Global climate and the distribution of plant biomes

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Biomes are areas of vegetation that are characterized by the same life-form. Traditional definitions of biomes have also included either geographical or climatic descriptors. This approach describes a wide range of biomes that can be correlated with characteristic climatic conditions, or climatic envelopes. The application of remote sensing technology to the frequent observation of biomes has led to a move away from the often subjective definition of biomes to one that is objective. Carefully characterized observations of life-form, by satellite, have been used to reconsider biome classification and their climatic envelopes. Five major tree biomes can be recognized by satellites based on leaf longevity and morphology: needleleaf evergreen, broadleaf evergreen, needleleaf deciduous, broadleaf cold deciduous and broadleaf drought deciduous. Observations indicate that broadleaf drought deciduous vegetation grades substantially into broadleaf ever-green vegetation. The needleleaf deciduous biome occurs in the world's coldest climates, where summer drought and therefore a drought deciduous biome are absent.

Traditional biome definitions are quite static, implying no change in their life-form composition with time, within their particular climatic envelopes. However, this is not the case where there has been global ingress of grasslands and croplands into forested vegetation. The global spread of grasses, a new super-biome, was probably initiated 30–45 Myr ago by an increase in global aridity, and was driven by the natural spread of the disturbances of fire and animal grazing. These disturbances have been further extended over the Holocene era by human activities that have increased the land areas available for domestic animal grazing and for growing crops. The current situation is that grasses now occur in most, if not all biomes, and in many areas they dominate and define the biome. Croplands are also increasing, defining a new and relatively recent component to the grassland super-biome. In the case of both grassland and croplands, various forms of disturbance, particularly frequent disturbance, lead to continued range extensions of the biomes.

Keywords: biome; climate; forest; grassland; cropland

1. INTRODUCTION

Biomes are large clusters of plant species that are defined in terms of the recognizable physiognomy of the dominant species. The classification by life-form is necessary because individual species are generally geographically too limited to encompass the full environmental and geographical range of the recognizable life-form and biome. It has also been typical to include a geographical or locational element in the definition, such as equatorial, tropical or boreal. Holdridge (1967) provided a detailed classification of different biomes in terms of both physiognomy and climate, often known as climate envelopes. This method deeply embeds climate in the definition of biomes. The approach moved away from earlier efforts, for example by Schimper (1898) and Walter (1931), to understand distributional limits in terms of critical biological processes.

A simplified view of the climate envelope of biomes (figure 1) indicates that geographical location, e.g. tropical and boreal plays as much a part in defining a biome as climate. Using location to define biomes should generally be avoided when investigating the geographical distribution of biomes as this leads to circularity. Including climate in the definition of a biome should also be avoided as climate itself defines the distribution of a biome (Woodward 1987), with further potential for circularity. Those biomes that include trees (figure 1) provide a starting point for the definition, as they occur in all but three of the biomes and are features that are readily recognizable.

An approach based solely on what can be seen has been developed by the remote sensing community. The IGBP–DIS has derived such a classification of biomes (table 1) in which geographical location plays no part. The traditional classification of biomes (figure 1) also creates sharp boundaries between biomes, whereas in reality, the majority of biomes have extensive interdigitation in an often wide transition between adjacent biomes. The IGBP–DIS (table 1) classification defines forests in the transitional zones between biomes as mixed forest, so the transitional zones are in effect considered as biomes. Tree-dominated biomes are defined as forests when tree cover exceeds 2 m in height and constitutes more than 60% of the canopy cover. The threshold effect will also lead to an artificial boundary between biomes, particularly when the transition zone is
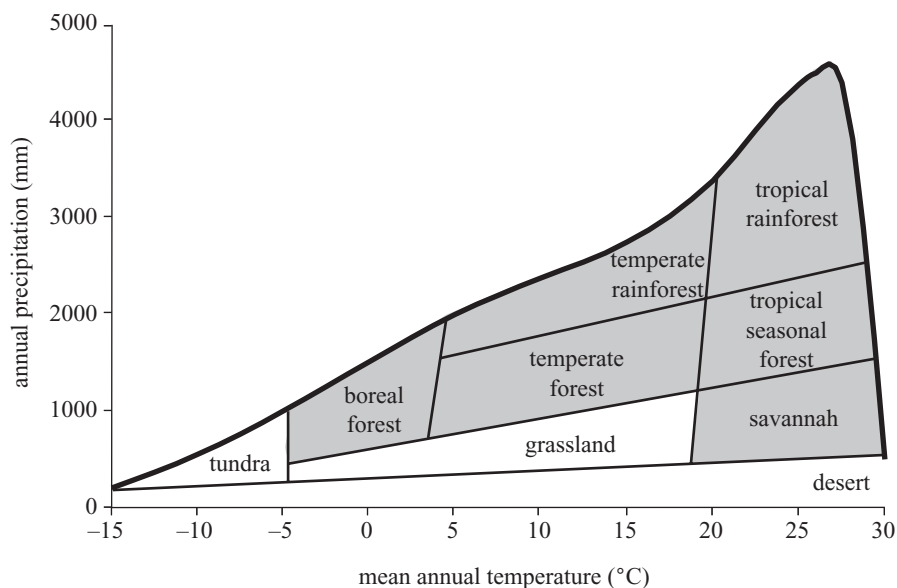
Figure 1. The distribution of traditionally defined biomes in terms of annual temperature and precipitation. The shaded area includes all biomes that contain trees. (Modified from Woodward & Lomas 2004.)

Table 1. The IGBP–DIS land cover classification. (Modified from Woodward *et al.* 2001.)

classification	comment
evergreen needleleaf forests	Lands dominated by trees with a canopy cover of more than 60% and height exceeding 2 m. Almost all trees remain green all year. Canopy is never without green foliage.
evergreen broadleaf forests	Lands dominated by trees with a canopy cover of more than 60% and height exceeding 2 m. Almost all trees remain green all year. Canopy is never without green foliage.
deciduous needleleaf forests	Lands dominated by trees with a canopy cover of more than 60% and height exceeding 2 m. Consists of seasonal needleleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
deciduous broadleaf forests	Lands dominated by trees with a canopy cover of more than 60% and height exceeding 2 m. Consists of seasonal broadleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
mixed forests	Lands dominated by trees with a canopy cover of more than 60% and height exceeding 2 m. Consists of tree communities with interspersed mixtures or mosaics of the other four forest cover types. None of the forest types exceeds 60% of the landscape.
closed shrublands	Lands with woody vegetation less than 2 m tall and with shrub canopy cover more than 60%. The shrub foliage can be either evergreen or deciduous.
open shrublands	Lands with woody vegetation less than 2 m tall and with shrub canopy cover between 10 and 60%. The shrub foliage can be either evergreen or deciduous.
woody savannahs	Lands with herbaceous and other understorey systems, and with forest canopy cover of between 30 and 60%. The forest cover height exceeds 2 m.
savannahs	Lands with herbaceous and other understorey systems, and with forest canopy cover between 10 and 30%. The forest cover height exceeds 2 m.
grassland	Lands with herbaceous types of cover. Tree and shrub cover is less than 10%.

extensive. IGBP–DIS (table 1) has also used remote sensing to identify and classify shrubland biomes. Analysis of shrublands has not been attempted here because of a real uncertainty, at least among the authors, of how to define shrublands. They may be considered to contain woody plants of less than 2 m tall (table 1), but there are many cases where woody plants of greater than 2 m tall are also classified as shrubs (Smith *et al.* 1997) and where woody plants of less than 2 m tall are defined as trees. This lack of clarity in definition has prevented their description here, although this biome is of major phylogenetic interest, for instance in the Australian flora (Crisp *et al.* 2004; Hill 2004).

It is also important to remove subjectivity when defining the distribution of biomes, particularly when investigating the importance of climate. Data from satellite imagery are well suited to such a requirement; even though the process of interpreting raw radiance data requires a model, it is generally objective. The approach taken here is to use interpreted remote sensing data (DeFries *et al.* 2000) to investigate the global-scale distribution of physiognomic classes of vegetation.

At present, the distribution of trees by satellite remote sensing has been carefully determined and validated (DeFries *et al.* 2000); however, no equivalent is available for shrubs and grasses. Therefore the initial approach is concerned with trees. This is expanded subsequently to include grasses in particular, using alternative sources of distribution data.

