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Considering the autogenic processes of the ecosystem to analyze the sensitivity of peatland carbon accumulation to temperature and hydroclimate change

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ABSTRACT

Peatland carbon accumulation plays a vital role in the global carbon pool and climate change dynamics. However, understanding how peatland carbon accumulation responds to climate change is challenging due to the influence of autogenic processes on carbon dynamics. In this study, we investigate the temporal variations of the Non-autogenic Carbon Accumulation Rate (NCAR) over approximately 1500 years in a peatland located in the Amur River Basin. To remove the effects of autogenic processes, we use conceptual models of peat development and employ plant macrofossils to identify vegetation changes, particularly the fen-bog phase transition. We apply different exponential decay models to capture autogenic processes in the fen and bog phases of the peatland. Subsequently, we analyze the sensitivity of peatland carbon accumulation to temperature and hydroclimate changes in the fen and bog phases, respectively. Our findings show that in the fen phase, higher temperature increases plant litter decomposition more than the plant net primary productivity (NPP) when water content is high, leading to lower NCAR. However, as temperature rises and water content is no longer a limiting factor, plant NPP surpasses plant litter decomposition, resulting in high NCAR. In the bog phase, we find no significant correlation between NCAR and precipitation but observe a positive relationship between NCAR and temperature. These results enhance our understanding of the connections between temperature, moisture, and peatland carbon accumulation by considering the influence of autogenic processes.

1. Introduction

Peatlands hold a significant amount of global soil carbon, estimated at around 30 % (Gorham, 1991; Page et al., 2011; Yu et al., 2010), making them crucial components of the global carbon cycle and important actors in the dynamics of climate change (Leifeld and Menichetti, 2018). The development of peatlands involves internal processes, known as autogenic processes, which can complicate the interpretation of peat records. Specifically, the lower layers of peat exhibit slower decay rate and longer decomposition times compared to the upper layers (Clymo, 1984). These autogenic processes can obscure climatic signals in the peat records, leading to a disconnect between peatland behaviour and climate (Morris et al., 2015). Consequently, when calculating past apparent Carbon Accumulation Rates (aCARs) in peatlands, the derived rates often deviate from the true carbon balance, which represents the

actual carbon gain or loss during a specific period (Young et al., 2021). Unfortunately, this issue has been insufficiently addressed by researchers utilizing the concept of carbon accumulation.

A range of conceptual models have been developed to enhance our understanding of peatland formation and peat accumulation processes. Clymo's Bog Growth Model (BGM) is one such model which assumes that the rate of peat addition (PAR) and peat decay (α) remain constant throughout the development of a bog. This generates a cumulative peat mass-age curve with a concave shape, reflecting the balance between peat production and decomposition. This means that as the time interval from the present increases, the peat mass-age curve becomes smoother due to prolonged peat decomposition. While Clymo's model is a relatively simple one which can be applied to all bogs, it may overlook certain influencing factors. Since being introduced in 1984, Clymo's model has been widely used to simulate peat development (Bunsen and

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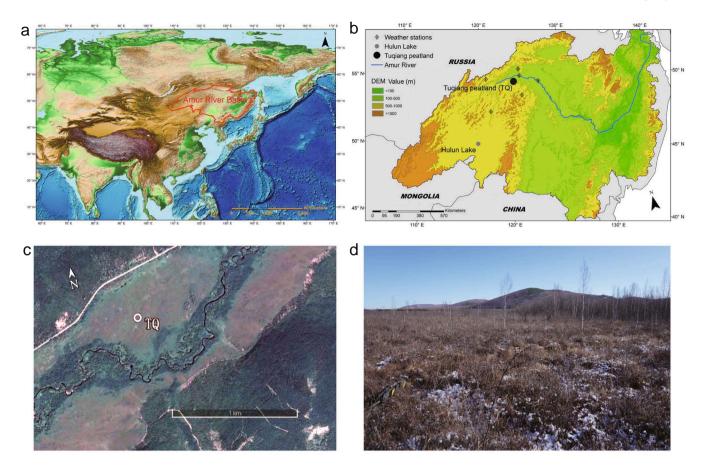


Fig. 1. Location maps and study site. (a) The topographic map was downloaded from https://ngdc.noaa.gov/mgg/global/relief/ETOPO1/image. (b) Topographic map of the Amur River Basin. The digital elevation model obtained from the Global Change Science Research Data Publishing System (Huang et al., 2017). This map illustrates the location of the Tuqiang peatland (TQ) and the local weather stations within the Basin. (c) The remote sensing image of the Tuqiang peatland, obtained from Google Earth, provides a visual representation of the peat core location. (d) Photo of the study site, capturing the view towards the north from the peat core location.

Loisel, 2020; Charman et al., 2013; Frolking et al., 2010; Gorham et al., 2012) and has also been adapted for fen development (Yu et al., 2003). However, while bogs have concave peat mass-age curves, fens display convex patterns, mainly due to a decrease in PAR. For instance, studies on Muskiki Fen in Alberta, Canada, and a fen in north-central Finland have shown convex peat mass-age curves (Kubiw et al., 1989; Mäkilä et al., 2001). In these cases, the shorter the time interval from the present, the smoother the peat mass-age curve, resulting in a convex shape. To address this, a PAR modifier was introduced into Clymo's model, permitting exponential changes in PAR which allowed for autogenic processes to be accounted for (Yu et al., 2003). Non-autogenic Carbon Accumulation Rates (NCAR) of each peat core were expressed as the deviations between aCARs and carbon accumulation rates derived from these models (Charman et al., 2013; Liu et al., 2019).

