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Water flux responses of tropical trees and lianas to foliage loss caused by a heavy hailstorm

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Abstract

Large-diameter hail is unusual in the lowland tropics; consequently, its impact on water flux responses of trees and lianas due to foliage loss is unknown. In December 2012, Xishuangbanna Tropical Botanical Garden (21°55′N) in southern Yunnan, China, experienced the most severe hailstorm in approximately 30 years, with hailstones of 8- to 17-mm diameter falling for 10–30 min. We assessed the effect of this hailstorm on sap flux density (SFD) in response to foliage loss in six tree and three liana species. Among the trees, for a given atmospheric vapour pressure deficit (VPD), *Tectona grandis* and *Dipterocarpus tuberculatus* showed a significant reduction in sap flux density and water use during the post-hailstorm week in comparison to pre-hailstorm week. In contrast, a liana *Ventilago calyculata* showed a significant increase in SFD during the first post-hailstorm week, whereas the other tree and liana species showed no significant change in their SFD and water use. *T. grandis* also showed visible wilting during the first 5 days post-hailstorm. However, this tree species showed recovery from wilting and also no more reduction in SFD after ~7–9 days. *D. tuberculatus* also showed SFD recovery a week post-hailstorm. We conclude that the impact of a heavy hailstorm on the water flux of tropical trees and lianas was mild or neglectable. Our study documented a rare severe hailstorm occurrence and its impact on ecosystem processes of tropical forest and enhances our understanding about water flux of tropical woody species exposed to hailstorm.

KEYWORDS
Asian tropics, hailstones, mechanical leaf damage, sap flow, woody plants

1 | INTRODUCTION

A hailstone of 15 mm in diameter has a mass of approximately 1 g and a terminal velocity of 15 m s^{-1} (Field et al., 2010), its formation requires an adequate depth of cold, and therefore, it is most common in mid-latitude. In low latitudes, the freezing level is high above ground; consequently, hail tends to melt as it falls (Knight et al., 2015). Nevertheless, hail has been widely reported from the tropics, although largely at higher altitudes (>1000 m a.s.l.) and latitudes (>18° from the equator), where it can cause serious damage to crops (Frisby &

Sansom, 1967). Ground-based hail records are patchy; however, a very large hail (>25-mm diameter) can be assessed from passive microwave satellite data and shows a rather different geographical distribution to that exhibited by the more common small hail (Cecil & Blankenship, 2012). Areas with the most frequent occurrence of large hail include a broad region in subtropical north eastern Argentina and southern Paraguay, and smaller areas in Bangladesh and eastern India. These areas are followed by the central United States, northern Pakistan, north-western India, and a significant fraction of Africa. Except Africa, large hail is very rare in the core tropics (± with 15° latitude) and but common in some mountainous regions.

Reports on the impact of hail damage to wild plants in the tropics are rare and cover only a few species (e.g., Fernandes et al., 2012; Houston, 1999); therefore, they do not provide an overall picture of plant vulnerability and the effect of hail damage on ecosystem processes in low-land tropics. The province of Yunnan, southwest China, has a lower incidence of hail than most of southern China (Cao & Peters, 1997; Zhang et al., 2008), and the highest frequency occurs in the northern region of Yunnan. Consequently, tropical Xishuangbanna in the south is considered at a 'low risk' of hailstorm (Li et al., 2012). The occurrences of hail are rare in the Xishuangbanna (low altitude) but are relatively common in high altitude area of Xishuangbanna. Currently, tropical Xishuangbanna is considered at a 'low risk' of hailstorm. However, the frequency of hailstorm has increased during the last decade with climate change.

Canopy transpiration of woody plants can be assessed through sap flow, which is correlated with canopy photosynthesis (Meinzer et al., 2018). The sap flow is driven by both biotic factors such as canopy leaf biomass, sapwood hydraulic conductivity, water storage, and so forth (Meinzer et al., 2003; Scholz et al., 2007; Siddiq et al., 2017; Siddiq & Cao, 2016) and abiotic factors such as vapour pressure deficit (VPD), solar radiations, and soil water status (Siddiq et al., 2019; Zeppel et al., 2004). The response of water flux to VPD can vary among different species, and knowledge of this variation can assist an understanding of canopy stomatal regulation behaviour (Oren et al., 1999).

Hailstorm can damage the various plant parts, including foliage, branches, stems, fruits, and seeds, and extensive damage to forests, trees, crops, vegetables, and fruits has been reported (Bal et al., 2014; Wang, 1990; Xu, 1991). Fernandes et al. (2012) found that damages caused by hailstorms differed among the plants based upon their height, growth form, leaf traits, and stem type. The most visible impact of hail is the leaf damage and loss (Dwyer et al., 1994). Reduction in foliage due to mechanical damage or herbivory can have impacts on the water fluxes of plants (Nabity et al., 2009). Previous studies on the effect of hailstorm on water flux of trees have yielded variable results. An increased rate of leaf gas exchange have been observed in some species as a result of foliage loss (Craine et al., 2016; Pataki et al., 1998; Reich et al., 1993), whereas other species have shown a decrease in their photosynthetic rate (Delaney & Higley, 2006; Ellsworth et al., 1994). There are also species that do not alter their water fluxes after the defoliation (Peterson et al., 1992, 1996, 2004; Snyder et al., 2010). Pattison et al. (2011) found that the foliar damage can cause less control over water use in some species, indicating the responses may vary across species depending the microclimatic conditions of remaining leaves and the leaf anatomical features.

