#### RESEARCH



# Effects of drought and moisture stress on the growth and ecophysiological traits of *Schima superba* seedlings

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#### Abstract

Changes in rainfall patterns are important environmental factors affecting plant growth, especially when larger precipitation events and prolonged drought periods occur in subtropical regions. There are many studies on how drought reduces plant biomass through drought-sensitive functional traits, but how excess water affects plant growth and ecophysiology is still poorly understood. Therefore, a greenhouse experiment was conducted on *Schima superba* (Theaceae), a dominant tree species in subtropical forests and commonly used in forestry, in a closed chamber under control (25% soil water content (SWC) as in local forests), drought stress (D, 15% SWC) and moisture stress (W, 35% SWC). Plant growth and ecophysiological traits related to morphology, leaf gas exchange, water potential and structural traits were measured. Compared to control, *S. suberba* under dry conditions significantly decreased its aboveground biomass, photosynthetic rate (A), leaf water potential and nitrogen use efficiency, but increased intrinsic water use efficiency, root to shoot ratio and specific root length. *S. superba* under wet conditions also significantly decreased its total biomass, aboveground biomass and specific root length, while W had no effect on A and leaf water potential. Our results indicate that *S. superba* shows a decrease in carbon gain under drought stress, but less response under wet conditions. This emphasizes the need to consider the strength and frequency of rainfall pattern changes in future studies because rainfall may either alleviate or intensify the effects of drought stress depending on the moisture level, thus suitable water conditions is important for better management of this tree species in subtropical China.

Keywords Altered precipitation · Plant productivity · Gas exchange · Soil moisture · Plant ecophysiology

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# Introduction

Climate change is expected to have significant impact on various ecosystems, causing seasonal and spatial variations in temperature and precipitation (Greaver et al. 2016). Precipitation regimes are expected to become more unpredictable, posing a growing challenge for forest managers. In addition, the hydrological cycle is expected to intensify globally (Knapp et al. 2015; O'Brien et al., 2024), increasing the frequency and severity of climate extremes such as severe droughts and heavy rainfall (Beier et al. 2012; Ke et al. 2022). Drier regions are increasing and will be most catastrophic in Central and Southwest Asia by 2050 (Agrawala et al. 2001) and climate change could have significant negative impact on trees growing in the wetter, hotter areas (Heilmayr et al. 2023). Droughts have become increasingly frequent in China (Duan et al. 2022), and have led to significant losses in productivity (Zhou et al. 2017). This phenomenon holds particular relevance in southern China,

which is distinguished by a transition from a hot and humid summer to a warm dry winter, thereby leading to fluctuating moisture levels. Therefore, such moisture level shifts due to changing precipitation patterns would have a dramatic influence on plant ecophysiological processes, understanding of which is of utmost importance.

Insufficient rainfall or low soil moisture can cause drought stress in plants, which can lead to a range of physiological, biochemical, and genetic responses, and severely limit plant growth (Seki et al. 2007; Vadez et al. 2012). Plants exposed to a water deficit can reduce leaf water potential and stomatal conductance (Bohnert et al. 1995; Bray 1997). Measuring leaf water relations can serve as a valuable method for assessing overall plant growth. According to (Junior et al. 2020), the water potential at dawn and minimum transpiration at dawn is considered the most accurate indicator of a plant's water status. Plant ecophysiological and nutritional traits of leaves, can indicate how plants respond to environmental changes both individually and in combination (Pratt and Mooney 2013). Additionally, these traits offer insights into the adaptation strategies and survival abilities of plants. However, trees have developed a variety of survival mechanisms to adapt effectively to fluctuations in precipitation patterns. By implementing drought avoidance or drought tolerance strategies, a well-adapted tree species may exhibit either more flexible adaptability to or an improved performance, for instance, some plants close stomata to avoid extreme transpiration under drought, or adjust above-belowground allocation to maintain water access, while other plants with a more negative turgor loss point to achieve drought tolerance (Li et al. 2023). However, how subtropical tree species respond to water deficits is still controversial. Subtropical forests make up a large part of the global carbon pool and are expected to be more vulnerable to climate change, which brings risks to biodiversity and influences forest growth (Wu et al. 2020). Therefore, more attention needs to be paid to different aboveground and belowground responses of subtropical forest species to increasing drought events in the future.

