**Climate
of the Past**

Late Quaternary vegetation-climate feedbacks

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Abstract. Feedbacks between vegetation and other components of the climate system are discussed with respect to their influence on climate dynamics during the late Quaternary, i.e., the last glacial-interglacial cycles. When weighting current understanding based on interpretation of palaeobotanic and palaeoclimatic evidence by numerical climate system models, a number of arguments speak in favour of vegetation dynamics being an amplifier of orbital forcing. (a) The vegetation-snow albedo feedback in synergy with the sea-ice albedo feedback tends to amplify Northern Hemisphere and global mean temperature changes. (b) Variations in the extent of the largest desert on Earth, the Sahara, appear to be amplified by biogeophysical feedback. (c) Biogeochemical feedbacks in the climate system in relation to vegetation migration are supposed to be negative on time scales of glacial cycles. However, with respect to changes in global mean temperature, they are presumably weaker than the positive biogeophysical feedbacks.

1 Introduction

Daisyworld paradigms

With their conceptual Daisyworld model, Watson and Lovelock (1983) demonstrated that, in theory, feedbacks between biosphere and atmosphere may stabilize the climate[1] without any teleological foresight of flora and fauna. The stabilizing feedback in the Daisyworld is designed to be a vegetation-albedo feedback in which dark daisies absorb more sunlight than the grey, bare planet and much more than white daisies. Thereby, dark daisies provide favourable conditions for life on the Daisyworld planet in cold climate when insolation is weak. White daisies, on the other hand, reflect sunlight more strongly and tend to cool the planet which is the key for survival in hot climate with relatively strong insolation. When dark and white daisies co-exist, Daisyworld's mean temperature is nearly constant over a wide range of changes in solar energy flux (see Fig. 1).

Watson and Lovelock formulated the Daisyworld model as a proof of concept rather than any realistic description of the dynamics of the Earth's climate system. Therefore, it is instructive to explore the concept further by varying one of the decisive ecological parameters. In the original Daisyworld model, the same set of ecological parameters is used for white and dark daisies. In particular, their growth rates peaks at the same optimum temperature. Alternatively, one could assume that for some reason, white daisies like it cooler than dark daisies. The boreal biosphere of tundra and taiga might serve as a real-world example. With this assumption, everything else being unchanged, the Daisyworld paradigm changes completely. With a difference of 15 K in optimum temperatures, the Daisyworld sees stable temperatures if daisies – either white or dark daisies, respectively – exist. At a certain insolation threshold, however, a change

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[1]Here, climate is defined in terms of state and statistics of the climate system which encompasses the atmosphere, the biosphere, the cryosphere, the hydrosphere, and the pedosphere.
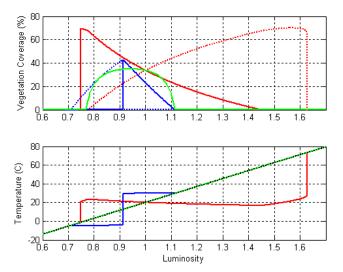
Fig. 1. Variants of Watson and Lovelock's (1983) Daisyworld model. The red lines depict results of the original model where the full red line and the dotted red line in the upper figure indicate the fractional coverage of the Daisyworld planet by dark and white daisies, respectively, as function of luminosity, i.e. the relative solar energy flux density. The lower figure shows the mean temperature of the Daisyworld planet. The dotted black line represents the temperature of the bare planet. (The dotted black line and the green line in the lower figure are identical.) For details of the equations of Daisyworld's vegetation and temperature dynamics, see Weber (2001). The parameter such as albedo values of 0.25, 0.5, 0.75 for dark daisies, bare planet, and white daisies, respectively, are the same as in the original model of Watson and Lovelock. In the original model, dark and white daisies have the same temperature for optimum growth (i.e., 20°C). This assumption is modified here: the blue curves refer to results, if white daisies grow at an optimum temperature which is 15°C lower than that of dark daisies. If the optimum temperature of white daisies is chosen to be 10°C lower, then the green curves result. In the latter case dark and white daisies occupy the same fraction of the planet, and the mean temperature of the Daisyworld planet does not differ from that of the bare planet. Hence the dotted black line and the green line in the lower figure are identical.

in the biosphere is triggered, and the vegetation-albedo feedback causes an abrupt increase in global mean temperature and an abrupt change in vegetation cover from white to dark daisies (Fig. 1, blue curves). A particularly interesting, special solution emerges for a difference of 10 K in optimum temperatures. In this case, white and dark daisies grow in harmony covering precisely the same fraction of their planet. Although the vegetation-albedo feedback causes local climate changes, an observer from space would not detect any difference in global mean temperatures between the living Daisyworld and a bare planet (Fig. 1, green curves; in the lower figure, the green curve and the dotted black curve are identical).

The question of which paradigm most appropriately characterizes the Earth's climate system – (a) the original conjecture of homoeostatic system (Lovelock and Margulis, 1974), (b) the system with locally important, but on global scale non-detectable, effects of biospheric feedbacks on global climate, or (c) the "mixed" case of a piecewise homoeostatic system in which long phases of a negative, stabilizing feedback exist as well as the possibility of abrupt climate changes – is hard, if not impossible, to answer. Indeed, it has been questioned whether falsifiable hypotheses could be posed in this context at all (Kirchner, 1989). However restriction to specific geological epochs and to subcomponents of the biosphere might lead to formulation of tractable questions.

