

Vegetation cover in a warmer world simulated using a dynamic global vegetation model for the Mid-Pliocene

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Abstract

In this study we employ the TRIFFID (Top-down Representation of Interactive Flora and Foliage Including Dynamics) Dynamic Global Vegetation Model (DGVM) and the Hadley Centre Atmospheric General Circulation Model version 3 (HadAM3 GCM) to investigate vegetation distributions and climate–vegetation feedbacks during the Mid-Pliocene, and examine the implications of these results for the origins of hominid bipedalism. The TRIFFID model outputs support extant palaeoenvironmental reconstructions for the Mid-Pliocene provided by the PRISM Group (Pliocene Research Interpretations and Synoptic Mapping). Compared to the pre-industrial, TRIFFID simulates a significant increase in forest cover during the Mid-Pliocene, composed of needle leaf trees in the higher latitudes of the Northern Hemisphere and broad leaf trees in other regions. Needle leaf trees extend from the Arctic Coast into the northern mid latitudes. The fractional coverage of bare soil declines in North Africa, the Arabian Peninsula, Australia and southern South America, a pattern that is consistent with PRISM's assertion of less extensive arid deserts. A significant increase in the fractional coverage of both broad leaf trees in Africa and South America in the Mid-Pliocene scenario is not indicative of a major expansion of tropical rainforests. Rather, it represents an expansion of general woodland type habitats. The principal impact of using a DGVM on the GCM predicted climatology for the Mid-Pliocene is to reduce minimum and maximum temperature extremes, thus reducing the seasonality of temperature over wide regions. The predicted Pliocene expansion in broad leaf trees in Africa is difficult to reconcile with the 'savannah hypothesis' for the evolution of hominid bipedalism. Rather the results lend credence to an alternative hypothesis which suggests that bipedalism evolved in wooded to forested ecosystems and was, for several million years, linked to arborealism.

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1. Introduction

1.1. Vegetation during the Mid-Pliocene warm period

The Mid-Pliocene warm period (ca 3.29 to 2.97 Ma BP; Dowsett et al., 1999) represents one of the most

intensively studied, scientifically challenging and controversial time periods in Cenozoic Earth history. For the last 15 years, the combined efforts of numerous individuals and research teams have been focussed on documenting the palaeoenvironmental and palaeoclimatic characteristics of the period (e.g., Dowsett et al., 1992, 1994, 1996; Thompson and Fleming, 1996; Poore and Sloan, 1996; Chandler et al., 1994; Sloan et al., 1996; Williams et al., 2005).

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Table 1

List and characterization of all terrestrial localities used within the PRISM2 vegetation reconstruction (Thompson and Fleming, 1996; Dowsett et al., 1999)

No.	Locality	Pliocene vegetation	References
1	Ocean Point	EVE, DEC	Nelson and Carter (1985)
2	Lost Chicken Mine	EVE	Ager (1994), Adam (1994)
3	Oak Grove Fork	EVE	Wolfe (1990)
4	Tulelake	EVE, GSS	Adam et al. (1989, 1990)
5	Sonoma Flora	EVE, DEC	Axelrod (1944), Evernden and James (1964)
6	Bruneau	EVE, GSS	Thompson (1992), Thompson (1996)
7	Fossil Gulch	EVE, GSS	Leopold and Wright (1985)
8	INEL	EVE, GSS	Thompson (1991)
9	Black Rock	EVE, GSS	Thompson et al. (1995)
10	DSDP Site 32	EVE	Fleming (1992, 1994)
11	DSDP Site 467	GSS, EVE, DEC	Heusser (1981), Ballog and Malloy (1981)
12	Meighen Island	EVE, TUN	Matthews (1987, 1990), Matthews and Ovenden (1990)
13	ODP 645b	EVE, TUN	De Vernal and Mudie (1989a)
14	ODP 646b	EVE, DEC	De Vernal and Mudie (1989b), Willard (1994)
15	Yorktown Formation	DEC, EVE	Litwin and Andrie (1992a), Willard (1994)
16	Duplin Formation	EVE, DEC	Litwin and Andrie (1992a), Willard (1994)
17	Raysor Formation	EVE, DEC	Groot (1991), Litwin and Andrie (1992a), Willard (1994)
18	Pinecrest Beds	EVE	Willard et al. (1993), Willard (1994)
19	Paraje Solo	DEC, EVE	Graham (1989, 1994)
20	Gatun Formation	RAI, DEC	Graham (1989, 1994)
21	Plain of Bogotá	DEC	Sarmiento (1991), Van der Hammen (1985), Wijninga and Kuhry (1990)
22	East-Central Pampas	GSS	Zarate and Fasana (1989)
23	Tjornes Section	EVE	Schwarzbach and Pflug (1957), Akhmetiev et al. (1978), Akhmetiev (1991), Willard (1992), Willard (1994)
24	ODP 642	EVE	Willard (1994)
25	Red and Walton Craggs	EVE, DEC	Zalasiewicz et al. (1988), Hunt (1989)
26	Brunssum/Reuver	DEC	Suc and Zagwijn (1983), Zagwijn (1992)
27	Northwest Germany	DEC	Mohr (1986)
28	Bresse Basin	DEC	Rousseau et al. (1992)
29	Stirone River Section	EVE	Bertolani Marchetti et al. (1979), Gregor (1990)
30	Le Castella Section	EVE	Bertolani Marchetti (1975)
31	Garraf 1	EVE	Suc (1984)
32	Autan 1	EVE	Cravatte and Suc (1981), Suc and Zagwijn (1983)
33	Southern Poland	EVE, DEC	Stuchlik and Shatilova (1987)
34	Slovakia	EVE, DEC	Planderová (1974)
35	Kozani Basin	EVE	Van de Weerd (1983)
36	NW Black Sea Coast	DEC, EVE, GSS	Svetlitskaya (1994)
37	Russian Plain #1	EVE, DEC	Grichuk (1991)
38	Russian Plain #2	EVE, DEC	Grichuk (1991)
39	Russian Plain #3	EVE, DEC	Grichuk (1991), Borisova (1991, 1994)
40	Russian Plain #4	EVE, DEC	Grichuk (1991), Borisova (1991, 1994)
41	Russian Plain #5	EVE, DEC	Grichuk (1991), Borisova (1991, 1994)
42	DSDP 380	EVE	Traverse (1982)
43	Western Georgia	DEC, EVE	Shatilova (1980, 1986), Shatilova et al. (1991)
44	Azerbaijan	DEC, EVE	Mamedov (1991)
45	Hula Basin	EVE, DEC, GSS	Horowitz (1989), Horowitz and Horowitz (1985)
46	ODP 658	GSS	Leroy and Dupont (1994), Dupont and Leroy (1994)
47	Hadar	GSS	Bonnefille et al. (1987)
48	Turkana Basin	GSS	Williamson (1985)
49	East Africa	GSS	Cerling et al. (1988), Cerling (1992)
50	South Africa	GSS, DEC	Partridge et al. (in press), Scott and Partridge (1994)
51	West Siberia	EVE, DEC	Volkova (1991)
52	northern Pakistan	GSS	Quade et al. (1989)
53	Kathmandu Valley	EVE, DEC	Igarashi et al. (1988)
54	Yunnan and Xizang	DEC, EVE	Hsü (1983)
55	East China Sea	GSS?	Zhou et al. (1989)
56	Bugpyeong area	EVE	Choi and Bong (1986)

