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Seed germination requirements of *Ficus virens* (Moraceae) as adaptation to its hemi-epiphyte life form

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ABSTRACT

Epiphytes and hemi-epiphytes are important floristic, structural and functional components of tropical rainforests. Their specific responses to light, temperature and water conditions during seed germination allow them to coexist with tropical forest trees. Here we investigated the effects of temperature, red to far-red light ratio (R:FR ratio) and water stress on seed germination of *Ficus virens* in tropical seasonal rainforest in Southwest China. We used incubators to create required temperature regimes, polyester filters to produce R:FR ratio gradients and mannitol solutions to simulate water stress. It was found that seed germination of *F. virens* was inhibited in the simulated understory conditions, i.e., at lower temperature (22/23°C), especially when combined with the R:FR ratio of 0.25, for which the germination percentage was less than 20%. In contrast, the seed germination percentages in the simulated canopy environment (22/32°C) showed no significant difference between R:FR ratios, with an average seed germination percentage as high as 65.8%. Seed germination delayed and decreased along with increasing water stress and was completely inhibited at -2.5 MPa, which might suggest that it is a kind of adaptation for *F. virens* seeds to detect the rainy season as germination chance on the canopy. Therefore, our study revealed the physiological mechanism for *F. virens* to be able to adapt to canopy environment.

INTRODUCTION

Canopy is the key ecological interface between forest and atmosphere (Liu *et al.* 2006, Nakamura *et al.* 2017). It was estimated that 40% of the world's terrestrial species live in the forest crown due to the heterogeneous physical and biotic conditions, with 10% of those species being the canopy-specific group (Ozanne *et al.* 2003, Hopkin 2005, Leroy *et al.* 2016). Among them, epiphytes and hemi-epiphytes were reported to play an important role in tropical rainforest (Zotz 2013, Hao *et al.* 2016).

It is important to understand the ecological and physiological adaptation characteristics of canopy-specific trees. Differing from parasitic plants, epiphytes and hemi-epiphytes remove no nutrients from their 'host', only regard the latter as physical support (Baskin and Baskin 1988). Hao *et al.* (2013) found that epiphytes and hemi-epiphytes use strategy different from free-standing plant to adapt to canopy environment of rainforest, including seed size, seed germination and seedling development. Compared with the understory trees, the canopy-specific trees have to avoid or endure extreme water shortage (Chazdon and Fetcher 1984, Liu *et al.* 2014), although they have more opportunity to get higher temperature and more light. Due to the high canopy density in the closed forest, light intensity, light spectral composition and temperature in the canopy differ markedly from those on the forest floor, for example, the red to far-red light ratios (R:FR, 660:730 nm) above the canopy can reach to 1.2 ~ 1.3, while only 0.1% ~ 1.9% of the total light could reach to the forest floor and the R:FR ratio decreased to 0.25 ~ 0.41 (Bazzaz and Pickett 1980, Vázquez-Yanes *et al.* 1990, Orozco-Segovia *et al.* 1993). The decreased light also leads to the decrease of understory temperature and the diurnal fluctuation. Moreover, epiphytes and hemi-epiphytes, living in the canopy, experience an extremely water shortage different from the understory, which only recaptures water from fog and canopy humus (Liu *et al.* 2014).

Seed germination is the most vulnerable processes in plant life cycle, which relates to the establishment of seedlings, survival and competition of individuals, distribution of vegetation and biodiversity (Teketay 1997, Nicotra *et al.* 1999, Donohue *et al.* 2010, Bače *et al.* 2012, Boelter *et al.* 2014, Song *et al.* 2016). Seed germination is highly susceptible to temperature, light and moisture (Swagel *et al.* 1997, Daws *et al.* 2002, Chen *et al.* 2013). The germination of large seeds is mainly temperature-controlled, while the germination of small seeds (< 2 mg) shows more photosensitivity (Pearson *et al.* 2002). Water potential is also a very important constraint in the early stages of seed germination and seedling establishment (Daws *et al.* 2002; Bunker and Carson 2005, Poorter and Markesteijn 2008). Furthermore, it has been suggested that seedlings from small seeds have higher risk of mortality when subjected to fire, flood, herbivores, soil water shortage, soil nutrients deficiency and damage or coverage by falling debris than those from large seeds (Daws *et al.* 2005, Hao *et al.* 2016). It is the supreme moment for small seeds to germinate or not, under the diversified and changeful natural environment.