Here, discussion is focused on the late Quaternary terrestrial vegetation-climate feedbacks, more precisely: feedbacks between terrestrial vegetation and other components of the climate system. The late Quaternary (by and large the last several glacial-interglacial cycles) is more accessible to falsification of models than the "deep past", because of its wealth of palaeoclimatic and palaeobotanic reconstruction. Moreover, the late Quaternary is the current geological epoch which is now being strongly affected by human activities. It is seems conceivable that humans might trigger destabilizing biospheric feedbacks – if they exist.

Discussion focuses on palaeoclimate questions, however, not on anthropogenic land-cover change. It centres on biogeophysical and, to a lesser extent, on biogeochemical feedbacks. Biogeophysical feedbacks directly affect near-surface energy, moisture, and momentum fluxes via changes in surface structure and plant physiology. These feedbacks include the biogeographical aspect, if vegetation pattern change. Biogeochemical feedbacks affect the chemical composition of the atmosphere. In nature, biogeophysical and biogeochemical feedbacks do not operate in isolation. Nonetheless, it is useful for many purposes to differentiate between them (e.g., Claussen, 2004).

This paper points in a similar direction as Bonan's (2008) recent review of biosphere-atmosphere interactions of tropical, boreal, and temperate forests. Also Bonan (2008) highlights the role of biogeophysical and biogeochemical feedbacks, and he focuses on the uncertainty of modelling these feedbacks. Here the topic is tackled from the palaeoclimatic and palaeobotanic perspective in the belief that interpretation of palaeoclimatic and palaeobotanic records by using climate system models could offer an inroad to testing hypotheses on the role of vegetation-climate feedbacks in climate system dynamics.

2 Biogeophysical aspects

2.1 Boreal feedbacks

2.1.1 Mid-Holocene warming

During the mid-Holocene some 6000 years ago, boreal forests extended north of the modern tree line (Frenzel et al., 1992; TEMPO et al. 1996; Cheddadi et al., 1997; Tarasov et al., 1998; Prentice and Webb III, 1998; MacDonald et al., 2000). These differences between mid-Holocene and present boreal biome patterns were presumably caused by steady changes in the Earth's orbit which led to stronger insolation (incoming solar energy flux density) than today and stronger near-surface warming during Northern Hemisphere summer.

Mid-Holocene boreal winter insolation was weaker than today (Berger, 1978). Hence by assuming that near-surface climate responds to changes in insolation linearly, one would expect mid-Holocene boreal winters to be colder than today. However at least in North-East Europe, mid-Holocene winters were reconstructed to be warmer than present (Cheddadi et al., 1997). This seeming paradox has been called the "biome paradox" by Berger (2001) who supposes that mid-Holocene winter time warming might have been caused by strong vegetation-snow albedo feedback. According to Otterman et al. (1984), more extended boreal forest, as reconstructed for mid-Holocene climate, could lead to a decrease in the surface albedo during the snowy season as snow-covered tall vegetation appears to be darker than snow-covered flat vegetation or bare ground. This, in turn, favours further warming due to reduced reflection of sunlight and further expansion of boreal forests (see also Foley et al., 1994; deNoblet et al., 1996; Texier et al., 1997; Foley, 2005).

Coupled atmosphere-ocean-vegetation models yield an ambiguous answer. Crucifix et al. (2002) report on strong vegetation-snow albedo feedback in their model. In other model studies (e.g. Ganopolski et al., 1998; Wohlfahrt et al., 2004), the vegetation-snow albedo feedback is too small to yield mid-Holocene winters which are warmer than present (pre-industrial) winters. Only in synergy with the sea-ice climate feedback, warmer winters can be found at northern, extra-tropical latitudes (see Fig. 2). (The sea-ice climate feedback encompasses two loops: the sea-ice albedo feedback and the sea-ice heat flux feedback. Both are positive as a change in sea-ice extent is amplified by near-surface warming/cooling due to changes in albedo or in heat flux from open water into the atmosphere; see Fig. A.22 in Claussen, 2004.) More recent studies by Gallimore et al. (2005) and Otto et al. (2009, Fig. 2) suggest a smaller effect of vegetation dynamics on mid-Holocene warming at high northern latitudes. They attribute the mid-Holocene warm winters mainly to ocean and sea-ice dynamics.

In the numerical models cited above, the effect of the vegetation-snow albedo on near-surface temperatures is strongest in spring by enhancing snow melt in a warmer cli-
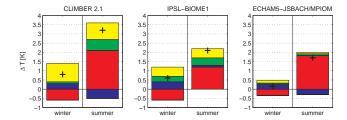

Fig. 2. Factors contributing to differences in winter and summer temperatures between mid-Holocene (some 6000 years ago) and pre-industrial climate for the Northern Hemisphere. The factor separation proposed by Stein and Alpert (1993) has been applied to CLIMBER 2.1, a model of intermediate complexity (data taken from Ganopolski et al., 1998, left figure), to the comprehensive atmosphere-ocean model IPSL asynchronously coupled to a (static) biome model (Wohlfahrt et al., 2004, middle figure), and to the comprehensive coupled atmosphere-vegetation-ocean model ECHAM5-JSBACH/MPI-OM (Otto et al., 2009, right figure). Temperature changes between mid-Holocene and present-day climate are considered over ice-free land areas north of 0° N for CLIMBER 2.1 and north of 40° N, for the comprehensive models. Red colours indicate the results in cases in which only the atmospheric dynamics are switched on in the climate models, i.e. the direct response of atmospheric dynamics to changes in orbitally induced solar energy flux is computed. Blue colours reveal the contribution due to ocean and sea-ice dynamics, i.e., additional warming or cooling due to ocean-atmosphere interaction. Green colours indicate the contribution to changes in vegetation patterns, i.e., the difference between the results of the atmosphere-vegetation models and the atmosphere-only models. Yellow colours show the contribution of a synergy between atmosphere-ocean and atmosphere-vegetation feedback.