The low-land tropics of southwest China host tropical rainforests (Zhu et al., 2006). Lianas are an important component of tropical forests. They occupy the canopies of trees and, consequently, have leaves exposed to the direct sunlight. This exposure also has the adaptive mechanisms for their stomatal regulations and water flux control (Chen et al., 2015). Trees–lianas interactions are a characteristics of tropical forests (Bongers et al., 2002, 2005; Liu et al., 2004), but lianas have several advantages over trees including large xylem vessels that enable them to have high rates of sap flow and hydraulically support a much larger leaf area than that of the trees (Ewers et al., 1991). Lianas also have softer and more flexible tissues than trees, which makes them less susceptible to mechanical damage and enhances the rate of recovery when damage occurs (Fisher & Ewers, 1989; Putz & Holbrook, 1991). Lianas also have high canopy: stem ratio, resulting in a higher proportion of photosynthetic leaves and thus higher stomatal conductance and transpiration rates than trees. This is further supported by the deeper roots of lianas than of trees, favouring them during dry season (Chen et al., 2015).

In order to assess the impact of an unusual and severe hailstorm on trees and lianas in the XTBG, we compared our on-going sap flow measurements pre- and post-hailstorm. Our main questions for this investigation were as follows: (1) How much loss of transpiration is exhibited by trees and lianas and are lianas more affected than trees? And (2) How long does it take for recovery of transpiration after the hail damage?

2 | MATERIALS AND METHODS

2.1 | Study site and species

This study was conducted in Xishuangbanna, southern Yunnan Province, Southwest China, in the Xishuangbanna Tropical Botanical Garden (21°55′N, 101°15′E; 750 m a.s.l.) from 20 December 2012 to 4 January 2013. This area is a global biodiversity hotspot (Myers et al., 2000). Liana abundance is high in Xishuangbanna (Zhu et al., 2006) but similar to other liana-rich areas (e.g. DeWalt et al., 2010; Schnitzer, 2005). XTBG was established in 1959, covering an area over 900 ha, and displays more than 10,000 plant species in 30 living plant collections, including both indigenous and exotic species. Trees and lianas form the most important and unique display in the garden's natural landscape. The XTBG is a globally renowned research and education institute of the Chinese Academy of Sciences. Because of the exceptional display of plant diversity, plant scientists from various parts of the globe conduct research in the XTBG (Cao et al., 2006; Song et al., 2006).

The region has a typical tropical monsoon climate and a pronounced dry season from November to April. The mean annual precipitation is approximately 1560 mm, nearly 80% of which occurs during the wet season (May to October). The mean annual temperature is 21.7°C with a monthly mean temperatures of 15.9°C in the coldest month (December) and 25.7°C in the hottest month (June) (Cao et al., 2006).

Six tree and three lianas species in the XTBG were being measured for sap flow, 6 days pre-hail and 9 days of post-hail sap flow data were used to compare impact of the hailstorm. Details about studied species, their scientific names, family, diameter at breast height (DBH range) number of replicates, and comparative pre-and post-hail sap flux density are presented in Table 1. The studied trees are important timber species and have been widely planted in tropical areas for timber production (ITTO, 2008).

2.2 | Measurement of sap flux density and water use

Sap flow was measured at DBH (diameter at 1.3-m height). Each tree was equipped with two sets of 2-cm-long lab-made thermal dissipation sap flow measuring sensors (Granier, 1987). Each liana had one set of sap flow measuring sensors, which was installed near the base of the plant. The sensors were connected to data loggers with the continuous supply of electricity. The data were scanned every 30 s and an average stored every 30 min in the data loggers. All the sensors were covered with aluminium foil to protect them from any mechanical damage and direct solar radiations. The sensors were monitored regularly to ensure the proper functioning. The Granier equation was used to calculate the sap flux density (Granier, 1987). Water use was estimated by multiplying the daily integrated sap flux density with the active sapwood area of studied species. Active sapwood area was determined using the dye method as described by Siddiq et al. (2017). We used the pre- and post-hailstorm data from our ongoing sap flow measurements of trees and lianas for assessment of the hailstorm effect. The mean water use (kg per day) per unit of transpirational demand (VPD) was calculated by normalizing the mean daytime water use to the mean daytime VPD.

2.3 | Climatic data

The climatic data (temperature, relative humidity, and solar radiation) was obtained from the climatic station of XTBG, which is situated approximately 900 m away from the sap flow measurement site. The hourly mean values of the above-mentioned climatic variables were used in the analysis. The VPD was calculated from the values of temperature and relative humidity (Campbell & Norman, 1998).

2.4 | Data analysis

The difference in sap flow during the pre-hailstorm 6 days and post-hailstorm 9 days for each species was analysed using a *t*-test. These above-mentioned days were selected based upon the similar climatic conditions in both pre and post-hail duration, except the fifth and sixth post-hail days when VPD was lower (<0.4 kPa) than that of the other days. These 2 days were excluded during the comparison of pre- and post-hailstorm SFD. The statistical analyses and graphics were made using sigma plot v. 12. We used scatter plots of hourly VPD versus hourly SFD for the comparison of each species pre- and post-hailstorm. The recovery of water flux was estimated by the hysteresis of the post-hail SFD diurnal curve with the similar day's SFD for the pre-hailstorm conditions. The leaves wilting in *Tectona grandis* was absorbed by calculating the ratio between the number of wilted and non-wilted leaves at the middle and top of the canopy.

