

# LPJ-GUESS – an ecosystem modelling framework

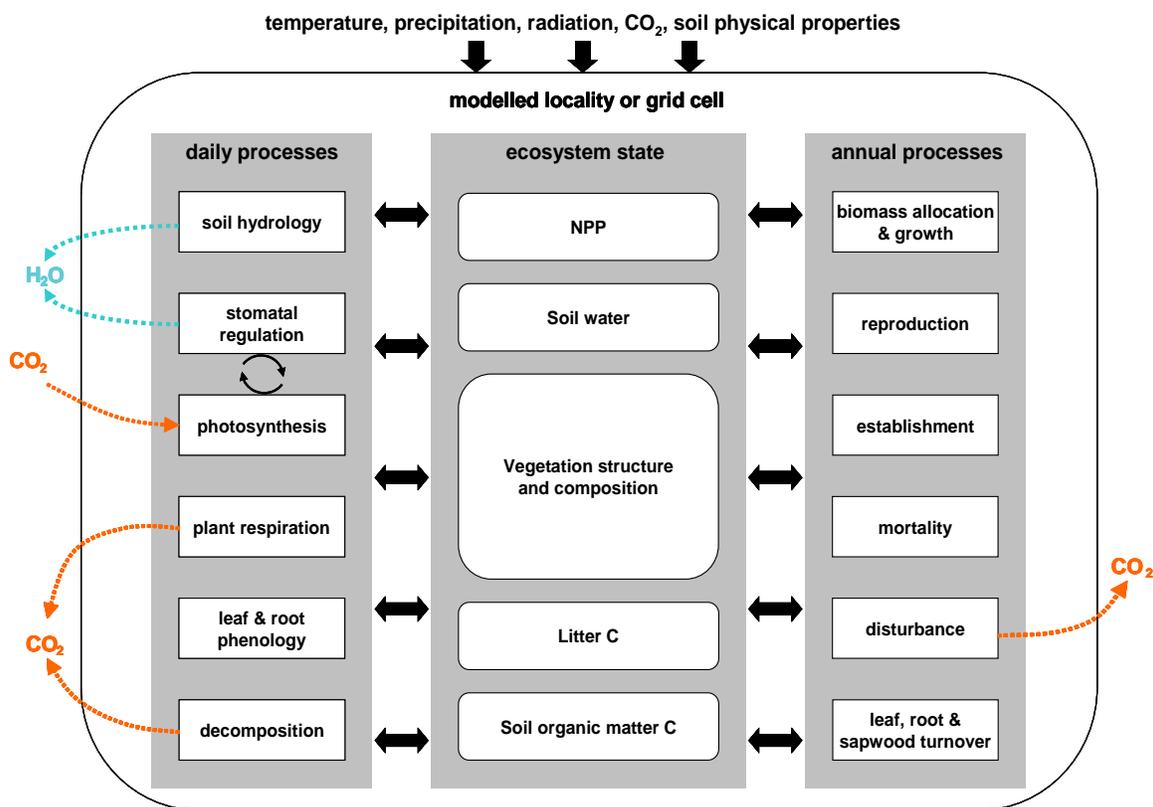
Ben Smith

## Contents

<b>1. Modular structure</b>	2
<b>2. Alternative vegetation modes</b>	3
2.2 Average individual	3
2.3 Population mode	4
2.4 Cohort and individual mode	5
<b>3. Plant functional types</b>	6
3.1 Bioclimatic niche	6
3.2 Growth form	6
3.3 Leaf phenology	6
3.4 Photosynthetic pathway	7
3.5 Life history	7
<b>4. Simulated processes</b>	8
4.1 Net primary production	8
4.2 Growth and allocation	10
4.3 Phenology	12
4.4 Soil hydrology	12
4.5 Litter and soil organic matter turnover	12
4.6 Population dynamics	13
4.6.1 <i>Establishment</i>	13
4.6.2 <i>Mortality</i>	15
4.7 Disturbance	16
<b>5. Further reading</b>	17
<b>6. References</b>	18

## 1. Modular structure

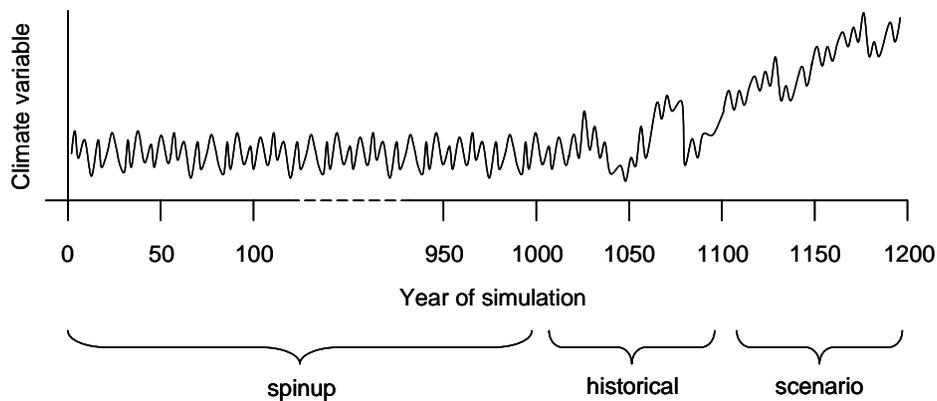
LPJ-GUESS is a flexible framework for modelling the structure and dynamics of terrestrial ecosystems at landscape, regional and global scales. The framework is made up of a number of modules (or submodels), each containing formulations of a relatively well-defined, related subset of ecosystem processes with a distinct spatial and/or temporal signature (characteristic scale). “Fast” process, such as photosynthesis, respiration and stomatal regulation are implemented on a time step of one day (or one month, interpolating between output values for adjacent months to obtain a value for each day). The “slow” processes of individual allocation and growth, population dynamics and disturbance are implemented once each simulation year (Figure 1). The input data to the model consist of climate parameters, atmospheric CO<sub>2</sub> concentrations and a soil code. The climate data are monthly or daily values of mean daily air temperature, precipitation and either incoming shortwave radiation or sunshine (the complement of percentage cloudiness). The soil code is used to derive texture-related parameters governing the hydrology and thermal diffusivity of the soil. Processes modify the values of state variables such as the cumulative annual net primary production (NPP), soil water availability, or aspects of the vegetation composition and structure. The rate or mode of a process may also be affected by the current values of the state variables, as well as by the input data to the model. Output data from the model include current values of state variables, as well as biogeochemical fluxes of CO<sub>2</sub> and H<sub>2</sub>O from ecosystems to the atmosphere or hydrosphere (Figure 1).



**Figure 1.** Conceptual representation of LPJ-GUESS showing the main process, time steps, state variables, and input environmental data. The potential output of the model include current values of the ecosystem state variables (e.g. biomass for different plant functional types, PFTs) as well as biogeochemical fluxes of CO<sub>2</sub> and H<sub>2</sub>O from ecosystems to the atmosphere or hydrosphere.

The model may be applied to simulate the potential ecosystem of a particular area or region, or across a grid made up of many adjacent areas (grid cells). In the latter case, the grid cells are modelled independently of each other, i.e. results for one grid cell do not affect the neighbouring grid cells. This is a simplifying assumption because, in reality, adjacent areas might be affected by, for example, species dispersal and runoff fluxes between areas.

The simulation for a particular area or grid cell normally follows two or three phases, separated in simulation time (Figure 2). The simulation begins with “bare ground,” which means that the modelled area is empty, with no vegetation present. The first phase of the simulation is known as the **spinup**, and normally takes 1000 years in population mode, or three times the generic disturbance interval in cohort or individual mode (see Section 2.3). The input data to the spinup are normally based on the first few years of available (historical) data, possibly with some interannual variation and with any trend removed. During the spinup, the vegetation as well as soil and litter carbon pools accumulate and approach an equilibrium with the climate at the beginning of the subsequent, **historical** phase of the simulation. During the historical phase, the model uses as input “observed” (usually, derived by interpolation from climate station data) climate and CO<sub>2</sub> data, for example average climate for the last 30 years, or climate for each year of the 20th century. In many cases there will be a third **scenario** phase simulating a future climate change.