2. CLIMATE AND THE GLOBAL DISTRIBUTION OF TREES

(a) *Data sources*

DeFries *et al.* (2000) describe techniques for mapping the global distribution of trees at a 1 km resolution from satellite data when their canopy cover ranges between *ca.* 10% and 80%. The lower limit is related more to the detection limits of the approach, while it does not appear that particular tree physiognomies exceed *ca.* 80% of canopy cover. The data are available at http://glcf.umiacs.umd.edu/data/treecover/latlongProjection.shtml. The procedure classifies trees into two recognizable physiognomies and two phenologies: evergreen, deciduous, broadleaf and needleleaf. These basic classes are not only recognizable but there is considerable understanding of the critical interactions between climate and biological processes that limit their distributions in both climatic and geographical space (Woodward 1987).

The correlation between the distribution of biomes and climate has traditionally been achieved using the geographical distributions of annual temperature and precipitation (figure 1). The climate data for this and other comparisons are for the period from 1901 to 1970, and have been derived by New *et al.* (2000). This data series avoids the increases in temperature observed over the last two decades and to which vegetation may be responding, but incompletely so (Woodward & Lomas 2004). The data have been interpolated to provide a global coverage, on a monthly basis, for the twentieth century; the finest resolution of the database is 0.5° of latitude and longitude.

(b) *Observations*

The four physiognomic classes of trees show contrasting but overlapping geographical distributions (figures 2–5), which indicates the extent of transition zones between biome types. Indeed, it appears that mixed classes of trees, generally as forests, dominate the global scene. Hard transitions between vegetation types (figure 1) are not observable in contemporary terrestrial vegetation. Broadleaf evergreen trees (figures 2 and 4) dominate, with evergreen and deciduous needleleaf trees (figures 3 and 5) being primarily confined to the Northern Hemisphere. Deciduous trees are widely distributed but rather rarely dominate any particular biome; this may in part be a result of the ingress of agriculture and grassland in different parts of the world.

Mean annual temperature (figure 6) and precipitation (figure 7) (modified from New *et al.* 2000) indicate some obvious correlations with tree distribution. The northern limits of evergreen needleleaf trees (figure 5) correspond approximately with the −5 °C isotherm (figure 6), and the broadleaf evergreen forests of Amazonia and Central Africa occur where the mean monthly precipitation exceeds *ca.* 140 mm. Water supply by precipitation is critical for plant growth, with plant water contents often being greater than 95% of fresh weight. Carbon dioxide taken up by photosynthesis is at a cost of simultaneous water loss, so productivity is strongly correlated with plant water loss and therefore water requirement (Woodward 1987).

Direct mechanistic relationships exist between precipitation and biome type (Woodward 1987). However, any process relationships between mean annual temperature and tree distributions are not straightforward, although more physiologically relevant characteristics, such as growing season temperature and absolute minimum temperature, may be correlated with mean annual temperature. Large areas of the terrestrial biosphere have mean annual temperatures below the freezing point of water, when little if any growth occurs. So if temperature is critical in the control of distribution then it must be some component of mean annual temperature, such as growing season temperature, for example .

Mean annual temperature has no directly obvious mechanistic relationship with plant distribution. By contrast, minimum temperature but not maximum temperature is causally related. Woodward (1987) established from observations the presence of cardinal temperatures for the survival of different functional types of trees. Chilling-sensitive species are sensitive to, or killed by temperatures above the freezing point of pure water and *ca.* 10 °C, respectively. Temperatures below freezing to *ca.* −15 to −20 °C kill frost-sensitive evergreen, broadleaf species. Species dependent on deep supercooling to avoid injury, and which are typically broadleaf deciduous species, survive to a threshold of *ca.* −40 °C. These temperature extremes (recorded as absolute minimum temperatures at meteorological stations (Müller 1982)) may only occur occasionally (Woodward 1987) but are of a sufficient frequency to influence tree survival.

Unfortunately, the global climate dataset does not contain observations of absolute minimum temperature. However, the mean temperature of the coldest month is strongly correlated with the absolute minimum temperature (Müller 1982). The map of mean minimum annual temperature (figure 8) identifies the terrestrial biosphere's coldest region, in Siberia, where deciduous needleleaf forest dominates (figures 3 and 5). By contrast, the minimum temperatures in areas where broadleaf evergreen trees dominate exceed any lethal freezing points (figures 2 and 4).

(c) *Climatic envelopes*

A resolution of 0.5° of latitude and longitude provides 33 000 points of comparison between the occurrences of different physiognomic and phenological classes of trees and climate. Therefore scatter diagrams between climatic variables and distribution, for all points, provide highly resolved indications of the climate envelopes, underpinned directly by an understanding of critical processes that limit survival.

The evergreen and deciduous classes of tree (figure 9*a,b*) show wide distributions in the climatic envelope defined by annual minimum temperature and total precipitation. This contrasts with the needleleaf class, which is only distributed in climates with a minimum temperature below 15 °C. Although deciduous vegetation occurs in most but the wettest of climates, there are notable discontinuities. The deciduous needleleaf class occurs only in climates with a minimum temperature of less than −30 °C. The cold deciduous class occurs at minimum temperatures of
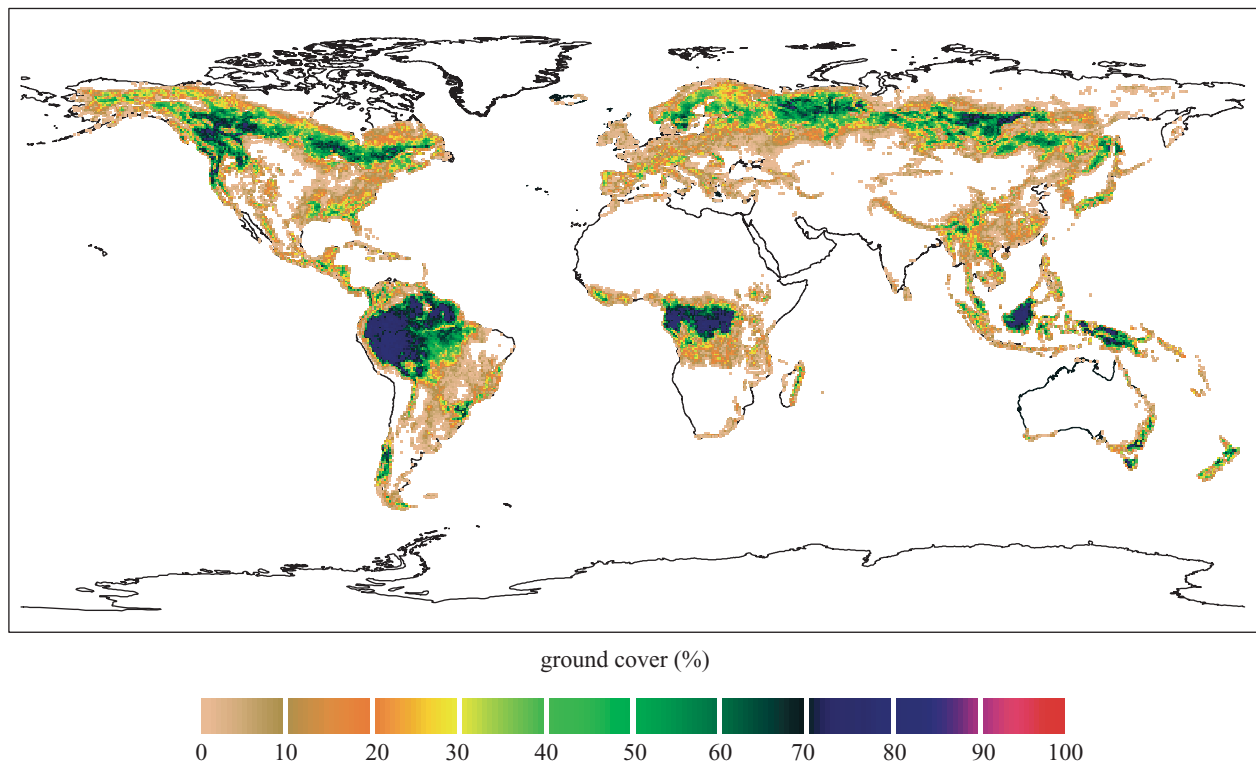
Figure 2. Global-scale distribution of evergreen trees (percentage of ground cover). All tree data are from the University of Maryland Global Land Cover Facility, continuous fields tree cover project, available at: http://glcf.umiacs.umd.edu/data/treecover/latlongProjection.shtml.
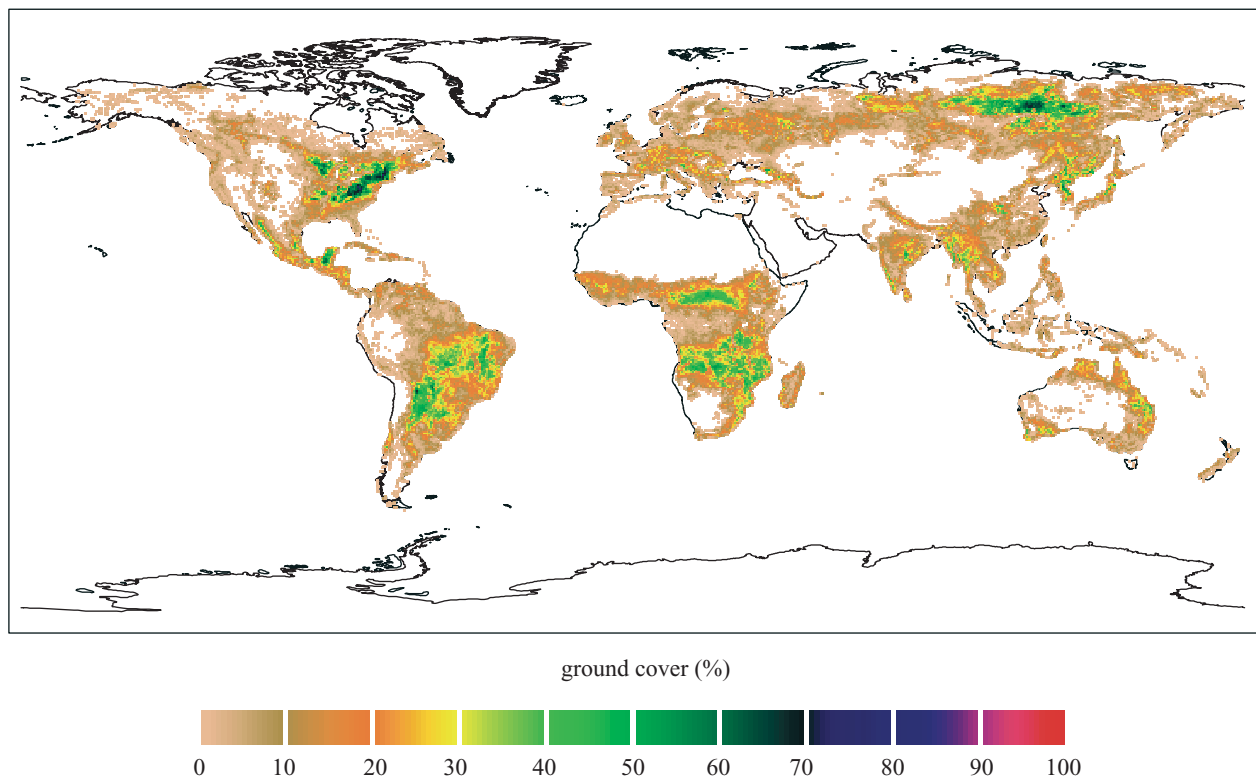