3 | RESULTS

3.1 | Pre- and post-hail climatic variables

The mean daytime VPD during the pre-hailstorm week was 0.57 (±0.04) kPa, whereas during in the post-hailstorm week, it was

TABLE 1 The tree and liana species that were measured for sap flow and their abbreviations, family, the diameter at breast height (DBH) range, number of replicates, and mean daily integrated sap flux density (g m^{-2} s^{-1}, ±SE) recorded over six of pre-hail and nine post-hailstorm days

Sr no.	Scientific name	Species abbreviations and family	DBH range (cm)	Replicates	Height (m)	Pre-hail	Post-hail	*P* value
Trees								
1.	*Beilschmiedia brachythyrsa*	BB, Lauraceae	23–25	2	19–20	261.1 ± 28.5	285.7 ± 11.0	0.39
2.	*Dipterocarpus alatus*	DA, Dipterocarpaceae	30–55	3	27–33	212.4 ± 16.3	216.6 ± 10.3	0.94
3.	*Dipterocarpus tuberculatus*	DT, Dipterocarpaceae	19–39	4	24–29	188.32 ± 11.86	151.46 ± 7.57	0.04
4.	*Hopea hainanensis*	HH, Dipterocarpaceae	19–30	3	18–24	210.3 ± 17.3	194.89 ± 9.0	0.08
5.	*Tectona grandis*	TG, Verbenaceae	17–57	4	18–20	143.44 ± 6.44	101.89 ± 6.44	0.007
6.	*Vatica guangxiensis*	VG, Dipterocarpaceae	16–24	3	13–17	242.45 ± 13.36	222.68 ± 10.56	0.1
Lianas								
1.	*Celastrus peniculatus*	CP, Celasteraceae		2		722.9 ± 46.7	888.74 ± 67.33	0.09
2.	*Dregea volubilis*	DV, Apocynaceae		2		275.2 ± 10.8	318.5 ± 17.5	0.2
3.	*Ventilago calyculata*	VC, Rhamnaceae		2		508.7 ± 22.6	709.82 ± 34.65	<0.001

0.53 (±0.02) kPa. The mean photosynthetically active radiation (PAR) during the pre-hailstorm week was 561.91 (±54.1) μmol m^{-2} s^{-1}, whereas in the post-hailstorm week, it was 595.13 (±23.65) μmol m^{-2} s^{-1} (Figure 2). Neither VPD nor PAR was significantly different between the pre- and post-hailstorm days ($P > 0.05$).

3.2 | Hailstorm foliage damage

In the late afternoon of 26 December 2012, the XTBG experienced a severe hailstorm that lasted for 10–30 min, with hailstones 8–17 mm in diameter. Both native and cultivated plants were damaged.

Outside the XTBG, the storm damaged 900 ha of crops, particularly vegetables, bananas, and maize, causing an estimated 8 million-yuan renminbi loss due to crop damage (Xishuangbanna Civil Affairs Bureau). In the XTB, the presence of near-pristine limestone forest, disturbed tropical seasonal forest, forest regrowth, and >10,000 cultivated plant species closely monitored by experienced horticulturalists provided an exceptional opportunity to observe the susceptibility of tropical plants to hail damage. The hail damage in the tree plantation stands was observed from the fallen foliage on the ground (Figure 1). The leaves of some plants were completely removed, and holes were observed in the surfaces of leaves on the ground. Greater foliage damage and loss was observed in stands of *T. grandis* (teak) plantation than in the other tree plantation stands. Approximately 40% of the top canopy and 25% of mid-canopy leaves of *T. grandis* exhibited wilting in the initial five to seven post-hailstorm days.

3.3 | Hailstorm impact on water flux

The comparison of daily integrated SFD in the pre- and post-hailstorm weeks also showed the hailstorm did not significantly affect the water flux of the most studied species except for a reduction in two of the tree species (*Dipterocarpus tuberculatus*, and *T. grandis*) and an increase in one liana species (*Ventilago calyculata*). Among the trees, the difference in mean daily integrated water flux pre- and post-hailstorm ranged from 2.5% to 27%. A minimum and non-significant reduction was observed in *Vatica gaunagxiensis*, while the maximum reduction was observed in *T. grandis*, (−27%) followed by *D. tuberculatus* (−21%). The other three species, *Beilschmiedia brachythyrsa*, *Dipterocarpus alatus*, and *Hopea hainaniensis* did not show the significant difference in water flux after the hailstorm as

FIGURE 1 The morning of post-hailstorm Day 1 at the study site. (a) Fallen *Tectona grandis* leaves along the hailstones, (b) a hole in the surface of *T. grandis* leaf made by hailstone, (c) foliage damage at the sap flow measuring site in *T. grandis* stand. (d) Foliage damage at the sap flow measuring site in a dipterocarp stand

compared to the pre-hailstorm week. Both *D. tuberculatus* and *T. grandis* showed the significant post-hailstorm reduction, especially during the initial post-hailstorm days (from Days 1 to 5), where the SFD was 40% lower during the first day in *T. grandis*, and 15% lower in *D. tuberculatus* than the pre-hailstorm values. However, on Day 9, the SFD was reduced by 4% and 5% for both *T. grandis* and *D. tuberculatus*, respectively. Following this recovery from the reduction of the SFD of *T. grandis*, the wilted leaves resumed their normal position as the days progressed. Hence, with the passage of time, gradual increase in SFD was observed, and it approached the mean pre-hail SFD value (Figures 2 and 3).

The hourly mean SFD was non-linearly correlated with hourly mean VPD for both trees and lianas during the pre- and post-hailstorm weeks, respectively (Figure 4). At a given VPD, two tree species *D. tuberculatus* and *T. grandis* showed reduced SFD during the post-hailstorm week as compared to the pre-hailstorm week, whereas a liana species *V. calyculata* showed increased SFD during the post-hailstorm week as compared to pre-hailstorm week. Other species showed the overlapped regression lines for the relationship of SFD against VPD between the pre- and post-hailstorm weeks.