(continued on next page)

Table 1 (continued)

No.	Locality	Pliocene vegetation	References
57	Lake Biwa	EVE, DEC	Tanai and Huzioka (1967), Fuji (1988)
58	Magadan District	EVE, DEC	Fradkina (1991)
59	Lena River	EVE, DEC	Fradkina (1991)
60	Kolyma Basin	EVE, DEC	Giterman et al. (1982)
61	Anadyr Basin	EVE, DEC	Fradkina (1991)
62	Blao	RAI	Kedves (1984)
63	Mahakam Delta	RAI	Caratini and Tissot (1988)
64	Papua	RAI	Khan (1974)
65	Lake Tay	DEC	Bint (1981)
66	Regatta Point	RAI	Hill and Macphail (1985)
67	Ohinewai, S. Auckland	RAI	Nelson et al. (1988)
68	North Island	DEC	Mildenhall and Pocknall (1984)
69	Waipipian section	RAI	Mildenhall and Harris (1970)
70	South Island	DEC	Mildenhall and Suggate (1981)
71	South Island	DEC	Mildenhall and Pocknall (1984)
72	Dusky Sound	DEC	Turnbull et al. (1985)
73	CIRO-S-1	DEC	Webb and Harwood (1993)
74	Oliver Bluffs	DEC	Webb and Harwood (1993)

Full references can be found in Dowsett et al. (1999; <http://pubs.usgs.gov/openfile/of99-535/>).

Key: DEC=deciduous forest, DES=desert, EVE=evergreen forest, GSS=grassland, steppe or savanna, RAI=rainforest, TUN=tundra (Thompson and Fleming, 1996).

A synthesis of Mid-Pliocene palaeoenvironmental conditions can be found within the United States Geological Survey's PRISM2 data set (Pliocene Research Interpretation and Synoptic Mapping; Dowsett et al., 1999). This data set contains information on both Mid-Pliocene terrestrial and marine environmental conditions (<http://pubs.usgs.gov/openfile/of99-535/>, <http://geology.er.usgs.gov/eespteam/prism/prism3main.html>). PRISM2 interpolates global Mid-Pliocene vegetation cover from an initial global data set of 74 terrestrial sites (Table 1). Abundant data for the period exist in North America and Europe. However in other regions, such as South America, virtually no geological data exist from which to reconstruct the character of Mid-Pliocene biomes. In such areas, the PRISM Group was forced to prescribe modern biome conditions (Fig. 1). Since the mid-1990s, when the PRISM vegetation reconstruction was completed, data on Mid-Pliocene vegetation, and terrestrial palaeoenvironmental conditions in general, have continued to be gathered by workers affiliated to PRISM and by those working independently (for summary see Haywood et al., 2002a). However, the geographical distribution of data points for Mid-Pliocene terrestrial proxy data remains incomplete and skewed towards the Northern Hemisphere, in particular North America and Europe. Therefore, our knowledge of Mid-Pliocene vegetation distributions actually represents a mixture of true Mid-Pliocene conditions and interpolated present-day characteristics.

The Mid-Pliocene vegetation distribution displayed in Fig. 1a is significantly different from a modern

vegetation distribution in the following ways. Evergreen (in particular coniferous) vegetation was more widespread in the Northern Hemisphere during the Mid-Pliocene. Boreal forest extended from the Arctic Coast southward to the northern mid-latitudes where it grades into temperate mixed-conifer forest and conifer hardwood forest. The geographical coverage of arid deserts appears to have declined, being replaced by grasslands. In other areas, tropical rainforests appear to have expanded. In Antarctica, the PRISM2 reconstruction indicates that the continent may have supported deciduous species of vegetation (*Nothofagus*), implying significant warming. The PRISM group attributed this change in vegetation distributions to be a reflection of the reconstructed warmer than present temperatures at high-latitudes grading southward to present-day temperatures at low latitudes (Thompson and Fleming, 1996).

Haywood et al. (2002a,b,c) used a mechanistically based biome model (BIOME 4) offline to an atmospheric general circulation model (AGCM) to predict global Mid-Pliocene biome distributions. These studies were useful in that they helped to quantify Pliocene climate-vegetation feedbacks and aid in the identification of Mid-Pliocene vegetation patterns that are in equilibrium with different ice-sheets and insolation scenarios. However, to better understand Mid-Pliocene climate-vegetation feedbacks, the land-cover must be treated as an interactive element (i.e., actively growing vegetation) by incorporating a dynamic global vegetation model (DGVM). In this study we employ a DGVM

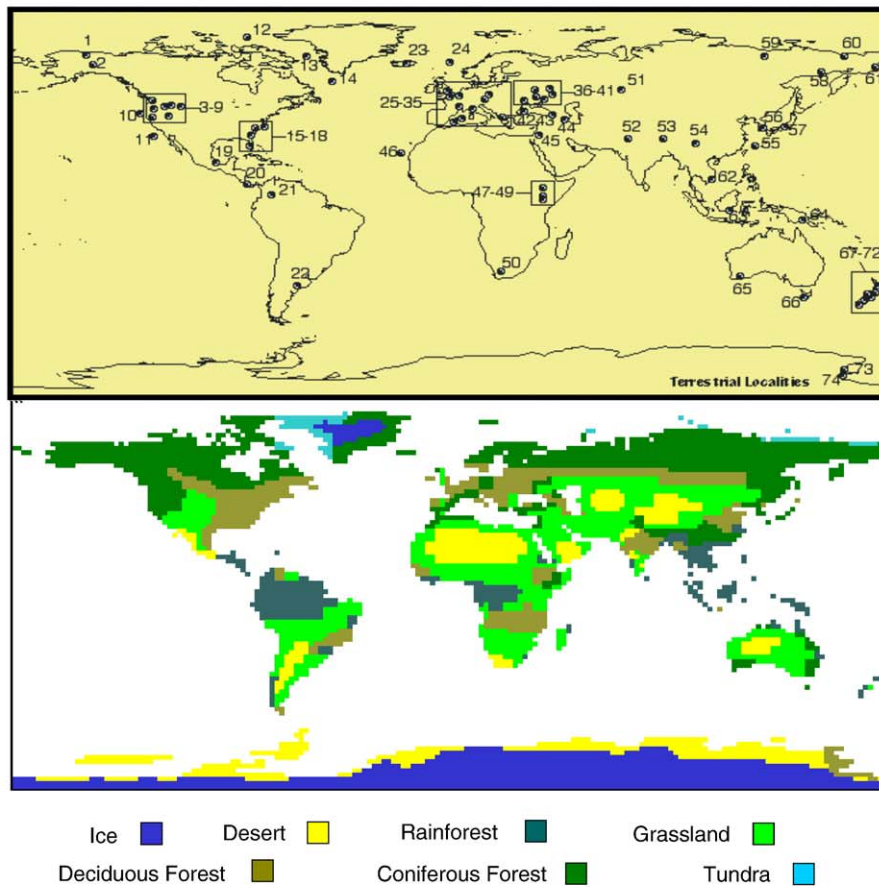
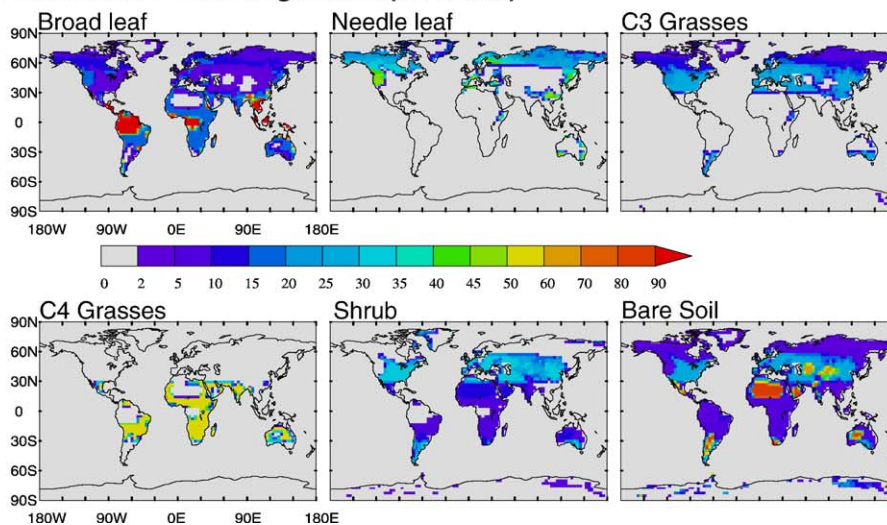
(a) Mid Pliocene Vegetation Reconstruction**(b) Translated PRISM Vegetation (MPTrans)**