Figure 3. Global-scale distribution of deciduous trees (percentage of ground cover).

between −30 °C and 5 °C, whereas the drought deciduous class occurs where the minimum temperature exceeds 7 °C and over a very wide range of annual precipitation. The drought deciduous broadleaf trees show a considerable overlap with the climatic envelope of the evergreen broadleaf trees.

Five classes of tree type can be recognized and defined as biomes. The five classes are needleleaf evergreen, broadleaf
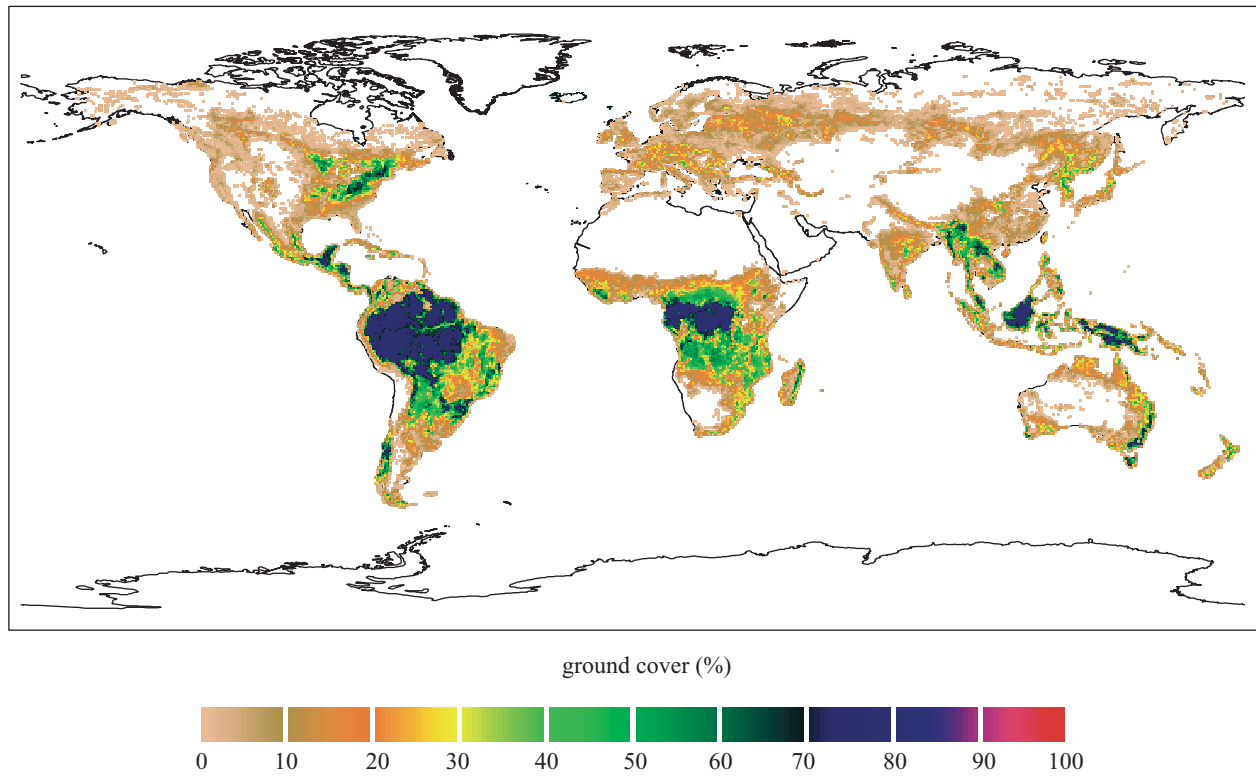
Figure 4. Global-scale distribution of broadleaf trees (percentage of ground cover).
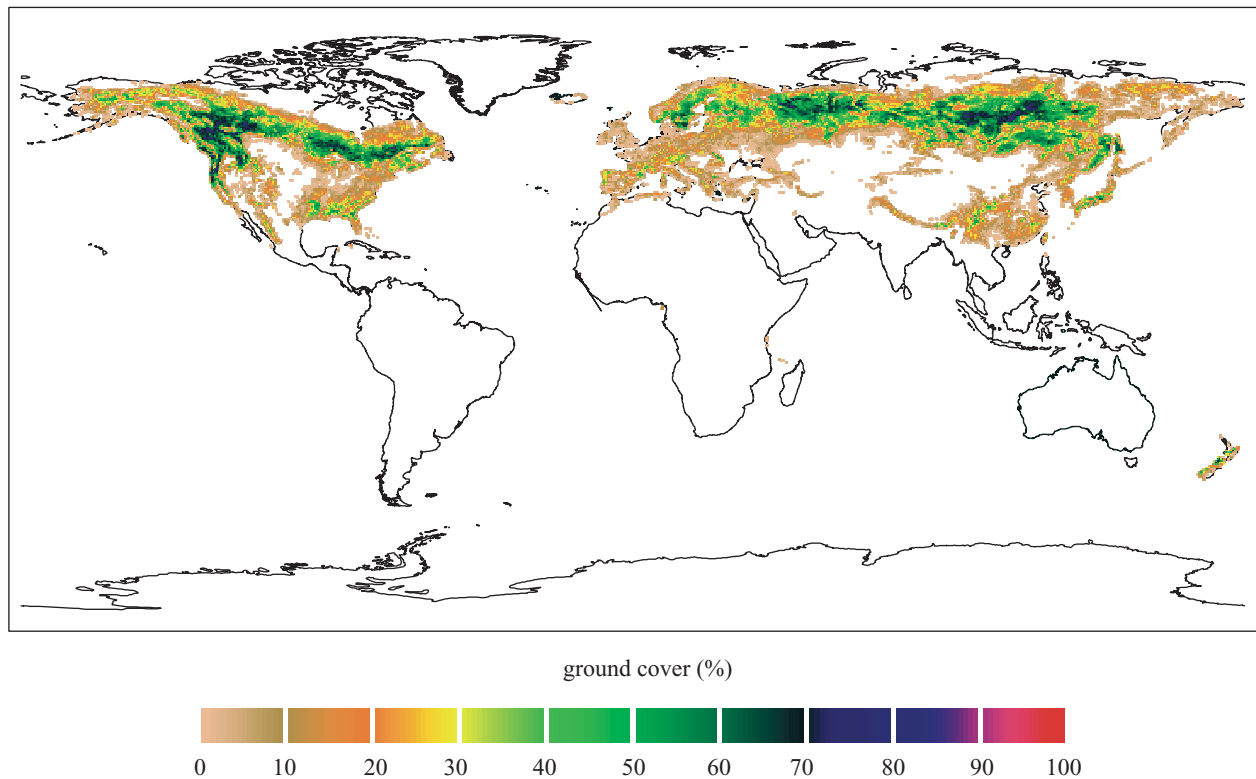

