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Early Paleogene Arctic terrestrial ecosystems affected by the change of polar hydrology under global warming: Implications for modern climate change at high latitudes

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Our understanding of both the role and impact of Arctic environmental changes under the current global warming climate is rather limited despite efforts of improved monitoring and wider assessment through remote sensing technology. Changes of Arctic ecosystems under early Paleogene warming climate provide an analogue to evaluate long-term responses of Arctic environmental alteration to global warming. This study reviews Arctic terrestrial ecosystems and their transformation under marked change of hydrological conditions during the warmest period in early Cenozoic, the Paleocene and Eocene. We describe a new approach to quantitatively reconstruct high latitudinal paleohydrology using compound-specific hydrogen isotope analysis which applies empirically derived genus-specific hydrogen isotope fractionations to *in situ* biomolecules from fossil plants. We propose a moisture recycling model at the Arctic to explain the reconstructed hydrogen isotope signals of ancient high latitude precipitation during early Paleogene, which bears implications to the likely change of modern Arctic ecosystems under the projected accelerated global warming.

Paleogene climate, Arctic ecosystems, global warming, global hydrology, vegetation change

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1 Introduction

A recent accelerated global warming has been confirmed by independent studies and is widely believed to be caused primarily by greenhouse gases (especially CO_2) emission generated through human activities [1–3]. The most recent assessment report from the Intergovernmental Panel of Climate Change (IPCC, [3]) predicted that the global surface temperature in the 21st Century would increase 1.8–4°C if no measure is taken to control the emission of greenhouse gases, and this will undoubtedly cause immense changes for the Earth ecosystems.

Polar regions play an important role in the Earth dynamics by both actively influencing global climate changes and passively receiving feedback of such alterations. Largely due to the ice “blanket” covering the polar areas, the polar climate generally amplifies the global climate change. For example, data show that in the past 100 years, the average Arctic temperatures increased at almost twice the global average rate [3]. Such an amplified impact would certainly have feedbacks to the global climate elsewhere in a way that we know little in terms of the long term consequences. To better understand the current global climate change and predict the magnitude and impact of future climate changes, we should turn to our geologic record as a “treasure trove”

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to assess its long term impact, particularly those concerning with the polar regions.

The history of global climate changes is best illustrated (and well documented) by the alterations of greenhouse (warm) periods and icehouse (cool) periods [4]. Compared with features of the current global warming and its possible magnitude increase in the future, the early Paleogene warmth (about 60–40 Ma ago) provides a unique analogue. Paleogene fossil assemblages unearthed in the Arctic area, particularly those exceptionally-preserved fossil leaves found in Axel Heiberg and Ellesmere Islands in the Canadian Arctic as far north as 80°N have illustrated a general picture of the paleoecosystem of a much warmer past in the Arctic: Lush deciduous conifers, such as trees of *Metasequoia* Miki, *Larix* Miller, and *Glyptostrobus* Endlicher [5–7] occupied swamps (sometimes *Metasequoia* trees formed pure swamp woods) and streamside lowlands; while the surrounding uplands were covered by a deciduous mixed conifer and hardwood forest [7–11]. The early Paleogene warmth is composed of a series of hyperthermals among which the Paleocene-Eocene Thermal Maximum (PETM, ~55 Ma) is the most prominent and best studied event. The PETM elevated global mean annual temperature (MAT) by ~5°C in less than 10000 years with more than 2000 Gt carbon injected into the atmosphere and ocean [12–14]. As its rate and magnitude of both temperature increase and greenhouse gas emission are comparable to those predicted to occur over the coming centuries [14, 15], PETM as well as the background early Paleogene warmth are considered as one of the geological analogues for modern climate change. Due to the sensitivity and greater feedbacks of the polar region climate to the global warming, our paper will focus on the early Paleogene ecosystems of the Arctic area, with the main purpose of learning "lessons" for the present as well as the future.

Conventional paleontological research on both plant and animal fossils during the past ~140 years (reviewed in ref. [7]) as well as the application of new geobiological techniques (such as the compound-specific isotope analysis) in the recent decades has greatly improved our understanding of Arctic paleoecosystems during the early Paleogene global warmth. Among available proxy based techniques to track long-term climate changes in the Arctic, stable hydrogen isotopic analysis is a powerful tool in diagnosing large scale ancient hydrological processes which were unable to be measured before but critical to our understanding of paleoclimate changes [16, 17]. Modern hydrogen isotope compositions of high-latitude precipitation is largely a result of isotopic distillation during progressive rainout [18], as well as changes in the magnitude of fractionation between vapor and liquid phases forced by meridional changes in air temperature [19, 20]. Modern isotopic compositions of precipitation in the high Arctic (i.e., on Axel Heiberg and Elsmere Islands) have estimated mean annual δD values of −190‰ to −195‰ with summer growing season δD values of ~−165‰. Substantially, more D-depleted precipitation during winter and early spring months (December–March) has been recorded [20].

In this paper we summarize our latest understanding of early Paleogene Arctic ecosystems, particularly those under abrupt climate events. We outline a new approach to infer paleohydrology of the Arctic region by quantitatively reconstructing ancient precipitation using genus-specific stable hydrogen isotopic analysis of *in situ* biomolecules from fossil plants. Based upon our new data, we propose a new model regarding the source of high Arctic moisture during the Paleogene warmth. Finally, we draw parallels between the early Paleogene warmth and the current and future alarming trend of warming in the Arctic.

2 Arctic ecosystems under early Paleogene warmth

After the Cretaceous-Tertiary (K-T) mass extinction that eliminated all dinosaurs on land and approximately 60%–80% of marine invertebrate species [21], the Earth entered the Cenozoic, known as the Age of Mammals and Flowering Plants (Angiosperms). Compared with the very warm Cretaceous, the very beginning of Paleocene was a cooler period; but close to the middle and late parts of the Paleocene (~59 Ma), a long-term global warming trend was initiated, launching a warming period for almost 25 million years until before the Eocene-Oligocene boundary (33.9 Ma) that resulted in an ice free Arctic under a much more reduced latitudinal temperature gradient [12–14, 22]. Superimposed on this early Paleogene warm background is a series of small-scaled hyperthermals, including the very short-lived PETM (~55.8 Ma, formerly known as the Latest Paleocene Thermal Maximum (LPTM), also named Eocene Thermal Maximum 1 (ETM1)); the Eocene Thermal Maximum 2 (ETM2, ~53.5 Ma; also known as Elmo, see ref. [23]); the 2-million-year-long Early Eocene Climatic Optimum (EECO, 53–51 Ma, the maximum warmth during early Paleogene), and the more transient Middle Eocene Climate Optimum (MECO, ~41 Ma) [14, 24] (also see Figure 2 in ref. [13]).

The first discovery of the early Paleogene (originally referred to as Miocene in age, e.g., ref. [25]) biota in the Arctic area was dated back to the late 19th and early 20th Century polar explorations (reviewed in ref. [7], and reference therein). These pioneering discoveries, along with subsequent findings, particularly fossil *Lagerstätten* sites yielding exceptionally preserved fossils from the Canadian Arctic Archipelago discovered since the 1980s (reviewed in ref. [26]) revealed the existence of a mixed deciduous circumpolar vegetation. Termed either as the Arcto-Tertiary Flora [25] or the Polar Broad-leaved Deciduous Forest [8], such a Paleogene polar vegetation has been found virtually every-where north of the Arctic circle in non-marine strata during the early Paleogene warmth [7, 8, 27].

These fossil assemblages offer scientists opportunities for inferring environmental parameters or climate signals (e.g., MAT; mean annual temperature range, MAR; mean winter temperature, MWT; sea surface temperature, SST; relative humidity, RH; precipitation; and atmospheric CO_2 partial pressure, P_{CO_2}) through both conventional paleontological methods and proxy-based geobiochemical techniques. Based on our own data as well as literature surveys, the general features of the Arctic ecosystems under the early Paleogene global warmth are summarized chronologically as the following.

2.1 Paleocene

In general, climate in the Paleocene was mild, with periods of drought occurring, but not severe [11]. With many ecological niches vacant after the K-T extinction, the Early Paleocene experienced a profound radiation of mammals, mostly small-sized insect feeders, into previously unoccupied niches [28, 29]. But the taxonomic turnover of plants was not as obvious as that of animals in the initial stage of Paleocene [29]. Later, in a more gradual way, the plants, mainly deciduous taxa of angiospermous families including Betulaceae, Ulmaceae, Palmaceae, Fagaceae, Juglandaceae, etc. and the conifers such as *Metasequoia* formed forests in the Arctic area, permitting the radiation of small, arboreal, fruit-eating birds and mammals [11, 29]. Probably due to the absence of large herbivorous dinosaurs, the forests became denser and more close-canopied and started to produce seeds larger than those in Early Paleocene, thus providing better food resources for mammals and other animals [28, 30].

