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Seed viability as a function of moisture and temperature in the recalcitrant rainforest species *Baccaurea ramiflora* (Euphorbiaceae)

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Abstract

- *Context* Fragmentation is a common and increasingly serious problem in tropical rainforests through the world, resulting in changes in species composition and subsequent species extinctions.
- *Aim* The aim of this study was to test the hypothesis that changes in species composition can originate from the different selection pressures on pioneer and climax seeds as the habitat changes.
- *Methods Baccaurea ramiflora* seeds were placed on the ground in six quadrats in five different habitats in the field, while graded temperature and relative humidity treatments in the laboratory were used to mimic the changed microclimate in rainforest fragments. Changes in seed moisture and viability were monitored.
- *Results B. ramiflora* seeds are recalcitrant and highly sensitive to both high temperatures and dehydration, with a reduced lifespan when temperature increased or relative humidity decreased, and viability is lost when dehydrated to 0.198 g/g or warmed to≥35 °C. Germination was delayed in non-rainforest conditions compared with the rainforest understory, and only one-third of the seeds assigned to an open site germinated and emerged.
- *Conclusion* The results support our hypothesis that recalcitrant-seeded species have a high dependence on intact rainforests, and that fragmentation and disturbance will reduce their germination and establishment while favoring orthodox-seeded pioneers.

Keywords Desiccation tolerance · High-temperature stress · Microhabitat changes · Rainforest fragmentation · Species shift · Seedling establishment

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Contribution of the co-authors The contribution of individual authors: Bin Wen designed the experiment, wrote the manuscript and supervised the work. Yifan Cai ran the experiment and analyzed the data.

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1 Introduction

Southern Yunnan is on the north margin of the Asian tropics and is a hotspot for global biodiversity (Myers 1998), with the largest area of tropical rainforest remaining in China (Cao et al. 2006; Zhu 1997). Protecting this rainforest and its biota is a national conservation priority, but its marginal position latitudinally and climatically make it particularly vulnerable to disturbance (Zhu 2004). Unfortunately, the remaining rainforest has become seriously fragmented in recent decades because of the expansion of rubber and other cash crops (Li et al. 2009). Fragmentation results in edge effects, first changing the microclimate near the forest margins by increasing temperature and decreasing moisture, and subsequently changing the tree-community composition, with pioneer and successional species increasing and large-seeded and old-growth taxa declining (Gascon et al. 2000; Laurance et al. 1998a, 1998b, 2006; Ma et al. 1998; Zhu et al. 2004). This may result in the extinction of some species endemic to tropical forests (Turner 1996; Zhu et al. 2010), but the mechanism for species shifts in fragmented rainforest is still not fully understood. We hypothesize that this shift in species composition originates, at least in part, from the different selection pressures on pioneer and climax seeds as the habitat changes, since these ecological species groups have different germination requirements, and seed germination and seedling establishment are the basis of forest dynamics. Swaine and Whitmore (1988) suggested that pioneer seeds germinate only in full sun, clearings or canopy gaps open to the sky, and require full sun for survival and growth, while climax seeds germinate in shade, or rarely in full sun, and seedlings can survive and grow in shade, although the difference between these seed groups is quantitative rather than qualitative and variation within them is continuous. We therefore expect that environmental changes in fragmented forests will stimulate germination of pioneer seeds and depress that of climax seeds.

Many climax species in tropical rainforests are known to produce recalcitrant seeds. Such seeds are sensitive to abiotic stresses (Roberts and King 1980; Tweddle et al. 2003), so it is necessary to assess their potential response to habitat fragmentation. *Baccaurea ramiflora* (Euphorbiaceae) is distributed widely in southern China and Southeast Asia. It is one of the most common species in Southern Yunnan tropical rainforests, with the third highest importance value in a 20-ha plot in the tropical seasonal rainforest in Xishuangbanna (3,212 individuals≥1 cm diameter; Cao et al. 2008). Previous studies reported that *B. ramiflora* produces recalcitrant seeds (Yu et al. 2008). To assess the vulnerability of germination to fragmentation and edge effects, we tested whether habitat damage causes a decrease in germination of *B. ramiflora* seeds in the field, and whether increased temperature and decreased moisture truncate seed longevity in the laboratory.

2 Materials and methods

2.1 Seed materials

Mature fruits of *B. ramiflora* were collected in July 2011 from trees growing in the rainforest patch within the Xishuangbanna Tropical Botanical Garden (hereafter XTBG) (for climate see: Cao et al. 2006). Seeds were extracted and cleaned manually, and then kept in polyethylene bags at 15 °C for a maximum of 3 days before use.