Figure 5. Global-scale distribution of needleleaf trees (percentage of ground cover).

evergreen, needleleaf deciduous, broadleaf cold deciduous and broadleaf drought deciduous, based on leaf size and longevity, but with the added necessity of recognizing cold and drought deciduous behaviour. This could be achieved by remote sensing of canopy temperature (Schmugge &

Kustas 1999) and canopy water status (Park *et al.* 2004). The climatic envelopes of these biomes are very wide and incompatible with the finer climatic-based resolutions, such as employed by Holdridge (1967), but they have the considerable advantage of being observable.
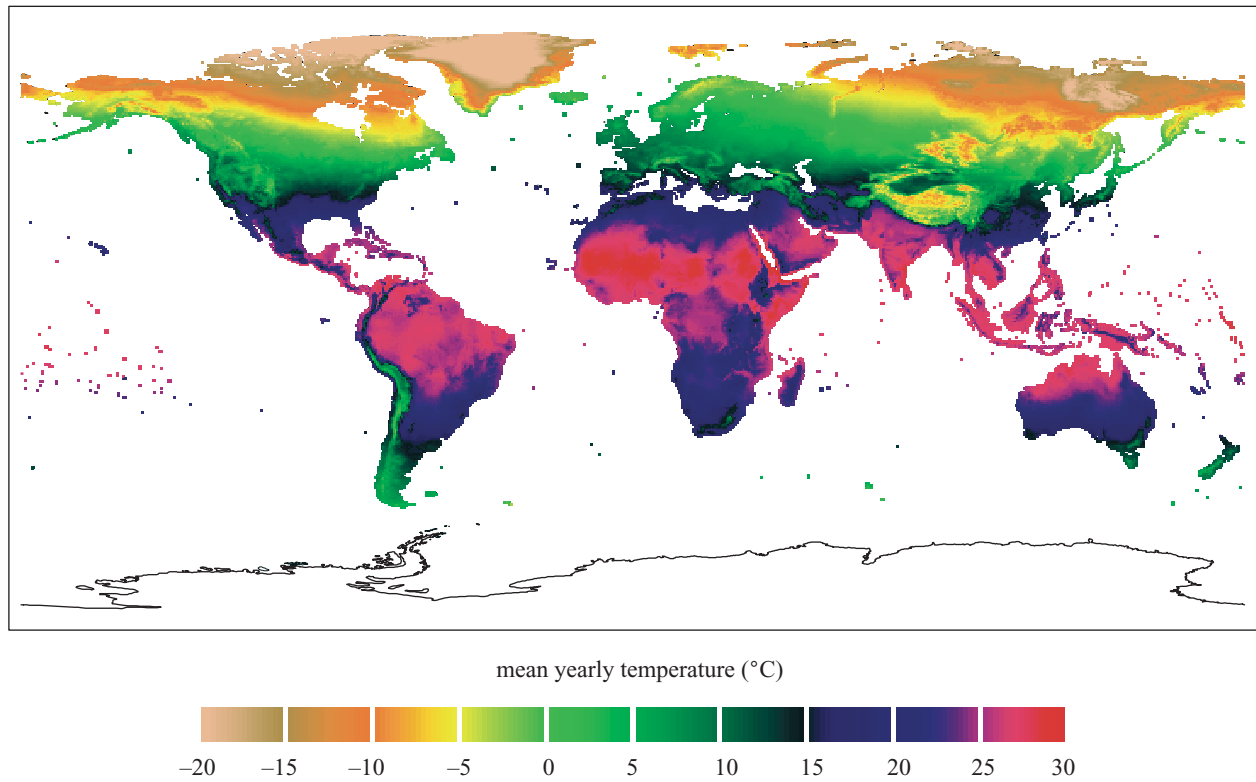
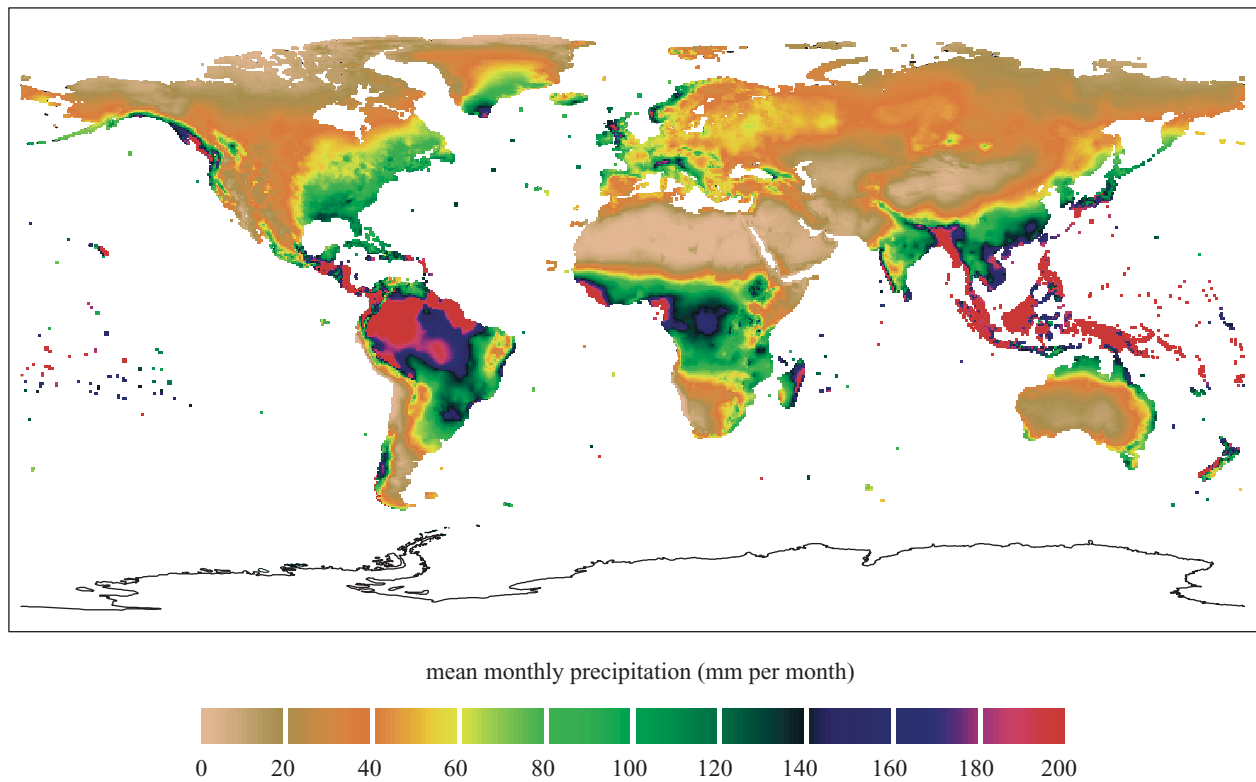Figure 6. Mean annual temperature for 1901 to 1970. (Modified from New *et al.* 2000.)

