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Linking Climate Change and Forest Ecophysiology to Project Future Trends in Tree Growth: A Review of Forest Models

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1. Introduction

Climate change is already altering tree species ranges, with tree lines shifting upwards and polewards around the world (Dullinger et al., 2004; Soja et al., 2007; Harsch et al., 2009). A recent analysis of the potential effects of climate change on tree distribution in British Columbia (western Canada) suggested that important timber species including white spruce and lodgepole pine may lose suitable habitat and suffer adversely from a combination of warming trends and reduced growing season precipitation (Hamann & Wang, 2006). In contrast, species such as Douglas fir and ponderosa pine may actually expand their range and potentially show improved growth rates in parts of their existing range. A recent study in the mountains of interior British Columbia showed how at high elevation, trees historically responded positively to increased temperatures, while at low elevations trees showed a negative response to growing season maximum temperature and a positive correlation with growing season precipitation (Lo et al., 2010a, 2010b).

Given these species-specific responses it is not surprising that recent research has failed to identify direct links between warmer temperatures and observed changes in species ranges (Dullinger et al., 2004; Wilmking et al., 2004). The important ecological and socio-economic consequences of such changes have prompted multiple modelling efforts to predict the future location of habitat suitable for tree species and to assess the potential implications for tree growth of changes in climate. Defining such areas and estimating the losses or gains due to climate change in timber production have important consequences on forest management and conservation.

The most popular approaches to project future areas of suitable habitat for commercial tree species have involved analysis of historical records of tree lines in boreal and alpine environments (Dullinger et al., 2004), using climate envelope models (Hamann & Wang, 2006). Similarly, dendroclimatology (studying historical tree growth rates by analyzing tree ring width) has been used to link climate and tree growth rates (Wilmking et al., 2004; Lo et al., 2010a, 2010b). These approaches are based mostly on climatic information, although their combination with other information such as soil or topography has been used to

produce maps of potential future habitat suitability (e.g. Iverson et al., 2008). Such predictions are useful to understand the relationships between climate and tree distribution, abundance and growth, and could be a starting point for helping to plan forest management at broad scales under changing climate. However, such approach has several shortcomings, which have been discussed in the scientific literature before but it seems that this discussion has not been translated into the forest management community yet. Readers can find detailed discussions on these shortcomings in Pearson & Dawson (2003) and Thuiller et al. (2008), with only a basic description following below.

2. Basic shortcomings of climate-based models for their use in forest management

The vegetation that can be seen around the globe at the present has persisted through significant climatic changes, especially in forests with ancient trees. Herb and shrub growth and distributions often respond more to changes in soil moisture and nutritional gradients, which are determined by many non-climatic variables. However, additional non-climatic factors such as competition, seed production, invasibility and migration rates will be equally or more important (Davis et al., 1998; Grace et al., 2002; Dullinger et al., 2004), as well as factors only indirectly related to climate such as rate, type and intensity of disturbances (Bergeron et al., 2004). If the ecological effects of these other determinants are well correlated with climate, climate-based models may prove useful for general planning at broad regional scales. However, at landscape and stand scales (the most meaningful for forest planning), topography, geology, slope, aspect and soils will, among other ecosystem characteristics, modify the direct effects of climate on trees (Pearson & Dawson, 2003).

Previous studies have advanced maps of future suitable habitat for commercial tree species under different climate scenarios (Hamann & Wang, 2006; Iverson et al., 2008). These models are based on the assumption that present-day tree distributions are in an equilibrium state determined by the interaction of climate with topographic and edaphic conditions. However, without accounting for dynamic changes in inter-specific competition, migration rates, seedling production, invasibility or disturbances, climate envelope models lack practical utility to support management decisions (Davis et al., 1998; Grace et al., 2002; Thuiller et al., 2008). This issue is increased when moving from continental and regional scales, where climate can be the main driver of current tree abundance and distribution, to landscape scales where local factors can be as important as climate, or even more (Pearson & Dawson, 2003).

Evidence from field studies shows that observed shifts in tree ranges are not always linked to changes in climate. For example, Harsch et al. (2009) found that only 50% of the reported treeline movements were connected to warmer temperatures, mostly because of the importance of non-climatic local factors. Bergeron et al (2004) showed that the limit between mixedwood and coniferous forest in north-eastern North America, which apparently matches climatic boundaries, is actually the result of wildfires. Therefore, climatic conditions of present species distributions are also not necessarily a valid proxy for possible future tree distributions, because forests, especially in the northern hemisphere, have not yet reached equilibrium after the last glaciation, neither fully occupy their current potential habitats (Bergeron et al., 2004; Sveming & Skov, 2004).

Responses to changing climate are species-specific and modulated through the ecophysiological responses of each tree species and their relationships with the rest of the

ecosystem. The same change in climate may be beneficial for the growth of some tree species, but detrimental or non-important for other species in the same ecosystem (Lo et al., 2010a, 2010b). At high elevation, trees usually respond with more growth to increased temperatures, while at low elevations trees typically show reductions in growth when growing season water stress increases in warmer environments. While tree growth has been shown to be correlated to climate variables, the direct or indirect causal factors are often less clear. Climate can influence photosynthesis and respiration rates, nutrient dynamics and subsequently productivity through its impact on organic matter decomposition rates. Recent litter decomposition studies have shown that soil temperature and soil moisture influence mass loss and mineralization rates (Trofymow et al., 2002; Prescott et al., 2004).

As climate changes, different species will respond differently and at different speeds: some will migrate, grow faster or stop growing, but many current tree populations will remain in their present ranges (just modifying their growth rates), making it difficult for southern and lowland species to successfully establish themselves outside of their current ranges, unless the present populations at those locations are eliminated via disturbances. In addition, it is known that many species can grow well in environments warmer than their current ranges, but are prevented from doing so through mechanisms of competition with faster-growing species, not because of poor adaption to climate (Hurtley, 1991).

As a result of these changes at species and population levels, new biological communities will be created. These new communities will be established on biotopes also different from the present (i.e., same geology and topography but different climate). As a consequence, new ecosystems will appear, in a process similar to post-glaciation colonization, which in some areas is still underway. Therefore, planning future forest management under the wrong assumption that current ecosystems will just be displaced northwards or upwards and keeping their current species ensemble and growth rates seems condemned to fail (Lo et al., 2010b).

Taking into account the mentioned shortcomings, it is clear that predicting changes in tree distribution and tree growth with models based only on climatic information is not a suitable approach. Predicting geographical changes in soils, trees, lesser vegetation and wildlife at scales meaningful for forest management involves greater complexity than is included in climatic envelope models. Therefore, we advocate the use of more complex, process-based models that incorporate a greater proportion of the key determinants of possible forest futures to deal adequately with the increasing uncertainty of future tree growth and climate change effects on forests, and that account for a more detailed description of the ecophysiological processes involved in tree growth rates (Kimmins et al., 2008). A review of the most important forest models of this kind follows below.

3. Forest models linking climate and ecophysiology

There is a wide variety of forest models available nowadays, simulating ecophysiological processes from leaf to landscape levels. Among them, fifteen stand level models used for predicting climate change effects have been reviewed and compared in this chapter. Although nowadays there are many simulation models capable to access climate change impacts, we have focused our review on those whose conceptual models or model structures are defined at stand level, which is the most meaningful level for forest management. A list of the basic features of these models can be found in Tables 1 and 2.

3.1 PnET

PnET is a process model of stand dynamics. It uses monthly time steps because the developers assumed the aggregation of daily data into months would not cause a significant loss of information. This assumption has been tested and proven before (Aber & Federer, 1992). The model structure focuses on water and carbon balances. It deals with climate change via temperature and precipitation (water balance), but it does not include the effects of atmospheric CO_2 concentration. The physiological process used to produce biomass is similar to the CENTURY model (described below). PnET has similar structures to simulate carbon and water balance to FOREST-BGC and BIOMASS (see below) models, with the exception that their time steps are different (Aber & Federer, 1992). The central concept behind the PnET model is that photosynthesis is a function of foliage nitrogen, and water use efficiency is a function of vapour pressure deficit. Therefore, the function of maximum net photosynthesis per unit leaf area (NetPsnmax, $\mu mol\ CO_2\ m^{-2}\ sec^{-1}$) and foliage N content (N%) is:

$$NetPsnmax = -5.98 + 4.86 \times N\% \tag{1}$$

Aber & Federer (1992) assume that the basal respiration of the foliage is 10% of the basic photosynthesis rate, and therefore the maximum gross photosynthesis (GrossPsnmax) is 1.1 times the maximum net photosynthesis. In this model, the authors assumed the actual gross photosynthesis (GrossPsn) would be affected by temperature (DTemp), water stress (Dwater) and vapour pressure deficit (DVPD) as indicated in Equation (2).

$$GrossPsn = GrossPsnmax \times DTemp \times Dwater \times DVPD \tag{2}$$

The latest improvement of this model includes the development of a soil organic submodel to enhance the model description of carbon and nitrogen coupling and to study changes in ecosystem carbon storage across a nitrogen deposition gradient (Tonitto et al., 2009).

