News & Views

Optimum temperature for photosynthesis: from leaf- to ecosystem-scale

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Terrestrial plants uptake carbon dioxide from the atmosphere by photosynthetic carbon dioxide assimilation. This flux, known as gross primary productivity, is the largest carbon dioxide flux between the atmosphere and the land surface, and accounts for approximately 120 billion tonnes of carbon per year [1]. Global terrestrial gross primary productivity varies with environmental conditions, and, according to an analysis of atmospheric carbonyl sulfide records, increased by 31% over the twentieth century [2]. Air temperature plays a key role in the process of photosynthetic carbon dioxide assimilation [3]. The effect of climate warming on terrestrial vegetation productivity is spatially heterogeneous, and may change over the twenty-first century [4]. Clarifying how terrestrial plant photosynthesis varies with air temperature is critical for understanding and projecting carbon cycle-climate feedbacks against the background of climate warming [5].

The instantaneous response of photosynthesis to temperature change has been widely studied based on measurements made at the leaf-scale. The temperature response curve of leaf-scale photosynthesis is generally bell shaped, with the optimum temperature ranging from 30 to 40 °C [6]. Here, leaf photosynthesis is net photosynthesis, equating to the uptake of carbon dioxide by gross photosynthesis, minus the release of carbon dioxide by both photorespiration and dark respiration at the leaf-scale. Leaf-scale photosynthesis-temperature response is usually obtained from gas exchange measurements made at different temperatures, while the other environmental conditions are left unchanged [7]. The optimum temperature for leaf-scale photosynthesis varies with plant species, background climates, soil nutrients, etc. Farquhar et al. [3] provided a mechanistic representation of leaf-scale photosynthetic carbon dioxide assimilation response to temperature in C_3 plants. This model suggests that leaf-scale photosynthetic carbon dioxide assimilation is generally limited by the maximum carboxylation rate of Rubisco at lower temperatures, and by the maximum rate of electron transport at higher temperatures [8]. Terrestrial ecosystem models usually incorporate these leaf-scale photosynthesis-temperature response functions. However, terrestrial ecosystem models generally use the knowledge from leaf-level (not ecosystem level), e.g., the Farquhar photosynthesis equations, to project the gross primary productivity response to air temperature at ecosystem level [8]. Accurate under-

standing of the ecosystem-scale optimum temperature for photosynthesis (T_{opt}^{eco}) is important for improving the representation of ecosystem-scale photosynthesis in global terrestrial ecosystem models.

The recent work of Huang et al. [9], published in *Nature Ecology & Evolution*, provides the first global distribution of ecosystem-scale optimum temperature for photosynthesis. This work used eddy covariance measurement datasets of half-hourly gross primary productivity along with half-hourly air temperature observations, satellite-derived proxies of gross primary productivity (16-day near-infrared reflectance of vegetation [NIRv], 16-day normalized difference vegetation index [NDVI], 16-day Enhanced Vegetation Index [EVI], and monthly solar-induced chlorophyll fluorescence [SIF]), and 6-hourly gridded climate data for 1982–2013 from the Climatic Research Unit/National Centers for Environmental Protection. Huang et al. [9] specifically define T_{opt}^{eco} as "the daytime air temperature at which gross primary productivity is highest over a period of several years" (Fig. 1a). Here, the daytime air temperature is represented by daily maximum air temperature, and the gross primary productivity is represented by daily-accumulated gross primary productivity. As shown in Fig. 1a, the variation of ecosystem-scale photosynthesis across temperature bins is not only directly driven by temperature variation, but may also be influenced by other ecosystem-scale factors, such as leaf age, seasonal and interannual variation of water conditions, seasonal rhythm of plant growth, and stand age of perennial plants. This specific definition of T_{opt}^{eco} is helpful for promoting the study of T_{opt}^{eco} in that, firstly, it enables T_{opt}^{eco} to be empirically examined using ecosystem-scale gross primary productivity measurements or proxies, and, secondly, it means that the large-scale spatiotemporal characterization of T_{opt}^{eco} can be quantitatively investigated.

