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Smoke-water effect on the germination of Amazonian tree species

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ABSTRACT

Smoke stimulates seed germination of a range of species from ecosystems that may or may not be fire prone. We evaluated the effects of smoke-water on germination of ten tree species of economic value in the Amazon region. Two materials were burnt to produce smoke-water: germination paper and the wood of *Cecropia palmata* Willd. Seven dilutions of the solutions were tested. Seeds of nine forest trees were germinated under controlled laboratory conditions (25 °C ± 2 °C) in the laboratory. *Bertholletia excelsa* Humb. & Bonpl., was tested in the nursery (approximately 25–36 °C) because of its large seeds. Irrespective of the material burned, smoke-water significantly increased seed germination of three species: *Cordia goeldiana* Hub., *Ochroma pyramidale* (Cav. ex Lam.) Urb. and *Jacaranda copaia* (Aubl.) D. Don. and there was a significant inhibitory effect on *Swietenia macrophylla* King. Germination was accelerated by smoke in *J. copaia*, *B. excelsa* and *Bellucia grossularioides* (L.) Triana. The most pronounced effect was observed in *B. excelsa*, as the mean germination time of 108 d (control) was reduced to 76 d with smoke-water made from germination paper (dilution of 1:25) and to 61 d with the one from *Cecropia* wood (dilution of 1:250). For five of the ten species studied, smoke-water either increased or accelerated seed germination, irrespective of the materials used for its production. Seeds with low vigour and prolonged germination time seemed to be more receptive to smoke.

1. Introduction

Human action may be the main cause of fire in the Amazon. Itinerant cultivation is part of indigenous culture and the use of fire after clearing an area is customarily used to transform forest into pasture for cattle ranches or agriculture (Lima et al., 2007). Even though the trees in this region do not experience regular fire in their natural habitat, we were interested in studying the effect of smoke-water on seed germination, as previous studies have shown a stimulatory effect on a variety of cultivated and non-cultivated plants, regardless of whether the plants occur in fire-prone ecosystems (Brown and Van Staden, 1997; Light and Van Staden, 2004; Light et al., 2009). The action of smoke does not appear to be restricted to a certain group of species, life form, geographical extension, habitat or seed weight (Van Staden et al., 2000; Crosti et al., 2006), or reproductive strategy and type of seed dispersal (Brown et al., 2003). Smoke can improve germination performance (Brown et al., 2003) and plant development (Van Staden et al., 2007), increase secondary roots in seedlings (Kulkarni et al., 2006), and seedling fresh weights (Sparg et al., 2006; Van Staden et al., 2006).

Production of smoke-water is relatively easy and inexpensive, as only simple devices are necessary. Thus smoke-water could be very useful for local producers, both by its wide applicability and the ease of production. At the laboratory level, smoke-water is often produced with germination paper (Jäger et al., 1996). This is impractical for obtaining larger volumes and for local producers. Smoke-water produced with several raw materials from the Amazon region, including the wood of a pioneer secondary forest species (*Cecropia palmata* Willd), sawdust of several trees from the Lauraceae family, or palm leaves, did improve the germination performance of tomato seeds (Arruda et al., 2012).

For this study, *Cecropia* wood was chosen for smoke production. This species grows vigorously after a pasture or field is abandoned throughout the Amazon region (Mesquita et al., 2001). Besides being a common species, it can be readily accessed, and the wood has no economic value. The wood is also easier to handle than large palm leaves. Smoke-water was tested on seed germination of ten economically important trees from the Amazon. These species differed in seed shape, size and consequently fresh weight, desiccation tolerance (recalcitrant and orthodox), dormancy (physical limitations, mechanical and physiological), dispersal behaviours (i.e. by wind and animals) and belonged to different ecological groups (pioneer and climax). The aim of this study was to compare smoke-water produced with germination paper or *Cecropia* wood on seed germination of economically important trees which do not experience regular fire in their natural habitat.

2. Materials and methods

The smoke-water was produced according to Farley (2005), at a ratio of 6 kg of raw plant material for 10 L of distilled water

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(Flematti et al., 2004). Thin Germitest® germination paper (GP) and *Cecropia* wood (CW) were used as raw materials. Before burning, the wood was cut into small pieces and dried at 105 °C for 24–48 h. Seven smoke-water dilutions were tested (1:1000, 1:500, 1:250, 1:100, 1:50, 1:25 and 1:10).