The carbon accumulation in peatlands is influenced by a delicate balance between plant carbon uptake and microbial respiration. The impacts of temperature and precipitation on these processes remain incompletely understood, and it remains uncertain which of these effects will dominate peatland response (Gallego-Sala et al., 2018; Loisel et al., 2021). This uncertainty elevates the importance of peatland carbon dynamics in climate projections (IPCC, 2014). Previous studies have generally suggested that elevated temperatures can promote carbon accumulation and peatland expansion on both a broad scale, such as in the Northern Peatlands (Charman et al., 2013; Yu et al., 2010), and regionally in Western Siberia (Smith et al., 2004), Central-eastern Europe (Longman et al., 2021), Alaska (Jones and Yu, 2010), South America (Loisel and Yu, 2013a), and Northeast China (Wang et al.,

2014; Zhao et al., 2014). The positive correlation between temperature and carbon accumulation in these regions may result from the elevated plant productivity under warmer temperatures (Jones and Yu, 2010; Morris et al., 2018). However, other studies have presented evidence suggesting that increased temperatures may lead to lower water levels in peatlands, thereby reducing the rate of carbon accumulation throughout the pan-Arctic region (Chaudhary et al., 2020; Zhang et al., 2020). Precipitation patterns also play a vital role in shaping peatland development, as changes in water levels significantly impact vegetation growth. Therefore, the synergistic influences of temperature and precipitation on non-autogenic carbon accumulation in peatlands should be further investigated.

This study utilized a well-dated, high-resolution carbon accumulation record derived from a fen-bog shift peatland situated in the Amur River Basin. By applying peat development models, we examined non-autogenic carbon accumulation in response to long-term climate variations. The study had two main objectives: (1) to reconstruct the autogenic processes occurring during different stages of peatland development, and (2) to establish links between observed changes in non-autogenic carbon dynamics and temperature as well as precipitation patterns. Through investigating the relationship between carbon accumulation and climate change, we aimed to evaluate the magnitude and direction of the future global carbon cycle feedback, while considering the ecosystem's autogenic processes.

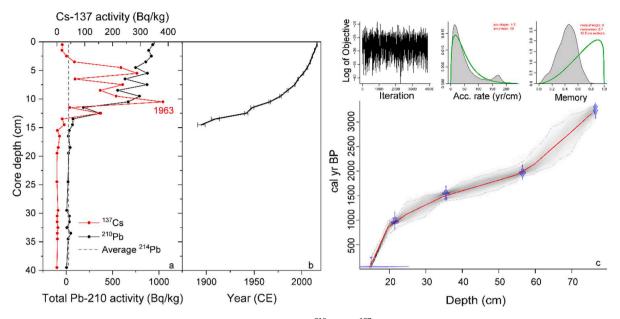


Fig. 2. Age-depth model for Tuqiang peat core over the past 3000 years. (a) ²¹⁰Pb and ¹³⁷Cs (red line) specific radioactivities of Tuqiang core. The dash line represents the average ²¹⁴Pb radioactivities. (b) The above 15 cm age-depth frame was derived from ²¹⁰Pb specific radioactivities by applying the constant rate of supply (CRS) model. (c) AMS ¹⁴C constructed the age-depth frame of 16–77 cm. The upper panels depict the Markov Chain Monte Carlo (MCMC) iterations (left, good runs show a stationary distribution with little structure among neighbouring iterations), the prior (green curves) and posterior (grey histograms) distributions for the accumulation rate (middle panel) and memory (right panel). The bottom panel shows the calibrated ¹⁴C dates (transparent light blue) and the age-depth model (grey stippled lines represent 95 % confidence intervals, and the red curve shows a single 'best' model based on the weighted mean age for each depth interval).

2. Materials and methods

2.1. Study site and fieldwork

Tuqiang peatland (52.94296°N, 122.85485°E), located in the Amur River Basin in northeastern China, serves as a representative example of a northern peatland with an elevation of 477 m above sea level (m a.s.l.) (Fig. 1b). The Amur River Basin is among the few accessible regions in East Asia (Fig. 1a) that host a substantial number of peatlands and is characterized by a cold temperate continental monsoon climate, featuring short, warm, wet summers, and long, cold, dry winters (Liu et al., 2019). The annual mean temperature in the area is -4.16 °C, and the average annual precipitation is approximately 469 mm, based on data from the nearest weather station in Huzhong.

The Tuqiang peatland, occupying approximately 0.75 km², is situated in a valley within the upper Amur River region (Fig. 1c). The vegetation in the peatland is primarily composed of *Ericaceae*, with *Vaccinium uliginosum* being the dominant species (Fig. 1d). *Sphagnum* moss is also prevalent, alongside other species such as *Betula fruticosa*, *Ledum palustre*, *Salix rosmarinifolia*, *Eriophorum vaginatum*, *Sanguisorba tenuifolia*, *Saussurea japonica*, *Smilacina trifolia*, and *Deyeuxia angustifolia*. In the surrounding upland vegetation, *Larix gmelinii* and *Betula platy-phylla* are the dominant tree species. By considering micro-landform observations and nutrient sources, it has been established that the peatland is presently classified as a bog.