Figure 7. Mean monthly precipitation for 1901 to 1970. (Modified from New *et al.* 2000.)

3. GRASSLAND

(a) *The origin of grasses*

The majority of the 400 Myr of life on land has been dominated by the presence of trees (Beerling & Woodward 2001). Their height and longevity have driven their dominance of terrestrial biomes. Grasses, by contrast, have a much shorter lifespan, evolving some 55 to 70 Myr ago (Kellogg 2001) and extending their distribution away from their origins in tropical woodland (Bredenkamp *et al.* 2002) only *ca.* 30 to 45 Myr ago. This spread and subsequently
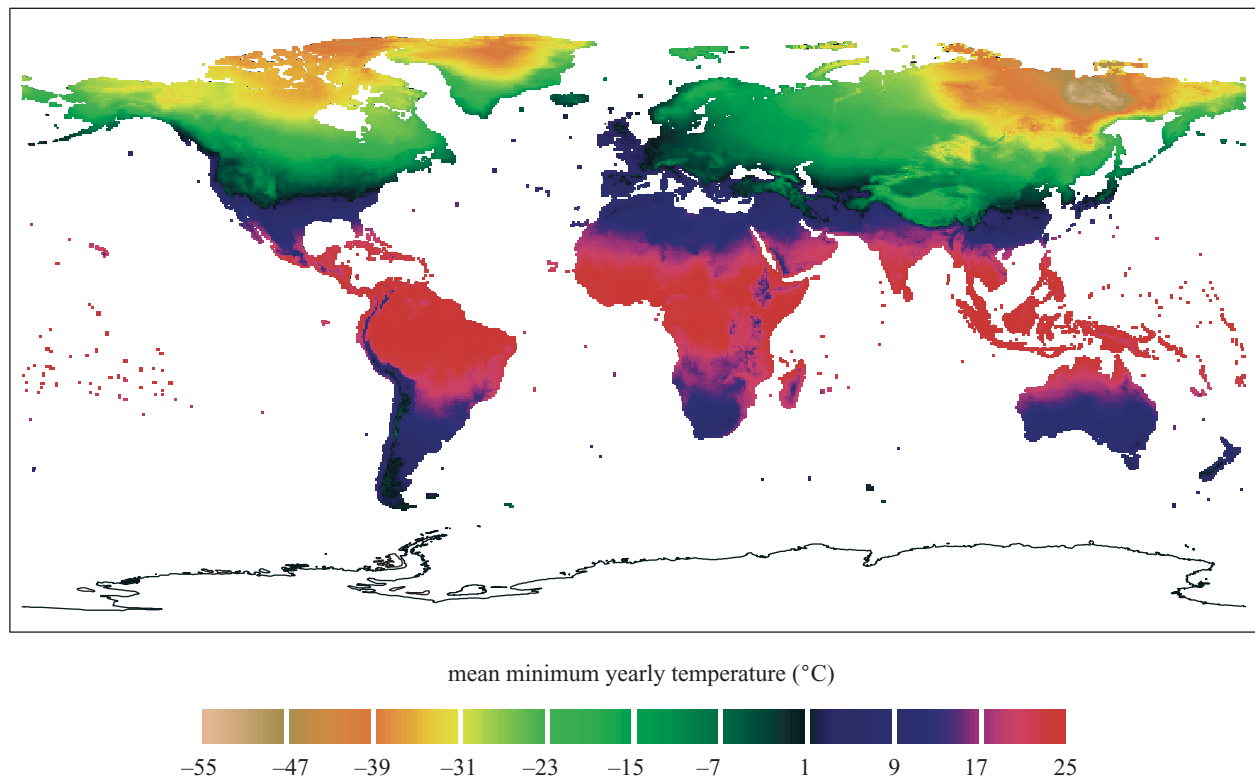
mean minimum yearly temperature (°C)

Figure 8. Mean minimum annual temperature (on a monthly basis) between 1901 and 1970. (Modified from New *et al.* 2000.)

rapid diversification appears to have been initiated by global environmental change, in particular greater aridity (Zachos *et al.* 2001). The geographical spread of grasslands to the Northern and Southern Hemispheres was aided by disturbance, in addition to climatic change. Grazing, rather than browsing animals increased in abundance and evolved rapidly as the range of grassland increased (Retallack 2001). Grazing animals reduced the regeneration of tree species in combination with the spread of fire, both of which significantly impacted tree survival but with less impact on the grasses owing to the positioning of their protected meristems at or below the soil surface.

A major evolutionary step in the grasses was the emergence of species with C4 photosynthetic metabolism. This origin is not known with certainty, but probably first occurred at *ca.* 25 Myr ago (Kellogg 2001). The initial spread and evolution of the C4 grasses was slow but notable range extensions, seen in many palaeoecological records, occurred *ca.* 8 Myr ago. Grasses with C4 photosynthetic metabolism have among the highest rates of photosynthesis (Pagani *et al.* 1999) but are generally confined to warm and hot climates, because the metabolism as a whole, which includes photosynthesis and growth (Lawlor 1993) is sensitive to chilling temperatures, a feature that strongly curtails the growing season in cool climates.

The rapidity of growth by C4 grasses, tied to their general occurrence in warm and at least semi-arid, seasonally dry climates, indicates that such biomes are particularly fire-prone (Bond *et al.* 2003). Fires can occur with high frequency, effectively preventing tree regeneration and even spreading into forested areas (Bond & Van Wilgen 1996).

Disturbance is therefore a key factor in grasslands and this is generally at odds with the spread and even survival of forest trees. It can be argued, therefore, that the current biome maps of the world represent not a stable distributional state but much more a gradual spread by attrition of grasslands, in place of trees.

(b) *The current distribution of grasses*

The combination of climatic change and disturbance has therefore strongly favoured the spread of grasses. Objective techniques for mapping open grasslands by remote sensing are available (Yamano *et al.* 2003), but these can fail to identify the presence of grasses as forest and woodland understorey. C4 grasslands cannot be differentiated from C3 grasslands on the basis of their particular physiology and leaf structure. There is some possibility for detection based on phenological dynamics (Davidson & Csillag 2001). However, this approach has not been attempted at the global scale. By contrast, it is relatively simple and accurate to simulate the occurrence of both C3 and C4 grasses, using an understanding of basic physiology (Still *et al.* 2003). Global scale maps of C3 (figure 10) and C4 (figure 11) grass distribution have been simulated (Woodward & Lomas 2004). The models compare well with independent observations of grassland distribution (Beerling & Woodward 2001; Woodward & Lomas 2004).

