Association plant leaf longevity to the increasing warm and arid environment

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Abstract. The longevity of plant leaves is an important factor relating to their growth strategies and responding to global climate change. The focus of this study is to present a meta-analysis of leaf life spans through an extensive literature survey. As to our knowledge, no comprehensive synthesis has yet been presented to reveal the response of leaf longevities to changing external abiotic factors, including elevated levels of carbon dioxide, increasing temperatures and shorter availability of moisture. We screened 146 abstracts from the Web of Science and summarized the results of 78 specific studies dealing with plants leaf longevity including herbaceous, shrub and tree species. The reaction of tree species was assessed in field studies while shrub and herb species were studied under experimental or field conditions. The leaf longevities of tree species are most affected by elevated levels of CO2, but not by the other two factors. Shorter leaf longevities of herbaceous species are observed in response to rising temperatures and greater moisture levels. Shrub species did not show significant changes in leaf longevity responding to any of the studied external factors. Herbaceous species were more affected by combined changes in temperature, moisture, and CO2 than shrub and tree species. In view of the whole plant biome, there are no significant responses, neither.

1. Introduction
Leaf longevity plays an important role in both plant nutrient cycling and adaptation to environmental change [1]. The carbon assimilation of the leaves and their life span during the vegetation period determines the carbon gain and loss [2]. Leaves represent significant nutrient capital in plant ecosystems [3] and their longevity or lifespan, relates to the period in which a leaf can carry out the photosynthetic function in the plant. Leaf longevity is an integral part of functional traits that organize the function of leaves as photosynthetic organs such as photosynthetic capacity, leaf mass per unit area, foliar nitrogen content and leaf dry matter content [4, 5]. Like the changing of extrinsic nutrients ability, leaf longevity might alter the nutrients amounts allocated in leaf production [6], turn the old leaves into the nutrient bank [7], or nutrient sources for new leaves [8].

It has been known for years that different biome zones have different dominating vegetation. The cold temperate and tropical (dry) seasonal climate zones are dominated (or co-dominated) by deciduous species while the wet tropics, areas with infertile soils and the boreal biome are dominated by evergreens [9]. As an essential part of plant function traits, leaf longevity is closely associated with plant phenology which is sensitive to extrinsic abiotic factors as elevated levels of carbon dioxide (CO2), increasing temperatures and shorter availability of moisture [10]. Plants are adapting to the changing biotopes caused by global warming faster than ever. Changing habitats compared to the original ones will have a definitely impact on plant function traits, leaf longevity included.
Several studies have been performed to analyze the leaf longevity patterns in relation to changing abiotic factors. The strategies of plants in their adaptation to variable resource conditions and abiotic environment [11, 12] are indicated by changed leaf longevity which could cause further shifts in community composition [13, 14]. Increasing mean annual temperature increases the leaf longevity across deciduous species, while decreases across evergreen species [15]. Kloke et al. [16] found the temperature to be the sole best predictor of the favorable period for leaf growth for deciduous plants, while water availability had only marginal effects on that. However, one conspicuous pattern remains poorly understood all across the whole plant biome.

Under the context of global warming and wetting, the elevated levels of CO₂, increasing temperatures and shorter water accessibility could be the major changes of plant habitats. We hypothesized that the elevated levels of CO₂, increasing temperatures and, lower levels of moisture had a species-specific influence on plant leaf longevity across biomes. Therefore, we investigated the overall patterns of leaf longevity in response to changing extern abiotic factors caused by global warming under the global climate change scenario.

2. Methods

2.1. Data collection

We conducted this search using the terms “leaf longevity or leaf lifespan or leaf duration and temperature or CO₂ or precipitation or water” in December 2019 using the Web of Science. For the sake of publication bias, peer-reviewed publications which satisfied the following criteria were included in the meta-analysis: (1) leaf longevity data was directly measured and at least one of the considered variables was measured; (2) the experimental and control plots were established under the same abiotic and biotic conditions, or a continuous field study and the time span of the experimental treatment was no more than five years; (3) only one variable was selected in an experiment if the experiment included more than one considered variables; (4) the amount of increment of the variables were clearly demonstrated, including the means, standard deviations and sample sizes of the selected variables which were available or could be referred to from related publications or database.