Excessive water can also impede plant growth and development by disrupting physiological and biochemical processes (Liu et al. 2020; Li et al. 2021a). According to previous studies, excessive water stress causes leaf stomata to close, stomatal resistance to  $CO_2$  diffusion to increase and net photosynthetic rate (A), stomatal conductance ( $g_s$ ) and transpiration rate (E) to decrease significantly. There is also a decrease in chlorophyll content and a slowdown in the transport of photosynthetic products (Rao et al. 2021; Chen et al. 2023). Previous studies using precipitation gradients at multiple sites (Biederman et al. 2016) or along a temporal scale at a single site (Ren et al. 2017) generally found positive correlations between precipitation and aboveground

net primary productivity. The benefits of increased precipitation on the ecosystem are evident at various levels, such as enhanced leaf photosynthesis (Niu et al. 2008; Ren et al. 2017) and improved soil nutrient availability (Li et al. 2019). However, there is a significant difference between seasonal and annual precipitation variability and variations in the frequency of heavy rainfall events. These severe rainfall events have various repercussions, including soil water saturation or flooding, which cause oxygen depletion and impaired nutrient transport, ultimately limiting plant growth (Chen et al. 2005; Voesenek et al. 2004), or even cause rot of roots through pathogen infection (Savian et al. 2020). Nonetheless, apart from these few cases, not much is known about the effects of wet conditions on plant ecophysiology due to excessive rainfall. Understanding how plants currently respond to excessive water is crucial for predicting their response to increased rainfall events in the future, as it serves as a proxy for the more frequent rain pulses expected in future climates. Therefore, the effects of dry and wet conditions on the growth and ecophysiological functions of tree species in subtropical areas need to be further investigated.

Schima superba is a dominant tree species in the subtropical evergreen deciduous forests of southern China and a well-known evergreen tree native to East Asia (Kuang et al. 2017). This tree species is ecologically and economically important, as it provides functions such as carbon sequestration, fire prevention, soil and biodiversity conservation, and traditional Chinese medicine. However, the responses of S. superba to different precipitation patterns are only known to a limited extent. Therefore, elucidating the responses of S. superba under dry and wet conditions is vital for sustainable forest management and conservation of subtropical forests. In this experiment, we aimed to investigate the responses of growth and ecophysiological traits of S. superba seedlings to different water conditions. Specifically, we hypothesized that: (1) dry conditions would promote belowground biomass and leaf nitrogen content, but reduce leaf water potential and photosynthetic rate. (2) Wet conditions would impair respiration and nutrient uptake, ultimately leading to stunted growth and lower ecophysiological activity of S. superba. (3) Including both excess water and drought conditions, physiological traits may be more sensitive to the water gradient than morphological traits, and in turn explain the growth responses of S. superba. The aim of this study was to assess the potential alterations in the dominant tree species within subtropical forests of China under future climate scenarios characterized by drier dry season and wetter wet season, while maintaing constant annual precipitation levels (Zhou et al. 2013).

# Materials and methods

#### **Experimental site**

The study was conducted in a closed glass chamber greenhouse of the South China Botanical Garden in Guangzhou, Guangdong Province, China (23°20' N, 113°30' E). The area has a subtropical climate with an average annual temperature of 21.7°C, with the coldest month being January (13.1°C) and the warmest month being July (28.7°C). The average annual precipitation over the last four decades has been around 1700 mm. The dry season, which lasts from October to March, differs from the rainy season, which lasts from April to September and during which 70% of the precipitation falls. The soil used for this experiment was taken from the top 0-30 cm of a subtropical evergreen broadleaved forest in Heshan National Field Research Station of Forest Ecosystems, Guangdong Province, China (22°43' N, 112°50' E). The chemical properties of the soil were as follows: pH 4.17, total carbon 11.5 g kg<sup>-1</sup>, total N 0.75 g  $kg^{-1}$ , total phosphorus (P) 0.21 g  $kg^{-1}$ , available P 1.32 mg  $kg^{-1}$ . For this experiment, 10 kg of 5 mm sieved soil was filled into each square plastic pot with an inner size of 20 cm width  $\times$  20 cm height  $\times$  25 cm length.