B. ramiflora seeds are flat-elliptic, arillate and endospermous, with a white or pinkish arillode. Inside the testa there is a tiny embryonic axis with two large, flat cotyledons, encapsulated by two fleshy endosperm pieces from each side. The seeds in this study had an initial germination percentage of 95.3±1.9 % and 93.3±1.3 %, for seeds with a pinkish and white arillode, respectively. Their moisture contents were 1.54±0.09 and 1.51±0.11 g/g (dry weight basis), respectively, and their 100-seed weights 32.96±0.26 and 36.36±0.27 g.

2.2 Laboratory experiments

Moisture contents, expressed as g water/g dry mass (g/g), were determined gravimetrically for eight individual seeds before and after drying for 17±1 h in a ventilated oven at 103±2 °C. The response of germination to temperature was assessed by sowing fresh seeds in 1 % distilled water agar in Petri dishes placed in constant temperatures of 10, 15, 20, 25, 30, 35, or 40 °C in temperature-controlled incubators, with 14 h light (20 μmol m^{-2} s^{-1})/10 h dark per day provided by white fluorescent tubes. Desiccation tolerance was assessed by placing seeds in a desiccator containing plenty of silica gel in an air-conditioned room at 20 °C. The seeds were placed on the surface of silica gel for up to 48 h, with the silica gel renewed regularly, and sampled for moisture and viability determination at regular intervals. Seed viability assessment in this and the following experiments was carried out at 25± 1 °C in light as described above.

The response of seeds to desiccation at different temperatures was assessed by a method used previously (Wen 2011). Seeds were placed in a monolayer in dishes put in incubators set at constant temperatures between 15 and 40 °C. The relative humidity recorded in these incubators was 45–78 % during the experiment. The response to desiccation under different relative humidities was assessed by exposing seeds in a monolayer in desiccators at relative humidities of 30 %, 43 %, 62 %, 75 %, 93.6 % and 100 %, regulated by saturated solutions of $CaCl_2$, K_2CO_3, NH_4NO_3, NaCl, KNO_3 and distilled water, respectively, at 25 °C in a temperature-controlled room. Seeds were sampled for moisture and viability determination regularly in both experiments.

2.3 Field experiments

Six 50 cm×50 cm quadrats (A–F) in five distinct habitats were chosen within XTBG. After removing covering plants and litter, approximately 1,200 seeds were placed in a monolayer on the ground in each quadrat, covered by a metal net to exclude seed predators, and sampled regularly for moisture and viability assessment until to the 10 days. Subsequently, germination of the seeds remaining in field was monitored once a week for 6 weeks. The quadrats and habitats were as follows:

Quadrats A and B:	in a valley of the XTBG rainforest, altitude 562 m, initial soil moisture content 38 % (determined using surface soil sampled on the day the experiment was set up and expressed on a fresh weight basis), with a diverse plant cover and dense canopy;

Quadrat C: on a slope in the XTBG rainforest, altitude 565 m, soil moisture content 35 %, with a diverse plant cover and dense canopy;

Quadrat D: in a plantation of *Mesua ferrea* near the XTBG rainforest, altitude 570 m, soil moisture content 23 %, with a dense canopy and dark, clean understory;

Quadrat E: in a pomelo orchard far away from the XTBG rainforest, altitude 580 m, soil moisture content 20 %, with an open canopy and clean and clear understory;

Quadrat F: in a grassy area close to buildings, with direct sunlight between 10:00 a.m. and 16:00 p.m. on sunny days, soil moisture content 28 %.

2.4 Seed germination test

The germination test was performed for six Petri dishes containing 25 seeds each for each treatment. Seeds were incubated for at least 3 months and those that failed to germinate were then subjected to a crush test to confirm that they were nonviable. At least 1 cm radicle protrusion was considered as germination, while formation of a normal seedling was considered as emergence.

2.5 Dehydration rate and desiccation tolerance assessment

The seed moisture loss rate index (SMLRI) defined by Samarah et al. (2009) was modified to quantity the drying rate under different regimes by the following equation:

$$SMLRI = \sum_{i=1}^{n} (SMC_i - SMC_{i+1})/day_{i+1}$$

where SMC_i and SMC_{i+1} are seed moisture contents (on a dry weight basis) of the sample numbers i and i+1, and day $_{i+1}$ is the number of days after imposing drying treatment for the sample number i+1. This differs from Samarah et al. (2009), who used moisture content expressed on a fresh weight basis. The units are g water g dry mass^{-1} day^{-1}.

