

The global distribution of ecosystems in a world without fire

W. J. Bond¹, F. I. Woodward² and G. F. Midgley³

¹Botany Department, University of Cape Town, Private Bag, Rondebosch, 7701, South Africa; ²NERC Centre for Terrestrial Carbon Dynamics and Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK; ³Climate Change Research Group, National Botanical Institute, P/Bag X7, Claremont 7735, South Africa & CAMP; Conservation International, Center for Applied Biodiversity Science 1919 M St., NW, Washington, DC 20036, USA

Summary

Author for correspondence:
W. J. Bond
Tel: +27 21 6502439
Fax: +27 21 6504041
Email: bond@botzoo.uct.ac.za

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- This paper is the first global study of the extent to which fire determines global vegetation patterns by preventing ecosystems from achieving the potential height, biomass and dominant functional types expected under the ambient climate (climate potential).
- To determine climate potential, we simulated vegetation without fire using a dynamic global-vegetation model. Model results were tested against fire exclusion studies from different parts of the world. Simulated dominant growth forms and tree cover were compared with satellite-derived land- and tree-cover maps.
- Simulations were generally consistent with results of fire exclusion studies in southern Africa and elsewhere. Comparison of global 'fire off' simulations with landcover and treecover maps show that vast areas of humid C₄ grasslands and savannas, especially in South America and Africa, have the climate potential to form forests. These are the most frequently burnt ecosystems in the world. Without fire, closed forests would double from 27% to 56% of vegetated grid cells, mostly at the expense of C₄ plants but also of C₃ shrubs and grasses in cooler climates.
- C₄ grasses began spreading 6–8 Ma, long before human influence on fire regimes. Our results suggest that fire was a major factor in their spread into forested regions, splitting biotas into fire tolerant and intolerant taxa.

Key words: climate–vegetation relationships, dynamic global vegetation models, fire ecology, global biomes, plant biogeography.

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Introduction

It is generally believed that climate exerts the key control over the distribution of the world's major ecosystems. On different continents, with distantly related floras, similar vegetation formations occur under similar climatic conditions (Schimper, 1903). The distribution of the major biomes of the world – desert, tundra, grasslands, savannas and forests (tropical, temperate and boreal) – can be broadly predicted from temperature and precipitation (Holdridge, 1947; Whittaker, 1975) and correlate well with water balance (Woodward, 1987; Stephenson, 1990). Ecosystem properties, such as biomass, leaf area and net primary productivity, also vary along gradients of temperature and moisture. Total plant biomass

increases with temperature, for example increasing from 650 g m⁻² in Arctic tundra to 8300 g m⁻² in boreal forests to 26 700 g m⁻² in temperate forests (Chapin *et al.*, 2002).

Here we argue that several of the world's major biomes owe their distribution and ecological properties to the fire regime. Fire is under-appreciated as a global control of vegetation structure, even though fires are a common and predictable feature of the world's grasslands, savannas, mediterranean shrublands and boreal forests (e.g. Goldammer, 1993; Archibold, 1995). Together these fire-prone formations cover some 40% of the world's land surface (Chapin *et al.*, 2002). Fires always reduce plant biomass and, depending on their frequency and severity, can also replace trees with shrublands or grasslands. The implication therefore is that some flammable ecosystems

may be far from physiognomic limits set by climate. There is direct and indirect evidence that this is often the case. First, patches of forest are common in many landscapes dominated by fire-prone grasslands and shrublands suggesting a mismatch between climate and vegetation (Sarmiento, 1983; Bond & van Wilgen, 1996; Midgley *et al.*, 1997; Bowman, 2000). Second, experimental exclusion of fire has often led to biome switches from flammable formations to forested ecosystems (Pickett & White, 1985; Bond & van Wilgen, 1996). Third, anthropogenic fires introduced to island ecosystems have transformed forests to flammable shrublands and grasslands (e.g. Hawaii, D'Antonio & Vitousek, 1992, New Zealand, Ogden *et al.*, 1998, Madagascar, Koehlin, 1972). Finally, plantation forestry, and the invasion of nonnative trees into flammable grasslands and shrublands (Richardson, 1998) shows that tree biomass in these ecosystems is far from the limit set by climate. These observations suggest that fire may be a primary factor in determining biome distributions, promoting flammable ecosystems where the climate can support forests.

In this paper, we provide the first global assessment of the importance of fire in determining world biome distribution. We do so by asking: how different the distribution of global biomes would be if we could 'switch fire off'; and to what extent would global vegetation change if fires were suppressed and succession allowed to proceed until the growth forms present were limited only by climate? To address these questions, we used simulation models to predict global ecosystem structure and growth form composition as if plant growth were limited only by climate. Until recently, analyses of determinants of the global distribution of vegetation have been largely correlative. Correlative methods cannot discriminate between the roles of climate and fire. In the last decade, process-based models for predicting global vegetation have become available. Dynamic Global Vegetation models (DGVMs) are designed to simulate vegetation responses to changing climates. DGVMs 'grow' plants according to physiological processes (Woodward *et al.*, 1995; Haxeltine & Prentice, 1996; Cramer *et al.*, 2001). They simulate carbon and water dynamics and structure of vegetation using input data of climate, soil properties, and atmospheric CO₂ (Woodward *et al.*, 1995; Beerling & Woodward, 2001; Cramer *et al.*, 2001). The models generate predictions of the composition and structure of vegetation for a given climate in terms of relatively few plant functional types (PFTs, e.g. Woodward *et al.*, 1995; Haxeltine & Prentice, 1996). Several DGVMs include fire modules (Cramer *et al.*, 2001). No mechanistic model to generate fire on a global scale exists. Instead DGVMs simulate fire from empirical relationships between moisture content of plant litter (which can be simulated from climate) and fire return intervals (Thonicke *et al.*, 2001; Venevsky *et al.*, 2002). The fire modules assume that ignition is not limiting (Woodward *et al.*, 2001).

DGVMs provide a useful biogeographical tool for exploring potential vegetation. Because they are based on an under-

standing of the first principles of plant photosynthesis, carbon allocation and growth, DGVMs allow the simulation of global ecosystem structure and growth form composition as if plant growth were limited only by climate. The real global biome distribution can then be compared with the simulated climate potential vegetation to ascertain the importance of fire in determining global biome distribution. In this paper, we use the Sheffield Dynamic Global Vegetation Model (SDGVM; Woodward *et al.* 1995, 2001) to investigate the importance of fire vs climate as determinants of global biome distribution. The SDGVM is a global-scale model that includes a fire module. Output of the SDGVM has been tested against measured ecosystem properties over a wide range of climates worldwide and gives a satisfactory fit (Cramer *et al.*, 2001; Woodward *et al.*, 2001). The DGVM is particularly useful for our purpose because the model is mechanistic and not based on correlations of existing vegetation with climate. We were therefore able to separate effects of climate from those of fire by 'switching off' the fire module in the simulations. We used long-term fire experiments to test model simulations of woody biomass and dominant plant functional type. By comparing model simulations with global maps of landcover, tree cover and the distribution of fires, we could assess the extent of fire-controlled vs climate-controlled global biome distribution.