2.2 Paleocene-Eocene boundary (the PETM event)

The Paleocene-Eocene Thermal Maximum (PETM) at ~55.8 Ma, thought to have fueled global warming by a rapid increase of greenhouse gas levels [13, 31–33], marking one of the warmest periods during the Earth history. This remarkably rapid event caused a marked negative carbon isotope shifts in both marine [31] and terrestrial [34] stratigraphic records.

This geologically sudden warming was associated with a perturbation of the hydrological cycle and an increased ocean acidification [12, 15, 24, 35–37] and was accompanied by 5–7°C rise in global surface temperature making a warm Arctic with MAT as high as 25°C at 75°N [38]. These elevated global temperatures were accompanied by an abrupt increase in seasonal extreme precipitation in the subtropical regions and an increase in moisture delivery and heavy precipitation in high latitudes [39–41]. Such a high level of precipitation was believed to have largely reduced the salt concentration of the Arctic Ocean [36]. Although the amount of carbon released to the atmosphere is still uncertain [42–44], the absorption of the carbon had caused a rapid acidification shoaling of the calcite compensation depth (CCD) of the Paleogene Ocean [45]. All these changes happened within a geologically transient (~170000 years) episode [24] which caused disturbance in ecosystems as indicated by a rapid dispersal of early mammals across high latitudes [46, 47], a polar-ward migration of insects [15], subtropical marine plankton [48, 49], and terrestrial plants [50–53], and extinction events for nannoplankton [54] and benthic faunas [55].

2.3 Eocene

The Early Eocene is featured by a general warming trend with two hyperthermals, ETM2 (~53.5 Ma) and EECO (53–51 Ma) superimposed. Although these two hyperthermals are not as thoroughly studied as the PETM event, the currently available information indicates that they are also associated with massive injections of ^{13}C-depleted carbon, ocean acidification, and perturbations of the hydrological cycle, though less pronounced than those during the PETM [24]. Their impacts on the terrestrial ecosystems are thus believed to be similar to that of the PETM. After the EECO, the global temperature started to drop gradually, but still in high level in most of the Middle and Late Eocene until the Earth entered into the icehouse period close to the Eocene-Oligocene boundary, which is marked by the Terminal Eocene Event (TEE), probably the greatest cooling event of the Cenozoic [8, 13, 28, 56]. Before the icehouse phase started, the Earth experienced the final hyperthermal of the early Paleogene warmth, the Middle Eocene Climate Optimum (MECO, ~41 Ma).

In general, the Arctic area during most of the Eocene is believed to be warm and extremely humid with relative humidity about two times higher than that of the modern Arctic level [57], thus sustaining rainforest-like ecosystems covering the high latitudinal region [26]. The vegetation was characterized by tall and dense forests that yielded a primary productivity similar to modern subtropical areas [58]. The mammalian diversity reached to its peak in the early Middle Eocene and large-sized reptiles (e.g., alligators and land tortoises) whose modern equivalents now live in subtropical regions appeared in the high Arctic area [28, 29, 59, 60]. Coal deposits in terrestrial sediments and rock-salt, gypsum, and coral reefs in marine strata are common in Eocene high Arctic [61]. However, the Late Eocene showed a cooling and drying trend, gradually replacing the dense tropical to subtropical forests of the Early and Middle Eocene with temperate mixed coniferous and deciduous woodland [8, 28, 29]. Toward the end of Eocene, the early Paleogene warmth came to an end, and the Earth entered the Neogene (Miocene and Pliocene) icehouse period [56]. Recent study suggested that the highly productive and stratified Arctic Ocean had significant exchange with surrounding seas and water bodies with a mixed salinities [62, 63].

In summary, during the early Paleogene warmth and elevated atmospheric CO_2 and CH_4 concentrations, ecosystems throughout the Arctic area were consistent with a warm and humid climatic regime. Recent estimates of continental MAT at the high Arctic during Late Paleocene to Middle Eocene were around 17–19°C [38]; while those of growing season relative humidity (RH) around 67%, and the end of growing season RH close to 100% [57]. The atmospheric CO_2 concentration was at least over 1000 ppm [64–67] compared with the present day of average ~360 ppm, and soil methanogenesis-generated CH_4 was as high as 24 gC_{CH_4} $M^{-1}yr^{-1}$ [68]. These unique high-latitude paleoecosystems were illuminated by ~4 months of continuous and low-intensity light irradiation during the Arctic summer [69, 70] and nurtured an extensive deciduous vegetation composed primarily of a mixture of deciduous conifers (dominated by *Metasequoia*, which sometimes formed pure forests) and deciduous angiosperms [7–11]. In the animal world, the Early Eocene Arctic faunas were composed of both subtropical vertebrates (fishes, amphibians, reptiles, birds and mammals) and invertebrates recovered from a mixed aquatic-riparian-terrestrial assemblage [28, 59, 71]. Lower-latitude animal species such as alligators, tortoises, and a diverse mammal fauna were year-round residents in Eocene Arctic. Certainly, along with the global warming trend, animals exhibited increased diversity and complexity from Paleocene to Eocene. As climatic fluctuations (small-scaled warming and cooling events) occurred on the warming trend background, animals and plants migrated polar-ward and equator-ward respectively [7, 11].

3 A new approach to estimate Paleogene atmospheric hydrology in the Arctic

Reconstruction of paleoenvironment and paleoclimate has relied heavily on fossil materials [72], sediments from ocean drilling cores [36], ice cores [73], and computer modeling [74]. Until recently [40, 75], sedimentary drill core from the Arctic region was not available, and fossil materials have been rare compared with other areas. However, biomolecules detected from exceptionally preserved fossil plants from the Canadian Arctic provided unique materials for applying geobiological techniques to address Arctic paleoclimate [76]. Among the techniques related to fossil biomolecule analysis, the compound-specific hydrogen isotope analysis is considered as a useful tool to quantitatively reconstruct palaeoclimate (hydrology and temperature) [77–79]. As hydrogen isotope in lipid compounds is also controlled by plant types, the taxon-specific molecular hydrogen isotopic analysis (i.e., molecules from *in situ* plant fossil with known identification) has been successfully applied to reconstruct Arctic paleoclimate [16, 17, 80].

Attempts to better understand the photosynthesis of high-latitude deciduous conifers during the summer months by continuous, low angle, and low intensity illumination [69] led to a hypothesis that photosynthesis under such unique Arctic light should influence the opening of stomata and activation of Rubisco, thus impact both the carbon and hydrogen isotopic compositions of deciduous plants [81–83]. We collaborated with colleagues at the University of Maine, the United States, to test this hypothesis in a greenhouse with controlled light, water, and CO_2 conditions [84].

Two-year old seedlings of three living deciduous conifers, *Metasequoia glyptostroboides* Hu et Cheng and *Taxodium distichum* (L.) L. C. Rich of the family Cupressaceae, and *Larix laricina* (Du Roi) K. Koch of the family Pinaceae that represent living counterparts of the dominant plants in Early Paleogene Arctic ecosystems were grown in the greenhouse under controlled temperature, humidity, and light conditions. These genetically identical plants were separated into two blocks: one block was under diurnal light (DL) (45°N) and the other was exposed to 4 months (May–August) of continuous light (CL) conditions with added artificial light provided by six metal-halide lamps and with overhead shading during day time in order to simulate the low-intensity summer light regime of the high Arctic [84]. Other conditions including temperature (22–25°C), CO_2 concentrations (357–361 ppm), relative humidity (85%– 92%), and water with known hydrogen isotope compositions ($\delta D = -65.7‰ \pm 1.7‰$) are identical for the two blocks. Then the carbon and hydrogen isotopic compositions ($\delta^{13}C$ and δD) were measured from bulk leaf tissues and leaf wax *n*-alkane lipids respectively. The obtained empirical data of molecular hydrogen isotope composition were used to calculate the apparent hydrogen isotope fractionation factors between leaf wax lipids and source water ($\varepsilon_{\text{lipid-water}}$) and subsequently applied to evaluate the hydrological characteristics of ancient precipitation during the Early Paleogene Arctic.