In November 2016, a peat core was extracted from the central area of Tuqiang peatland. Monoliths ($20 \times 20 \times 40~\text{cm}^3$) were collected for the uppermost sections (up to 40 cm) using an iron shovel and a hacksaw. To retrieve the permafrost layers (41–77 cm), percussion drilling techniques were employed. Subsequently, the peat sediments from the 1–40 cm depth were sliced at 1-cm intervals on site using a stainless-steel knife, while those from the 41–77 cm depth were divided at 5-cm intervals. A total of 47 samples were collected and transported to the laboratory for further analysis.

2.2. 210 Pb/ 137 Cs and 14 C dating

The chronology of the Peat core was established using Accelerator Mass Spectrometry (AMS) radiocarbon (¹⁴C) dating, ²¹⁰Pb dating, and a ¹³⁷Cs time-marker (Fig. 2). The AMS dating involved nonaquatic plant macrofossils, which were carefully selected and cleaned with distilled water. The samples were sent to the Poznań Radiocarbon Laboratory in Poland, and the results were given in years before the present (BP), where "present" is defined as the year 1950 Common Era (CE). Bayesian age-depth modeling was conducted using OxCal v4.2.2 and a Poisson-process (P-sequence) single depositional model at 1-cm increments, with a K value of 100 to produce the age-depth model (Blaauw and Christen, 2011).

The ²¹⁰Pb and ¹³⁷Cs measurements were performed using low background gamma spectroscopy (ORTEC Instruments Ltd., USA) at the Analysis and Test Center of the Northeast Institute of Geography and Agroecology of the Chinese Academy of Sciences. The age-depth framework was constructed using the Constant Rate of Supply (CRS) model based on the specific radioactivities of unsupported ²¹⁰Pb (Appleby and Oldfield, 1978). The radionuclide ¹³⁷Cs reflects nuclear tests and leaks worldwide, with a notable peak in 1963 CE (Robbins and Edgington, 1975). The specific radioactivities of ¹³⁷Cs were plotted against depth to calibrate the CRS dating model.

2.3. Plant macrofossils identification and statistics

The peat sub-samples were subjected to a thorough washing process using a powerful water jet through a sieve with a mesh size of 125 $\mu m.$ Prior to this, the percentage of Unidentifiable Organic Matter (UOM) in the total sample by volume was estimated. The remaining residue was carefully examined under a stereomicroscope at magnification of 7.3–120×, and in some cases, 400× was utilized for better visibility. By using a 10 \times 10 square grid salver, the relative abundance of each macrofossil type and plant species was assessed for each depth interval, following the methodology outlined in Barber et al. (1994).

To establish ecological community zones, the constrained incremental sum of squares (CONISS) cluster analysis was employed, utilizing

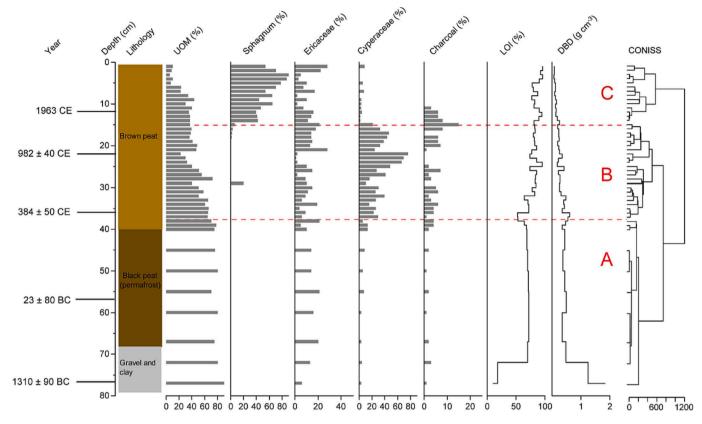


Fig. 3. Stratigraphic profile showing the relative abundances of plant macrofossils from the Tuqiang peatland, along with the sediment units, Loss On Ignition (LOI), and Dry Bulk Density (DBD) measurements of the peat core. The total sum of squares results from the cluster analysis (CONISS) and three main zones (A/B/C, separated by the red lines) identified in the plant macrofossils data. The boundary between Zone B and C was considered to be the depth of transition from fen to bog. UOM stands for the Unidentifiable Organic Matter. The different colours of the rectangular column on the left represent the changes in lithology.

the R function 'chclust' (Grimm, 1987). In order to minimize the impact of abundant species on the analysis, the plant data from Tuqiang peatland were subjected to Hellinger transformation. Principal component analysis (PCA) was then conducted to extract the scores of the first principal component (PC1) from the ecological communities, capturing the most important information regarding the community compositions.

2.4. Carbon measurements and modelling

Volumetric peat samples, measuring 17 cm³, were collected using an aluminum specimen box. These samples were then dried at 105 °C for 12 h to determine their Dry Bulk Density (DBD), which is the ratio of dry weight to volume. A portion of dried subsamples was combusted at 550 °C in a muffle furnace for four hours to measure the Loss On Ignition (LOI), which provides an estimate of Organic Matter content (OM) (Craft et al., 1991). To calculate the Organic Carbon content (OC), the OM was multiplied by 50 % (Chambers et al., 2011). Based on the chronologies and the measured DBD (g cm $^{-3}$) and OC (%), the peat aCAR was calculated as:

$$aCAR = \frac{h}{t} \times DBD \times OC \times 100 \tag{1}$$

where h (cm) is the thickness of the peat during time t (yr).

