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The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model

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ABSTRACT

1 Disturbances from fire, wind-throw, insects and other herbivores are, besides climate, CO_2, and soils, critical factors for composition, structure and dynamics of most vegetation. To simulate the influence of fire on the dynamic equilibrium, as well as on potential change, of vegetation at the global scale, we have developed a fire model, running inside the modular framework of the Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ-DGVM).
2 Estimated litter moisture is the main driver of day-to-day fire probability. The length of the fire season is used to estimate the fractional area of a grid cell which is burnt in a given year. This affected area is converted into an average fire return interval which can be compared to observations.
3 When driven by observed climate for the 20th century (at a 0.5° longitude/latitude resolution), the model yielded fire return intervals in good agreement with observations for many regions (except parts of semiarid Africa and boreal Siberia). We suggest that further improvement for these regions must involve additional process descriptions such as permafrost and fuel/fire dynamics.

Key words disturbance, dynamic global vegetation model, fire model, fire return intervals, fire season, plant functional types, vegetation dynamics.

INTRODUCTION

Disturbance, defined as irregularly occurring destruction of vegetation structure, whether natural or human-induced, plays an integral part in shaping global vegetation (Sousa, 1984; Glenn-Lewin & van der Maarel, 1992). Disturbance usually acts as an additional component, which together with climate and soil conditions drives vegetation structure and functioning. Sites opened by disturbance allow regeneration of vegetation, thereby often maintaining vegetation composition and successional cycles. Depending on the post-disturbance environment, disturbance can also accelerate changes in vegetation composition, possibly resulting in different vegetation dynamics and altered biodiversity. Consequently, inclusion of disturbance in vegetation models is required to simulate vegetation dynamics correctly.

In this study, we consider fire as a primary disturbance agent, because of its overwhelming importance in many ecosystems — other agents could be considered using a similar approach. The long history of fire ecology and fire modelling studies provides process understanding and suitable algorithms for including fire disturbance in a vegetation model (see, e.g. Gardner *et al.*, 1999).

The role of fire for natural vegetation

Fire is one of the major disturbance agents on the global scale, affecting biogeochemical cycling, playing an important role in atmospheric

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chemistry and the global carbon cycle. Globally, approximately 3.9 Gt of carbon (Gt C) are released annually into the atmosphere through biomass burning (Andreae, 1991), equivalent to over 70% of the annual anthropogenic fossil fuel emissions. With its inherent sensitivity to climatic conditions, and with the prospect of rapid future climate change, fire has been a focus of intensive investigation in recent years (Levine, 1996). Vegetation composition and biogeochemical cycling in many European ecosystems are strongly affected by fire and therefore must be included in any European regional study (Sykes *et al.*, 2001).

The season of burning and the time between recurring fires determine the plant species composition through selection in most ecosystems. In semi-arid and arid grasslands the season of burning determines the final assemblage of C_3 and C_4 grasses and forbs, while the length of the fire return intervals governs the invasion of woody plants on a site, given sufficient precipitation (Bragg, 1995). By initiating successional cycles, a larger number of species can often be maintained, as is observed in tropical rain forests (Goldammer, 1992), Mediterranean-type ecosystems (Keeley & Keeley, 1988; Walter & Breckle, 1991a), boreal forests (Walter & Breckle, 1991a; Treter, 1993) and in the transition zone between boreal and temperate deciduous forest (Burrows, 1990).

The nutrient cycle is accelerated by fire, with the formation of ash rapidly mobilizing nutrients for the plants regenerating in the newly opened understorey. This is important in ecosystems with long decomposition cycles, e.g. in the boreal forest (Treter, 1993) or where soils are nutrient poor, e.g. in South-African fynbos (Kruger & Bigalke, 1984), Californian chaparral (Rundel, 1981; Walter & Breckle, 1991a) or the African savanna (Scholes & Walker, 1993). A changing fire regime may cause an overall loss of nutrients in the ecosystem.

Fire can influence the hydrological cycle and soil chemistry by transferring heat into the soil, thereby changing microclimate and soil conditions. In the boreal forest, removal of the litter layer leads to intensified soil heating during the growing season, increasing the melting depth in permafrost soils, and thus tree-rooting depth (Treter, 1993). In Mediterranean-type shrublands, oxidation and erosion of soil organic matter due to intense fire affects water-holding capacity and erosivity (Christensen, 1994).

In the long history of human intervention in nature, different and changing interests have influenced fire regimes, and hence vegetation. The existence of ecosystems such as the African savannas, the Brazilian cerrado, many Mediterranean-type ecosystems and Prairie grasslands cannot be adequately explained without the consideration of human burning activities, which shifted the periodicity of fire, consequently changing vegetation composition (Bourlière & Hadley, 1983; Coutinho, 1990; Schüle, 1990; Davis & Richardson, 1995). After a change in management, previously adapted plants may no longer be adapted to the new fire regime, as changes in pastoralism (e.g. Davis & Richardson, 1995) or North-American fire suppression policy have shown. It was believed initially that suppression would reduce fire hazard and economic loss, but in fact it merely demonstrated how fire is a key driver in vegetation dynamics. Fire suppression reduced the number of medium to large-scale fires, with the effect that a small number of huge fires account for 98% of the total area burnt (Stocks, 1991). Such a change in fire dynamics has important influences on stand-age structure, e.g. in the western Canadian boreal forest (Johnson *et al.*, 1998).

Simulating fire within a Dynamic Global Vegetation Model

Many fire models have been developed for various spatial and temporal scales and application purposes. The state-of-the art process-orientated fire models (e.g. Albini, 1976; Keane *et al.*, 1996) include processes of topography-dependent lateral fire spread and are designed for GIS systems at relatively fine scales (1 km or less). They are therefore not directly applicable on the coarse $0.5°$ (≈ 50 km) scale, i.e. cannot be directly incorporated into Dynamic Global Vegetation Models (Cramer *et al.*, 2001). Modelling fire at this coarse spatial scale requires a top-down approach, which considers only major regional characteristics but is sufficiently general to be applicable to every grid cell on the global scale.

To link fire regime and its effects on vegetation dynamics we have developed a general fire model Glob-FIRM (*Glob*al *FIR*e *M*odel) that has been incorporated into the LPJ-DGVM (Sitch *et al.*, 2000; Smith *et al.*, 2001). Our approach is a compromise between the fire history concept

(a statistical relationship between the length of the fire season and area burnt) and a process-orientated model methodology (estimation of fire conditions based on soil moisture). A relationship between the daily litter moisture status and the length of the fire season is derived from observed data to develop the function for probability of fire occurrence. Observed data are also used to calibrate a function that describes the relationship between the length of the fire season and annual area burnt. The fire module is validated against observations of typical fire return intervals.