The global terrestrial average value of T_{opt}^{eco} is estimated to be 23 ± 6 °C, with a large spatial heterogeneity, manifested as clear latitudinal gradients [9]. Across spatial gradients, T_{opt}^{eco} is positively linearly related to background climate (mean daily maximum air temperature during the growing season). When the background temperature increases by 1 °C, T_{opt}^{eco} increases by 0.61 °C. The largest value of T_{opt}^{eco}, of about 30 °C, occurs in tropical regions, while high latitudes and mountainous regions have relatively lower values, with the minimum value close to 10 °C. The value of T_{opt}^{eco} is lower
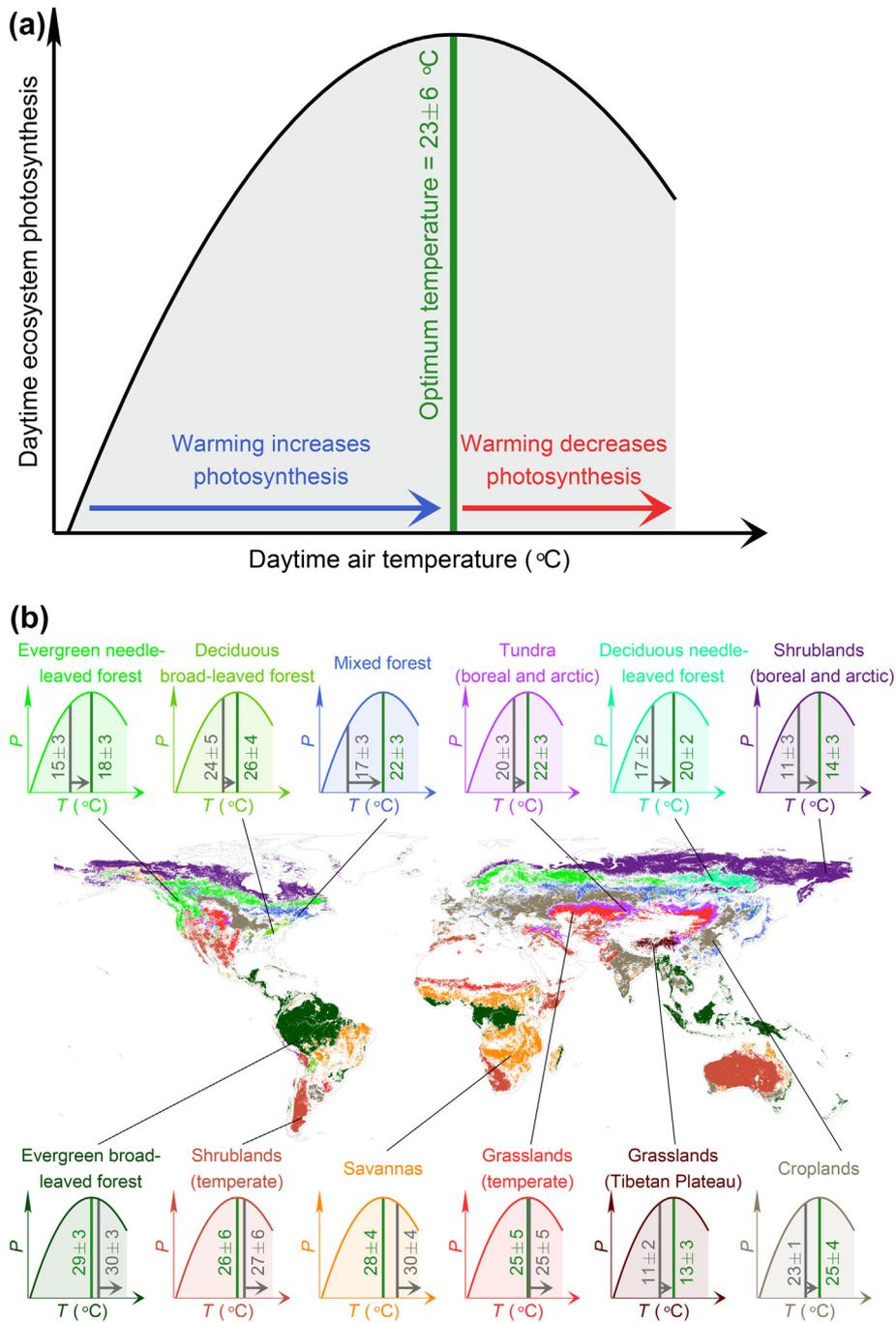
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Fig. 1. Photosynthesis-temperature relationship at ecosystem-scale. (a) The definition of ecosystem-scale optimum temperature for photosynthesis (T_{opt}^{eco}). The calculation of T_{opt}^{eco} is based on the daytime ecosystem photosynthetic response to changing daytime air temperature over several years. The daytime air temperature has seasonal-, interannual- and even decadal-dynamics, which co-vary with other conditions such as leaf age, foliar density, canopy architecture, light intensity, atmospheric carbon dioxide concentration, soil moisture, and humidity. Thus, there are usually multiple values of daytime ecosystem photosynthesis for any specific value of daytime air temperature. In the work of Huang et al. [9], daytime ecosystem photosynthesis is represented by daily-accumulated ecosystem gross primary productivity or satellite-derived proxies, and daytime air temperature is represented by daily maximum air temperature for the days in the growing-seasons of 2001–2013. The grey area indicates the range of the daytime ecosystem photosynthesis values for each value of daytime air temperature. The bell-shaped curve indicates the maximum daytime ecosystem photosynthesis for a specific value of daytime air temperature. The green vertical line indicates T_{opt}^{eco}. The average T_{opt}^{eco} across global terrestrial ecosystems is 23 ± 6 °C. Warming increases daytime ecosystem photosynthesis when the daytime air temperature is below T_{opt}^{eco}, but decreases daytime ecosystem photosynthesis when the daytime air temperature is above T_{opt}^{eco}. (b) Ecosystem-scale optimum temperature for photosynthesis for 12 vegetation types. The spatial distribution and the name of each vegetation type are shown with the same color. For each vegetation type, T_{opt}^{eco} is calculated using the relationship between daytime ecosystem photosynthesis (P) and daytime air temperature (T), as in Fig. 1a. T_{opt}^{eco} (°C) is indicated by the green vertical line and associated green numeral. The grey vertical line and associated grey numeral indicates the mean growing-season daily maximum air temperature during 2001–2013. The vegetation distribution dataset, T_{opt}^{eco}, and the mean growing-season daily maximum air temperature for 2001–2013 are from Huang et al. [9].