Most fig species occur in tropical area, especially in tropical rainforests (Berg 1989). There are more than 800 species of *Ficus* (Moraceae), and about 500 of them are hemi-epiphytes, which begin their life as epiphytes in canopy then develop aerial roots to establish on the forest floor (Hao *et al.* 2016). At least 20 *Ficus* species in Xishuangbanna are hemi-epiphytes, but only a few reports on their germination traits in this area (Flora of China Editorial Committee 2003, Chen *et al.* 2013).

Ficus virens is native to Xishuangbanna tropical rainforests, which produces tiny seeds with a 1000-seed-weight of only 0.25 g (Royal Botanic Gardens Kew 2017). As it was reported as a hemi-epiphytic species (Flora of China Editorial Committee 2003), we hypothesized that its seed germination should have special adaptation strategy to canopy conditions: its seeds are photosensitive, they can germinate at lower water potentials, and the higher temperature fluctuation of the canopy can promote their germination. Thus we investigated the effects of light quality (R:FR light ratios), temperature and water potentials on seed germination of *F. virens* to help us understand the physiological mechanism why the plant adapt to the canopy.

MATERIAL AND METHODS

This study was carried out at the Xishuangbanna Tropical Botanical Garden (XTBG), Mengla, Yunnan, Southwest China (21°50′N, 101°12′E; altitude 590 m). The climate here is characterized by two distinct seasons: a rainy season (May to October) and a dry season (November to next April, Cao *et al.* 1996, Zhang *et al.* 2010). The dry season can be subdivided into foggy cool and hot dry seasons (Wu *et al.* 2016). The annual mean temperature is 21.8°C, mean annual precipitation is 1,493mm, of which about 85% occur during the rainy season (Cao *et al.* 2008).

Ficus virens is a hemi-epiphyte tree, with a wide distribution in South China, South Asia and Southeast Asia, altitude from 300 to 2700 m (Flora of China editorial committee 2003). In Xishuanbanna, it grows in seasonal tropical rainforests, especially in closed forests along valleys and stream sides. where it is a common strangler.

Material

Ripe fruits of *F. virens* were collected in XTBG in April 2016. Seeds were extracted by mashing the fruits and decanting the fruit pulp in water. They were then air-dried for 2–3 days, and then stored at room temperature (~26°C) until the start of the experiments on the 9th September, 2016.

Methods

Seed germination

Germination tests were carried out in two incubators (MGC-350HP-2 instrument, Yiheng Shanghai, Shanghai, PR China). Each treatment included six replicates of 25 seeds placed on the surface of filter paper in 60-mm-diameter Petri dishes. Seeds were incubated in 12 h /12 h temperature regimes, with the high temperature corresponded to the 12 h daily light periods.

Temperature and light treatment

Two temperature treatments (22/23 and 22/32°C) were applied to simulate the temperature on understory soil surface (23°C, 7 July 2016) and in canopy (22~31°C, 4 July 2016), respectively (data from Xishuangbanna Station for Tropical Rainforest Ecosystem Studies).

Four R:FR ratios were set up following Chen *et al.* (2013). For full dark, we used aluminum foil to wrap dishes after they were covered by black cloth to ensure that the seeds could not be affected by light leakage resulting from aluminum foil breakage.

Seeds were checked after 42 days incubation and then non-germinated seeds were incubated at 22/32°C (12 h dark /12 h light) under fluorescent light for 28 days to determine whether seeds were viable or not.