Human-changed fire regimes as well as other land use impacts are not considered in the LPJ-DGVM at the present stage. As a first step, the impact of simulating fire is studied for natural conditions to demonstrate the applicability of this model before combining impacts of fire and land use on vegetation. The coupled model (i.e. the DGVM including the fire module) is used to study the interaction between fire and global vegetation over the historic period 1901–98.

MODEL DESCRIPTION

The Lund–Potsdam–Jena Dynamic Global Vegetation Model

The LPJ-DGVM (Sitch *et al.*, 2000; Smith *et al.*, 2001) was constructed in a modular framework. Individual modules describe key ecosystem processes, including vegetation establishment, resource competition, growth and mortality. Vegetation structure and composition are described by nine plant functional types (PFTs), which are distinguished according to their plant physiological (C_3, C_4 photosynthesis), phenological (deciduous, evergreen) and physiognomic (tree, grass) attributes. The model is run on a grid cell basis with inputs of soil texture, monthly fields of temperature, precipitation and percentage sunshine hours. These fields are interpolated to obtain daily values for processes calculated on a daily time-step, such as evapotranspiration and soil moisture status. Each grid cell is divided into fractions covered by the PFTs and bare ground. The presence and fractional coverage of an individual PFT depends on its specific environmental limits, and on the outcome of resource competition with the other PFTs.

The two-layer soil–water balance model is based on Haxeltine & Prentice (1996). Moisture in each layer, expressed as a fraction of water holding capacity, is updated daily. Percolation from the upper to the lower layer, and absolute water-holding capacity are soil texture-dependent.

Establishment and mortality are modelled on an annual basis. Plant establishment, in terms of additional individuals, depends on the fraction of bare ground available for seedlings to establish successfully. Natural mortality is taken as a function of plant vigour, and corresponds to an annual reduction in the number of individuals. Dead biomass enters the litter pool and the soil pools. Mortality also occurs due to disturbance (explained in the fire model section below).

The fire module Glob-FIRM in the LPJ-DGVM

Fire is modelled as the combination of fire occurrence and its effects. In order to model both processes on a global scale some simplifying hypotheses are made. First, fire occurrence is dependent only upon fuel load and litter moisture (i.e. the amount of dry material available), which combines both the influence of climate and vegetation. Ignition is assumed to take place sooner or later, without specific consideration. Secondly, fire effects are mainly driven by the length of the fire season and the PFT-dependent fire resistances.

Fire occurrence

To start a fire the fuel has to reach a minimum temperature at which it ignites. Combustion will start if there is sufficient fuel present at the site. If fuel moisture is above a certain level, then all available energy in the preheating process is consumed to vaporize water, thus ignition temperature is not reached and ignition, either spontaneously or due to fire spread, fails (Viegas, 1997b). The threshold of fuel moisture content above which a fire would not spread is named the 'moisture of extinction'. Albini (1976) reports moisture of extinction for dead fuel in the range of 15–30% in temperate ecosystems, similar to values reported by Kauffman & Uhl (1990) in tropical rain forest, Viegas (1998) in the Mediterranean Basin and De Ronde *et al.* (1990) in tropical industrial pine plantations.

Even if the fuel is dry enough, a fuel load of less than approximately 200 g/m^2 reduces fire spread to zero (Schultz, 1988). In ecosystems with high climate variability and consequently fluctuating vegetation productivity, periods with a discontinuous fuel bed, i.e. insufficient fuel load, are characterized by little or no area burnt despite favourable climatic conditions. Above the threshold, fuel load is sufficient to sustain fire and is therefore not limiting fire spread. Instead, climate conditions become more important. This is in agreement with observations from boreal forests (Bessie & Johnson, 1995; Schimmel & Granström, 1997), where climate conditions vary more over time than available fuel load (which is in ample supply) and have a larger impact on fire behaviour and fire spread.

In our model, the influence of fuel load on fire spread and thus the final area burnt, is described by a threshold function. Below a threshold of 200 g/m^2 fire is not permitted. If a sufficient amount of dead fuel exists with a moisture content below the moisture of extinction, then both live and dead fuel will start to burn. As a first approximation it is assumed that an ignition source is always available, either natural or anthropogenic.

Experimental data on dead fuel (pine needles) moisture have been used to develop a function to estimate the probability of fire in a grid cell. Measurements were made by Viegas *et al.* (1992) in three zones in Central Portugal, differing in both climate and land use. The results of these experiments express the probability of at least one fire occurring on a day with a given moisture content. They show that, for this part of the world, the daily moisture content of dead fuel has similar dynamics and similar extinction values in all three zones. The measurements of dead fuel moisture content were corrected for a consistent bias, associated with the specific measurement technique (Viegas *et al.*, 1992), using the fire behaviour model BEHAVE (Rothermel *et al.*, 1986). The resulting relationship between measured and predicted dead fuel moisture content, $\tilde{m}$ and m, respectively, is:

$$m = 0.4994 * \tilde{m} + 1.02 \tag{1}$$

with $r^2 = 0.852$, where $\tilde{m}$ and m are percentages (see equation 8 in Viegas *et al.*, 1992). In our fire model, m is taken as the daily moisture status in the upper soil layer.

The exponential power function (equation 2) is used to approximate the probability of the occurrence of at least one fire in a day in a grid cell:

$$p(m) = e^{-\pi * \left(\frac{m}{m_e}\right)^2} \tag{2}$$

where m_e is the moisture of extinction. Statistically, fire is considered to be absent when m exceeds m_e with probabilities lying within the 95% confidence interval (see equation 3). The smooth non-linear function provides the better fit and continuity over the entire range for possible daily moisture status (m ranging from 0.0 to 1.0), than a simple linear function.

$$1 - p(m_e) = 1 - e^{-\pi} \approx 0.956 \tag{3}$$

Equation 2 yields good fit to the experimental data for the three zones in Central Portugal with the moisture of extinction equal to approximately 30% (see Fig. 1), which is well within the range of the published data.