**Figure 2.** In a typical model experiment with LPJ-GUESS the simulation for each modelled area or grid cell consists of a spinup phase to establish vegetation, litter carbon pools and soil carbon pools at equilibrium with the long-term average climate, a historical phase using observed climate as input data, and a scenario phase simulating a future climate change.

## 2. Alternative vegetation modes

LPJ-GUESS currently implements two different, but related, ecosystem models as alternative “vegetation modes”. **Population mode** is a version of the dynamic global vegetation model LPJ-DGVM (Sitch et al. 2003); **cohort mode** and **individual mode** correspond to the General Ecosystem Simulator, GUESS (Smith et al. 2001). The two models have many components in common, but differ in the way vegetation is represented internally in the model. There are also differences in the way certain processes that control vegetation dynamics, i.e. changes in the physical structure, composition and distribution of vegetation through time, are implemented in the model.

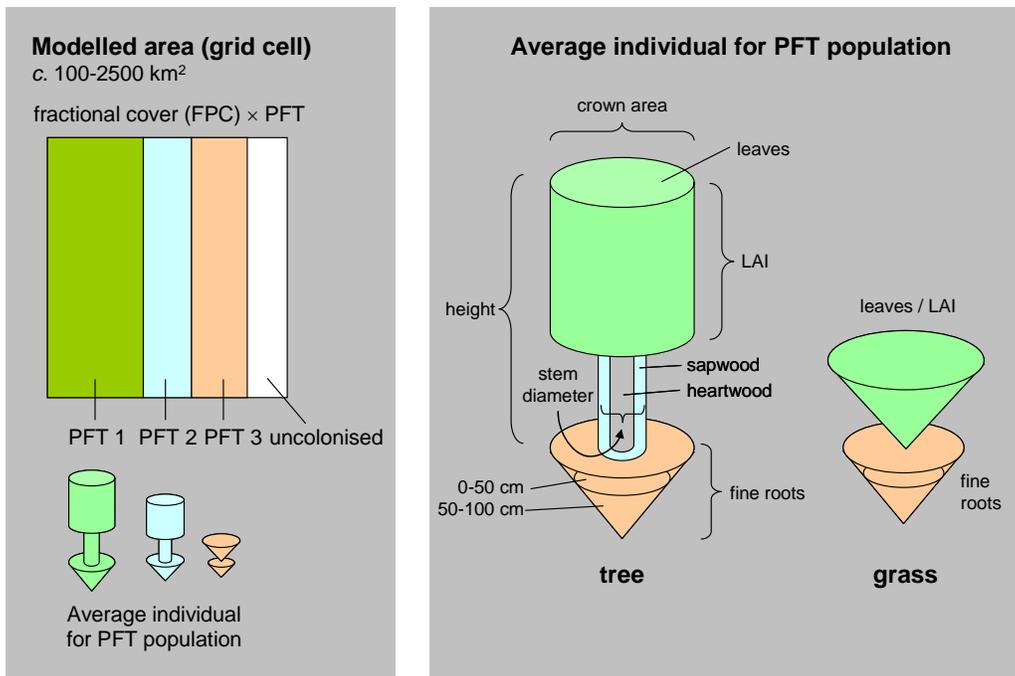
### 2.1 Average individual

The **average individual** is an important concept in LPJ-GUESS. An average individual consists of a series of state variables describing different properties of an individual plant: a tree, shrub or herb

(including grass). For example, an average individual tree includes information about the individual’s height, stem diameter, crown area, leaf area index, and carbon biomass, divided into leaves, fine roots, heartwood and sapwood. These properties are updated each day or year of the simulation. The different vegetation modes are named after the vegetation component that the average individual represents. In population mode, each average individual represents the average properties of an entire population of a **plant functional type (PFT)**, i.e. all individuals of the PFT occupying a particular modelled area or “stand”. In cohort mode, average individuals represent average properties of an age class, or **cohort**, of a PFT in a particular patch. In individual mode, there is one average individual for each true individual. (An exception is made for herbs or grasses, where there is just one average individual per patch).

## 2.2 Population mode

Population mode is simpler and much faster, but also less mechanistic, than cohort and individual modes. Each unit modelled area, often a cell within a grid, is assumed to be large, normally at least 100 km<sup>2</sup>. A unit model area is known as a **stand**, but does not normally equate to a single stand of vegetation in reality, but rather an extensive landscape consisting of many individual stands, and possibly some areas uncolonised by vegetation. The assumption that the modelled area is large is important because it implies that all of the state variables represent averages over many individuals, distributed among many vegetation patches at different stages of development (following local disturbances in the past). This means, in turn, that environmental variability at smaller scales, such as the microhabitat, patch and local scales, can be ignored – effects of environmental variability are assumed to “average out” at the larger scale being modelled. It also means that stochastic (random) processes, which result in highly variable outcomes (but with a certain expectation) at small scales, can be treated as deterministic at the larger scale being modelled. Examples of stochastic processes include the demographic processes of establishment and mortality which add or remove individuals from the population, as well as certain types of disturbance.



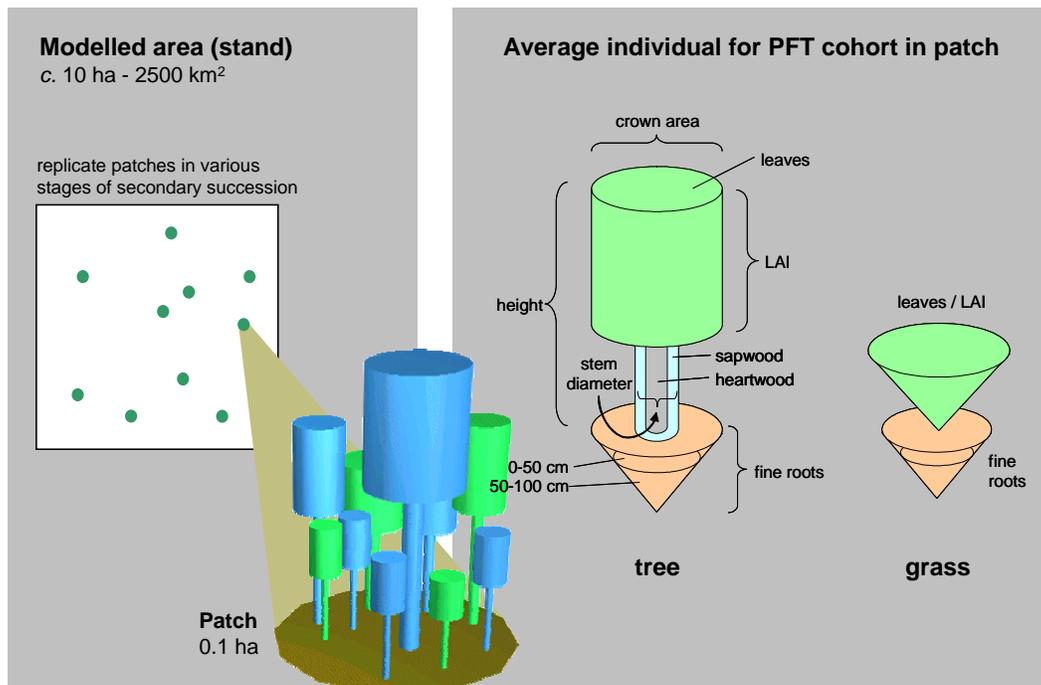
**Figure 3.** The representation of vegetation in “population mode”.