To assess carbon accumulation on decadal and centurial scales, it is important to identify the boundary between the acrotelm (upper, more aerobic layer) and the catotelm (lower, more anaerobic layer). The acrotelm is exposed to oxygen and therefore experiences higher rates of decomposition compared to the catotelm. The long-term maximal depth of the summer water table, which reflects the maximum depth of oxygenated conditions, is commonly used to define this boundary (Ingram, 1982). The water level was measured under steady-state

conditions using a meter ruler subsequent to the peat core drilling. Carbon accumulation was then computed exclusively for the catotelm layer.

Assuming a constant PAR (g cm $^{-2}$ yr $^{-1}$) driven by plant NPP and a constant peat decay coefficient (α , yr $^{-1}$), the following exponential decay model was used to represent the autogenic peat decomposition process of the bog:

$$M = \frac{PAR}{\alpha} \times (1 - e^{-\alpha t}) \tag{2}$$

where M is the cumulative peat (g cm $^{-2}$) at time t (yr) (Clymo, 1984). The PAR and α of the peat core were evaluated using a curve-fitting procedure. We adapted this approach to model the catotelm only. As the PAR and α of the fen and bog are different, the PAR and α of the fen can change over time. PAR is more sensitive to the vegetation type and environmental conditions involved than the α in the fen. Following a suggestion by Clymo, Yu et al. (2003) added a PAR modifier to model (2). Thus, the extended model is:

$$M = \frac{PAR}{\alpha - b} \times (e^{-bt} - e^{-at}) \tag{3}$$

where b is the coefficient of the PAR modifier. The estimated values for PAR, α , and b were used to derive the model CAR. Changes in Non-autogenic Carbon Accumulation Rate (NCAR) (Charman et al., 2013) for the peat core were expressed as differences between observed accumulation rates and those derived from models (2) and (3).

2.5. Regression models

Generalized Additive Models (GAMs) is a type of regression model

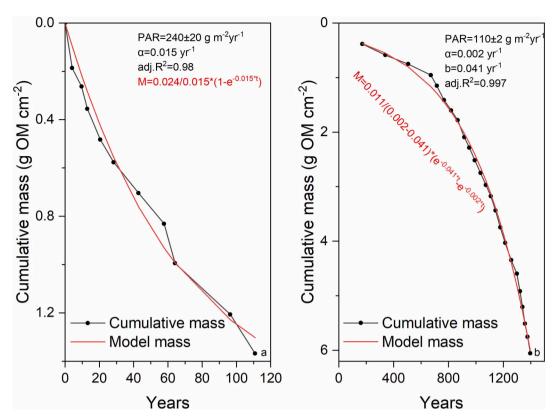


Fig. 4. Cumulative peat mass and exponential decay model of the bog (a) and fen (b) phases within the Tuqiang peatland ecosystem. The black dots represent the cumulative peat mass during different years, and the red lines represent the fitted model's results. Here the focus was only on the peat sediments above the permafrost used to do fitting, spanning the past ~ 1400 years.

that utilizes smoothing splines instead of linear coefficients for covariates (Hastie and Tibshirani, 1986). The aim of using GAMs is to establish the connection between NCAR and climate factors in the Amur River Basin. The reconstructed century-scale precipitation and temperature data are derived from Wen et al. (2010). Meteorological data from the National Oceanic and Atmospheric Administration (NOAA) databases were obtained to calculate the temperature and precipitation in the study area over the past century. This involved incorporating data from multiple weather stations (Nerchinskij Zavod, Mogoca, Dzalinda, Skovorodino, Chernjaevo, and Huzhong weather stations) in the region (Fig. 1b). GAMs were subsequently employed to analyze the correlations between NCAR and climate factors, specifically temperature and precipitation. The ultimate model was selected based on the lowest Akaike information criterion (AIC).

3. Results

3.1. Core lithostratigraphy and chronology

The Tuqiang peat core retrieved from the Amur River Basin was visually categorized into three distinct sedimentary units (Fig. 3). The uppermost unit, spanning 0–40 cm, consisted of brown peat. In contrast, the second unit (41–67 cm), which belonged to the permafrost layer, was primarily composed of dark brownish peat. The bottom unit (68–77 cm) comprised gravel and clay, also within the permafrost layer.

The basal age of the Tuqiang core was determined to be 3260 \pm 97 cal yr BP, with peat accumulation starting around 2619 cal yr BP (at 66.5 cm into the core). There was a total of four ^{14}C ages obtained from the 77 cm core, yielding an overall accumulation rate of 0.24 mm/yr. However, there was a notably lower mean peat accumulation rate of 0.08 cm/yr between depths of 14.5 and 21.5 cm.