#### Experimental design and treatment description

One-year-old seedlings of the species S. superba were taken from a nursery and transplanted into pots without damaging the roots in September, 2021. After two-month plant incubation and acclimation, the pots with healthy seedlings were arranged in randomized complete blocks and treatments were started from December, 2021. Each block was assigned as an individual treatment with four pots per treatment and two seedlings per pot, totally 12 pots. The treatments were: CK (controlled condition, with a soil water content of 25%, which is the average annual soil moisture in the local subtropical evergreen broad-leaved forest in Heshan National Field Research Station of Forest Ecosystems), D (dry conditions with 15% soil water content, which is 60% less than the soil moisture in CK) and W (wet conditions with 35% soil water content, which is 60% more than the soil water content in CK) (Wang et al. 2020). Stevens HydraProbe II sensors (Stevens Water Monitoring Systems, Inc., USA) were used to monitor soil volumetric water contents of each treatment, and data were recorded by A755 GRPS (Adcon, Klosternueburg, Austria) to indicate the soil moisture content dynamics, and the pots were watered every day to maintain the target soil water content.

#### **Functional trait measurements**

All the measurements in this study were carried out in the summer growth season from June to July, 2023, one and a half year after all the treatments started.

#### Growth traits

Plant height (Height) was first quantified as the vertical distance from the apex of the tree in the pot to the level of the soil in the container at the point of soil-tree contact.

At the end of the experiment in August, 2023, all the plants were harvested and separated into roots, stems and leaves, after which the roots were thoroughly washed with tap water to remove any soil. Subsequently, all organs were dried in an oven at 70°C for 72 h to determine the dry weight of each organ. Total biomass was calculated as the sum of aboveground biomass (stems and leaves) and belowground biomass (roots). The biomass distribution including the root-to-shoot ratio (R/S) was determined by dividing the root biomass (M) ratio (L/M), the shoot biomass (S) to total biomass (S/M), and the root biomass (R) to total biomass (R/M).

#### **Ecophysiological traits**

Five fully developed leaves from each plant were randomly selected, scanned and the leaf area (LA) measured using LI-3000 Portable Leaf Area Meter. The leaves were then placed in an envelope and oven-dried at 72°C for 72 h. The dry mass of the leaves was also measured and the specific leaf area (SLA) and leaf mass per area (LMA) were calculated. The dried leaves were then ground into powder. The leaf nitrogen content (LNC) was measured using the 5E-CHN2200 CHN elemental analyser, at a combustion temperature of 1050 °C. Approximately 800 mg of the ground leaf was placed in a tin capsule, which was placed in the elemental analyzer, where the sample was combusted at a temperature of 1050 °C. The root length of each plant was measured using a WinRHIZO Root Analyzer System (WinRHIZO 2012b, Regent Instruments Inc., Montreal, Canada) to scan and analyse the selected fine roots (diameter < 2 mm) by cutting a small portion from the roots with sharp blade (Guo et al. 2016). Specific root length (SRL) was calculated as the root length divided by the dry weight of the roots.

The gas exchange parameters of the leaves were measured on two continuous sunny days between 9:00 and 11:00 on July, 2023 to minimize variation. Photosynthetic rate (A) and stomatal conductance (gs) of *S. superba* were determined in situ using a portable infrared photosynthesis system (LI-6800 Li-Cor Inc., Lincoln, NE, USA). Measurements were made on five randomly selected mature leaves of each individual and averaged, and then four individuals were used as replicates of each treatment. Measurements were performed with a red and blue light source at a photosynthetic photon flux density of 1500  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, a relative humidity of 50%, a CO<sub>2</sub> concentration of 400  $\mu$ mol mol<sup>-1</sup> and an ambient temperature of 25–30 °C. After all measurements, the intrinsic water use efficiency (WUE<sub>i</sub>) was calculated as A/gs and the nitrogen use efficiency (NUE) as A/LNC.