mate. For example in the model of Gallimore et al. (2005), more wide-spread boreal forests in mid-Holocene high latitudes cause the strongest warming due to reduced snow cover in May. At mid latitudes more extended grass and shrub area produces a cooling between mid-Holocene and present climate mainly by enhanced snow cover which appears to be strongest in April. The situation in summer is more complex as other processes than changes in snow cover become important. For example, enhanced forest cover during mid-Holocene could increase evaporation thereby leading to a cooling. Increased evaporation, on the other hand, increases atmospheric water content and thereby, the wet greenhouse effect. In summary, however, biogeophysical feedback and associated synergies yield some amplification of mid-Holocene warming at high northern latitudes in most models.

Reconstructions of transient changes in boreal biomes suggest a rather steady southward shift of tree line and steady changes in pollen records during the Holocene (Brovkin et al., 2002) with perhaps some faster retreat between 4000 and 2000 years (uncalibrated ^{14}C ages) ago (MacDonald et al., 2000). This has been recaptured by numerical simulations
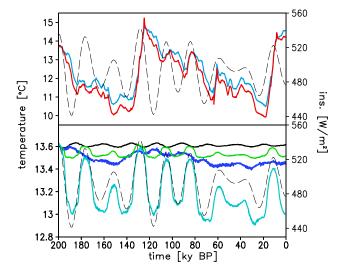
Fig. 3. Simulated global annual mean near-surface air temperatures for the last 200 ky BP (thousand years before present). The red line in the upper figure indicates results of a model run in which changes in inland ice and atmospheric CO_2 concentration are prescribed to force an atmosphere-ocean-vegetation model. The blue line in the upper figure indicates results of an atmosphere-ocean model in which vegetation cover is kept constant at initial values. The lower figure depicts results of the atmosphere-only model in which inland ice, atmospheric CO_2 concentration, vegetation cover, sea-surface temperature, and sea-ice cover are prescribed at values reconstructed or simulated (in the case of vegetation cover and ocean state) at 200 ky BP (black line). The green line indicates results of the atmosphere-vegetation model, the dark blue line, results of the atmosphere-ocean model, and the light blue line, results of the atmosphere-ocean-vegetation model. The dashed line shows the monthly mean insolation in June at 60° N. (This figure is taken from Claussen et al., 2006.)

(e.g. Brovkin et al., 2002; Crucifix et al., 2002). Theoretical studies in which the stability of boreal forest dynamics has been analysed (Levis et al., 1999; Brovkin et al., 2003) do not reveal any bifurcation of the atmosphere-biosphere system. Hence shifts in boreal vegetation patterns seem to follow orbital forcing rather steadily without any indication of abrupt changes in vegetation and climate.

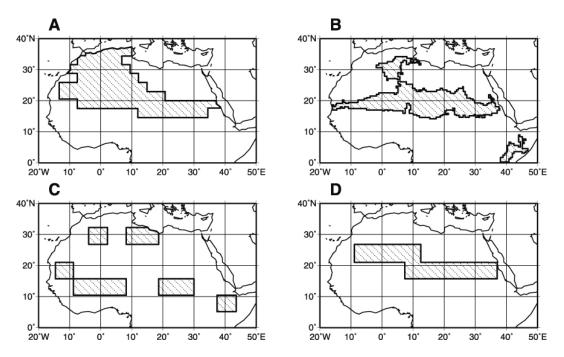### 2.1.2 Amplification of glacial-interglacial temperature change

Suppose that biogeophysical feedback, directly of by synergy with other feedbacks, tend to enhance global temperature change. What would be the consequence for late Quaternary climate dynamics? Firstly, it is to be expected that during the last interglacial, the Eemian some 126 000 years ago, the amplifying effect on global mean temperature should have been stronger than during the mid-Holocene due to stronger changes in orbital forcing. This surmise is consistently recaptured by models (e.g. Crucifix and Loutre, 2002;

Kubatzki et al., 2000; Schurgers et al., 2006). Secondly, the disappearance of the last remnants of the Laurentian ice sheet between 8000 to 6000 years ago presumably induced a warming associated with the vegetation-snow-albedo feedback which overcomes the Holocene cooling trend due to orbital forcing (Wang et al., 2005b)

For glacial climate, the opposite effect of vegetation migration on global mean temperature is expected. In an increasingly colder climate, the retreat of boreal forests to the south tends to cool the climate more strongly than without any vegetation shift (Kubatzki and Claussen, 1998). The same effect is found by Berger (2001) for the last glacial inception. Ganopolski (2003) and Jahn et al. (2005) quantify the overall effect of biogeophysical feedbacks (and synergies with other feedbacks) to account for some 0.6–0.7 K of the global mean cooling of approximately 5 K. Although biogeophysical feedbacks at northern high latitudes tend to be stronger in colder climate than in warmer climate due to a longer snow season (Brovkin et al., 2003), Jahn et al. (2005) show that during glacial climate (i.e., Marine Isotope Stages 3 and 2), the biogeophysical effect of vegetation on global mean temperature is still smaller than other processes such as changes in ice sheets and atmospheric CO_2 concentration.