The vegetation of a modelled area is represented as a mixture of PFTs, each represented by a single average individual, and each covering a certain proportion of the modelled area, termed the **foliar**

**projective cover (FPC)** (Figure 3). The sum of the FPCs of all PFTs cannot exceed 1 (or 100%), which means that there can be no vertical overlap among PFTs. The areas occupied by different PFTs are assumed to be well-mixed and are not necessarily contiguous areas. Properties of the average individual are scaled to the modelled area by multiplying by the current “population density” (the number of average individuals per unit area, averaged over the entire modelled area). Population mode provides no direct information on the demography or size structure of PFTs, stages of stand development (succession) or vertical stand structure. This means that interactions among PFTs for the uptake of resources (especially light) can be represented only in very simplified, non-mechanistic ways.

### 2.3 Cohort and individual mode

In cohort and individual modes, tree or shrub populations and their dynamics are represented in similar ways to forest dynamic models (“gap” models), which simulate the growth of individuals within a number of replicate **patches**, corresponding in size approximately to the maximum area of influence of one large adult individual on its neighbours (Figure 4). In LPJ-GUESS, each modelled stand or grid cell is normally represented by 100 patches each 0.1 ha in size. The patches are assumed to be identical in terms of climate and soil type. Establishment, mortality and disturbance are normally implemented as stochastic processes and may result in different dynamics in different patches. Over many patches, however, modelled properties tend to converge on a single average value. In cohort mode, one average individual represents each PFT cohort in a patch (Figure 3), which implies that all individuals of the same age in a particular patch are identical in structure. Individual mode offers the possibility of representing differences among individuals in the same cohort, for example in initial size; however, this feature is not implemented in the current version of the model so that, in practice, individual mode is identical to cohort mode, but considerably slower! Because cohort mode distinguishes age classes and patches, vegetation is represented in much more detail compared with population mode. Competition for light, interactions between shade-tolerant and shade-intolerant PFTs, and succession following patch-destroying disturbances can be simulated in realistic ways.



**Figure 4.** The representation of vegetation in “cohort mode”.

### 3. Plant functional types

Modellers define plant functional types (PFTs) in order to represent the enormous structural and functional variety among the half million or so higher plant species of the world in a tractable way, capable of being simulated by a model. Any number of PFTs could in theory be defined in LPJ-GUESS, but the “standard” set consists of about 10 PFTs that cover all major higher plant types (Table 1). These are distinguished mainly according to their bioclimatic niche (distribution in climate space), growth form (tree/shrub or herb), leaf phenology type (evergreen, summergreen or raingreen), photosynthetic pathway ( $C_3$  or  $C_4$ ) and, in cohort and individual modes, life history type. These differences among PFTs affect their performance in the model under different climates, at different  $CO_2$  concentrations, and at different stages in the vegetation development. The characteristics of PFTs are controlled by values of a number of **PFT parameters**, defined in the **instruction (ins) file**, which is read in at the beginning of each model run.

**Table 1.** General characteristics of the global PFTs defined by Sitch et al. (2003)

PFT	Min. coldest month temperature(°C)	Leaf phenology	Drought tolerance	Shade tolerance	Fire tolerance	Production sensitive to $CO_2$
TrBE (tropical broadleaved evergreen tree)	+15.5	evergreen	low	high	low	yes
TrBR (tropical broadleaved raingreen tree)	+15.5	drought deciduous	high	high	high	yes
TeNE (temperate needleleaved evergreen tree)	-2	evergreen	medium	high	low	yes
TeBE (temperate broadleaved evergreen tree)	+3	evergreen	medium	high	low	yes
TeBS (temperate broadleaved summergreen tree)	-17	winter deciduous	low	high	low	yes
BNE (boreal needleleaved evergreen tree)	-32.5	evergreen	low	high	low	yes
BS (boreal summergreen tree)	no limit	winter deciduous	low	high	low	yes
C3G (boreal/temperate grass)	no limit	drought+winter deciduous	high	low	high	yes
C4G (tropical grass)	+15.5	drought+winter deciduous	high	low	high	no

#### 3.1 Bioclimatic niche

The standard global PFT set comprises three bioclimatic types: boreal, temperate and tropical. Boreal trees are able to survive at the lowest average coldest-month temperatures ( $T_{c,min}$ ), but cannot establish in climates where  $T_{c,min}$  is higher than  $-2^\circ C$ . Tropical trees are able to survive only in climates where  $T_{c,min}$  is  $15.5^\circ C$  (above zero!) or higher. Temperate trees have intermediate tolerance limits. Boreal and temperate trees also require a minimum growing season temperature sum ( $GDD_5$ , i.e. the annual sum of daily temperatures above  $5^\circ C$ ) to enable establishment. The boundary between  $C_3$  (boreal-temperate) and  $C_4$  (primarily tropical) herbaceous PFTs follows the  $15.5^\circ$  coldest-month isotherm.

#### 3.2 Growth form

Trees and herbaceous plants are distinguished. Shrubs can be implemented in principle, but are not part of the standard PFT sets for either population or cohort/individual modes. The herbaceous (non-woody) types mainly represent grasses, which are by far the most important herbs in terms of total biomass and cover at the global scale.

#### 3.3 Leaf phenology

Summergreen, or winter-deciduous, PFTs, which are characteristic for cool temperate and boreal biomes, shed their leaves (or needles, in the case of *Larix* [larch] species) in winter. Raingreen PFTs are common

in drier reaches of the tropics, and shed their leaves during the dry season. Remaining tree PFTs do not shed their leaves and have evergreen phenology. Most grasses are inactive under extremely cold or extremely dry conditions. Herbaceous PFTs are therefore classified as both summergreen and raingreen in LPJ-GUESS.

Evergreen PFTs have (by definition) a leaf longevity (life span)  $\geq 1$  year. Plants with longer-lived leaves generally invest greater resources in their leaves, for example, to promote leaf survival through periods of stress (winter, dry season) and to reduce damage by herbivory. Long-lived leaves are thus more “expensive” individually, but cheaper in that they do not have to be replaced as often. In LPJ-GUESS this aspect of leaf economics is implemented by relating the **specific leaf area** (SLA, the ratio of the one-sided leaf surface area to leaf carbon mass,  $\text{m}^2 \text{kgC}^{-1}$ ) to leaf longevity, according to an empirical relationship given by Reich et al. (1997):

$$SLA = 0.2 \cdot \exp(6.15 - 0.46 \cdot \ln 12a)$$

where  $a$  is leaf longevity, in years.

### 3.4 Photosynthetic pathway

The majority of plants have the  $\text{C}_3$  biochemical pathway of photosynthesis, in which the first product formed from  $\text{CO}_2$  contains three carbon atoms per molecule. The first set of biochemical reactions involved in converting  $\text{CO}_2$  to carbohydrates are known as carboxylation and are catalysed by the enzyme **Rubisco**. In the presence of molecular oxygen,  $\text{O}_2$ , however, rubisco can also catalyse an alternative reaction which consumes energy and releases  $\text{CO}_2$ . This process, known as **photorespiration**, reduces photosynthesis. Higher atmospheric  $\text{CO}_2$  concentrations reduce photorespiration and can enhance the productivity of  $\text{C}_3$  plants.

Most tropical grasses and some other plants of warmer environments possess the alternative  $\text{C}_4$  pathway, in which the first product of photosynthesis contains four carbon atoms. In addition, carboxylation takes place within a special cell structure separated from the site of initial  $\text{CO}_2$  fixation, where the  $\text{O}_2$  concentration is kept low. This reduces photorespiration and results in more efficient photosynthesis. However, it also means that the productivity of  $\text{C}_4$  plants is much less sensitive to changes in atmospheric  $\text{CO}_2$  concentrations.

### 3.5 Life history

In cohort and individual modes, where the vertical structure of vegetation and separate tree age classes are represented, it is meaningful to implement PFTs differing in life history and possible to simulate the interactions (competition) between them and how these affect the vegetation dynamics (Table 2).