Methods

The basic workings of the DGVM are described in Appendix 1. Climate data for DGVM simulations were taken from the University of East Anglia global data set for the 20th century. The DGVM incorporates soil depth and texture from a global database (FAO, 1998). It assumes soils are freely drained. Model output includes ecosystem properties, such as plant biomass, and also the cover of several major growth forms. Stem biomass (above-ground woody biomass) indicates relative dominance of trees and is therefore a pointer to biome type. To test model output, we compared simulated above-ground biomass with measured above-ground biomass reported for five long-term fire experiments.

There are difficulties in using long-term fire-exclusion experiments to test 'climate potential' in terms of biomass. Although there are many such experiments, results are generally reported as changes in cover or density of trees and other growth forms, rather than as changes in biomass. A second problem is that many decades of fire exclusion may be needed before woody plants colonise a site and grow to their climate-limited potential biomass. For much of the data available, the effects of fire exclusion are best measured qualitatively as a tendency for increased woody cover. Three qualitative outcomes can be expected from long-term fire exclusion experiments:

- 1 no change (vegetation is climate limited)
- 2 increased density or size of woody plants but no change in species (climate-limited, fire modified)

3 increased density and size of woody plants and successional tendency to forest with invasion of fire-sensitive trees and shrubs (fire-limited).

The third case indicates meta-stable vegetation with alternate fire-dependent or climate-dependent states. As an additional test of the utility of the SDGVM for exploring determinants of vegetation, we simulated plant functional types (PFTs) with 'fire on' and 'fire off' for the southern African region. The region is relatively arid, with semiarid shrublands in the west, grasslands and savannas in the east, and Mediterranean shrublands in the south-west. Small patches of forest occur throughout the higher rainfall regions suggesting the potential for biome switches (Midgley *et al.*, 1997; O'Connor & Bredenkamp, 1997). We compare the simulations with results from numerous long-term fire exclusion studies in the region (Bond *et al.*, 2003a).

We simulated the dominant growth form based on both cover and biomass for global comparisons. Cover, in mixed tree/grass ecosystems, emphasises grasses, while biomass emphasises trees because of the large amount of biomass contained in tree stems. As indicators of major biomes we used model output for four key growth forms: gymnosperm trees (mostly conifers, deciduous and evergreen), angiosperm trees (deciduous and evergreen), temperate grasses or shrubs with C_3 photosynthesis (C_3) and tropical grasses with C_4 photosynthesis (C_4). Areas of low cover or biomass are indicated as 'bare'. We compared simulated global vegetation with 'fire off' to a map of observed vegetation. Producing a global map of vegetation is not without its own problems of interpretation. A number of vegetation maps are available (e.g. Matthews, 1983; Olson *et al.*, 1983; Haxeltine & Prentice, 1996; Hansen *et al.*, 2000). We used the land cover map produced by ISLSCP (Meason *et al.*, 1995), which shows dominant functional types similar to those simulated by the DGVM. The land cover map is primarily determined from the annual variations in a satellite-derived vegetation index, Normalized Difference Vegetation Index, NDVI, for each $1^\circ \times 1^\circ$ pixel of the terrestrial surface. The approach (De Fries & Townshend, 1994) builds on previously established techniques of analysis and classification of NDVI data (Los *et al.*, 1994; Sellers *et al.*, 1994). In addition, the classifications based on the NDVI data have been trained, and therefore constrained, by established vegetation maps, such as those of Matthews (1983) and Olson *et al.* (1983). The ISLSCP map includes land cover modified by agriculture and so is an attempt to map actual vegetation. The map derived by the SDGVM is for potential vegetation and does not account for any human impacts on vegetation.

Since reduction in tree cover is one of the major effects of fire, we also compared median tree cover for the 20th century, simulated with and without fire, with a satellite derived map of global tree cover (FAO, 2001). The FAO tree cover map was derived from satellite imagery for the period from 1995 to 1996 obtained from the Advanced Very High Resolution

Radiometer (AVHRR), and archived in the Global Land Cover Characteristics Database (GLCCD). This imagery consists of five calibrated AVHRR bands and a NDVI band. The preliminary map was reviewed by experts from around the world and tested against International Geosphere Biosphere Programme (IGBP) validation points and full land-cover data sets from the governments of USA and China. The evaluations showed that the average accuracy of the maps for all tree cover classes is about 80% with greatest accuracy for closed forest (FAO, 2001).

Results

Biomass change

Where fires are frequent, woody biomass should be reduced relative to climate potential. Fig. 1 compares stem biomass