3.2 Forest-BGC and tree-BGC

Forest-BGC (Running & Coughlan, 1988; Coughan & Running, 1997) is a process-based ecosystem model that runs in a mixed time scale (daily and yearly; Running & Coughlan, 1988; Korol et al., 1995). It is used to predict stand growth and to provide site quality index estimations. The key processes considered in this model are the effects of carbon, nutrient and water availability on forest ecosystems. Short-wave radiation, air temperature, dew point and precipitation are daily input data used to drive the model (Running & Coughlan, 1988). The model calculates daily canopy photosynthesis (PSN; $kg\ CO_2\ day^{-1}$) by multiplying CO_2 diffusion gradient (ΔCO_2; $kg\ m^{-3}$), radiation and temperature-controlled mesophyll CO_2 conductance (CM; $m\ s^{-1}$).

$$PSN = [(\ \Delta CO_2 * CC * CM)\ /\ (CC + CM)] * LAI \times DAYL \tag{3}$$

The other parameters of this equation are CC: canopy conductance ($m\ s^{-1}$), LAI: leaf area index ($m^2\ m^{-2}$), and DAYL: day length for a flat surface ($s\ day^{-1}$). The mesophyll CO_2 conductance (CM) is calculated from three modifier functions: nitrogen (CMn), light (CMq) and temperature (CMt). These modifiers are all scaled from 0 to 1.

$$CMn = 67.0\ LEAFN \tag{4}$$

$$CMq = (Q - Q_0) / (Q + Q_{0.5}) \tag{5}$$

$$CMt = (TMAX - TAIR) \times (TAIR - TMIN) / TMAX^2 \tag{6}$$

LEAFN is leaf nitrogen concentration (fraction of dry weight). Q is canopy average radiation (kJ m^{-2} day^{-1}). Q_0 is the photosynthesis light compensation point (kJ m^{-2} day^{-1}). $Q_{0.5}$ is radiation level where CMq is 0.5 of maximum (kJ m^{-2} day^{-1}). TMAX and TMIN are high and low temperature (°C) at photosynthesis compensation points. TAIR is daylight average air temperature. Based on those values, the model calculates daily canopy photosynthesis, then subtracts the value of night canopy respiration (calculated from night average temperature and LAI) and gets daily net canopy carbon fixation.

This model considers respiration because it is a key process of the carbon budget. Daily maintenance respiration of stem and root biomass is calculated from compartment size and average air and soil temperature under a $Q_{10} = 2.3$ assumption

$$R_{l,s,r} = \alpha \exp (0.085 \, TEMP) \times C_{l,s,r} \tag{7}$$

where $R_{l,s,r}$ is maintenance respiration of leaf, stem and root compartments (kg day^{-1}); α is scaling factor for leaf, stem and root compartments (0.00015, 0.0010 and 0.0002 kg^{-1}kg^{-1}) ; and 0.085 is a scalar that gives a Q_{10} value of 2.34. In Equation 7, TEMP (°C) represents night and daily average air temperature and soil temperature. Night time average temperature is used for leaf respiration, daily average is used for stem respiration, and soil temperature is used for root respiration. $C_{l,r}$ is carbon storage either in the leafs or roots. C_s is stem respiration calculated by the function

$$C_s = \exp (0.67 \ln (\text{stem carbon storage})) \tag{8}$$

The yearly growth respiration is calculated as a fixed fraction of the carbon allocated to the leaf, stem and root compartments. The coefficients are usually obtained from literature and are independent of temperature. Unlike PnET, Forest-BGC considers nutrient cycling and therefore it has a decomposition component. The annual litter decomposition function is:

$$DECOMP = (-3.44 + 0.100AET) - ((0.0134 + 0.00147 \, AET) \times LIG) \tag{9}$$

where DECOMP is annual percent weight loss of fresh litter (% year^{-1}) and LIG is initial litter lignin concentration (% dry weight). Actual annual evapotranspiration (AET; mm year^{-1}) is calculated from a daily model of evapotranspiration.

One of the shortcomings of Forest-BGC is that the canopy is homogeneous. Therefore, although the leaf area index is proportional to the depth of the canopy, it may not capture the water and carbon budgets accurately (Running & Coughlan, 1988). Because of the lack of a management component, it cannot be a management tool for foresters. However, it is a suitable research tool to predict the impact of climate change. In addition, the model offers a link between input data and GIS databases which is useful for application of data collected from regional studies. This model has also been expanded into a series of related models (Tree-BGC, Fire-BGC) and it has also been combined with other models (PnET-BGC) to overcome its weaknesses. Forest-BGC has been widely used to predict climate change effects on natural disturbances, being the latest application of Forest-BGC estimating carbon dynamics in forests in Portugal (Rodrigues et al., 2010).

Tree-BGC, a variant of FOREST-BGC model, is also a stand level, process-based, mixed time scale (daily and yearly) ecosystem model. Most parts of these two models are very similar except the spatial scales are different (e.g. tree-level model vs. stand-level model). The purpose of Tree-BGC is the same as Forest-BGC: to calculate carbon, water and nitrogen flows in forest ecosystems (Korol et al., 1995). The only difference of these two models is that in Tree-BGC, all the simulated processes are based on individual tree physiological characteristics, and it focuses on light competition and ignores decomposition. To scale up the simulation results from individual tree level to the stand level, Tree-BGC has to make an important assumption: the responses of individual photosynthesis processes under different constraining factors at tree level are same at stand level (Korol et al., 1995). Most structures of Tree-BGC are very similar to the ones in Forest-BGC. Therefore, each tree annual canopy photosynthesis (PSNi; kg C tree^{-1} year^{-1}) is calculated as:

$$PSN_i = PSN \times \left(\frac{PAR_i}{\sum PAR_i} \right) \tag{10}$$

where PSN is stand annual canopy photosynthesis (kg C stand^{-1} year^{-1}); PARi is individual tree's photosynthetically active radiation (MJ m^{-2}), and the stand annual canopy photosynthesis is the sum of tree annual canopy photosynthesis. Not only the photosynthesis, but also the maintenance respiration has been modified in Tree-BGC compared to Forest-BGC. The maintenance respiration of each stem (MRs; kg C) is multiplied by stem respiration coefficient (f; kg C^{-1} day^{-1} kg^{-1}); temperature (T) controlled function and respiration volume (RV; m^3 ha^{-1}) which is the sum of phloem and live sapwood volume.

$$MRs = f \exp (0.085T) \, RV \tag{11}$$

The maintenance respirations of leaves (MRLi; kg C) and roots (MRri; kg C) are allocated to each tree (i) proportionally to its leaf and root carbon. Each tree's yearly maintenance respiration (MRi; kg C year^{-1}) is calculated by following the function:

$$MRi = MRLi \times MRsi + MRri \tag{12}$$

As mentioned before, Tree-BGC does not simulate litter decomposition, and therefore is not suitable to explore the link between tree and soil processes.

3.3 BIOMASS

BIOMASS (McMurtrie et al., 1990) is a stand-level process model that works at daytime steps. It has been used to simulate forest carbon, water-balance and to predict forest growth (McMurtrie et al., 1990; McMurtrie & Landsberg, 1992). The two main components of the model are the canopy assimilation of atmospheric carbon and plant-soil water balance. Canopy carbon assimilation is simulated as a function of an elaborated simulation of stomata processes (involving radiation, CO_2 concentration, temperature, soil water, etc.) and foliage nitrogen content (McMurtrie et al., 1990, 1992; McMurtrie & Landsberg, 1992; McMurtrie & Wang, 1993). Tree respiration is used to estimate biomass production, carbon allocation to different tree components, and litterfall rates (McMurtrie et al., 1989). There is no decomposition component in this model.

The model separates the canopy vertically into three homogenous layers and simulates detailed stomata processes for each layer. BIOMASS can be calibrated with standard daily weather data (McMurtrie et al., 1990). Because it simulates the details of the stomata to control photosynthesis and it uses climatic inputs including CO_2 concentration, temperature and soil moisture, it is a powerful tool for predicting climate change impact as long as the calculated rates of all the physiological process remain the same.

As for the water balance component, BIOMASS considers the impacts of different silviculture strategies on the dynamics of soil water. Therefore, in regions where soil moisture is the major growth limiting factor, BIOMASS can be used as a management tool to explore the impacts of different practices designed to increase water availability for trees. One downside of this model is that BIOMASS is a purely physiological process-based model, which means it shares the strengths, but also the main shortcoming of all mechanistic models: the requirement of many and complex data for calibration (McMurtrie et al., 1990). BIOMASS has been recently used to estimate the carbon balance of coniferous forests in response to different harvesting strategies in Sweden (Bannwarth, 2009).

3.4 LINKAGES

The LINKAGES model is designed to help to understand the ecosystem carbon and nitrogen storage and cycling under climate and soil moisture constraints (Pastor & Post, 1985). It can be seen as an offspring of the JABOWA model (Botkin, 1993). The model time step is yearly, but simulations of the effects of temperature and precipitation are based on monthly data (Pastor & Post, 1985). The model contains two parts: the environment and the tree species population components. The environmental component includes three subcomponents: TEMPE (temperature), MOIST (soil moisture) and DECOMP (decomposition), which are used to determine the site conditions. The population component also has three subroutines: BIRTH, GROW and KILL. These are used to calculate the population dynamics. These two groups are connected by GMULT (modifier for optimal birth rate, annual stem growth and mortality; Pastor & Post, 1985). Although the model structure and concepts are inherited from JABOWA, LINKAGES focuses more on how stand structure changes than on how stand productivity changes (the main focus of JABOWA).

