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Author for correspondence:
Kun-fang Cao
e-mail: kunfangcao@gxu.edu.cn

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The physiological cold tolerance of warm-climate plants is correlated with their latitudinal range limit

Yin Wen[1,2], De-wen Qin[1,2], Bing Leng[1,2], Yun-fei Zhu[3,4] and Kun-fang Cao[1,2]

[1]Plant Ecophysiology and Evolution Group, State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, and [2]Guangxi Key Laboratory of Forest Ecology and Conservation, College of Forestry, Guangxi University, Nanning, Guangxi 530004, People's Republic of China
[3]School of Life Sciences, University of Science and Technology of China, Hefei, Anhui Province 230026, People's Republic of China
[4]Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan Province 666303, People's Republic of China

YW, 0000-0002-0262-8876; K-fC, 0000-0002-2253-7189

Plants are moving poleward and upward in response to climate warming. However, such movements lag behind the expanding warming front for many reasons, including the impediment of plant movement caused by unusual cold events. In this study, we measured the maximum photochemical efficiency of photosystem II (F_v/F_m) in 101 warm-climate angiosperm species to assess their cold tolerance at the end of a severe chilling period of 49 days in a southern subtropical region (Nanning) in China. We found that 36 of the 101 species suffered from chilling-induced physiological injury, with predawn F_v/F_m values of less than 0.7. There was a significant exponential relationship between the predawn F_v/F_m and northern latitudinal limit of a species; species with a lower latitudinal limit suffered more. Our results suggest that the range limits of warm-climate plants are potentially influenced by their physiological sensitivity to chilling temperatures and that their poleward movement might be impeded by extreme cold events. The quick measurement of F_v/F_m is useful for assessing the cold tolerance of plants, providing valuable information for modelling species range shifts under changing climate conditions and species selection for horticultural management and urban landscape design.

1. Introduction

With increasing atmospheric temperatures, the species compositions of global ecosystems are expected to change [1]. Previous studies have shown that plants living at lower altitudes and latitudes are migrating upward and poleward, respectively [2,3]. However, the rate of the movement of plant species is slower than the warming rate [2,4–6], even when surface temperatures approach the upper thermal niche limits of many plant species [7,8]. Moreover, the current tropical forest plant species are mainly survivors of the last glacial maximum, when the temperatures in the tropics were approximately 4–5°C lower than those in the present, and heat-tolerant species might have been eliminated during glaciations [9,10]. Hence, the current tropical forest plants may have narrow thermal niches and may therefore be unable to adapt to increasing temperatures [11,12]. These species will have to migrate poleward and upward for survival [4,11]. In support of this statement, Freeman & Freeman [6] observed that the geographical ranges of tropical organisms are shifting at a higher rate than those of temperate organisms [6].