Leaf water potential was measured predawn ( $\Psi_{pd}$ , MPa) and midday ( $\Psi_{md}$ , MPa) on four full-grown mature leaves from each treatment using a Scholander-type pressure chamber (PMS 1505D, PMS Instruments, Corvalis, Oregon, USA). We randomly selected and measured three mature leaves and averaged their data for one individual value, and then measured four individuals as replicates of each treatment. Measurements were done in the greenhouse for the  $\Psi_{pd}$  before dawn between 6:00 and 7:00 am. On the same day, leaf samples were excised again and carried to laboratory where they were measured between 12:00 and 2:00 pm for the  $\Psi_{md}$  at noon.

#### Statistical analysis

R software R.4.3.1 (R Core Team 2023) was used for a one-way statistical analysis of normality and homogeneity of variance between control, dry and wet treatments (one-way ANOVA) followed by Tukey's tests for further multiple comparisons (detailed values of each trait are in Table S1). In addition, correlation analyses were performed using the *lm* function in R, focusing on the relationships between predawn water potential, midday water potential with photosynthetic rate (A), and stomatal conductance (gs).

# Results

#### **Growth response**

No significant differences were observed in plant height under both dry and wet conditions as compared to control (Fig. 1a). However, aboveground biomass decreased by 25% under dry and 33% under wet conditions (Fig. 1b), and belowground biomass also showed 21% increase under dry, and a slight decrease under wet conditions compared to control (Fig. 1c). Total biomass underdry conditions decreased but did not differ significantly from the control, while total biomass under wet conditions decreased significantly by 26.5% (Fig. 1d). The biomass allocation of *S. superba* reacted differently under dry and wet conditions. On the other hand, under dry conditions, there was a significant difference in the proportion of root to total biomass (R/M ratio) and the proportion of root to shoot biomass (R/S ratio), while all other biomass allocation ratios were not significantly different (Fig. 2).

#### **Ecophysiological traits**

Schima superba exhibited significant variations in leaf water potential both at predawn and midday (Fig. 3). The  $\Psi_{pd}$  and  $\Psi_{md}$  water potential decreased significantly (87%, 22%), under dry, (P < 0.05), but there was no difference between predawn and midday water potential of plants under wet stress (Fig. 3).

According to ANOVA, dry and wet conditions had no significant effects on LNC and SLA, but LMA showed slightly higher values under dry D (13%) (Fig. 4a, b, c). Root growth showed significant differences in both treatments. The specific root length increased by 9.2% under dry, but it decreased by 9.5% under wet conditions (Fig. 4d).

The seedlings of *S. superba* grown in different treatments showed considerable differences in photosynthetic rate. Both photosynthetic rate (A) and conductance rate (gs) decreased significantly under dry treatment by 31% and 68%, respectively. However, wet treatment only slightly decreased A (11%) and gs (14%) but did not show statistical significance compared to controlled treatment plants (Fig. 5a, b). In addition, intrinsic water use efficiency (WUEi) was improved and highly significant under dry conditions (134%) and under wet conditions showed nonsignificantly reduced under dry (37%), but NUE was not affected by wet condition (Fig. 5c, d).

# Correlation between ecophysiological traits and water potential

There was a significant positive correlation between photosynthetic rate (A) and  $\Psi$ pd as well as  $\Psi$ md potential (R<sup>2</sup>=0.72 and 0.66, respectively, both p < 0.01) (Fig. 6, a, b). Stomatal conductance exhibited positive correlations with predawn and midday water potential, (R<sup>2</sup>=0.78 and 0.77, respectively, both p < 0.001) (Fig. 6c-d). Specific root length showed negative correlation with both predawn, and midday water potential (R<sup>2</sup>=0.69 and 0.72, respectively, both p < 0.001) (Fig. 6e-f). **Fig. 1** Development of plant height, aboveground biomass (AGB), belowground biomass (BGB), and total biomass (TB) of *S. superba* under dry and wet conditions. The bars represent means  $\pm$  standard deviations (*n*=4). Different lowercase letters above the error bars indicate significant differences between dry and wet treatments compared to plants under controlled condition







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Fig. 3 Response of leaf water potential of S. superba at predawn and midday under dry and wet conditions. The bars represent means  $\pm$  standard deviations (n=4). Different lowercase letters above the error bars indicate significant differences between treatments