The amounts of carbon isotope offsets ($\Delta^{13}C_{DL\text{-}CL}$) between the two conditions (CL *vs* DL) vary among species. In *Larix*, the offset was up to 4.6‰; whereas in *Metasequoia*, it was only 1.9‰ (Figure 1). But in all cases, leaves under CL condition are depleted in ^{13}C compared with DL leaves, and this observed depletion in ^{13}C in CL leaves can be attributed to a higher ratio of intercellular to atmospheric CO_2 concentration (C_i/C_a) compared to their DL counterparts. Furthermore, CL condition has a significant impact on hydrogen isotope fractionation factors ($\varepsilon_{\text{lipid-water}}$) of *n*-alkanes. In all tested species, leaf wax *n*-alkanes from the CL condition are D-enriched relative to those from the DL condition (Figure 2). Our results also indicate that the values of $\varepsilon_{\text{lipid-water}}$ for all tested plants are substantially smaller (for example, $\varepsilon_{\text{lipid-water}} = -62‰ \pm 1.4‰$ for *Metasequoia* C_{27} and $-74‰ \pm 1.5‰$ for *Larix* C_{27}) than

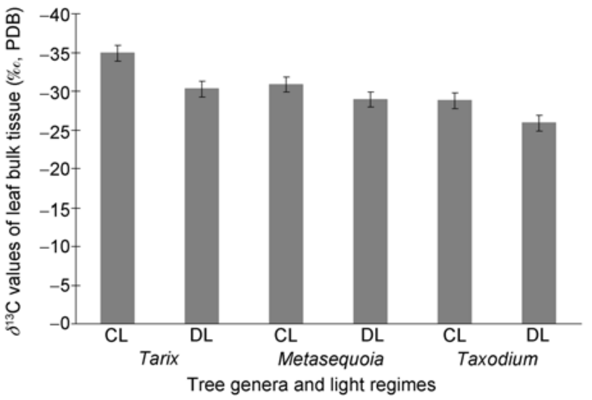


Figure 1 Carbon isotope compositions of bulk leaf tissue under different light regimes under greenhouse conditions.

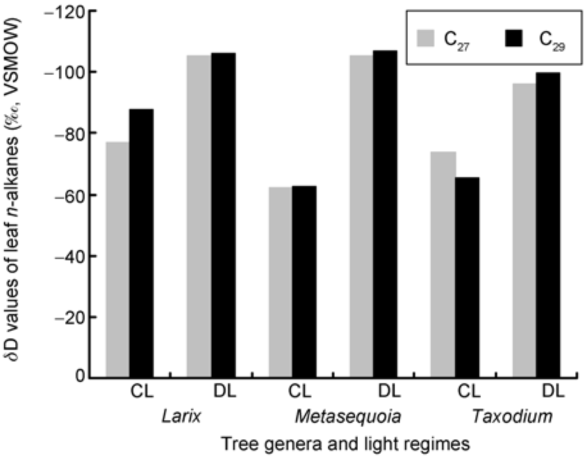


Figure 2 Hydrogen isotope compositions of leaf wax *n*-alkanes under different light regimes under greenhouse conditions.

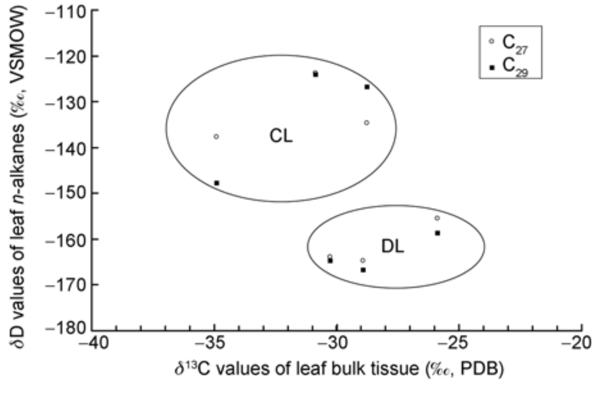


Figure 3 A cross plotting of δD of leaf *n*-alkanes and $\delta^{13}C$ of leaf bulk tissue showing distinct patterns for isotope signals registered under CL and DL in the greenhouse.

previously published values of modern angiosperms and gymnosperms in natural ecosystems [85, 86] where a rigorous constraint on source water D/H composition was lacking. Lipid D-enrichment under CL conditions can be attributed to the extended period of water transpiration under 24-h CL growth. Cross plotting of $\delta^{13}C$ and δD (Figure 3) clearly separates CL and DL leaves, illustrating the impact of continuous light illumination on isotope signals from plant leaves. In contrast to other studies [57], our reconstructed ancient Arctic hydrological data inferred from identifiable and three-dimensionally-preserved fossil leaves of *Metasequoia* and *Larix* from Canadian Arctic Archipelago (paleolatitude ~80°N) suggested contributions of local moisture to the wet Paleogene Arctic [80].

4 Implications for the reconstruction of Paleogene paleohydrology for the Arctic

Given that deciduous conifers in the Paleogene Arctic produced most of the organic matter during the summer growing season under continuous light conditions, hydrogen isotopic ratios of leaf wax *n*-alkanes from these leaves should reflect summer precipitation δD. Celebrated as “living fossils”, *Metasequoia* and *Larix* are known for their slow evolutionary rates and morphological stasis through geological times [87–90], and hence have likely conserved their physiological characteristics [70]. Thus, it is warranted to apply our empirically obtained apparent hydrogen fractionation factors to hydrogen isotope compositions of *in situ* *n*-alkanes recovered from well-preserved early Paleogene deciduous conifer fossils from the Arctic area. By using compound-specific lipids and genus-specific hydrogen isotope fractionation factors, we obtained summer growing season δD of −186‰ for the Late Paleocene, −157‰ for the early Middle Eocene, and −182‰ for the late Middle Eocene respectively [80]. Thus, our newly reconstructed precipitation δD values for growing seasons during the early Middle Eocene are similar to δD values for the present-day summer precipitation in the high Arctic (~−165‰ for summer precipitation and −190‰ for mean annual precipitation respectively, ref. [20]); whereas the late Paleocene and the late middle Eocene values are slightly more D-depleted relative to the modern values, consistent with previously obtained oxygen isotope records from the region [91–93]. To explain their low $\delta^{18}O$ values, Jahren and Sternberg [92] proposed a meridional moisture transportation pattern from the low latitudes (Pacific Ocean) towards the Arctic (Figure 4(a)). Such a proposed long transportation trajectory requires a driving force of a strong meridional temperature gradient, similar to that of today. However, all available evidence has indicated a much lower meridional temperature gradient during early Paleogene than the present day [7, 12, 24]. Furthermore, the proposed progressive rainout process would not result in a well-proved wet Arctic climate [26, 39, 57, 94, 95] as the low latitude water would be lost along the long distance transportation. Hence, these facts made a strong latitudinal D/H distribution rather unlikely [36, 75, 96, 97]. In order to reconcile the newly detected D-depleted precipitation and high humidity in early Paleogene Arctic, an additional source of D-depleted moisture other than solely transported from low latitudes maybe required.

Early studies on hydrogen isotope ratios in plant tissues linked variations of the D/H in terrestrial plant cellulose with mean annual temperature [98, 99] in addition to precipitation. Recent studies using a worldwide database have shown that hydrogen isotope compositions of modern leaf wax from higher plants are largely controlled by global precipitation pattern that is influenced by the temperature gradient [100] and by different plant life forms [16, 101]. As air mass movement and delivery of moisture to the Arctic is largely controlled by global temperature gradient [18, 96], precipitation and temperature are ultimately linked in controlling hydrogen isotope compositions in leaf wax of terrestrial plants [16, 78] as well as in aquatic plants [86]. Such a co-variant nature of precipitation and temperature should be carefully considered while explaining early Paleogene D/H record from plants and sediments deposited under a unique Arctic terrestrial ecosystem that was influenced by a high atmospheric humidity and low global temperature gradient.

Through continental convection of vapor, both ocean source and evapo-transpiration from land plants and water bodies can significantly influence isotopic signature in precipitation as documented in the tropical [102] and temperate [103, 104] regions. Considering the extensive *Metasequoia* dominated forests in the early Paleogene Arctic area, we have proposed a new model of the moisture source for the high Arctic area during the Paleogene which encompassed both the evaporation from the Arctic Ocean and the transpiration of the extensive local forests (Figure 4(b)). This new model takes the unique polar terrestrial vegetation-climate dynamics under the condition of 24-h continuous light into consideration. Due to the lack of modern analogue and the difficulty of quantifying climatic features, the dynamics between the climate and the extensive Arctic vegetation during early Paleogene has previously been overlooked. In our new quantified model, we argue that the relationship between the climate and the local vegetation may have played a much more important role in the Paleogene Arctic ecosystems than previously believed, particularly during the summer growing seasons. Our new model effectively explains the relatively negative hydrogen isotope signals which were largely modified by the recycled precipitation through evapo-transpiration, and at the same time confirms the theoretical prediction of the vegetation feedback based upon modern ecosystems [105].