Classical ecological theory suggests that species vary in their life history syndromes or “strategies” because of functional trade-offs: a function that maximises performance under some conditions (e.g. a high establishment rate) carries a cost in terms of inferior functioning under other conditions (e.g. poor tolerance of shading). In LPJ-GUESS, differences in the strategies of shade-tolerant and shade-intolerant PFTs are represented by different values of the PFT parameters governing the maximum establishment rate ( $\text{est\_max}$ ), the rate at which establishment declines with declining potential productivity at the forest floor ( $\alpha_r$ ), the minimum growing-season PAR (light) level at the forest floor required for establishment ( $\text{parff\_min}$ ), the growth-efficiency threshold for stress mortality ( $\text{greff\_min}$ ), the annual sapwood-to-heartwood turnover fraction ( $\text{turnover\_sap}$ ), and the expected life span under non-stressed conditions ( $\text{longevity}$ ).

Shade-intolerant trees specialise in colonising a newly cleared surface quickly, and growing rapidly in height, to remain above other developing trees and thus avoid being shaded. This requires a high maximum establishment rate and a greater relative investment in stems compared with other woody PFTs (increased investment in stems leads to greater height growth). For this reason, shade-intolerant PFTs have

a higher annual sapwood-to-heartwood turnover fraction, which represents the fraction of active transport tissue in stems that is converted to structural wood each year. The larger this fraction, the faster trees grow, but the converted sapwood needs to be replaced, which is a cost in terms of NPP.

Shade-intolerant trees have markedly reduced establishment under light shade (a high value of  $\alpha_r$ ; see Section 4.6.1), and cannot establish beneath a closed forest canopy (when the PAR level at the forest floor is lower than the threshold value specified by `parff_min`). Shaded adults experience low growth efficiency, defines as the ratio of individual NPP to leaf area. If growth efficiency falls below the threshold value specified by `greff_min`, the risk of mortality is increased so that death is likely to occur within a few years. This threshold is higher for shade-intolerant PFTs, which have lower survivorship in the shade compared with shade-tolerant trees.

Shade-tolerant trees have lower establishment under high-PAR conditions and grow more slowly in height for the same NPP compared with shade-intolerant PFTs. However, they are more tolerant of shade both in the seedling and adult phases, and for this reason are able to dominate a closed-forest, in which shade-intolerant species are unable to regenerate. Finally, shade-tolerant PFTs tend to be longer-lived (even in the absence of stress mortality) than shade-intolerant PFTs.

Taken together, differences in the life-history strategies of shade-tolerant and shade-intolerant PFTs imply that shade-tolerant trees will come to dominate the community in the absence of disturbances, and so long as temperatures and/or water availability are sufficient for canopy closure. In all but the driest or coldest environments, shade-intolerant PFTs are dependent on regular disturbances creating open areas for them to colonise.

**Table 2.** Major European PFTs implemented in LPJ-GUESS individual mode by Smith et al. (2001).

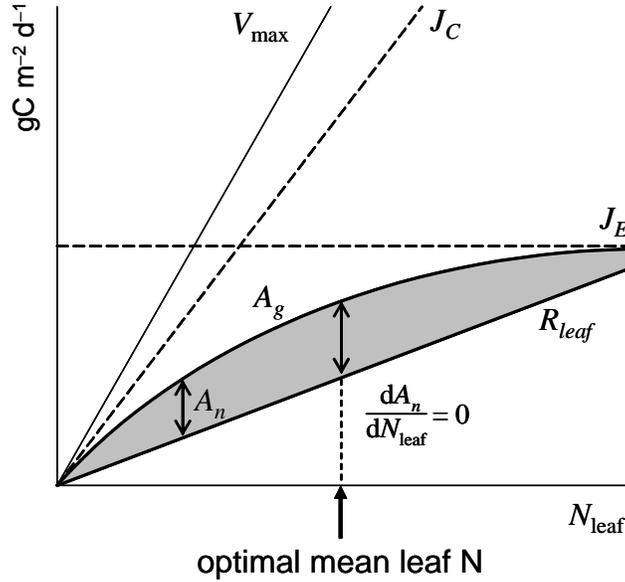
PFT	Min. coldest month temperature(°C)	Leaf phenology	Drought tolerance	Shade tolerance	Fire tolerance	Production sensitive to CO <sub>2</sub>
BNE (boreal needleleaved evergreen tree)	no limit	evergreen	medium	high	medium	yes
TBS (shade-tolerant broad-leaved summergreen)	-18	winter deciduous	medium	high	low	yes
IBS (shade-tolerant broad-leaved summergreen)	no limit	winter deciduous	medium	low	low	yes
BE (broadleaved evergreen tree)	+1.7	evergreen	medium	high	medium	yes
MNE (mediterranean needle-leaved evergreen tree)	+1.7	evergreen	high	low	high	yes
C3G (boreal/temperate grass)	no limit	drought+winter deciduous	high	low	high	yes

## 4. Simulated processes

### 4.1 Net primary production

Net primary production (NPP) is the balance of photosynthesis and autotrophic (plant) respiration, averaged over one year. Photosynthesis, stomatal conductance, plant water uptake and evapotranspiration are modelled concurrently on a daily time step by a coupled photosynthesis and water module adapted from the model BIOME3 (Haxeltine & Prentice 1996b). The photosynthesis sub-model is an adapted Farquhar scheme (Farquhar et al. 1980; Collatz et al. 1991; Haxeltine & Prentice 1996a), which computes net CO<sub>2</sub> assimilation at the canopy scale for each average individual each simulation day (or once per month, interpolating to derive a daily value). The input variables are absorbed photosynthetically-active radiation (APAR), air temperature ( $T_a$ ) and the CO<sub>2</sub> concentration of the intercellular spaces in the leaf mesophyll ( $c_i$ ). The maximum carboxylation rate,  $V_{max}$ , which must normally be specified as a parameter

in the Farquhar model, is computed prognostically based on the assumption of optimal nitrogen allocation in the vegetation canopy, assuming further that sufficient nitrogen is available to satisfy the “demand” by leaves (Figure 5).



**Figure 5.** LPJ-GUESS uses an adapted Farquhar photosynthesis scheme to compute net carbon assimilation at the canopy scale. The Farquhar model requires the maximum carboxylation rate,  $V_{max}$ , as a parameter, but this parameter varies e.g. with species, climate and canopy position. At a given temperature,  $V_{max}$  depends on the abundance of the nitrogen-rich enzyme rubisco. Leaf respiration, which reduces net  $\text{CO}_2$  assimilation, is linearly related to  $V_{max}$ . Following Haxeltine & Prentice (1996a) a canopy-average value of  $V_{max}$  is computed for each average individual and day based on the assumption that leaf nitrogen is distributed through the canopy in such a way as to optimise rubisco activity and maximise net assimilation (the balance of photosynthesis and leaf respiration) at the canopy level. The nitrogen supply is assumed to be sufficient to satisfy the leaf “demand”. Symbols:  $N_{leaf}$  = leaf nitrogen content;  $V_{max}$  = carboxylation capacity;  $J_c$  = carboxylation (rubisco)-limited photosynthesis rate;  $J_E$  = light-limited photosynthesis rate;  $A_g$  = gross photosynthesis;  $R_{leaf} = b \cdot V_{max}$  = leaf respiration ( $b$  is a constant parameter);  $A_n = A_g - R_{leaf}$  = net assimilation rate.