First studies with interactive ice sheets highlight the importance of vegetation dynamics on glacial inception. Meissner et al. (2003) conclude that land related feedbacks double the atmospheric cooling, and the introduction of vegetation related feedbacks increases the surface area with perennial snow significantly. In turn, keeping vegetation at interglacial level might mitigate glacial inception (Wang et al., 2005; Kageyama et al., 2007) or even inhibit glacial inception (Kubatzki et al., 2006, 2007).

So far, no complete factor separation of feedbacks has been performed over the course of several glacial-interglacial cycles, i.e., many precessional cycles. A first modelling study with prescribed varying ice sheets and atmospheric CO_2 concentrations (Claussen et al., 2006) indicates that the biogeophysical feedback of boreal biomes and its synergy with the sea-ice albedo feedback could be an important amplifier of the precessional signal such that this signal appears in global mean temperature variations (Fig. 3). (The climatic precession itself induces only a seasonal cycle in solar energy flux, but no change in the annual mean flux.) More interestingly, the signal of precessional forcing emerges in simulated global mean temperature if only atmospheric and vegetation dynamics are included, and this signal is amplified by including ocean and sea-ice dynamics. This example illustrates that not only ice sheet dynamics could amplify the precessional signal (e.g. Köppen and Wegener, 1924), but also, albeit with a presumably much smaller amplitude, biogeophysical feedbacks and synergies.

Fig. 4. Differences between present-day and mid-Holocene Sahara as simulated by various coupled vegetation (or biome)-climate models. The hatched area indicates the vegetated fraction irrespective of the density of vegetation coverage. Results are shown from **(A)** Claussen and Gayler (1997), **(B)** Doherty et al. (2000), **(C)** Schurgers et al. (2006), and **(D)** Liu et al., (2007).

2.2 Subtropical desert feedbacks

2.2.1 North African wet phase

The largest subtropical desert, the Sahara, was much greener and moister than today during the early and mid-Holocene according to palaeobotanic reconstructions (Jolly et al., 1998; Hoelzmann et al., 1998; Prentice et al., 2000), and lake level and water balance reconstructions (e.g. Yu and Harrison, 1996; Coe and Harrison, 2002). Like the difference in boreal biomes, the difference between the smaller ("greener") mid-Holocene Sahara and more extended modern Sahara has been attributed to changes in orbital forcing and associated changes in ocean-continent temperature contrast (e.g., Spitaler, 1921; Kutzbach and Guetter, 1986). The stronger mid-Holocene summer monsoon triggered by changes in the Earth's orbital around the sun and in the tilt of the Earth's axis, however, did not seem to be large enough to explain a large areal difference between mid-Holocene and modern Sahara (Joussaume et al., 1999).

Claussen and Gayler (1997) find a strong positive feedback between vegetation and precipitation – mainly in the western part of the Sahara – which could amplify the summer monsoon to foster a stronger coverage of the Sahara with Sahelian vegetation in the mid-Holocene. Claussen and Gayler explain the positive feedback by an interaction between high albedo of Saharan sand deserts and tropical atmospheric circulation. This desert-albedo feedback was originally proposed by Otterman (1974) and described in a model by Charney (1975) to explain the opposite process of desertification in the Sahel region. Charney (1975) hypothesizes that the high albedo over subtropical deserts causes a radiative cooling above deserts because the sum of incoming solar radiation, reflected solar radiation and outgoing long-wave radiation is negative at the top of the atmosphere: more radiation leaves than enters the atmosphere above a subtropical desert. The local radiative cooling induces a subsidence of air masses which compensates the cooling by adiabatic heating. The sinking motion suppresses convective precipitation. The reduction of precipitation is supposed to cause further vegetation degradation, thus enhancing the growth of desert-like conditions. Xue and Shukla (1993) and Eltahir and Gong (1996) argue that the albedo changes in the Sahel are too weak to explain any strong feedback in relation to albedo. But for the region of the Sahara, the desert-albedo feedback seems to work both to amplify a decrease in precipitation with an increase in desert area and to amplify an increase in precipitation with a decrease in desert area (Claussen and Gayler, 1997).

The extent of Saharan vegetation coverage during the mid-Holocene wet phase is still not fully known. Areal reconstructions (e.g. Petit-Maire and Guo, 1996; Hoelzmann et al., 1998; Anhuf et al., 1999), differ, so do model simulations (Claussen and Gayler, 1997; Texier et al., 1997; Broström et al., 1998; Doherty et al., 2000; Schurgers et al., 2006; Liu et al., 2007) (Fig. 4). Summarizing the results of the Paleoclimate Modeling Intercomparison

Project 2, Braconnot et al. (2007) conclude that the biogeophysical feedback might be weaker than previously thought. However this statement is based on results obtained from an ensemble of models which strongly differ in present-day values of North African albedo as well as calculated albedo differences between present-day and mid-Holocene Sahara. Moreover, most model simulations were not set up such that a consistent feedback and factor separation could have been derived.

