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Driving forces of mid-Holocene vegetation shifts on the upper Tibetan Plateau, with emphasis on changes in atmospheric CO_2 concentrations

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ABSTRACT

Numerous pollen records across the upper Tibetan Plateau indicate that in the early part of the mid-Holocene, *Kobresia*-rich high-alpine meadows invaded areas formerly dominated by alpine steppe vegetation rich in *Artemisia*. We examine climate, land-use, and CO_2 concentration changes as potential drivers for this marked vegetation change. The climatic implications of these vegetational shifts are explored by applying a newly developed pollen-based moisture-balance transfer-function to fossil pollen spectra from Koucha Lake on the north-eastern Tibetan Plateau (34.0°N; 97.2°E; 4540 m a.s.l.) and Xuguo Lake on the central Tibetan Plateau (31.97°N; 90.3°E; 4595 m a.s.l.), both located in the meadow-steppe transition zone. Reconstructed moisture-balances were markedly reduced (by ~150–180 mm) during the early mid-Holocene compared to the late-Holocene. These findings contradict most other records from the Indian monsoonal realm and also most non-pollen records from the Tibetan Plateau that indicate a rather wet early- and mid-Holocene. The extent and timing of anthropogenic land-use involving grazing by large herbivores on the upper Tibetan Plateau and its possible impacts on high-alpine vegetation are still mostly unknown due to the lack of relevant archaeological evidence. Arguments against a mainly anthropogenic origin of *Kobresia* high-alpine meadows are the discovery of the widespread expansion of obviously 'natural' *Kobresia* meadows on the south-eastern Tibetan Plateau during the Lateglacial period indicating the natural origin of this vegetation type and the lack of any concurrence between modern human-driven vegetation shifts and the mid-Holocene compositional changes. Vegetation types are known to respond to atmospheric CO_2 concentration changes, at least on glacial–interglacial scales. This assumption is confirmed by our sensitivity study where we model Tibetan vegetation at different CO_2 concentrations of 375 (present-day), 260 (early Holocene), and 650 ppm (future scenario) using the BIOME4 global vegetation model. Previous experimental studies confirm that vegetation growing on dry and high sites is particularly sensitive to CO_2 changes. Here we propose that the replacement of drought-resistant alpine steppes (that are well adapted to low CO_2 concentrations) by mesic *Kobresia* meadows can, at least, be partly interpreted as a response to the increase of CO_2 concentration since 7000 years ago due to fertilization and water-saving effects. Our hypothesis is corroborated by former CO_2 fertilization experiments performed on various dry grasslands and by the strong recent expansion of high-alpine meadows documented by remote sensing studies in response to recent CO_2 increases.

1. Introduction

Land cover on the Tibetan Plateau strongly affects regional atmospheric circulation (e.g. Yasunari, 2006). Studying its (palaeo)-environmental character is thus essential to understand past and future climatic changes in the Asian monsoonal realm. In this context, the early- to mid-Holocene environmental situation on the Tibetan

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Plateau is of particular interest because, due to globally increasing temperatures, the mid-Holocene may serve as an analogue for the future. A marked feature of the mid-Holocene is the replacement of drought-resistant *Artemisia*-rich steppes by *Kobresia*-dominated high-alpine meadows as recorded by numerous pollen sequences (Figs. 1 and 2). This vegetation shift has been assumed to reflect a moisture increase (Shen et al., 2008; Herzschuh et al., 2009), although such pollen-based climatic reconstructions contradict the general observation of an weakening Asian summer monsoon during the mid-Holocene (Fleitmann et al., 2003; Wang et al., 2005). Recently, the mid-Holocene expansion of *Kobresia* meadows has been interpreted as a response to the establishment of nomadic herding on the upper Tibetan Plateau (Miehe et al., 2009; Schlütz and Lehmkuhl, 2009).

In glacial times, low atmospheric CO_2 concentrations that globally promoted the expansion of drought-resistant vegetation (Polley et al. 1993; Prentice and Harrison, 2009), are also assumed to have affected Tibetan vegetation (Herzschuh et al., 2010a). Inverse vegetation modelling for Africa, however, indicates that Holocene vegetation, in contrast to glacial vegetation, was not sensitive to CO_2 variations because either CO_2 concentrations already exceeded a critical threshold value or they were too small (Wu et al., 2007). Likewise, changing CO_2 concentrations have not previously been considered to be a driving force for Holocene Tibetan vegetation change. However, experimental CO_2 fertilization of dry grassland and desert vegetation performed in several regions world-wide has stimulated plant growth directly through enhanced photosynthesis and indirectly through enhanced water-use efficiency (Morgan et al., 2004).

Palaeovegetational investigations that include pollen-based quantitative moisture-balance reconstructions concentrate on Koucha Lake (north-eastern Tibetan Plateau, Herzschuh et al., 2009) and Xuguo Lake (Xuguo Lake, central Tibetan Plateau, Shen, 2003). Both medium-sized lakes have a regional-scale relevant pollen-source area and are situated in the transition zone between *Kobresia*-meadows and alpine steppe and are thus ideal for tracing vegetational transitions at a regional scale. Furthermore, we provide preliminary results of vegetation modelling using the BIOME4 model that test the sensitivity of Tibetan vegetation to atmospheric CO_2 changes. In the discussion, we critically review possible driving forces for early- to mid-Holocene vegetation shifts on the upper Tibetan Plateau (including precipitation, growing season length, radiation, human impact) with particular emphasis on changing CO_2 concentrations to better predict future environmental change and impacts on the Tibetan Plateau in a rapidly changing world.

2. Regional setting

The climate of the Tibetan Plateau is dominated by the Asian monsoonal circulation. There is a general gradient from high summer temperature (up to 19 °C) and high precipitation (>700 mm) on the south-eastern Plateau to low precipitation (<100 mm) and low summer temperature (~6 °C) on the north-western Tibetan Plateau.

Montane conifer and mixed forests grow in the warm and wet southern, south-eastern, and eastern margins of the Tibetan Plateau up to ~3000 m in the north and ~4000 m in the south (Fig. 3). Due to intensive logging, forest patches only persist in remote areas and on steep slopes. The north-eastern, northern, central, and western Tibetan Plateau is covered by non-forest vegetation (Hou, 2001). Cold and wet areas on the eastern Tibetan Plateau above 4500 m support high-alpine meadows mainly composed of different *Kobresia* species (e.g. *Kobresia pygmaea*, *Kobresia capillifolia*). Ranunculaceae, *Polygonum*, Fabaceae, and Caryophyllaceae are common in these vegetation types which grade into alpine steppe – a mixture of *Artemisia*, Cyperaceae (e.g. *Kobresia littledalei*, *Kobresia royleana*, *Carex moorcroftii*), and Poaceae (*Stipa subsessiliflora*, *Stipa purpurea*) in areas with less than 350 mm annual precipitation. This steppe vegetation type dominates large areas of the north-eastern and central-western Tibetan Plateau. Only the dry north-central and westernmost regions of the Plateau are occupied by alpine desert steppes, where the dominant Chenopodiaceae (e.g. *Ceratoides compacta*) are accompanied by *Artemisia*, Poaceae, *Ephedra*, and *Nitraria*. Most areas of the Plateau are regularly grazed, especially the eastern, southern, and central parts.