Fig. 1. (a) Location of data sites used in the construction of the Mid-Pliocene vegetation reconstruction and the vegetation reconstruction itself derived from the PRISM2 data set (Thompson and Fleming, 1996; Dowsett et al., 1999; see also Table 1). Note the reduction in arid desert regions, the loss of Northern Hemisphere tundra vegetation, the expansion of coniferous forests and the existence of deciduous forest on Antarctica along with polar desert. (b) The PRISM2 Mid-Pliocene vegetation reconstruction translated into the fractional coverage (%) of TRIFFID plant functional types used in experiment MPTrans. This was achieved by designing a vegetation look-up-table that documented, for the present-day, what the average fractional coverage of TRIFFID plant functional types was for each of the biome types used with the present-day PRISM vegetation reconstruction.

and the HadAM3 GCM (Hadley Centre Atmospheric General Circulation Model version 3) to investigate vegetation distributions during the Mid-Pliocene and assess the significance of the results to hypotheses regarding the origin of hominid bipedalism.

1.2. Increasing role of vegetation models in palaeoclimate studies

The need to consider vegetation within palaeoclimate modelling experiments, particularly the interaction between vegetation and climate is well documented (e.g., Cosgrove et al., 2002). A growing number of studies have demonstrated the importance of climate–vegetation interaction in understanding climate sensitivity and climate change (e.g., Bonan et al., 1992; Foley et al., 1994; Gallimore and Kutzbach, 1996; Dutton and Barron, 1996, 1997; Otto-Bleisner and Upchurch, 1997; DeConto et al., 1999; Cosgrove et al., 2002). Initial vegetation modelling efforts concentrated on coupling the outputs from global climate models to empirical models of vegetation (e.g., Handerson-Sellers, 1993). However, the complexity of vegetation models quickly increased to allow for the representation of numerous physiological processes such as photosynthesis, respiration, transpiration, and soil water uptake (e.g., Prentice et al., 1992; Neilson, 1995; Woodward et al., 1995; Haxeltine and Prentice, 1996; Foley et al., 1998). Whereas initially, output from global climate models were simply used offline to the vegetation model itself, many of the vegetation models are now asynchronously or dynamically coupled to global climate models (VEMAP, 1995; de Noblet et al., 1996; Betts et al., 1997; Texier et al., 1997; Claussen et al., 1998; Ganopolski et al., 1998; Doherty et al., 2000; Levis et al., 1999a,b,c, 2000; Cosgrove et al., 2002).

The rapid development of vegetation models has greatly expanded the number of applications for which they can be used, and therefore the usefulness of the models themselves (Cosgrove et al., 2002). These applications now include investigating the effects of changing carbon dioxide levels on primary productivity and competition (Culotta, 1995; Jolly and Haxeltine, 1997; Levis et al., 1999b, 2000) and the exploration of transient vegetation dynamics (Foley et al., 1996, 1998; Beerling et al., 1997; Friend et al., 1997). Examples of the use of vegetation models in deep time palaeoclimatology include Dutton and Barron (1996, 1997) who examined a series of sensitivity experiments for the Miocene time period that focused on the global and regional specification of different vegetation types. Cosgrove et al. (2002) developed the Simple Interactive

Vegetation Model (SIVM). The SIVM was evaluated by: (a), determining the extent to which the simplified vegetation alters the simulation of the present-day climate; (b), determining the extent to which SIVM produces a realistic present-day vegetation distribution given observed climate parameters; and (c), examining the performance of the coupled GENESIS-SIVM system when applied to the Miocene and Oxygen Isotope Stage 3 (Cosgrove et al., 2002).

2. Methods

2.1. Model description (GCM & DGVM)

The particulars of the version of the AGCM (HadAM3) used in this study are well documented (Pope et al., 2000). However, some discussion of the model itself and how it differs from HadAM2 is necessary. HadAM3 was developed at the Hadley Centre for Climate Prediction and Research, which is a part of the UK Meteorological Office. The horizontal resolution of the model is 2.5° in latitude by 3.75° in longitude. This gives a grid spacing at the equator of 278 km in the North–South direction and 417 km East–West and is approximately comparable to a T42 spectral model resolution. The model has 19 layers in the vertical, a time step of 30 min and includes a new radiation scheme that can represent the effects of minor trace gases (Edwards and Slingo, 1996). A parametrization of simple background aerosol climatology is also included (Cusack et al., 1998). The convection scheme has also been improved (Gregory et al., 1997) and a land-surface scheme includes the representation of the freezing and melting of soil moisture. The representation of evaporation now includes the dependence of stomatal resistance on temperature, vapour pressure and CO₂ concentration (Cox et al., 1999). The sea ice component is, in large part, the same as that employed within HadAM2. It uses a simple thermodynamic scheme and contains parameterizations of ice drift and leads (Cattle and Crossley, 1995).

As part of this study we have employed the TRIFFID dynamic vegetation model coupled to the HadAM3 GCM. The TRIFFID model, developed by the Hadley Centre, defines the state of the terrestrial biosphere in terms of soil carbon and the structure and coverage of five different plant functional types (broad leaf trees, needle leaf trees, C3 grass, C4 grass and shrub) within each model grid box (Cox, 2001). The areal coverage, Leaf Area Index and canopy height of each type are updated based on a carbon balance approach in which vegetation change is driven by the net carbon fluxes

calculated within the MOSES2 (Met Office Surface Exchange Scheme) land surface scheme, which is part of the HadAM3 GCM (Cox, 2001).

