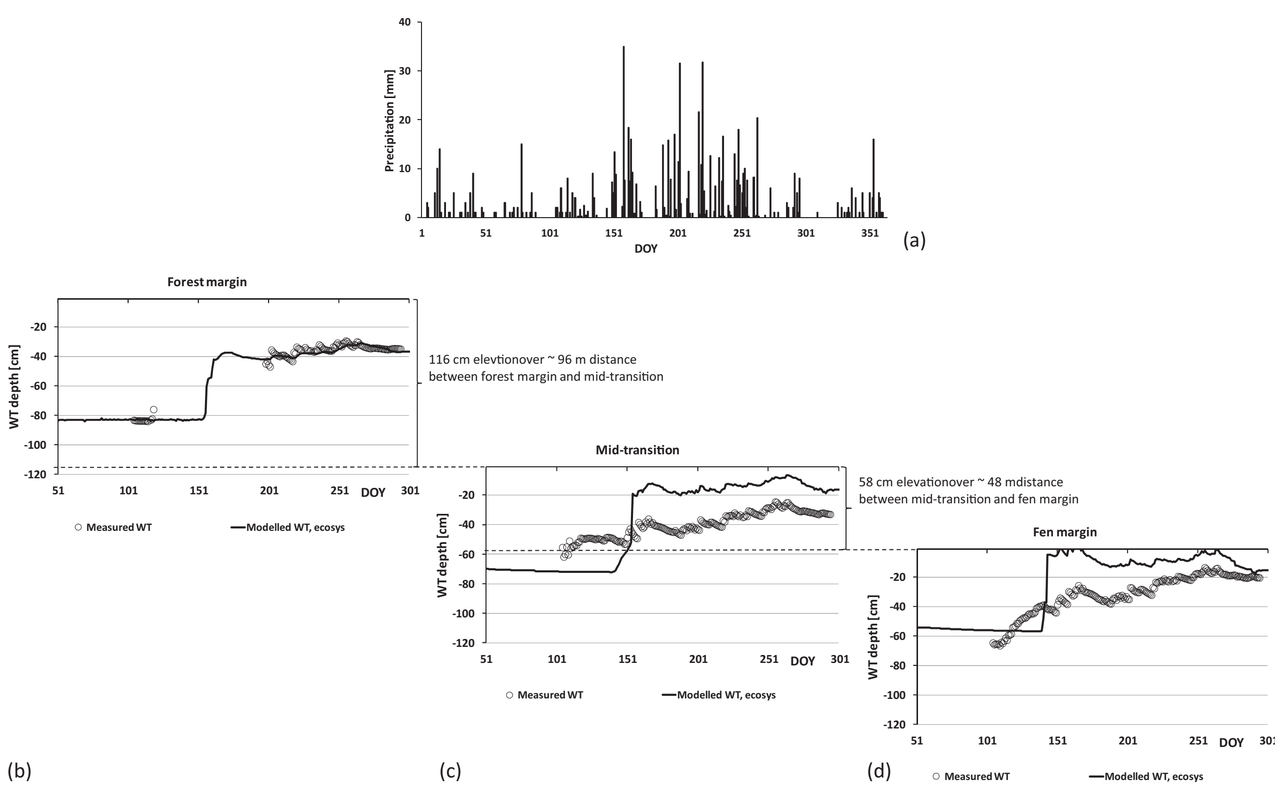


Fig. 4. Daily precipitation at Old Black Spruce Fen (OBSF) transition zone (a), modelled vs. measured daily water table (WT) at OBSF upper (forest margin) (b), middle (mid-transition) (c), and lower (fen margin) (d) positions, with terrain elevations and distances between them, during the very wet year 2004; DOY is day of year.