Koucha Lake (34.0°N; 97.2°E; 4540 m a.s.l.) is situated on the north-eastern Tibetan Plateau (Fig. 1). This freshwater lake (18 km^2 area) has a maximum depth of ~6 m. Mean annual precipitation and

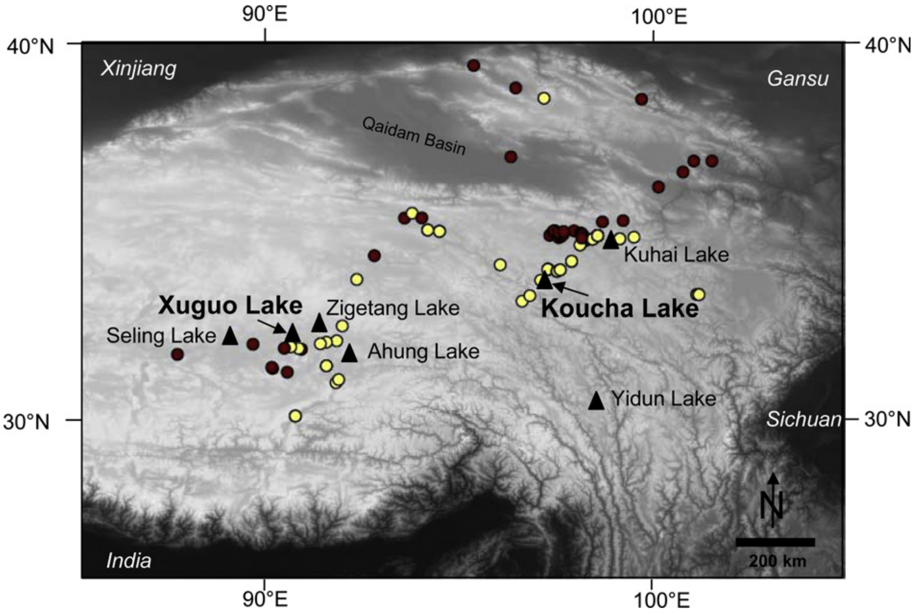

Fig. 1. Map of the eastern Tibetan Plateau with locations of palynological sites (black triangles). Coloured circles indicate *Artemisia*/Cyperaceae ratios (>0.4 in yellow; <0.4 in purple) inferred from lake sediment surface samples from alpine vegetation on the eastern Tibetan Plateau. A ratio of 0.4 is in rough agreement with the alpine steppe–*Kobresia* meadow borderline according to Hou (2001). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

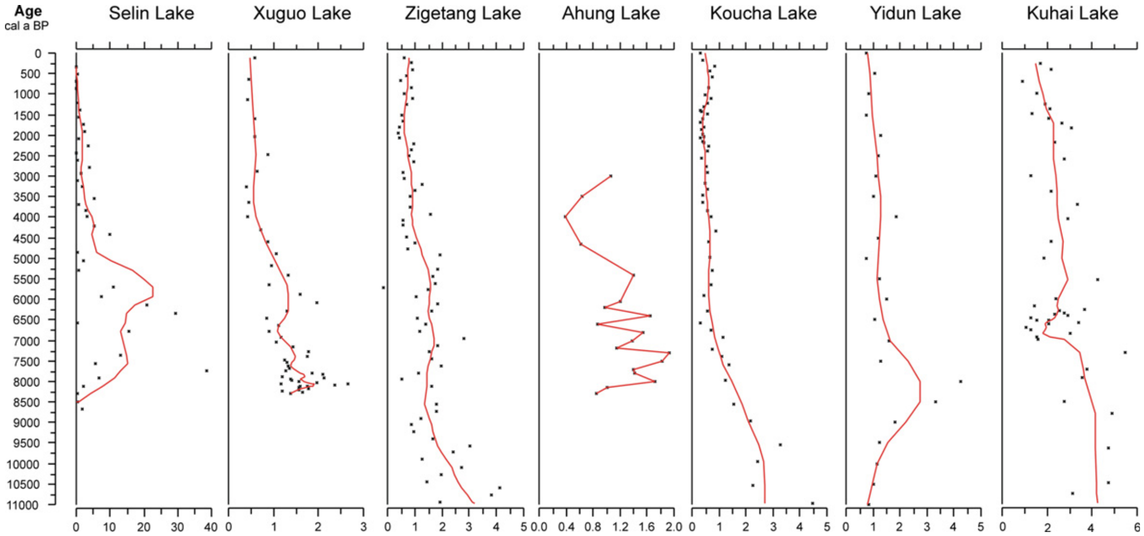

Fig. 2. *Artemisia*/Cyperaceae ratios of Holocene pollen profiles from the upper Tibetan Plateau arranged along a west–east transect across the steppe-meadow transition. All sites show a declining trend in the *Artemisia*/Cyperaceae ratio since the early mid-Holocene. Most sequences show an early- to mid-Holocene maximum indicating that alpine steppe had its maximum extension during that time. The fitted lines are LOESS smoothers (span = 0.1) (References: Selin Lake, Sun et al. (1993); Xuguo Lake and Ahung Lake, Shen (2003); Zigetang, Herzschuh et al. (2006a); Koucha Lake, Herzschuh et al. (2009); Yidun Lake, Shen et al. (2006); Kuhai Lake, Wischnewski et al. (2011)).

mean annual temperature as inferred from the Chengduo climate station (33.8°N; 97.13°E; 4418 m a.s.l.) are 469 mm and −4.4 °C, with a modern moisture balance of about −300 to −400 mm. The immediate vicinity of Koucha Lake is covered by high-alpine *Kobresia* meadows, whereas the lower plains are covered by alpine steppe (Herzschuh et al., 2009).

Xuguo Lake (31.97°N; 90.3°E; 4595 m a.s.l.) is situated on the central Tibetan Plateau. This brackish-water lake (23 km^2 area) has a maximum depth of ~3.5 m. Mean annual precipitation and mean annual temperature as inferred from the Bange climate station (31.38°N; 90.02°E; 4701 m a.s.l.) are 323 mm and −0.4 °C, respectively, with a moisture balance of about −400 to −500 mm. Xuguo Lake is situated in the transition between *Kobresia*-dominated meadows and *Stipa*-*Artemisia* steppes (Hou, 2001).

3. Methods

To obtain a quantitative estimate of Holocene moisture-balance changes from the upper Tibetan Plateau, we developed a pollen-based transfer function using the modern pollen data-set presented in Herzschuh et al. (2010a) and modern moisture-balance data from Böhner (2005). The transfer functions were applied to two fossil data-sets; 1) Koucha Lake (original pollen data in Herzschuh et al., 2009) and 2) Xuguo Lake (digitized data from Shen, 2003).