Although the fuel composition and its surface-to-volume ratio are important parameters for fuel ignition (Albini, 1993; Viegas, 1997a), fuel flammability is species dependent (Heinselman, 1981; Walter & Breckle, 1991a). The present PFT definition is too general, with PFTs not characterized in terms of fuel flammability. This could be implemented in a future definition of fire-related subsets of PFTs. As a first approximation, m_e is kept constant at 30% for the set of woody PFTs (e.g. trees and large shrubs) and 20% for herbaceous PFTs. The latter value is obtained by averaging observed values for grasses of different height and small shrubby vegetation according to Albini (1976).

The annual length of the fire season is estimated by adding the probability of at least one fire in a day over the whole year:

$$N = \sum_{n=1}^{365} p(m_n) \tag{4}$$

Fire effects

After ignition, the temporal and spatial change in burning conditions determine fire spread, and thus fire size. The lower the moisture content of the fuel, the less energy is consumed in the preheating process, the faster the fire can propagate. The
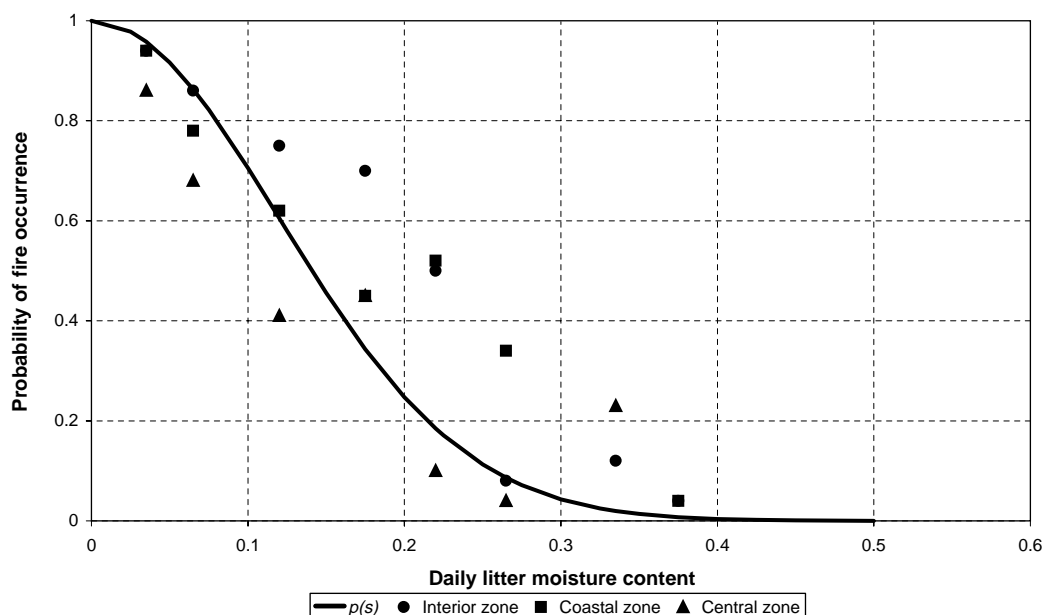
Fig. I The probability of at least one fire occurring on a day with a given litter moisture content. The points represent the experimental data for each investigated zone in Central Portugal (Viegas *et al.*, 1992), averaged over the four years of investigation.

area burnt is inversely related to the daily moisture content of dead fine fuels as field measurements in Portugal have shown (Viegas *et al.*, 1992; Viegas, 1998). The longer the burning conditions persist, the larger the fire can grow (Viegas, 1998). This leads to the assumption that, on the meso-scale of our grid cells, the same relative annual sum s of days with particular fire conditions N (see equation 4) with $s = N/365$ gives the same annual fractional area burnt, A, expressed in terms of a fraction of the grid cell. We assume that this relationship is the same in all geographical regions. A is zero when fire conditions were absent during the year, and reaches 1 when fire conditions continue throughout the entire year. As a non-linear function, $A(s)$ can be expressed as follows

$$A(s) = s * f(s) \qquad (5)$$

where $f(s)$ is equal to 1, when $s = 1$. Assuming that $f(s)$ is

$$f(s) = e^{((s-1)*\alpha(s-1))} \qquad (6)$$

$\alpha(s-1)$ is a function, which provides the rate of exponential growth in annual fractional area burnt with increasing length of fire season. The

shape of $f(s)$ defines the rapid change of behaviour in $A(s)$ from an almost linear slow increase of the annual fractional area burnt, when the length of the fire season is less than half a year, to a rather rapid increase, when the length of the fire season exceeds half a year (see Fig. 2).

If we combine equations 5 and 6, $\alpha(s-1)$ can be expressed in terms of $A(s)$ and s,

$$\alpha(s-1) = \frac{\ln(A(s)) - \ln(s)}{s-1} \qquad (7)$$

The observed data of area burnt, converted into fraction $\tilde{A}$, with corresponding length of fire season $\tilde{s}$, were used in equation 7 to obtain estimates of $\alpha(s-1)$. A non-linear regression of these values satisfying the least mean square criteria gives the following formulation:

$\alpha(s-1) =$

$$\left(\frac{1}{0.45 * (s-1)^3 + 2.83 * (s-1)^2 + 2.96 * (s-1) + 1.04} \right) \qquad (8)$$

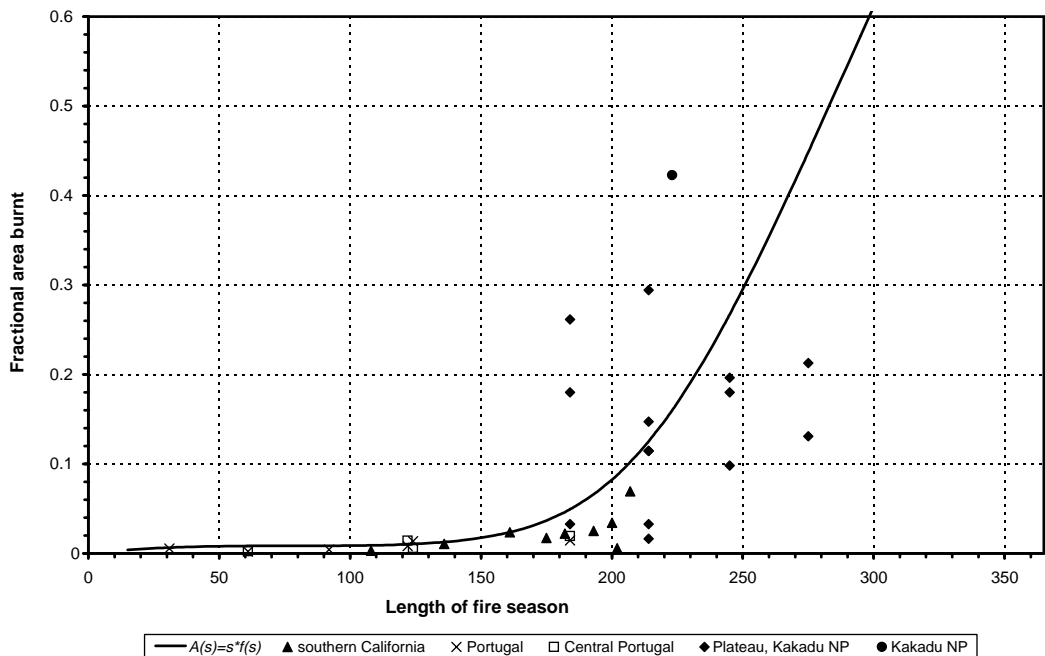which provides the fractional area burnt with length of the fire season (see Fig. 2),