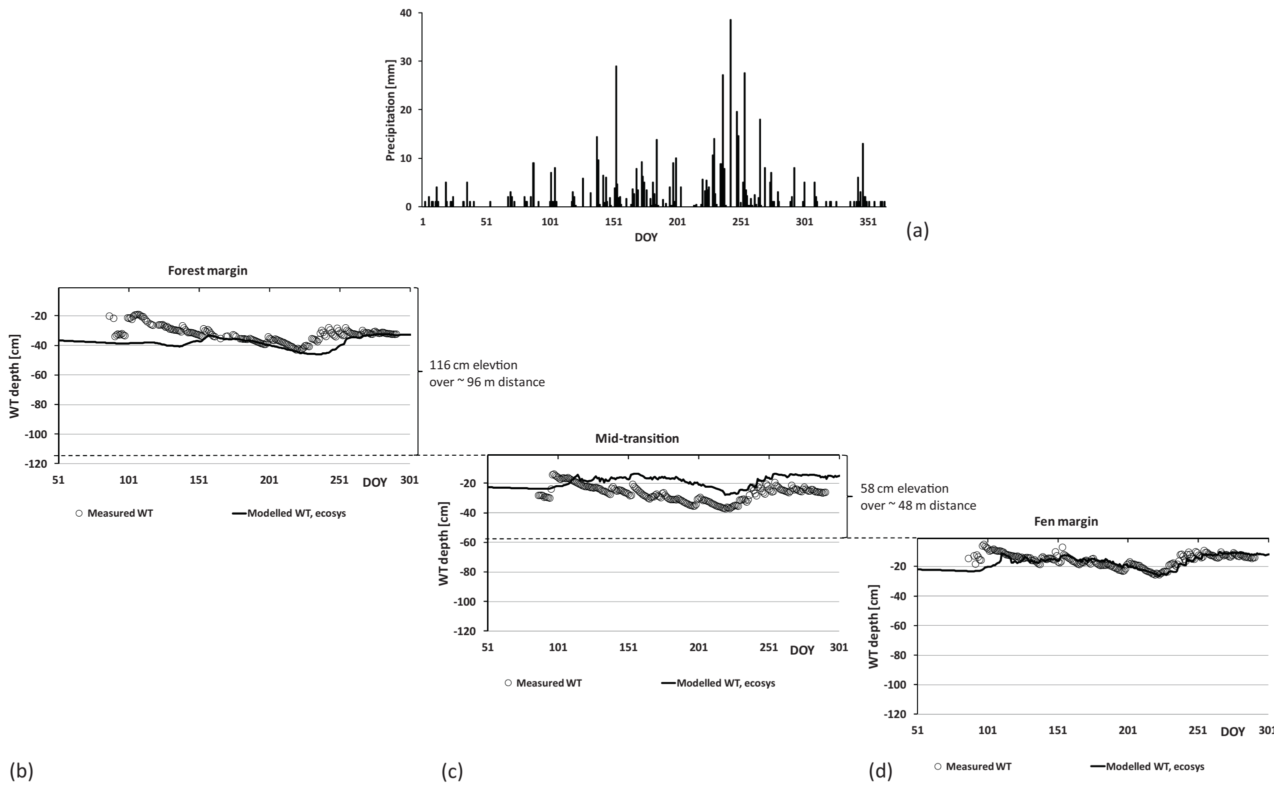


Fig. 5. Daily precipitation at Old Black Spruce Fen (OBSF) transition zone (a), modelled vs. measured daily water table (WT) at OBSF upper (forest margin) (b), middle (mid-transition) (c), and lower (fen margin) (d) positions, with terrain elevations and distances between them, during the hydrologically average year 2005; DOY is day of year.

indicated the importance of lateral boundary conditions, representing the watershed hydraulic gradients in the model, for proper recharge and WT simulations. General inability of *ecosys* to simulate properly WT rise during the spring thaw at mid-transition (Fig. 4c) and fen margin (Fig. 4d) was due to erroneous detection of saturated soil in the freezing zone, in result of capillary rise from deeper soil drawn by declining ψ_s towards the freezing front, as a perched WT (Grant et al., 2012), above the basal WT calculated according to the algorithms described in Section 2.1.

Excessive precipitation in 2004 caused rapid rise of simulated WT at the upland forest towards $WT_{ext,W}$ so that the total water recharge through the western boundary was only 19 mm, much less than that in 2003. Subsurface soil water movement down the simulated landscape topography resulted in high WT at the lowland fen that was above $WT_{ext,E}$, forcing total water discharge through the eastern model boundary of 306 mm, much more than in 2003. The net water discharge of 287 mm indicated that *ecosys* simulated landscape water fluxes driven by watershed hydraulic gradients down to the fen in the very wet 2004.