Sunlight is the driving variable for stand dynamics (Pastor & Post, 1985). In the TEMPE subroutine, LINKAGES uses a random number generator algorithm to generate daily temperature based on each month's mean and standard deviation, and sums the number of degree days for the year. In MOIST, it uses Thornthwait and Mather's water-balance method to calculate actual evapotranspiration as the input to DECOMP. LINKAGES also considers soil physical characters (depth, texture), monthly temperature and rainfall to calculate the dry days of the year as an input to the GMULT subroutine. In the DECOMP subroutine, it calculates mass loss, nitrogen immobilization and mineralization, lignin decay and CO_2 loss from decomposing litter cohorts and humus. LINKAGES has been lately adapted to the conditions of New Zealand by McGlone et al. (2010).

As mentioned above, the simulation objective of LINKAGES is different from the other models reviewed. Unlike other models that calculate either GPP or NPP, LINKAGES calculates annual diameter and height increment as a function of site and climate variables (Pastor & Post, 1985). Because it follows the ideas of JABOWA, it could be considered more similar to a plant dynamics model than to a stand production model. Therefore, it does not contain any management tools. As a consequence, it can be considered more of a research model than a model applied to forestry. However, because many stand production dynamic simulation models in use today use the concepts in LINKAGES, it is worth considering.

3.5 G'DAY

G'DAY is more a plant-soil model than a stand simulation model (Medlyn et al., 2000). It describes how photosynthesis and nutrient factors interact with each other (Comins & McMutrie, 1993). The model is designed to predict the forest growth response to elevated atmospheric CO_2 concentrations and temperature. It predicts the response from decadal to century time scales (Medlyn et al., 2000). Earlier versions of G'DAY were linked to CENTURY (Parton et al., 1993). The latest version uses the BEWDY model (Medlyn, 1996) to replace the plant production calculated by CENTURY, but it still keeps other components of this soil model (i.e. soil carbon and nutrient dynamic components). This is because the model developers think BEWDY is more mechanistic and therefore it considers the temperature and CO_2 effects on plant photosynthesis and respiration better than CENTURY (Medlyn et al., 2000). When developing G'DAY, the authors considered two approaches to represent plant respiration biomass loss because how to deal with this process is still under discussion among ecosystem modellers (Medlyn et al., 2000). In the first approach, respiration is separated into maintenance respiration (Rm) and growth respiration (Rg). Maintenance respiration is assumed to be proportional to the non-structural nitrogen content of the plant. The growth respiration is calculated by a ratio (Yg; between 0 and 1) of the difference between potential photosynthesis (or gross primary production, growth canopy photosynthesis; Pg) and maintenance respiration (Rm). Therefore, net primary production (NPP) is the result after potential photosynthesis minus maintenance respiration minus growth respiration:

$$NPP = (1 - Yg) \times (Pg - Rm) \qquad (13)$$

For the second approach, Medlyn et al. (2000) assumed that respiration is a constant fraction of the canopy photosynthesis, similarly to the assumption in PnET (see above):

$$NPP = f\,Pg \qquad (14)$$

being f a factor of carbon use efficiency independent of atmospheric CO_2 and air temperature (Medlyn et al., 2000). Gross primary production (Pg) is calculated from the BEWDY model in which the photosynthesis rate depends on canopy leaf area index, the intensity of beam (direct) and diffuse radiation, leaf N content, air temperature and CO_2 concentration. Details can be found in Medlyn (1996).

There is no decomposition rate function in the model, but decomposition is implicit in each component of the nitrogen cycle, with the decomposition rates being temperature dependent. G'DAY is an annual time step model dealing with atmosphere CO_2 and temperature effects. No management tools are included in this model, but it does predict long-term forest production as an index of the impact of climate change. The model can also be used to estimate the effects of other human impacts on the environment, such as nitrogen deposition (Dezi et al., 2010).

3.6 3-PG

3-PG (Physiological Principles in Predicting Growth) is a model based on similar ideas on how forest stands grow to the ones used in LINKAGES and other models developed later. It is a physiological process stand-level growth model that uses monthly weather data as input (Landsberg & Waring, 1997). The model is based on well-established physiological principles and empirical data and therefore does not need much local calibration to predict forest growth. Generally speaking, it uses absorbed photosynthetically active radiation to

calculate gross primary production (PG) and then uses the ratio (Cpp) of net primary production (PN) to gross primary production (Cpp = 0.45 ± 0.05) to calculate net primary production. The model developers assume that the ratio is a constant. 3-PG employs data and functions of growth effects under different growing conditions from the literature to create a simple relationship between root growth and turnover rate to estimate the below-ground carbon allocation. To simulate the above-ground components, the model uses carbon allometric ratios, age effects and the 3/2 power law to constrain tree growth patterns and stand dynamics (Landsberg & Waring, 1997). Gross primary production is the product of $\varphi_{p.a.u.}$ (utilizable, absorbed photosynthetically active radiation) and α_c (canopy quantum efficiency coefficient = 0.03 mol C (mol photon)$^{-1}$ or 1.8 g C MJ^{-1}). The model uses α_c as a constant. The utilizable, absorbed photosynthetically active radiation $\varphi_{p.a.u.}$ is calculated from modifiers that come from monthly means of day-time vapour pressure deficit, soil water, temperature, and tree age:

$$PG = \varphi_{p.a.u.} \times \alpha_c \tag{15}$$

3-PG does not have a strong nutrient component; the only consideration of nutrients in 3-PG is that nutrient availability will affect root growth therefore changing carbon allocation (Landsberg & Waring, 1997). This nutrient availability is defined by an empirical, site-dependent coefficient. Although 3-PG is not as complicated as other models (BIOMASS, G'DAY, etc.), it incorporates important ideas about how forest stands produce biomass. However, some of the parameters used in the model are not regularly measured in the field and could be very difficult to be accurately calibrated. The model does not consider canopy complexity, does not have a water balance component, and does not attempt to be a management tool, but it contains the simulation of physiological processes which have been proven good enough to produce accurate prediction for some experimental sites (Landsberg & Waring, 1997).

3-PG is becoming an increasingly popular model for forest research, due to its capacity of being used for landscape modelling by linking it to satellite observations, and its relative lower calibration requirements (Coops et al., 2010). However, the model can be very sensitive to parameters that are very difficult to measure and are not easily related to physiological data measured in the field (Rodríguez-Suárez et al., 2010).

3.7 CENTURY, TREEDYN3 and TRIPLEX

Combining the strengths of 3-PG, CENTURY and TREEDYN3, TRIPLEX was built as a meta-model of existing models, to avoid the difficulties of the model development stage. Linkages of existing models as a meta-model instead of spending time and money to develop a completely new model to represent the ecosystem is a global trend (Peng et al., 2002). As we have already introduced 3-PG, here we will introduce CENTURY and TREEDYN3, and then describe the TRIPLEX model.

CENTURY (Parton et al., 1993) is a terrestrial biogeochemistry model. It focuses on the plant-soil linkage, which therefore is the target of the simulation, rather than the forest stand. It has a detailed soil nutrient component (Parton et al., 1993). CENTURY represents the relationship between climate, forest management, soil characters, plant productivity and decomposition. It incorporates key process relating to carbon assimilation and turnover from existing models. It contains three main components: soil organic C model, N submodel and an aboveground production model. The soil organic matter submodel contains three

major components: active soil organic matter, a slow organic matter pool, and a passive stable organic component. This well developed submodel, which is used in many other models (G'DAY and TRIPLEX), uses temperature and moisture as two of the factors, which control decomposition rate. For temperature, it uses mean monthly soil temperature as the input. For moisture, the input is the ratio of stored soil water plus monthly precipitation to potential evapotranspiration. The decomposition model is as follows:

$$\text{For I = 1,2} \qquad \frac{dC_I}{dt} = K_I L_C A C_I \tag{16}$$

$$\text{For I = 3} \qquad \frac{dC_I}{dt} = K_I A T_m C_I \tag{17}$$

$$\text{For I = 4,5,6,7,8} \qquad \frac{dC_I}{dt} = K_I A C_I \tag{18}$$

$$T_m = (1 - 0.75T) \tag{19}$$

$$L_C = e^{(-3Ls)} \tag{20}$$

C_I and K_I stand for carbon in different pools and the maximum decomposition rate (year^{-1}) of that pool; I = 1: surface material (K_1 = 3.9); I = 2: soil structure material (K_2 = 4.9); I = 3: active soil organic matter (K_3 = 7.3); I = 4: surface microbes (K_4 = 6.0); I = 5: surface metabolic material (K_5 = 14.8); I = 6: soil metabolic material (K_6 = 18.5); I = 7: slow soil organic matter (K_7 = 0.2) and I = 8: passive organic matter (K_8 = 0.0045). A is the combined effect of soil moisture and soil temperature. Tm is the soil texture effect (silt plus clay content) on the active soil organic matter component. Ls is the structural material and Lc is the impact of lignin content. The nitrogen submodel is similar to the soil C submodel. Organic N is the product of the carbon and the N: C ratios of the soil stable component that receives the C.

CENTURY can simulate plant production for different ecosystems (i.e. grasslands, agricultural crops, forests and savannah). However, the model has been developed to simulate grasslands. The general idea is that above-ground production is a function of soil temperature, available water and self-shading factor. But it also relates the soil nutrient supply (nitrogen, phosphorus and sulphur).