APAR, at the canopy level, is computed assuming that 50% of incoming shortwave radiation ( $R_s$ ) is of wavelengths usable for photosynthesis. Light extinction within the canopy depends on the **leaf area index (LAI)**, the ratio of leaf area to ground area) and is taken to follow Beer’s law, with an extinction coefficient  $k$ . In population mode, a parameter,  $\alpha_a$ , accounts for additional light losses via scattering and absorption by non-photosynthetic surfaces:

$$APAR = \alpha_a \cdot 0.5 \cdot R_s \cdot [1 - \exp(-k \cdot LAI)]$$

The leaf intercellular  $\text{CO}_2$  concentration  $c_i$  depends on the ambient (i.e. atmospheric)  $\text{CO}_2$  concentration and stomatal conductance,  $g_c$ . Plants are assumed to partially close their stomata, thereby reducing conductance, in order to avoid drying out when the potential transpiration rate exceeds the maximum uptake rate via the roots. This means that  $c_i$  is controlled by a complex relationship involving soil water content, plant root distributions, temperature and humidity as well as ambient  $\text{CO}_2$ . In LPJ-GUESS, part of

this relationship is parameterised by an empirical relationship between the equilibrium transpiration rate  $E_q$ , the potential maximum uptake rate (“supply”) of water from the roots ( $S$ ), and  $g_c$  (Monteith 1995):

$$g_c = -g_m \ln \left[ 1 - \frac{S}{E_q \alpha_m} \right]$$

Where  $g_m$  and  $\alpha_m$  are empirical parameters. This relationship describes the canopy conductance under water-limited condition, when the stomata are partially closed.

Autotrophic respiration is the sum of energy-demanding processes in vegetation, which result in release of  $\text{CO}_2$  and reduce NPP. Maintenance respiration, the cost of metabolic processes in living tissues, differs according to tissue C:N ratio:

$$R_m = r \frac{C}{C:N} g(T)$$

and follows a modified Arrhenius response to temperature (Lloyd & Taylor 1994):

$$g(T) = \exp \left[ 309 \cdot \left( \frac{1}{56} - \frac{1}{T + 46} \right) \right]$$

Where  $T$  = temperature in °C;  $C$  = tissue C biomass;  $r$  is a constant scaling factor (respiration coefficient). The temperature sensitivity term  $g(T)$  may be described as an exponential response that declines (becomes less steep) at higher temperatures. The Arrhenius relationship it is based on has been found to describe the behaviour of many biochemical processes. The modification introduced by Lloyd & Taylor (1994) represents a decline in the parameter for activation energy with temperature.

Growth respiration, the energetic cost of synthesising new tissue, is insensitive to temperature. It is set to a constant one-third of NPP.

## 4.2 Growth and allocation

The growth of average individuals is implemented at the end of each simulation year by allocating the annually-accrued individual NPP to three tissues or “compartments”: leaves, sapwood (which primarily corresponds to the outer ring of living transport tissue in the stems of trees) and fine roots. At the same time, a proportion of the existing sapwood is transferred to the non-living heartwood pool (the inner core of tree stems). It is the accumulation of sapwood and heartwood that controls height and diameter growth in trees. The allocation – i.e. the relative proportions of the NPP assigned to the three living compartments – is adjusted so that the following four allometric equations, or “constraints”, which control the structural development of the average individual, remain satisfied (Figure 6):

### Constraint 1. Leaf area to sapwood cross-sectional area relationship

An assumption based on the so-called Pipe Model (McDowell et al. 2002), which suggests that the ratio of the total leaf area ( $LA$ ) to the area of the sapwood, in cross-section ( $SA$ ), remains constant, irrespective of tree size:

$$LA = k_{lasa} \cdot SA$$

### Constraint 2. Functional balance

Following a period of water limitation, plants will tend to invest more in roots at the expense of leaves and stems, as an adaptation to ameliorate potential water limitation the following growing season:

$$C_{leaf} = k_{lr} \cdot \omega \cdot C_{root}$$

where  $\omega$  is the mean annual value of a drought-stress factor which varies between 0 and 1, higher values representing greater water availability.

**Constraint 3. Stem mechanics**

As trees grow, an increased stem diameter is required to support a heavier crown (Huang et al. 1992):

$$H = k_2 \cdot D^{2/3}$$

**Constraint 4. Crowding constraint**

This relationship describes the development of the crown projective area as trees grow under closed canopy conditions, competing with their neighbours for a share of the limited area available in the canopy. The relationship is derived from Reineke’s Rule (Reineke 1933) which suggests that mortality of suppressed individuals during the development of a young, even-aged stand of trees will lead to a power relationship between stem diameter and population density with an exponent of about 1.6:

$$N \approx D^{-1.6}$$

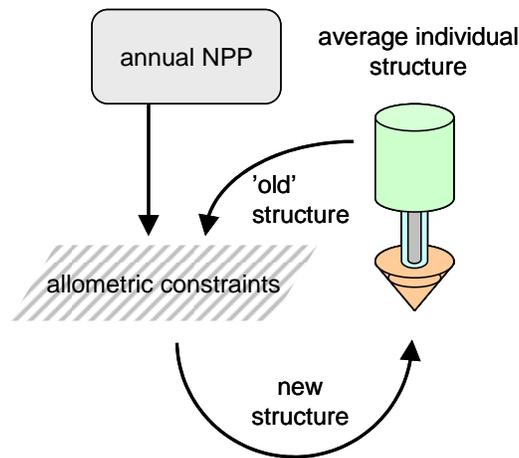
If the canopy is assumed to be divided equally between the crowns of all individuals, then crown area (m<sup>2</sup> per individual) will be the inverse of population density (individuals per m<sup>2</sup>):

$$CA = 1 / N$$

Combining the above equations gives a relationship between crown area and stem diameter:

$$CA = k_1 \cdot D^{1.6}$$

Herbaceous PFTs lack stems in the model, and follow only constraints 1 and 2.



**Figure 6.** Growth is simulated by adding the current year’s NPP of an average individual to its current biomass, partitioning the available carbon this represents among the living biomass compartments (leaves, fine roots and sapwood) such that the four allometric constraints remain satisfied.

### 4.3 Phenology

Leaf onset in summergreen (winter deciduous) PFTs is related to a cumulative temperature sum above a 5°C threshold (GDD<sub>5</sub>), counting from the beginning of the growing season. A PFT-specific parameter “phengddramp” defines the minimum GDD<sub>5</sub> required for full leaf cover. Leaf cover increases linearly with accumulated GDD<sub>5</sub> below this target value.

Raingreen (drought deciduous) PFTs retain their leaves until the daily value of the drought stress factor ( $\omega$ ) falls below a threshold value (normally 0.35). Full leaf cover is resumed once  $\omega$  rises above the threshold value again. The drought stress factor is calculated daily for each average individual, based on the balance between water supply via the roots and transpirative demand (potential transpiration). It ranges between 0 and 1, with smaller values representing increasing drought stress.

Herbaceous PFTs normally follow both summergreen and raingreen phenology.

### 4.4 Soil hydrology

Availability of water for plant growth is based on storage and flow within a two-layered soil profile. Water enters the upper soil layer (0-0.5 m) through precipitation, or melting of snow from a dynamic snow pack. On days with an average temperature  $\leq -2^\circ\text{C}$ , precipitation does not enter the soil directly but replenishes the snow pack. Transpiration by vegetation (see Section 4.1) and evapotranspiration from bare soil surfaces deplete the water content of the soil. Uptake by plants is partitioned according to the PFT-specific fraction of roots situated in each layer. Trees and shrubs are usually assumed to have a larger proportion of their roots in the lower soil layer, while herbaceous plants are shallow-rooting. This feature affects the relative performance of woody and herbaceous PFTs in dry environments differing in the seasonality of rainfall. Additional depletion of soil water may occur through percolation beyond the lower soil layer (0.5-1.5 m) and out of reach by plant roots, while precipitation onto a saturated upper soil layer is lost as surface runoff.

In the individual-based model, water content in each soil layer, and storage in the snow pack, are modelled independently for each patch, based on the overall precipitation and temperature and patch-specific vegetation dynamics; i.e. there are no horizontal fluxes of water between patches.

### 4.5 Litter and soil organic matter turnover

Biomass is converted to litter through shedding of leaves and roots by living individuals, and through vegetation mortality. Leaves and fine roots have a prescribed longevity, which may differ among PFTs. For summergreen and raingreen PFTs, leaf longevity is (by definition)  $\leq 1$  year. Leaves and roots converted to litter are replaced as part of the normal allocation process of the current year’s NPP.