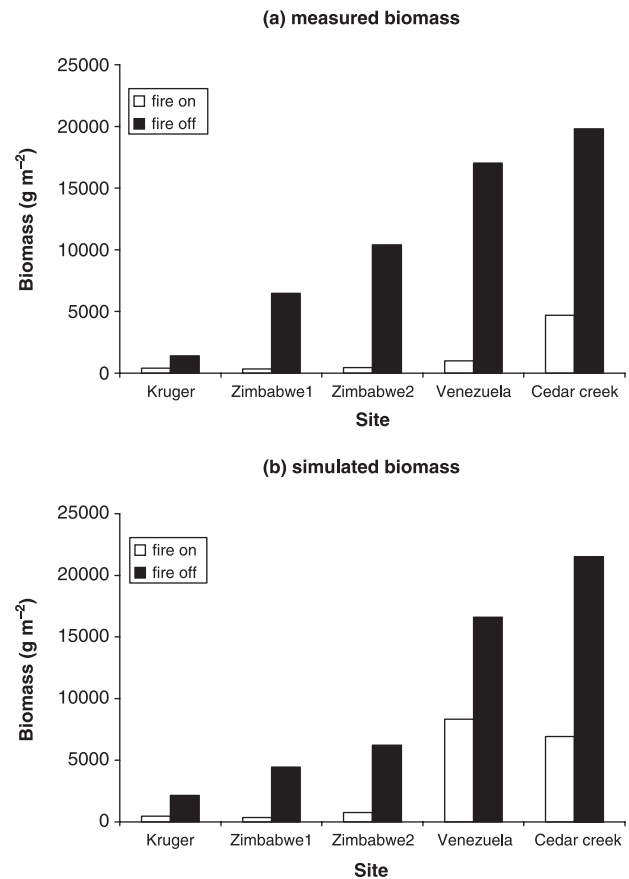


Fig. 1 Above-ground woody biomass in savannas with 'fire on' (burnt every 2–3 yr) and 'fire off' (unburnt for 40+ yr). (a) Measured biomass in $g\ m^{-2}$ dry weight; (b) simulated biomass using the Sheffield Dynamic Global Vegetation Model (SDGVM; maximum values for fire off, median values for fire on). Sites are Kruger National Park (Shackleton & Scholes, 2000); Zimbabwe 1, Matopos (Kennan, 1972, P. Frost pers. comm., 2003), Zimbabwe 2, Marondera (Barnes, 1965; Tsvuura, 1998, and P. Frost pers. comm., 2003); Venezuela (San Jose *et al.*, 1998); Cedar Creek, USA (Tilman *et al.*, 2000).

in frequently burnt savannas with plots where fire has been excluded for at least 30 yr in experiments from Africa, the USA and Venezuela. These studies show very large differences in woody biomass between frequently burnt and unburnt treatments in the more humid sites. The biomass differences are comparable in magnitude with differences between major biomes such as tundra and temperate forests (Chapin *et al.*, 2002). The DGVM simulations with 'fire off' showed a good fit between observed and simulated maximum biomass for fire exclusion treatments, although biomass was somewhat underestimated for two of the African savannas. The 'fire on' simulations showed a good fit between median biomass and observed data at relatively arid sites but overestimated woody biomass at more mesic sites. In part, this is because the fire module generated too few fires in more humid climates. The simulated fire return intervals (fri) for the 20th century were 200 yr for the North America site and 73 yr for the Venezuela site, both of which burnt at intervals of 2–5 yr. By contrast, the African sites had simulated fris of 3–5 yr, close to the actual fri of 2–5 yr.

Regional biome simulations

Fig. 2 shows simulated tree cover (angiosperms) for southern Africa with and without fire. The simulations of 'fire on' are consistent with the actual vegetation, which is grassland with very low tree cover except near the eastern sea-board (savanna vegetation), and in the south-west, which supports evergreen forests. The 'fire off' simulation shows a striking contrast with trees dominating all the higher rainfall regions of the east. The simulations imply that most of this region would be forest in the absence of burning. The figure also shows the locality of a number of fire exclusion studies and whether exclusion treatments resulted in biome switches (to fire-intolerant forest) or merely structural or no change as defined above (Bond *et al.*, 2003a). The simulations are generally consistent with the results of fire exclusion studies (Bond *et al.*, 2003a).

Global biome simulations

Functional types The regional test of the SDGVM gives some confidence in the use of the model for simulating global biome distribution as affected by fire. Fig. 3 shows the ISLSCP landcover map (Meason *et al.*, 1995) of the world using similar broad growth form categories to the DGVM output (see Table 1 for ISLSCP and DGVM map units). The locations of several long-term fire exclusion studies are also indicated on the map and the successional trends reported for the experiments are shown in Table 2. Fig. 4 shows the dominant growth form, as measured by relative cover, simulated with fire 'off'. Simulations of the dominant growth form as measured by biomass produced similar results with only slightly larger areas of C_4 and C_3 cover and are not shown

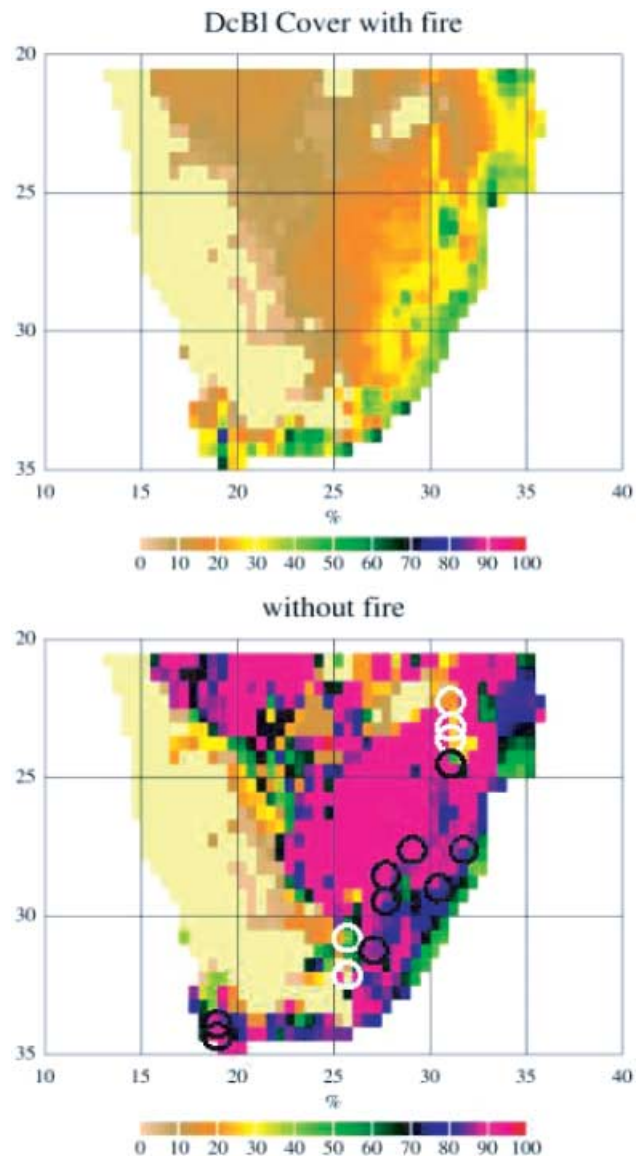


Fig. 2 Tree cover for southern Africa simulated with and without fire by the Sheffield Dynamic Global Vegetation Model (SDGVM). Fire exclusion studies are indicated on the 'without fire' simulation. Black rimmed circles indicate sites in which there was a successional trend to closed forest; white rimmed circles indicate sites that showed no trend to forest (see Bond *et al.*, 2003b for sources).

here. A map of fires in 1998, derived from satellite imagery, is shown in Fig. 5 to give an indication of the global distribution of fires in a single year. A large proportion of C_4 grassy ecosystems burn on an annual basis relative to other biome types.