than the optimum temperature for leaf-scale gross photosynthetic capacity, which usually ranges from 30 to 40 °C. This difference may be partly due to that higher temperature leads to a higher vapour pressure deficit [9]. For instance, during hot periods, T_{opt}^{eco} is partly limited by high vapour pressure deficit, but leaf-scale optimum temperature is usually measured under constant vapour pressure deficit conditions across temperatures such as ranging from 15 to 25 °C [7,9]. Besides vapour pressure deficit, the other factors may influence the difference between leaf- and ecosystem-scale optimum temperature for photosynthesis such as leaf age controlled by phenology, foliar density, and vitality [9]. The global distribution of T_{opt}^{eco} is useful for identifying vulnerable regions, or biomes, against the background of climate warming, and can also be used to validate and calibrate model simulations.

Vegetation-specific T_{opt}^{eco} was investigated for 12 vegetation types: evergreen needle-leaved forest (ENF); evergreen broad-leaved forest (EBF); deciduous needle-leaved forest (DNF); deciduous broad-leaved forest (DBF); mixed forest; shrublands (temperate); shrublands (boreal and arctic); savannas; grasslands (temperate); grasslands (Tibetan Plateau); and croplands [9]. Fig. 1b shows the spatial distribution and the conceptual ecosystem photosynthesis-temperature relationship for the 12 vegetation types. Daytime air temperature is generally lower than T_{opt}^{eco} in ENF, DNF, DBF, mixed forest, shrublands and tundra in boreal and arctic regions, grasslands in Tibetan Plateau, and croplands, indicating that climate warming has potential to enhance vegetation growth in high latitude and alpine ecosystems. Daytime air temperature is generally close to, or slightly higher than, T_{opt}^{eco} in EBF, temperate shrublands and grasslands, and savannas, indicating a limited safety margin for mid- and low- latitude ecosystems.