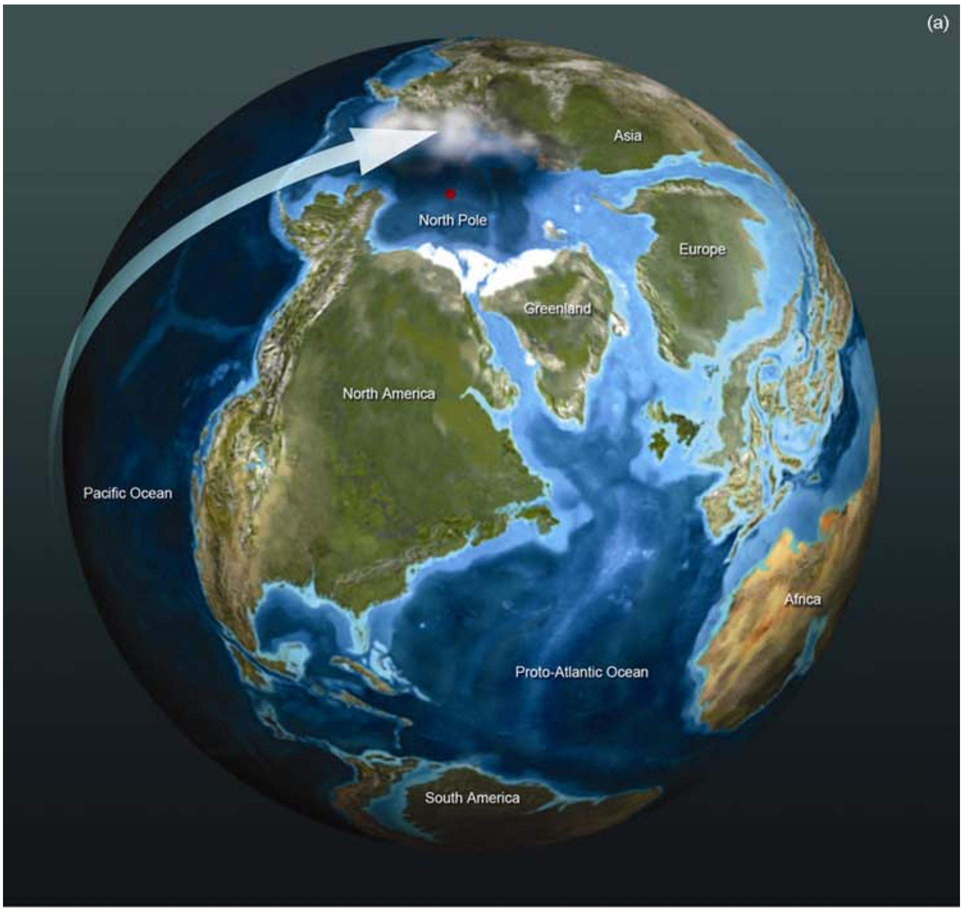
In addition, if we apply our empirically obtained apparent hydrogen fractionation factors to published δD of *n*-alkanes across polar PETM [40], the reconstructions are in good agreement with our pre- and post-PETM baseline precipitation δD values (−160‰ to −170‰). The dramatic positive shift (up to 50‰) at the onset of PETM may indicate a sudden change of precipitation δD, representing a possible alteration of atmospheric circulation dynamics which may have been resulted from an abrupt increase of global temperature and moisture [39]. Caballero and Langen [97] has pointed out that while the temperature reaches to a certain level, the static stability decreases, reaching to the critical threshold to change global atmospheric circulations, and in turn to alter the source of moisture delivered to the high Arctic. If this is true, our new model would also explain the extremely wet conditions, the major δD shift at PETM, the relatively stable baseline precipitation δD, and the relative low values of growing season precipitation δD recorded in lipids from the deciduous plant fossils.

5 Implications for modern Arctic ecosystem changes under climate warming

The modern Arctic is drastically different, in every aspect, from what it was during early Paleogene. However, since the permanent Arctic ice cap probably was not built up until late Pliocene [74], a fairly recent time at the geological time scale, the ecosystem and climate in the Arctic, as well as in other parts of the Earth, should be viewed as a continuum dynamic. Indeed, from the historical perspective, the hemispheric-scale warmth of the past decade, likely due to human impact, for the Northern Hemisphere is anomalous for the past two millennia [2].

Modern Arctic ecosystems, situated above 66.7°N with strong seasonal differences in climate, include tundra and taiga vegetation and transitional ecotones between them. The tundra vegetation covers about 5.6×10^6 km^2 of the high Arctic, marked by frost-tolerant plants with low stature and low productivity, such as mosses, lichens, and herbaceous and cushion-forming plants. This high Arctic area is a region of low precipitation with less than 50 mm yr^{-1} in the north, while the southern part of this zone is the polar semi-desert. Mean July temperatures of this high Arctic area range from 6°C in the south to 2°C in the north. Animals in this area include vole, bumble bee, ptarmigan, lemming, Arctic hare, caribou, musk ox, Arctic fox, weasel, snowy owl, Jaeger, and wolf [106–108].

Conditions associated with high Arctic tundra are influenced by three interacting forces: the permafrost which is a deep soil layer permanently frozen year-round, an overlying active layer of organic matter and soil that freezes and thaws on an annual cycle, and vegetation that retards thawing in the summer. Freezing and thawing of the upper layer of soil forms a patterned structure of frost hummocks, frost heaves and stone polygons, accompanied by the formation of ridges and other irregularities in topography.



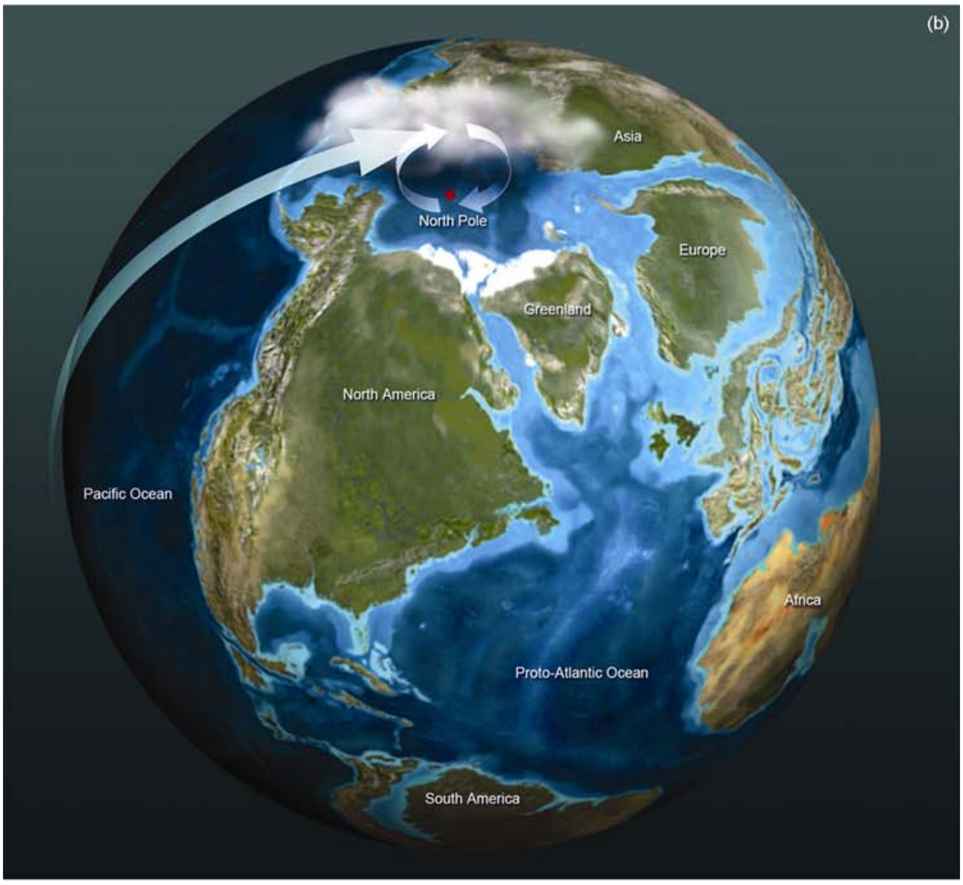


Figure 4 Conceptual models of atmospheric moisture fluxes over the Arctic area during early Paleogene warmth. (a) The previous model showing moisture of tropical source (shown by arrow) based on ref. [92]; (b) our new model based upon data from ref. [80], showing moisture composed of tropical source flux (arrow) and evapotranspiration from local forests and water bodies (cycled arrows). Both figures are drawn based on the Eocene (50 Ma) global paleogeographic map (Oblique West-hemispheric view) from the Northern Arizona University's Web Server "jan" (http://jan.ucc.nau.edu/~ rcb7/globaltext2.html).