Tree cover Fig. 6(a,b) shows simulated angiosperm tree cover with 'fire off' and 'fire on'. The FAO map of tree cover is shown in Fig. 6(c) for comparison. The DGVM simulated greater tree cover than that recorded in the FAO map probably, in part, because of the underestimation of fire

Table 1 ISLSCP Mapping units and plant functional type (PFT) equivalents in the dynamic global vegetation model (DGVM) simulations used in Fig. 3

ISLSCP number	Land cover type	DGVM PFT
1	Broadleaf evergreen forest	Angio
	Broadleaf deciduous forest and woodland	Angio
2		
3	Mix of 2 and coniferous forest	Angio
4	Coniferous forest and woodland	Gymno
5	High latitude, deciduous forest and woodland	Gymno
6	Wooded C ₄ grassland	C ₄
7	C ₄ grassland	C ₄
9	Shrubs and bare ground	Bare
10	Tundra	C ₃
11	Desert, bare ground	Bare
12	Cultivation	Cultivation
13	Ice	Bare
14	C ₃ wooded grassland, shrublands	C ₃
15	C ₃ grassland	C ₃

frequency in humid C₄ grasslands. However areas with closed forest in the FAO classification (60–100% tree cover) show a good correspondence with areas with a simulated tree cover of 80–100% in the DGVM simulations. Fire has a significant effect on the extent of global forest cover. According to the simulations, forest cover (80–100% tree cover) would double from 26.9% of vegetated grid cells to 56.4% in the absence of burning. More than half (52.3%) of grid cells with C₄ grasses present (> 20% cover) in the 'fire on' simulation would change to closed angiosperm forest in the absence of burning. None would be replaced by gymnosperm forest. Ecosystems with C₃ grasses or shrubs (> 20% cover) are somewhat less dependent on fire with 41% being lost to forest in the 'fire off' simulations. Of these, 53% would be replaced by gymnosperm, 34% by angiosperm, and 13% by mixed forests

Discussion

The aim of our study was to evaluate the extent to which fire determines the global distribution of vegetation after climate limitations are accounted for. Where would global vegetation change if fires were suppressed and succession allowed to proceed until the growth forms present were limited only by climate? Comparisons of the ISLSCP land cover map (Fig. 3) with fire-off simulations (Fig. 4) suggest that biomes of large parts of the world are far from their climate potential supporting flammable formations (Fig. 5) such as grasslands and savannas. We label these fire-dependent ecosystems. They are fire-dependent in the sense that the dominance of grasses or shrubs (measured as biomass or cover) depends on burning. FDEs are meta-stable. In the absence of burning, FDEs would be replaced by forest. FDEs, according to the simulations, are of much greater extent in the tropics and southern hemisphere than the temperate and boreal north (Figs 3–5). Vast areas of Africa and South America, and smaller areas of Australia are dominated by C₄ grassy ecosystems, which have the climate potential to support woodlands and forest. Satellite maps of fire occurrence show that these biomes experience by far the most extensive fires in the world (Fig. 6; Dwyer *et al.*, 1998; Barbosa *et al.*, 1999; Dwyer *et al.*, 2000; Tansey *et al.*, 2004). In the northern hemisphere, outside the tropics, these systems are of much smaller extent, occurring as prairies in North America, and in relatively small areas of savanna in India, south-east Asia and northern China. It is perhaps not coincidental that fire is barely mentioned in general ecological textbooks written in the northern hemisphere (Bond & van Wilgen, 1996). By contrast, fire ecology has been a central theme of ecologists in Australia (e.g. Gill, 1975; Whelan, 1995; Bradstock *et al.*, 2002) and Africa (Phillips, 1930; Booysen & Tainton, 1984; Bond & van Wilgen, 1996). In South America, too, there is an extensive literature on fire in savannas (e.g. Beard, 1944; Coutinho, 1982, 1990; Sarmiento, 1983; Hoffmann,

Table 2 Long-term fire-exclusion studies in savannas (see Fig. 3)

Site	Locality	Years of fire protection	Trend	MAP mm	T °C	Source
1	USA	35	Forest	790	6.0	Tilman <i>et al.</i> (2000)
2	Venezuela	> 100	Forest	1249	27.9	San Jose <i>et al.</i> (1998), San José & Farinas (1983)
3	Brazil	18	Woodland	1491	21.3	Moreira (2000)
4	South Africa	45	Savanna	548	12.0	Shackleton and Scholes (2000)
5	Zimbabwe	46	Woodland	581	18.2	Kennan (1972); P. Frost (pers. comm. 2003)
6	Zimbabwe	46	Woodland	924	17.2	Barnes (1965); Tsvuura (1998); P. Frost (pers. comm. 2003)
7	Zambia	22	Forest	1200	25.6	Trapnell (1959)
8	Ghana	32	Forest	1190	34.5	Swaine <i>et al.</i> (1992)
9	Australia	15	Woodland/forest	1420	28.2	Bowman and Panton (1995)

In all studies, tree density increased with fire protection. Successional trends were obtained from the listed sources. Forest, change to closed tree canopies with no grass understorey, shift to forest tree species; woodland, increase in tree cover with canopies closing but sufficient grass to carry a fire, increase in fire-intolerant species; savanna, no tendency to closed tree cover, no change in tree composition. Y, years of fire protection; MAP, mean annual precipitation; T, mean annual temperature.

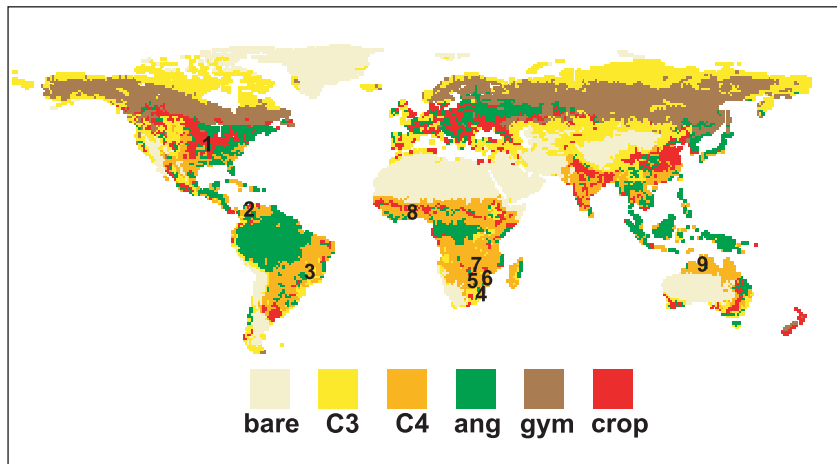


Fig. 3 ISLSCP Landcover according to dominant functional types. See Table 1 for conversion of landcover classes to dominant functional types. Squares indicate the location of long-term fire exclusion studies listed in Table 2. Source: ftp://daac.gsfc.nasa.gov/data/inter_disc/biosphere/land_cover