C3 grasses occur predominantly in the Northern Hemisphere (figure 10), in particular the steppes of central Asia and around the margins of cool deserts, but also with notable occurrences in southern Australia, New Zealand and South America. C4 grasses dominate in the warmer areas of the world (figure 11) in which C3 grasses have low abundance. C4 grasses occur at the margins of warm and
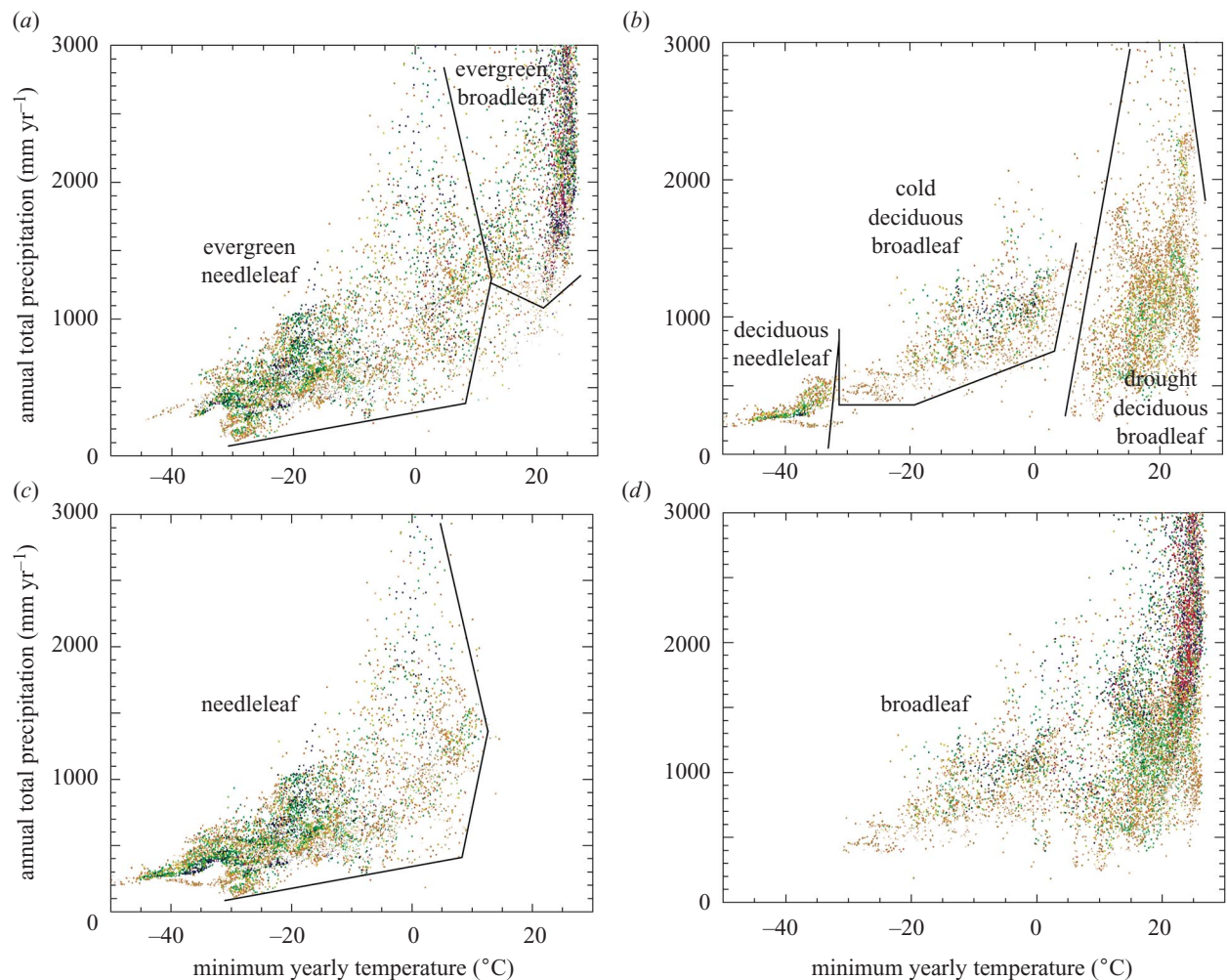
Figure 9. Scatter diagrams of tree cover (percentage of ground cover) against mean minimum annual temperature (°C) and annual total precipitation (mm). (*a*) Evergreen; (*b*) deciduous; (*c*) needleleaf; and (*d*) broadleaf. Precipitation totals are capped at 3000 mm to provide greater resolution for climates with low precipitation. The colour scheme is as for figure 2 to 5. Boundary lines are drawn by eye.

hot deserts, but readily spread into forested areas after fire (Bond & Van Wilgen 1996).

(c) *Climatic envelopes*

Grasses are simulated to occur across a wider range of minimum temperature and precipitation (figure 12) than any class of tree (figure 9). C3 grasses occur where the minimum temperatures are less than 15 °C, whereas C4 grasses occur where the minimum temperatures exceed −20 °C. In all locations, C4 growth and activity will be limited to periods of the year when the temperature rises above the chilling range (Woodward 1987). Although there is considerable overlap in their climatic envelopes this is not realized geographically, with C4 grasses dominating tropical and Southern Hemisphere latitudes.

The cosmopolitan nature of grassland distribution indicates that all biomes should, in principle, be considered as physiognomic mixtures, such as cold deciduous broadleaf forest and grass: not a simple definition. The more remarkable observation is that in the space of at most 40 Myr, grass has evolved and spread into all terrestrial biomes: it is the new super-biome. Its capacity to change the nature of disturbance by favouring grazing animals and fire in particular, has

provided unfamiliar pressures for the existing global suite of forests.

4. CROPLAND

(a) *Cultivated and managed biomes*

Humans have influenced the landscape for over one million years, in search of food. A major influence was the use of fire to this end (Goudie 1990), which has led to gradual geographical extensions of grasslands. However, the major impacts of humans on the terrestrial biosphere have occurred from the beginning of the Holocene, *ca.* 10 000 years ago (Goudie 1990). This time was characterized by the domestication of crops and animals for food. Cultivated grasses became a major food source, as did the meat from domesticated animals, which in turn were reared particularly on natural grasslands. These major changes led to considerable expansions in the areas of grasslands, now differentiable as crops and pastures: approximately 12 million km^2 of forests have been cleared for crop production since the seventeenth century (Ramankutty & Foley 1999). Currently, *ca.* 18 million km^2 are under cultivation and domestic animals now graze an area of land 2.5 times greater than that used for growing crops (Loomis & Connor 1992).
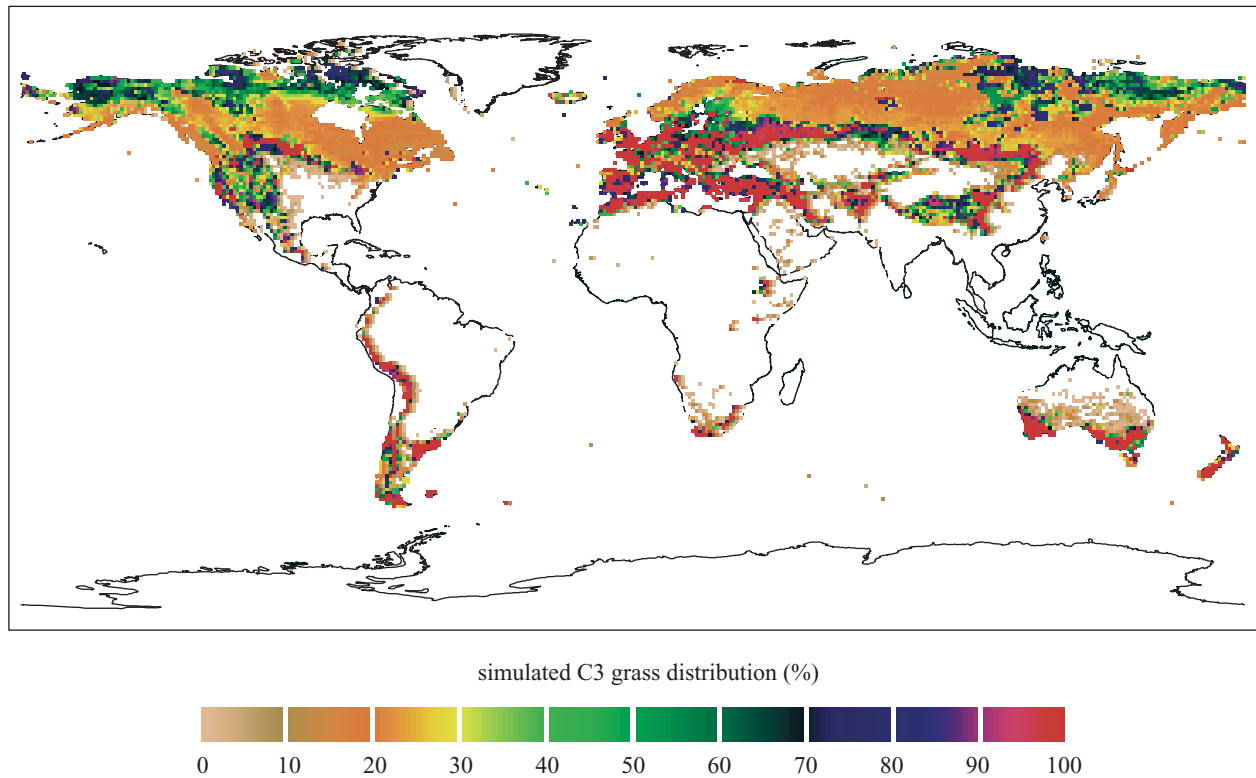
simulated C3 grass distribution (%)