On the other hand, the taiga (boreal forest) represents more southerly located forested areas of deciduous or evergreen coniferous trees in the Arctic. It supports a more diverse animal population such as elk, snowshoe hare, arboreal red squirrel, porcupine, vole, wolf, lynx, weasel, ermine, owl, and raven. At its northern edge the taiga becomes the forest tundra, or subarctic, characterized by small trees that do not form a continuous layer. The permafrost is found at the northern edge of the low Arctic, and forms a continuous cover northward. The low Arctic vegetation is characterized by low thicket-forming shrubs, sedges, and tussock-forming sedges with dwarf shrubs, with precipitation reaching about 1000 mm yr^{-1} and annual net production of 100–1200 g m^{-2} [106–108]. Obviously, biodiversity decreases along a latitudinal gradient from the taiga and forest tundra in the south to the polar deserts in the high Arctic.

Polar regions are very sensitive to climate change, and the Arctic ecosystems are highly vulnerable to rising temperatures and changing precipitation patterns. The climate of the Arctic has warmed substantially since the end of the Little Ice Age to present [109], and in the period from the mid-1800s to the mid-20th Century, the Arctic warmed to the highest temperatures in 400 years [110]. A variety of evidence synthesized from marine, terrestrial, and atmospheric studies indicates that the Arctic warmth was accelerated during the last 30 years with some Arctic areas warmed as much as 4.5°C MAT and 6°C MWT [3, 107, 109, 111]. Global circulation models predict that warming is at the greatest in the polar region during winter times, with 1–5°C changes in comparison with 2–4°C changes in summer for a doubling of atmospheric CO_2 concentration [112].

Later freezing and earlier thawing of Arctic lakes and rivers appear to mirror Arctic-wide and even worldwide changes in air temperatures [113, 114]. Hinzman et al. [109] noted that with a warming global climate, first-order impacts to the terrestrial ecosystems of the Arctic are associated with a longer thawing period combined with increased precipitation. Meanwhile, longer snow-free seasons and greater winter insulation will produce deeper thawing and greater melting of Arctic permafrost and glaciers, accompanied by an increased biological productivity and changes in vegetation. Furthermore, additional impacts will emerge as wildlife and people respond to climatic and ecosystem changes. The permafrost region occupies approximately 23 km×106 km or 24% of the land area in the Northern Hemisphere, and the temperature at the top of the permafrost layer has increased by up to 3°C since the 1980s in the Arctic, thawing at a rate ranging up to 0.04 m yr^{-1} in Alaska to 0.02 m yr^{-1} [3]. The maximum extent of seasonally frozen ground has decreased by about 7% from 1901 to 2002, with a decrease in spring of up to 15%, coupled with maximum seasonal thaw depth over the permafrost increasing by about 0.2 m in the Russian Arctic from 1956 to 1990 [3]. The degradation of permafrost layers also leads to changes in land surface characteristics and draining systems; yet recent data indicate that our knowledge of the response of permafrost to the warming climate is still inadequate to evaluate possible future changes [115].

Satellite data since 1978 show that the annual average Arctic sea ice extent has shrunk by 2.7% per decade [3]; other independent evidence, derived from submarine records, indicates that the thickness of sea ice has likely been decreasing by up to 1 m from 1987 to 1997 [3]. The Greenland ice sheet has shown increased surface melting trend since 1995, and the year of 2007 has observed the fastest melting record that led to an extensive water runoff [116]. This reduction of Arctic ice sheet in 2007 was accompanied by a rapid decline of Arctic sea ice to unprecedented low extents in the summer of 2007 [117]. Arctic sea ice coverage during February 2009 was at its fourth lowest measurement since satellite records were initiated in 1979, reaching only 14.8×10^6 km^2 (NOAA-National Oceanic and Atmospheric Administration data of March 13, 2009, from "http://www.noaanews.noaa.gov"). Other changes associated with temperature rise in Arctic regions include enlargement and increased numbers of glacial lakes, increasing ground instability in permafrost regions, warming of northern seas, a northward shift of zooplankton assemblages in Nordic Seas, a northward shift in the spawning location of cod stocks along the Norwegian coast, and a northward shift in the ecosystem of the Bering Sea [3, 118]. Recent estimates indicate that if the warming trend continues, by as early as the 2030s, the Arctic Ocean will change from a perennially ice-covered to a seasonally ice-free ocean [119]. As a result, the plausible 0.8 m increase in sea level by the end of the year of 2100 has been proposed [120]. Recent estimates based upon numerical modeling work have shown that the growth of continental ice sheets in the Northern Hemisphere required much lower global atmospheric CO_2 concentration than maintaining ice sheets in the Southern Hemisphere [74]. With the accumulation of CO_2 concentration in the atmosphere due to human activities, we have crossed the CO_2 threshold of 280 ppm that is required for significant growth of continental ice sheet in the Northern Hemisphere. All models from IPCC have predicted a much higher atmospheric CO_2 concentration by the year of 2100. Such a high level of CO_2 will undoubtedly continue to impact on Arctic climate and its ecosystems [3, 121].

As glaciers on land store about 75% of the world's freshwater, the volumes of the Greenland and Antarctic ice sheets are equivalent to approximately 7 m and 57 m of ocean level rise, respectively. As a direct consequence of melting of glaciers, global average sea level rose at an average rate of 1.8 mm yr^{-1} over 1961 to 2003, with an obvious faster rate of about 3.1 mm yr^{-1} over 1993 to 2003 [3]. Mass loss of glaciers and ice caps is estimated to be 0.50 ± 0.18 mm yr^{-1} in sea level equivalent (SLE) between 1961 and 2004, and 0.77 ± 0.22 mm yr^{-1} SLE between 1991 and 2004, probably as a result of post-1970 warming [3].

Taken together, the continuous melting of ice sheets in Greenland and Antarctica will contribute to significant sea level rise in the years to come.

Rising levels of CO_2 and observed global warming trends are significantly altering the carbon sequestration function associated with Arctic ecosystems, possibly adding a multiplier effect to the rate of climate change. Currently, the Arctic tundra ecosystems, with their low productivity but high carbon accumulation in soils and low rates of microbial decomposition in the cold soil, serve as a global carbon sink [107]. However, the stored carbon, estimated to be about 14% of the soil carbon stored globally [106], may be released back to the atmosphere, reinforcing the current global warming, although to what extent, or through which chemical pathways, is still under discussion [122–125]. As the climate is warmed up, the enhanced activity of soil microbes could speed up the release of carbon, in the form of CH_4 in water logged soils or CO_2 in drier locations. This could reverse the pattern of carbon uptake. Some evidence from northern Alaska has pointed to the shift in the carbon balance in the Arctic, from a carbon sink to a carbon source [126, 127]. However, scientists, particularly zoologists and botanists, continue to explore the detailed mechanisms of carbon transport in permafrost communities exposed to higher temperatures [122].

Many researchers have concluded that a warming climate will initiate a cascade of impacts that affect geophysical, hydrological, biological, and social systems in the far North [109]. The absence of snow or ice in polar regions will be associated with a decreased meridional temperature gradient, which affects winds and ocean currents as well as moisture transport to high latitudes. Because of the positive temperature-ice albedo feedback, some cryospheric components act to amplify both changes and variability. As the annual global fresh water budget is a balance between evaporation, atmospheric transport, precipitation, runoff, and storage, there is a potential for redistribution of water on the Earth, altering Arctic or even global hydrological cycles. Already, most areas of the Arctic have experienced increases in precipitation along with the increases in global rainfall [3, 128–130].

Using early Paleogene evidence to examine patterns in the distribution of Arctic vegetation associated with past climate change suggests that there will be undoubtedly future changes in vegetative patterns and local precipitation as the current warming continues. Although more long-term experimental validation is still needed [106], some models of vegetation redistribution predict that 30% of the Arctic tundra would be displaced by boreal forests based on a doubling of atmospheric CO_2 [131]. Such changes are associated with the increase in precipitation and productivity levels [132]. Thus, recent studies of the early Paleogene seem to validate some forecasts about future first-order changes in climate: extreme ocean warming in the Arctic; increase in regional precipitation, greater discharge from rivers and freshening of surface waters in the Arctic Ocean [14]. If our local moisture recycle model held and the Arctic hydrological circulation change can be triggered by the increase of deciduous vegetation coverage along with increased Arctic MAT and annual precipitation as seen during the early Paleogene, the long-term continuous increase of atmospheric CO_2 and other greenhouse gases may further alter Arctic hydrology in a significant way.