Days for mid-point viability loss (T50) and the critical moisture content for 85 % and 50 % germination (WC_{85} and WC_{50}) were calculated by probit analysis.

2.6 Statistical analyses

Moisture contents on a dry weight basis were estimated as means±SE of eight replicates of single seeds. Seed germination was expressed as means±SE of six replicates of 25 seeds. Analysis of variance (ANOVA) was conducted on final germination percentages after arcsin transformation and a general linear model chosen. We applied one-way ANOVA to test whether incubation temperature and desiccation intensity influence seed germination separately, and two-way ANOVA to test whether desiccation regime, i.e., temperature, relative humidity or habitat in different experiment, and treatment time, and interaction of these two factors, influence seed germination, respectively. Data was processed using SPSS version 19 (SPSS, Chicago, IL).

3 Results

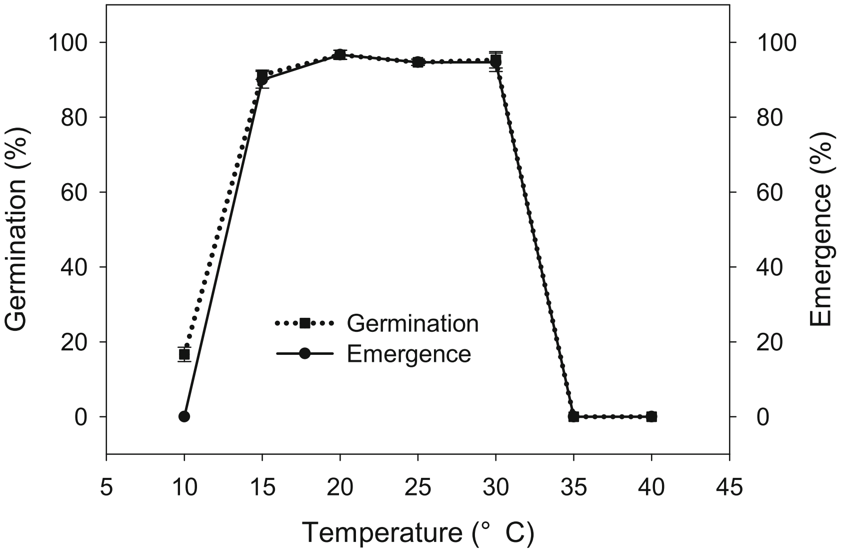
3.1 Effects of temperature on seed germination

Analysis of variance indicated that temperature significantly affected germination (F=360, P<0.001) and emergence (F=385, P<0.001). *B. ramiflora* seeds had maximum emergence percentage when incubated at 30 °C while maximum germination percentage was achieved at 20 °C, but neither emergence percentage nor germination percentage differ significantly between these two temperatures. No emergence was observed from seeds incubated at 10 °C, or at 35 °C or 40 °C. The same results were obtained for germination, except that 15 % of seeds germinated at 10 °C but failed to form seedlings (Fig. 1). Between 15 and 30 °C, the germination rate increased with temperature. One week after sowing, 23 % seeds were found to have radicle protrusion at 30 °C, while this value was 12 % for 25 °C and 20 °C, and nil for 15 °C. Seeds incubated at 15 °C to 30 °C all finished root and shoot formation within 1–2 months.

3.2 Desiccation tolerance of whole seeds under silica gel dehydration

B. ramiflora seeds lost moisture quickly under silica gel desiccation. This experiment lasted for only 48 h, but seed moisture decreased from 1.54 to 0.066 g/g. The wide shoulder of the desiccation time-moisture course for recalcitrant seeds was not observed for *B. ramiflora*. However, *B. ramiflora* seeds are very sensitive to desiccation, which significantly influenced the germination (F=78.1, P<0.001) and emergence (F=76.2, P<0.001) percentages. Twenty-four hours dehydration depressed seed moisture to 0.198 g/g, with germination decreasing linearly with moisture content from 96 % to zero. Probit analysis indicated that the critical moisture content is 1.38 and 0.818 g/g for 85 % and 50 % seedling emergence, respectively. The percentage germination and emergence differed from each other only slightly in the 0.667 to 1.13 g/g moisture range (Fig. 2). Overall, emergence was always closely linked with germination, with only slight differences (<5 %) detected, except for seeds incubated at