Three decomposable carbon pools are distinguished: the litter pool and a “fast” and “slow” soil organic matter (SOM) pool. The pools differ in their decomposition rates. Carbon entering the litter pool has a mean residence time of 3 years (corresponding to a turnover, or decomposition, rate of  $1/3 \text{ year}^{-1}$ ) at  $10^\circ\text{C}$ . Corresponding residence times for the fast and slow SOM pools are 33 and 1000 years, respectively. The decomposition rate is given by:

$$\frac{dC}{dt} = -\frac{1}{\tau} \cdot g(T) \cdot f(W) \cdot C$$

where  $C$  is the carbon mass of the pool;  $\tau$  is the residence time at  $10^\circ\text{C}$ ;  $g(T)$  represents the sensitivity of decomposition to temperature;  $f(W)$  represents the sensitivity of decomposition to soil moisture.

In reality, soil organic matter is not made up of different pools, but comprises a more-or-less continuous series differing in “quality” as a substrate for decomposer organisms. As more labile (easily metabolised) fractions are consumed, the remaining material approaches a lower average quality and takes longer to

consume. This is represented in the three-pool formalism of LPJ-GUESS by transferring a fixed proportion (29.5%) of the carbon lost to the litter pool to the fast SOM pool, and a fixed proportion (0.5%) to the slow SOM pool. The remainder (70%) is taken to be heterotrophic respiration and contributes to the ecosystem CO<sub>2</sub> flux to the atmosphere. Consumption of the fast and slow SOM pools makes up the remainder of the heterotrophic respiration flux.

Decomposition rates are sensitive to temperature and soil moisture. The sensitivity to these factors is the same for all three pools. The temperature sensitivity follows the modified Arrhenius relationship of Lloyd & Taylor (1994), which is also used to scale plant maintenance respiration (see above):

$$g(T) = \exp\left[309 \cdot \left(\frac{1}{56} - \frac{1}{T + 46}\right)\right]$$

where  $T$  is soil temperature in °C, estimated at 25 cm depth. Decomposition varies with linearly with soil moisture in the upper (50 cm) soil horizon, ranging from 25% to 100% as plant available soil water ( $W$ ) varies from 0-100% of field capacity (Foley 1995), i.e.

$$f(W) = 0.25 + 0.75 \cdot W$$

## 4.6 Population dynamics

Changes in PFT populations occur in LPJ-GUESS through the establishment and mortality of individuals. The implementation of these processes is different in population mode, compared to cohort and individual modes.

### 4.6.1 Establishment

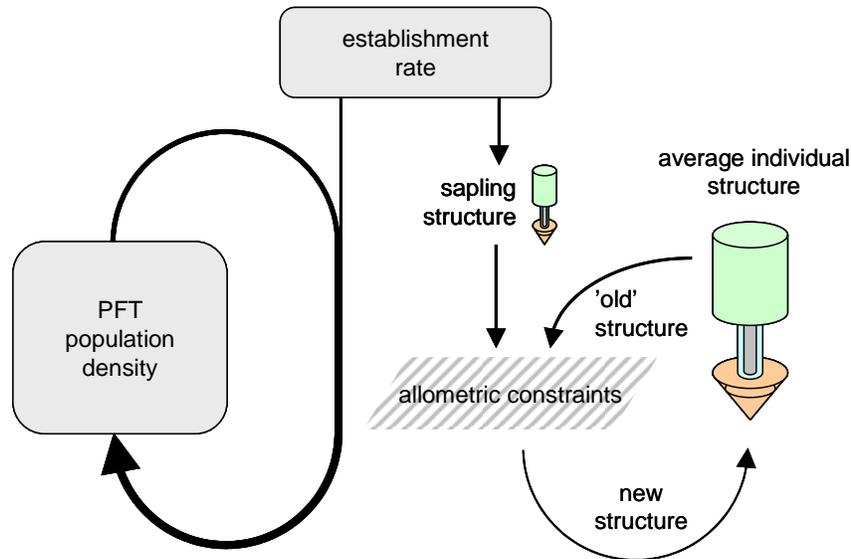
In all modes, bioclimatic limits determine which PFTs are able to establish under current climatic conditions for the modelled area (Table 1). The limits are applied to the average climate of the last 30 simulation years, to account for factors such as landscape heterogeneity and migration lags that might delay large-scale vegetation shifts as the climate changes. For PFTs within their bioclimatic limits, establishment is implemented at the end of each simulation year.

#### *Population mode*

In population mode, where individuals are not distinguished, tree establishment is implemented by increasing the “population density” of the PFT concerned, and adjusting the mass and structure of the average individual to reflect the addition of saplings (small trees) (Figure 7). As the saplings are invariably smaller than the average individual (which represents the average properties of all living individuals in the PFT population), the effect is that the average individual “shrinks”, while the population expands. The density of establishment (saplings m<sup>-2</sup>) declines as the modelled area fills, reflecting increasing competition for space and light. The dependency of establishment on total tree FPC (in the range 0-1) is given by:

$$est = est_{\max} \{1 - \exp[-5 \cdot (1 - FPC)]\} \cdot (1 - FPC)$$

Where  $est_{\max}$  is the potential establishment rate in the absence of competition from existing individuals. Herbaceous plants are assumed to be inferior in competition for light and establish only within areas not occupied by any woody PFT.



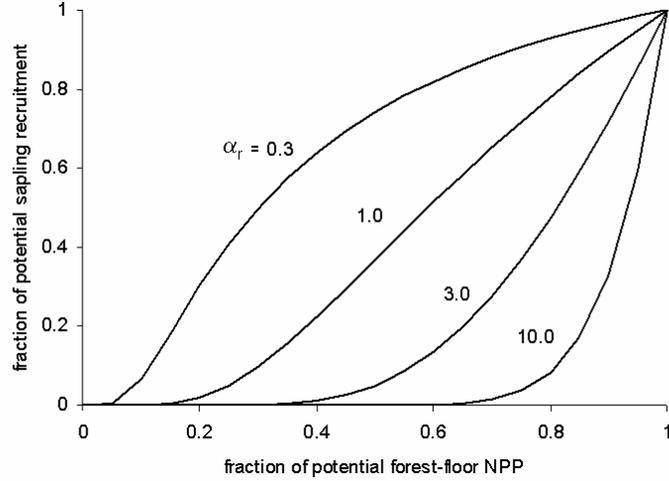
**Figure 7.** In population mode, establishment increments the PFT “population density”. The mass and structure of the average individual is adjusted to reflect the addition of saplings (small trees) at the density defined by the establishment rate.

#### *Cohort and individual mode*

Establishment is modelled directly as the addition of new individuals with the character of saplings. In cohort mode, a new cohort (age class), represented by one average individual object, is created in each patch. The density (individuals  $m^{-2}$ ) of each new cohort is a random number with an expectation affected by a PFT-specific maximum establishment rate ( $est_{max}$ ), the fraction of maximum potential productivity (NPP) at the forest floor ( $F$ ), and two constants,  $k$  and  $\alpha_r$ :

$$k \cdot est_{max} \cdot \alpha_r (1 - 1/F)$$

Generally conditions are best at the start of the simulation or following a disturbance, when there is no vegetation to cast shade onto the forest floor. Apart from shading, reduced soil water or temperature can also reduce potential forest-floor NPP, and therefore establishment rates. The rate at which establishment declines with declining forest-floor NPP is governed by the parameter  $\alpha_r$  (Fulton 1991) which is related to the life history class of the PFT. Higher values of  $\alpha_r$  represent a steeper decline in establishment rate as shading reduces potential seedling growth, as might be expected for shade-intolerant tree species (Figure 8).



**Figure 8.** Relationship of sapling recruitment to potential forest-floor NPP for different values of the PFT-specific parameter  $\alpha_r$ . Larger values of  $\alpha_r$  represent a steeper decline in establishment rate under shaded conditions, as expected for shade-intolerant trees. Smaller values are characteristic for shade-tolerant trees.