Ten economically important tree species, occurring on unflooded (terra firme) forest, were selected for this study (Table 1). Most are timber species (e.g., mahogany — *Swietenia*), others have other uses, such as the Brazil nut tree (*Bertholletia*). Most fruits and seeds were collected in the Brazilian Amazon region in the state of Amazonas, with *Swietenia* from the state of Para, and *Schizolobium* from the state of Mato Grosso.

Seed moisture (%) was determined on a fresh-weight basis, gravimetrically after drying the whole seed at 75 °C until the weight was constant. For *Bellucia*, ten samples of 5 g of seeds were used, because the seeds were small. The seeds were stored at 15 °C before commencement of the germination experiments, as indicated in Table 2. Only *Bertholletia* seeds, according to the recommendation of Kainer et al. (1999), were maintained in moist sand in the nursery (monthly average minimum temperature was 25 °C ± 2 °C and maximum 36 °C ± 3 °C). For the germination trials, germination substrate, containers and the number of seeds per trial were chosen according to seed size. The three species with physical dormancy, listed in Table 1 as having an impermeable seed coat, were scarified (Table 2). Germination was assessed under constant temperature (25 °C ± 2 °C) with a 12 h photoperiod and seeds were sown on top of the substrate. Only *Bertholletia* was sown in the rain-protected nursery and covered with a layer of 2 cm of vermiculite. The substrates were moistened with distilled water (control) or with one of the smoke-water dilutions of GP and CW, and remoistened when necessary. Germination was assessed every two days until no further germination occurred. In the laboratory, the germination criterion was a radicle protrusion of ≥2 mm, and in the nursery it was emergence above the substrate. The measured variables were: final percentage of seeds germinated, mean germination time and time for 50% germination of the germinable seeds (Santana and Ranal, 2004). The results were analyzed by Wilcoxon test at 5% probability.

3. Results

Regardless of whether GP or CW was used for the production of smoke-water, three distinct effects on seed germination could be observed: stimulatory, inhibitory or neutral. A stimulatory effect on seed germination with smoke-water was observed in three species: *Jacaranda*, *Ochroma* and *Cordia* (Fig. 1). In *Cordia*, the GP dilution of 1:50 caused an increase in germination from 56% (±9.6%) in the control, to 88% (±9.1%) with smoke-water. However, in *Ochroma*, a significant increase was observed with a GP dilution of 1:250 (88 ± 11.1% compared to 40 ± 27.0% control). In *Jacaranda*, several dilutions of smoke-water made from both raw materials increased germination percentage (≥79%) compared to the control (48 ± 20.5%), as well as all dilutions tested between 1:10 and 1:100 with GP, and 1:25, 1:50, 1:100 and 1:1000 with CW. Smoke-water had no effect on germination of six species. The slight increases observed with some dilutions were not significant (Fig. 1). Germination inhibition was observed with mahogany seeds (*Swietenia*); germination was quantitatively reduced with all dilutions, and significantly reduced after application of CW smoke-water at higher concentrations (1:10 and 1:50) (Fig. 1). In this species abnormalities of the primary root were also observed in ≤8% of the seedlings with CW and ≤12% with GP.

The smoke dilutions, which produced the highest increase in germination, varied between 1:10 and 1:1000, depending on the species. Regardless of the raw materials used, the relative increase in germination varied: *Cariniana* (GP — 4%; CW — 7%), *Schizolobium* (GP — 12%; CW — 7%), *Bellucia* (GP — 10%; CW — 10%), *Tabebuia* (GP — 12%; CW — 13%), *Bertholletia* (GP — 4%; CW — 29%), *Enterolobium* (GP — 19%; CW — 20%), *Cordia* (GP — 57%), *Jacaranda* (GP — 34%; CW — 83%), and *Ochroma* (GP — 114%). In *Cordia*, *Ochroma* and *Jacaranda* seeds, which had shown significant increases in germination with smoke, germination of the controls varied between 40% and 56%, indicating seed lots of low vigour. Particularly in *Ochroma* seeds the smoke-water effect was high, with an increase of 114% with GP — 1:250 compared to the control.

Germination rate was increased by smoke-water, as can be seen by the reduction of mean germination time of three species: *Jacaranda*, *Bellucia*, and *Bertholletia* (Fig. 2). All dilutions tested with GP smoke-water reduced mean germination time in *Bellucia* seeds, as well as two dilutions of CW (1:250 and 1:500). In *Bertholletia*, a reduced germination time was seen with both GP and CW, however due to germination spread over a long time after sowing (between 26 and 171 d) the differences in mean germination time were not statistically significant. Germination rate in *Jacaranda* seeds was reduced with all dilutions of CW. However, no influence was seen with GP, and the most

Table 1
Seed characteristics of species investigated in this study, ranked by seed weight.