Fig. 1 Germination and emergence percentages of *Baccaurea ramiflora* seeds incubated at 10–40 °C in temperature-controlled incubators. Values are expressed as means±SE of six replicates of 25 seeds

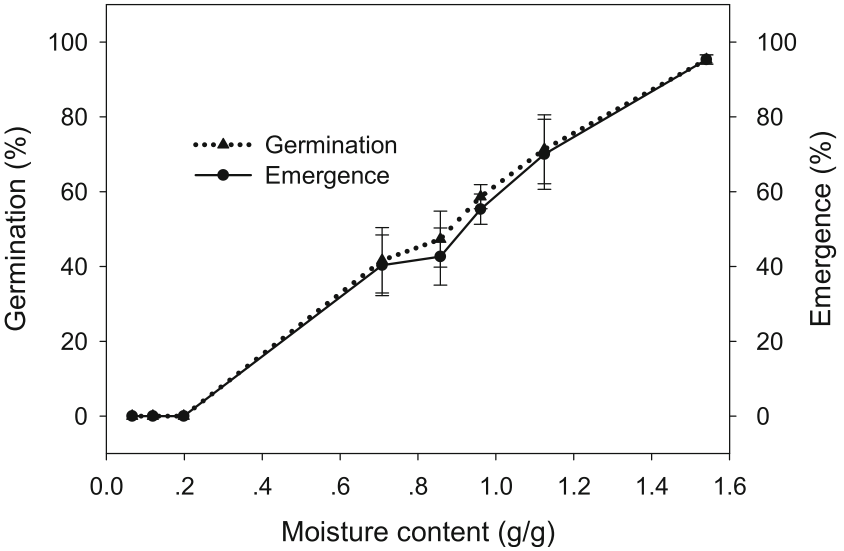


10 °C as mentioned above, so germination is not reported for the other experiments.

3.3 Effects of temperatures on moisture content and viability of whole seeds

As expected, temperature and treatment time both had a very significant influence on seed moisture ($F_{\mathrm{temperature}}$= 38.8, F_{time}=22.3, P<0.001 for both) and viability loss ($F_{\mathrm{temperature}}$=339, F_{time}=465, $F_{\mathrm{temperature\times time}}$=38.4, P<0.001 for all). Among all the temperatures investigated, seeds subjected to 20 °C had the slowest moisture and viability loss rate, with SMLRI=0.994 g g^{-1} day^{-1} and T50=3.5 days. As the treatment temperature increased, the seeds lost moisture and viability more and more rapidly (Fig. 3). Seeds at 35 °C and 40 °C behaved differently from those at lower temperatures, as at the higher temperature treatments equilibrium is reached quickly. Within the time period investigated, seeds at 15–30 °C lost moisture nearly linearly (Fig. 3a). Their emergence loss course had an obvious shoulder before they lost viability gradually, and these shoulders had almost the same width for the four temperatures (Fig. 3b). In contrast, temperatures of 35 °C and 40 °C depressed seed moisture to 0.25 g/g within 24 h, and these seeds reached their lowest values after 36 and 24 h (Fig. 3a), respectively, with T50s of only 0.64 and 0.35 days. From the co-plot between moisture content and emergence percentage, it can be seen that seeds at 40 °C lost most viability sharply at high moisture contents, so the curve had a convex slope; while those at 20 °C retained viability to lower moisture

Fig. 2 Viability loss of *B. ramiflora* seeds under dehydration by silica gel at 20 ºC. Moisture contents are determined by eight replicates of single seeds; germination and emergence percentages are means±SE of six replicates of 25 seeds