Analytical accuracy of 137 Cs and 210 Pb in this study was determined within a depth range of 1–20 cm, with a resolution of 1-cm. The total

 ^{210}Pb specific activities portrayed an exponentially decreasing trend with depth and reached relatively stable values around 15.5 cm below the core, and no measurable radioactivity was detected at a depth of 17 cm. Consequently, measurements beyond 20 cm were less frequent and primarily aimed at confirming the attainment of radioactive equilibrium. The average value of ^{214}Pb (supported ^{210}Pb) specific activities was 25.8 Bq/kg (Fig. 2). Thus, the bottom depth of the ^{210}Pb age-depth framework is 14.5 cm, corresponding to the year 1895 \pm 4 CE, derived from the CRS model. The age at 14.5 cm and the four ^{14}C ages were used to create a Bayesian age-depth model chronology. Thus, the age framework from a depth of 14.5 to 76.5 cm was constructed by ^{14}C ages. The highest ^{137}Cs specific activity appeared at 10.5 cm, and the highest ^{137}Cs specific activity was marked during 1963 CE, aligning with the age constructed by the ^{210}Pb CRS model.

3.2. Past vegetation change

In the Tuqiang core, the macrofossil results revealed substantial variations in the relative abundance of *Sphagnum* and *Cyperaceae* (Fig. 3). These two dominant species exhibited varying levels of abundance, ranging from absence to as high as 90 %, with occasionally peaks reaching 76 %.

Zone A (1250 BCE–350 CE, 77–38 cm) exhibited abundant UOM levels, reaching up to 90 %. The presence of *Ericaceae* accounted for approximately 21 %. *Sphagnum* was absent in this zone, while the abundance of *Cyperaceae* remained low, peaking at a maximum of 13 % around 1600 cal yr BP. Charcoal formation was minimal within this zone.

In contrast, Zone B (350–1895 CE, 38–15 cm) witnessed an increase in the abundance of *Cyperaceae*, becoming the most dominant species with fluctuations between 10 % and 76 %. UOM abundance decreased from 70 % to 37 %, while charcoal formation increased to 15 %. *Ericaceae* displayed fluctuations between 1 % and 28 %, with a noticeable

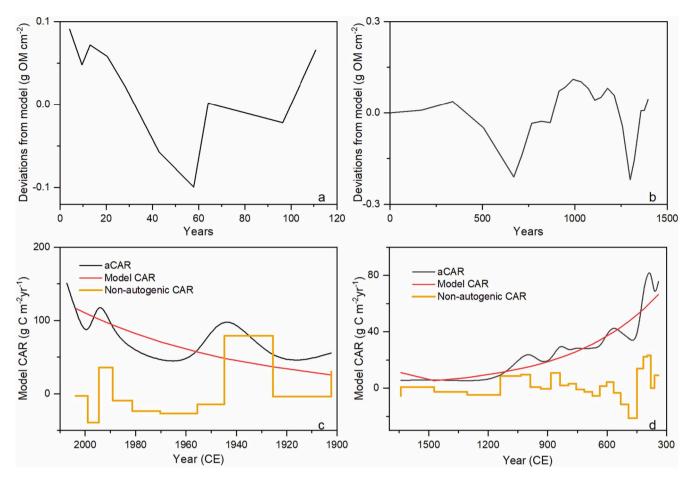


Fig. 5. Steps involved deriving a non-autogenic accumulation curve from the age profile after fitting the peat accumulation model in different ecosystem states. Deviations between observed cumulative peat mass and that simulated by the model in the bog (a) and fen (b) phases. Long-term observed CAR, the modelled (autogenic) CAR, and the non-autogenic CAR for the Tuqiang peat core in the bog (c) and fen (d) phases.

peak around 1010 CE. *Sphagnum* was generally absent, except for a brief occurrence near 1290 cal yr BP, reaching up to 20 %.

Transitioning to Zone C (1895 to 2016 CE, 15–0 cm), *Sphagnum* emerged as the most abundant species, averaging 60 % and fluctuating between 39 % and 90 %. The transition from the fen to bog ecosystem was considered to occur around the boundary between Zones B and C, at a depth of approximately 15 cm. In Zone C, the abundance of UOM decreased from 37 % to 10 %, while *Ericaceae* increased from 11 % to 28 %. *Cyperaceae* predominantly exhibited low abundance throughout this zone. Initially, Zone C showed a high abundance of well-preserved charcoal (up to 8 %), but charcoal gradually disappeared since 1960 cal yr BP.

3.3. Carbon accumulation dynamics

The Tuqiang core exhibited an average OM of 73 %, with peat DBD averaging $0.38~g/cm^3$ (Fig. 3). There was an inverse relationship between OC and DBD, with OC increasing while DBD decreased from the base to the surface of the core. Field observations indicated that the boundary between the acrotelm and catotelm layers of the Tuqiang peatland was approximately 3–4 cm below the core, based on the maximum depth of the summer water table over the long term.

In terms of peat mass accumulation, the cumulative peat mass over the last 120 years (1–15 cm, bog) was 1.4 g OM cm $^{-2}$, while the cumulative peat mass of 121–1400 years (16–40 cm, fen) was 6 g OM cm $^{-2}$ (Fig. 4). The lowest OM content of the peat was more than 70 %, leading to the use of OM to represent peat accumulation in this context. The PAR in the bog and fen areas was measured to be 240 \pm 20 g C m $^{-2}$ yr $^{-1}$ and

 $110\pm 2~g~C~m^{-2}~yr^{-1},$ respectively. The decay coefficient (α) of the bog $(0.015~yr^{-1})$ was higher than that of the fen $(0.002~yr^{-1}).$ Additionally, the PAR modification coefficient for the fen phase of the Tuqiang peatland was $0.041~yr^{-1}.$ The autogenic processes of the permafrost changed slowly over time, with the decay coefficient (α) approaching zero, indicating that the permafrost in the fen phase was not included in the model. Over the past 120 years, the observed peat C accumulation rate for the Tuqiang core averaged 84 g C m $^{-2}$ yr $^{-1}$ (Fig. 5). This value exceeds the average accumulation rate of 35 g C m $^{-2}$ yr $^{-1}$ for the last 1400 years.