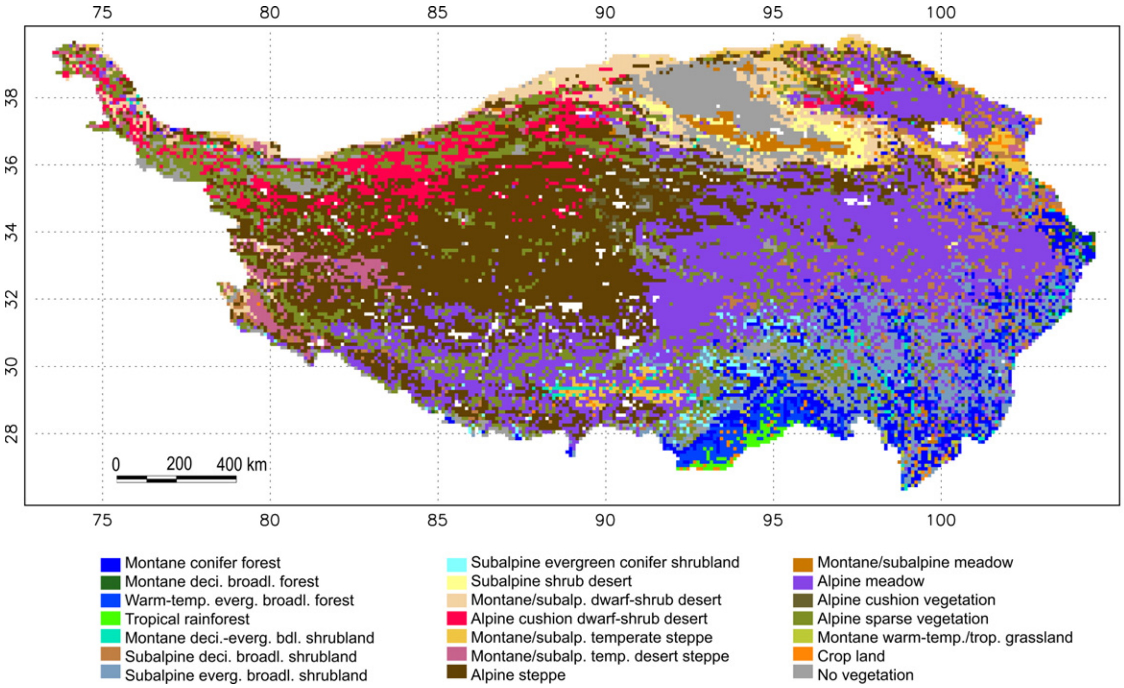

Fig. 3. Vegetation map of the Tibetan Plateau on a 10 km resolution. Map information obtained from the Vegetation Atlas of China (Hou, 2001).

To estimate quantitatively the annual moisture-balance (=annual precipitation − annual potential evapotranspiration), we developed a modern pollen-climate calibration data-set based on 132 lake surface-sediments from the eastern Tibetan Plateau, covering a wide moisture-balance range (−1287 to +1008 mm). The original modern pollen data are presented in Herzschuh et al. (2009, 2010a), Zhao and Herzschuh (2009), and Kramer et al. (2010a). Site-specific climate information on moisture-balance was obtained from Böhner (2006). Monthly resolution climate estimates (precipitation, temperature, radiation, evapotranspiration) where performed on a regular grid network (3500 × 4000 grid cells) covering the whole of Central and High Asia with a grid-cell spacing of 1 km^2 (Böhner, 2006). The statistical downscaling approach at the core of geospatial climate modelling integrates gridded circulation variables (GCM data, reanalysis series), available station observations (climate records from more than 400 climate stations) and advanced terrain parameterization methods (Böhner and Antonic, 2008) to account for the topoclimatic heterogeneity of Central Asia. A detailed description of the methods used is given in Böhner (2005).

Pollen and spore percentages were transformed to square roots to stabilise variances prior to further computations. Quantitative transfer functions were developed using weighted averaging partial least-squares regression (WA-PLS), one of the most robust techniques for transfer-function development (Birks, 1998). The number of WA-PLS components included was selected as the number producing the lowest root mean square error of prediction (RMSEP), as estimated by leave-one-out cross-validation (ter Braak and Juggins, 1993), along with a high coefficient of determination (r^2) between observed and predicted values, a low maximum bias, and the smallest number of useful components indicated by a decrease of at least 5% in RMSEP toward the lower component number (Birks, 1998). WA-PLS was implemented in C2 1.3 (Juggins, 2003).

We improved the global vegetation model BIOME4 (a coupled biogeographical and biogeochemical including carbon and water-flux model; Kaplan et al., 2003; Song et al. 2005) by re-parameterizing some bioclimatic factors of key plant functional types on the Tibetan Plateau (Ni and Herzschuh, in press). Biomes on the Tibetan Plateau were then simulated with different CO_2 concentrations – 375 (present-day), 260 (early Holocene), and 650 ppm (future scenario) – using the improved BIOME4-Tibet model driven by present-day climate and soil data, Monthly mean temperature, precipitation and sunshine percentages, and minimum temperature were interpolated to 10′ resolution from the 1971 to 2000 averaged meteorological records from 1814 weather stations across China. The soil properties of water-holding capacity and percolation rate were derived from the FAO digital global soil map (FAO, 1995; Kaplan et al., 2003).

The simulation using BIOME4-Tibet (Ni and Herzschuh, in press) has proved that modern biome distribution is in general agreement with the potential natural vegetation. Due to the limited number of vegetation types included in BIOME4, the model cannot differentiate between alpine shrub vegetation and high-alpine *Kobresia* meadows. However, the model initially determines leaf area index (LAI) to infer net primary productivity (NPP) for each given PFT and uses this information together with the climate data to predict biomes. To explore the effects of CO_2 changes we therefore investigated the changes and percentage changes of NPP.

4. Results

4.1. Pollen-based reconstructions

Holocene changes in the *Artemisia*/Cyperaceae (A/Cy) ratio for several pollen records arranged along a gradient from dry to wet sites today are shown in Fig. 2, giving a rough estimate of alpine steppe to meadow variations. The A/Cy values are relatively higher at the dry western sites and lower at the moist eastern sites, a picture that is also seen from modern lake-sediment pollen spectra from the upper eastern Tibetan Plateau (Fig. 1). All fossil pollen records show a significant decrease in the A/Cy ratio by the mid-Holocene due to the widespread expansion of *Kobresia* meadows, especially on the central (Silin Lake, Xuguo Lake) and north-eastern Tibetan Plateau (Koucha Lake).

Table 1
Model performance statistics as assessed by leave-one-out cross-validation of the first three components of the WA-PLS pollen-based moisture-balance transfer functions in terms of RMSEP – root mean square error of prediction (mm), r^2 – coefficient of determination between predicted and observed climate values, maximum (max.) bias (mm) and percentage change in RMSEP toward the lower component model. The selected model is shown in bold.