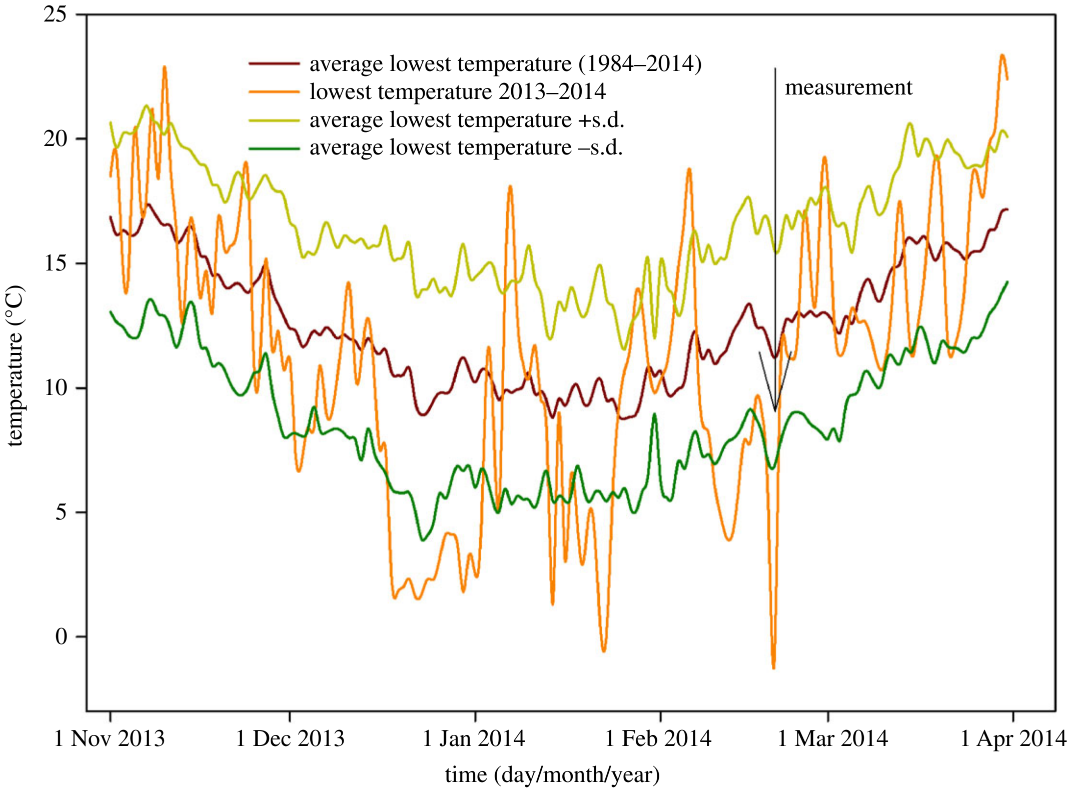

Figure 1. Comparison of daily minimum temperature during winter 2013 and early spring 2014, and the 30 yr average daily minimum temperature.

Despite the clear tendency of plants to migrate in response to climatic warming, recent findings suggest that the rate of this movement may lag behind that of warming for many reasons, especially the impediments caused by extreme cold events [13,14]. The latest report from the Intergovernmental Panel on Climate Change (IPCC) and other studies suggest that extreme cold events will continue to occur [15,16]. Plant species that have migrated or have been introduced to cooler areas from warmer regions may not adapt to or survive extreme cold events at the new sites. Extreme cold events could result in physiological stress, causing damage to warm-climate plants [13,17]. This would result in impeding the newly arrived species from establishing themselves in the plant communities.

Chlorophyll fluorescence techniques can quickly detect the efficiency of the photosynthetic apparatus of a plant. The maximum photochemical efficiency of photosystem II (PSII) (F_v/F_m) can be used as an indicator of damage to a plant's PSII [18,19]. For a healthy angiosperm plant, the predawn F_v/F_m is approximately 0.8; however, a lower predawn F_v/F_m value (e.g. of less than 0.7) indicates the effect of stress [20]. The quick and easy measurement of F_v/F_m in intact leaves has been used to assess the physiological effects of extreme cold events on tropical and subtropical plants [18,21–23].

Plants from diverse origins are cultivated in cities, providing an opportunity to assess their physiological performance in response to climate change. Here, to assess tolerance to chilling following a severe 49 day chilling event with a daily lowest temperature of less than 10°C, we measured the predawn F_v/F_m of 101 warm-climate angiosperm species in a southern subtropical city in China. We hypothesized that plants originating from warmer climates would be physiologically more sensitive to chilling, showing lower F_v/F_m values. We tested this hypothesis by examining the relationship between the predawn F_v/F_m at the end of the chilling period and the northern latitudinal range limit of the 77 species for which distribution data are available.

2. Material and methods

(a) Study sites

This study was carried out at two sites in Nanning City, China: Guangxi University (22°50′22″ N, 108°17′34″ E, 82 metres above sea level (m.a.s.l.)) and Qingxiushan Park (22°47′28″ N, 108°22′43″ E, 128 m.a.s.l.). These two sites contain cultivated native and introduced plant species, including many with tropical and subtropical origins. At these two sites, we selected 101 warm-climate angiosperm species for physiological measurements. In Nanning, the mean annual temperature is approximately 21.6°C, with the average air temperature in the coldest month (January) being approximately 12.8°C and a minimum recorded temperature of −2.4°C, and cold events with a temperature below 0°C are rare (figure 1). The meteorological data were obtained from the Nanning meteorological station (22°49′ N, 108°21′ E, 73.1 m.a.s.l.).