3.3. Modelling water table dynamics in a hydrologically average year following a very wet year

Once the soil profiles of topographic positions along the landscape transect were refilled in very wet 2004, simulated WT followed closely measured WT at the forest margin (Fig. 5b), mid-transition (Fig. 5c) and fen margin (Fig. 5d), driven by incoming precipitation during the hydrologically average year 2005 (Table 1, Fig. 5a). Consistent with field observations, simulated WT [Eq. D8b] at the three positions rose with the rainfall event sequence peaking up to DOY 151, then declined with declining precipitation pattern up to ~DOY 225, after which rose again with increasing rainfall pattern during DOY 225–253, and remained high with declining but still heavy rainfall up to DOY 310. The total water recharge through the western model boundary was only 71 mm, less than in 2003 and 2004, due to rather high WT maintained in 2004 and 2005 with respect to $WT_{ext,W}$. Even though precipitation in 2005 was less than in 2004 (Table 1), the total water discharge through the eastern model boundary was 335 mm, greater than in 2004, when lots of incoming water was retained to refill the peat after the 2001–2003 drought. The net water discharge of 331 mm showed that *ecosys* simulated landscape water fluxes driven by watershed hydraulic gradients down to the fen in hydrologically average 2005.

3.4. Goodness of fit of modelled water table along the boreal transition zone

Obs:exp plots for measured vs. simulated daily WT indicated that *ecosys* reproduced the seasonal dynamics of WT at different topographic positions under diverse weather conditions (Figs. 6a–c, 7a–c and 8a). Slope → 1 for all the three positions in hydrologically average 2005 compared to slopes in dry 2003 and wet 2004 (Fig. 6a–c) suggested that *ecosys* performed well for hydrologically moderate years, such as most of the years within the available weather period (Table 1). R^2 for 2005 was higher than R^2 for 2003, but slightly lower than R^2 for 2004 (Fig. 6a–c), which could be attributed to possible greater variability with extreme precipitation in 2004 associated with greater WT variation. Also, we found that *ecosys* performed best on forest margin, followed by mid-transition and worse on fen margin (Fig. 7a–c), possibly due to some cumulative uncertainty of drainage through the transect and out of the lower fen boundary. R^2 and slope of the obs:exp plot for the entire ecotone in 2003–2005 with $WT_{ext,W}$ = −62.5 cm, interpolated for the watershed (Fig. 8a), were similar to those of