Water stress treatment

Mannitol (M 4125, Sigma Chemical Co., St. Louis, MO) was used to set a gradient to simulate different water potentials. Mannitol concentrations varied (0, 0.04, 0.1, 0.2, 0.4, 0.48, 0.6, 0.8, 1.0, 1.2 mol/L) which generated a substrate water potential of 0, -0.1, -0.25, -0.5, -1.0, -1.2, -1.5, -2.0, -2.5, -3.0 MPa (Swagel *et al.* 1997). All of the water potential experiments were carried out at 22/32°C (12 h dark /12 h light). Petri dishes were covered by plastic to decrease changes in water potentials of the test solutions during experimental period. Pre-experimental results showed that about 1 g water was lost every 3 days, so 1 ml deionized water was added to each dish to compensate for water evaporation every 3rd day. Seeds were checked daily for germination, indicated by radical protrusion. Observations ended after 42 days, and then non-germinated seeds were removed to incubate on filter paper moisture with deionized water for viability determination as described above.

Seedling growth

Forty-two days after experiment started, one of the six replicated dishes for each treatment was sampled for seedlings assessment, with radical and whole seedling lengths of all seedlings in the dish measured.

Statistical analysis

Data were expressed as mean ± SE of six replicates. After arcsine transformation, germination data were subjected to analysis of variance (ANOVA) and means compared by the Kruskal-Wallis test and by the Mann-Whitney *U*-test. General linear model was used to analyze the correlation between the seed germination and osmotic stress, the radical length and the entire seedling length. Statistical analyses were performed by SPSS version 21 for Windows (SPSS, Chicago, Illinois).

RESULTS

Temperature and light treatment

The seeds used in this study had an initial viability of approximate 80%. None of the seeds germinated in total darkness. Through the two-way ANOVA, we found that there was a significant interaction between light and temperature on seed germination ($F = 6.782$, $P = 0.001$). The germination percentages at 22/32°C were significantly higher than those at 22/23°C ($H = 34.677$, $P < 0.001$). Seed germination responded positively to increased R:FR ratios at 22/23°C ($H = 14.529$, $P = 0.002$), but germination percentages were not affected by the R:FR ratios at 22/32°C ($H = 3.158$, $P = 0.368$) (Fig. 1).

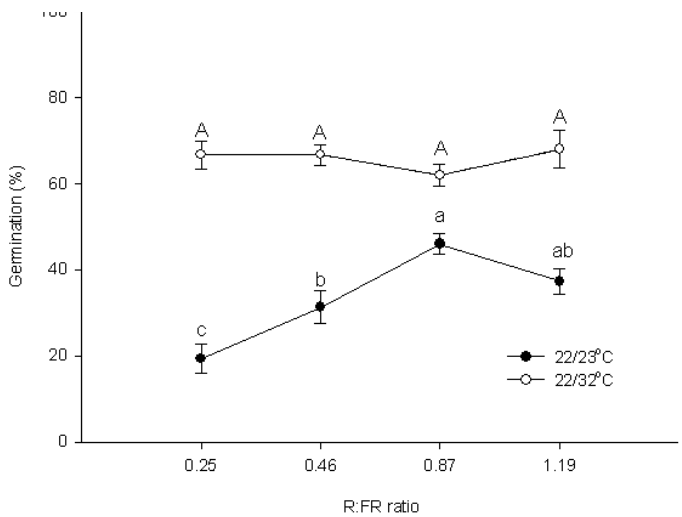

Fig. 1. Effects of the light and temperature on seed germination (means ± SE) of *Ficus virens*. Seeds were incubated for 6 weeks in the deionized water under light and temperature indicated. Different letters indicate significant differences between R:FR (red to far-red light) ratios, capital letters for 22/32°C, small letters for 22/23°C.

Water stress treatment

The seed germination declined with increasing osmotic stress ($R^2 = 0.813$, Fig. 2). The germination percentage under the control, -0.1 and -0.25 MPa were significantly higher than that under the lower water potentials. When the water potential decreased to -1.5 MPa, germination was almost completely inhibited (H = 8.768, $P = 0.003$).

Furthermore, the mean time to germinate (MTG) under the control, -0.1 and -0.25 MPa were significantly shorter than that under the lower water potentials (H = 26.691, $P < 0.001$) (Figs. 2 and 3).