All the three lianas species showed an increase in their daily integrated water flux after the hailstorm, ranging from 8% to 39%; the minimum increase was observed in *Dregea volubilis*, whereas the maximum was observed in *V. calyculata* (39.7%; Figure 2). Our further analysis of water use (kg) per unit of transpirational demand (kPa) also indicated the same results (Figure 5).

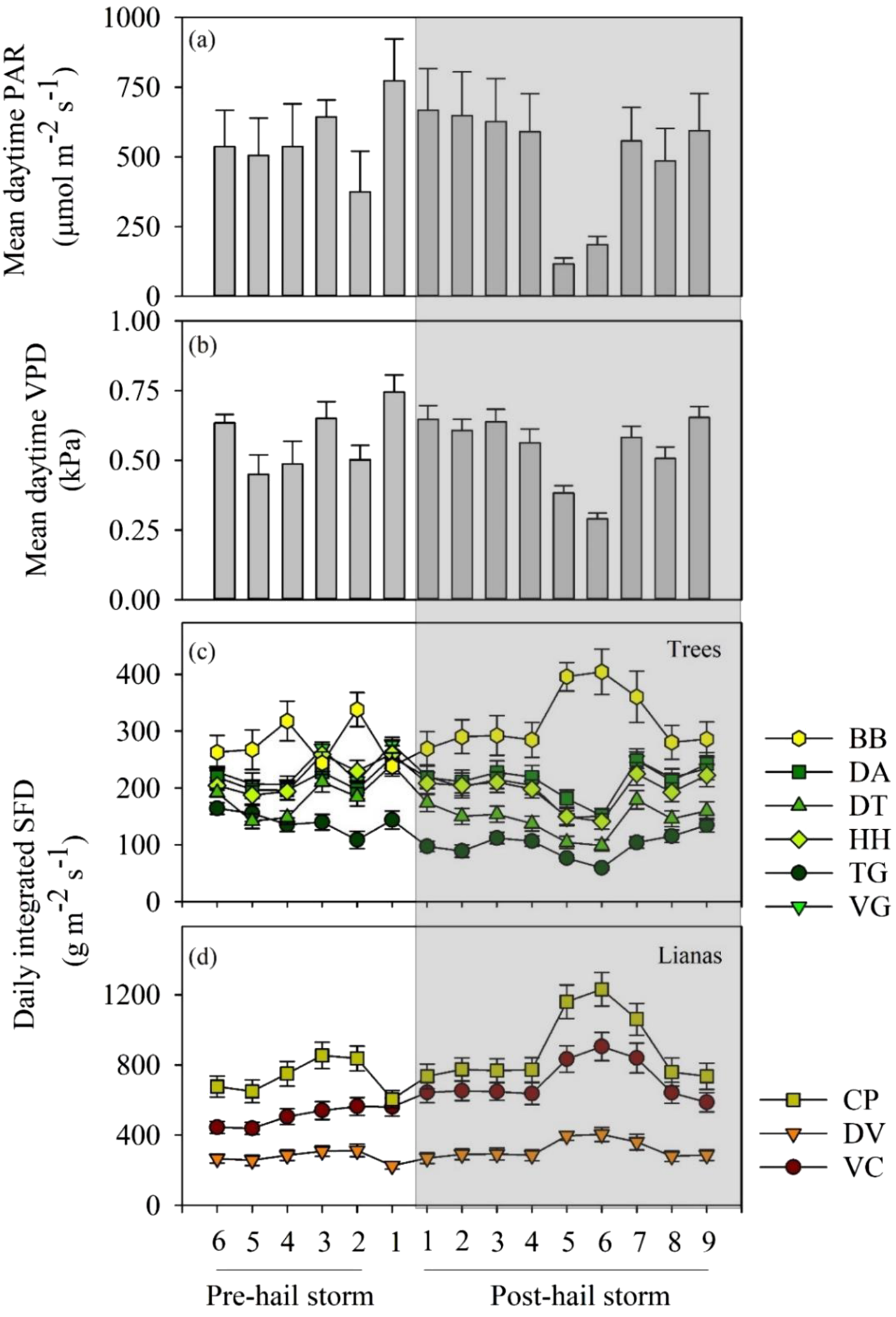

FIGURE 2 (a) Daytime mean vapour pressure deficit (VPD), (b) photosynthetically active radiations (PAR), (c) daily integrated sap flux density of trees ± SE, and (d) daily integrated sap flux density ± SE of three liana species in the pre- and post-hailstorm days. The fifth and sixth post-hailstorm days indicate cloudy conditions. The species abbreviations are listed in Table 1