Unlike most of the physiological models, CENTURY does not consider detailed solar radiation effects. The model developers did not consider the effects of changes in the plant community (Parton et al., 1993). Because the time step is monthly, it is not sensitive to daily rainfall patterns and there is a lag effect between nutrient effects and photosynthetic storage in plant. CENTURY is not considered to be a tool for foresters and there is no representation of silviculture strategies in this model, but it has been recently used to explore ecosystem dynamics in grasslands (Feng and Zhao, 2011)

TREEDYN3 is a process model, which predicts tree growth, carbon and nitrogen dynamic in a single species, even-aged forests stand (Bossel, 1996). It also has a description of stand structure. The model is different from other models in that it introduces diurnal and seasonal variation in physiological processes (i.e. photosynthesis; seasonal dynamic of respiration, phenology and soil processes) and it considers energy and mass balance of

carbon and nitrogen flow (Bossel, 1996). The reason for using diurnal and seasonal scales is because these physiological processes are sensitive to daily and seasonal variation. TREEDYN3 is designed to explore the effects of climate change, air pollution, and different forest management strategies (Bossel, 1996).

In this model the photosynthate storage A is the result of net photosynthetic production (α_{prod}) and assimilate relocation (α_{reloc}) minus the assimilate consumption from growth (α_{grow}), respiration ($\alpha_{resp)}$ and death (α_{dead}).

$$\frac{dA}{dt} = \alpha_{prod} + \alpha_{reloc} - \alpha_{resp} - \alpha_{grow} - \alpha_{dead} \tag{21}$$

For details of each part, please see Bossel (1996). The respiration submodel calculates respiration consumption from the following function:

$$\alpha_{resp} = k_{Tr}\left[\sigma_L\left(1 - \frac{h}{24}\right)L + \sigma_w bW + \sigma_F \tau_F F\right] + k_{Ts}\sigma_R R \tag{22}$$

where k_{Tr} and k_{Ts} are temperature modifiers of air and soil temperatures; σ_L, σ_W, σ_F and σ_R are the respiration rates of leaves, wood, fruits and fine roots; L is leaf mass, b is the proportion of respiring wood volume (sapwood) and τ_F is the respiration period when there is fruit, and R is fine root mass. The model developers considered respiration because it is a limiting factor for tree growth. Litter and humus decomposition (C_{GE}, C_{SE}) are calculated with the following two functions:

$$C_{GE} = (1 - \chi)\rho_{dec}k_{Ts}C_G \tag{23}$$

$$C_{SE} = \rho_{min}k_{Ts}C_s \tag{24}$$

where ρ_{dec} and ρ_{min} are normal decomposition rate and specific humus mineralization rate, χ is the humification ratio, C_G is the carbon in litter, and C_S is the carbon in humus.

The TREEDYN3 model has many features different from other models. First, it is the only model considering mass and energy balance of carbon and nitrogen flows as a constraint. Second, it follows the current trend of forest model development; it's a hybrid model (see section 4). Third, it introduces diurnal and seasonal variation. In addition, it is also a management tool for foresters who are considering thinning and harvest effects on forest yield (Bossel, 1996). The major shortcoming of the model is that it is only suitable for even-age artificial forest stands, because during the simulation, all trees are of uniform size. Therefore, when alternative silviculture strategies are simulated, it does not produce realistic results. However, it's still a good tool for predicting long-term effects of climate change, air pollution and managements. TREEDYN3 has also been used to simulate the tree sub-modules in other models (Miehle et al., 2010), with TRIPLEX as the best example of this linkage.

TRIPLEX is a hybrid, monthly-time step, stand model used for predicting forest growth and yield and ecosystem carbon and nitrogen dynamics. As noted above, it integrates three well-developed process-based models: 3-PG (Landsberg & Waring, 1997), CENTURY (Parton et al., 1993) and TREENYD3 (Bossel, 1996). It borrows the soil submodel from CENTURY, and the growth and yield components from 3-PG and TREENYD3. It has four major submodels: forest production submodel, soil C and N dynamics submodel, forest growth and yield

submodel and soil water balance submodel (Peng et al., 2002). The TRIPLEX model uses the approach from 3-PG to calculate gross primary productivity (GPP),

$$GPP = k \times I_m \times LAI \times f_a \times f_t \times f_w \times f_d \qquad (25)$$

where GPP is a function of monthly received photosynthetically active radiation; PAR (I_m), leaf area index (LAI), forest age (f_a), monthly mean temperature (f_t), soil drought (f_w), percentage of frost days in a month (f_d) and a conversion constant (k). It combines the idea that net primary production (NPP) is a fixed proportion of gross primary productivity (GPP), and NPP is affected by nutrient availability.

$$NPP = C_{NPP} f_r GPP \qquad (26)$$

C_{NPP} is a fixed fraction (0.47 ± 0.04) and f_r is the modifier indicating available N. As a result, there is no respiration component in this model. The decomposition part adapts the approach of CENTURY, but it also adds some additional components.

$$R_i = K_i \times C_i \times M_d \times T_d \qquad (27)$$

$$R_{i'} = \min\left(R_i, \frac{K_i S_N (B_s B_t)}{(p B_s - p B_t - (1-p) B_t R_e)}\right) \qquad (28)$$

where R_i and $R_{i'}$ are potential decomposition and actual decomposition of each carbon pool respectively; K_i, C_i, M_d and T_d are maximum decomposition rate, carbon stock in particular pool, soil moisture and temperature modifier respectively. In the restriction function, decomposition is obtained from the lower value between potential decomposition and restricted decomposition. In this function, S_N is soil mineral N, B_s and B_t are C:N ratio of source and target C pools, p is the proportion of decomposed C which flows into other pools and R_e is the fraction of soil organic N generated from C decomposition process which flows into the mineral N pool.

The approach developed in TRIPLEX is new in that it combines existing models instead of building a new model to predict the climate change effects. The difficulty with this approach is the need to combine different time scales. However, comparing the simulation results with observed data suggests good model performance. As TREEDYN3 incorporates silviculture strategies, TRIPLEX can be used as a management tool, as in its latest application to simulate forest response to pre-commercial thinning (Wang et al., 2010).

3.8 Carbon flux models: BEPS, EASS and CLASS

The common features of these models are that they are research tools that try to simulate short time spans (usually time steps are hours). These models can simulate large regions by using satellite data on vegetation cover combined with weather data as inputs. However, there are no management tools included in the models. This, together with the complex methods required to measure carbon fluxes (flux towers, eddy covariance measurements, etc.) make these models unsuitable for forest management.

BEPS (Boreal Ecosystem Productivity Simulator; Liu et al., 1997) was developed at the Canadian Centre for Remote Sensing (CCRS) and the University of Toronto for short-term carbon cycle simulations. This model has been used with remotely sensed estimates of leaf area index (LAI) and land cover, and with Soil Landscapes of Canada (SLC), forest

inventory and gridded meteorological data to make regional and national estimates of NPP, NEP and net biome productivity (NBP) (Chen et al., 2003). CO_2 fixation in BEPS is constrained by leaf stomatal conductance, calculated empirically from canopy temperature, humidity and global radiation (Humphreys et al., 2003).

EASS (Ecosystem–Atmosphere Simulation Scheme) is a remote sensing-based ecosystem model, developed at the University of British Columbia (Chen et al., 2007). EASS has the following characteristics: (i) satellite data are used to describe the spatial and temporal information on vegetation, and in particular, the use of a foliage clumping index, in addition to leaf area index to characterize the effects of three-dimensional canopy structure on radiation, energy and carbon fluxes; (ii) energy and water exchanges and carbon assimilation in the soil–vegetation–atmosphere system are fully coupled and are simulated simultaneously; (iii) the energy and carbon assimilation fluxes are calculated with stratification of sunlit and shaded leaves to avoid shortcomings of the "big-leaf" assumption.

CLASS (Verseghy, 2000) was developed by the Meteorological Service of Canada (MSC) for coupling with the Canadian General Circulation Model (CGCM) in regional climate–ecosystem interactions. This model includes physically based treatment of energy and moisture fluxes from the canopy as well as radiation and precipitation cascades through it, and incorporates explicit thermal separation of the vegetation from the underlying ground. Seasonal variations of canopy parameters are accounted for. The morphological characteristics of the 'composite canopy' associated with each grid square are calculated as weighted averages over the vegetation types present. Each grid square is divided into a maximum of four separate subareas: bare soil, snow-covered, vegetation-covered, and snow-and-vegetation covered. CLASS has participated in the International Project for Intercomparison of Land–Surface Parameterization Schemes (PILPS). Versions of the CLASS biospheric component (C-CLASS) are being developed at McMaster University (C-CLASSm) (Arain et al., 2002) and the University of Alberta (C-CLASSa) (Zhang et al., 2004). In C-CLASSa, soil water deficits effects constrained CO_2. In CCLASSm, CO_2 fixation was constrained directly by soil water content.

4. The hybrid modelling approach: FORECAST climate

As we have shown in the previous section, simulation models can organise the complexity of information and data into a coherent tool for analysing systems at these various scales (Messier et al., 2003). The process-based models described in the previous section use the scientific knowledge available to link several ecosystem variables trough equations, but the difficulty in getting the right coefficients used in those equations usually produces unrealistic or unreliable predictions. On the other hand, statistic, simple growth and yield models are based on field data and they usually produce good estimations if the simulated conditions are similar to the recorded ones, but they do not contain explanation and therefore cannot be used to explore ecological interactions or to generate estimations in areas outside of the range of recorded data (Kimmins, 2004). To reduce the inconvenient of both types of models but keeping the advantages of both approaches, hybrid models have been developed. Combination of historical bioassay models with process simulation can give it sufficient flexibility to produce believable yield predictions under the types of changed growth conditions that are expected. A more detailed analysis of the philosophy behind hybrid predictors is given in Kimmins et al. (2010).