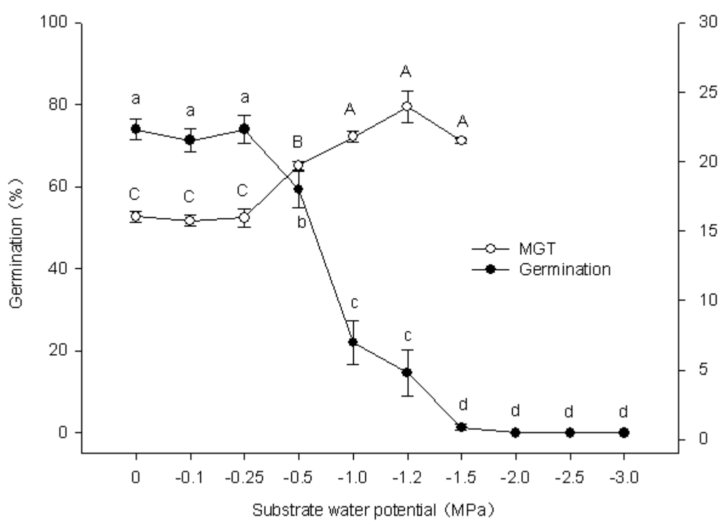

Fig. 2. Effects of the water potentials on seed germination (means ± SE) and the mean time to germinate (MTG) of *Ficus virens*. Seeds were incubated for 6 weeks in the substrate water potential created by different concentrations of mannitol solutions. Different letters indicate significant differences between substrate water potentials, capital letters for MGT, small letters for germination ($P < 0.05$).

Seedling growth

Temperature affected neither the radical length (F = 0.080, $P = 0.778$) nor germ length (F = 1.021, $P = 0.315$) much, but R:FR ratio had considerable impacts on both of them. With the increase of R:FR ratio, the radical growth was significantly promoted (H = 16.387, $P = 0.001$) whereas the germ growth was significantly inhibited (H = 25.052, $P < 0.001$) (Fig. 4). The percentage of radical length was not significantly affected by temperature (H = 0.894, $P = 0.344$), but it significantly increased (H = 18.054, $P < 0.001$) with increasing R:FR ratios (Fig. 4).

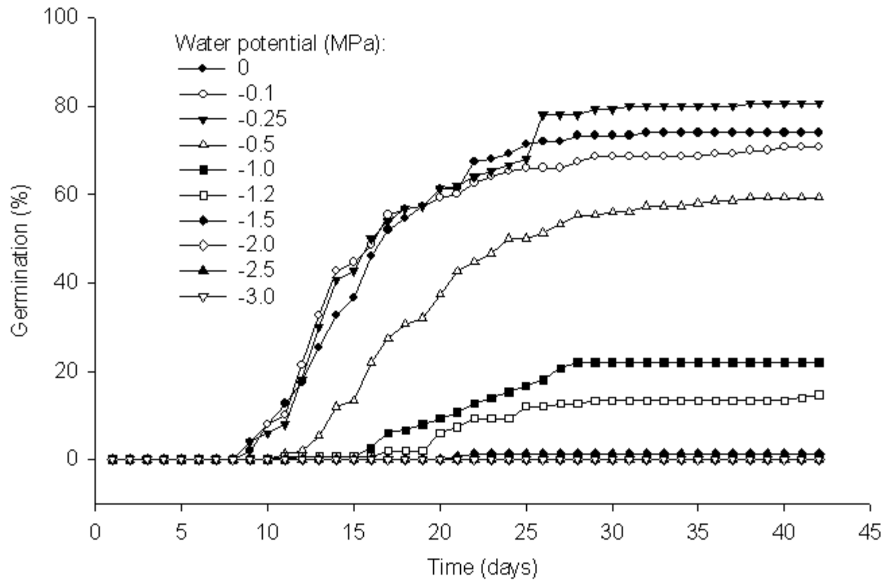

Fig. 3. Cumulative distributions of *Ficus virens* germinations over time for seeds incubated in the mannitol solutions of different concentration, simulating different water potentials (MPa).