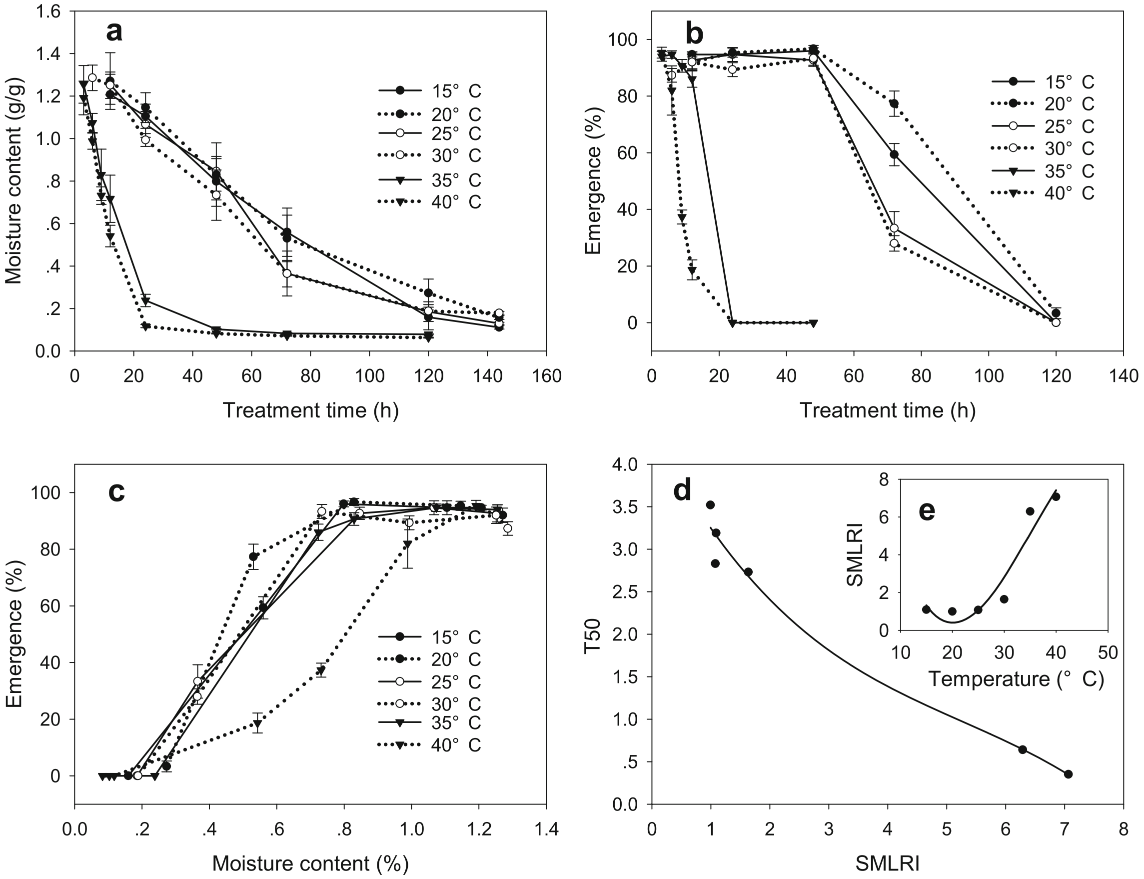


Fig. 3 **a**–**e** Moisture and viability loss of *B. ramiflora* seeds at different temperatures in temperature-controlled incubators. Moisture content expressed on a dry weight basis as means±SE of eight replicates of single seeds. Emergence percentages as means±SE of six replicates of 25 seeds. The *inset graph* (**e**) shows the seed moisture loss rate index (SMLRI) co-plotted with temperature

and then lost their most viability sharply, so the curve had a concave slope (Fig. 3c).

There was a varying relationship between temperature and moisture loss, as SMLRI increased abruptly when seeds were subjected to 35 °C and 40 °C, while it increased gradually at temperatures between 15 °C and 30 °C (Fig. 3e). Further, the drying rate provided a good explanation for variation in seed lifespan under different temperatures, as shown by T50 co-plotted against SMLRI (Fig. 3d). However, we failed to find a relationship between moisture loss rate and critical moisture content (data not shown).

3.4 Effects of relative humidity on moisture content and viability of whole seeds

Relative humidity is another factor significantly influencing seed moisture (F_{RH}=6.33, P=0.001; F_{time}=11.8, P<0.001) and viability loss (F_{RH}=223, F_{time}=668, $F_{\mathrm{RH \times time}}$=72.2, P<0.001 for all). *B. ramiflora* seeds had an initial moisture content as high as 1.54 g/g and seeds kept at RH 100 % had a slight increase in moisture content in the course of experiment (Fig. 4a), with their viability staying essentially constant for up to 80 days (Fig. 4b). Precocious germination was not observed, suggesting that an extra water supply is needed for germination and that wet storage could be used for short-term seed conservation. Seeds under RH 93.6 % lost moisture continuously (Fig. 4a) and exhausted viability over the course of the experiment (Fig. 4b). The lower the relative humidity, the faster the seeds lost moisture and the more rapidly they reached their equilibrium moisture content. Subsequently, they quickly lost their viability. From RH 93.6 % to 30 %, every decline in relative humidity notably accelerated moisture loss (Fig. 4a), increased seed moisture loss rate (Fig. 4e) and curtailed seed lifespan (Fig. 4d). It was found that *B. ramiflora* seeds reached their equilibrium moisture content within 30 days when relative humidity fell below 60 % (Fig. 4a). T50 was 22.1, 16.8, 10.4, and 2.24 days for seeds under RH 75 %, 62 %, 43 % and 30 %, respectively (Fig. 4d). Seeds at low relative humidity had short longevity as they lost both viability and moisture content rapidly, while those at high relative humidity had long longevity as they retained viability and moisture longer, and then lost viability sharply at a higher moisture content (Fig. 4c).