2.2. Experimental design, boundary conditions & model spin-up

Three coupled AGCM-DGVM experiments were conducted, one for the pre-industrial period and two for the Mid-Pliocene. For the Mid-Pliocene simulations a CO₂ concentration of 400 ppmv is used. This is a justifiable value given the numerous proxy estimates of Mid-Pliocene atmospheric CO₂ concentrations that are available. Estimates have been derived from the analysis of stomatal density of fossil leaves (Van der Burgh et al., 1993; Kürschner et al., 1996), through analyses of $\delta^{13}\text{C}$ ratios of marine organic carbon (Raymo and Rau, 1992; Raymo et al., 1996) and through measurement of the differences between the carbon isotope composition of surface and deep waters (Shackleton et al., 1992). All three methods suggest that absolute CO₂ levels during the time period range from 360 to 400 ppmv, compared to mid-19th century levels of approximately 280 ppmv and modern concentrations of 378 ppmv. The Mid-Pliocene simulation with dynamic vegetation (hereafter referred to as MPDV) is compared to a pre-industrial simulation with dynamic vegetation (hereafter referred to as PIDV) as well as a Mid-Pliocene experiment where vegetation coverage was specified from the PRISM2 data set and not allowed to vary (hereafter referred to as MPTrans). To facilitate this, PRISM2 vegetation categories first had to be translated into TRIFFID plant functional types before the model simulation commenced (Fig. 1b). This was achieved by designing a vegetation look-up-table that documented, for the present-day, what the average fractional coverage of TRIFFID plant functional types was for each of the biome types used in the present-day PRISM vegetation reconstruction. The MPDV, PIDV and MPTrans simulations were integrated for 30 HadAM3 years (for further details see Table 2).

The MPDV and MPTrans experiments were initialised with boundary conditions derived from the United States Geological Survey (USGS) PRISM2 enhanced $2^\circ \times 2^\circ$ digital data set. The particulars of the PRISM2 data set have been well documented in previous papers (e.g., Dowsett et al., 1994, 1999; PRISM Project Members, 1995; Haywood et al., 2000 and references therein). In brief, the prescribed boundary conditions cover the time slab between 3.29 and 2.97 Ma B.P. according to the geomagnetic polarity time scale (Berggren et al., 1995). Boundary conditions integrated into the model that are specific to the Mid-Pliocene include: (1), continental configuration, modified by a 25 m increase in global sea level; (2), modified present-day elevations; (3), reduced ice sheet size and height for Greenland (~50% reduction) and Antarctica (~33% reduction); (4), Pliocene vegetation distribution (MPTrans only); and (5), Pliocene SSTs and sea ice distributions (see Dowsett et al., 1999).

The geographical extent of the Greenland and Antarctic ice sheets within the PRISM2 data set was based on global sea-level estimates derived for the Mid-Pliocene by Dowsett and Cronin (1990). The PRISM2 reconstruction uses model results from Michael Prentice (personal communication to Harry Dowsett; cited in Dowsett et al., 1999) to guide the areal and topographic distribution of Antarctic and Greenland ice. For a more detailed description of the PRISM2 data set and how it differs from earlier PRISM data sets see Dowsett et al. (1999: <http://pubs.usgs.gov/openfile/of99-535>).

A multi-stage process was used to facilitate model spin-up for the MPDV and PIDV experiments. TRIFFID was initialised with 100% shrub coverage in all terrestrial model grid boxes not covered by the imposed pre-industrial or PRISM2 ice-sheets. Shrub was selected due to its relatively neutral characteristics of surface albedo and surface roughness. The first stage of the model spin-up involved an iterative coupling between the HadAM3 GCM and the TRIFFID model running in equilibrium mode. The HadAM3 GCM was integrated for 5 years after which the required fluxes of moisture and carbon were passed to the TRIFFID model. TRIF-

Table 2

Showing details of trace gas concentrations for all model experiments, length of model simulations and the period used to calculate climatological means

Model experiment	CO ₂ (ppm)	CH ₄ (ppb)	NO ₂ (ppb)	CFC ^{11&12} (ppt)	TRIFFID run	Length of model run	Climatological means
Pre-industrial run (PIDV)	279	790	284	0	Yes	30	Last 10 years
Mid-Pliocene run (MPDV)	400	790	284	0	Yes	30	Last 10 years
Mid-Pliocene AGCM run using fixed PRISM2 vegetation (MPTrans)	400	790	284	0	No	30	Last 10 years

FID was then integrated for a total of 50 years, after which the updated vegetation and soil variables were passed back to the HadAM3 GCM. This process continued for a total of 500 simulated TRIFFID years. This approach, similar to a Newton–Raphson algorithm for approaching equilibrium, is a proven and effective method in producing equilibrium states for the slowest variables (e.g., soil carbon and forest cover). The second stage involved using the HadAM3 and TRIFFID models in their fully dynamic mode in which the vegetation cover and other characteristics were updated every 10 simulated days. The model was integrated in this fully dynamic mode for a total of 30 simulated years to allow the model to adjust to short time scale vegetation variability.

3. Results

3.1. Fractional coverage of Mid-Pliocene plant functional types

The fractional coverage (%) for all TRIFFID plant functional types predicted for experiment MPDV is shown in Fig. 2a. Tropical and low latitude regions of South America, central and South Africa, India and South-east Asia and NW Europe have a high fractional coverage (80% or above) of broad leaf trees. A coverage of 5% to 30% is predicted in mid to high latitude regions of North America and Eurasia. Needle leaf trees have a high fractional coverage in Peru and Chile, around the fringes of the Himalayas, the Tibetan Plateau, Northern North America, Eurasia, Eastern Europe and Scandinavia. C3 grasses have a low fractional coverage on Antarctica and in most areas that are not either barren or dominated by broad leaf or needle leaf trees. Conversely, C4 grasses have a high-predicted coverage in the southern Sahara region, central Australia and southern North America, with low percentage coverage in equatorial regions and parts of the mid latitudes that are not dominated by trees. Shrub type vegetation is mostly restricted to high and mid latitude regions of the Northern Hemisphere and southern South America. The fractional coverage of bare soil is predicted to be high in North Africa, Arabia, central Eurasia, southwest Australia and southwest North America.

Compared to experiment MPTrans, experiment MPDV has a larger fractional coverage of broad leaf trees in South America, central southern Africa, India, northwest Europe and parts of Southeast Asia (Fig. 2c). Moderate increases are also predicted in regions of North America and Eurasia. Needle leaf trees are pre-

dicted to have a similar increase to broad leaf trees in northern North America, central Europe, Scandinavia and the interior of Eurasia/China and also in the Peru/Chile highlands. Grasses of C3 type decrease in fractional coverage by up to 40% in North America, Europe, and Eurasia. A small increase in coverage is predicted in equatorial and low altitude regions of Africa and South America. On Antarctica, coverage increases by 10% to 50%. Grasses of C4 type increase their fractional coverage in areas where the fractional coverage of bare soil decreases. Large reductions in C4 grass coverage are also predicted in regions where there have been significant increases in the coverage of broad leaf trees. The coverage of shrubs generally decreases in all areas apart from the high latitudes of the Northern Hemisphere, where significant increases in coverage are predicted, and on the Antarctic continent. Bare soil decreases in fractional coverage in most regions. Particularly in North Africa, southern South America and central parts of Australia. Large increases are noted along the North African coastal region, Arabian Peninsula, parts of central Eurasia and the Australian southwest.