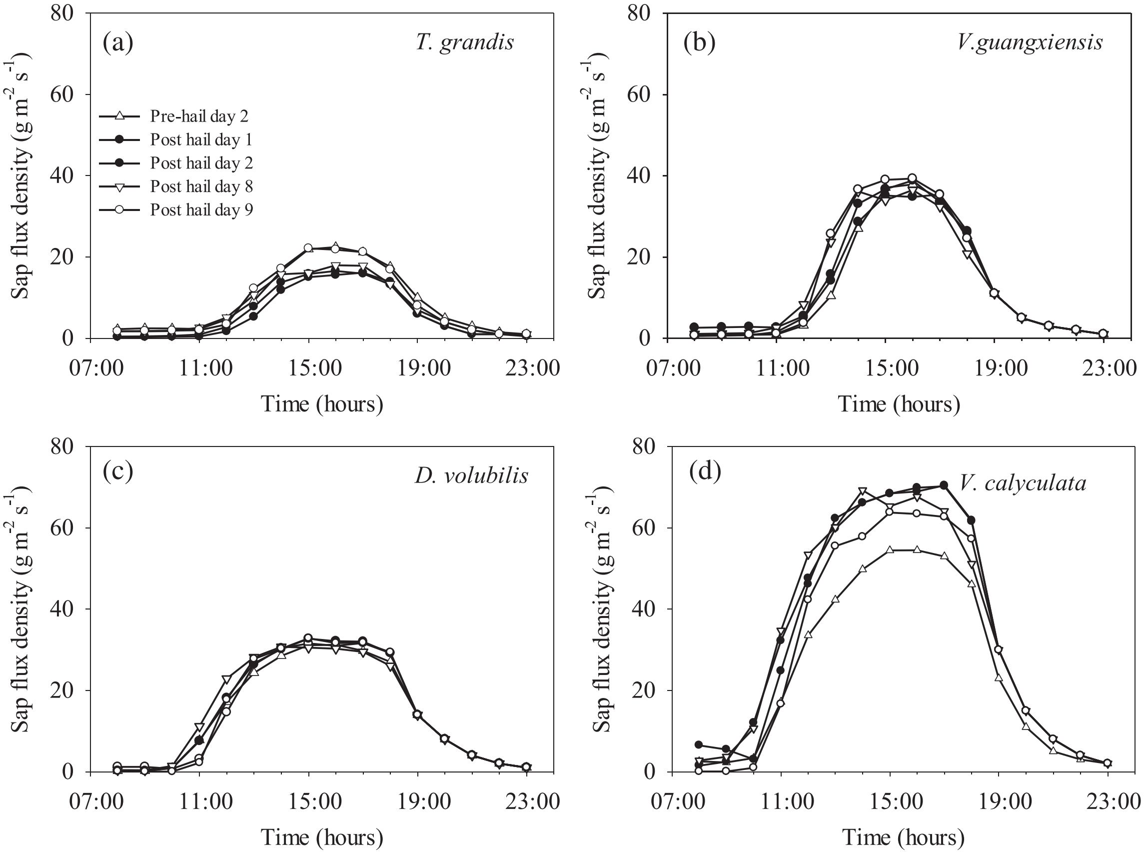

FIGURE 3 Diurnal pattern of sap flux density in the tree Tectona grandis and Vatica guangxiensis (a,b), and liana species Dregea volubilis, and Ventilago calyculata (c,d) during day 2 of the pre-hailstorm and the days 1, 2, 8 and 9 of the post-hailstorm periods

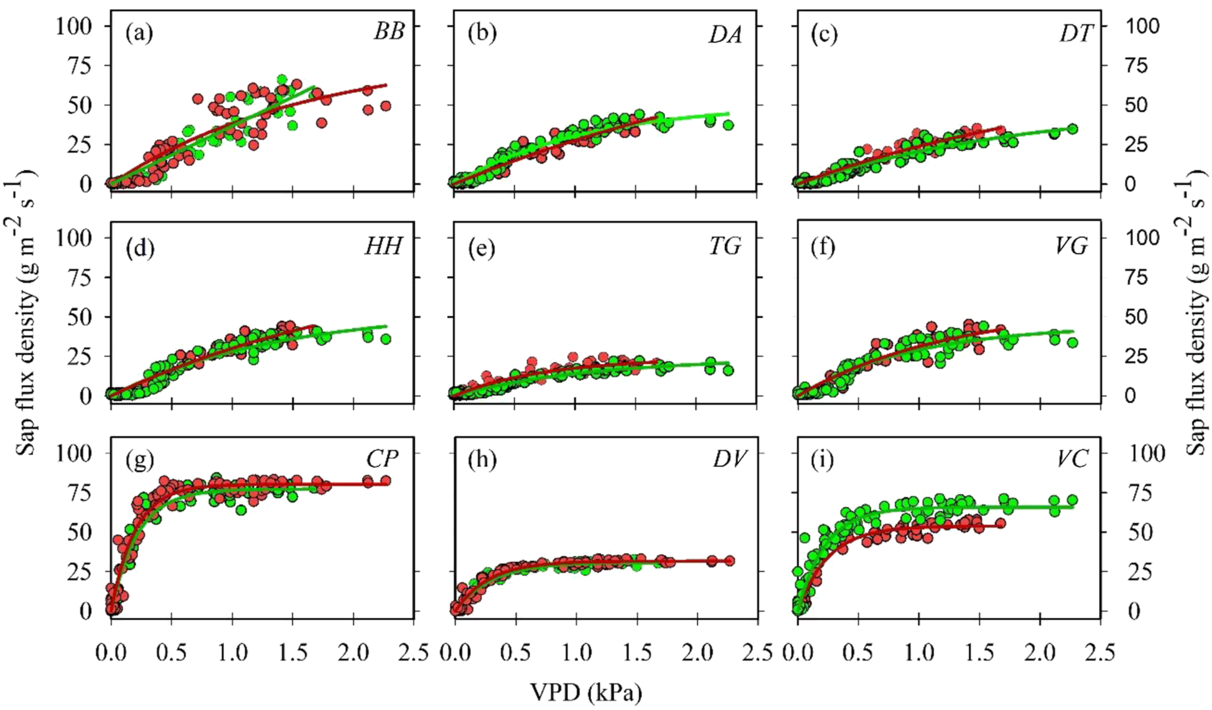

FIGURE 4 Relationship of daytime hourly mean vapor pressure deficit (VPD) with hourly mean sap flux density (SFD) for trees (a–f) and lianas (g–i) during the pre-hailstorm 6 days and post-hailstorm 9 days. The exponential rise to the maximum function was fitted for the regressions, R_2 was >0.85 and P < 0.0001 for all the species studied. Red symbols indicate pre-hailstorm while the green symbols indicate post-hailstorm data