Drying rate is an important cause for variation in seed lifespan under different relative humidities (Fig. 4d), and relative humidity provided a partial explanation for SMLRI (Fig. 4e).

3.5 Changes in seed moisture and viability in the field

Both habitat and treatment time had significant effects on seed viability ($F_{\mathrm{habitat}}=62.5$, $P<0.001$; $F_{\mathrm{time}}=2.66$, $P=0.035$; $F_{\mathrm{habitat}\times\mathrm{time}}=5.14$, $P<0.001$), but only habitat on seed moisture ($F_{\mathrm{habitat}}=32.5$, $P<0.001$; $F_{\mathrm{time}}=1.38$, $P=0.277$). A one-day treatment made the moisture content of seeds assigned to Quadrat F significantly lower than those assigned to Quadrats A–E, and it decreased further after 2 days. Although seed moisture rose again after a thunderstorm in the following days, these seeds had lower moisture content in the whole experiment (Fig. 5a). In accordance with this, seed emergence from Quadrat F decreased rapidly to 30 % (Fig. 5b).

Although seeds from Quadrats D and E had almost as high moisture (Fig. 5a) and viability (Fig. 5b) as those from Quadrats A–C, they behaved differently in the field. Six days after they were assigned to habitats, more than 60 % of seeds in Quadrats A and B had germinated in the field, but only 30 % and 13 % in Quadrats C and D, and none in Quadrats E and F. By the 10 days, more than 95 % of seeds in Quadrats A–C had germinated, with 5-cm long roots, while 20 days were needed for seeds to reach this germination stage in Quadrats D and E. One month later, almost all seeds had formed normal seedlings in the field except that emergence was only 35 % for Quadrat F.

4 Discussion

This study confirmed previous reports that *B. ramiflora* produces recalcitrant seeds (Yu et al. 2008). Under silica gel desiccation, they lost viability within 24 h as moisture content decreased from 1.54 to 0.198 g/g. Using graded temperatures and relative humidity to mimic the changed microclimate in rainforest fragments, this study showed that both increases in