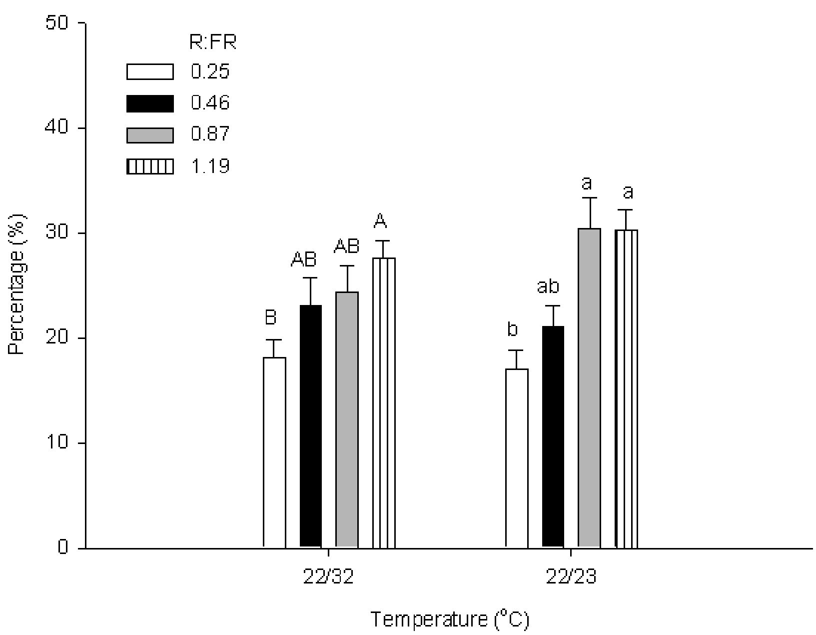

Fig. 4. The percentage of radical length (radical length/whole seedling length×100%) in *Ficus virens* germinated and grown for 6 weeks at temperature and light indicated. Vertical bars indicate means ± SE. Different letters indicate significant differences between R:FR (red to far-red light) ratios, capital letters for 22/32°C, small letters for 22/23°C.

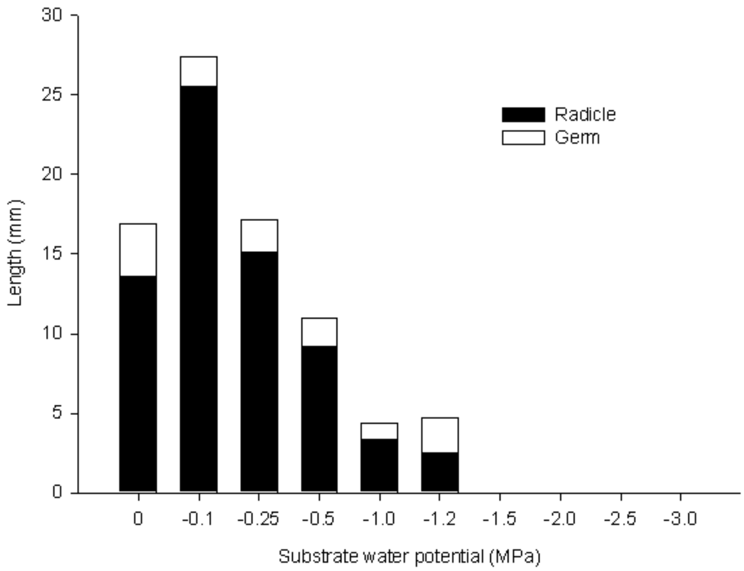

Fig. 5. Length of germ and radical of *Ficus virens* after 6-week's germination and growth at the substrate water potentials indicated.

The seedlings growing at -0.1 MPa had the longest whole length in this experiment, which were significantly longer than the control (H = 11.410, P = 0.01). But the seedling growth was significantly inhibited when germinating in progressively water stress (Fig. 5). The radical length is strongly correlated to the whole seedling length ($R^2 = 0.993$).