**Fig. 4** Response of leaf nitrogen content (LNC g cm<sup>-2</sup>), leaf mass area (LMA g cm<sup>-2</sup>), specific leaf area (SLA cm<sup>2</sup> g<sup>-1</sup>) and specific root length (SRL cm g<sup>-1</sup>) of *S. superba* under dry and wet conditions. The bars represent means  $\pm$  standard deviations (*n*=4). Different lowercase letters above the error bars indicate significant differences between dry and wet treatments compared to plants under controlled condition



**Fig. 5** Responses of dry and wet treatments on net  $CO_2$  assimilation rate (A,  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>), stomatal conductance (g<sub>s</sub>, mol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>), intrinsic water use efficiency (WUE<sub>i</sub>), and nitrogen use efficiency (NUE) of *S. superba* under dry and wet conditions. The bars represent

means  $\pm$  standard deviations (n = 4). Different lowercase letters above the error bars indicate significant differences between dry and wet treatments compared to plants under controlled condition



**Fig. 6** The relationships of predawn ( $\Psi$ pd) and midday water potential ( $\Psi$ md) with (**a**, **b**) photosynthetic rate (A), (**c**, **d**) stomatal conductance (g<sub>s</sub>), and (**e**, **f**) specific root length (SRL). Control treatment values

are shown in grey; dry treatment in brown, and wet treatment in cyan. Only statistically significant relationships (p < 0.05) are shown as solid lines

## Discussion

This study found that varying water levels differently impact the growth and ecophysiology of S. superba. Confirming our first hypothesis, S. superba exhibited significantly higher root/total mass and root/shoot mass ratios under drought conditions, mainly due to decreased aboveground biomass, despite an increasing trend in belowground biomass. This shift is attributed to the plant's strategy of reallocating resources to the roots, enhancing water exploration, nutrient absorption, and osmotic regulation, thus maintaining physiological processes under water stress (Mao et al. 2018). The decrease in both above and belowground biomass under wet conditions confirms our second hypothesis: excess water limits root oxygen supply, impairing root function, nutrient uptake, and physiological activity which has similarities with previous studies (Pan et al. 2021; Li et al. 2021a; Guasconi et al. 2023). Our findings align with recent studies. Feldman et al. (2024) reported that increased rainfall alters above-ground biomass and net primary productivity. Wet ecosystems experience a 28% decrease, while dry ecosystems experience a 29% increase. In addition, O'Brien et al. (2024) found growth reductions 48% of species and survival declines 92% during high rainfall periods. These results confirm that excessive water severely impacts S. superba's growth and ecophysiology. In this case, wetter wet seasons have worse ecological consequences than drier dry seasons in subtropical forests of China.

However, to explain the observed growth differences, we found that drought and excess water significantly affected root morphological traits, such as specific root length, and leaf physiological traits, including leaf nitrogen content, photosynthesis, and water potential, but had no significant effects on leaf morphological traits like SLA and LMA. Our findings are supported by Kuang et al. (2017), who reported that LMA and leaf nitrogen content did not change significantly under dry conditions. In this study, specific root length increased under dry conditions, aligning with Wang et al. (2023) and Rowland et al. (2023), showing enhanced moisture and nutrient absorption. This adaptation, involving reduced aboveground biomass and increased root growth, is a common drought mechanism. Schima superba exhibited high plasticity, adapting well to both drought and excess water stresses.

The increasing trend in leaf nitrogen content (LNC) of *S. superba* under drought may be attributed to higher nitrate content due to reduced nitrate reductase activity, likely caused by the synthesis and accumulation of nitrogen-based osmolytes like proline (Querejeta et al., 2022). Meanwhile, under the dry conditions, the photosynthetic rate (A) decreased due to a reduction in stomatal conductance (gs) and a slight increase in LNC, consistent with McAusland

et al. (2016), and Song et al. (2022). Our findings suggest that *S. superba* exhibits high plasticity in leaf and root ecophysiological traits, adapting well to drought. However, no significant differences in ecophysiological traits, except gs, were observed under wet conditions due to decreased root oxygen levels, which reduced gs and A. Low gs negatively impacts transpiration, disrupting water absorption and nutrient distribution, thus affecting growth and biomass (Colmer 2003; Voesenek and Bailey-Serres 2015).