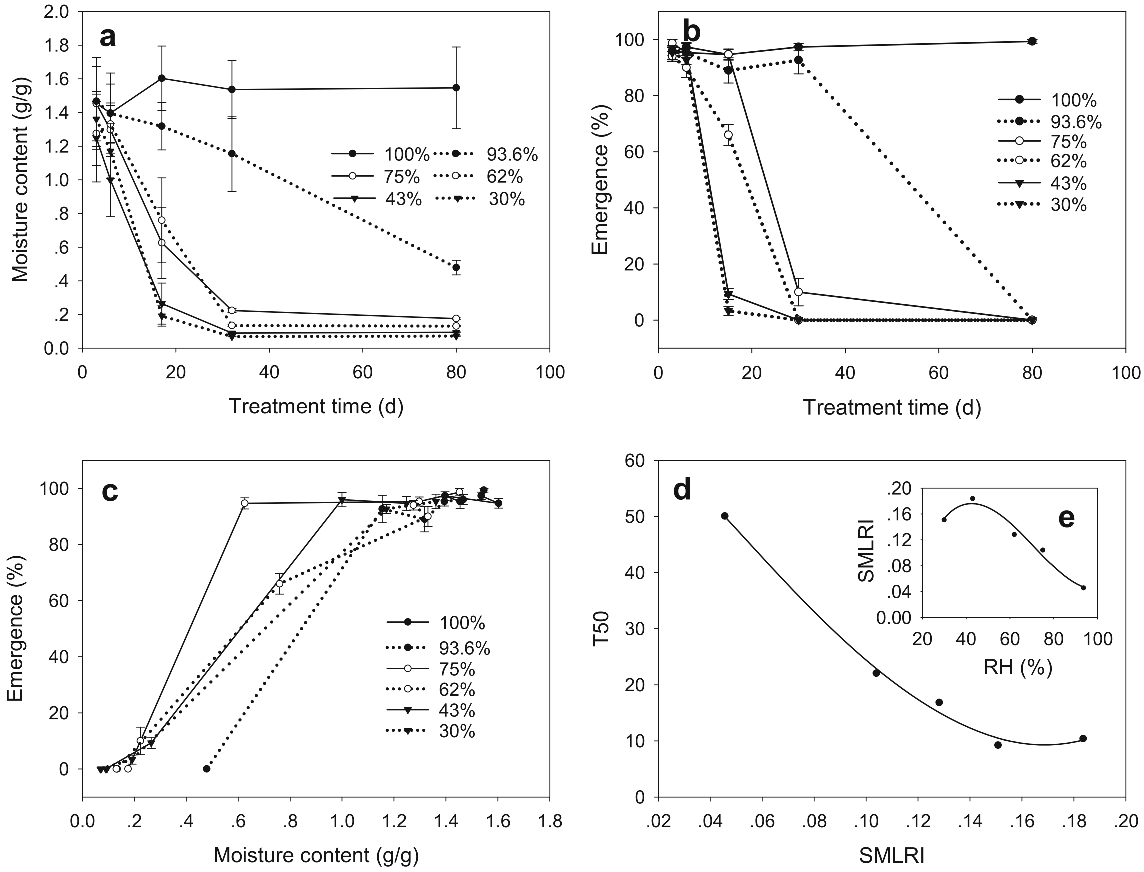


Fig. 4 **a**–**e** Moisture and viability loss of *B. ramiflora* seeds at different relative humidities regulated by saturated solutions of $CaCl_2$, K_2CO_3, NH_4NO_3, NaCl, KNO_3 and distilled water, in desiccators at 25 °C. Moisture contents are expressed on a dry weight basis as means±SE of eight replicates of single seeds; emergence percentages are means±SE of six replicates of 25 seeds. The *inset graph* (**e**) shows the SMLRI co-plotted with relative humidity (RH 100 % not included as there was no moisture loss under this regime)

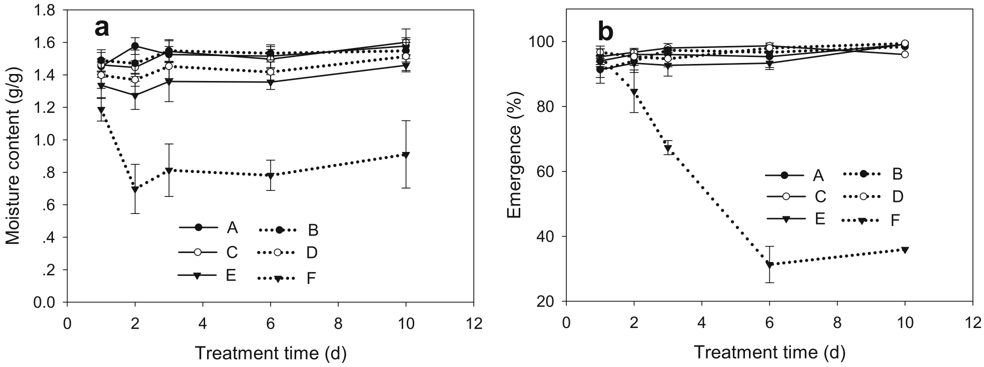


Fig. 5 **a** Moisture and **b** viability loss of *B. ramiflora* seeds placed on the soil surface in different habitats. Seeds were sampled from the field for viability and moisture determination. Quadrat *A* and *B* are in a rainforest valley, Quadrat *C* is on a slope in the same rainforest, Quadrat *D* is in an artificial forest of *Mesua ferrea* near the rainforest, Quadrat *E* is in a pomelo orchard far away from the rainforest, and Quadrat *F* is in grassland close to buildings where sunlight can reach directly between 10:00 a.m. and 4:00 p.m. on sunny days. Moisture contents are expressed on a dry weight basis as means±SE of eight replicates of single seeds; emergence percentages are means±SE of six replicates of 25 seeds

temperature and decreases in relative humidity accelerate loss of moisture and viability, although the response patterns were complex. *B. ramiflora* seeds had a higher initial moisture content than the *Hopea mollissima* seeds studied previously (Wen 2011) (1.54 vs 0.667 g/g), but we did not observe precocious germination under RH 100 % as occurred with *Hopea mollissima*, although both had an increase in moisture under this humidity.