No. of components	RMSEP	r^2	Max. bias	% change
1	190	0.81	367	–
2	**177**	**0.83**	**250**	**6.8%**
3	180	0.82	265	−1.6%

To estimate what moisture changes these vegetation shifts might reflect, we developed a modern pollen-based moisture-balance transfer function. A two-component WA-PLS model was chosen to be the most parsimonious model on the basis of the model performance statistics (Table 1). Root mean square error of prediction (RMSEP) is 177 mm, coefficient of determination (r^2) is 0.83 between observed and model-predicted values of moisture-balance, and maximum bias is 250 mm. RMSEP, when expressed as a percentage of the gradient, is 6.8%, illustrating the very good performance of the model. Plots of predicted moisture-balance against observed moisture-balance (Fig. 4) and of the residuals against the observed moisture-balance illustrate the robustness of the model over the modern annual moisture-balance range from −1287 to +1008 mm. The plots also indicate that biases are mostly below average for sites with −600 to −400 mm of annual moisture-balance found on the north-eastern and central Tibetan Plateau.

Pollen-based annual moisture-balance inferences (Fig. 5) for Xuguo Lake yield values around −480 mm until ca 6 ka BP followed by an steady increase to ∼−300 mm reached by 3 ka BP. The moisture-balance reconstruction for Koucha Lake generally shows considerable variability. A slight decreasing trend from ∼−400 to −500 mm is found between 11 and 8 ka BP, followed by a moisture increase to ∼350 mm towards the late-Holocene.

4.2. Sensitivity of net primary productivity and biomes to atmospheric CO_2 concentrations

The trends of the BIOME4 model-based NPP prediction for present-day CO_2 levels (375 ppm; Fig. 6) are in good agreement with modern remote-sensing based observations (Piao et al., 2006), i.e. a decrease in NPP from the south-east to north-west. However, the absolute values on the upper Tibetan Plateau, are slightly higher (by ∼50–100 gC/m^2/a) in the model than in the observations, especially in the north-western part. The model-based CO_2 effects on NPP distribution (Fig. 7) are distinct all over the Plateau both for CO_2 lowering from modern to early-Holocene levels (375–260 ppm) and for an increase from modern values to a future scenario (375–650 ppm). NPP is reduced at 260 ppm by >120 gC/m^2/a at moist alpine sites on the south-eastern Plateau, by ∼80 gC/m^2/a in the transition area on the central Tibetan Plateau, and by 30 gC/m^2/a on the north-western Plateau, which indicates a reduction by ∼25%. In the desert area of the Qaidam Basin, and on the north-western Tibetan margin it is lowered by 20 gC/m^2/a and by 60 gC/m^2/a in the surrounding temperate steppe and xerophytic

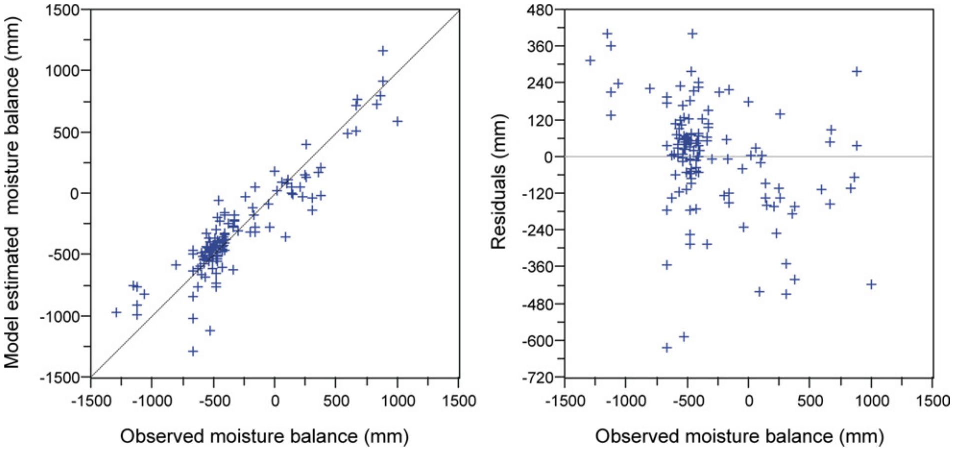

Fig. 4. Moisture-balance model evaluation: Scatter plots of (a) observed annual moisture-balance (mm) vs. weighted averaging partial least-squares regression (WA-PLS) predicted annual moisture-balance (mm); (b) observed annual moisture-balance (mm) vs. residuals (mm) as obtained from a pollen-climate calibration set based on 132 lake-sediment pollen spectra from the Tibetan Plateau.

shrubland, which indicates a NPP reduction of 30–40%. In contrast, positive NPP changes of 30–45% are predicted when CO_2 changes from 375 ppm to 650 ppm CO_2. The NPP in the desert area of the Qaidam Basin almost doubles.

The model-based CO_2 effects on biome distribution on the Tibetan Plateau are rather limited (supplementary online material Fig. a and b). A shift to dry vegetation occurs when CO_2 is changed from present-day (375 ppm) to early-Holocene conditions (260 ppm) with temperate conifer forest, cold mixed forest, and evergreen taiga changing to non-forest in the south, and grassland to shrubland, shrub tundra to steppe tundra, and shrubland to desert and grassland in the north-east and south-east. A trend to more mesic vegetation is found under higher CO_2 (650 ppm) with grassland and shrub tundra changing to conifer and mixed forests in the south, and desert, grassland, and shrubland changing to shrub tundra, and shrubland changing to desert and grassland in the east.

5. Discussion

5.1. Climatic changes are unlikely as the vegetation driver

In most palaeoecological studies from Central Asia it is assumed that climate is the dominant forcing parameter for Holocene vegetation change. Here we examine how several climate parameters could have changed to cause the observed vegetation patterns and how the inferred climatic change fits to earlier non-pollen climate