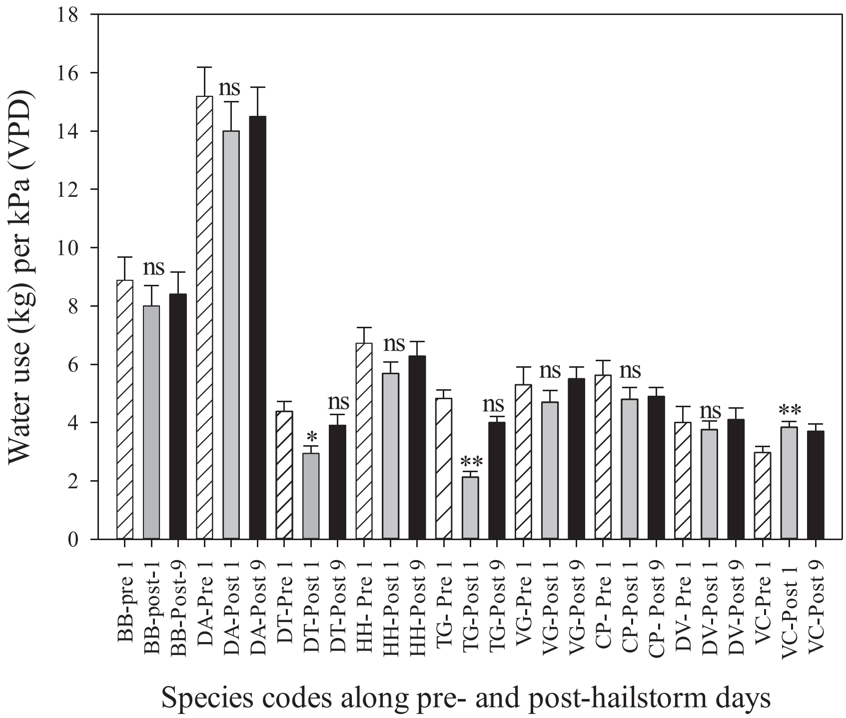

FIGURE 5 Pre- and post-hailstorm mean water use along with ±SE for trees and lianas. Species abbreviations are listed in Table 1. $^*P < 0.05$, $^{**}P < 0.01$, and ns indicates not significant

4 | DISCUSSION

This study provides the first report on the different water flux response between tropical trees and lianas exposed to a severe hailstorm. Given that climatic drivers of water flux (VPD and PAR) were not significantly different during the pre-hailstorm 6 days and post-hailstorm 9 days, it appeared that the observed differences in water flux are due to the foliage damage from hail. The observed recovery from damage of two species (*T. grandis* and *D. tuberculatus*) was gradual, and complete recovery of SFD had occurred by the ninth post-hailstorm day. Our observation of a post-hailstorm increase in water flux in the liana species could be because of the occurrence of these liana species on the top of tree canopies; consequently, the lianas leaves might have been more exposed to hailstorm than the tree leaves and hence incurred more damage. The lianas may be more responsive to injuries by increasing sap flux through physiological changes that help with repair or regrowth after foliage damage, as its leaves are potentially more frequently attacked by insects because of their location in the upper canopies of trees. Further, the damaged leaves and the canopy leaf losses could potentially have increased the exposure of the less-exposed lower canopy leaves to the solar radiations, which partly compensated for the leaf loss. Pattaki et al. (1998) observed 45% increase in water flux in *Pinus taeda* due to artificial leaf damage. Another factor contributing to such a response could be cuticular water loss, because when the leaves were injured, their cuticle layer would have been damaged (Aldea et al., 2006). Although the loss of foliage was evident from the freshly fallen leaves on the ground but the supply of water through the xylem was not affected, hence the water flux may have increased because of the increased exposure of the rest of the foliage to light (Pieruschka et al., 2010). According to Nadine et al. (2019) plants can be more responsive to achieving the recovery of their water status after the tissue damage if the water is available. Our previous study showed that water potentials of trees at the study site was the same during the dry season and the rainy season because of the access of their roots to ground water sources (Siddiq & Cao, 2016). Different levels of hail damage on plants and their non-uniform responses to such damage have also been reported by Fernandes et al. (2012). Our finding of a higher water flux in response to foliage damage by hail in a liana species is consistent with the study of Craine et al. (2016), who reported increased water consumption in *Tamarix* species resulting from defoliation. Similar findings of increased canopy photosynthetic activity after foliage loss were observed by Turnbull et al. (2007).

5 | CONCLUSION

We conclude that the effects of a heavy hailstorm on the canopy physiology of tropical woody plants were mild or neglectable as assessed through different short-period responses of water flux between trees and lianas. Tree species with large leaf sizes were more affected for a short duration. Whereas one of the liana species showed short-duration increase water flux during the post-hailstorm days. Our findings provide novel information on the effect of a severe hailstorm on physiological processes of a tropical forest.

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DATA AVAILABILITY STATEMENT

The data can be available upon request from the corresponding authors.

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REFERENCES

Aldea, M., Hamilton, J. G., Resti, J. P., Zangerl, A. R., Berenbaum, M. R., Frank, T. D., & DeLucia, E. H. (2006). Comparison of photosynthetic damage from arthropod herbivory and pathogen infection in understory hardwood samplings. *Oecologia*, *149*, 221–232. https://doi.org/10.1007/s00442-006-0444-x

Bal, S. K., Saha, S., Fand, B. B., Singh, N. P., Rane, J., & Minhas, P. S. (2014). Hailstorms: Causes, damage and post-hail management in Agriculture. Technical bulletin no. 5, National Institute of Abiotic Stress Management, Malegaon, Baramati. 413 115, Pune, Maharashtra (India) p. 44.