#### 4.6.2 Mortality

The death of individuals can result from stress, background factors such as senescence and small-scale disturbance, and large-scale disturbances. In addition, all individuals of a PFT are killed if coldest-month temperatures, averaged over the last 30 years, fall below a minimum threshold for survival of the PFT. Mortality results in a reduction in the population or cohort density. The biomass of killed individuals is transferred to the litter pool, except in the case of fire mortality, where the affected biomass is lost as a CO<sub>2</sub> flux to the atmosphere. Fire disturbance is discussed in more detail in the later section on disturbance.

##### *Population mode*

The annual mortality (fraction of individuals killed) is the sum of separate terms for mortality due to stress+background factors, shading and disturbance by fire, up to a maximum value of 1:

$$m = m_{stress} + m_{shade} + m_{fire}$$

Stress mortality is normally the result of chronic resource limitation or other factors that reduce productivity, such as low temperatures or a shortened growing season. Stress is characterised in the model by low values of growth efficiency, the ratio of NPP (in kgC m<sup>-2</sup> year<sup>-1</sup>) to leaf area index (m<sup>2</sup> leaves per m<sup>2</sup> ground):

$$m_{stress} = \frac{k_{mort}}{1 + 35 \cdot \frac{NPP}{LAI}}$$

Where  $k_{mort}$  is a constant parameter. Shading mortality is in reality a form of stress mortality, but is treated separately in the model as a mechanism to prevent the projective area of all tree PFTs together from exceeding the area of the grid cell following growth and establishment. Any excess in the summed FPC of all tree PFTs beyond a maximum value of 0.95 is reduced by “shading mortality”.

### *Cohort and individual mode*

Mortality within a tree cohort is typically highest at the seedling stage and later, as the surviving individuals approach their maximum potential life span. In LPJ-GUESS, the seedling stage is ignored, or rather, parameterised by the PFT-specific maximum sapling establishment rate and parameter  $\alpha_r$ , which take account of the effect of early-stage mortality factors on recruitment of seedlings to the adult (i.e. sapling and older) population. The individuals explicitly represented in LPJ-GUESS, therefore, face an increasing risk of mortality due to background factors as they approach their maximum potential life span. Mortality is stochastic with each individual having a certain probability of death each year. The expected annual background mortality ( $m_{\min}$ ) is given by:

$$m_{\min} = -\frac{3 \ln 0.001}{age_{\max}} \left( \frac{age}{age_{\max}} \right)^2$$

where  $age$  is the current cohort age and  $age_{\max}$  is the maximum expected life span or longevity.

Stress mortality may affect individuals whose growth efficiency, defined as the ratio of individual annual NPP to individual leaf area, averaged over five years, falls below a PFT-specific threshold. These individuals face a 30% likelihood of death each year that their growth efficiency is below the threshold. Low growth efficiency could be caused by low temperatures, drought or a shortened growing season, but the most likely cause is severe shading by taller individuals.

## 4.7 Disturbance

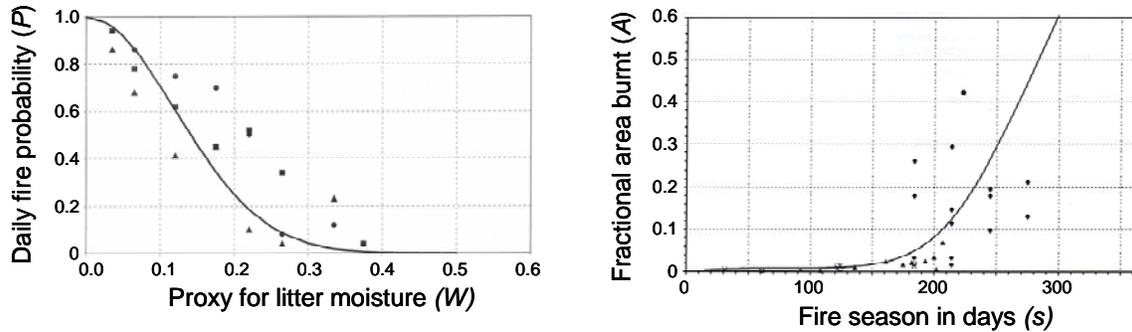
Fire is the most important class of disturbance, in terms of area affected globally each year. It is the only class of disturbance modelled in population mode. The fire sub-model is described in detail by Thonicke et al. (2001). The probability of a fire occurring within the modelled area is calculated each day based on the litter load, flammability and the available water content of the uppermost soil layer ( $W$ , in the range 0-1), as a surrogate for the litter moisture content, which is not modelled explicitly. Litter flammability is characterised by the “moisture of extinction”, which is a PFT-specific parameter in the range 0-1, with lower values representing increasing flammability. This daily probability of fire is given by the empirical relationship (Figure 9):

$$P = \exp\left[-3.14 \cdot (W / m_e)^2\right]$$

The sum of daily fire probabilities over a year gives the fire season length in days ( $s$ ). The proportion of the modelled area affected by fire is then determined as a function of the fire season length by the empirical equation (Figure 9):

$$A = s / 365 \cdot \exp\left[\frac{s - 1}{0.45 \cdot (s - 1)^3 + 2.83 \cdot (s - 1)^2 + 2.96 \cdot (s - 1) + 1.04}\right]$$

Fires result in mortality and combustion of biomass and litter over the affected area. The proportion of individuals affected is further controlled by a PFT-specific fire resistance parameter. The proportion of individuals from the affected area that are burned and killed is  $(1-R)$ , where  $R$  is the fire resistance, in the range 0-1. The biomass of burned individuals and carbon from burnt litter (which has a fire resistance equal to the PFT from which it originated) are lost to ecosystems as a flux to the atmosphere.



**Figure 9.** Relationships between daily fire probability and litter moisture, and between the annual fractional area burnt and the fire season length. The curves are empirical equations fitted to observational data (Thonicke et al. 2001).

In cohort and individual modes, fires are not usually modelled. Instead, generic disturbances with a certain expected interval ( $d$ ) may be prescribed. These kill all individuals on an affected patch, converting their biomass to litter. Disturbances occur at random, with a probability of  $(1/d)$  of affecting any given patch in a particular year.

## 5. Applications and further reading

A full description of earlier versions of LPJ-DGVM and GUESS is given by Smith et al. (2001). Note that many details, including a number of key equations, are given in the online appendix of that paper, not in the main text.

Further details of the physiological, biophysical and biogeochemical components of the models are given by Sitch et al. (2003). Some elements are inherited from the equilibrium biosphere model BIOME3 and are documented by Haxeltine & Prentice (1996b). The current version of LPJ-GUESS includes improved representations of soil hydrology, snow pack dynamics and soil-vegetation-atmosphere exchange of water, as documented by Gerten et al. (2004).

Numerous studies have employed LPJ-DGVM and LPJ-GUESS to explore impacts of climatic and environmental changes on vegetation and ecosystems:

- In a pioneering study using DGVMs, Cramer et al. (2001) simulated changes in global terrestrial ecosystem carbon balance under a climate change scenario for the 21st century. Five out of six DGVMs, including LPJ, simulated strong carbon sinks to 2100, with only one (Hybrid) showing saturation of primary production and strong declining sink strength after 2050. Results were reprinted and formed part of the Third Assessment Report of IPCC (Prentice et al. 2001), but have been questioned by, among others, Hungate et al. (2003).
- McGuire et al. (2001) used LPJ-DGVM and three other terrestrial carbon cycle models to assess the relative contributions of climate, atmospheric  $\text{CO}_2$  concentrations and changes in agricultural land cover in explaining changes in biospheric carbon storage through the 20th century. Three out of the four models, including LPJ, simulated net losses of carbon to the atmosphere prior to 1950 due mainly to expansion of agricultural areas at the expense of forest. In the final decades of the 1900s, increasing  $\text{CO}_2$  concentrations stimulated ecosystem carbon storage, causing all models to predict a net sink for carbon as also suggested by so-called inversion studies. The strongest sinks were inferred to occur in non-tropical parts of the northern hemisphere.
- Lucht et al. (2002) used LPJ-DGVM to explore the causes of increasing land surface greenness revealed by satellite data for the northern hemisphere from the early 1980s onwards. Both an observed advancement in the onset of greening (earlier spring leaf-out) and an increase in maximal LAI were

reproduced by the model when driven by climate data alone. Almost the same trends were predicted when the model was driven by temperature changes alone, leading to the inference that a longer growing season is the primary mechanism underlying the observed greening. A primary production anomaly associated with the cooling effect of the 1991 Mt Pinatubo eruption was apparent in both the satellite and model time series.