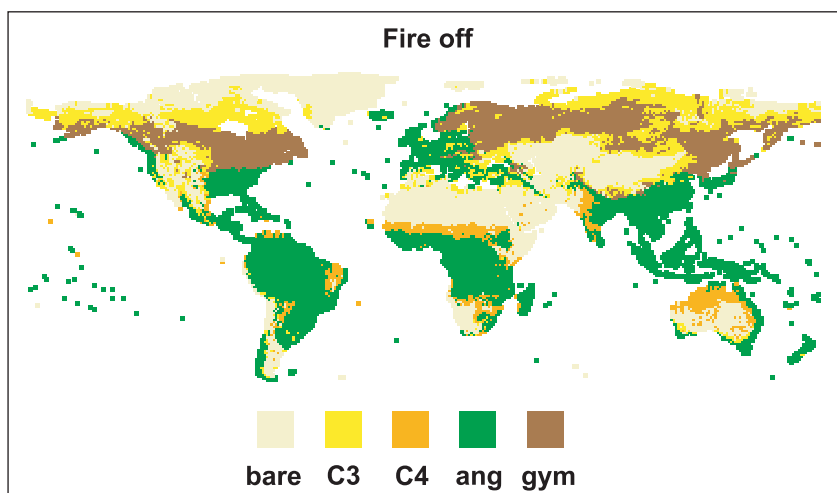


Fig. 4 Distribution of dominant functional types measured by cover and simulated with 'fire off'.

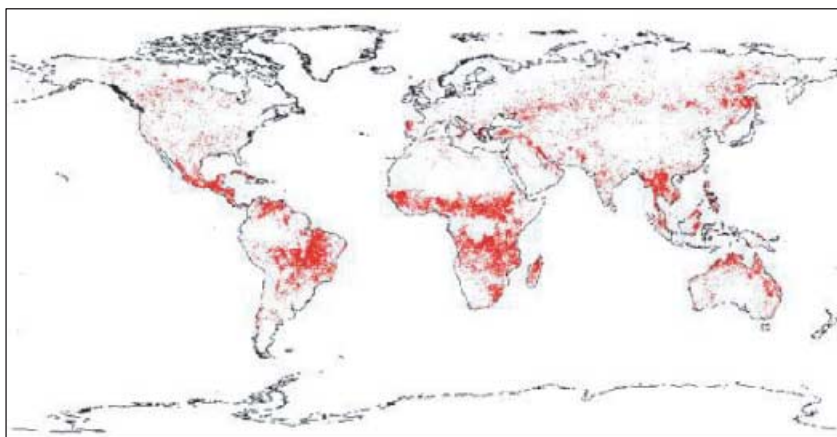


Fig. 5 Global distribution of fire in 1998 mapped by ATSR-2 World Fire Atlas (European Space Agency). Note that most fires occur in C_4 grass ecosystems. Source: ATSR World Fire Atlas web page: <http://shark1.esrin.esa.it/FIRE/AF/ATSR/>.

1999; Hoffmann & Franco, 2003) but a larger literature on forests.

Four of the world's major biomes experience frequent and/or predictable fire: temperate and tropical grasslands

and savannas, Mediterranean shrublands, and boreal forest (Archibold, 1995). Our results point to grasslands and savannas, dominated by C_4 grasses, as by far the most extensive FDEs. Most tropical and subtropical grasslands and savannas