Bongers, F., Parren, M. P. E., & Traoré, D. (Eds.) (2005). *Forest climbing plants of West Africa: Diversity, ecology and management*. Wallingford UK: CAB International.

Bongers, F., Schnitzer, S. A., & Traore, D. (2002). The importance of lianas and consequences for forest management in West Africa. *Bioterre*, *2002*, 59–70.

Campbell, G. S., & Norman, J. M. (1998). Water vapor and other gases. In G. S. Campbell & J. M. Norman (Eds.), *An introduction to environmental biophysics* (2nd ed.) (pp. 37–51). New York: Springer. https://doi.org/10.1007/978-1-4612-1626-1_3

Cao, K. F., & Peters, R. (1997). Species diversity of Chinese beech forests in relation to warmth and climatic disturbances. *Ecological Research*, *12*, 175–189.

Cao, M. X., Zou, M., Warren, M., & Zhu, H. (2006). Tropical forests of Xishuangbanna, China. *Biotropica*, *38*(3), 306–309. https://doi.org/10.1111/j.1744-7429.2006.00146.x

Cecil, D. J., & Blankenship, C. B. (2012). Toward a global climatology of severe hailstorms as estimated by satellite passive microwave imagers. *Journal of Climate*, *25*, 687–703. https://doi.org/10.1175/JCLI-D-11-00130.1

Chen, Y. J., Cao, K. F., Schnitzer, S. A., Fan, Z. X., Zhang, J. L., & Bongers, F. (2015). Water-use advantage for lianas over trees in tropical seasonal forests. *The New Phytologist*, *205*, 128–136. https://doi.org/10.1111/nph.13036

Craine, E. B., Evankow, A., Wolfson, K. B., Dalton, K., Swedlund, H., Bowen, C., & Heschel, M. S. (2016). Physiological response of *Tamarix ramosissima* (Tamaricaceae) to a biological control agent. *Western North American Naturalist*, *76*(3), 339–351. https://doi.org/10.3398/064.076.0310

Delaney, K. J., & Higley, L. G. (2006). An insect countermeasure impacts plant physiology: Midrib vein cutting, defoliation and leaf photosynthesis. *Plant, Cell & Environment*, *29*, 1245–1258. https://doi.org/10.1111/j.1365-3040.2006.01504.x

DeWalt, S. J., Schnitzer, S. A., Chave, J., Bongers, F., Burnham, R. J., Cai, Z., Chuyong, G., Clark, D. B., Ewango, C. E., Gerwing, J. J., & Gortaire, E. (2010). Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, *42*, 309–317. https://doi.org/10.1111/j.1744-7429.2009.00589.x

Dwyer, L. M., Stewart, D. W., Evenson, L., & Ma, B. L. (1994). Maize growth and yield following late summer hail. *Crop Science*, *34*, 1400–1403. https://doi.org/10.2135/cropsci1994.0011183X003400050047x

Ellsworth, D. S., Tree, M. T., Parker, B. L., & Skinner, M. (1994). Photosynthesis and water-use efficiency of sugar maple (*Acer saccharum*) in relation to pear thrips defoliation. *Tree Physiology*, *14*, 619–632.

Ewers, F. W., Fisher, J. B., & Fichtner, K. (1991). Water flux and xylem structure in vines. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 127–160). Cambridge: Cambridge University Press.

Fernandes, G. W., Oki, Y., de Sá, C. M., Sales, N. M., Quintino, A. V., Freitas, C., & Caires, T. (2012). Hailstorm impact across plant taxa: Leaf fall in a mountain environment. *Neotropical Biology and Conservation*, *7*, 8–15.

Field, P.R., Hand, W., Cappelluti, G., McMillan, A., Foreman, A., Stubbs, D., & Willows, M. (2010). Hail threat standardization: Final report for EASA.2008.OP.25. (Met Office, U. K).

Fisher, J. B., & Ewers, F. W. (1989). Wound recovery in stems of lianas after twisting and girdling injuries. *Botanical Gazette*, *150*, 251–265. https://doi.org/10.1086/337770

Frisby, E. M., & Sansom, H. W. (1967). Hail incidence in the tropics. *Journal of Applied Meteorology*, *6*, 339–354. https://doi.org/10.1175/1520-0450(1967)006%3C0339:HIITT%3E2.0.CO;2

Granier, A. (1987). Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology*, *3*(4), 309–319. https://doi.org/10.1093/treephys/3.4.309

Houston, W. A. (1999). Severe hail damage to mangroves at Port Curtis, Australia. *Mangroves and Salt Marshes*, *3*, 29–40. https://doi.org/10.1023/A:1009946809787

ITTO. (2008). *Annual review and assessment of the world's timber situation*. International Tropical Timber Organization: Yokohama.

Knight, C., Knight, N., & Brooks, H. E. (2015). Hail and hailstorms. In G. R. North, J. Pyle, & F. Zhang (Eds.), *Encyclopedia of atmospheric sciences* (2nd ed., Vol. 3) (pp. 334–338). Amsterdam: Elsevier.

Li, M., Zhu, Y., & Ji, W. (2012). Risk evaluation of hail disaster in Yunnan tobacco planting areas based on GIS. *Chinese Journal of Agrometeorology*, *33*, 129–133.

Liu, W. J., Meng, F. R., Zhang, Y. P., Liu, Y. H., & Li, H. M. (2004). Water input from fog drip in the tropical seasonal rain forest of Xishuangbanna, Southwest China. *Journal of Tropical Ecology*, *20*, 517–524.