(b) Data collection

For each of the 101 angiosperm species, at least three individuals were selected for leaf F_v/F_m measurements. For the herb, shrub and vine species, individuals between 0.6 and 2 m in height were selected, and for the tree species, individuals between 2.5 and 6 m in height were selected. The sampled plants were either mature or young individuals. At the end of the chilling period, from 17 to 24 February 2014, we measured the predawn (3–6 h) F_v/F_m of sun leaves ($n > 6$ for each species) in the canopy of all the selected individuals using a portable fluorescence meter (FMS2, Hansatech, Norfolk, UK). Prior to these measurements, there was slight rain, and the air temperature reached −1°C. Following the chilling period, we took three more measurements (on 6, 11 and 19 March) in 13 representative species (with predawn F_v/F_m values varying from 0.34 to 0.74) to assess the recovery of F_v/F_m (figure 2*b*).

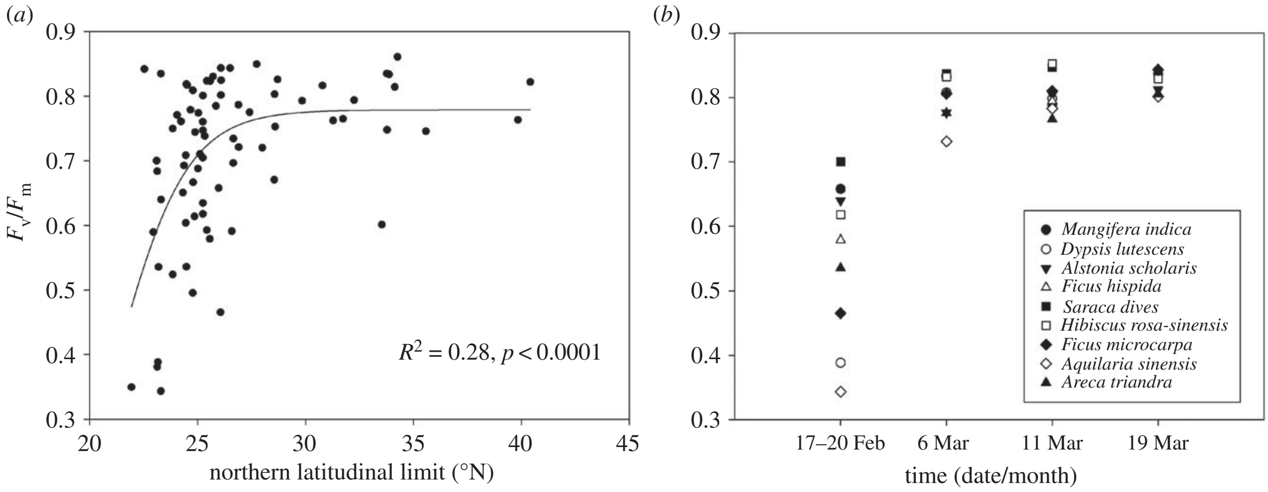

Figure 2. (*a*) The relationship between F_v/F_m at the end of the chilling period and the northern latitudinal limit of 77 plant species. (*b*) The recovery of F_v/F_m value in nine representative chilling-sensitive species (with $F_v/F_m < 0.7$ at the end of chilling period).

Of the 101 measured species, we found distribution data for 77 species on the Chinese Virtual Herbarium website (CVH) [24]. For the northern latitudinal limit of a species, we took the average latitude of its northernmost distribution using at least three distribution points that varied in latitude by less than 0.5°. Isolated extreme distributions at higher latitudes with fewer than three points were not taken into account, as they could be due to the specimens from greenhouses or unusual sites. The latitude values were obtained from Google Earth (Google, USA).

(c) Data analysis

We analysed the relationship between the predawn F_v/F_m at the end of chilling period and the latitude of the northern range limits across the 77 species using nonlinear regression analysis in SigmaPlot 12 (Systat Software, Inc., Chicago, IL, USA).