Fig. 2 Length of the fire season in relation to area burnt (expressed as fire fraction). Points are experimental data from Portugal (✕) 1987–94, Central Portugal (☐) 1987–90, southern California (▲) 1970–80, Plateau, Kakadu National Park in northern Australia (◆) 1980–94 and entire Kakadu National Park averaged over 1980–94 (●), representing the length of a fire season against area burnt (expressed as the fraction of a 0.5° × 0.5° longitude/latitude grid cell). The line presents the fitted function A, see equation 9.

$$A(s) = s * e^{\left(\frac{s-1}{0.45 * (s-1)^3 + 2.83 * (s-1)^2 + 2.96 * (s-1) + 1.04} \right)} \quad (9)$$

This formulation is based on the hypothesis that the annual fractional area burnt increases slowly at first, when the length of fire season s is relatively short, but increases more rapidly when s approaches the entire year. The hypothesis was tested against observations containing both annual areas burnt and length of fire season in four large regions on different continents, southern California (Minnich, 1998), Portugal (Viegas, 1998) and central Portugal (Viegas *et al.*, 1992), and northern Australia (Russell-Smith *et al.*, 1997). The data from northern Australia are considered in two ways. First, data obtained from the Plateau in Kakadu National Park are assumed to be the most representative for natural conditions, with the least human influence on vegetation through fire management. The second is an average value for the entire National Park and for all years, thereby

excluding the specific influence of local vegetation. Observed areas burnt are converted into fractions of 0.5° × 0.5° longitude/latitude grid cell and were used to calibrate function (6) (see Fig. 2).

The resulting fire effects on vegetation in the fractional area burnt are calculated for each PFT. The fraction of individuals killed depends upon the prescribed PFT fire resistance, which represents the PFT survivorship during a fire (see Table 1). In the fire model, grasses and litter are fully consumed. Interannual variability in climate, area burnt and therefore vegetation mortality provides bi-directional feedback between vegetation and fire.

Data

For the historical simulation we used the CRU05 (1901–98) 0.5° × 0.5° longitude/latitude monthly climate data, provided by the Climate Research Unit, University of East Anglia, U.K.

Table 1 PFT parameter values for fire resistance

PFT	Fire resistance (%)
Woody	
Tropical broad-leaved evergreen	12.0
Tropical broad-leaved raingreen	50.0
Temperate needle-leaved evergreen	12.0
Temperate broad-leaved evergreen	50.0
Temperate broad-leaved summergreen	12.0
Boreal needle-leaved evergreen	12.0
Boreal summergreen	12.0
Grasses	
C3 grass	100.0
C4 grass	100.0

Historical CO_2 concentrations were derived from ice core and atmospheric measurements (Enting *et al.*, 1994). Soil texture information was obtained from the FAO soil dataset (FAO, 1991).

A global validation of length of fire season or area burnt over long time-series is problematic due to the limited data available. Most of the fire statistics are gathered over administrative units, which often integrate different vegetation types. Therefore, data given for a specified vegetation type are preferred. An indirect method of validation is to convert the fractional area burnt into fire return intervals (FRI), which have been observed for a broad range of ecosystems. The fire return interval, according to the fire history concept of Johnson & Gutsell (1994), is the expected return time of the fire. It is defined as the time required to burn an area equal in size to the study area. Their annual percentage burn, here equivalent to average fractional area burnt, is the inverse of the fire return interval (averaged over a sufficiently long time period).

In using the FRI one must bear in mind its limitations and the difficulties associated with the implicit assumption of stable ecosystem conditions (see Clark, 1989; Turner & Romme, 1994). In reality, the observed fire regimes are a consequence of interannual variability in climate, of human influence and of changes in vegetation dynamics over different time scales.

RESULTS

Validation of the fire model within the LPJ-DGVM

The first step is to validate the complete fire model Glob-FIRM within the LPJ-DGVM for sample regions in California, Portugal and Australia. The observations used to construct functions (4) and (9) are valid only on the short-term and the fire-vegetation relationships are themselves dependent on not only the present but also the past climate and ecosystem conditions.

The four sample regions differ in climate (interannual and seasonal variabilities), vegetation composition and flammability. For all four, the simulated length of the fire season is generally in good agreement with the observations (Fig. 3). The largest differences between model and observation are at sites with a length of fire season greater than 160 days, with model over- and underestimates at the southern California and Kakadu National Park sites, respectively. Minnich (1998) describes a self-regulated fire regime for the Californian Chaparral, where fire risk is reduced during the early successional stage. The underestimated length of fire season for northern Australia in some years can be explained by the high flammability of the dominant *Eucalyptus* and *Spinifex* species, which promotes fire, a feature not considered in the model.