Meinzer, F. C., James, S. A., Goldstein, G., & Woodruff, D. (2003). Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell & Environment*, *26*, 1147–1155.

Meinzer, F. C., Woodruff, D. R., Domec, J.-C., Goldstein, G., Campanello, P. I., Gatti, M. G., & Villalobos-Vega, R. (2018). Coordination of leaf and stem water transport properties in tropical forest trees. *Oecologia*, *156*, 31–41.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858.

Nabity, P. D., Zavala, J. A., & DeLucia, E. H. (2009). Indirect suppression of photosynthesis on individual leaves by arthropod herbivory. *Annals of Botany*, *103*(4), 655–663.

Nadine, K. R., Rüdiger, G., Stefan, M., & Almut, A. (2019). Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress. *Tree Physiology*, *39*(8), 1285–1299. https://doi.org/10.1093/treephys/tpz032

Oren, R., Sperry, J. S., Katul, G. G., Pataki, D. E., Ewers, B. E., Phillips, N., & Schafer, K. V. R. (1999). Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapor pressure deficit. *Plant, Cell and Environment*, *22*(10), 1515–1526.

Pataki, D. E., Oren, R., & Phillips, N. (1998). Response of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *Journal of Experimental Botany*, *49*(322), 871–878.

Pattison, R. R., D'Antonio, C. M., & Dudley, T. L. (2011). Biological control reduces growth, alters water relations of saltcedar tree (*Tamarix* spp.) in western Nevada, USA. *Journal of Arid Environments*, *75*, 346–352.

Peterson, R. K. D., Danielson, S. D., & Higley, L. G. (1992). Photosynthetic responses of alfalfa to actual and simulated alfalfa weevil (Coleoptera: Curculionidae) injury. *Environmental Entomology*, *21*, 501–507.

Peterson, R. K. D., Higley, L. G., & Spomer, S. M. (1996). Injury by *Hyalaphora cecropia* (Lepidoptera: Saturniidae) and photosynthetic responses of apple and crabapple. *Environmental Entomology*, *25*, 416–422.

Peterson, R. K. D., Shannon, C. L., & Lenssen, A. W. (2004). Photosynthetic responses of legume species to leaf-mass consumption injury. *Environmental Entomology*, *33*, 450–456.

Pieruschka, R., Huber, G., & Berry, J. A. (2010). Control of transpiration by radiation. *Proceedings of the National Academy of Sciences, USA*, 107, 13372–13377. https://doi.org/10.1073/pnas.0913177107

Putz, F. E., & Holbrook, N. M. (1991). Biochemical studying of vines. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 73–97). Cambridge: Cambridge University Press.

Reich, P. B., Walters, M. B., Krause, S. C., Vanderdlien, D. W., Raffa, K. F., & Tabone, T. (1993). Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. *Trees*, *7*, 67–77.

Schnitzer, S. A. (2005). A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist*, *166*, 262–276.

Scholz, F. G., Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C., & Miralles-Wilhelm, F. (2007). Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant, Cell & Environment*, *30*, 236–248.

Siddiq, Z., & Cao, K. F. (2016). Increased water use in dry season in eight deiperocarp species in a common plantation in the northern boundary of Asian tropics. *Ecohydrology*, *9*, 871–881.

Siddiq, Z., Chen, Y. J., Zhang, Y. J., Zhang, J. L., & Cao, K. F. (2017). More sensitive response of crown conductance to VPD and larger water consumption in tropical evergreen than in deciduous broadleaf timber trees. *Agricultural and Forest Meteorology*, *247*, 399–407.

Siddiq, Z., Tomlinson, K. W., Zhu, S. D., & Cao, K. F. (2019). Does fluctuation of meteorological conditions across years influence stand transpiration of *Tectona grandis* plantation? *Ecohydrology*, *12*(6), 1–10.

Snyder, K. A., Uselman, S. M., Jones, T. J., & Duke, S. (2010). Ecophysiological responses of salt cedar (*Tamarix* spp. L) to the northern tamarisk beetle (*Diorhabda carinulata* Desbrochers) in a controlled environment. *Biological Invasions*, *12*, 3795–3808.

Song, F.-Q, Zhang, Y.-P, Yang, Q, Xu, Z.-F., Xiao, L.-Y., & Hu, J.-X. (2006). The adaptability of introduced plants in Xishuangbanna Tropical Botanical Garden. *Plant Diversity*, *28*(06), 615–623.

Turnbull, T. L., Adams, M. A., & Warren, C. R. (2007). Increased photosynthesis following partial defoliation of field-grown *Eucalyptus globulus* is not caused by increased leaf nitrogen. *Tree Physiology*, *27*, 1481–1492.

Wang, Y. S. (1990). Hailstorm hazard in China. In G. Z. Sun, Y. S. Wang, & P. Y. Zhang (Eds.), *Natural hazard; in China* (pp. 127–135). Beijing: Academic Press China. (in Chinese)

Xu, Y. H. (Ed.) (1991). *Climate of Southwest China*. Beijing: Meteorological Press China. (in Chinese)

Zeppel, M. J. B., Murray, B. R., Barton, C., & Eamus, D. (2004). Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia. *Functional Plant Biology*, *31*, 461–470. https://doi.org/10.1071/FP03220

Zhang, C., Zhang, Q., & Wang, Y. (2008). Climatology of hail in China: 1961–2005. *Journal of Applied Meteorology and Climatology*, *47*, 795–804.

Zhu, H., Cao, M., & Hu, H. (2006). Geological history, flora, and vegetation of Xishuangbanna, Southern Yunnan, China. *Biotropica: The Journal of Biology and Conservation*, *38*(3), 310–317.

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