3.4. Final model of the bog phase

The AIC values for the GAMs were as follows: $\log(NCAR) = s(tem) + s(pre)$ with an AIC of 59.7, $\log(CAR) = s(tem)$ with an AIC of 63.4, and $\log(CAR) = s(pre)$ with an AIC of 62.7. Here the function s() represents the smooth function of temperature or precipitation values. Therefore, the final GAM selected was $\log(CAR) = s(tem) + s(pre)$. This model was able to explain 49 % of the variance in NCAR (P < 0.1).

4. Discussion

4.1. Peatland ecosystem regime shift mainly caused by its autogenic processes

Over the past 120 years, there has been a rapid transition from a *Cyperaceae* fen peat to bog peat dominated by *Sphagnum* mosses at the

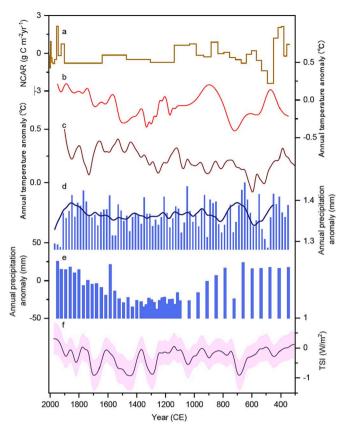


Fig. 6. Long-term trends in reconstructed Z-scores of the non-autogenic CAR (NCAR) during the fen phrase of Tuqiang peatland, compared with climate factors. (a) Z-scores of NCAR in the Tuqiang peatland. (b, e) Reconstructed temperature and precipitation based on pollen data from Hulun Lake (Wen et al., 2010). (c, d) Model-derived paleo temperature and precipitation (Fordham et al., 2017). The dark-blue line represents the 100-yr moving average of precipitation. (f) Reconstruction of total solar irradiance (TSI) by Steinhilber et al. (2012).

study site. Previously, the Tuqiang peatland ecosystem had been relatively stable as a fen ecosystem for the past 2500 years with Cyperaceae as the dominant the plant macrofossils. However, since 1895 CE, *Sphagnum*, a typical oligotrophic bog plant, has gradually become dominant in the plant community. The application of the Sequential Ttest Analysis of Regime-shifts (STARS) algorithm confirmed that the ecosystem regime shift occurred around 1900 CE (Supplementary Information, Fig. S1).

The causes of oligotrophic processes are multifaceted and can be triggered by diminished mineral water inputs into peatlands (Loisel and Yu, 2013b). Peatlands undergo autogenic processes as peat accumulates gradually above the water table, leading to the transition from fen to bog. Additionally, dry hydroclimatic conditions can augment peat decomposition and lower the water table, resulting in a dense, water-resistant peat layer that shields plants from groundwater influence (Hughes, 2000). In the Tuqiang peatland, the autogenic processes predominantly drove the fen-to-bog transition and the subsequent colonization by *Sphagnum*. Both pollen-based precipitation (Wen et al., 2010) and model-derived precipitation (Fordham et al., 2017) indicated low precipitation between 700 and 1800 CE (Fig. 6d, e). However, the peatland has long been viewed as a stable ecosystem where *Cyperaceae* consistently dominated the plant community during this period (Fig. 3).

It is increasingly recognized that the fen-to-bog shift exhibits nonlinear, step-like transitions from one stable state to another (Belyea, 2009; Swindles et al., 2018). The fen-to-bog transition in the Tuqiang peatland was rapid and drastic, which aligns with observations from other empirical studies on peat cores (Hughes and Barber, 2003; Loisel

and Bunsen, 2020). Sphagnum can flourish when peat accumulates above the water table (Granath et al., 2010; Rastogi et al., 2020). Once established, Sphagnum increases the acidity of its surroundings, reinforcing its persistence and enabling further invasion, leading to rapid oligotrophication of the ecosystem (van Breemen, 1995). Overall, positive feedback loops play a significant role in driving these catastrophic shifts in the ecosystem.

4.2. The fitting peat development models of different ecosystem stages

To represent the autogenic decomposition and accumulation processes of peat in the Tuqiang peatland, we employed a Clymo-type decomposition/accumulation modeling approach. This approach takes into consideration the concave cumulative mass-age curve of peat, which is commonly observed in the surface layer of the Tuqiang peatland (Fig. 4a) and other oceanic bogs (Yu et al., 2003).

Fens, characterized as groundwater-fed peatlands, exhibit more intricate hydrology compared to bogs. In fen ecosystems, the autogenic vertical growth of peat causes a long-term drying trend on the surface as they become increasingly isolated from surrounding upland water tables (Yu et al., 2003). Additionally, there has been a downward trend in precipitation in the region since 700 CE (Fig. 6). The combination of vertical growth and regional climate change has contributed to this longterm drying trend. As a result, the production of moisture-sensitive plant species has decreased, and acrotelm (the upper layer of peat) decomposition has increased, leading to a decrease in the PAR. Specifically, for the fen period of the Tuqiang peatland, the PAR was fitted to be 110e $^{0.041t}$ g C m $^{-2}$ yr $^{-1}$ (Fig. 4b). To account for the ongoing decline in PAR caused by peatland vertical growth and drying in continental fens, an extended model (model 3) was proposed by Yu et al. (2003). This extended model aims to mitigate the PAR decline and provide a more accurate representation of the peatland ecosystem state and its autogenic processes in continental fens.