The fate of non-germinated seeds

After transferred to incubation in fluorescent light at 22/32°C, the non-germinated seeds incubated in full dark in temperature and light experiment had germination percentages of only 28.7 and 41.3%, respectively. Besides, seeds from other treatments in this experiment germinated well after transferred to fluorescent light (data not shown).

The seeds that did not germinate in water potential experiment germinated well after rinsed in deionized water. Whatever the water potentials were used previously, seeds were able to sprout out within 4 weeks of incubation in deionized water and reached a final germination percentage quite close to the control, except the seeds from -2.5 MPa, which displayed significantly lower germination percentage (data not shown).

DISCUSSION AND CONCLUSIONS

Temperature significantly affected the seed germination of *Ficus virens*. Seed germination in the understory was inhibited obviously at lower temperature (22/23°C) and low R:FR ratio (0.25). This would render *F. virens* incompetent in terms of seed germination when competing for nutriments and sunlight with many other species that survived in the bottom of the forest under low light and temperature (Ross and Harper 1972, Fowler 1986, Weiner *et al.* 1997, Turk and Tawaha 2003). During a recent survey of a 20-ha tropical forest dynamics plot (21°37′08″N, 101°35′07″E) in Xishuangbanna, Southwest China (Cao *et al.* 2008), no seedlings of *F. virens* were found in the understory, only a few in the canopy (Chen, unpublished data). This indirectly revealed harsh situations faced by *F. virens* during germination and seedling establishment in the understory.

Light also played an important role in the seed germination of *F. virens*. Similar to many other *Ficus* seeds (Vázquez-Yanes *et al.* 1996, Chen *et al.* 2013), the seed germination of *F. virens* is positively photoblastic. No seeds germinated in the darkness, irrespective of the temperatures simulating those in canopy or understory. The low germination percentages could not be attributed to lack of seed viability or dormancy, since seed germination recovered well after they were transferred to fluorescent light under 22/32°C. This indicated that temperature alone could not initiate the seed germination of *F. virens*. Different R:FR ratios led to different seed germination percentages (Bewley and Black 1994, Smith 2000). Like other photoblastic seeds (Daws *et al.* 2002, Chen *et al.* 2013), the *F. virens* seed responded positively to increasing R:FR ratios at relatively low R:FR ratios under 22/23°C. We assumed that this might result in enhanced germination percentages for seeds at different tree heights of the canopy with temperatures lower than the surface of the canopy but high enough R:FR ratios.

This study found that water was another key limiting factor in the germination of *F. virens*, however, germination took place up to -1.2 MPa. This made *F. virens* listed among the few species with highest tolerance to water shortage, since much higher sensitivity to water stress was popular for seed germination, for example, *Eupatorium adenophorum Sprengel* (Li and Feng 2009), *Eclipta prostrata* (L.) L. (Chauhan and Johnson 2008), *Echinochloa colona* (L.) Link (Bhagiraths and Davide 2009) and *Piper aduncum* (Wen *et al.* 2015), retained only 20–70% seed germination under water stress up to -0.6MPa, and species whose seeds germinated up to -1.0 MPa is relatively rare, such as tomato, sunflower and corn (Swagel *et al.* 1997). The ability to germinate under low water potentials may be an important adaptive trait of hemi-epiphytes. Swagel *et al.* (1997) found that although the seed germination of *F. aurea* was highly sensitive to substrate water potential, palm crowns was an "micro-oasis" for establishment of figs since its condition of sustained moisture (substrate water potential of ≥ -1.2 MPa) was met in humus of palm leaf bases, which was thought to contribute to its survival during the dry season. Though this species can germinate under lower water potentials, the high preference for low osmotic stress in the germination of *F. virens* might imply that it was more likely to germinate in natural forests during the rainy season as new seedlings were more susceptible to drought stress and death (McLaren and McDonald 2003).

We conclude that by having hemi-epiphytes growth life, the *F. virens* seed germination and seedling establishment adapt to the complex and changeful light, temperature, and water environment. Thus, *F. virens* successfully colonize in the dense rainforest. This is mostly the ecological adaptation of *F. virens* during long-term evolution.

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