There is at least one model which indicates a negative biogeophysical feedback (Wang et al., 2008; Notaro et al., 2008) which sustains vegetation in a mid-Holocene vegetated Sahara. In this model, evaporation from bare ground appears to be stronger than transpiration from grassland in wet conditions. Thereby, the drying of soil is stronger in the absence of plants. Hence it is conceivable that on short time scales during the early and mid Holocene, negative feedbacks could dominate when changes in albedo were small. On longer time scales however, changes in soils from dark to bright soils should be considered. An illustrative example is the desiccation of the Lake Mega-Chad where today, very high values of albedo can be found (Knorr and Schnitzler, 2006). Therefore, on time scales of climatic precession, most models show a stronger response of climate change when vegetation dynamics are included (Braconnot et al., 2007). Alternative explanations include feedbacks between atmosphere and ocean via changes in cool updraft regions along the North African Coast (e.g. Kutzbach and Liu, 1997; Hewitt and Mitchell, 1998; Liu et al., 2004). However, the strength of these feedbacks is too weak to explain the climate change in North Africa alone. Also the synergy between vegetation-atmosphere and ocean-atmosphere feedbacks seems to be smaller than the vegetation-atmosphere feedback (Ganopolski et al., 1998; Braconnot et al., 1999).

2.2.2 Saharan dynamics

The transient dynamics of the Sahara appear to be more complex than boreal vegetation dynamics. Earlier model studies with asynchronous coupling of atmospheric and biome models demonstrate the possibility of multiple equilibrium solutions. For present-day climate Claussen (1994, 1997) found two solutions: a desert like today, if the model is initialized with present-day vegetation pattern, and a Sahara which is much greener than today in its western part, if the model is initialized with forest or grass or even dark deserts all over the world. Similar is valid for glacial conditions (Kubatzki and Claussen, 1998). For mid-Holocene conditions, however, only one solution of the model, the "green (West-)Sahara" is obtained irrespective of initial vegetation patterns (Claussen and Gayler, 1997).

The appearance of multiple equilibrium states of a dynamical system as function of varying forcing suggests the potential of abrupt transitions between states, if external forcing varies with time. This can happen either in the form of a single, abrupt transition or in the form of multiple switches, so-called flickering, until the system stays in one of the stable equilibria (for conceptual visualization see Scheffer et al., 2001).

Brovkin et al. (1998) have set up a mathematical conceptual model of subtropical vegetation-precipitation interaction. By applying this model to the results of the comprehensive asynchronously coupled atmosphere-biome model they found that the jump from the green to the desert state should have happened between 6000 and 3600 y BP. This conclusion has been corroborated by the Claussen et al. (1999) (Fig. 5a) who used a dynamically coupled global atmosphere-ocean-vegetation model of intermediate complexity, CLIMBER-2.1. They predicted a fast expansion of the Sahara around 5500 y BP.

More recent model simulations reveal a more mixed picture. In their model, ECBilt-CLIO-VECODE, Renssen et al. (2003) find a steady decline of Saharan vegetation on millennial average. However, variability in Saharan vegetation changes with particularly strong variations in vegetation cover between 7000 and 5000 y BP (Fig. 5b). Renssen et al. (2003), show that the change in variability in their model could be attributed to a bistability of the system during the period of strong variations. Using a zonally symmetric model of vegetation dynamics and air-flow over West Africa, Irizarry-Oritz et al. (2003) obtain bistability of the atmosphere - vegetation system for the mid-Holocene period thereby corroborating the results by Renssen et al. (2003). Liu et al. (2006b) have analysed the stability of the biogeophysical system in the presence of rainfall variability which is implicit in randomly varying atmospheric dynamics. They conclude that rainfall variability could induce abrupt vegetation change – as found in their model, the comprehensive atmosphere-ocean-vegetation model FOAM-LPJ (Fig. 5c). They conclude that their model reveals a strong non-linear response of vegetation to precipitation, but only a weakly non-linear feedback.

Shortly after Claussen et al. (1999) published their model predictions, deMenocal et al. (2000) reported on an abrupt increase in terrestrial dust flux around 5500 y BP in marine sediments of the coast of North Africa near Cape Blanc, Mauretania (Fig. 5d). They interpret the abrupt change in dust flux as abrupt aridification of West Africa. The dust record of deMenocal et al. (2000) has long been considered as corroboration of abrupt climate and vegetation change in the western part of the Sahara. However, this record should be interpreted with care since the abrupt change in the dust deposition might reflect not only a decrease in vegetation cover but also an increase in the source area of the dust caused by lake desiccations.

For the eastern part of the Sahara (east of approximately 10° E), Pachur (1999) found that aridification increased more gradually with a period of larger variability in between 7000 to 4500 y BP (Fig. 5e). Rapid swings between the arid and the wet state were detected in reconstructions from several

hundred ^{14}C dates around the Tropic of Cancer by Petit-Maire and Guo (1996) and from tree rings in the Central Sahara by Cremaschi et al. (2006). Recently, Kröpelin et al. (2008) presented fascinating details of desiccation from Lake Yoa located northeast of the ancient Lake Mega Chad. This record spans some 6000 years, and for the oldest 1000 years multiple swings with decreasing amplitude in tropical and grass pollen were detected. Kröpelin et al. (2008) (Fig. 5f) interpret their reconstruction as a rather smooth, non-abrupt transition in climate and vegetation cover. This could be a valid statement. However, the Lake Yoa record is just too short for a detailed statistical analysis to exclude the possibility that the multiple swings in vegetation are a manifestation of flickering of the system.
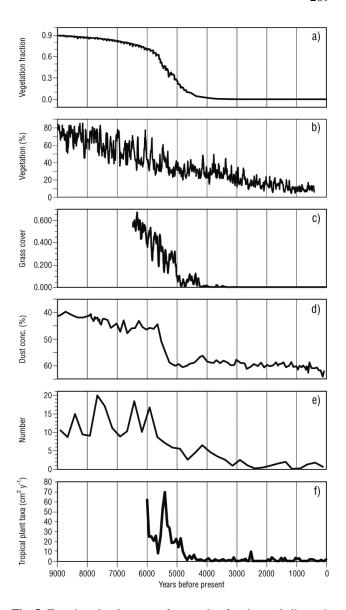
2.2.3 Long-term Saharan change