Out of all the biomes, evergreen broad-leaved forest in the tropics has the largest T_{opt}^{eco}, with a value of 29 ± 3 °C, slightly lower than the background temperature (30 ± 3 °C) (Fig. 1b). Eddy covariance measurements from a tropical forest site in Brazil show that this site is likely close to a temperature threshold of ~29 °C, above which the ecosystem photosynthesis rate sharply declines [10]. The whole-canopy CO_2 uptake rate declined by 35%–40% when air temperature increased from 28.5 to 31.5 °C, with an increase in evaporative demand and a reduction of canopy conductance [10]. The inhibitive effect of warming on tropical forest photosynthesis may be partly due to water limitation. The negative response of the tropical terrestrial carbon sink to warming is greater in drier regions [11]. Eddy flux observations suggest that stomatal processes play a key role in determining T_{opt}^{eco} in tropical forests, and that factors affecting stomatal conductance, e.g., rising atmospheric carbon dioxide concentration, will influence tropical forest T_{opt}^{eco} [12].

Alpine grassland on the Tibetan Plateau has the smallest T_{opt}^{eco} of the 12 biomes with a value of 13 ± 3 °C (Fig. 1b). This low value is still higher than the mean daily maximum air temperature during the growing season of 11 ± 2 °C, indicating the potential for the enhancement of gross primary productivity by climate warming in this biome. Nevertheless, it should be noted that the warming induced enhancement of alpine plant growth mainly occurs in the mid-eastern Tibetan Plateau, with vegetation growth being found to be water-limited in the northeastern and southwestern Tibetan Plateau during 2000–2015 [13]. In addition, the results of a multi-level nitrogen addition field experiment suggest that non-legume species growth is nitrogen-limited in Tibetan alpine steppe [14]. However, the atmospheric nitrogen deposition rate is relatively low, with the average wet deposition of atmospheric inorganic nitrogen for the whole Tibetan Plateau being 1.6 kg nitrogen per hectare per year [15]. The way in which T_{opt}^{eco} varies

with water and nutrient conditions in alpine ecosystems in the Tibetan Plateau remains to be clarified.

Huang et al. [9] further compared T_{opt}^{eco} with the projected daily maximum air temperature by the end of the twenty-first century (2091–2100), using the output from 20 Earth System Models which participated in Phase 5 of the Coupled Model Intercomparison Project. Under three climate scenarios of representative concentration pathways 2.6, 4.5, and 8.5, the projected temperature will exceed the current T_{opt}^{eco} in tropical evergreen forests. But the projected temperature is still below the current T_{opt}^{eco} in arctic and boreal ecosystems, except under representative concentration pathway 8.5, indicating the potential for future warming to affect ecosystem carbon uptake. The acclimation of T_{opt}^{eco} in the future was considered by assuming that the value of T_{opt}^{eco} changed proportionally with daily maximum air temperature variation during 2001–2100. In this case, the projected air temperature is still above the acclimated T_{opt}^{eco} in tropical evergreen forests. This fact highlights the risk of future climate warming suppressing tropical ecosystem photosynthesis.

Overall, Huang et al.'s [9] work represents an important step forward to quantitatively understand the spatiotemporal evolution of ecosystem-scale photosynthesis-temperature relationship. Nevertheless, more accurate understanding of the mechanisms underlying the spatiotemporal change of T_{opt}^{eco} is essential for predicting the response of the terrestrial carbon cycle to future climate change, e.g., a 1.5 or 2 °C global warming above pre-industrial levels. For instance, the thermal acclimation of T_{opt}^{eco} lags behind warming, with the potential mechanism remaining to be explored by further studies. T_{opt}^{eco} may change with other factors, besides warming, such as changes in atmospheric carbon dioxide concentration, precipitation, and vegetation community composition, factors which are closely related with the terrestrial carbon cycle. These factors' quantitative effect on temporal and spatial pattern of T_{opt}^{eco} may be investigated using new global-scale dataset, e.g., global terrestrial solar-induced chlorophyll fluorescence data from the first Chinese Carbon Dioxide Observation Satellite Mission (TanSat) launched in 2016 [16,17]. Furthermore, *in situ* observation at various terrestrial ecosystems is also needed to clarify the mechanisms underlying the difference between leaf- and ecosystem-scale photosynthesis-temperature relationships. This will provide theoretical support for improving the representation of ecosystem-scale photosynthesis response to temperature variations in terrestrial ecosystem models.

Conflict of interest

The author declares that he has no conflict of interest.

Acknowledgments

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