Distinguishing between concave and convex peat accumulation patterns is crucial for developing simulation models and projecting future peat carbon dynamics. Therefore, different models were employed to simulate these distinct accumulation patterns, aiming to accurately reflect the state of the peatland ecosystem and its autogenic processes. This step is crucial in investigating the external factors influencing peat carbon accumulation.

4.3. Impacts of temperature and moisture on peat carbon accumulation over the late holocene

The interaction between hydroclimate and temperature is crucial for peat carbon accumulation. In the fen phase from 300 to 700 CE, characterized by high and stable precipitation, changes in peatland carbon accumulation were found to have a negative correlation with temperature (* * P < 0.01, deviance explained 51.7 %; Fig. 6a, b and Fig. 7a). The temperature derived from pollen data was consistent with the modelderived temperature (Fig. 6b, c). In the context of climatic warming, changes in peatland carbon stocks are influenced by two conflicting processes. On one hand, warming stimulates plant growth and results in increased plant litter input, leading to increased peat carbon accumulation. On the other hand, warming accelerates microbial respiration, causing soil carbon loss and negatively impacting peat carbon stocks (Friedlingstein et al., 2006). In the fen phase of the Tuqiang peatland ecosystem, high temperatures were associated with low NCAR, indicating that the temperature increase promotes microbial decomposition more significantly than the increase in plant NPP. The composition of plant species in peatlands affects litter decomposition, with Cyperaceae decomposing at a faster rate compared to Sphagnum under similar climatic conditions (Bell et al., 2018; Moore et al., 2007). In the fen stage of the Tuqiang peatland, Cyperaceae is dominant and its litter decomposes more easily. Additionally, the over-saturation of peatland in the early fen stage, due to low terrain and abundant water sources, restricts

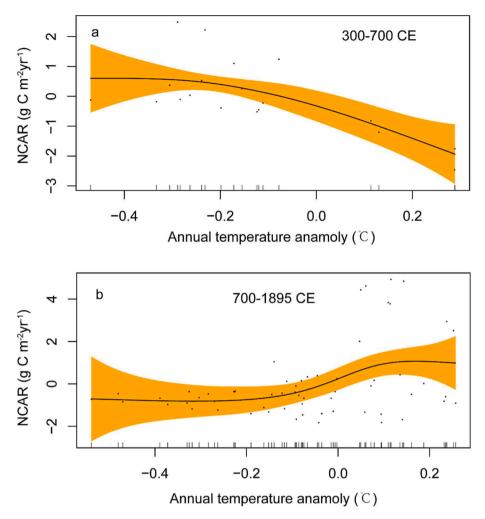


Fig. 7. Correlation analysis employing Generalized Additive Models (GAMs) between the non-autogenic CAR (NCAR) during the fen phase and annual temperature.

vegetation growth. Consequently, higher temperatures promote plant litter decomposition more readily, resulting in a lower peat accumulation rate

From 700 to 1000 CE, there was a sharp decline in precipitation, despite which the NCAR indicated a positive trend with temperature, even though the ecosystem state remained in the fen phase during this period (Fig. 6a, b). This trend can be ascribed to the decrease in water level, resulting in the peatlands no longer being oversaturated. With water content no longer constraining vegetation growth, the increase in temperature enhanced plant NPP, outweighing the impact of temperature on plant decomposition during the fen phase between 700 and 1895 CE. Previous studies have also noted that temperature and growing season length have a more pronounced effect on plant NPP in northern peatlands (Jones and Yu, 2010; Morris et al., 2018). Although precipitation increased from 1500 to 1895 CE, it remained lower than the rainfall between 300 and 700 CE. Adequate but not excessive water conditions are crucial for the growth of wetland vegetation. Therefore, the relationship between carbon accumulation and temperature was found to be positive (*p < 0.1, deviance explained 21.8 %) during the 700–1895 CE period (Fig. 7b). When water levels were excessively high and peatlands were over-saturated, an increase in temperature did not significantly enhance plant NPP but instead accelerated plant litter decomposition. In contrast, when water levels were appropriate and no longer limiting for plant growth, higher temperatures promoted greater plant NPP relative to plant litter decomposition.

During the bog phase, the peaks in the NCAR corresponded to periods of high temperature in the 1940s and 1990s. Over the last century,

there has been a 3°C increase in temperature in the region (Fig. 8b), leading to an increase in vegetation's NPP. However, the higher temperatures also caused greater evaporation and microbial activity, affecting peat accumulation. Therefore, temperature showed a positive correlation (*p < 0.1, deviance explained 48.9 %) with peat accumulation (Fig. 9b), while rainfall did not exhibit a clear relationship. Precipitation levels in the Amur River Basin have shown fluctuations over time, with an increase from the 1910s to the 1960s, followed by a stable pattern. Ombrotrophic bogs rely solely on precipitation for their water supply. Any changes in the bog's hydrology are directly influenced by climate factors, specifically precipitation and temperature, which determine the magnitude of water evaporation. The effect of evaporation surpasses the impact of rainfall on carbon accumulation due to the significant temperature increase observed during the past century (Fig. 8b, c; Fig. 9).