Broad-scale observations of fire regimes around the world are still rare. The observational methods used over the last decades are remote sensing or on-ground fire inventories conducted by national forest services. Application of remote sensing to identify areas burnt and numbers of fires has started only recently and is still in development, therefore results vary markedly (1.5–2 times, e.g. Barbosa *et al.*, 1999). Hence, national fire statistics for forested and open woodland lands (FAO, 1999) were used to check the credibility of our fire model. This data source contains total areas of fires in hectares for forests and other woodlands over the period 1987–96 (for republics of the former Soviet Union over the period 1991–96). The forest fire statistics for 10 countries of Europe and North America, where the annual average of total area burnt over the entire period exceeds 10^3 ha (i.e. significant for the spatial resolution of the LPJ-DGVM)
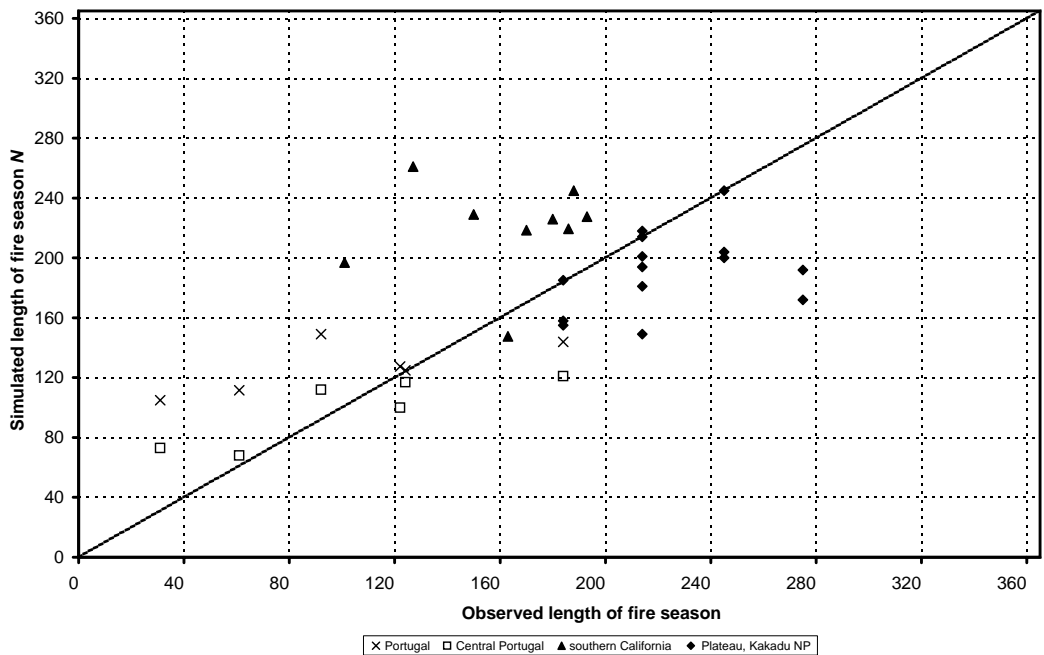
Fig. 3 Verification of the simulated length of fire season using LPJ-DGVM against observations in the sample regions.

were taken for validation purposes. The average annual fractional area burnt over the period 1987–96 (1991–96 for Russia and Ukraine) for an entire forested land by country $A_{country}$ was derived using FAO data on national forest cover for 1995 (FAO, 1999). The average annual fractional area burnt for the 10 countries was converted into fire return intervals (FRI) and then compared with the values produced by the LPJ-DGVM for the same time period (grid cells with non-forested lands were masked out and $A_{country}$ was calculated by spatial averaging of the average annual fractional area burnt over the period 1987–96 in the remaining grid cells and then converted to the FRI). The observed vs. simulated FRI by country is shown in Fig. 4.

The comparison allows us to conclude that the fire model within the LPJ-DGVM captures broad-scale fire regimes reasonably well. The FRIs for seven countries, including the United States and Canada (which are covered by vast forest areas), are reproduced with moderate to high accuracy. However, big discrepancies are seen for France, the Russian Federation and the Ukraine. A possible reason for disagreement in

simulated against observed results in FRI for the Ukraine and France is that potential plant functional types modelled by the DGVM differ from the actual vegetation. Although Canada and Russia have similar vegetation, the official fire statistics show a seven times longer FRI in Russia compared with Canada. This may be due to an underestimation in area burnt in Russia over the period 1991–96 due to differences in registration or definitions used by the Russian Federal Forest Service. Indeed, other sources (see Table 33 in Nilsson *et al.* 2000) estimate the annual area burnt during 1988–92 in the Russian forests as 3.5 million ha, compared with 1.16 million ha presented by the official Russian fire statistics over the period 1991–96 (FAO, 1999).

Global historical fire simulation

The simulated historical fire return intervals, averaged over the period 1901–98, are in reasonable agreement for most regions with observations given in the literature and compiled in Fig. 5. Regions which are unsuitable to carry fires (e.g. deserts) are shown in Fig. 6 as having intervals of
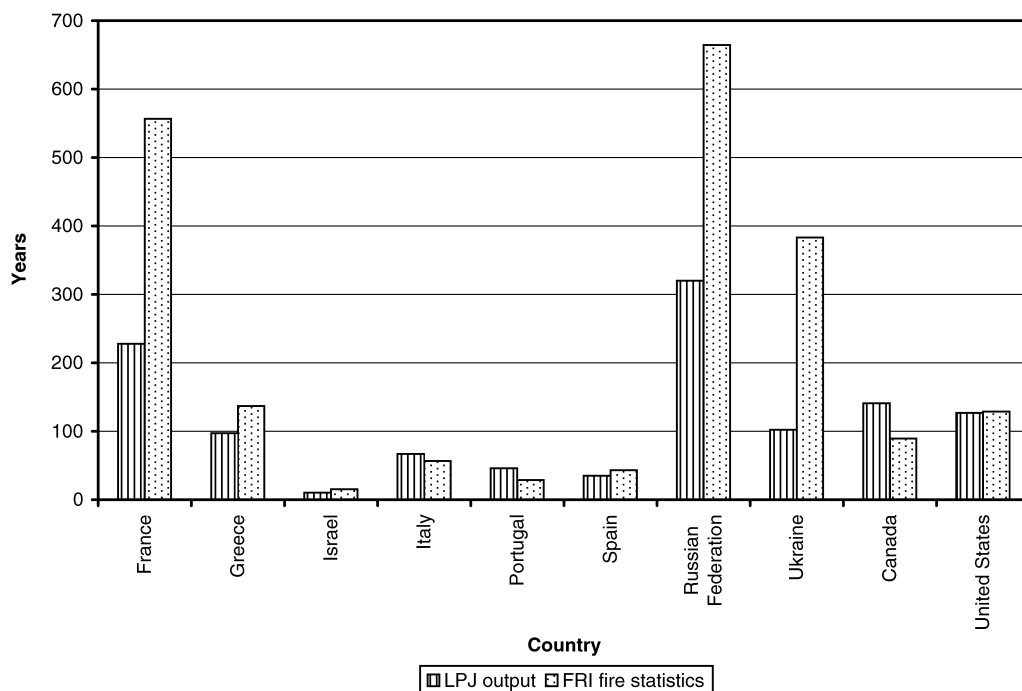
Fig. 4 Fire return intervals for the period 1987–96 derived from the national fire statistics of forest services and simulated for the same period by the LPJ-DGVM (the data for the Russian Federation and Ukraine are given for the period 1991–96).

more than 900 years. The transition between infrequent to frequent fires is well captured by the model in Africa (Trollope, 1984; van Wilgen *et al.*, 1990; Gillon, 1992; Scholes & Walker, 1993), in South and South-east Australia (Walker, 1981; Walter & Breckle, 1991b; Gill, 1994), South America (Soares, 1990) and in northern North America. In the following sections a few regions covering a range of global ecosystems and ecotones, will be discussed in more detail.