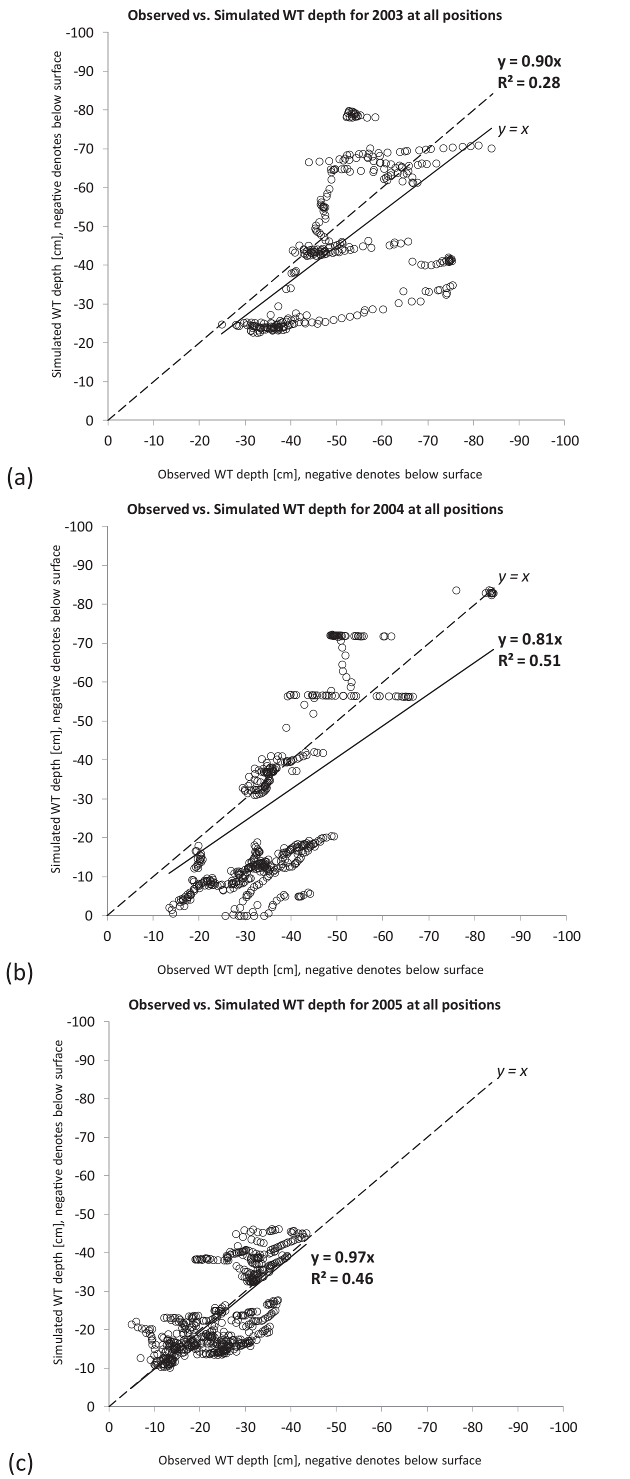


Fig. 6. Observed:expected (obs:exp) plot for measured vs. simulated daily water table (WT) for combined positions of forest margin, mid-transition and fen margin of Old Black Spruce Fen (OBSF) transition zone during the very dry year 2003 (a), the very wet year 2004 (b), and hydrologically average year 2005 (c). Both simulated and measured WT are in negative values, indicating their positions below soil surface.

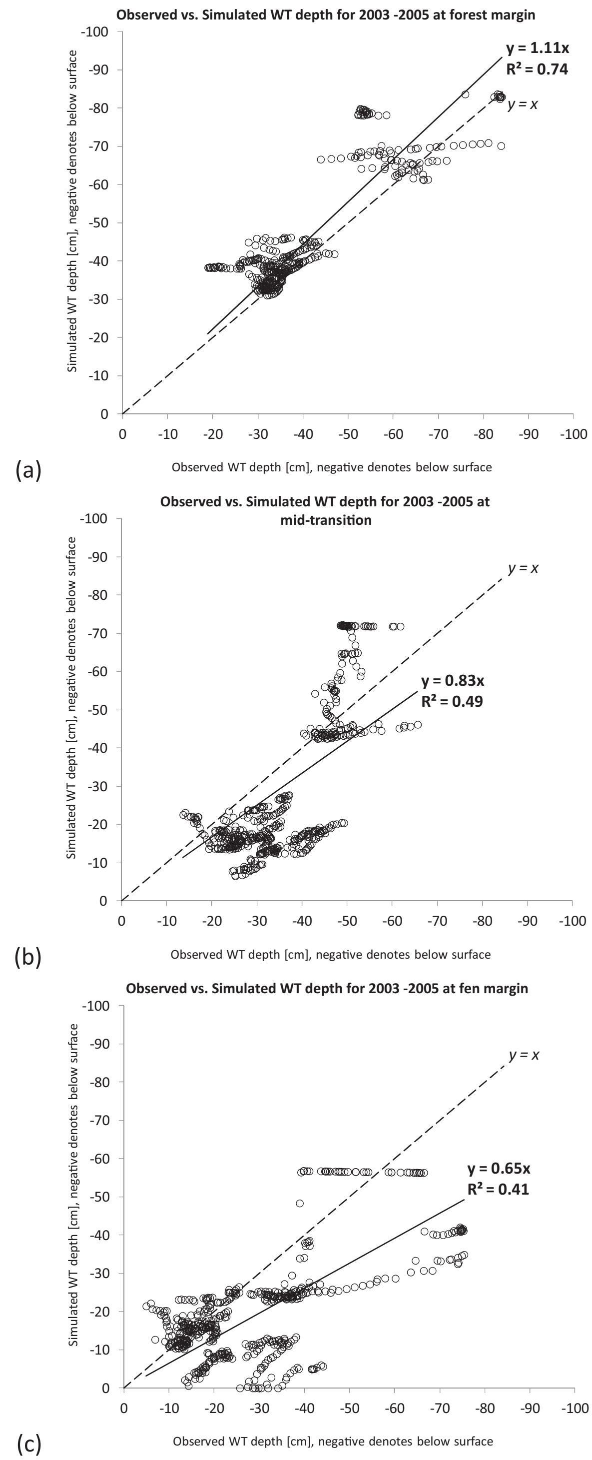
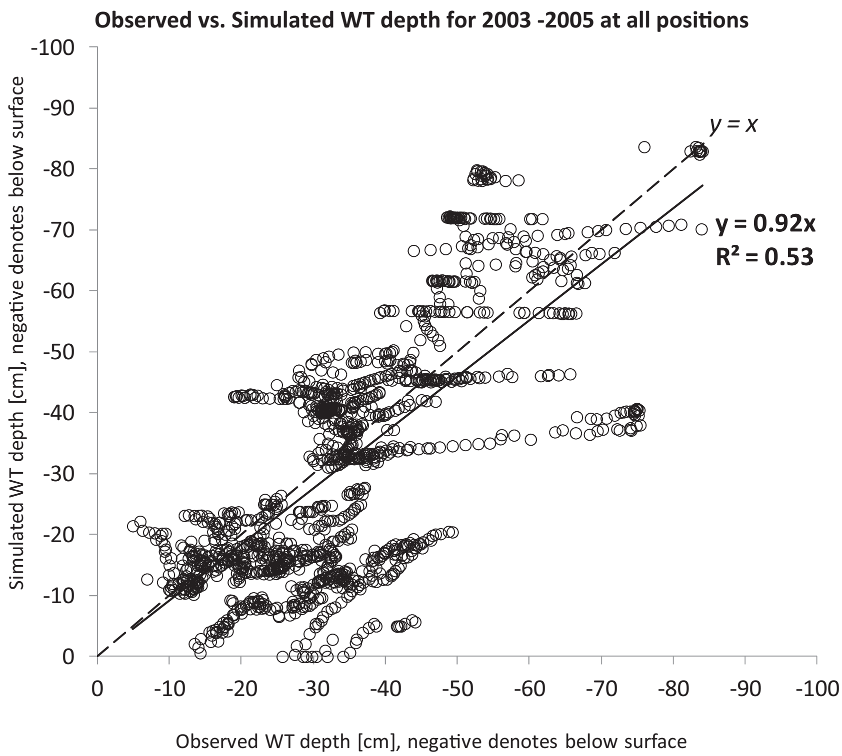