One example of process-based, ecophysiological model that accounts for the effects of climate change but that is designed for real forest management applications is FORECAST-

Climate. This model has been developed and designed to give it the capability to explicitly represent the potential impacts of climate change on forest growth and development. In the general version of FORECAST (Kimmins et al., 1999), tree growth is limited by light and nutrient availability, and no climate is represented. The projection of stand growth and ecosystem dynamics is based on a representation of the rates of key ecological processes regulating the availability of, and competition for, light and nutrient resources (Figure 1). The rates of these processes are calculated from a combination of historical bioassay data (biomass accumulation in component pools, stand density, etc.) and measures of certain ecosystem variables (e.g. decomposition rates, photosynthetic saturation curves) by relating 'biologically active' biomass components (foliage and small roots) with calculations of nutrient uptake, the capture of light energy, and net primary production. The model generates a suite of growth properties used to model growth as a function of resource availability and competition (Kimmins et al., 1999). They include (but are not limited to): 1) Photosynthetic efficiency per unit of foliage biomass; 2) Nutrient uptake requirements; 3) Light-related measures of tree and branch mortality. Nutrient cycling is simulated through a mass balance approach. Nitrogen that is incorporated into the soil solution through atmospheric deposition, seepage, mineral weathering, and litter mineralization is calculated.

Model	Scale		Climate input			Physiological processes				LAI	Driving function Foliage [N]	Nutrient Cycling
	Spatial	Temporal	Tem.	Moist.	[CO2]	Photosynthesis[1] GPP	/ NPP	Resp.	Decom.	LAI	Foliage [N]	N
PnET	stand	monthly	Y	Y	-	2nd	1st	Y	-	-	Y	-
FOREST - BGC	stand	daily / yearly	Y	Y	Y	1st	2nd	Y	Y	Y	-	Y
TREE-BGC	tree to stand	daily	Y	Y	-	1st	2nd	Y	-	Y	-	Y
BIOMASS	stand	daily to monthly	Y	Y	Y	1st	2nd	Y	-	Y	?	-
LINKAGES	tree to stand	monthly	Y	Y	-	-	1st	-	Y	?	-	Y
G'DAY	stand	yearly	Y	-	Y	1st	2nd	Y	Y	Y	Y	Y
3-PG	stand	monthly	Y	Y	-	1st	2nd	-	-	Y_2	Y_2	-
CENTURY	stand	monthly	Y	Y	-	Y_3	Y_3	-	Y	Y_4	Y_4	Y
TREEDYN3	stand	monthly/ seasonal	Y	-	-	1st	2nd	Y	Y	Y_5	Y	Y
TRIPLEX	stand	monthly	Y	Y	Y	1st	2nd	-	Y	Y	-	Y
FORECAST	stand	yearly	-	-	-	-	1st	-	Y	-	Y	Y
FORECAST Climate	stand	daily	Y	Y	-	-	1st	-	Y	-	Y	Y

Table 1. Comparison of different ecosystem processes, climate input included and main features in several stand-level models. Abbreviations: Y: Yes, Tem: Temperature, Moist: soil moisture, [CO2]: atmospheric CO_2 concentration, Resp: respiration, Decom: litter decomposition, LAI: Leaf Area Index, Foliage [N]: N concentration in foliage. Notes: 1) Photosynthesis 1st / 2nd indicates the order in which GPP and NPP are calculated; 2) Driving function is Canopy Quantum Efficiency Coefficient; 3) Potential production; 4) Driving function is biomass; 5) LAI affects radiation.

Model	Stomata	Canopy Layers	Ecological levels			Management tool	GIS input	Reference
			Soil	Tree	Forest			
PnET	-	Y	-	-	Y	-	-	Aber & Federer (1992)
FOREST-BGC	Y	-	Y	-	Y	-	Y	Running & Coughlan (1988)
TREE-BGC	-	shade effect	-	-	Y	-	-	Korol et al. (1995)
BIOMASS	Y	Y	-	-	Y	Y	-	McMurtrie et al. (1989)
LINKAGES	-	shade effect	-	-	Y	-	-	Pastor & Post (1985)
G'DAY	Y	shade effect	Y	-	Y	-	-	Medlyn (1996)
3-PG	-	-	-	-	Y	-	Y	Landsberg & Waring (1997)
CENTURY	-	-	Y	Y		-	-	Parton et al. (1993)
TREEDYN3	-	Y	-	-	Y	Y	-	Bossel (1996)
TRIPLEX	-	-	Y	-	Y	Y	Y	Peng et al. (2002)
FORECAST	-	Y	Y	Y	Y	Y	-	Kimmins et al. (1999)
FORECAST Climate	-	Y	Y	Y	Y	Y	-	Seely et al. (1997), Kimmins et al. (2010)
BEPS	Y	-	Y	-	Y	-	Y	Liu et al. (1997)
EASS	Y	clumping index	Y	-	Y	-	Y	Chen et al. (2007)
CLASS	Y	shade effect	Y	-	Y	Y	Y	Verseghy, (2000)

Table 2. Comparison of main features in several process forest models; Y: Yes.

If this amount is more than what the combination of what the soil can retain (as defined by the cation and anion exchange capacities) and trees can uptake, the difference leaches out of the system. Soil fertility in FORECAST is represented based on a bioassay approach in which empirical input data describing decomposition rates and changes in chemistry as decomposition proceeds allow for calculation of nutrient release from litter and humus (Fig. 1). Carbon allocation in response to soil fertility and tree nutrition is based on empirical biomass ratios and biomass turnover rates (e.g. number of years of leaf retention for evergreens) for sites of different fertility, and on literature or locally-obtained values for variation in fine root turnover along fertility gradients. Moisture limitation on growth is currently based on moisture-determined maximum foliar biomass and thus maximum foliar N. FORECAST has shown high accuracy when applied to real management operations (Blanco et al., 2007).
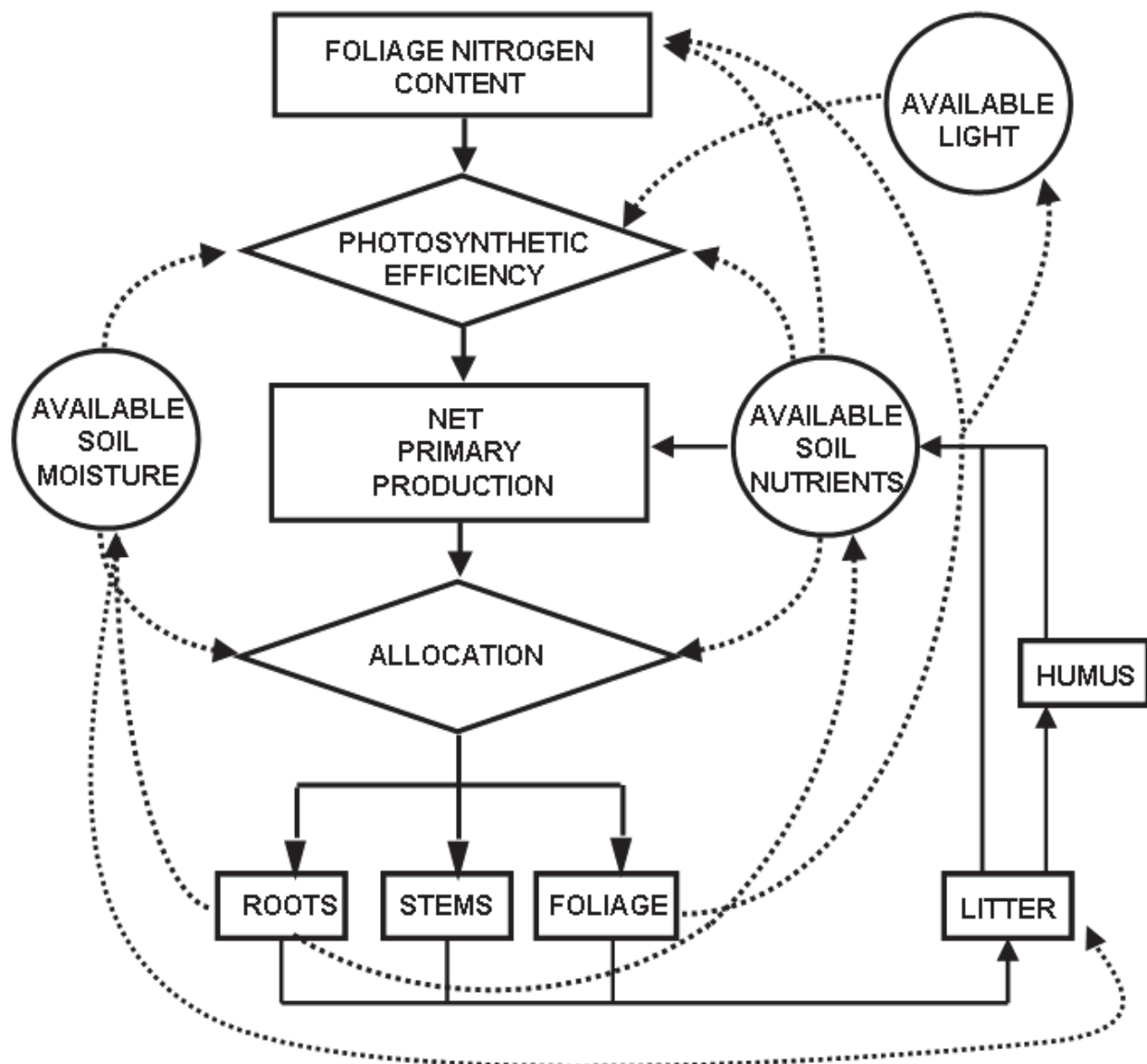
Fig. 1. Diagram representing FORECAST and FORECAST-Climate main processes and pools. The difference between both models is the influence of Available Soil Moisture, simulated in FORECAST-Climate but not in FORECAST (modified with permission from Kimmins et al., 1999).