Because of its wide distribution and high importance value (Cao et al. 2008), *B. ramiflora* is a critical species in Xishuangbanna tropical rainforests, as well as being representative of other climax species with recalcitrant seeds. *B. ramiflora* sheds seeds in the rainy season, and can complete germination within 10 days in the rainforest. In contrast, they lost moisture and viability rapidly when subject to drying, with a high critical moisture content. Almost all seeds germinated in the intact rainforest (Quadrats A–C), while in artificial forests (Quadrats D and E) germination was delayed. *B. ramiflora* seeds have been reported previously to have a high germination percentage in both the forest understory and in a canopy gap (Yu et al. 2008), but in this study two-thirds of the seeds failed to germinate in the non-forest habitat (Quadrat F), which is more open than the gap in the previous study.

Tropical recalcitrant seeds often initiate germination on the parent plants or shortly after release, so species with such seeds persist as an understory seedling bank rather than a soil seed bank (Dickie and Pritchard 2002; Farnsworth 2000; Thompson 2000; Vázquez-Yanes et al. 2000). In this study, *B. ramiflora* seeds had high final emergence in understory conditions, both in closed rainforest and artificial forests. Generally, recalcitrant seeds are spherical/ovoid while seeds of this species are flat. The seeds are also rather small compared to most typical recalcitrant seeds, such as mango and chestnut, with 100-seed weight of 30 g vs>100 g. This is likely to mean less resistance to desiccation, as small and flat seeds lose moisture more quickly under dry conditions, in addition to limited food reserves for germination and establishment at low levels of solar radiation.

Rainforest fragmentation results in both microclimate changes and changes in species composition. Though the relationship between them is likely to be complex, microclimate changes may influence germination, as shown by Bruna (1999), and thus lead to changes in species composition. Accumulated evidence from ecological studies supports this inference, although studies of the effects of fragmentation on seed germination are limited. For example, by investigating the germination of 43 tree species native to the lowland forests of Malaysia in three different habitats, Raich and Khoon (1990) found that most forest canopy species germinated in the gap, but germination in the large clearing was reduced dramatically. Conversely, canopy-induced inhibition of germination was apparent in pioneer species. They concluded that germination requirements play a very important role in controlling the species composition of regeneration in forest understorey, gap, and large clearing habitats (Raich and Khoon 1990). Many other studies, such as those of Kyereh et al. (1999), Vásquez-Yanes and Orozco-Segovia (1990), Metcalfe (2001), Souza and Válio (2001), Daws et al. (2002), and Chen et al. (2013), covering both field and/or laboratory work, have reported differences in seed germination response of pioneer and non-pioneer species. These studies show that forest fragmentation will favor the germination and seedling establishment of pioneer species because this will cause increased sunlight and temperature fluctuations, in the same way as gap formation, but why and how the microclimate changes in fragmented rainforests reduces germination and truncates the longevity of climax seed species is still not fully understood, in part because of the difficulty in assessing the effects of multiple, changing, factors under field conditions. Wen (2011) studied the effects of increased temperature and decreased relative humidity on moisture content and viability of *Hopea mollissima* seeds using graded temperatures and relative humidity. *B. ramiflora* seeds are similar to *H. mollissima* seeds in that they exhibit high sensitivity to changes in temperature and relative humidity, but differ in that they lose moisture and viability more rapidly when subjected to high temperature and low RH. Both of these seed species need forest habitats to germinate in the field.

Seeds at the open site were subject to high temperatures as well as low humidity. Although high temperatures accelerate seed moisture loss (Fig. 3a), these seeds lost viability at relatively higher moisture contents (Fig. 3c), implying that high temperature itself is lethal to *B. ramiflora* seeds, as was also shown under the experimental temperature treatments. Ground temperatures in forest gaps in Xishuangbanna can reach>40 °C (Liu et al. 2000), suggesting that the thermal tolerance of rainforest seeds deserves further study.

In conclusion, *B. ramiflora* seeds are very sensitive to dehydration and high temperatures and require rainforest habitats for germination. Fragmentation and deforestation will impair germination and make seedling establishment a bottleneck in the plant life cycle. The vulnerability of recalcitrant seeds to high temperatures needs further investigation. In fragmented tropical rainforests, species like *B. ramiflora* producing recalcitrant seeds have more difficulties than those producing orthodox seeds, thus favoring pioneers over climax species. Rainforest conservation managers need to pay more attention to the germination and establishment of species with recalcitrant seeds. To prevent extinction of recalcitrant-seeded climax species from tropical rainforests, management should focus on maintaining interior forest conditions.

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