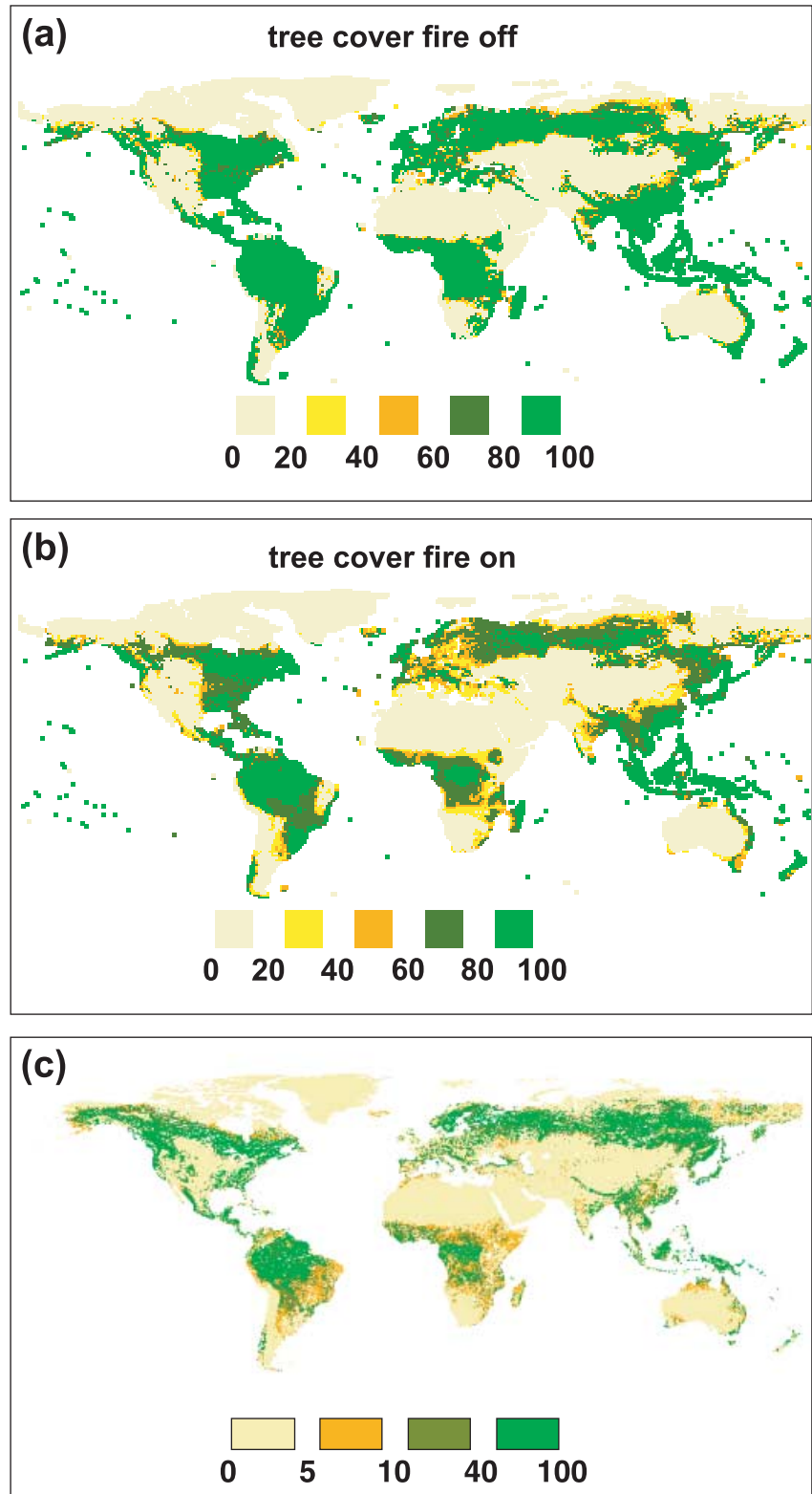


Fig. 6 Tree cover (%) (a) simulated with 'fire off' (b) simulated with 'fire on' (c) observed tree cover derived from satellite imagery in 2000 (FAO, 2001). Simulated cover values are median tree cover for 20th century simulations. Observed tree cover classes are: 40–100%, closed forest with no grass understorey; 10–40% more closed forms of savanna and other types of 'forest'; 5–10% scattered trees. The map does not discriminate between natural forests and plantations.

are not at their climate potential according to these simulations and would be replaced by woodlands and forests in a 'fire off' world. However the simulations also point to significant areas of climate-limited C_4 ecosystems in the more arid regions of the world, which are not dependent on burning (Fig. 4). Mediterranean shrublands are of much smaller extent but also have the climate potential to be forest, not shrublands, according to the simulations. The implication is that fire, and not just a combination of winter rainfall and summer drought (Specht, 1969; Mooney, 1977), is responsible for the peculiar dominance of shrubs. Mediterranean climate regions are characterised by steep climate gradients and the global simulation averages conditions over heterogeneous landscapes. At finer scales of resolution, a mosaic of fire-maintained and climate maintained shrublands seems more likely. The third major fire-prone biome, boreal forests, are often dominated by fire-adapted trees with serotinous cones that release seeds only after crown fires (Johnson, 1992; Keeley & Zedler, 1998). However, by our measure of fire dependence, the dominance of the gymnosperm tree growth form does not depend on burning according to the simulations. If fire dependence were measured by changes in species composition, rather than broad functional type, large areas of boreal forest (and other ecosystems?) might be considered 'fire-dependent'.

Testing the simulations

'Fire-off' DGVMs are relatively new tools for exploring biogeographical questions. How valid are the simulations? The 'fire-off' simulations of stem biomass gave a reasonable fit to observed biomass in vegetation where fire had been excluded for long periods (Fig. 1). Simulations of tree cover, a functional type which varies greatly with fire, also gave a satisfactory fit to southern African vegetation. The 'fire on' simulations predicted low tree cover (Fig. 2), consistent with the grassy and shrubby vegetation that dominates most of the region (Acocks, 1953; Cowling & Richardson, 1997). 'Fire-off' simulations are strikingly different with forests dominating the more humid eastern and south-western areas. Studies of successional trends following long-term fire exclusion support these predictions (Fig. 2; Bond *et al.*, 2003a). The locations of several experimental studies from other parts of the world are shown in Fig. 3. All of these are consistent with the 'fire-off' simulations, with those in more humid sites showing successional trends to woodland or closed forest (Table 2). We suspect there are many more fire-exclusion experiments around the world that could be used to test the DGVM simulations but no global compilation is available.

A major problem with using fire exclusion experiments to test the potential for biome switches is the time lag before all potential forest trees have colonised an area and grown to maturity. However there are many 'natural experiments' where, in landscapes dominated by flammable ecosystems,

forest patches persist in fire refugia adjacent to water bodies, in deep ravines, and at the edges of barren or rocky areas (Sarmiento, 1983; Furley *et al.*, 1992; Bond & van Wilgen, 1996; Bowman, 2000). Since forest patches often differ in other environmental factors too, there has been much debate on which of them limit forest distribution (e.g. Manders, 1990; Furley *et al.*, 1992; Bowman, 2000). Bowman (2000) has recently comprehensively reviewed the evidence on factors limiting rainforest distribution in Australia. He concluded that intolerance of recurrent fire, rather than climate or soil, is the only factor that consistently explains the distribution of Australia's archipelago-like rainforest patches in a sea of flammable vegetation.

Potential for afforestation also provides clues on the extent of climate control of vegetation. Many grasslands and shrublands in the southern hemisphere have been planted up to conifers and eucalypts or have been invaded by these trees (Richardson, 1998). Replacement of these systems by trees of much greater biomass is one indication that the native vegetation is not at climate potential. In the Cape region of South Africa, Le Maitre *et al.* (1996) reported above-ground biomass for fynbos, a flammable Mediterranean shrubland, of *c.* 1500–3500 g^{-2} where the SDGVM predicted 1000–2600 g^{-2} for 'fire-on'. In the same landscapes, they reported biomass of invasive conifer forests of 11 500–18 600 g^{-2} close to the SDGVM prediction of 12 000–22 000 g^{-2} for 'fire off' for these localities. Both empirical and simulated data support the idea that these shrublands are fire-maintained and not at their climate potential.

Fire-on simulations Although there is clearly room for refinement, the SDGVM predictions of climate-limited ('fire off') biome properties are well supported by available evidence. The 'fire on' simulations are more problematic, especially for humid grassy areas. The DGVM simulated very low fire return intervals (200 and 73 yr, respectively) for the North American and Venezuelan sites (Fig. 1) over the 100-yr simulation period. In reality, both sites burnt at intervals of 2–5 yr (San Jose *et al.*, 1998; Tilman *et al.*, 2000). Other attempts to simulate fire for DGVMs also underestimate fire frequency in humid savannas. Thonicke *et al.* (2001) predicted fire return intervals of 50 to > 200 yr for humid savanna regions of Brazil, Africa and tall grass prairies in North America. In practise, these C_4 grass-dominated systems may burn every year and at least several times in a decade. Current versions of fire modules used in DGVMs are therefore likely to greatly overestimate tree cover in humid savannas (Fig. 1; Venezuela site). This is apparent in comparisons of simulated and observed tree cover (Fig. 6b, c). While the tree cover classes are difficult to equate, the SDGVM cover class of > 90% tree cover for the 'fire on' simulation is largely coincident with the FAO 'closed forest' cover class. However the SDGVM simulated high tree cover in, for example, the Brazilian cerrados. This vast (> 2 million km^2) region of humid savannas (mean

annual rainfall of 800–2000 mm) has strikingly low tree cover, especially when compared with the patches of closed forest that occur as isolated patches within cerrado (Sarmiento, 1992; Ratter *et al.*, 1997; Oliveira-Filho & Ratter, 2002). Since humidity is a major driver of current fire modules in global DGVMs, it is not surprising that simulated fire frequencies are greatly underestimated in humid savannas. More work is needed on developing fire models, perhaps by including differences in flammability among PFTs, to improve simulations of the very high fire frequencies of humid tropical grassy biomes. However our aim was to determine which parts of the world support vegetation very different from the potential set by climate. To this end, the ‘fire-off’ simulations of DGVMs are currently the best available tool for exploring the biogeography of a world without fire. It is clear that humid savannas are the prime candidate.