- Hickler et al. (2004) demonstrated the skill of LPJ-GUESS in reproducing successional pathways and compositional variation in forests growing in different climates of the Great Lakes region of North America.
- Gritti et al. (2005) explored the possible effects of future climatic and vegetation changes on the vulnerability of Mediterranean islands to invasions by exotic weeds. Simulations with LPJ-GUESS in which invasive plants were introduced to the simulated natural ecosystems under a climate warming scenario suggested that climate change alone might have a relatively minor influence on invasibility compared with the effects of different disturbance regimes.
- Zaehle et al. (2005) used Monte-Carlo methods to examine parameter-based uncertainty in the population mode of LPJ-GUESS. The analysis revealed that uncertainty surrounding a number of parameters scaling physiological processes, such as photosynthesis, was responsible for much of the uncertainty in output variables such as NPP, heterotrophic respiration and net carbon exchange. Potential future trends in ecosystem carbon balance, as simulated in Cramer et al. (2001), were, however, found to be relatively robust to uncertainty propagating from the parameters of the model.
- In one of the first studies to apply a species-based model on the regional scale, Koca et al. (2006) simulated changes in the composition, carbon balance and growth of potential natural vegetation under future climate scenarios for Sweden.
- In a future scenario-based study, Scholze et al. (2006) used LPJ-DGVM to identify risk areas for dangerous ecosystem changes: forest/non-forest shifts, increased wildfire, and reduced water supplies. The risks of dangerous changes in ecosystems and their services, and the areas affected by such changes, were predicted to be substantially greater under  $>3^{\circ}\text{C}$  global mean warming compared with  $<2^{\circ}\text{C}$ .
- Morales et al. (2007) investigated the sensitivity of future trends in the carbon exchange of European ecosystems to the assumptions underlying scenarios generated by different climate models and different future concentrations of atmospheric  $\text{CO}_2$ . When driven by different scenarios, LPJ-GUESS predicted contrasting patterns of future change in NEE, especially in drier parts of central and southern Europe. For Europe as a whole, the uncertainty propagating from different global climate models (GCMs) was found to be greater than the uncertainty due to different regional climate models (RCMs) or emissions scenarios.

## 6. References

- Collatz, G.J., Ball, J.T., Grivet, C. & Berry, J.A. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* 54: 107-136.
- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A. & Young-Molling, C. 2001. Global response of terrestrial ecosystem structure and function to  $\text{CO}_2$  and climate change: results from six dynamic global vegetation models. *Global Change Biology* 7: 357-373.
- Farquhar, G.D., von Caemmerer, S. & Berry, J.A. 1980. A biochemical model of photosynthetic  $\text{CO}_2$  assimilation in leaves of  $\text{C}_3$  plants. *Planta* 149: 78-90.
- Foley, J.A. 1995. An equilibrium model of the terrestrial carbon budget. *Tellus* 47B: 310-319.
- Fulton, M.R. 1991. Adult recruitment rate as a function of juvenile growth in size-structured plant populations. *Oikos* 61: 102-105.

- Gerten, D., Schaphoff, S., Haberlandt, U., Lucht, W. & Sitch, S. 2004. Terrestrial vegetation and water balance—hydrological evaluation of a dynamic global vegetation model. *Journal of Hydrology* 286: 249-270.
- Gritti, E.S., Smith, B. & Sykes, M.T. 2005. Vulnerability of Mediterranean basin ecosystems to climate change and invasion by exotic plant species. *Journal of Biogeography* doi:10.1111/j.1365-2699.2005.01377.x
- Haxeltine, A., Prentice, I.C. 1996a. A general model for the light-use efficiency of primary production, *Functional Ecology* 10: 551-561.
- Haxeltine A. & Prentice I.C. 1996b. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochemical Cycles* 10: 693-709.
- Hickler, T., Smith, B., Sykes, M.T., Davis, M.B., Sugita, S. & Walker, K. 2004. Using a generalized vegetation model to simulate vegetation dynamics in the western Great Lakes region, USA, under alternative disturbance regimes. *Ecology* 85: 519-530.
- Huang, S., Titus, S.J., Wiens, D.P. 1992. Comparison of nonlinear height-diameter functions for major Alberta tree species. *Canadian Journal of Forest Research* 22: 1297-1304.
- Hungate, B.A., Dukes, J.S., Shaw, M.R., Luo, Y. & Field, C.B. 2003. Nitrogen and climate change. *Science* 302: 1512-1513.
- Koca, D., Smith, B. & Sykes, M.T. 2006. Modelling regional climate change effects on Swedish ecosystems. *Climatic Change* 78: 381-406.
- Lloyd, J. & Taylor J.A. 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8: 315-323.
- Lucht, W., Prentice, I.C., Myneni, R.B., Sitch, S., Friedlingstein, P., Cramer, W., Bousquet, P., Buermann, W. & Smith, B. 2002. Climatic control of the high-latitude vegetation greening trend and Pinatubo effect. *Science* 296: 1687-1689.
- McDowell, N., Barnard, H., Bond, B.J., Hinckley, T., Hubbard, R.M., Ishii, H., Köstner, B., Magnani, F., Marshall, J.D., Meinzer, F.C., Phillips, N., Ryan, M.G., Whitehead, D. 2002. The relationship between tree height and leaf area: sapwood area ratio. *Oecologia* 132: 12-20.
- McGuire, A.D., Sitch, S., Clein, J.S., Dargaville, R., Esser, G., Foley, J., Heimann, M., Joos, F., Kaplan, J., Kicklighter, D.W., Meier, R.A., Melillo, J.M., Moore, B. III, Prentice, I.C., Ramankutty, N., Reichenau, T., Schloss, A., Tian, H., Williams, L.J. & Wittenberg, U. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO<sub>2</sub>, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles* 15: 183-206.
- Morales, P., Hickler, T., Rowell, D.P., Smith, B. & Sykes, M.T. 2007. Changes in European ecosystem productivity and carbon balance driven by Regional Climate Model output. *Global Change Biology* 13: 108-122.
- Prentice, I.C., Farquhar, G.D., Fasham, M.G.R. et al. 2001. The Carbon Cycle and Atmospheric Carbon Dioxide. Ch. 3 in Houghton, J.T. et al. *Climate Change 2001 - The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the IPCC. Cambridge University Press, pp 183-237.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences USA* 94: 13730-13734.
- Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research* 46: 627-638.
- Scholze, M., Knorr, W., Arnell, N.W. & Prentice, I.C. 2006. A climate-change risk analysis for world ecosystems. *Proceedings of the National Academy of Sciences USA* 103: 13116-13120.
- Sitch, S., Smith, B., Prentice, I.C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J., Levis, S., Lucht, W., Sykes, M., Thonicke, K. & Venevsky, S. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. *Global Change Biology* 9: 161-185.
- Smith, B., Prentice, I.C. & Sykes, M.T. 2001. Representation of vegetation dynamics in modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography* 10: 621-637.
- Thonicke, K., Venevsky, S., Sitch, S. & Cramer, W. 2001. The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. *Global Ecology and Biogeography* 10: 661-677.
- Zaehle, S., Sitch, S., Smith, B. & Hatterman, F. 2005. Effects of parameter uncertainties on the modeling of terrestrial biosphere dynamics. *Global Biogeochemical Cycles* 19: 3020.