Such a change in the Arctic and global ecosystems will cause major latitudinal and intercontinental migrations in terrestrial plants and mammals resulting declines or even extinction of vulnerable species such as the polar bear (*Ursus maritimus*). Some changes in response to Arctic climate changes are indirect. For example, the increase in Arctic precipitation will change nutrient structure of Arctic lakes which impacts on high latitude lacustrine food web from algae growth to fish colonization. Furthermore, an increasing warm Arctic has significant consequences far beyond natural ecosystems, ranging from the increased accessibility to northern states to the opportunities of mining, energy extraction, and shipping channels at the high latitudes.

6 Conclusions

Arctic ecosystems during the early Paleogene warmth provide a useful analogue to examine both the causes and possible consequences of Arctic climate changes under the current global warming context. In reviewing the paleoecosystem changes and the latest progress on the reconstruction of Arctic hydrology during early Paleogene, we show that a climate model built upon paleo-data may provide insightful information toward a better understanding of the future impact of Arctic climate changes. If the current global warming trend continues, Arctic warming and northward migration of animals and plants will not only further alter the Arctic landscape but may change the climate dynamics in the Arctic region. Under a warmer global climate with elevated atmospheric CO_2 concentration and less ice coverage, the percentage of local moisture contributing to the Arctic humidity may increase. If the global meridional temperature gradient continues to reduce, along with the increase of greenhouse gases, a hydrological threshold to change current hydrological and atmospheric circulation may be approached. Such an event may cause unpredictable severe global climate disturbance. This study, along with recent advancement on paleoclimate reconstruction for the Arctic region, illustrates the importance of paleoecological information associated with long-term climate changes derived from the geological and historical records. There is a clear need for more information from high latitudinal sites in the Northern Hemisphere, and new research approaches and advanced technology will continue to offer such data to address environmental changes at Arctic that will have significant implications for global social-economic conditions.

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1 Steffen W, Sanderson A, Tyson P D, et al. Global Change and the Earth System: A Planet Under Pressure. Berlin-Heidelberg-New York: Springer-Verlag, 2004. 336

2 Mann M E, Zhang Z, Hughes M K, et al. Proxy-based reconstructions of hemispheric and global surface temperature variations over the past two millennia. Proc Natl Acad Sci USA, 2008, 105: 13252–13257

3 The Core Writing Team of IPCC. Climate Change 2007: Synthesis Report. Valencia, Spain: IPCC (International Panel on Climate Change), Geneva, Switzerland, 2007. 104

4 Frakes L A, Francis J E, Syktus J I. Climatic modes of the Phanerozoic. Cambridge: Cambridge University Press, 1992. 274

5 Christie R L, McMillan N J. Tertiary fossil forests of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago. Geo Surv Can Bull, 1991, 403: 1–226

6 Greenwood D R, Basinger J F. The paleoecology of high-latitude Eocene swamp forests from Axel Heiberg Island, Canadian High Arctic. Rev Palaeobot Palyno, 1994, 81: 83–97

7 McIver E E, Basinger J F. Early Tertiary floral evolution in the Canadian high Arctic. Ann Mo Bot Gard, 1999, 86: 523–545

8 Wolfe J A. Distribution of major vegetational types during the Tertiary. In: Sundquist E T, Broecker W S, eds. The Carbon Cycle and Atmospheric CO_2, Natural Variations Archean to Present. Geophysical Monographs, No. 32. Washington, DC: American Geophysical Union, 1985. 357–375

9 Spicer R A, Chapman J L. Climate change and the evolution of high-latitude terrestrial vegetation and flora. Trends Ecol Evol, 1990, 5: 279–284

10 Basinger J F, Greenwood D R, Sweda T. Early Tertiary vegetation of Arctic Canada and its relevance to paleoclimatic interpretation. In: Boulter M C, Fisher H C, eds. Cenozoic Plants and Climates of the Arctic. Berlin: Springer-Verlag, 1994. 175–198

11 Askin R A, Spicer R A. The Late Cretaceous and Cenozoic History of Vegetation and Climate at Northern and Southern High Latitudes: A Comparison, Effects of Past Global Change on Life. Washington DC: National Academy Press, 1995. 156–173

12 Sluijs A. Global Change During the Paleocene-Eocene Thermal Maximum. Dissertation for Doctoral Degree. Utrecht: Institute of Environmental Biology, Department of Biology, Faculty of Science, Utrecht University, 2006. 227

13 Zachos J C, Pagani M, Sloan L C, et al. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science, 2001, 27: 686–693

14 Zachos J C, Dickens G R, Zeebe R E. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature, 2008, 451: 279–283

15 Currano E D, Wilf P, Wing S L, et al. Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. Proc Natl Acad Sci USA, 2008, 105: 1960–1964

16 Yang H, Leng Q. Molecular hydrogen isotope analysis of living and fossil plants—*Metasequoia* as an example. Prog Nat Sci, 2009, 19: 901–912

17 Leng Q, Yang H. A new approach to reconstruct Paleogene atmospheric hydrology at high latitudes. Sci Found China, 2009, 17: 46–49

18 Gat J R. Oxygen and hydrogen isotopes in the hydrologic cycle. Annu Rev Earth Planet Sci, 1996, 24: 225–262

19 Bowen G J, Wilkinson B. Spatial distribution of $\delta^{18}O$ in meteoric precipitation. Geology, 2002, 30: 315–318

20 Bowen G J, Revenaugh J. Interpolating the isotopic composition of modern meteoric precipitation. Water Resour Res, 2003, 39 (SWC9): 1–13

21 MacLeod N. K-T mass extinction. In: Enclyclopedia of Life Sciences. John Wiley & Sons, Ltd. www.els.net, 2001. 1–4

22 Moran K, Backman J, Brinkhuis H, et al. The Cenozoic palaeoenvironment of the Arctic Ocean. Nature, 2006, 441: 601–605

23 Lourens L J, Sluijs A, Kroon D, et al. Astronomical pacing of late Palaeocene to early Eocene global warming events. Nature, 2004, 435: 1083–1087

24 Sluijs A. Rapid carbon injection and transient global warming during the Paleocene-Eocene thermal maximum. 2008 Gussow-Nuna Geoscience Conference, Banff, Alberta, 2008

25 Chaney R W, Axelrod D I. Miocene floras of the Columbia Plateau. Part II: Systematic considerations. Carnegie Inst Washington Publ, 1959, 617: 135–229

26 Jahren A H. The Arctic forest of the Middle Eocene. Annu Rev Earth Planet Sci, 2007, 35: 509–540

27 Akhmetiev M A. Paleocene and Eocene floras of Russia and adjacent regions: Climatic conditions of their development. Paleont J, 2007, 41: 1032–1039

28 Janis C M. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. Annu Rev Ecol Syst, 1993, 24: 467–500

29 Elias S A. Terrestrial ecosystems in the past 100 million years. In: Encyclopedia of Life Sciences. John Wiley & Sons, Ltd. www.els.net, 2001. 1–5

30 Wing S L, Tiffney B H. Interactions of angiosperms and herbivorous tetrapods through time. In: Friis E M, Chaloner W G, Crane P R, eds. The Origins of Angiosperms and Their Biological Consequences. Cambridge: Cambridge University Press, 1987. 203–224

31 Kennett J P, Stott L D. Abrubt deep-sea warming, palaeoceangraphic changes and benthic extinctions at the end of the palaeocene. Nature, 1991, 353: 225–229

32 Thomas D J, Zachos J C, Bralower T J, et al. Warming the fuel for fire: Evidence for the thermal dissociation of methane hydrate during the Paleocene-Eocene thermal maximum. Geology, 2002, 30: 1067–1070

33 Pancost R D, Steart D S, Handley L, et al. Increased terrestrial methane cycling at the Palaeocene-Eocene thermal maximum. Nature, 2007, 449: 332–335

34 Koch P L, Zachos J C, Gingerich P D. Correlation between isotope records in marine and continental carbon reservoirs near the Palaeocene/Eocene boundary. Nature, 1992, 358: 319–322

35 Katz M E, Cramer B S, Mountain G S, et al. Uncorking the bottle: What triggered the Paleocene/Eocene thermal maximum methane release? Paleoceanography, 2001, 16: 549–562

36 Sluijs A, Schouten S, Pagani M, et al. Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene Thermal Maximum. Nature, 2006, 441: 610–613

37 Zachos J C, Schouten S, Bohaty S, et al. Extreme warming of mid-latitude coastal ocean during the Paleocene-Eocene thermal maximum: Inferences from TEX86 and isotope data. Geology, 2006, 34: 737–740

38 Weijers J, Schouten S, Sluijs A, et al. Warm arctic continents during the Palaeocene-Eocene thermal maximum. Earth Planet Sci Lett, 2007, 261: 230–238