Different combinations of hydroclimate and temperature play varying roles in carbon accumulation, dependent on whether these factors fall within the suitable range for peatland development (Sullivan et al., 2008). During the fen phase, wetland vegetation growth was limited by unsuitable precipitation conditions, resulting in a negative relationship between NCAR and temperature from 300 to 700 CE (Fig. 6e; Fig. 7a). From 700 to 1895 CE, precipitation conditions became favorable for peatland vegetation growth (Fig. 6d, e), leading to a positive relationship between NCAR and temperature (Fig. 7b). In the bog phase, the increase in peat height did not result in precipitation oversaturation during the period from 1895 to 2010 CE, and the rise in temperature was conducive to the peatland vegetation growth. However, the evaporation

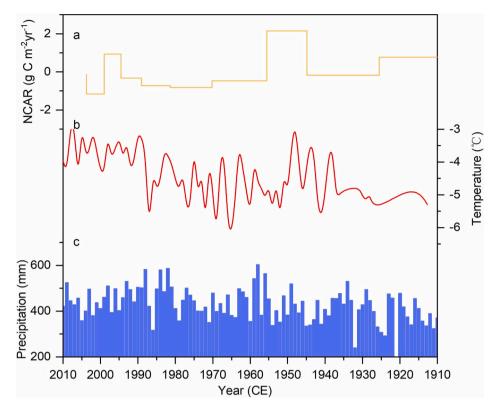


Fig. 8. Comparison of recent trends in reconstructed Z-scores of non-autogenic CAR (NCAR) during the bog phase of Tuqiang peatland with climate factors.

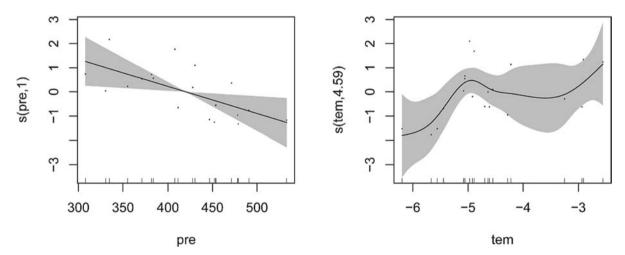


Fig. 9. The GAMs model between non-autogenic CAR (NCAR) of bog phase and climate factors. (a) The GAMs of NCAR and precipitation. (b) The GAMs of NCAR and temperature. The black fitted line results from the application of GAMs with a continuous-time first-order autoregressive process estimated using the generalized cross-validation method. The shaded light-dark bands enclosing the estimated trends are the \sim 97.5 % across-the-function confidence intervals. The dots show the distribution of observed values for the NCAR and climate factor values (precipitation and temperature). The number in parenthesis is the effective degrees of freedom (edf) of the smooth function.

effect on peat carbon accumulation exceeds the effect of rainfall due to the significant increase in temperature observed in the past century, leading to insignificant correlation between NCAR and precipitation (Fig. 9a). The consideration of different ecosystem states within the peatland ecosystem, such as fen and bog, is crucial for a comprehensive understanding of the relationship between carbon accumulation and climate factors. The Tuqiang peatland ecosystem shifted from fen to bog, and the relationships between carbon accumulation and climate factors differed in each state.

Assuming no external influences, it is expected that the ecosystem will remain in a bog state in the next century. Based on the established

relationship between carbon accumulation and climate factors, as well as future climate change scenarios, it is possible to predict the carbon accumulation rate. The NCAR of the Tuqiang peatland was modeled using GAMs to link them to temperature and precipitation. The model showed no significant correlation between NCAR and precipitation, while a positive relationship was observed between NCAR and temperature (Fig. 9). Under all Representative Concentration Pathway (RCP) scenarios, temperatures in the Amur River Basin are projected to increase and remain above $-2\ ^{\circ}\mathrm{C}$ in the coming century. On the other hand, precipitation is projected to exhibit dynamic stability under the RCP scenarios, ranging from 500 to 1000 mm (Supplementary

information, Fig. S2). The Amur River Basin peatlands, located in high latitude regions, have experienced increasing temperatures since the Industrial Revolution. Additionally, current environmental protection policies in the Amur River Basin, including strict wetland conservation measures and no ongoing wetland draining or farmland reclamation, further support the notion of increased carbon accumulation in the bog in the coming century.

5. Conclusions

This study presents an analysis of the non-autogenic carbon accumulation in a peatland located in the Amur River Basin over a period of nearly 1500 years. The peatland underwent a transition from a fen to a bog, and the research demonstrates that carbon sequestration in the peatland is influenced by a combination of hydroclimate and temperature. The findings indicate that the autogenic processes of the peatland mainly caused the fen-bog transition and recent *Sphagnum* colonization. During the fen phase, higher temperatures led to increased decomposition of plant litter only under conditions of water oversaturation in the peatland. However, in the presence of suitable moisture conditions, a rise in temperature promoted plant NPP more than plant litter decomposition. In the bog phase, there was no significant correlation observed between NCAR and precipitation, while a positive relationship between NCAR and temperature was evident during this phase.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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