Fig. 7. Observed:expected (obs:exp) plot for measured vs. simulated daily water table (WT) for combined years 2003, 2004 and 2005 at each position forest margin (a), mid-transition (b), and fen margin (c) of Old Black Spruce Fen (OBSF) transition zone. Both simulated and measured WT are in negative values, indicating their positions below soil surface.

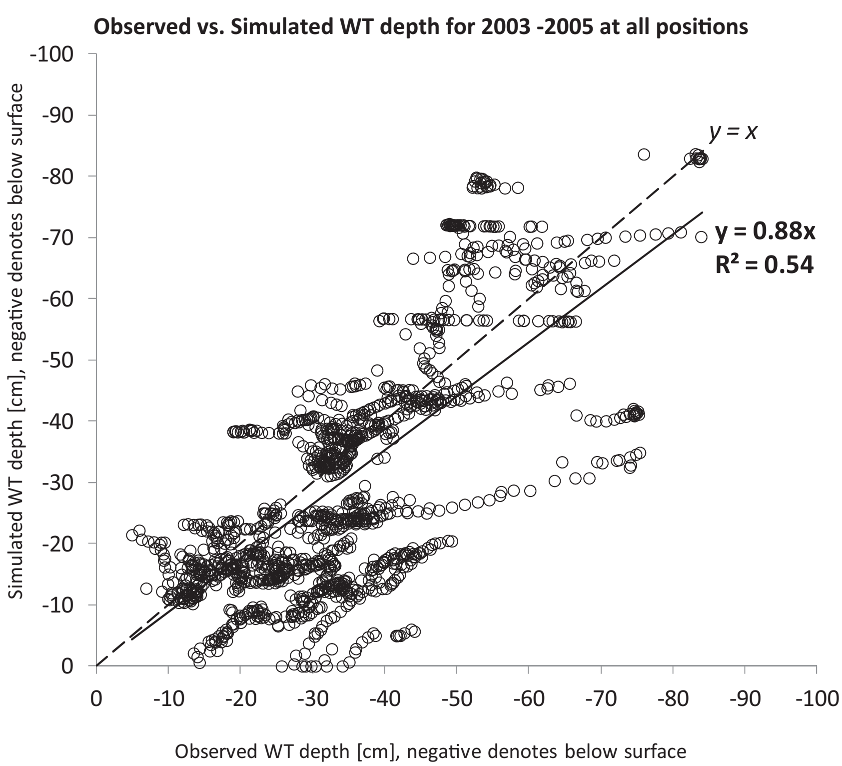
the obs:exp plot with $WT_{ext,W} = -50$ cm, the average observed WT at the upper ecotone boundary in 2003–2005 (Fig. 8b). This similarity indicated little relative impact of uncertainty in evaluating boundary hydrological gradients and confirmed that simulations of landscape hydrology can be placed within the larger context of watershed hydrological gradients, as well as within the specific context of local ones.