Seventy-eight plant species including trees, shrubs and herbaceous species were referred into this meta-analysis. Original data were extracted from the text, tables, figure and appendices of 43 publications, which were optimized from 146 initially selected peer-reviewed publications after screening the abstract, methods and results. Engauge software 10.4 was employed to obtain the numeric data from figures (http://digitizer.sourceforge.net). In some continuous field study e.g. measurements with leaf longevity and without direct given temperature and precipitation, climate data was extracted from the Global Climate database (http://www.worldclim.org/) using latitude and longitude. Regardless of the fact of the original experiment, higher temperature, greater moisture availability and elevated levels of CO₂ were taken as the experimental groups.

2.2. Meta-analysis

We used the effect size, AKA natural log response ratio (lnRR) to assess the responses of leaf longevity to increasing temperature, greater moisture availability and elevated levels of CO₂ to avoid biased effect estimates because the natural logarithm of a ratio has better statistical properties [17]. Response ratio (RR) was calculated as a ratio of leaf longevity change in the greater moisture levels, increasing temperature and elevated levels of CO₂ treatment (Xd) to that in the blank treatment (Xc) (Equation (1)). The log transformation is more favourable to conduct statistical analysis [17].

\[
\ln RR = \ln \frac{\bar{x}_d}{\bar{x}_c} = \ln \bar{x}_d - \ln \bar{x}_c
\]  

(1)

Variances of response ratio (v) were calculated using the following equation:
\[ v = \frac{(SD_d)^2}{n_d \bar{x}_d^2} + \frac{(SD_c)^2}{n_c \bar{x}_c^2} \]  

where \(SD_d\) and \(SD_c\) are the standard deviations of leaf longevity for control and blank treatments, respectively; \(n_d\) and \(n_c\) are the sample sizes for the respective treatments. Some un-given SDs were calculated using the mean value multiplied by the average coefficient of variance (CV) of each complete data set [18]. The mean effect sizes were calculated using means and SDs by OpenMEE [19]. If the Ln RR<0, effect is considered as negative and vice versa. The 95% confidence intervals (95% CI) were calculated by bootstrapping with 9999 iterations. Control treatment was considered as statistically significant when the 95% CIs did not include zero. Subgroup analysis was performed during the continuous random-effects meta-analysis, using Der Simonian-Laird random effects methods (Confidence level = 95%). Funnel plot and fail-safe test were both performed to explore the potential publication bias (Appendix). All statistical analyses and figures were performed using R 3.4.3 [20].

3. Results

The leaf longevity of herbaceous species (-10%) was also shortened significantly while the moisture levels got greater. The leaf lifespan of trees and shrubs had no significant responses to the greater moisture levels. Considering the whole plants, higher moisture availability had a similar response to increasing temperature, with no significant changes. In the future climate scenario accompanying by shorter moister availability, herbaceous species may have longer leaf life span (Figure 1).

![Figure 1](image1.png)

**Figure 1.** Mean effect sizes of plants leaf longevity in response to greater moisture availability. Diamond patterns represent 95% confidence intervals (CIs).

Higher temperature significantly shortened the leaf longevity of herbaceous species (-14.9%). As to trees and shrubs, they both had no significant responses to increasing temperature, neither from the point of whole plants. In the warmer future, the herbaceous species will obtain a shorter theoretical leaf life span (Figure 2).

![Figure 2](image2.png)

**Figure 2.** Mean effect sizes of plants leaf longevity in response to higher temperature. Diamond patterns represent 95% confidence intervals (CIs).
Elevated levels of CO\(_2\) significantly prolonged the leaf longevity of trees (+15.6\%) and herbaceous species (+9.5\%) but did not significantly change the leaf lifespan of shrubs. The estimated 95\% CI value of shrubs was -0.015 (-0.171, 0.140), which meant different shrub species had a different response to the elevated levels of CO\(_2\). Shrub species might even have totally adverse responses to the elevated levels of CO\(_2\) (Figure 3).

**Figure 3.** Mean effect sizes of plants leaf longevity in response to the elevated levels of CO\(_2\). Diamond patterns represent 95\% confidence intervals (CIs).