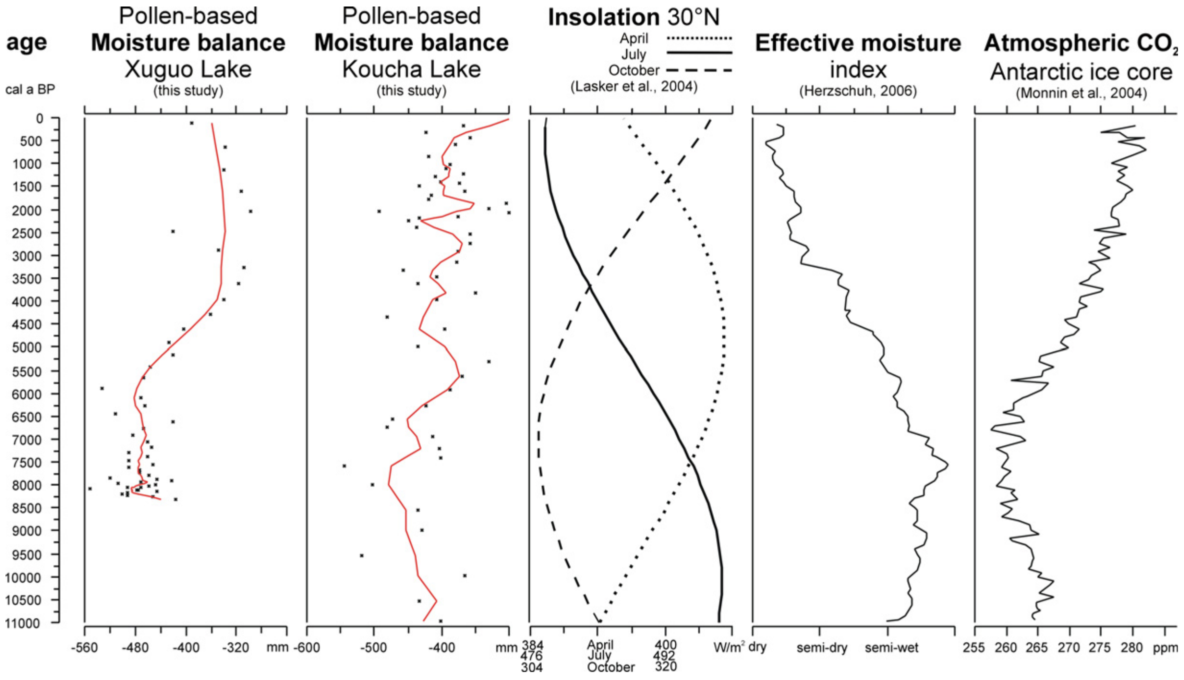

Fig. 5. Quantitative moisture-balance reconstructions based on the transfer functions for Xuguo Lake and Koucha Lake on the Tibetan Plateau. The variation of the curve rather than the absolute deviations from the present level at the sites (Xuguo Lake: −324 mm; Koucha Lake: 470 mm) should be interpreted, as the pollen signal integrates the environmental signal over the entire pollen source area. Implications of the curves would be that either moisture-balance was minimal during the early mid-Holocene (which contradicts most other records from the monsoonal realm – see the effective moisture index of Herzschuh (2006) inferred from a review of proxy records from monsoonal Central Asia) or that low moisture-balance is reconstructed as a result of the expansion of drought resistant vegetation due to the early- to mid-Holocene low atmospheric CO_2 levels. For comparison the Antarctic ice-core CO_2 data and calculated insolation at 30°N for the Holocene are shown.

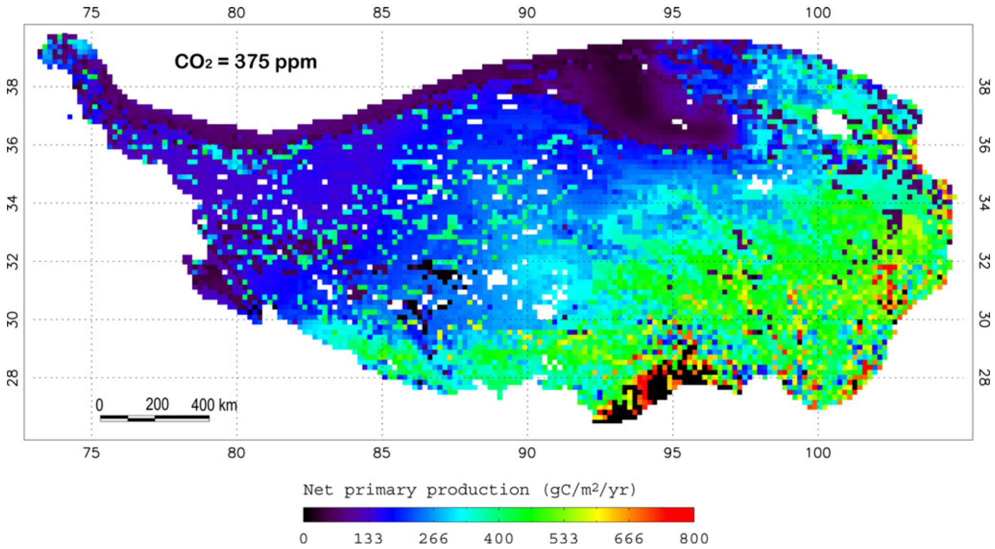

Fig. 6. Distribution of net primary productivity on the Tibetan Plateau as predicted by the BIOME4 vegetation model for current atmospheric CO_2 concentration (375 ppm).

reconstructions from monsoonal Asia. Plant-available moisture is the decisive parameter for vegetation distribution and productivity on the upper Tibetan Plateau (Fu et al., 2009; Yang et al., 2009). Characteristic elements of early-Holocene steppes (*Artemisia*, *Ephedra*) that today dominate the relatively dry north-eastern and north-central Plateau, are well adapted to water limitation as indicated by their high water-use efficiency (i.e. the ratio of carbon gained to water lost in leaf gas exchange), morphology, and chemical leaf traits compared to mesic *Kobresia*-meadows that today occupy comparatively mesic areas on the eastern and southern Plateau (Pyankov and Kondrachuk, 2003; Song et al., 2008). Quantitative moisture-balance reconstructions from Koucha Lake and Xuguo Lake (Fig. 5) have a Holocene minimum of 200 mm below present-day conditions during the early mid-Holocene and an increasing moisture-balance trend thereafter. Hence, pollen-inferred moisture changes from the *Kobresia* meadow-alpine steppe transition area on