4. Discussion

Ecosys with constant lateral boundary conditions (Section 2.4) simulated general rise of WT observed from forest margin to fen margin and observed changes of WT with precipitation from low in 2003 (Fig. 3a–d) to high in 2004 (Fig. 4a–d), and then returning to near-average in 2005 (Fig. 5a–d). *Ecosys* performance was



(a)



(b)

Fig. 8. Observed:expected (obs:exp) plot for measured vs. simulated daily water table (WT) for combined years 2003, 2004 and 2005, and combined positions of forest margin, mid-transition and fen margin of Old Black Spruce Fen (OBSF) transition zone with an external WT preset at −62.5 cm, interpolated for the watershed (a) and with an external WT preset at −50 cm, the average observed WT at the upper ecotone boundary in 2003–2005 (b). Both simulated and measured WT are in negative values, indicating their positions below soil surface.

consistent with our hypotheses that lateral boundary conditions represented by WT_{ext} need to be well defined in the model to simulate WT accurately along boreal transition zones, even when their topography is relatively flat as at the OBSF ecotone (Fig. 2a). Also, we tested a newly developed method for modelling WT dynamics along a boreal transition zone with different landscape positions, each with different organic–mineral soil profiles, thus extending an earlier test at a site scale for a fen in Wisconsin (Grant et al., 2012). Many studies have shown that changes in WT influenced net ecosystem productivity (NEP) through impacting its components gross ecosystem productivity (GPP) and ecosystem respiration (ER), as shown in many experimental studies (Sulman et al., 2009; Dunn et al., 2007; Strack and Waddington, 2007; Strack et al., 2006; Lafleur et al., 2001) and modelling studies (Grant et al., 2012; Dimitrov et al., 2011; Sonnentag et al., 2008; Grant, 2004). Hence, proper modelling of WT along ecotone landscape trasnsects is a prerequisite for proper modelling of ecotone productivity gradients along these transects. The latter is subject to a related study on hydrological effects on ecotone productivities and respiration along the same boreal transition zone, based on the same model run (submitted manuscript ECOMOD-13-538).

4.1. Uncertainties in modelling hydrology of boreal transition zones

Modelling of landscape-scale WT dynamics relies on accurate representation of external hydraulic gradients by hydrological boundary conditions in the model (WT_{ext} in *ecosys*) and of hydrological properties of simulated landscape soil profiles (Table 2). Uncertainties in these conditions and properties, combined with inherent model limitations, resulted in: (i) too slow recharge while WT at the upland forest boundary was below $WT_{ext,W}$ and consequent inability to raise WT to that measured in the well drained peat at the forest margin during the dry year 2003 (Fig. 3b); (ii) too slow discharge while WT at the lowland fen boundary was above $WT_{ext,E}$ and consequently maintaining WT higher than that measured at the mid-transition (Fig. 4c) and fen margin (Figs. 3d and 4d). Analysing WT sensitivity to boundary conditions, we raised $WT_{ext,W}$ by 33% to increase recharge at the forest boundary and lowered $WT_{ext,E}$ by 33% to increase discharge at the fen boundary (model output not shown here). However, these changes caused either too high WT at the fen boundary with increased recharge at the forest boundary, or too low WT at the forest boundary with increased discharge at the fen boundary. This analysis indicated that setting $WT_{ext,W}$ and $WT_{ext,E}$ should comply to hydrological gradients along the watershed in order to simulate accurately the landscape ecotone hydrology.