3. Results

Across the 101 species, the predawn F_v/F_m values at the end of the chilling period ranged from 0.34 to 0.86. Thirty-six species suffered from chilling-induced physiological injury, as indicated by predawn F_v/F_m values of less than 0.7. Tropical species, such as *Aquilaria sinensis*, *Lagerstroemia speciosa*, *Pouteria campechiana* and *Raphia vinifera*, suffered the most, with predawn F_v/F_m values of less than 0.4. Following the chilling event, the F_v/F_m values of nine of the 13 selected chilling-affected species had recovered to approximately 0.8 within approximately 10 days, and all 13 species completely recovered within 20 days (figure 2*b*), indicating that the prior low value of F_v/F_m was owing to chilling.

For the 77 species for which we found northern latitudinal limit data, there was a significant exponential relationship between the predawn F_v/F_m at the end of the chilling period and the northern latitudinal limit of a species ($n = 77$, $R^2 = 0.28$, $p < 0.001$; figure 2*a*). Between 20° N and 27° N, the F_v/F_m values sharply increased with an increasing latitudinal limit; however, this relationship plateaued at latitudinal limits greater than 27° N.

4. Discussion

The exponential relationship between the predawn F_v/F_m at the end of the chilling period and the northern latitudinal limit suggests that the sensitivity of warm-climate plant species to chilling is related to their northern range limit—species with a lower northern latitudinal limit are more sensitive to sudden and extreme chilling. Tropical plants are typically never subjected to subzero temperatures in their native habitats; thus, sudden and extreme chilling events at sites where they are cultivated are harmful to them. However, for most subtropical plants, such chilling events are not rare. It should be noted that the intraspecific variation in the cold tolerance of widespread species cannot be ignored [23,25]; thus, if the locations of origin of the sample plants are taken into account, the regression of chilling sensitivity and the range limit of a species could be improved.

Tropical plants are particularly sensitive to subzero temperatures because of their low investment in chemical resistance and physiological structure. Cold events cause injury to them by disturbing their physiological processes, such as photosynthesis and cell membrane integrity [26]. The decline in F_v/F_m mainly results from the interruption of linear electron transport and a reduction in the Calvin cycle. The effects of chilling on photosynthesis in a tropical plant that has newly colonized a region owing to climate warming could reduce its competitive ability within a cold-adapted plant community. This implies that extreme cold events might prevent the establishment of warm-climate plants in new sites outside of their ranges despite the new regions becoming progressively warmer.

Despite the exposure of most individuals in the present study to an extreme cold event in 2008, they still suffered from chilling stress in 2014. This suggests that even when they are exposed to prior extreme cold events, tropical plants have limited physiological acclimation to cold. In addition, our recovery measurements showed that the predawn F_v/F_m of most of the representative chilling-sensitive species recovered within approximately 10 days after the chilling period. This indicates that subzero temperatures may not be lethal to the plants included in the present study, although chilling injury might weaken their competitive vigour in the local plant community at a new site [25,26].

Recent studies have suggested the expansion of tropical areas [27,28]; this could facilitate plant migration, thus changing forest community structures. However, occasional cold events might also influence the dynamics of community composition. Quick and easy F_v/F_m measurements can be used to assess the cold tolerance of a species, thus enabling the prediction of the potential poleward or upward movement of a plant species, the prediction of changes in the natural plant community structure owing to climatic warming, and the selection of plant species for horticultural management and landscape design.

Data accessibility. Data available at http://dx.doi.org/10.5061/dryad.dp08c26 [29].

Authors' contributions. Y.W., D.-w.Q. and K.-f.C. designed the study. Y.W., D.-w.Q., B.L. and Y.-f.Z. conducted the measurements. Y.W., B.L. and Y.-f.Z. analysed the data. Y.W. and K.-f.C. wrote the manuscript. All authors critically contributed to the drafts, gave final approval for publication and agree to be held accountable for the content herein.

Competing interests. We declare no conflicting interests.

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