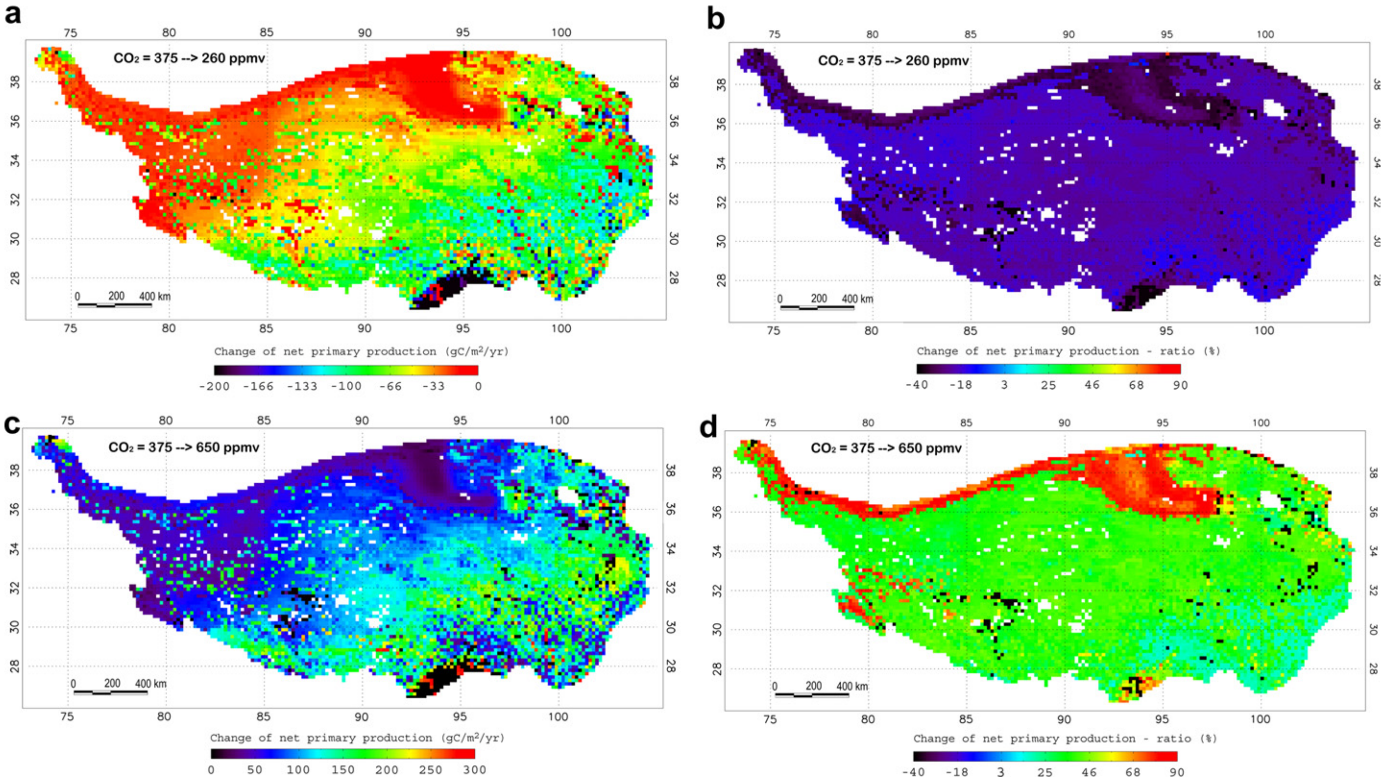

Fig. 7. Results of modelling the sensitivity of Tibetan vegetation to CO_2 changes using the BIOME4 vegetation model. Difference maps of net primary productivity (NPP) and percentage differences (in % relative to NPP at 375 ppm CO_2) for 260 ppm minus 375 ppm CO_2 (early mid-Holocene – modern CO_2 level; a/b) and for 650 minus 375 ppm (future scenario – modern CO_2 level; c/d) are shown. Compared to the modern CO_2 level (375 ppm), NPP is reduced at the early Holocene CO_2 level (260 ppm) but enhanced at the future scenario level (650 ppm).

the upper Tibetan Plateau are in marked contrast to most non-vegetation records from the Tibetan Plateau that indicate a wet first half of the Holocene and a drying trend thereafter, being in line with other high-resolution proxy records from the monsoonal realm and with modelling results (e.g. Zhao et al., 2005; Herzschuh, 2006). Declining moisture is generally interpreted as a response to monsoonal weakening as a result of low-latitude summer insolation decrease. However, vegetation records from rather moist marginal areas at lower altitudes on the Tibetan Plateau (Shen et al., 2005; Herzschuh et al., 2006a; Kramer et al., 2010a) are in line with this general trend. The continuous decline of forest since 6 cal ka BP can be most reasonably explained by a precipitation and/or temperature reduction (Herzschuh et al., 2010c).

Beside precipitation, changing seasonality may have impacted Holocene vegetation on the upper Tibetan Plateau. The annual growing season today extends from May to September and is mainly a function of air temperature (Fu et al., 2009). The total amount of annual insolation was higher during the early-Holocene compared with today. This was proposed to have resulted in the upward shift of temperate steppe-meadow vegetation in continental Asia (Herzschuh et al., 2006b). The insolation sum of the growing season-boundary months, April and October, however, was slightly lower than today during the early-Holocene (Laskar et al., 2004; Fig. 5), indicating that the length of the growing season was not longer. Due to low winter insolation, the soil probably required even more time to thaw in spring and this may have shortened the growing season further.

Field and laboratory investigations on Tibetan alpine vegetation show that carbon gain and biomass production are limited in time by high light intensities, and that the limitation is even exacerbated by high leaf temperature and water stress (Cui et al., 2004). Due to photo-inhibition, a 5% loss in gross primary productivity is modelled for present-day *Kobresia* meadows (Zhang and Tang, 2005). Under clear sky conditions, early-Holocene summer radiation would have been higher than today as a result of higher summer insolation (Fig. 5). However, the influences of radiation on primary productivity of Tibetan vegetation (e.g. reduction of water-use efficiency under strong radiation) are largely dependent on cloudiness (Gu et al., 2003) which is difficult to reconstruct. Greater early- and mid-Holocene cloudiness as a result of an enhanced Indian summer monsoon is modelled by Liu et al. (2004) and Zhao et al. (2005), and is assumed to be a result of high cosmogenic ray fluxes (linked to the earth`s magnetic field) by Knudsen and Riisager (2009). However, whether these effects compensate for the stronger insolation, especially in largely cloud-free areas of the central Tibetan Plateau, is unlikely because neither of the described radiation/cloudiness effects could reasonably explain the relatively high effective moisture at the very beginning of the Holocene compared to the mid-Holocene.

To conclude, precipitation changes and changes in seasonality probably do not account for the wide expansion of steppe vegetation during the early- or mid-Holocene. Variations of Holocene radiation effects on vegetation are still largely unknown.