Slow soil discharge/recharge in the model might also be due to poorly understood hydrological properties along the diverse mineral–organic soil gradients of the transition zones (especially of the upper peat). Properties such as K_s (Table 2) determined hydraulic conductances [Eq. D9a,b], hence subsurface water fluxes between adjacent model cells and across the model boundaries [Eqs. D7, D10]. Following previous studies in peatland hydrology (Dimitrov et al., 2010a; Letts et al., 2000), we tested different values of K_s along the ecotone in the course of simulations. However, larger K_s than those in Table 2 did not result in improved discharge/recharge and WT in the model, possibly due to the complexity of the simulated peat-mineral soil gradient. Furthermore, earlier spring rise in WT in the field vs. model partially might be due to unknown regional flow pathways/gradients through the transition zone that brought water from other watershed locations where snowmelt and spring thaw occurred earlier, thus not captured by *ecosys*. Findings of numerous studies on water balance of prairie wetlands in central Canada also report that springtime water influx from snowmelt and spring thaw, including runoff from the watershed above, is one of the principal sources of water for those wetlands that is essential and critical for their existence (Hayashi et al., 1998; Winter and Rosenberry, 1995; Price, 1993).

The slow soil discharge/recharge in the model might also have been due to inherent limitations of *ecosys*, which currently does not represent hydrological gradients across the model boundaries in the unsaturated zone above the water table, or to some eventual effects of seasonal dynamics of WT_{ext} in the filed, unlike WT_{ext} in the model currently assumed constant. However, simulating generally unknown seasonal dynamics of WT_{ext} outside of our study site will not only increase uncertainty in simulations, but will also reduce the principle of simplicity in modelling.

4.2. Implications for modelling hydrology of ecotone ecosystems at watershed scale

Previous studies have focused on modelling forest hydrology, as summarized in Ju et al. (2006), and especially wetland hydrology, as summarized in Su et al. (2000). Although some of these studies simulated lateral water fluxes, recognizing them as an important part of the overall ecosystem water balance (Sonnentag et al., 2008), others treated ecosystem hydrology outside of the context of watershed hydrology, or considered wetlands as focal points of water influx from small, hydrologically closed basins (Winter, 1989). Our modelling approach considers explicitly the importance of external lateral hydraulic gradients at different model boundaries as inherent components of the watershed hydrology driving water through ecosystems on a landscape scale. *Ecosys* provides an option to simulate different external hydraulic gradients at different lateral model boundaries, which is critically important for proper ecohydrological modelling, e.g. at the ecotone ecosystems with diverse WT dynamics through complex organic–mineral soil gradients.

Field studies suggested that importance of the surrounding watershed for lateral hydraulic gradients along boreal transition zones would depend on their positions within the groundwater flow system, hydrogeological properties of soils and underlying rock material, and climatic zone through vegetation cover (Sophocleous, 2002; Winter, 1999, 2000; Toth, 1999). Findings of our study are especially important for WT modelling in relatively flat terrains in central and western Canada (Price et al., 2005), where the OBSF transition zone is located. In these boreal plain regions the groundwater flow (lateral and vertical recharge/discharge) is driven by complex hydraulic gradients due to the low relief and deep glacial deposits. Hence, a modelling approach as ours is a prerequisite for proper ecohydrological modelling of these ecosystems.

5. Conclusions

This study summarizes emerging knowledge about WT dynamics in boreal transition zones. Our findings suggest that even though many of these ecotone ecosystems occur in relatively flat areas, their WT dynamics depend on the regional scale watershed hydrology. Therefore, detailed ecohydrological models should be able to simulate different lateral hydraulic gradients acting at different model boundaries, thereby coupling ecotone landscape hydrology directly to the watershed hydrology. However, modelling of ecotone hydrology may still be limited by such hydrological uncertainties as poorly understood external hydraulic gradients, complex soil hydraulic properties, or unknown surface/subsurface pathways that bring water from other watershed locations. To the best of our knowledge, *ecosys* is the only ecological model applied so far in boreal transition zones and simulating reasonably well their WT dynamics.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2013.11.030.

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