Alternative explanations for nonforested ecosystems

Our study indicates large differences between climate potential and actual vegetation, especially in tropical grasslands and savannas. But is fire really the culprit? There has long been a debate on determinants of savanna distribution (Frost & Robertson, 1987; Scholes & Archer, 1997). Savannas generally occur in seasonally dry climates. But, as revealed by the DGVM simulations, fire exclusion studies, the presence of closed forests in savanna landscapes, and extensive conversion of humid grassy ecosystems to plantation forestry, seasonally dry climates can also support closed forests. In South America, forests occur over the entire rainfall range of savannas (Sarmiento, 1992; Oliveira-Filho & Ratter, 2002). Soil factors are frequently invoked to explain the absence of tree-dominated vegetation. Seasonally waterlogged soils are a common feature of bottomlands and lower slopes of soil catenas in many tropical savanna landscapes of low relief. Grasslands typically dominate on these soils with few, widely scattered trees. The Pantanal, a vast South American wetland (*c.* 400 000 km²), is probably the only area, at a global scale, where seasonal waterlogging is so extensive that it can account for the sparse tree cover (Eiten, 1975).

Low soil nutrients in ancient weathered landscapes, including most of Australia and large areas of South America and Africa, have also been invoked as an explanation for the lack of forest in humid regions (e.g. Cole, 1986 for savannas; Specht & Moll, 1983 for shrublands). However long-term fire exclusion studies and growth experiments suggest that, although soil nutritional properties may influence the rate of tree invasion into grasslands and shrublands, they do not prevent tree incursion (e.g. Kellman, 1984; Manders, 1990; Bowman & Panton, 1993). Forest trees tend to accumulate nutrients more than savanna trees and such enrichment may sometimes (but not always; e.g. Hoffmann & Franco, 2003) be an essential precursor to their invasion of fire-protected savannas (Bowman & Fensham, 1991). Where fires are

frequent, any factor that slows tree growth will tend to favour dominance by fire-tolerant shrubs or grasses (Kellman, 1984).

Other than fire, and anthropogenic activities, few (if any) disturbance agents reduce tree biomass at a global scale. The extent to which herbivores control ecosystem structure has been long debated (Hairston *et al.*, 1960; Polis, 1999). Fire, as an alternative consumer of plants, has not been part of this debate. Yet Africa, despite having the largest extant diversity of ungulate herbivores, also has the most frequent and extensive fires in humid grassy ecosystems (Fig. 5; Barbosa *et al.*, 1999; Dwyer *et al.*, 2000). Grasses of the humid tropics are typically coarse and inedible and support low grazer biomass (Bell, 1982). In Africa, large elephant populations confined in protected areas have major impacts on tree cover (e.g. Cumming *et al.*, 1997). They may (or may not) have been influential in reducing tree cover over larger areas in the past. Stand die-back from insect out-breaks is a common feature of higher latitude forests and can limit tree biomass, especially of conifers (Kurz & Apps, 1999). These and other disturbance agents may be of local importance in limiting tree biomass. None have the global extent and influence of biomass burning (Fig. 5).

Origins of fire-dependent biomes

The vast extent of flammable biomes, especially in the tropics and subtropics, has often been attributed to anthropogenic burning. Although anthropogenic fires have undoubtedly extended areas of flammable vegetation, there is now abundant evidence that natural fires occurred long before humans (Scott, 2000) and that flammable ecosystems predate anthropogenic burning by millions of years. C₄ grassy ecosystems first began to form a distinct vegetation type some 6–8 Ma according to isotope evidence from fossil bone and soil carbonate (Cerling *et al.*, 1997). Their appearance has been attributed to decreasing atmospheric [CO₂], which favours the C₄ photosynthetic mechanism (Ehleringer *et al.*, 1997, but see Keeley & Rundel, 2003), but increased fire frequencies must have been a major factor in their rapid spread at the expense of forests (Sage, 2001; Bond *et al.*, 2003b; Keeley & Rundel, 2003). It is interesting to note that these grassy ecosystems were even more extensive at the last glacial maximum (Harrison & Prentice, 2003) when anthropogenic effects were minor but fires continued to burn (Scott, 2002).

The very extensive flammable formations in Australia (woody and grassy) seem, from fossil charcoal and palynological records, to have begun carving out forests from the Miocene (Bowman, 2000; Kershaw *et al.*, 2002; Hassell & Dodson, 2003). Mediterranean shrublands, whose origin has usually been attributed to the onset of mediterranean-type climates, seem also to have expanded in the late Tertiary more or less coincidentally with flammable C₄ grassy biomes (California Axelrod, 1989, Europe Herrera, 1992, Australia Hassell & Dodson, 2003; South-west Africa Linder, 2003).