The improved FORECAST-Climate model includes an explicit representation of soil moisture and forest hydrological processes based on a linkage to the Forest Water Dynamics (ForWaDy) model (Seely et al., 1997). ForWaDy is a vegetation-oriented model originally developed as a companion forest hydrology model to FORECAST. The model was designed to provide a representation of the impacts of forests management activities on water competition among different tree species and between trees and minor vegetation. Potential evapotranspiration (PET) in ForWaDy is calculated using an energy balance approach. Incoming radiation is partitioned among vertical canopy layers (vegetation type) and the forest floor to drive actual evapotranspiration (AET) calculations. A schematic of the model showing the various flow pathways represented in the model is provided in Fig. 2.
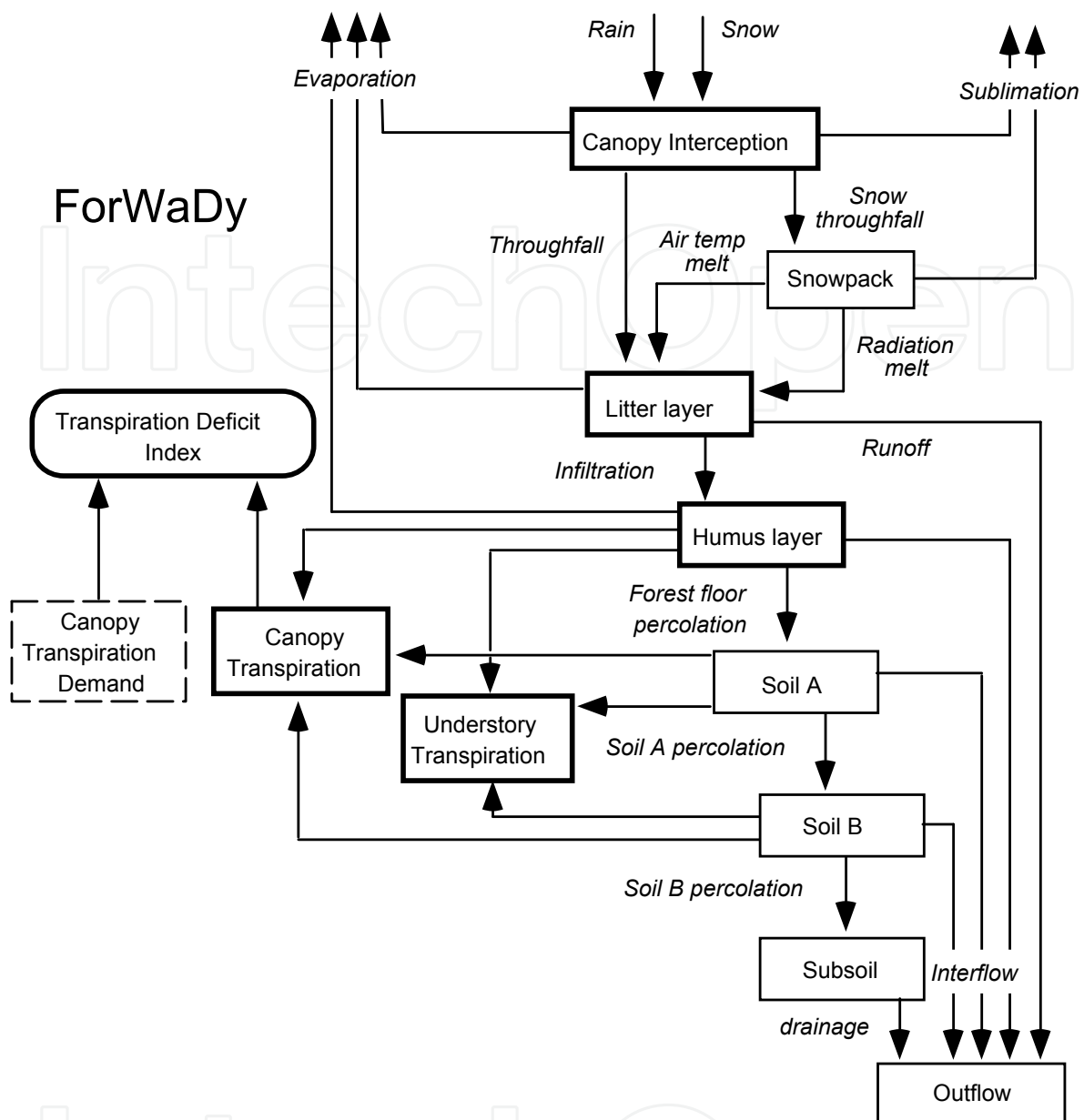
Fig. 2. Diagram representing energy and water flows in ForWaDy (adapted with permission from Seely et al., 1997).

The model is structured for portability, with minimum soil data requirements and parameter values that are relatively easy to estimate. It has a simplified representation of the soil physical properties dictating moisture availability, storage, and infiltration. ForWaDy is a forest hydrology model used to simulated forest water dynamics under given climate and forest stand structure conditions. It uses a daily time step to capture precipitation events (Seely et al., 1997). ForWaDy uses an energy budget approach to calculate PET as a function of climate (solar radiation, mean air temperature, precipitation and snow depth), stand structure and soil texture (Seely et al., 1997). It simulates precipitation interception by the vegetation canopy and competition between plants for water in the soil under different forest stand conditions, and calculates water demand by different canopy layers and within different soil layers. After calculating the difference between water supply and water

demand of the tree, ForWaDy provides a tree water stress index: TDI (transpiration deficit index), which will be used as a modifier of tree growth in FORECAST. The advantages of this model are that it is written in a user-friendly language (i.e. STELLA) and it does not have a high input data requirement to run the model. Also, the processes within the model come from well-tested existing models or equations where possible (Seely et al., 1997) and it has been successfully tested in Canada and Argentina (Dordel, 2009; Kimmins et al., 2010). A detailed description is provided in Seely et al. (1997).

The linkage of FORECAST with ForWaDy to create FORECAST-Climate provides an additional feedback on tree growth rates based on a climate-driven quantification of tree water stress (Fig. 1). Moreover, the simulation of soil and litter moisture content in FORECAST-Climate facilitates a climate-based representation of organic matter decomposition and associated nutrient mineralization rates. These developments in combination with a simulation of temperature effects on length of growing season and forest growth rates will provide the foundation for the representation of climate impacts on forest growth in FORECAST. The completed model allows users to explore the potential impacts on varying climate scenarios on indicators of multiple forest values and it is directly applicable as a forest management.

5. Conclusions

Process-based models could be important tools to support decisions in forest management (Blanco et al., 2005). Such modelling tools are required to help forest planners navigate the potential implications of climate change on timber supply through the use of scenario analysis and case studies. Although detailed physiological models have been useful in exploring climate impacts on tree growth and ecosystem processes at research level, they are often data intensive and difficult to apply for management related applications (e.g. Grant et al., 2005). These models also have to be supported by accurate weather records or estimations (Lo et al., 2011). To be effective for guiding management, such tools must be able to capture the current understanding of the effect of specific climate variables on ecosystem processes governing forest growth, but still be practical for estimating impacts on tangible projections of forest growth and yield and other ecosystem values (Landsberg, 2003; BC Ministry of Forests and Range, 2006). Only then meaningful assessments for forest managers of the effects of climate change on forests could be carried out.

6. References

Aber, J.D. & Federer, C.A. (1992). A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia*, Vol. 92, pp. 463-474. ISSN 0029-8549.

Aber, J. D.; Ollinger, S.V. & Driscoll, C.T. (1997). Modelling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling*, Vol. 101, pp. 61–78. ISSN 0304-3800.

Arain, M.A.; Black, T.A.; Barr, A.G.; Jarvis, P.G.; Massheder, J.M.; Verseghy, D.L. & and Nesic, Z. (2002). Effects of seasonal and interannual climate variability on net ecosystem productivity of boreal deciduous and conifer forests. *Canadian Journal of Forest Research*, Vol. 32, pp. 878–891. ISSN 1208-6037.

Bannwarth, M. (2009). *Carbon balance of coniferous forests in response to different harvesting strategies : a model based analysis.* MSc thesis, University of Uppsala, Uppsala.

B.C. Ministry of Forests and Range (2006). *Preparing for Climate Change:Adapting to Impacts on British Columbia's Forest and Range Resources.* B.C. Ministry of Forests and Range, Victoria, BC, Canada.