5.2. Holocene land-use changes unrelated to expansion of Kobresia meadows

Miehe et al. (2009) hypothesised that the present-day *Kobresia*-dominated high-alpine meadows as a whole represent largely an artificial vegetation complex resulting from anthropogenic land-use practices reaching back to 8.8 cal ka BP. In support of this hypothesis, there is growing evidence from different marginal areas of the Tibetan Plateau that herding of domesticated yak started sometime during the early- or mid-Holocene (Guo et al., 2006; Dearing et al., 2008; Meyer et al., 2009). However, wide-spread, intensive, and persistent human land-use is not documented by archaeological evidence: although there exists a number of late-Pleistocene sites, only one archaeological site (Xidatan 2 from the Kunlun Mountains at the northernmost Plateau margin) of Epi-Palaeolithic culture has been found on the upper (>3500 m) Tibetan Plateau from 11 to 3.7 ka BP (Aldenderfer and Zhang, 2004; Brantingham and Gao, 2006; Brantingham et al., 2007). Chugong (5 km north of Lhasa, 3680 m a.s.l.), is the only Neolithic site in the present-day *Kobresia* meadow or alpine steppe area that provides evidence for year-round occupation on the upper Plateau. It is dated to ~3.7 cal ka BP (Aldenderfer, 2007). This observation is roughly in line with the marked increases of grazing indicators by 3.4 cal ka BP in a lake pollen record from the south-eastern Tibetan Plateau (Kramer et al., 2010a) and with increases of grazing indicators by 2.2 cal ka BP in a peat record from the eastern Tibetan Plateau (Schlütz and Lehmkuhl, 2009). The differentiation between natural-zoogenic and anthropo-zoogenic grazing from pollen records remains very problematic (Miehe et al., 2009), especially when interpreting the very local palynological information from peat and soil sequences. Such very local sequences are inappropriate archives of regional grazing intensity (Jacobson, 1988). Modern vegetation studies involving exclosure experiments (Miehe et al., 2008; Wu et al., 2009), show that (1) fencing promotes the expansion of Poaceae, (2) *Kobresia* is still the dominant element of ungrazed meadows, and (3) *Artemisia* is favoured rather than replaced by grazing. This is in clear contrast to the fossil pollen record as (1) Poaceae shows no trend during the Holocene in regional pollen records (e.g. Zigetang Lake, Herzschuh et al., 2006b; Koucha Lake, Herzschuh et al., 2009); (2) *Artemisia* declines, and (3) *Kobresia* expands after the onset of proposed anthropo-zoogenic grazing. Evidence for *Kobresia* meadows being a natural element on the Tibetan Plateau is indicated by >80% Cyperaceae in lake pollen assemblages of Lateglacial (Allerød) age, indicating the widespread occurrence of *Kobresia* meadows on the south-eastern and north-eastern Tibetan Plateau under cool and wet climate conditions (Herzschuh et al., 2006a; Kramer et al., 2010b). Still, due to the impossibility of differentiating *Kobresia* pollen morphologically from other Cyperaceae we cannot be absolutely sure that it was *Kobresia* that expanded during the Lateglacial. However, the composition of the Lateglacial high-alpine meadow at Naleng Lake e.g. the co-occurrence of *Polygonum bistorta*-type and *Swertia* (Kramer et al., 2010b) is very similar to modern *Kobresia* meadow pollen assemblages.

To conclude, the extent and timing of anthropogenic land-use on the upper Tibetan Plateau and its possible impacts on high alpine vegetation are still mostly unknown. However, it is unlikely that modern *Kobresia* meadows are mainly of artificial origin.

5.3. Changes in atmospheric CO_2 concentration as the driving force of vegetation change

Partial CO_2 pressure decreases strongly with altitude while the molar CO_2 concentration in air remains constant. Earlier plant physiological modelling studies concluded that the pressure reduction is largely mitigated by physical mechanisms such as faster molecular gas diffusion and parallel lowered O_2, which competes with CO_2 at the Rubisco reaction site (Terashima et al., 1995). However, experimental investigations have shown that the photosynthetic capacity of upland population increases to the same extent as the partial CO_2 pressure is artificially raised (Körner and Diemer, 1987; Bresson et al., 2009). Transferred to the central Tibetan Plateau (~4500 m), this finding implies that alpine vegetation suffers from 40% lower carbon availability compared to sea-level. However, the photosynthetic capacity of alpine plants is not correspondingly lowered, probably as a result of physiological adaptation and acclimation, thereby accepting higher energetic costs to compensate for the low efficiency of physiological processes at high altitudes (Reich and Oleksyn, 2004). High-alpine plants have high leaf nitrogen concentrations indicating lower plant nitrogen-use efficiency (for the Tibetan Plateau, see He et al., 2006) and low water-use efficiency (Körner et al., 1988; for Tibetan Plateau, see Wei and Jia, 2009). Thus plants with xeromorphic leaf anatomies such as increased stomatal densities (Pyankov and Kondrachuk, 2003) are at a competitive advantage. Hence, the central physiological adaptations to dry ecosystems and to high altitudes (i.e. low leaf nitrogen-use efficiency and high water-use efficiency) are similar and such adaptations are demonstrated in gradient studies of Tibetan vegetation (He et al., 2006; Wei and Jia, 2009). Experimental and modelling investigations have shown that plant-growth response to elevated CO_2 concentrations is amplified in vegetation types with high nitrogen but limited water supply (Nowak et al., 2004; McMurtrie et al., 2008). Hence, Tibetan vegetation composition, especially on comparatively high and dry sites, might be especially sensitive to lowering of CO_2 concentration as the adaptive capacity of single plant taxa may then be exceeded.

According to Antarctic ice-core records (Indermühle et al., 1999; Monnin et al., 2004), Holocene CO_2 concentrations were comparatively high between 11 and 10 ka, decreased during the early-Holocene, showed a minimum at less than 260 ppm around 7000 a, increased afterwards to pre-industrial levels of 285 ppm (Fig. 5), and then increased to present-day values of ~375 ppm that are markedly above early- or mid-Holocene conditions. Hence, minimum CO_2 concentrations correlate with the maximum expansion of low-biomass and drought-resistant alpine steppe vegetation on the Tibetan Plateau. Furthermore, our CO_2 sensitivity studies confirm that a CO_2 increase from early-Holocene to present-day levels strongly enhances NPP on the Tibetan Plateau, reducing the expansion of low-biomass and drought-resistant vegetation.

Even though the trends of vegetation-inferred moisture-balance parallel CO_2 concentration changes well and vegetation modelling results confirm that the lowering of CO_2 concentration to early-Holocene levels markedly reduces the NPP of Tibetan vegetation, four questions remain open that need to be answered before CO_2 concentrations can be proposed as a main driving force for Holocene vegetation change:

(1) Do modern CO_2 fertilization experiments indicate that water-limited alpine vegetation, such as Tibetan steppes and meadows, are especially vulnerable to CO_2 concentration changes? CO_2 enrichment studies from the Tibetan Plateau or from other high-alpine steppe vegetation are completely lacking. However, there is growing evidence that water-limited grassland vegetation is amongst those vegetation types that show the strongest positive reactions to CO_2 enrichment, especially due to reduced water consumption (Nelson et al., 2004; Niklaus and Körner, 2004). The few free-air enrichment studies performed at (water-saturated) alpine sites yielded no amplification of CO_2 enrichment due to low CO_2 pressure (Körner et al., 1997). However, comparison of CO_2 enrichment effects to pairs of a lowland and an upland species yielded a stronger biomass increase for the upland species (Körner and Diemer, 1994; Olivo et al., 2002), indicating that upland vegetation is more vulnerable to CO_2 concentration changes.

(2) Can changing CO_2 account for species turnover as has been inferred for the mid-Holocene on the Tibetan Plateau? Species shifts in grasslands as a result of CO_2 fertilization have been reported by many authors (e.g. Potvin and Vasseur, 1997; Niklaus et al., 2001). A CO_2 enrichment experiment on dominant species from the North American sagebrush steppe showed that water-use efficiency of grass species (*Stipa*, *Elymus*) increased more strongly than for *Artemisia* (Lucash et al., 2005). This is in agreement with the review of Ainsworth and Rogers (2007) on the reaction of different plant functional types to CO_2 enhancement that suggested that, on average, grasses were twice as strongly stimulated by CO_2 enhancement as shrubs. An extensive enrichment study of a calcareous seasonally water-limited grassland dominated by *Bromus* (Poaceae) and *Carex* spp. (Cyperaceae) probably represents the best vegetation analogy to alpine Tibetan vegetation (Niklaus and Körner, 2004). This study showed that biomass gains were disproportionately large for mesic *Carex* species and were mainly indirectly caused through water savings. It was concluded that the increase of soil moisture was the major effect of elevated CO_2 and this was translated to various characteristics of the ecosystem. By analogy, the increase of soil moisture as a result of lower water consumption during the early- to mid-Holocene on the Tibetan Plateau may have promoted the expansion of mesic *Kobresia* at the expense of xeromorphic shrubby *Artemisia* while the abundance of intermediate Poaceae was unaffected.