Looking further back into the past, it appears that there is a strong link between Dansgaard-Oeschger cycles, Heinrich events and climate changes in North Africa (Claussen et al., 2003a; Chang et al., 2008; Tjallingii et al., 2008). No or only very small changes are detectable in the Sahara which during the cold MIS 4, 3 and 2 remains an extended desert. In the Sahel region, however, stadials lead to a reduction in precipitation and vegetation cover where the effect of Heinrich events is stronger than the effect of Dansgaard-Oeschger cycles. Superimposed on these effects is the imprint of precessional forcing.

As mentioned above, the Sahara was much greener than today during the Eemian and MIS 5e according to model simulations and archaeological evidence (e.g. Osborne et al., 2008). Interestingly not only MIS 5e, but also MIS 5c and MIS 5a had seen a greener Sahara than today according to palaeoclimate reconstructions and model results (Tjallingii et al., 2008) (Fig. 6). From these studies one can conclude that in sufficiently warm climate states, such as interglacials, the Sahara expands and retreats following precessional forcing. Precessional forcing, however, is only the trigger, as the change in vegetation and climate appears to be much faster than the subtle change in forcing. In cold and dry climate states like glacials (e.g. MIS 4, 3, and 2), no great changes are expected in the Sahara.

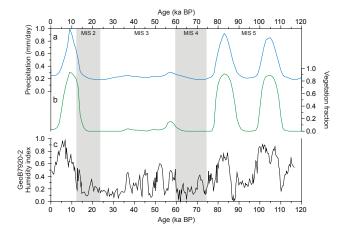## 3 Biogeophysical vs. biogeochemical aspects

3.1 Carbon cycle-climate feedbacks

In the previous sections, biogeophysical processes have been considered, and it has been concluded that from the biogeophysical point of view, vegetation dynamics tend to be an amplifier of late Quaternary climate change. However changes in vegetation cover not only affect the energy fluxes, but also biogeochemical fluxes which modify the chemical composition and subsequently, the energy cycle of the atmosphere. When focussing on the carbon cycle, mainly three

Fig. 5. Transient development of vegetation fraction and climate in the Sahara. **(a)** Simulated changes in vegetation fraction on average over the entire Sahara by Claussen and Gayler (1997). **(b)** Simulated changes in vegetation fraction in the Western Sahara/Sahel region (14° W to 3° E, 17° N to 28° N) by Renssen et al. (2003). **(c)** Simulated changes in grass cover in the Eastern Sahara (11° E to 34° E, 18° N to 23° N) by Liu et al. (2007). **(d)** Reconstructed dust concentration in North Atlantic marine sediment (at approximately 20.8° N, 18.5° W) by deMenocal et al. (2000). **(e)** Number of ^{14}C dates in the Sahara east of 11° E by Pachur (1999). **(f)** Reconstructed change in tropical plant taxa from Lake Yoa (at approximately 19° N, 20.3° E) by Kröplin et al. (2008).

feedbacks stand out: the so-called climate-greenhouse, or climate-carbon, feedback, the CO_2 fertilization-CO_2 uptake feedback and a biogeochemistry-climate feedback caused by shifts in vegetation patterns.

Fig. 6. Simulated annual mean daily precipitation (mm/day) (upper, blue line) and relative vegetation coverage (middle, green line) over the Saharan region between 20° N and 30° N over the last 120 ka (ka BP = thousand years before present). The black line depicts temporal variations of the proportion of non-aeolian terrigeneous sediment reconstructed from marine core GeoB7920-2 (at approximately 20.5° N, 18.5° W). (This figure is taken with modifications from Tjallingii et al., 2008.)

The climate-carbon feedback implies that warming increases soil emissions of CO_2 and reduces carbon storage in terrestrial and ocean ecosystems. The net result is an increase in atmospheric CO_2 concentration which, in turn, leads to further warming. The CO_2 fertilization-CO_2 uptake feedback is considered a negative feedback. It increases uptake of CO_2 with increasing atmospheric CO_2 concentrations, thereby reducing atmospheric CO_2 concentrations (House et al., 2006).

Both feedbacks are considered to exist with high certainty (House et al., 2006). The net effect seems to be positive, as Scheffer et al. (2006) found from analysing past trends in atmospheric CO_2 concentration. This is supported by numerical simulations with prescribed, increasing CO_2 emissions from fossil fuel burning. They yield an amplification of the increase in atmospheric CO_2 concentration owing to a reduced uptake of CO_2 by the terrestrial biosphere and the ocean (e.g. Cox et al., 2000; Friedlingstein et al., 2006; Raddatz et al., 2007). However the strength of these feedbacks is much less certain (Denman et al., 2007). Bonan (2008) summarizes that in a comparison of eleven models, feedbacks related to the terrestrial carbon cycle could increase atmospheric CO_2 concentrations by 4 to 44% at the end of the 21st century. Much of the model uncertainty arises from the CO_2 fertilization-CO_2 uptake feedback.