Figure 10. Simulated distribution of C3 grasses for 1990 to 2000. (Modified from Woodward & Lomas 2004.)
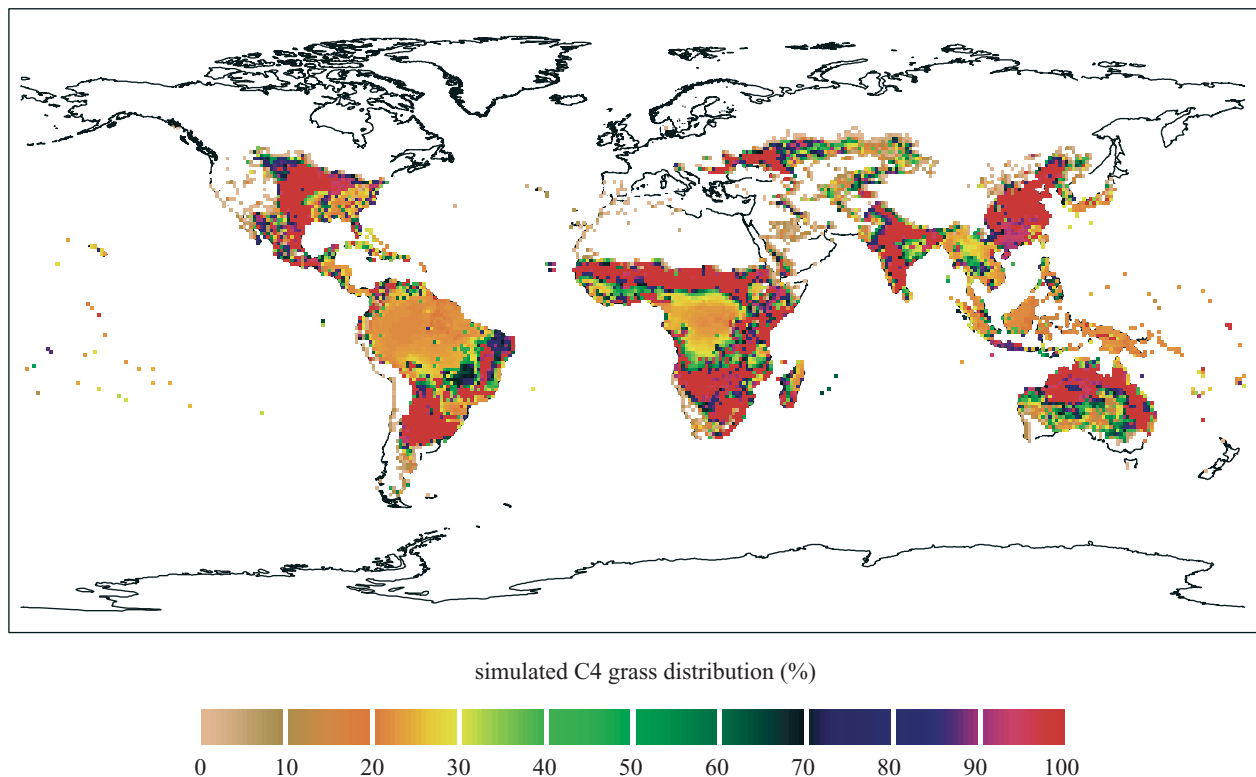

simulated C4 grass distribution (%)

Figure 11. Simulated distribution of C4 grasses for 1990 to 2000. (Modified from Woodward & Lomas 2004.)

These human disturbances, over a very short period of time (Ramankutty & Foley 1999), have made marked inroads into natural vegetation (figure 13). The current extent of cultivated and managed land has been quantified (GLC 2000) from satellite data (figure 13). The area of cultivated land overlaps considerably with the simulated areas of C3 and C4 grasses (figures 10 and 11), which is unsurprising because such natural areas would be readily adaptable for managing livestock. However, there is also considerable ingress into forested areas, in particular the cold and drought deciduous vegetation (figures 3 and 9) and the evergreen broadleaf areas of Southeast Asia
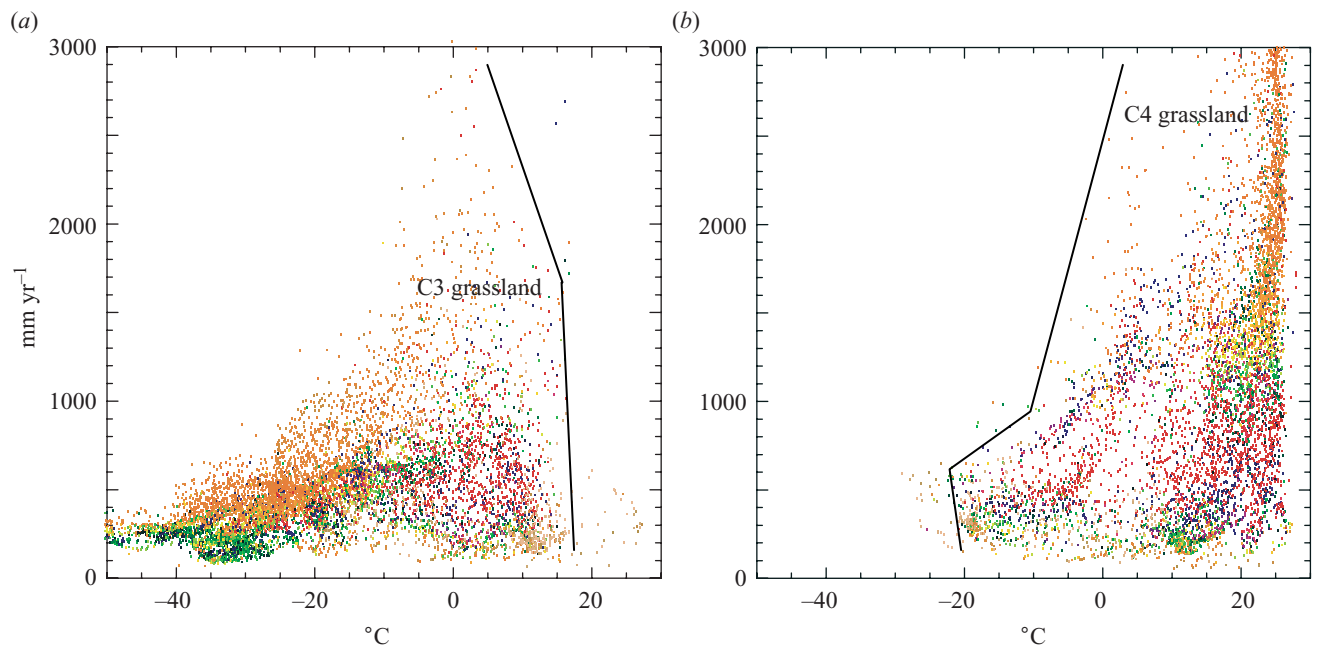
(a)

(b)

Figure 12. Scatter diagrams of grass cover (percentage) against mean minimum annual temperature (°C) and annual total precipitation (mm). (*a*) C3 grasses; and (*b*) C4 grasses. The colour scheme is as for figures 10 and 11. Boundary lines are drawn by eye.
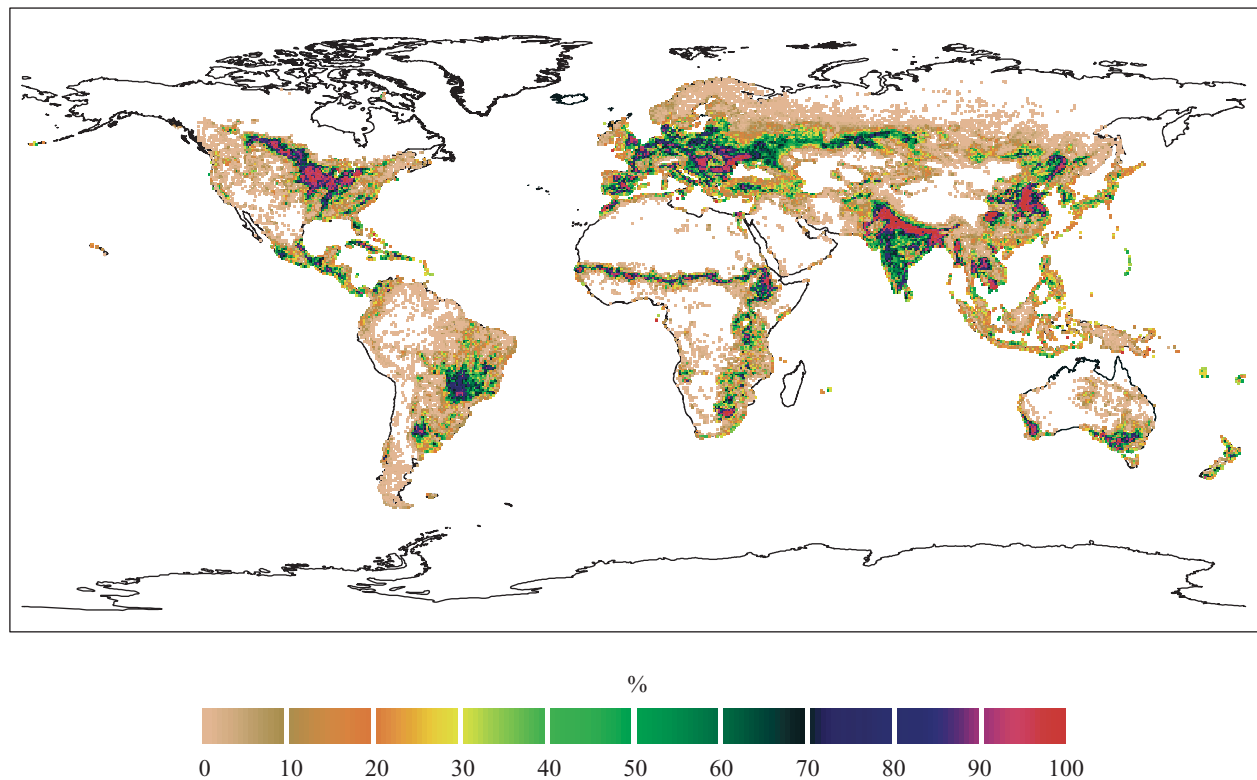
%