Bergeron, Y.; Gauthier, S.; Flannigan, M. & Kafka, V. (2004). Fire regimes at the transition between mixedwood and Coniferous boreal forest in northwestern Quebec. *Ecology,* Vol. 85, pp. 1916-1932. ISSN 0012-9658.

Blanco, J.A.; Zavala, M.A.; Imbert, J.B. & Castillo, F.J. (2005). Sustainability of forest management practices: Evaluation through a simulation model of nutrient cycling. *Forest Ecology and Management,* Vol. 213, pp. 209-228. ISSN 0378-1127.

Blanco, J.A.; Seely, B.; Welham, C.; Kimmins, J.P. & Seebacher, T.M. (2007). Testing the performance of FORECAST, a forest ecosystem model, against 29 years of field data in a *Pseudotsuga menziesii* plantation. *Canadian Journal of Forest Research*, Vol. 37, pp. 1808-1820. ISSN 1208-6037.

Bossel, H. (1996). TREEDYN3 forest simulation model. *Ecological Modelling*, Vol. 90, pp. 187-227. ISSN 0304-3800.

Botkin, D.B. (1993). *Forest Dynamics: An Ecological Model.* Oxford University Press, ISBN-13: 978-0195065558, New York, NY, USA.

Chen, J.M.; Ju, W.; Cihlar, J.; Price, D.; Liu, J.; Chen, W.; Pan, J.; Black, T.A. & Barr, A. (2003). Spatial distribution of carbon sources and sinks in Canada's forests based on remote sensing. *Tellus B,* Vol. 55, pp. 622–642. ISSN 0280-6509.

Chen, B.; Chen, J.N. & Ju, W. (2007). Remote sensing-based ecosystem–atmosphere simulation scheme (EASS)—Model formulation and test with multiple-year data. *Ecological Modelling,* Vol. 209, pp. 277-300. ISSN 0304-3800.

Comins, H.N. & McMutrie, R.E. (1993). Long-term response of nutrient limited forests to CO2 enrichment; equilibrium of plant-soil models. *Ecological Applications*, Vol. 3, pp. 666-681. ISSN 1051-0761.

Cosby, B.J.; Hornberger, G.M. & Galloway, J.N. (1985). Modeling the effects of acid deposition: assessment of a lumped parameter model of soil and streamater chemistry. *Water Resources Research*, pp. 21: 51-63. ISSN 0043-1397.

Coops, N.C.; Hember, R.A. & Waring, R.H. (2010). Assessing the impact of current and projected climates on Douglas-fir productivity in British Columbia, Canada, using a process-based model (3-PG). *Canadian Journal of Forest Research,* Vol. 40, pp. 511-525.

Coughlan, J.C. & Running, S.W. (1997). Regional ecosystem simulation: A general model for simulating snow accumulation and melt in mountainous terrain. *Landscape Ecology*, Vol. 12, pp. 119 – 136. ISSN 0921-2973.

Davis, A.J.; Jenkinson, L.S.; Lawton, J.H.; Shorrocks, B. & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature,* Vol. 391, pp. 783-786. ISSN 0028-0836.

Dezi, S.; Medlyn, B.E.; Tonon, G. & Magnani, F. (2010). The effect of nitrogen deposition on forest carbon sequestration : a model-based analysis. *Global Change Biology,* Vol. 16, pp. 1470-1486. ISSN 1354-1013.

Dordel, J. (2009). *Effects of nurse tree species on growth environment and physiology of underplanted* Toona ciliata *Roemer in subtropical Argentinean plantations.* PhD thesis. Unviersity of British Columbia, Vancouver.

Dormann, C.F. (2007). Promising the future? Global change projections of species distributions. *Basic Applied Ecology,* Vol. 8, pp. 387-397. ISSN 1439-1791.

Dullinger, S.; Dirnböck, T. & Grabherr, G. (2004). Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. *Journal of Ecology,* Vol. 92, pp. 241-252. ISSN 1365-2745.

Feng, X.M. & Zhao, Y.S. (2011). Grazing intensity monitoring in Northern China steppe : Integrating CENTURY model and MODIS data. *Ecological Indicators,* Vol. 11, pp. 175-182. ISSN 1470-160X.

Grace, J. ; Berninger, F. & Nagy, L. (2002). Impacts of climate change on tree line. *Annals of Botany,* Vol. 90, pp. 537-544. ISSN 0305-7364.

Grant, R.F.; Araina, A.; Arora, V.; Barr, A.; Black, T.A.; Chen, J.; Wang, S.; Yuan, F. & Zhang, Y. (2005). Intercomparison of techniques to model high temperature effects on CO_2 and energy exchange in temperate and boreal coniferous forests. *Ecological Modelling,* Vol. 188, pp. 217–252. ISSN 0304-3800.

Hamann, A. & Wang, T. (2006). Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology,* Vol. 87, pp. 2773-2786. ISSN 0012-9658.

Harsch, M.A. ; Hulme, P.E. ; McGlone, M.S. & Duncan, R.P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters,* Vol. 12, pp. 1040-1049. ISSN 1461-023X.

Humphreys, E.R.; Black, T.A.; Ethier, G.A.; Drewitt, G.B.; Spittlehouse, D.L.; Jork, E.-M.; Nesic, Z. & Livingston, N.J. (2003). Annual and seasonal variability of sensible and latent heat fluxes above a coastal Douglas-fir forest, British Columbia, Canada. *Agricultural and Forest Meteorology,* Vol. 115, pp. 109–125. ISSN 0168-192.

Hurtley, B. (1991). How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany,* Vol. 67, pp. 15-22. ISSN 0305-7364.

Heikkinen, R.C. ; Luoto, M. ; Araújo, M.B. ; Virkkala, R. ; Thuiller, W. & Sykes, M.T. (2006). Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography,* Vol. 30, pp. 751-777. ISSN 0309-1333.

Iverson, L.R. ; Prasad, A.M. ; Matthews, S.N. & Peters, M. (2008). Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management,* Vol. 254, pp. 390-406. ISSN 0378-1127.

Kimmins, J.P. (2004). *Forest Ecology. A Foundation for Sustainable Management and Environmental Ethics in Forestry.* 3rd ed. Prentice Hall, ISBN 9-780130-662583. New Jersey, NJ, USA.

Kimmins, J.P. ; Mailly, D. & Seely, B. (1999). Modelling forest ecosystem net primary production: the hybrid simulation approach used in FORECAST. *Ecological Modelling,* Vol. 122, pp. 195-224. ISSN 0304-3800.

Kimmins, J.P. ; Blanco, J.A.; Seely, B. & Welham, C. (2008). Complexity in Modeling Forest Ecosystems; How Much is Enough? *Forest Ecology and Management*, Vol. 256, pp. 1646-1658. ISSN 0378-1127.

Kimmins, J.P.; Blanco, J.A.; Seely, B.; Welham, C. & Scoullar, K. (2010). *Forecasting Forest Futures: A Hybrid Modelling Approach to the Assessment of Sustainability of Forest Ecosystems and their Values*. Earthscan Ltd., ISBN 978-1-84407-922-3, London, UK.

Korol, R.L.; Running, S.W. & Milner, K.S. (1995). Incorporating intertree competition into an ecosystem model. *Canadian Journal of Forest Research*, Vol. 25, pp. 413-424. ISSN 1208-6037.

Landsberg, J. (2003. Modelling forest ecosystems: state of the art, challenges, and future directions. *Canadian Journal of Forest Research*, Vol. 33, pp. 385-397. ISSN 1208-6037.

Landsberg, J.J. & Waring, R.H. (1997). A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest. Ecology and Management*, Vol. 95, pp. 209-228. ISSN 0378-1127.

Lo, Y.-H. (2009). *Relationships between climate and annual radial growth in three coniferous species in interior British Columbia, Canada.* PhD thesis. University of British Columbia, Vancovuer, BC, Canada.

Lo, Y.-H.; Blanco, J.A. & Kimmins, J.P. (2010a). A word of caution when projecting future shifts of tree species ranges. *The Forestry Chronicle*, Vol. 86, pp. 312-316. ISSN 1499-9315.

Lo, Y.-H.; Blanco, J.A.; Seely, B.; Welham, C. & Kimmins, J.P. (2010b). Relationships between Climate and Tree Radial Growth in Interior British Columbia, Canada. *Forest Ecology and Management,* Vol. 259, pp. 932-942. ISSN 0378-1127.

Lo, Y.-H.; Blanco, J.A.; Seely, B.; Welham, C. & Kimmins, J.P. (2011). Generating reliable meteorological data in mountainous areas with scarce presence of weather records: the performance of MTCLIM in interior British Columbia, Canada. *Environmental Modelling & Software*, Vol. 26, pp. 644-657. ISSN 1364-8152.

McGlone, M.S.; Graeme, M.J. & Wilmshurst, J.M. (2010). Seasonality in the early Holocene : Extending fossil-based estimates with a forest ecosystem process model. *The Holocene*, in press. ISSN 0959-6836.

McMurtrie, R.E. & Landsberg, J.J. (1992). Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata*. *Forest Ecology and Management*, Vol. 52, pp. 243-260. ISSN 0378-1127.

McMurtrie, R.E. & Wang, Y.-P. (1993). Mathematical models of the photosynthetic response of tree stands to rising CO_2 concentrations and temperature. *Plant, Cell and Environment*, Vol. 16, pp. 1-13. ISSN 0140-7791.