The climate-carbon feedback and the CO_2 fertilization-CO_2 uptake feedback have been explored in simulations of the recent past, the last centuries, and the near future. So far no estimates of their effect on long time scales of glacial cycles seem to exist. On these longer time scales, shifts in vegetation patterns have presumably provided a negative feed-

back in the climate system. During glacial inception forest were reduced in their extent which led to an increase in atmospheric CO_2 concentration, while during deglaciation, atmospheric CO_2 concentration should have decreased due to the built up of forest. In the following, only the last, long-term feedback will be considered, and a quantitative estimate is given below.

Possibilities of a positive feedback on long time scales of glacial cycles due to burial of terrestrial carbon during glacials have been discussed (Zeng, 2003), but have not yet been corroborated. A burial of vegetation and soils by ice sheets during a glacial inception would inhibit the exchange of CO_2 between the terrestrial biosphere and the atmosphere thereby lowering the atmospheric CO_2 concentration and, hence, the atmospheric greenhouse effect. When ice sheets retreat, the buried carbon is released to the atmosphere thereby increasing the warming during deglaciation by strengthening the greenhouse effect.

3.2 A thought experiment

Is it possible to evaluate the strength of biogeophysical versus biogeochemical effects of large-scale land cover change? Claussen et al. (2001) tried to quantify the relative magnitude of these processes and their synergism by using the CLIMBER-2 model. Their sensitivity studies show that when the climate system has reached an equilibrium, changes in forest fraction and changes in atmospheric CO_2 are negatively correlated, i.e., deforestation yields an increase in atmospheric CO_2 concentration and afforestation, a decrease (Fig. 7). With respect to global mean temperature, however, correlation changes sign. Tropical deforestation tends to warm the climate, because the increase in atmospheric CO_2 and hence, the greenhouse effect, outweighs the biogeophysical effects. In mid and high northern latitudes, however, biogeophysical processes – mainly the vegetation-snow albedo feedback in synergy with the sea-ice albedo feedback – win over biogeochemical processes, thereby eventually leading to a global cooling in the case of deforestation and to a global warming, in the case of afforestation. Since CLIMBER-2 does not explicitly simulate synoptic variability, the question of significance of the biogeophysical and biogeochemical signals in the presence of ubiquitous climate variability has not been answered. Furthermore, the question of time scales has not been addressed. It is conceivable that time scales of biogeophysical and biogeochemical processes differ. Hence the study by Claussen et al. (2001) should be considered a thought experiment. The result of this experiment is, however, consistent with model simulations by Betts (2000) and Bala et al. (2007). Betts (2000) compared estimates of a positive radiative forcing and associated warming due to decreasing albedo caused by afforestation of current agricultural land with the estimates of a negative radiative forcing caused by a lowering of atmospheric CO_2 due to enhanced carbon uptake by new forests. Bala et al. (2007) used

a coupled atmosphere-ocean-vegetation model to assess temperature changes in potential future climate change with deforestation of global, tropical, temperate, and boreal forests, respectively.

3.3 Glacial implications

How does the thought experiment apply to the question on the role of vegetation-climate feedback on late Quaternary climate? Tropical forests were presumably reduced in their extent during glacial climate, (Crowley, 1995) with tropical rainforest being replaced by tropical seasonal forest in tropical lowlands and by xerophytic woods in tropical highlands (Elenga et al., 2000). Model simulations yield a slight areal increase (Prentice et al., 1993), little change (Jahn, 2004), and a slight decrease (Kubatzki and Claussen, 1998; Kutzbach et al., 1998) in tropical forests. Boreal forests, however, regressed equatorwards with a compression and fragmentation of the forest zones (Prentice et al., 2000) covering a much smaller fraction, roughly 1/3, of its present-day area according to the model studies cited above. Hence one might conclude that because of its strong areal changes, boreal biogeophysical feedbacks could have been the dominant factor in modifying global mean temperature during glacial-interglacial cycles

These considerations are corroborated by an estimate of the strength of the effect of changes in terrestrial carbon on atmospheric CO_2 concentration and on glacial cooling The amount of carbon stored in the glacial biosphere is estimated to be at least by 500 GtC less than during the pre-industrial period (Crowley, 1995; Francois et al., 1999; Joos et al., 2004). Most of the resulting increase in CO_2 flux into the atmosphere was likely to be buffered by the oceanic biogeochemical processes including carbonate compensation, so that atmospheric CO_2 concentration should have increased by no more than 20–25 ppmv due to the shrinkage of the terrestrial biosphere (Archer et al., 2002; Brovkin et al., 2007). A change in atmospheric CO_2 concentration by 20–25 ppmv would lead to a change in global mean temperature by some 0.2–0.3 K, if a best guess of present-day climate sensitivity is considered (i.e., an increase in global mean temperature by 3 K caused by a doubling in atmospheric CO_2 concentration). An alternative estimate of climate sensitivity to changes in atmospheric CO_2 concentration in glacial climate is given by Jahn et al. (2005). From their model they found a decrease in global mean temperature of some 1.5 K due to a drop in atmospheric CO_2 concentration by 90 ppmv. This value implies a temperature change of some 0.3–0.4 K for a change in atmospheric CO_2 concentration by 20–25 ppmv. Hence the biogeochemical feedback caused by changes in vegetation patterns between glacial and interglacial climate may have resulted in a temperature change by some 0.2–0.4 K which is – in absolute values – smaller than the global mean temperature of some 0.6–0.7 K due to biogeophysical feedback according to Ganopolski (2003) and Jahn et al. (2005).
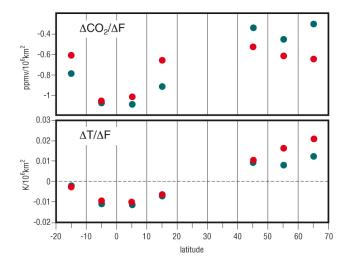

Fig. 7. Simulated ratio of changes in global atmospheric CO_2 concentration (upper figure) and global mean near-surface temperature (lower figure) to changes in forest area due to deforestation (red dots) and afforestation (green dots) in latitudinal belts of 10 degrees width. (This figure is taken with modifications from Claussen et al., 2001.)