Differences in the fractional coverage of plant functional types between the MPTrans and PIDV experiments (Fig. 2c) should reflect the differences noted between the basic PRISM2 vegetation reconstruction for the Mid-Pliocene and present-day. The fractional coverage of broad leaf and needle leaf trees increases in the high latitudes of the Northern Hemisphere (particularly needle leaf trees). C3 grasses increase their coverage in the mid to high latitudes of North America and Eurasia, whereas C4 grass coverage increases in parts of central and southern Africa, the Arabian Peninsula and central and southern South America. Coverage is reduced in parts of North America and in Australia. Shrubs generally increase in coverage in Africa, South America and mid latitude regions of North America/Eurasia. Their coverage decreases in the high latitudes of the Northern Hemisphere. The coverage of bare soil increases in the mid to high latitudes of North America/Eurasia and on Antarctica (reflecting the reduced extent of the EAIS). Bare soil decreases in North Africa, the Arabian Peninsula, parts of central Asia and Australia.

The difference in the fractional coverage of plant functional types between the MPDV and PIDV experiments is shown in Fig. 2d. The TRIFFID model predicts a large increase (10% to 90%) in the fractional coverage of broad leaf trees in NW Europe, the high latitudes of North America and Eurasia, India, central Africa and eastern Australia. Needle leaf trees exhibit a similar expansion in the high latitudes of the Northern

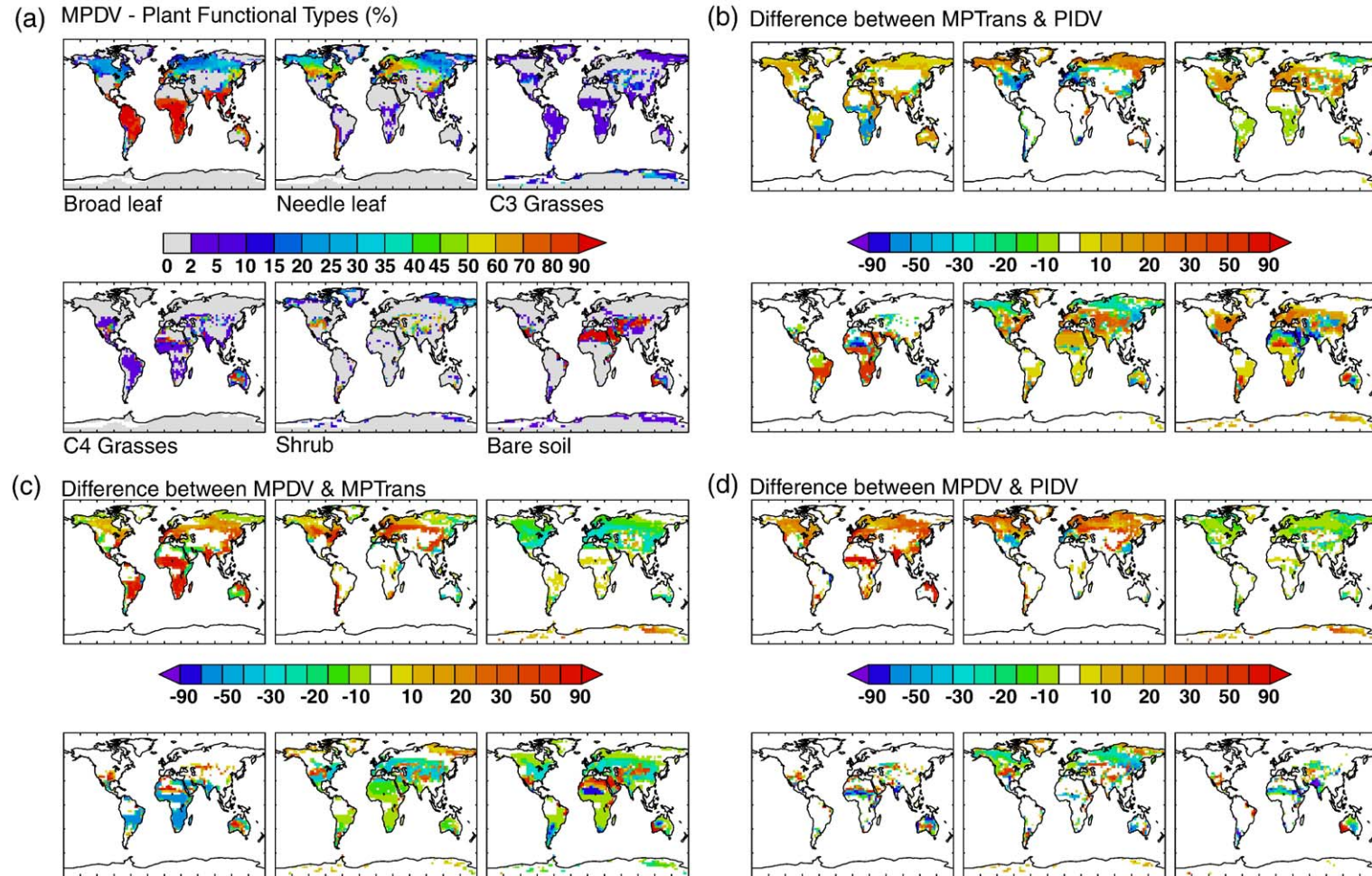


Fig. 2. Showing: (a), absolute fractional coverage (%) of TRIFFID plant functional types (broad leaf trees, needle leaf trees, C3 grasses, C4 grasses, Shrubs and bare soil) for experiment MPDV (Mid-Pliocene experiment with dynamic vegetation); (b), difference in fractional coverage of all TRIFFID plant functional types between the MPTrans (Mid-Pliocene experiment using fixed vegetation translated from the PRISM2 data set) and PIDV (pre-industrial experiment with dynamic vegetation); (c), difference in fractional coverage of all TRIFFID plant functional types between the MPTrans and MPDV experiments; and (d), difference in the fractional coverage of all TRIFFID plant functional types between experiments MPDV and PIDV.

Hemisphere. However, fractional coverage decreases in areas of Europe and central North America and in China, where broad leaf trees replace them. Needle leaf trees are predicted to occur on deglaciated regions of Greenland. The coverage of C3 grasses declines (10% to 20%) over a wide area, being replaced by forests. However, coverage increases by up to 50% on Antarctica. C4 grasses display a clear reduction, by as much as 50%, in central Africa, India and North Australia being replaced by broad leaf trees. The fractional coverage of shrubs increases significantly on Antarctica and Greenland whilst generally decreasing in the Northern Hemisphere where broad leaf and needle leaf trees expand their coverage. The coverage of bare soil significantly decreases in North Africa, India, central Asia and Australia.

3.2. Impact on AGCM climatology

In this section it is our intention to examine the impact on predicted Pliocene climatologies of using a DGVM model coupled to the HadAM3 GCM. Therefore, we will be comparing the climatological results from experiments MPDV and MPTrans. The difference between predicted annual mean and seasonal mean surface temperature ($^{\circ}\text{C}$) and total precipitation rate (mm/day) is shown in Fig. 3.