North America

An almost complete picture of observed FRI is available for the North American continent (Fig. 5). The shape of the simulated FRI follows the climate gradients for boreal North America. Long intervals with almost no fire occur around the Hudson Bay, with a shortening, i.e. more fires, going westward in the boreal zone. Relatively short FRI are observed in central Alaska

and neighbouring regions in the Canadian North-west Territories, but intervals were much longer (implying almost no fire) in the coastal zone of the Pacific North-west. In both of these regions the model is in reasonable agreement with observations.

It was more difficult to model the FRI for temperate grasslands (prairie) and for the boreal Labrador peninsula, where the modelled FRI were too long, while for some parts of the Appalachian Mountains fires should be less frequent. Due to sparse vegetation, very long FRI would be expected in the North American deserts, instead of intervals between 12 and 50 years (Fig. 6).

The transition between no fire occurrence and frequent fires in the tundra near the tree-line, e.g. near St James Bay, Western Quebec, is modelled further south than reality in the boreal forest in Quebec, North-west Ontario and Labrador (compare Fig. 5 and Fig. 6). Here, simulation of the fire season was less successful — the impact of other environmental factors on its length, e.g. the
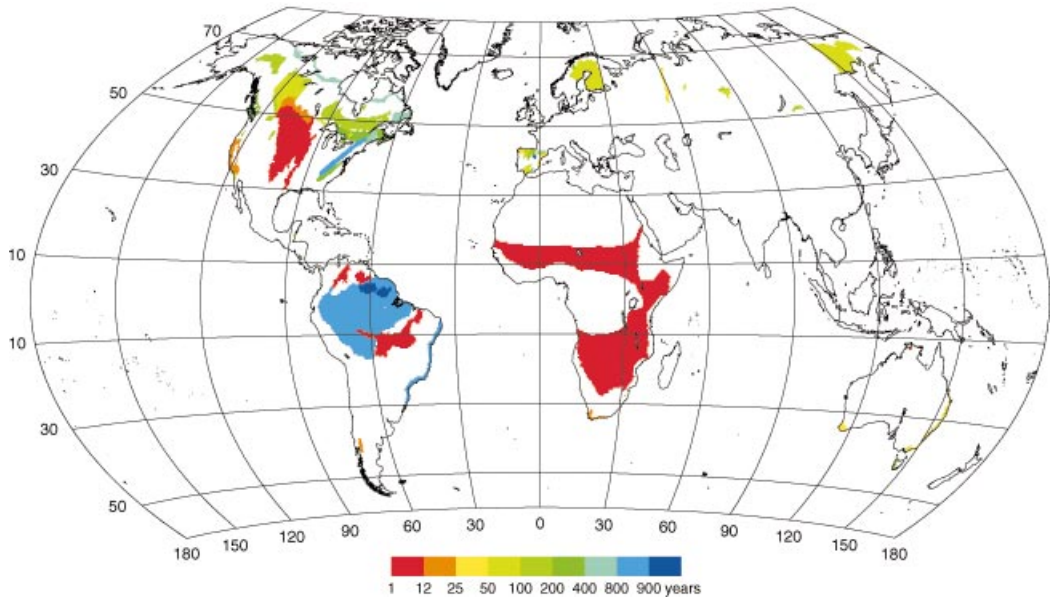
Fig. 5 Observed fire return intervals. Values are either given as an average for a vegetation type or estimated for a specific study area. According to the two categories of data sources, boundaries of the areas shown here correspond to the extension of the study area or were defined according to the defined extension of the major vegetation zone after Walter & Breckle (1983). (Sources: Swain, 1973; Mooney *et al.*, 1981; Suffling *et al.*, 1982; Runkle, 1985; Green, 1986; Delisle & Hall, 1987; Collins & Gibson, 1990; Goldammer, 1990; Johnson & Larsen, 1991; Scholes & Walker, 1993; Groves, 1994; Turner & Romme, 1994; Bragg, 1995; Briggs & Knapp, 1995; Whelan, 1995; Goldammer & Furyaev, 1996; Kellman & Meave, 1997; Larsen & MacDonald, 1998; Lavoie & Sirois, 1998; Taylor & Skinner, 1998; Vázquez & Moreno, 1998; Veblen *et al.*, 1999; Niklasson & Granström, 2000).
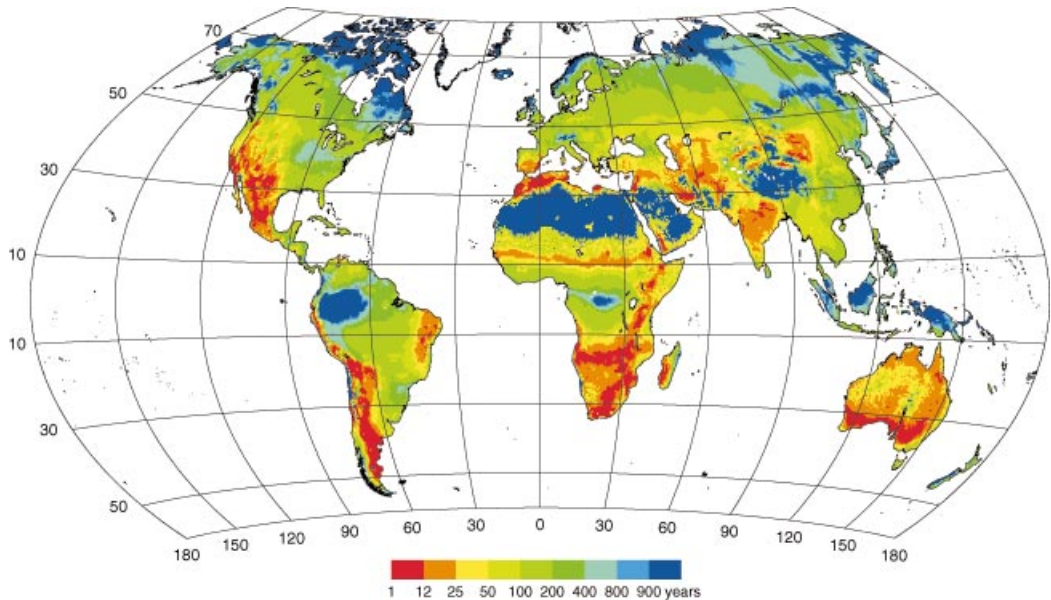

Fig. 6 Historical fire intervals simulated by the LPJ-DGVM (averaged over the period 1901–98).

influence of permafrost and/or snow cover on the soil moisture regime needs to be investigated further.