(3) Can the absolute values in moisture and biomass change largely be explained by the relatively small pre-industrial Holocene CO_2 concentration variations? The global CO_2 increase of 25 ppm between 6 and 1 cal ka BP is paralleled by a leaf-area increase of ~20% on the Tibetan Plateau (Herzschuh et al., 2010b) assuming a moisture-balance increase by ~30%. Free-air CO_2 treatment of a natural C3 steppe (with a total CO_2 gradient between 250 and 550 ppm) showed a biomass increase of ~20%, a water-use efficiency increase of ~40%, and a soil water content increase of ~15% for a CO_2 concentration increase from 260 to 285 ppm (Fay et al., 2009). These investigations indicate that the Holocene vegetation changes are in the same order of magnitude as experimental results though the latter neglected acclimation and long-term effects (Arp, 1991). Furthermore, our CO_2 sensitivity study indicates that NPP is lowered at 260 ppm atmospheric CO_2 by as much as ~25% in the moist tundra–steppe tundra transition zone of the Central Tibetan Plateau compared to present-day CO_2 concentrations.

(4) Has the modern global CO_2 fertilization affected Tibetan vegetation during recent decades? Sophisticated remote-sensing studies show that increasing biomass in North America is related to the direct fertilization effect of increasing atmospheric CO_2 concentration (e.g. Lim et al., 2004). Increases in biomass and NPP during recent decades are also found by several remote-sensing studies (partly with ground-truthing) from the Tibetan Plateau but with strong regional differences. Grassland biomass changes are not or only moderately correlated to meteorological variables such as increasing temperature, increasing precipitation, and decreasing evapotranspiration (Chu et al., 2007). NPP prediction of a carbon model driven with NDVI data (Normalised Difference Vegetation Index – a measure of standing biomass) for 1982–1999 indicates that the strongest increase in NPP occurred in high-alpine meadows in the period from 1992 to 1999 (Piao et al., 2006). Furthermore, in an investigation of biomass changes from 1981 to 2001 in the Tibetan Autonomous Region (Zhang et al., 2007a,b), the strongest NDVI increase was found in the transition area from *Kobresia* to steppe vegetation (roughly 87°–93°E; 30°–33°N, comprising Xuguo Lake area) despite a population density increase of 23% from 1989 to 2002. The results from all these studies are further indications that the transition from steppe to meadow on the Tibetan Plateau could be partly driven by CO_2 concentration changes.

Our results indicate that Holocene CO_2 changes should be taken into account when vegetation records are interpreted in terms of either climate or land-use changes. However, our study design is not appropriate to draw firm conclusions about the influence of Holocene CO_2 variations on Tibetan vegetation change. We have considered the potential of single factors to trigger changes in upper Tibetan Plateau vegetation from a theoretical perspective. Furthermore, we have restricted our investigation to the transition area between alpine steppe and high-alpine meadows and do not extend our hypothesis to other vegetation types. Pollen-based inverse vegetation modelling (Guiot et al., 2008) may help to overcome some of the limitations in our study design. However, for that purpose the vegetation models first need to be adjusted for specific Tibetan vegetation types and probably also for altitudinal effects on photosynthesis and human land-use changes.

5.4. Implications of a strong CO_2 sensitivity of Tibetan vegetation for future global change

According to this CO_2 hypothesis, the expansion of *Kobresia* was promoted by globally increasing CO_2 concentrations from 7000 years ago mainly due to the effects of fertilization and improved water economy. In contrast to the hypothesis of Ruddiman (Ruddiman, 2003; Ruddiman and Ellis, 2009), Elsig et al. (2009) assigned the early-mid Holocene CO_2 changes to ocean carbon release but at least the CO_2 increase during the last centuries is of anthropogenic origin (Friedli et al., 1986). Independent of the cause of CO_2 increase, because of its dryness and probably also due to its high-elevation, the Tibetan Plateau was probably among the first ecosystems that responded to these greenhouse-gas increases. A stabilisation at 650 ppm CO_2 concentration after 2100 is one that was investigated in the context of IPCC (2007). Experimental treatment of vegetation with increased CO_2 concentration yields higher biomass production in natural water-limited grassland and desert ecosystems (Morgan et al., 2004). Steppe-*Kobresia* meadow transition areas on the central Tibetan Plateau that are probably most sensitive to CO_2 changes, are likely to turn into *Kobresia* meadows which would act as a carbon sink. Our results from vegetation modelling of the Tibetan Plateau with 650 ppm prescribed CO_2 yields a strong increase in NPP all over the Tibetan Plateau (Fig. 7d). The relative increase is particularly high in the desert areas of the Qaidam Basin and in Central Tibet. However, the responses of other global change-related climatic parameters, especially temperature, precipitation, and cloudiness, and changing human impact will almost certainly modify the vegetation response to changing atmospheric CO_2 concentrations. An experimental doubling of CO_2 at a *Kobresia* meadow site enhanced the apparent quantum-use efficiency of vegetation though the strength of the increase is dependent on a related climate change (Xu et al., 2007). An earlier modelling study revealed that CO_2 enhancement together with a warmer and a more humid climate would cause an increase in NPP (Ni, 2000). Investigations show that soil carbon and nitrogen cycling in a grassland ecosystem are much more responsive to increases in the past than to those predicted for the coming century (Gill et al., 2002). Körner (2006) pointed out that the relative influence of any given increment of CO_2 concentration declines with the absolute concentration which is confirmed by our modelling results which similarly do not show a linear relationship.

6. Conclusions

Numerous pollen records from across the upper Tibetan Plateau indicate that *Kobresia*-dominated high-alpine meadow invaded alpine steppes during the mid- to late-Holocene. However, our investigation using a pollen-moisture transfer function yielded that this marked vegetation change cannot be satisfactorily explained by climate change. A literature review did not reveal convincing evidence for any widespread human impact on mid-Holocene vegetation. Here we propose that the vegetation changes can, at least partly, be interpreted as a response to Holocene CO_2 concentration changes. Our theoretical argument is based on the findings that high-elevation vegetation is particularly sensitive to CO_2 changes due to lowered CO_2 partial pressure; that water conservation of steppe vegetation in response to experimental CO_2 enrichment was of the same order of magnitude as inferred from mid-to late Holocene Tibetan pollen records, and that modern remote sensing-aided vegetation monitoring of the Central Tibetan Plateau yielded an increase in biomass, most probably as an response to modern CO_2 increase, despite increasing land-use by herding.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.quascirev.2011.03.007.

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