The main differences in annual and seasonal mean surface temperatures are as follows. Surface temperatures over parts of North America and the western fringes of Greenland warm by 2 to 5 $^{\circ}\text{C}$ in experiment MPDV compared to experiment MPTrans. This warming is a clear response to the significantly increased fractional coverage of broad leaf and needle leaf trees. In central and southern regions of South America, surface temperatures decline by a maximum of 2 $^{\circ}\text{C}$ that similarly reflects the increase in the fractional coverage of broad leaf trees. In northern North Africa, parts of East Africa, Arabia and central/southern Eurasia, surface temperatures rise by 2 to 10 $^{\circ}\text{C}$ because of the increase in the fractional coverage of bare soil. In most other areas of Africa surface temperatures decrease by up to 2 $^{\circ}\text{C}$ due to the increase in fractional coverage of broad leaf trees. In western Australia surface temperatures decline due to an expansion of C4 grassland. However, in coastal regions of western Australia the fractional coverage of bare soil increases and so surface temperatures rise by up to 10 $^{\circ}\text{C}$. On Antarctica, surface temperatures increase, over deglaciated regions, due to the insulating effect of the higher fractional coverage of C3 grasses and shrubs. Examining model diagnostics for the annual and seasonal mini-

mum and maximum surface temperature (Fig. 4) demonstrates that an additional impact of using a DGVM is to reduce minimum and maximum temperature extremes, thus effectively reducing the seasonality of temperature over wide regions.

Model predictions for total precipitation rate (mm/day) from experiment MPDV (Fig. 3) indicate an increase in annual mean and seasonal precipitation, by as much as 4 mm/day, over wide regions of the African continent. This rise in African precipitation relates to the significant increase in the fractional coverage of broad leaf trees. Increased tree cover not only alters surface albedo but also changes local evapo-transpiration rate providing a greater flux of moisture into the atmosphere that later falls as rain. Other regions that are predicted to have increased forest cover also display modest enhancements in total precipitation rate. Conversely, precipitation in regions with increased fractional coverage of bare soil declines. Precipitation in the Inter-tropical Convergence Zone (ITCZ) is generally increased with indications of an enhanced West African monsoon.

4. Discussion

4.1. Model/data comparison

Specific geographical regions, such as Europe and North America, contain enough information on Mid-Pliocene vegetation cover to facilitate a comparison with predicted TRIFFID plant functional types. The aim of such an approach is to assess how accurate the simulated climate and character of vegetation cover produced by the HadAM3 GCM and TRIFFID is for the Mid-Pliocene. If the model predictions are robust, then the plant functional types predicted by TRIFFID for experiment MPDV should closely approximate those of experiment MPTrans, which utilised a translated version of the PRISM2 vegetation scheme (this assumes that the initial PRISM2 reconstruction is accurate and the translation algorithm used faithfully converts this scheme into TRIFFID plant functional types).

The main problem of this approach relates to the initial boundary conditions used by HadAM3. If any of the boundary conditions within the PRISM2 reconstruction are erroneous, or perhaps more likely, inconsistent with one another, the resulting climate simulated by HadAM3 will be wrong, and thus the initial climatology utilised by TRIFFID will be not a real representation of a Mid-Pliocene state. Under these circumstances, it is likely that the equilibrium distribution of plant functional types produced by TRIFFID

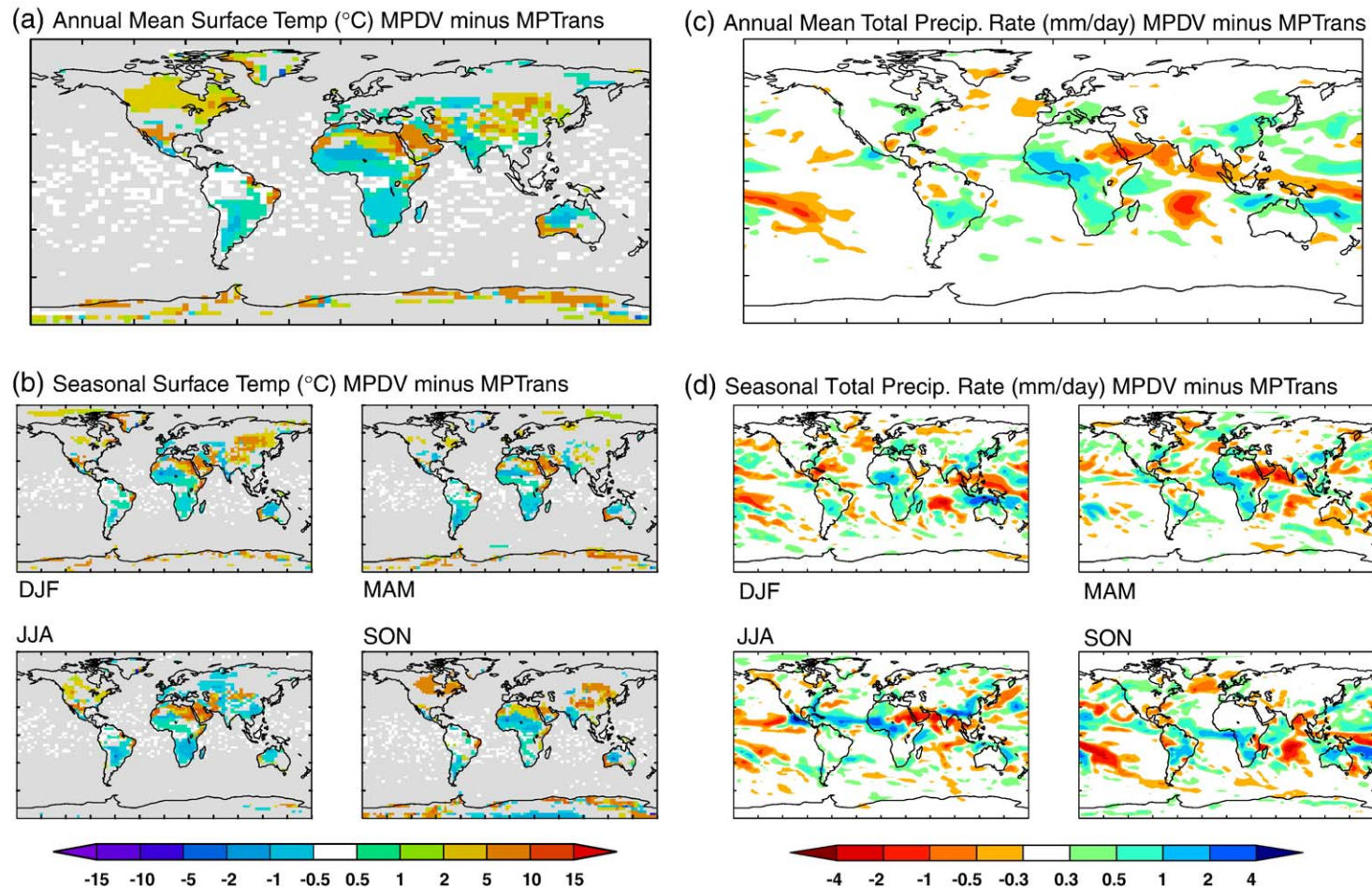


Fig. 3. Showing climate results from HadAM3 for: (a), statistically significant differences (tested to a 95% statistical significance level using Student's t test) in annual mean surface temperature (°C) between experiments MPDV (Mid-Pliocene experiment with dynamic vegetation) and MPTrans (Mid-Pliocene experiment using fixed vegetation translated from the PRISM2 data set); (b), statistically significant differences in seasonal surface temperatures between experiments MPDV and MPTrans (DJF: December, January and February, MAM: March April May, JJA: June, July and August, SON: September October and November); (c), the difference in annual mean total precipitation rate (mm/day) between experiments MPDV and MPTrans; and (d), the difference in seasonal total precipitation rate between experiments MPDV and MPTrans (DJF, MAM, JJA and SON).