McMurtrie, R.E.; Landsberg, J.J. & Linder, S. (1989). Research priorities in field experiments of fast growing tree plantation: implication of a mathematical model. In: *Biomass Production by Fast-Growing Trees,* Pereira, J.S.. & Landsberg, J.J., pp. 181-207. Kluwer, ISBN 0-7923-0208-7, Dordrecht, The Netherlands.

McMurtrie, R.E.; Rook, R.A. & Kelliher, F.M. (1990). Modelling the Yield of Pinus radiata on a site limited by water and nitrogen. *Forest Ecology and Management*, Vol. 30, pp. 381-413. ISSN 0378-1127.

McMurtrie, R.E.; Leuning, R.; Thompson, W.A. & Wheeler, A.W. (1992). A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf CO_2 exchange. *Forest Ecology and Management*, Vol. 52, pp. 261-278. ISSN 0378-1127.

Medlyn, B.E. (1996). *The representation of photosynthetic productivity in an ecosystem model used to assess plant response to climate change.* Ph.D. thesis, University of New South Wales, Sydney, Australia.

Medlyn, B.E.; McMutrie, R.E.; Dewar, R.C. & Jeffreys, M.P. (2000). Soil processes dominate the long-term response of forest net primary productivity to increased temperature and atmospheric CO_2 concentration. *Canadian Journal of Forest Research,* Vol. 30, pp. 873-888. ISSN 1208-6037.

Messier, C.; Fortin, M.-J.; Schmiegelow, F.; Doyon, F.; Cumming, S.G.; Kimmins, J.P.; Seely, B.; Welham, C. & Nelson, J. (2003). Modelling tools to assess the sustainability of forest management scenarios. In *Towards sustainable management of the Boreal Forest* Burton, P.J.; Messier, C.; Smith, D.W. & Adamowicz, W.L. (eds). NRC Research Press, ISBN 9-780660-187624, Ottawa, ON, Canada.

Miehle, P.; Grote, R.; Battaglia, M.; Feikema, P.M. & Arndt S.K. (2010). Evaluation of a process-based ecosystem model for long-term biomass and stand development of *Eucalyptus globulus* plantations. *European Journal of Forest Research,* Vol. 129, pp. 377-391. ISSN 1354-1013.

Parton, W.J.; Scurlock, J.M.O.; Ojima, D.S.; Gilmanov, T.G.; Scholes, R.J.; Schimel, D.S.; Kirchner, T. ; Menaut, J.-C. ; Seastedt, T.; Garcia Moya, E.; Kamnalrut, A. & Kinyamario, J.L. (1993). Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, Vol. 7, pp. 785-809. ISSN 0886-6236.

Pastor, J. & Post, W.M. (1985). *Development of a Linked Forest Productivity-Soil Process Model*. U.S. Dept. of Energy, ORNL/TM-9519. Oak Ridge, TN, USA.

Pearson, R.G. & Dawson, T.G. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography,* Vol. 12, pp. 361-371. ISSN 1466-822X.

Peng, C.; Liu, J.; Dang, Q.; Apps, M.J. & Jiang, H. (2002). TRIPLEX: a generic hybrid model for prediction forest growth and carbon and nitrogen dynamics. *Ecological Modelling*, Vol. 153, pp. 109-130. ISSN 0304-3800.

Pojar, J. ; Klinka, K. & Meidinger, D.V. (1987). Biogeoclimatic Ecosystem Classification in British Columbia. *Forest Ecology and Management,* Vol. 22, pp. 119-154. ISSN 0378-1127.

Prescott, C.E.; Blavins, L.L. & Staley, C. (2004). Litter decomposition in B.C.forests: controlling factors and influences of forestry activities, *BC Journal of Ecosystems and Management*, Vol. 5, pp. 30-43. ISSN 1488-4666.

Rodrigues, M.A.; Lopes, D.M.; Leite, S.M. & Tabuada, V.M. (2010). Analyzing the carbon dynamics in north western Portugal : calibration and application of Forest-BGC. *Earth System Dynamics Discussions,* Vol. 1, pp. 41-62. ISSN 2190-4979.

Rodríguez-Suárez, J.A.; Soto, B.; Iglesias, M.L. & Diaz-Fierros, F. (2010). Application of the 3PG forest growth model to a *Eucalyptus globulus* plantation in Northwest Spain. *European Journal of Forest Research*, Vol. 129, pp. 573-583. ISSN 1354-1013.

Running, S.W. & Coughlan, J.C. 1988. A General model of Forest ecosystem process for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling,* Vol. 42, pp. 125-154. ISSN 0304-3800.

Seely, B.; Arp, P. & Kimmins, J. P. (1997). A forest hydrology submodel for simulating the effect of management and climate change on stand water stress. In *Proceedings of Empirical and Process-based models for forest, tree and stand growth simulation,* Amaro A. & Tomé M. (ed) Edições Salamandra, Lisboa, Portugal, September 1997.

Soja, A.J.; Tchebakova, N.M.; French, N.H.M.; Flannigan, M.D.; Shugart, H.H.; Stocks, B.J.; Sukhinin, A.I.; Parfenova, E.I.; Chapin, F.S. & Stackhouse Jr., P.W. (2007). Climate-induce boreal forest change: predictions versus current observations. *Global and Planetary Change,* Vol. 56, pp. 274-296. ISSN 0921-8181.

Svenning, J.-C. & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecological Letters,* Vol. 7, pp. 565-573. ISSN 1461-023X.

Thornton, P.E.; Running, S.W. & White, M.A. (1997). Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology,* Vol. 190, pp. 214-251. ISSN 0022-1694.

Thuiller, W.; Albert, C.; Araújo, M.B.; Berry, P.M.; Cabeza, M.; Guisan, A.; Hickler, T.; Midgley, G.F.; Paterson, J.; Schurr, F.M.; Sykes, M.T. & Zimmermann, N.E. (2008). Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology,* Vol. 9, pp. 137-152. ISSN 1433-8319.

Tonitto, C.; Goodale, C. L.; Ollinger, S. V. & Jenkins, J. (2009). Soil organic carbon dynamics across a nitrogen deposition gradient: application of the PnET-SOM model to northeastern forest ecosystems. *Proceedings of American Geophysical Union*, *Fall Meeting 2009*, abstract #B13C-0532. San Francisco, December 2009.

Trofymow, J.A.; Moore, T.R.; Titus, B.; Prescott, C.; Morrison, I.; Siltanen, M.; Smith, S.; Fyles, J.; Wein, R.; Camire, C.; Duschene, L.; Kozak, L.; Kranabetter, M. & Visser, M. (2002). Rates of litter decomposition over six years in Canadian forests: Influence of litter quality and climate, *Canadian Journal of Forest Research*, Vol. 32, pp. 789-804. ISSN 1208-6037.

Verseghy, D.L. (2000). The Canadian Land Surface Scheme (CLASS): its history and future. *Atmosphere-Ocean*, Vol. 38, pp. 1–13. ISSN 0705-5900.

Wang, W.; Peng, C.; Zhang, S.Y.; Zhou, X.; Larocque, G.R.; Kneeshaw, D.D. & Lei, X. (2010). Development of TRIPLEX-Management model for simulating the response of forest growth to pre-commercial thinning. *Ecological Modelling,* in press. ISSN 0304-3800.

Wilmking, M. ; Juday, G.P. ; Barbier, V.A. & Zald, H.S.J. (2004). Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology,* Vol. 10, pp. 1-13. ISSN 1354-1013.

Yuan, F.; Arain, M.A.; Black, T.A. & Morgenstern, K. (2007). Energy and water exchanges modulated by soil–plant nitrogen cycling in a temperate Pacific Northwest conifer forest. *Ecological Modelling,* Vol. 201, pp. 331–347. ISSN 0304-3800.

Yuan, F.; Arain, M.A.; Barr, A.G.; Black, T.A.; Bourque, C.P.-A.; Coursolle, C.; Margolis, H.A.; McCaughey, J.H. & Wofsy, S.C. (2008). Modeling analysis of primary controls on net ecosystem productivity of seven boreal and temperate coniferous forests across a continental transect. *Global Change Biology*, Vol. 14, pp. 1765–1784. ISSN 1354-1013.

Zhang, Y.; Grant, R.F.; Flanagan, L.B.; Wang, S.S. & Verseghy, D.L. (2004). Recent developments and testing of a carbon-coupled Canadian land surface scheme in a water-stressed northern temperate grassland. *Ecological Modelling,* Vol. 181, pp. 591–614. ISSN 0304-3800.

Climate Change - Research and Technology for Adaptation and Mitigation
Edited by Dr Juan Blanco

This book provides an interdisciplinary view of how to prepare the ecological and socio-economic systems to the reality of climate change. Scientifically sound tools are needed to predict its effects on regional, rather than global, scales, as it is the level at which socio-economic plans are designed and natural ecosystem reacts. The first section of this book describes a series of methods and models to downscale the global predictions of climate change, estimate its effects on biophysical systems and monitor the changes as they occur. To reduce the magnitude of these changes, new ways of economic activity must be implemented. The second section of this book explores different options to reduce greenhouse emissions from activities such as forestry, industry and urban development. However, it is becoming increasingly clear that climate change can be minimized, but not avoided, and therefore the socio-economic systems around the world will have to adapt to the new conditions to reduce the adverse impacts to the minimum. The last section of this book explores some options for adaptation.

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