This study partially supported our third hypothesis, revealing that both physiological traits (photosynthesis and stomatal conductance, gs) and root morphological traits responded to the water potential gradient. Ypd became more negative under dry conditions, while no change was observed under wet conditions, consistent with findings on S. superba and O. pinnata (Li et al. 2021a). We observed a positive correlation between photosynthetic rate and gs with leaf predawn and midday water potential and a negative correlation between specific root length and both water potentials. Previous research shows that higher water potential promotes stomatal opening, enhancing CO2 uptake and photosynthesis, and is crucial for maintaining turgor pressure in plant cells (Wang et al. 2023). Conversely, reduced water potential due to water stress lowers turgor pressure, negatively impacting photosynthesis (Buckley and Mott 2013; Flexas & Carriqui, 2020). During drought, plants optimize water uptake by redistributing water within their root systems. Zhou et al. (2018) and Carrillo et al. (2022) emphasized the role of specific root length in maximizing water absorption under drought.

We found that drought increased intrinsic water-use efficiency (WUEi) and decreased nitrogen-use efficiency (NUE). Previous studies have shown that drought raises WUEi (Swap et al. 2004; Mariotte et al. 2013) and lowers NUE (Guo et al. 2022) in grassland plants like *L. chinensis* (Yue et al. 2019) due to reduced stomatal conductance, transpiration, and nutrient flux (Hu et al. 2023). This indicates a trade-off between WUEi and NUE, consistent with prior research (Field et al. 1983). Under wet conditions, no difference was observed, as soil saturation provides consistent water availability, allowing plants to modulate stomata and root adaptations to maintain stable internal water potential.

Dry and wet conditions have significant impacts on tree growth and ecophysiology. Drought induces water stress, which leads to a reduction in forest productivity (Yu and He 2017) and often results in widespread tree mortality due to hydraulic failure, carbon starvation, or increased vulnerability to pests (Anderegg et al. 2013; McDowell et al. 2008). On the other hand excessively wet periods have negative effects on tree demographic rates caused by physiological factors such as hypoxia or anoxia resulting from prolonged waterlogging, as well as meteorological factors like increased cloud cover which limits photosynthesis (Esteban et al. 2021). Furthermore, storms and heavy rainfall increase tree mortality (Aleixo et al., 2019). This study provides valuable insights into the growth dynamics and ecophysiology of *S. superba*, common in subtropical forests. However, further research is needed to determine if these patterns apply to other species, investigate mechanisms driving population dynamics, and identify thresholds for entire plant communities. Future studies also need more replicates of each treatment, as some of our traits showed trends but no statistical significance, which may be avoided by a larger n-value. Overall, understanding species' growth and ecophysiology in response to seasonal precipitation changes will aid in conserving plant diversity and ensuring the long-term sustainability of forest ecosystems.

# Conclusion

This study provides evidence that both drought and moisture stress negatively affect the growth and ecophysiological activities of S. superba. Under drought, the plant significantly decreased its aboveground biomass, photosynthetic rate, leaf water potential and nitrogen use efficiency, but increased water use efficiency, root to shoot ratio and specific root length. Meanwhile, S. superba under wet conditions significantly decreased its total biomass, aboveground biomass and specific root length, but no changes in photosynthesis and leaf water potential. In addition, S. superba exhibits a decrease in carbon increment under both dry and wet stress. This emphasizes the need to consider the interactive effects of changing rainfall patterns in future studies and to provide a theoretical basis for better management of this important forestry tree species in subtropical China. Further longer-term field studies are needed to fully understand the impact of changing precipitation patterns on tree species. In addition, it's crucial to anticipate how plants will react to shifting rainfall patterns in upcoming years to accurately assess their impact on the land carbon sink, fluctuations in global carbon uptake, and trends in vegetation greening.

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Author contributions Kashif Hussain, Hui Liu and Yanxia Nie conceived the ideas and designed methodology; Kashif Hussain, Emily Patience Bakpa and Asif Riaz collected the data; Kashif Hussain analyzed the data; Kashif Hussain, Defu Wang, Guilin Wu, Emily Patience Bakpa, Suping Liu and Hui Liu led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability Data will be made available on request.

### Declarations

Competing interest The authors declare no competing interests.

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