The fire regime in the mixed-conifer northern hardwood forest in eastern North America is successfully modelled (e.g. Swain, 1973; Grimm, 1983; Abrams & Orwig, 1996), although the longer FRI reported for the northern Appalachian Mountains are not captured. These intervals may be a result of intense land use or of policies of fire suppression (Elliott *et al.*, 1999).

North American tall-grass prairie and aspen-parkland are burnt every 10–20 years, and in the other prairie types fires are even more frequent (Fig. 5). During the last centuries fire management practice of native Americans together with a favourable abiotic environment have created self-perpetuating fire conditions, leading to very frequent fires. This has led to the exclusion of primarily non-resistant woody plants in areas where the climate would allow forests or at least woodlands (Grimm, 1984; Bragg, 1995). The complex interactions between drought, soil conditions, topography, grazing and fire (Collins & Wallace, 1990; Joern, 1995) make the correct simulation of the FRI very difficult. Addressing all of these factors, although important, is beyond the scope of the current analysis.

Central and South America

The impact of fire has been observed in many South American ecosystems, ranging from natural or anthropogenic savannas to burning in tropical rain forests (Kauffman & Uhl, 1990; Soares, 1990; Walter & Breckle, 1991b). The spatial pattern of simulated FRI appears to follow the main gradients, with shorter FRI in the savanna regions of the Brazilian Cerrado, the Venezuelan Orinoco plains and the high plains in Guyana, and very long FRI for the tropical and temperate forests, including the coastal rain forest, as well as the Atacama desert (Figs 5 and 6). The reasons for the establishment of savannas are manifold and appear to be critical for a correct simulation of the fire regime, furthermore complicating the definition of fire drivers in these ecosystems (Coutinho, 1990; Walter & Breckle, 1991b).

The moist microclimate in closed tropical rain forests permits burning only in extremely dry years (e.g. during El Niño events) and in canopy openings following tree cuts (Kauffman & Uhl, 1990). Since the LPJ-DGVM does not consider gap dynamics explicitly, the FRI of all the tropical rain forests are between 400 and greater than 900 years, indicating almost no fire occurrence (see Fig. 6). However, more detailed and spatially explicit information about the natural fire regime in seasonal rain forest is needed to understand the gradient of increasing fire occurrence from the evergreen rain forest towards the savanna region.

Boreal Eurasia

The FRI simulated for Scandinavia are close to the observed 70 and 100 years (Bradshaw & Zackrisson, 1990; Parviainen, 1996). The length of the fire season for central and far eastern Siberia is incorrect, however. Observations by Korovin (1996) of a decreasing length of fire season with increasing latitude and a subsequent decrease in area burnt is not captured by the model (Fig. 6) in the region to the east of the Yenissey river and to the north of lake Baikal. The simulated FRI are close to those reported by Furyaev (1996) of between 20 and 70 years for southern Siberia and between 70 and approximately 150 years for western Siberia (for location of the study areas see Fig. 5). Ecological differences in Siberia from those found in the western part of Eurasia, e.g. permafrost soils, extensive lichen coverage and complex topography, which are not explicitly modelled in LPJ-DGVM, are important for litter hydrology and need further investigation. In many cases LPJ-DGVM estimates high soil moisture contents, which lead to almost no days with burning conditions. In the model, the onset of the snowmelt fills the top soil layer, and the short growing season is insufficient to reduce the soil moisture content to the stage where it drops below the moisture of extinction.

Mediterranean-type ecosystems

In Mediterranean-type ecosystems fragmentation of the landscape is naturally very high, and fire regimes have been changed for centuries due to human activities. Thus, the reported natural FRI for these ecosystems vary from 10 to 60 years up to more than 120 years depending on the subtype investigated (Hanes, 1981; Kilgore, 1981; van Wilgen *et al.*, 1990; Walter & Breckle, 1991b).

Whereas the simulated FRI for the Australian and South African ecosystems compares well with those given in van Wilgen *et al.* (1990) and Gill (1994), those simulated for Californian chaparral were slightly overestimated (6–50 years compared with the observed 58–77 years, Minnich, 1998). The geographical distribution of FRI for the Iberian peninsula generally agrees with the estimates given in Vázquez & Moreno (1998).

Africa

On the African continent the FRI vary with latitude in a bimodal manner with peaks in the Sahara and the tropical rain forest. Moving southwards into the Sahel the FRI decrease with increasing fuel load, and are progressively lengthened further south with increasing precipitation, resulting in no fire activity in the tropical forest. Due probably to human intervention, more frequent fires than simulated are observed in the African savannas, especially in the Sahelian and Guinean savanna. In southern Africa, the small coastal area of the Namib desert, which has no fire, is captured well in the simulation (Fig. 6), while the area of longer simulated FRI would be expected to be larger in surrounding areas of the Karoo and Kalahari ecosystems in central southern Africa, where the vegetation is presumably too sparse to carry a fire (Werger, 1986; Schultz, 1988).

In water-limited ecosystems such as the African savannas, a sequence of years with lower annual precipitation, which kills a large part of the vegetation, leads to extreme fire events that reduce carbon pools and vegetation coverage (compare Fig. 7a–d, especially after simulation year 1945). Litter carbon is fluctuating close to the defined limit for supporting fire spread (see section 'fire occurrence'), therefore fire does not occur in all years when annual precipitation declined. Re-vegetation takes several years depending on climate condition and plant competition. Tropical broad leaved rain-green woody trees compete strongly with C_4 herbs for the remaining resources. The dominance of these two PFTs, which shed their leaves during the dry season, leads to an increase in the litter pool, and thus large fractional area burnt due to the higher annual precipitation in the years after simulation year 1955 (see Fig. 7b–d).