39 Bowen G J, Beerling D J, Koch P L, et al. A humid climate state during the Palaeocene/Eocene thermal maximum. Nature, 2004, 432: 495–499

40 Pagani M, Pedentchouk N, Huber M, et al. Arctic hydrology during global warming at the Palaeocene/Eocene thermal maximum. Nature, 2006, 442: 671–675

41 Schmitz B, Pujalte V. Abrupt increase in seasonal extreme precipitation at the Paleocene-Eocene boundary. Geology, 2007, 35:

215–218

42 Beerling D J. Increased terrestrial carbon storage across the palaeocene-Eocene Boundary. Palaeogeography, 2000, 161: 395–405

43 Higgins J A, Schrag D P. Beyond methane: Towards a theory for the Paleocene-Eocene Thermal Maximum. Earth Planet Sci Lett, 2006, 245: 523–537

44 Pagani M, Caldeira K, Archer D, et al. An ancient Carbon mystery. Science, 2006, 314: 1556–1557

45 Zachos J C, Röhl U, Schellenberg S A, et al. Rapid acidification of the ocean during the Paleocene-Eocene thermal maximum. Science, 2005, 308: 1611–1615

46 Bowen G J, Clyde W C, Koch P L, et al. Mammalian dispersal at the Paleocene/Eocene bounday. Science, 2002, 295: 2062–2065

47 Smith T, Rose K D, Gingerich P D. Rapid Asia-Europe-North America geographic dispersal of earliest Eocene primate *Teilhardina* during the Paleocene-Eocene thermal maximum. Proc Natl Acad Sci USA, 2006, 103: 11223–11227

48 Kelly D C, Brallower T J, Zachos J C, et al. Rapid diversification of planktonic foraminifera in the tropical pacific (ODP site 865) during the late Paleocene thermal maximum. Geology, 1996, 24: 423–426

49 Crouch E M, Heilmann-Clausen C, Brinkhuis H, et al. Global dinoflagellate event associated with the late Paleocene thermal maximum. Geology, 2001, 29: 315–318

50 Wing S L, Harrington G J, Smith F A, et al. Transient floral change and rapid global warming at the Palaeocene-Eocene boundary. Science, 2005, 310: 993–996

51 Wing S L, Harrington G J. Floral response to rapid warming in the earliest Eocene and implications for concurrent faunal change. Paleobiology, 2001, 27: 539–563

52 Smith F A, Wing S L, Freeman K H. Magnitude of the carbon isotope excursion at the Paleocene-Eocene termal maximum: The role of plant community change. Earth Planet Sci Lett, 2007, 262: 50–65

53 Schoutena S, Woltering M, Rijpstra W I C, et al. The Paleocene-Eocene carbon isotope excursion in higher plant organic matter: Differential fractionation of angiosperms and conifers in the Arctic. Earth Planet Sci Lett, 2007, 258: 581–592

54 Gibbs S J, Bown P R, Sessa J A, et al. Nannoplankton extinction and origination across the Paleocene-Eocene thermal maximum. Science, 2005, 314: 1770–1773

55 Kaiho K, Arinobu T, Ishiwatari R, et al. Latest Paleocene benthic foraminiferal extinction and environmental changes at Tawanui, New Zealand. Paleoceanography, 2003, 11: 447–465

56 Liu ZH, Pagani M, Zinniker D, et al. Global cooling during the Eocene-Oligocene climate transition. Science, 2009, 323: 1187–1190

57 Jahren H A, Sternberg L S L. Humidity estimate for the middle Eocene Arctic rain forest. Geology, 2003, 31: 463–466

58 Williams C J, Johnson A H, LePage B A, et al. Reconstruction of Tertiary *Metasequoia* forests. II. Structure, biomass, and productivity of Eocene floodplain forests in the Canadian Arctic. Paleobiology, 2003, 29: 271–292

59 Estes R, Hutchinson J H. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeog Palaeoclimat Palaeoecol, 1980, 30: 325–347

60 Eberle J, Storer J E. Northernmost record of brontotheres, Axel Heiberg Island, Canada—Implications for age of the Buchanan Lake Formation and brontothere paleobiology. J Paleontol, 1999, 73: 979–983

61 Hickey L J, West R M, Dawson M R, et al. Arctic terrestrial biota: Paleomagnetic evidence of age disparit with Mid-Norhtern latitudes during the Late Cretacous and Early Tertiary. Science, 1983, 221: 1153–1156

62 Onodera J, Takahashi K, Jordan R W. Eocene silicoflagellate and ebridian paleoceanography in the central Arctic Ocean. Paleoceanography, 2008, 23: PA1S15

63 Waddell L M, Moore T C. Salinity of the Eocene Arctic Ocean from oxygen isotope analysis of fish bone carbonate. Paleoceanography, 2008, 23: PA1S12

64 Peason P N, Palmer M R. Atmospheric carbon dioxide concentrations over the past 60 million years. Nature, 2000, 406: 695–699

65 Royer D L, Wing S L, Beerling D J, et al. Paleobotanical evidence for near present-day levels of atmospheric CO_2 during part of the Tertiary. Science, 2001, 292: 2310–2313

66 Pagani M, Zachos J C, Freeman K, et al. Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. Science, 2005, 309: 600–603

67 Lowenstein T K, Demicco R V. Elevated Eocene atmospheric CO_2 and its subsequent decline. Science, 2006, 313: 1928

68 Jahren A H, LePage B A, Werts S P. Methanogenesis in Eocene Arctic soils inferred from $\delta^{13}C$ of tree fossil carbonates. Palaeogeogr Palaeoclimatol Palaeoecol, 2004, 214: 347–358

69 Pielou E C. A Naturalist's Guide to the Arctic. Chicago: University of Chicago Press, 1994. 327

70 Jagels R, Day M E. The adaptive physiology of *Metasequoia* to Eocene high-latitude environments. In: Hemsley A R, Poole I, eds. The Evolution of Plant Physiology: From Whole Plants to Ecosystems. London: Elsevier, 2004. 401–425

71 Novacek M J. 100 million years of land vertebrate evolution: The Cretaceous-Early Tertiary transition. Ann Mo Bot Gard, 1999, 86: 230–258

72 Greenwood D R, Wing S L. Eocene continental climates and latitudinal temperature gradients. Geology, 1995, 23: 1044–1048

73 Ahn J, Brook E J. Atmospheric CO_2 and climate on millennial time scales during the last glacial period. Science, 2008, 322: 83–85

74 DeConto R M, Pollard D, Wilson P A, et al. Thresholds for Cenozoic bipolar glaciation. Nature, 2008, 455: 652–656

75 Sluijs A, Röhl U, Schouten S, et al. Arctic late Paleocene-early Eocene paleoenvironments with special emphasis on the Paleocene-Eocene thermal maximum (Lomonosov Ridge, Integrated Ocean Drilling Program Expedition 302). Paleoceanography, 2008, 23(PA1S11): 1–17

76 Yang H, Huang Y-S, Leng Q, et al. Biomolecular preservation of Tertiary *Metasequoia* fossil *lagerstätten* revealed by comparative pyrolysis analysis. Rev Palaeobot Palyno, 2005, 134: 237–256

77 Sessions A L, Burgoyne T W, Schimmelmann A, et al. Fractionation of hydrogen isotopes in lipid biosynthesis. Org Geochem, 1999, 30: 1193–1200

78 Xie S, Nott C J, Avsejs L A, et al. Palaeoclimate records in compound-specific δD values of a lipid biomarker in ombrotrophic peat. Org Geochem, 2000, 31: 1053–1057

79 Yang H, Huang Y-S. Preservation of lipid hydrogen isotope ratios in Miocene lacustrine sediments and plant fossils at Clarkia, northern Idaho, USA. Org Geochem, 2003, 34: 413–423

80 Yang H, Pagani M, Briggs D E G, et al. Carbon and hydrogen isotope fractionation under continuous light: Implications for paleoenvironmental interpretations of the High Arctic during Paleogene warming. Oecologia, 2009, 160: 461–470

81 Smith B N, Oliver J, McMillan C. Influence of carbon source, oxygen concentration, light intensity, and temperature on $^{13}C/^{12}C$ ratios in plant tissues. Bot Gaz, 1976, 137: 99–104

82 Farquhar G D, Hubick K T, Condon A G, et al. Carbon isotope fractination and plant water use efficiency. In: Rundel W, Ehleringer J R, Nagy K A, eds. Stable Isotopes in Ecological Research. New York: Springer, 1989. 21–40

83 Ögren E, Sundin U. Photosynthetic responses to variable light: A comparison of species from contrasting habits. Oecologia, 1996, 106: 18–27