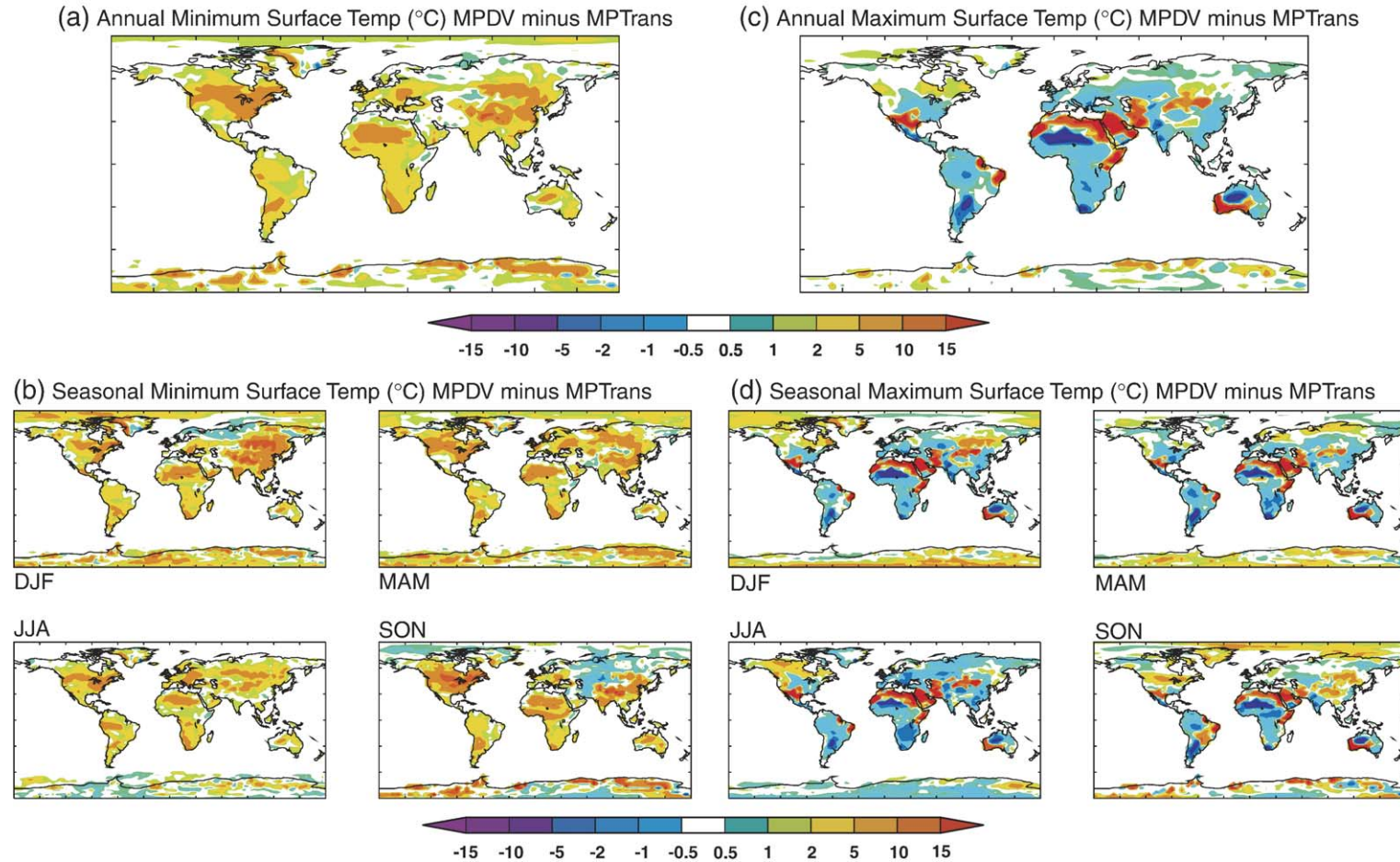


Fig. 4. Showing climate results from HadAM3 for: (a), the difference in annual mean minimum surface temperature ($^{\circ}\text{C}$) between experiments MPDV (Mid-Pliocene experiment with dynamic vegetation) and MPTrans (Mid-Pliocene experiment using fixed vegetation translated from the PRISM2 data set); (b), the difference in seasonal mean minimum surface temperatures between experiments MPDV and MPTrans (DJF: December, January and February, MAM: March April May, JJA: June, July and August, SON: September October and November); (c), the difference in annual mean maximum surface temperature between experiments MPDV and MPTrans; and (d), the difference in seasonal mean maximum surface temperature between experiments MPDV and MPTrans (DJF, MAM, JJA and SON).

for experiment MPDV will diverge away from the PRISM2 vegetation reconstruction as represented in experiment MPTrans to a new equilibrium state. This makes the task of identifying the cause of the differences between predicted TRIFFID plant functional types for the Pliocene and PRISM2 vegetation scheme difficult.

Broadly, TRIFFID outputs from experiment MPDV support the PRISM reconstruction. In particular, TRIFFID simulates a significant increase in tree cover, particularly needle leaf trees in the higher latitudes of the Northern Hemisphere (needle leaf trees extend from the Arctic Coast into the northern mid latitudes) and broad leaf trees in other areas. The fractional coverage of bare soil declines in North Africa, the Arabian Peninsula, Australia and southern South America and is consistent with PRISM's assertion of reduced coverage of arid deserts.

Whilst the TRIFFID outputs support the broad vegetation trends identified in the PRISM2 vegetation reconstruction, significant differences are noted in detail. TRIFFID predicts an expansion of bare soil, meaning arid desert, in the North African coastal region, parts of the Arabian Peninsula and SW Australia. In North Africa and the Arabian Peninsula, the PRISM2 vegetation scheme is based on extrapolation rather than actual data so it is not possible to determine if the discrepancy is real or simply an artefact. However, in the SW Australian case the Lake Tay site (Bint, 1981) indicates that forest existed in SW Australia during the Mid-Pliocene not arid desert. This may indicate that the climate model does not simulate sufficient precipitation in this region, although it is unclear how certain this discrepancy really is since it is based on a single data point.