4 Conclusion and perspective

The interaction between vegetation and climate must be considered an important component in climate system dynamics. This sentence, today, sounds almost trivial owing to advances in empirical and theoretical research. But some ten years ago, it was not. In fact in a review article in 2000 (Grassl, 2000), the distribution of global vegetation pattern was considered a boundary conditions to climate system models. Only short-term plant physiology and, to some extent, fractional vegetation and leaf area were allowed to change with meteorological conditions. Over the last decade, some climate system models have been developed in which not only atmospheric and oceanic, but also vegetation dynamics are simulated explicitly including biogeochemical cycles. Hence only now, comprehensive feedback analyses of the interaction between these climate system components can be tackled.

Despite great advances in modelling feedbacks between most components of the climate system, the question on the overall role of biogeophysical and biogeochemical feedbacks in the climate system is not yet solved. This is partly due to the lack of rigorously accounting for these feedbacks in numerical studies. Both feedbacks can be positive or negative, thereby partly compensating each other. When weighting current understanding based on the interpretation of palaeobotanic and palaeoclimatic evidence by using numerical climate system models, a number of arguments speak in favour of vegetation dynamics being an amplifier of orbital forcing in the late Quaternary.

Firstly, the vegetation-snow albedo feedback in synergy with the sea-ice-climate feedback tends to amplify global

mean temperature changes between glacial-interglacial states. In one model of intermediate complexity, the climatic precession (which itself induces only a seasonal cycle in solar energy flux, but no change in the annual mean flux) can be detected in annual mean temperature variations even if ice sheet cover and atmospheric CO_2 concentrations are held constant over many precessional periods. Other simulations, which include interactive atmosphere-ocean-vegetation-ice sheet dynamics, suggest that glacial inception could be strongly weakened or even suppressed, if vegetation pattern is kept constant at interglacial values.

An amplifying effect caused by migrating boreal vegetation is seen in most models. However regarding the magnitude of the biogeophysical feedback and any synergy associated with it, models differ. It is hard to judge on which model is "correct". In most cases, a formally complete factor separation analysis (following Stein and Alpert, 1993) has not been done. Further insight could be gained by undertaking model intercomparison in the form sensitivity studies with identically prescribed land-cover change. Moreover, comparison of present-day climate simulations with satellite-derived information could be helpful (Wang et al., 2005a). Based on the statistical analysis of remote sensing observations, for example, Liu et al. (2006a) suggest strong positive boreal vegetation-temperature feedback.

Secondly, variations in the extent of the largest desert on Earth, the Sahara, appear to be amplified by biogeophysical feedback when considering orbital time scales. This is seen in most models. Furthermore, it seems to be safe to state that expansion and retreat of the Sahara occurs at a faster pace than the driving orbital forcing. The dynamics of the Sahara is, however, still being explored. Theoretically it seems possible that the biosphere-atmosphere system in this region exhibits multiple steady states which would imply the potential of abrupt changes.

This aspect is interesting also for projections of potential future climate and precipitation change in the Sahel region and the Southern Sahara. If Saharan precipitation would increase in a greenhouse gas induced warmer climate and if a strong positive vegetation-climate feedback would exist, then an abrupt Saharan greening is likely to occur (Claussen et al., 2003b). So far, model simulations of potential future precipitation change disagree even with respect to the sign of change in this region (Meehl et al., 2007). For a step towards solving this problem, sufficiently long, multi-millennia records of climate archives are needed. These should provide independent palaeoclimatic and palaeobotanic information to reconstruct the dynamics of individual climate system components separately. Only then model-based interpretation of such records will allow an assessment of the strength of feedbacks between relevant climate system components.

Thirdly, biogeochemical feedbacks (the climate-carbon feedback, the CO_2 fertilization-CO_2 uptake feedback and a biogeochemistry-climate feedback caused by shifts in vegetation patterns) can be positive or negative, but on time scales of glacial cycles, they are supposedly negative: the land surface and terrestrial vegetation looses carbon during the transition from interglacial to glacial climate and gains carbon during the transition from glacial to interglacial climate thereby opposing the general trend of atmospheric CO_2 concentration.

Unfortunately no estimates on the relative strength of different biogeochemical feedbacks seem to exist. First estimates suggest that biogeochemical vegetation feedbacks in the climate system are, at the end, weaker than biogeophysical feedbacks. However, this assertion is based on reasoning and on analysing results of simplified models. Important processes with respect to terrestrial carbon cycle such as the storage and loss of carbon in peat and wetlands have not yet been explicitly included in this analysis.

In terms of the Daisyworld paradigms introduced in the beginning of this discussion, one might tentatively conclude that for the late Quaternary, the picture of a biosphere-atmosphere system that could trigger abrupt vegetation and climate changes is more appropriate than the picture of a purely homoeostatic biosphere-atmosphere interaction. Implicit in this conclusion is the assumption that the biosphere does not adjust itself to climate via evolution on orbital time scales – an assumption which awaits falsification.

Edited by: J. Guiot

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