84 Equiza M A, Day M E, Jagels R. Physiological responses of three deciduous conifers (*Metasequoia glyptostroboides, Taxodium distichum* and *Larix laricina*) to a continuous-light environment: Adaptive implications for the early Tertiary polar summer. Tree Physiol, 2006, 26: 353–364

85 Chikaraishi Y, Naraoka H. Compound-specific δD-$\delta^{13}C$ analysis of *n*-alkanes extracted from terrestrial and aquatic plants. Phyochemistry, 2003, 63: 361–371

86 Sachse D, Radke J, Gleixner G. Hydrogen isotope ratios of recent

lacustrine sedimentary *n*-alkanes record modern climate variability. Geochim Cosmochim Acta, 2004, 68: 4877–4889

87 LePage B A, Basinger J F. Early Tertiary *Larix* from the Buchanan Lake Formation, Canadian Arctic Archipelago, and a considerartion of the phytogeography of the genus. Geol Surv Can Bull, 1991, 403: 67–82

88 Yang H. From fossils to molecules: The *Metasequoia* tale continues. Arnoldia, 1999, 58/4-59/1: 60–71

89 Yang H. Biomolecules from living and fossil *Metasequoia*: Biological and geological applications. In: LePage B A, Williams C J, Yang H, eds. The Geobiology and Ecology of *Metasequoia*. Dordrecht-Norwell: Springer Netherlands, 2005. 253–281

90 Leng Q, Yang H, Wang L, et al. Discovery and evolution history of *Metasequoia*. In: Sha J G, ed. Centennial Celebration of Chinese Palaeontology (in Chinese). Beijing: Science Press, 2009. 360–368

91 Tripati A, Zachos J C, Marincovich L, et al. Late Paleocene Arctic coastal climate inferred from molluscan stable and radiogenic isotope ratios. Palaeogeogr Palaeoclimatol Palaeoecol, 2001, 170: 101–113

92 Jahren H A, Sternberg L S L. Eocene meridional weather patterns reflected in the oxygen isotopes of Arctic fossil wood. GSA Today, 2002, 12: 4–19

93 Richter S L, Johnson A H, Dranoff M M, et al. Oxygen isotope ratios in fossil wood cellulose: Isotopic composition of Eocene- to Holocene-aged cellulose. Geochim Cosmochim Acta, 2008, 72: 2744–2753

94 Greenwood D R, Basinger J F, Smith R Y. How wet was the Arctic Eocene rain forest? Estimates of precipitation from Paleogene Arctic macrofloras. Geology, 2010, 38: 15–18

95 Jahren A H, Sternberg L S L. Annual patterns within tree rings of the Arctic middle Eocene (ca. 45 Ma): Isotopic signatures of precipitation, relative humidity, and deciduousness. Geology, 2008, 36: 99–102

96 Boyle E A. Cool tropical temperatures shift the global δ^{18}O-T relationship: An explanation for the ice core δ^{18}O-borehole thermometry conflict? Geophys Res Lett, 1997, 24: 273–276

97 Caballero R, Langen P L. The dynamic range of poleward energy transport in an atmospheric general circulation model. Geophys Res Lett, 2005, 32: L02705

98 Yapp C J, Epstein S. Climatic significance of the hydrogen isotope ratios in tree cellulose. Nature, 1982, 297: 636–639

99 Feng X-H, Epstein S. Climatic temperature records in D data from tree rings. Geochim Cosmochim Acta, 1995, 59: 3029–3037

100 Liu W-G, Yang H. Multiple controls for the variability of hydrogen isotopic compositions in higher plant *n*-alkanes from modern ecosystems. Glob Change Biol, 2008, 14: 2166–2177

101 Liu W-G, Yang H, Li L-W. Hydrogen isotopic compositions of *n*-alkanes from terrestrial plants correlate with their ecological life forms. Oecologia, 2006, 150: 330–338

102 Worden J, Noone D, Bowman K. Importance of rain evaporation and continental convection in the tropical water cycle. Nature, 2007, 445: 528–532

103 Bonan G, Pollard D, Thompson S L. Effects of boreal forest vegetation on global climate. Nature, 1992, 359: 716–718

104 Bonan G. Ecological Climatology. 2nd ed. Cambridge-New York-Melbourne-Madrid: Cambridge University Press, 2008. 550

105 Brubaker K L, Entekhabi D, Eagleson P S. Estimation of continental precipitation recycling. J Climate, 1993, 6: 1077–1089

106 Callaghan T V. Arctic ecosystems. In: Encyclopedia of Life Sciences. John Wiley & Sons, Ltd. www.els.net, 2002. 1–8

107 Nuttall M, Callaghan T V, eds. The Arctic: Environment, People, Policy. Amsterdam: Harwood Academic Publishers, 2000. 647

108 Bonan G B, Shugart H H. Environmental factors and ecological processes in boreal forests. Ann Rev Earth Planet Sci, 1989, 20: 1–28

109 Hinzman L D, Bettez L D, Bolton W R, et al. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. Clim Change, 2005, 72: 251–298

110 Overpeck J, Hughen K, Hardy D, et al. Arctic environmental change of the last rour centuries. Science, 1997, 278: 1251–1256

111 Serreze M C, Walsh J E, Chapin F S I, et al. Observational evidence of recent change in the northern high-latitude environment. Clim Change, 2000, 46: 159–207

112 Cattle H, Crossley J. Modelling Arctic climate change. Philos Trans Roy Soc London B, 1995, 352: 201–213

113 Magnuson J J, Robertson D M, Benson B J, et al. Historical trends in lake and river ice cover in the Northern Hemisphere. Science, 2000, 289: 1743–1746

114 Chapman W L, Walsh J E. Recent variations of sea ice and air temperature in high latitudes. Bull Amer Meteorol Soc, 1993, 74: 33–47

115 Froese D G, Westgate J A, Reyes A V, et al. Ancient permafrost and a future, warmer Arctic. Science, 2008, 321: 1648

116 Mote T L. Greenland surface melt trends 1973–2007: Evidence of a large increase in 2007. Geophys Res Lett, 2007, 34: L22507

117 Stroeve J, Serreze M, Drobot S, et al. Arctic sea ice extent plummets in 2007. EOS Transe Am Geophys Union, 2008, 89: 13–14

118 Dickson R R. The integrated Arctic Ocean Observing System (iAOOS) in 2008. Cambridge: IPY (International Polar Year) International Project Office, 2009. 82

119 Gascard J C, Festy J, le Gogg H, et al. Exploring arctic transpolar drift during dramatic sea ice retreat. EOS Trans Am Geophys Union, 2008, 89: 21–28

120 Pfeffer W T, Harper J T, O'Neel S. Kinematic constraints on glacier contributions to 21st-Century sea-level rise. Science, 2008: 1340–1343

121 Lunt D J, Foster G L, Haywood A M, et al. Late Pliocene Greenland glaciation controlled by a decline in atmospheric CO_2 levels. Nature, 2008, 454: 1102–1105

122 Callaghan T V. Special issue of climate change and UV-B impacts on Arctic Tundra and polar desert ecosystems. AMBIO—A J Human Environ, 2004. 385–479

123 Nordstroem C, Soegaard H, Christensen T R, et al. Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in NE-Greenland. Theoret Appl Climat, 2001, 70: 149–166

124 Oechel W C, Vourlitis G L, Hastings S J, et al. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature, 2000, 406: 978–981

125 Stieglitz M, Giblin A, Hobbie J, et al. Simulating the effects of climate change and climate variability on carbon dynamics in Arctic tundra. Glob Biogeochem Cycle, 2000, 14: 1123–1136

126 Oechel W C, Hastings S T, Vourlitis G, et al. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature, 1993, 361: 520–523

127 Malmer N, Wallén N. Peat Formation and mass balance in Subarctic Ombrotrophic Peatland around Abisko, Northern Scandinavia. Ecol Bull, 1996, 45: 79–92

128 Serreze M C, Maslanik J A, Scambos T A, et al. A new record minimum Arctic sea ice and extent in 2002. Geophys Res Lett, 2003, 30: 1110

129 Serreze M C, Bromwich D H, Clark M P, et al. The large-scale hydro-climatology of the terrestrial Arctic drainage system. J Geophys Res, 2003, 108(D2): 8160

130 Kattsov V M, Walsh J E. Twentieth-century trends of Arctic precipitation from observational data and a climate model simulation. J Clim, 2000, 13: 1362–1370

131 Chapin F S III, Shaver G R, Giblin A E, et al. Responses of Arctic tundra to experimental and observed changes in climate. Ecology, 1995, 76: 694–711

132 Nemani R R, Keeling C D, Hashimoto H, et al. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science, 2003, 300: 1560–1563