Around the deglaciated margins of Greenland, the TRIFFID model simulates the occurrence of needle leaf trees, C3 grasses and shrubs, whereas the PRISM2 vegetation scheme makes a clear demarcation between East and West Greenland. East Greenland is dominated by coniferous vegetation whilst West Greenland is exclusively tundra. The TRIFFID model does not support this result. On Antarctica, TRIFFID predicts the occurrence of only Shrubs and C3 grasses whereas PRISM suggests that deciduous vegetation should exist in parts of East Antarctica. This interpretation was based on fossil wood and leaves of *Nothofagus* (southern beech) from the CIROS-1 core and the Oliver Bluffs locality (Webb and Harwood, 1993). However, the environmental interpretation of this material has now been revised to tundra based on the studies of Francis and Hill (1996), a result that is more consistent with TRIFFID outputs.

Needle leaf trees are predicted to extend north to the Russian Arctic coast. However, the dominant predicted plant functional type in this region is shrubs rather than trees. PRISM indicates a dominance of coniferous forests but again a scarcity of data points makes this discrepancy hard to assess.

4.2. Mid-Pliocene expansion of tropical rainforests and significance for hominid evolution

One of the most striking results of the TRIFFID model for experiment MPDV is the increase in fractional coverage of broad leaf and needle leaf trees compared to experiments MPTrans and PIDV. If taken literally the increase in broad leaf trees in Africa and South America could be viewed as representing a massive expansion in the geographical coverage of tropical rainforest. However, closer inspection of the TRIFFID results suggests that only a modest increase in rainforests occur. TRIFFID diagnostics for plant respiration, Leaf Area Index and canopy height reveal that the characteristics of the broad leaf trees in southern Africa and parts of central and southern South America are significantly different from the Amazon and central African rainforest regions. Specifically, plant respiration is reduced and canopy height is lower. So whilst there is no doubt that broad leaf trees expand in Africa and South America in experiment MPDV, it does not represent a major expansion in rainforest per se, but rather a different type of forest. However, there is evidence for a genuine increase in geographical coverage of tropical rainforest in central and East Africa.

Of particular interest is the significance of these results to the theories surrounding hominid evolution and dispersal from East Africa. One theory regarding the origin of hominids states that the family evolved in open country from a quadrupedal precursor (e.g., Washburn, 1967; Richmond and Strait, 2000). The central theme of the hypothesis is that the opening up of the landscape due to rifting and domal uplift caused the aridification of East Africa and led to the emergence of Hominidae at the end of the Miocene. In the 'savannah hypothesis', the emergence of the family is visualised as occurring in open country (Pickford et al., 2004). The results from the TRIFFID model presented in this study indicate that broad leaf trees dominate East Africa even during the Pliocene (up to 90% fractional coverage) with C3 and C4 grasses normally only achieving a fractional coverage of ~15%. Such a result is not consistent with the savannah hypothesis.

The savannah hypothesis is not universally accepted by palaeoanthropologists. For example, a specimen of

Australopithecus antiquus seu afarensis from Ethiopia, which is approximately 3 million years old, the ‘Lucy’ specimen, inhabited montane forest rather than savannah (Bonnefille et al., 1987). Pickford et al. (2004) stated that recent discoveries of Late Miocene and Early Pliocene hominids have revealed that the sites are often reconstructed as representing well wooded to forested palaeohabitats. For example, *Orrorin tugenensis*, a 6–5.7 Ma bipedal hominid, is associated with abundant colobine monkey fossils, suggesting an abundance of trees in the basin (Pickford and Senut, 2001). The same applies to the Western Margin sites in the Middle Awash (5.7–5.2 Ma; Haile-Selassie, 2001) and the 4.2 Ma site of Aramis, Ethiopia (White et al., 1994). The Lothagam hominid mandible (Apak Member), which was for many years thought to be Late Miocene in age (Patterson et al., 1970) has recently been re-dated (McDougall and Feibel, 1999) and is more likely to be Early Pliocene in age (older than 4.2 Ma and younger than 5 Ma). It appears to be associated with well-vegetated conditions with some open country habitats nearby, while two slightly older specimens (Upper Nawata Member: 6.5–5 Ma) are also associated with well-vegetated palaeoenvironments (cited in Pickford et al., 2004).

Williamson (1985) proposed, on the basis of the freshwater snail genus *Potadoma* found in Late Pliocene to Early Pleistocene deposits of West Turkana, that there was an extension of the tropical rainforest to the Turkana Basin, Kenya at that time. Today, this snail is confined to rivers in heavily forested areas. On the basis of faunal studies, Pickford (1991) concluded that during the Late Miocene and Early Pliocene the Tugen Hills region was considerably more humid and better vegetated than it is today. The recent discovery of tragulids in the Early Pliocene deposits of the region confirms that rainforest was present in Kenya from about 5.3 to 4.5 Ma, while forest and dense woodland has been inferred even earlier in the basin, in the Lukeino Formation (ca. 6 Ma; Pickford and Senut, 2001) and the Mpesida Beds (6.3 Ma; Kingston, 1999). The faunal studies and examination of palaeosols in the Lukeino, Kaparaina and Mabaget Formations indicate that throughout the period represented by these formations (6–4.5 Ma), the Tugen Hills area was close to or within tropical forest, and that signs of semi-arid to arid conditions are rare to non-existent.

Pickford et al. (2004) concluded on the basis of this evidence that it is now unlikely that protohominids ventured into the savannah as quadrupeds that then went through a knuckle-walking stage before becoming

bipedal. It now seems possible that bipedalism evolved in wooded to forested ecosystems and was, for several million years, linked to arborealism and that only after it was perfected did hominids spread into more open environments as fully functional bipeds. The results from this study appear to support this conclusion in as much as they support the reconstructions of forested palaeohabitats that are believed to be associated with hominid sites of Pliocene age, and give credence to the idea that forest cover was much more extensive in East Africa and Africa in general, until at least 3 million years ago.

5. Conclusions

In this study we employ the TRIFFID Dynamic Global Vegetation Model (DGVM) and the HadAM3 GCM to investigate vegetation distributions and climate–vegetation feedbacks during the Mid-Pliocene ~3 Ma BP, and examine the significance of these results to established hypotheses regarding the origin of hominid bipedalism.

- TRIFFID outputs support extant palaeoenvironmental reconstructions provided by the PRISM Group (Pliocene Research Interpretations and Synoptic Mapping).
- TRIFFID simulates a significant increase in forest cover, composed of needle leaf trees in the higher latitudes of the Northern Hemisphere and broad leaf trees in other regions. Needle leaf trees extend from the Arctic Coast into the northern mid latitudes.
- The fractional coverage of bare soil declines in North Africa, the Arabian Peninsula, Australia and southern South America and is consistent with PRISM's assertion of reduced coverage of arid deserts.
- A significant increase in the fractional coverage of both broad leaf trees in Africa and South America is not indicative of a major increase in the coverage of rainforest. Rather, it represents an expansion of wooded and forest habitats in these regions.
- The principal impact on the GCM predicted climatology of using a DGVM is to reduce minimum and maximum temperature extremes, thus effectively reducing the seasonality of temperature over wide regions.
- Our results are not compatible with the ‘savannah hypothesis’ for the evolution of hominid bipedalism. Rather they lend credence to an alternative hypothesis stating that bipedalism evolved in wooded to forested ecosystems and was, for several million years, linked to arborealism.

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