DISCUSSION

The fire model, which is a compromise between fire history and process-orientated models, successfully simulates fire regimes in many of the world's ecosystems. In many regions it is apparently sufficient to consider only fuel load and litter moisture as the key drivers of the fire regime. In these cases, extrapolating experimental data from regional studies in order to construct globally applicable fire functions and the assumption that the accumulated length of fire season gives the annual fractional area burnt are both valid steps.

In some regions, the simulated results differed from the observations indicating that processes or environmental conditions (i.e. permafrost, lichen cover and edaphic conditions) not described in the LPJ-DGVM are important. Additional physical properties of fuel seem to be necessary for inclusion into the model in order to obtain better results, especially for grassland regions. In other regions human activities, both directly and indirectly, influence the fire regime through fire management and modification of land cover, respectively. It was therefore not possible to validate fully the fire model against natural fire regimes in these regions. This question should be addressed in later studies, e.g. inclusion of human population as an additional fire driver. The present model functions are based on a limited amount of observed data, since data should cover a sufficient number of years in order to capture the climate variability at any location. Despite intensive literature surveys, more data showing both area burnt and length of fire season in other ecosystems are needed. Therefore, as new data become available the function can change.

Our fire module Glob-FIRM, coupled into a Dynamic Global Vegetation Model, provides a bi-directional feedback between fire and vegetation. PFT-specific fire effects and the ability of PFTs to establish, influence postfire vegetation dynamics in the opened sites. The new assemblage of PFTs has an impact on fire occurrence through competition, plant growth and thus water demand of each PFT. An increase in fire can enhance the expansion of fire-tolerant PFTs, i.e. those with higher survivorship after fire. Their vegetation dynamics will then feed back on the fire regime.
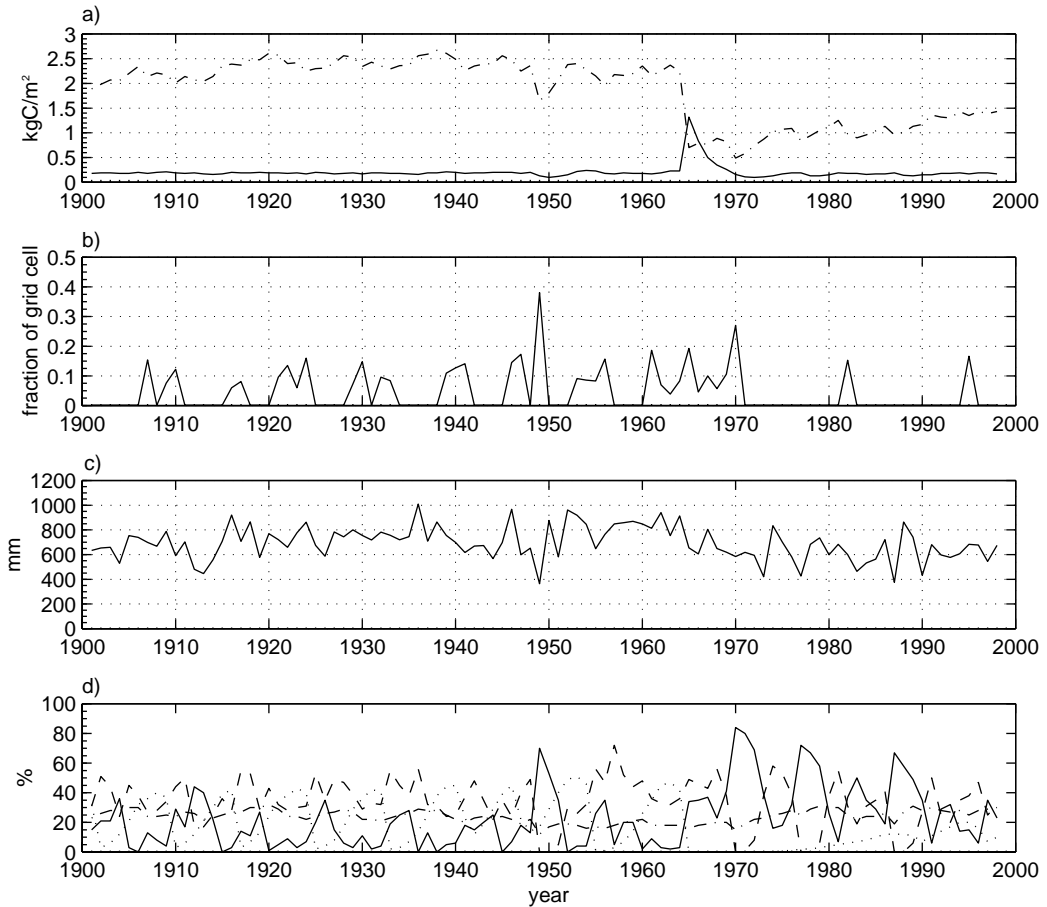
Fig. 7 Temporal dynamics of (a) vegetation carbon (dash-dotted line) and litter carbon (solid line), (b) fractional area burnt, (c) annual precipitation and (d) fractional PFT coverage (dashed = C$_4$ herbaceous; dotted = tropical broadleaved raingreen woody; dash-dotted = tropical broadleaved evergreen woody; and solid = barren) for a grid cell in the northern African savanna (10.75°E, 11.75°N).

The effects of climate change on plant water demand can indirectly buffer or intensify fire occurrence and effects depending on vegetation productivity. These patterns and their consequences for vegetation composition and the global carbon cycle should be addressed in a detailed study. Glob-FIRM, implemented in the LPJ-Dynamic Global Vegetation Model, is a suitable tool for this, since feedbacks between vegetation composition, productivity and fire, through moisture conditions and litter accumulation, are considered in one combined model. Changes in either vegetation pattern or fire can be investigated with respect to their effects on

other modelled processes. Under climate change conditions, it can show new aspects of the atmosphere–biosphere interaction, which could be different from existing studies, where projections of fire danger indices independent of the influence of vegetation dynamics on fire drivers were studied (Flannigan *et al.*, 1998).

The modified LPJ-DGVM allows a further insight into the global role of fire for biosphere dynamics. To provide a full range of successional dynamics, however, other disturbance agents such as insects or wind-throw, must be included in DGVMs, thus completing the picture of biotic and abiotic interactions in ecosystems.

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