### 4. Discussion

In this short brief, we conducted a simple variable study which was not applicable in real biome. Even though the changes of leaf longevity under a certain environmental pressure was sole and specific, the mechanisms behind this is still hard to be exhibited on the same page. Species-specific differences of plant leaf longevity responding to changing habitat characteristics resulted in the different reactions across biomes [21]. Foliar life span was analyzed through specific sources of variation but that in environmental conditions they’ll influence leaf life span together. The plant’s communities are complicated and the changes among plant leaf longevity-related environmental factors are coupling.

Moisture levels are a major constraint on plant growth and productivity in most terrestrial plant communities [22, 23]. In our study, greater moisture levels significantly shortened the leaf longevity of herbaceous species. Implications of temporal water shortage on plants with respect to leaf photosynthesis [24, 25] have been studied extensively. Leaf longevity was prolonged during drought and this difference was mainly due to delayed discoloration and leaf fall [26]. Water stress triggers senescence and consequent abscission of leaves, which resulted in a shorter the leaf longevity [27]. There also are existing contradictory evidence that irrigation experiments did not alter the timing of leaf fall in many species [28]. Such results might be a consequence of factors other than soil water influencing patterns of leaf fall [29]. Moreover, water applied to plants in different ways (directly to canopy or soil) had different effects on leaf lifespan of different plants communities [30]. The fact that moisture levels induced the change in leaf lifespan was still poorly understood.

With respect to increasing temperature, only herbaceous species exhibit negative correlations. The nutrients sensitive tiller characteristics, especially the nitrogen usage was leaf lifespan-related [31], and leaf longevity is conditional on photosynthetic nitrogen use efficiency [32], which is temperature related. We extrapolated that those herbaceous species with a larger proportion of photosynthetic area are more affected by temperature based on the fact that evergreen species have longer leaf longevity than that of deciduous species [16, 33]. Leaf longevity of Mediterranean winter-deciduous shrubs were short compared to that found in temperate deciduous plants and co-occurring Mediterranean evergreens [34]. Photosynthetic nitrogen use efficiency decreased with leaf age. The shorter the leaf longevity, the greater the rate of decrease in photosynthetic nitrogen use efficiency. A similar relationship between leaf longevity was observed in 23 Amazonian tree species [35], but no significant relationship was reported in a comparison of seven tree species in an evergreen broadleaf forest in central Japan [36]. Trees, shrubs and herbaceous species have totally different photosynthetic nitrogen
use efficiency and nutrients threshold value. If we regress nutrient use efficiency of various forests against nutrient absorption rate, we obtain a decreasing relationship between the two [37], while if there is a lower limit of the nutrient amount to achieve positive net production, the relationship should be an optimum curve [38].

The results in this study demonstrate that the leaf longevity of trees and herbaceous species benefit from the increase of CO₂ level. The elevated levels of CO₂ change the exhibit anatomical and physiological structure of plants, through enhancing the carbon fixation rates [39, 40]. Leaf phenology is species-specific in response to elevated levels of CO₂. Former studies show that enhanced CO₂ tends to be less favourable to non-leguminous plants [41] and to wild plant species [39, 42, 43], than to leguminous plants and trees. What’s more, elevated levels of CO₂ did not increase the growth of roots, but greater shoots production, especially in C₃ plants [44, 45]. C₃ species and C₄ species overlapped broadly in the range of leaf nutrients concentrations and photosynthetic pathway explained some [46]. Thus, elevated levels of CO₂ prolonged the carbon gain capacity of leaves during autumnal senescence to increase their functional leaf lifespan [47], which is also species-specific. The average leaf life longevity in sunlit microhabitats has different responses to elevated levels of CO₂ compared to the shaded plants [48]. We speculate that the complexity of light availability leads to different results among trees, shrubs and herbaceous species.

5. Conclusions

Herbaceous species are most sensitive to the changing external environmental factors. The leaf longevity will shorten significantly with the increase in temperature concomitant with reduced water availability. In contrast, elevated levels of CO₂ will prolong the leaf life span of herbaceous species. Shrub species do not show significant changes in leaf longevity durations response to any of these studied environmental factors. Compared with shrubs, the leaf longevity of tree species is positively related to the elevated levels of CO₂, and the same to the other two factors. In view of the whole plant species, there are no significant responses at all.

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