Figure 13. The global distribution of cultivated and managed land. (Modified from GLC 2000.)

(figures 2, 4 and 9). The high fraction of cultivated lands in the Indian sub-continent and areas of Europe indicate considerable conversion of natural forested vegetation (Goudie 1990) to cultivated lands.

(b) *Climatic envelopes*

The cultivated and managed biome occurs across a very wide range of climatic conditions (figure 14), only being absent from the coldest climate, characteristic of the deciduous needleleaf forests. The biome can also be sustained under very low annual precipitation, of less than 100 mm yr^{-1}. The greatest fraction of cultivated land is in the climatic envelope of the cold deciduous broadleaf forests, whereas the lowest fraction occurs in the climatic envelope of the evergreen broadleaf forests. This contrast also reflects very different soil conditions between these
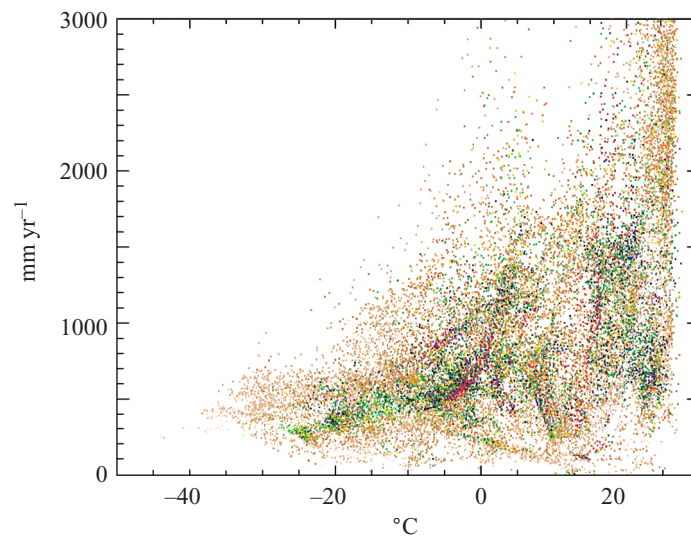
Figure 14. Scatter diagram of cultivated and managed land cover (percentage) against mean minimum annual temperature (°C) and annual total precipitation (mm). The colour scheme is as for figure 13.
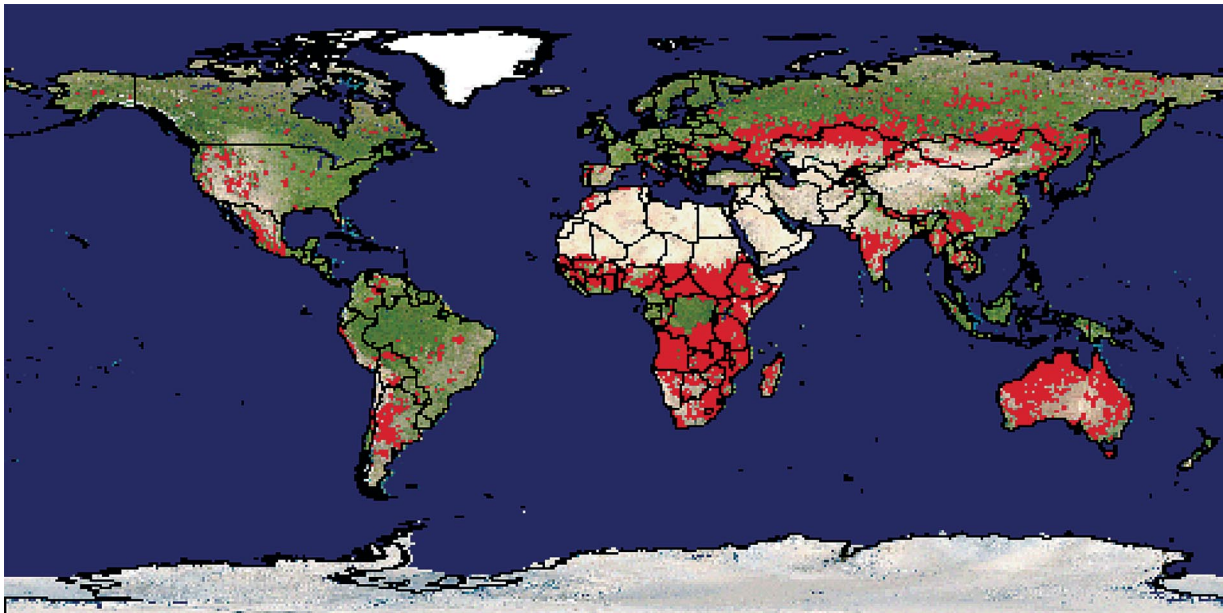

Figure 15. Global map of area burned (in red) determined from the analysis of satellite observations. (Modified from GBA 2000).

two vegetation types, the former being much more nutrient rich (Trudgill 1988).

Human presence in this managed biome, in addition to the large areas of grassland, leads to frequent disturbance by livestock and by fire. In 2000, the total burn area recorded by satellite was 3 505 184 km² (GBA 2000), with the largest fractions occurring in grasslands and managed lands (figure 15). This map shows the relentless nature of the spread of disturbance into the world's natural forests.

5. CONCLUSIONS

Biomes have been defined traditionally by plant physiognomy and geographical distribution or climate. There has been a trend away from this non-observable biome type to one that is based on plant features that are wholly observ-

able by remote sensing satellites. This offers the potential for objective classifications, although this may be difficult to achieve. The approach also offers a high frequency of repeat observations through the year, providing unrivalled large-scale measures of biome phenology and dynamics. Satellite observations, in addition to global fields of climate, indicate that there is only one biome with a unique climatic envelope: the deciduous needleleaf forest (figure 9). Although this biome escapes the cultivated biome there is clear overlap with C3 grassland, and also shrubs, which have not been considered here. The climatic envelope of the evergreen needleleaf forests overlaps with the cold deciduous broadleaf forests, and there is considerable overlap between the drought deciduous and evergreen broadleaf forests. In all of these cases, grassland and cultivated and managed land are also present at varying frequencies.

The biome concept can be supported by obvious physiognomic and phenological differences, such as between evergreen and deciduous behaviour and between broadleaf and needleleaf structure. However, the climatic overlap between most of these major biomes suggests that long-term history and migration are crucial in underpinning the actual geographical locations. The historical perspective is further amplified when it is realized that grasses, which constitute the new super-biome, through their linkage with all forms of disturbance are slowly advancing on ancient forests, in addition to changing the climate *en route* (Hoffmann & Jackson 2000). In bringing ecology and history together there is, therefore, a need for much greater emphasis on disturbance, in all its guises, and how it has impacted on land and biome history and phylogeny.

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GLOSSARY

IGBP–DIS: International Geosphere Biosphere Programme, Data and Information Systems