If the extent of fire-dependent ecosystems were an anthropogenic artefact, then the biota should reflect a very recent origin with just a few widespread species profiting from burning along with some fire-tolerant survivors. Flammable grassy ecosystems with just such characteristics occur on islands such as Madagascar and Hawaii altered by relatively recent human settlement (D'Antonio & Vitousek, 1992). However the biota of flammable ecosystems on continents show evidence of greater antiquity. Among grasses, the Andropogoneae dominate many humid grassy ecosystems with the climate potential to form forests worldwide (Hartley, 1958; Barkworth & Capels, 2000). They have several characteristics that promote frequent fires (Bond *et al.*, 2003a). The sudden appearance of C₄ grass-fuelled fire regimes in the late Tertiary must have presented a formidable obstacle to tree recruitment and survival, especially in the context of falling CO₂ levels (Bond *et al.*, 2003b). Tree floras of flammable formations would be expected to have evolved independently on different continents with little time for dispersal across ocean barriers between continents. Evidence for this is that dominant tree taxa differ from one savanna region to the next and have diversified greatly within regions. Examples include *Eucalyptus* (Myrtaceae) in Australia (Ladiges *et al.*, 2003), Caesalpiniaceae and *Acacia* in Africa (White, 1983), Dipterocarpaceae in savannas of south-east Asia (Stott, 1988; Stott *et al.*, 1990), and diverse lineages in the vast cerrados of Brazil (Sarmiento, 1983; Ratter *et al.*, 1997; Hoffmann & Franco, 2003). From the few studies available, savanna tree species are not a fire-tolerant subset of forest tree species. They are generally endemic to flammable formations with an entirely different suite of species occurring in closed forests (Prance, 1992; Sarmiento, 1983 for South America; Bowman, 2000 for Australia; White, 1983 for Africa). However, at least in some genera, sister taxa in forests and savannas have apparently arisen independently several times (Prance, 1992; Hoffmann & Franco, 2003) and few genera, and no families appear to be endemic to fire-dependent grassy biomes consistent with the relatively recent origin of flammable floras. Our point is that the global extent of fire-dependent ecosystems is not merely an artefact of recent anthropogenic burning. They have existed long enough to evolve distinctive biotas.

Conclusion

Although the importance of fire in determining vegetation structure and composition has been extensively studied in many parts of the world, this is the first integrated report on the global extent of fire-dependent ecosystems. It is made possible by the recent development of DGVMs, which, for the first time, allow an evaluation of the mismatch between climate potential and actual world vegetation measured, largely, by the importance of trees. The reduction of trees by fire has resulted in the evolution of some of the most biodiverse ecosystems in the world, and facilitated the rise of essentially

modern C₄ grass-dominated floras and associated faunas. The great extent of apparently fire-dependent grasslands and shrublands raises a number of questions. What limits the occurrence of fire and what determines particular fire regimes? What caused changes in fire regimes in the past initiating the spread of FDEs? How do humans alter fire regimes, often promoting, but also consciously or inadvertently, suppressing fires? How should fire be incorporated in global change scenarios, not only through atmospheric impacts of biomass burning but also as a major determinant of global ecosystem structure and composition? Answers to these questions will help fill the large gaps in our current understanding of global ecology and biogeography.

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Appendix. Description of the Sheffield Dynamic Global Vegetation Model (SDGVM)

The SDGVM is a generalised global-scale model that predicts vegetation structure and dynamics from input data of climate, [CO₂] and soil texture. The basic processes and assumptions in the SDGVM are outlined in Cramer *et al.* (2001). The SDGVM requires input data of climate, [CO₂] and soil texture. The climate data are monthly mean and minimum temperatures, water vapour pressure deficit, precipitation and cloudiness. The physiology and biophysical module simulates carbon and water fluxes from vegetation (Woodward *et al.*, 1995) with water and nutrient supply defined by the water and nutrient flux module. The soil module incorporates the Century soil model of carbon and nitrogen dynamics (Parton *et al.*, 1993), with a model of plant water uptake. Eight soil carbon and nitrogen pools are modeled: surface and soil structural material, active soil organic matter, surface microbes, surface and soil metabolic material, slow and passive soil organic material.

The carbon and nitrogen dynamics are described by linear autonomous differential equations with parameters that depend on soil texture, temperature, precipitation, humidity, soil moisture, water flow, potential evapotranspiration and litter. These variables are held constant over a given period and the differential equations are solved by standard means for these conditions. The set of parameters is updated at each successive period, and the carbon calculation is advanced using the final state in the previous period as the initial state in the current period. These equations are solved each month. The organic nitrogen flows are equal to the product of the carbon flow and the nitrogen to carbon ratio of the state variable that receives the carbon (Parton *et al.*, 1993). The carbon to nitrogen ratios of the soil state variables receiving the flow of carbon, are linear functions of the mineral nitrogen pool. The mineral nitrogen pool is an additional pool, which stores surplus nitrogen. The dynamics imposed by the linear functions ensure that this pool is always positive.

Water fluxes are modelled using a 'bucket' model. The model is composed of four buckets: one thin (5 cm) layer at the surface and three buckets of equal depth, which make up the remainder of the soil layer. The depth of the total soil layer is set to a default of 1 m. The effects of bare soil evaporation, sublimation, transpiration and interception (each of which represents a loss of water available to the vegetation system) are incorporated into the model.

The primary productivity model simulates canopy CO₂ and water vapour exchange and nitrogen uptake and partitioning within the canopy. Nitrogen uptake is linked directly with the Century soil model, which simulates the turnover of carbon and nitrogen in plant litter, of differing ages and depths within the soil, in addition to soil water status.

The primary productivity model determines the assimilated carbon available for the growth of plant leaves, stems and roots. The plant structure and phenology module defines the vegetation leaf area index and the vegetation phenology. Leaf phenology is defined by temperature thresholds for cold deciduous vegetation and by drought duration for drought deciduous vegetation (Cramer *et al.*, 2001).

The vegetation dynamics module (Cramer *et al.*, 2001; Woodward *et al.*, 2001) simulates the establishment, growth, competition and mortality of plant functional types (evergreen and deciduous broad leaved and needle leaved trees, grasses with the C₄ photosynthetic metabolisms and C₃ grasses and shrubs). Functional types of plants compete for light and soil water and all suffer random mortality that increases with age. The densities (plants per unit area), heights and ages of all of the functional types, except grasses, are simulated at the finest spatial resolution (pixel) of the model. A fire module, based on temperature and precipitation, burns a fraction of the smallest pixel of study (Woodward *et al.*, 2001). The fire model simulates disturbance by fire for a small fraction of the pixel. It is assumed that 80% of above-ground carbon and nitrogen are lost as a consequence of the fire and fire only occurs when, in effect, leaf litter reaches a critical point of dryness, at which point fire will occur at a random time and for a random subset of the pixel (Woodward *et al.*, 2001).

The SDGVM simulations start from a soil, defined by texture and depth, climate and atmospheric CO₂ concentration. Therefore there is a necessary initialisation stage in which the soil carbon and nitrogen storage of the soil is determined, with the appropriate vegetation for the simulated climate. The model initialisation is determined by running with a repeated and random selection of annual climates from 1901 to 1920. The soil carbon and nitrogen values are first determined by solving Century analytically. Then the model is run until the vegetation structure is at equilibrium, typically after, at most 500 yr. When initialisation is completed the SDGVM then simulates vegetation for the whole climate series. Fire was simulated from the same initial values as the fire-off simulation for the 20th century.



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