Species	Family	Dispersal type	Dormancy type	Seed reserve	Seed weight	Seed moisture
					(g)	(%)
Bellucia grossularioides (L.) Triana	Melastomataceae	Zoochorous	Light-required[a]		0.00007 (±0.000008)[a]	8.6 (±0.2)
Ochroma pyramidale (Cav. Ex Lam.) Urb. (Balsa wood)	Malvaceae	Anemochorous	Impermeable seed coat[b]	Endosperm	0.007 (±0.001)	7.5 (±4.4)
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	Anemochorous	Light-required[a]	Cotyledons	0.012 (±0.003)	9.9 (±1.0)
Tabebuia serratifolia (G. Don) Nichols.	Bignoniaceae	Anemochorous	Non-dormant[c]	Cotyledons	0.016 (±0.006)	21.4 (±5.7)
Cordia goeldiana Hub.	Boraginaceae	Anemochorous	Non-dormant[d]	Embryo[d]	0.017 (±0.002)	13.2 (±1.2)
Enterolobium schomburgkii Benth.	Fabaceae	Zoochorous	Impermeable seed coat[e]	Cotyledons[e]	0.069 (±0.014)	9.2 (±2.6)
Cariniana micrantha Ducke	Lecythidaceae	Anemochorous	Non-dormant[f]	Embryonic axis[f]	0.094 (±0.038)	21.6 (±2.0)
Swietenia macrophylla King (Mahogany)	Meliaceae	Anemochorous	Non-dormant[g]	Cotyledons[g]	0.542 (±0.115)	7.9 (±0.9)
Schizolobium amazonicum Huber ex Ducke	Fabaceae	Barochorous; anemochorous	Impermeable seed coat[h]	Endosperm[h]	0.923 (±0.135)	4.0 (±0.9)
Bertholletia excelsa Humb. & Bonpl. (Brazil nut)	Lecythidaceae	Barochorous	Immaturity; mechanical restriction by seed coat[i]	Hypocotyl[i]	12.933 (±5.103)	38.1 (±11.2)

[a] Aud and Ferraz (2012).
[b] Sandi and Flores (2002).
[c] Ferreira et al. (2004).
[d] Kanashiro and Vianna (1982).
[e] Ramos and Ferraz (2008).
[f] Camargo et al. (2003).
[g] Lima Júnior and Galvão (2005).
[h] Sousa et al. (2005).
[i] Kainer et al. (1999).

Table 2
Storage before commencement of germination experiments and conditions of germination trials.

Genus	Storage period	Germination treatments	Replications × seeds	Substrate	Container	Container dimensions (cm)
Bellucia	1 year	None[a]	5 × 50-100	Paper	Petri dish	8.5 × 8.5 × 6.0
Ochroma	5 months	Manual scarification	5 × 20	Vermiculite	Plastic box	11.0 × 11.0 × 3.0
Jacaranda	1 month	None[a]	5 × 20	Paper	Plastic box	21.0 × 11.5 × 4.5
Tabebuia	11 days	None	4 × 25	Paper	Paper roll	38.0 × 28.0
Cordia	5 months	None	5 × 20	Vermiculite	Glass dish	24.5 × 16.0 × 6.0
Enterolobium	8 years	Manual scarification	4 × 25	Paper	Paper roll	38.0 × 28.0
Cariniana	11 days	Wing size reduced by cutting	4 × 25	Vermiculite	Plastic box	21.0 × 11.5 × 4.5
Swietenia	7 months	Wing size reduced by cutting	4 × 25	Vermiculite	Glass dish	24.5 × 16.0 × 6.0
Schizolobium	4 months	Manual scarification	4 × 25	Vermiculite	Glass dish	24.5 × 16.0 × 6.0
Bertholletia	7 months	Seed coat removal	3 × 25	Sand and vermiculite	Plastic box	30.0 × 20.0 × 10.0

[a] Sowing above substrate was sufficient to overcome light requirement.

concentrated solution (1:10) increased germination time. In the remaining seven species no influence of smoke-water on the germination rate was seen, either by the raw materials or by the tested dilutions.

Time needed for 50% germination of germinable seeds (T_{50}) is shown in Fig. 3. The best performance of the respective smoke-water dilutions were compared with the control. Smoke-water effects became more pronounced with increasing germination time, as in *Bertholletia* and *Bellucia*. In *Cordia* seeds germination time (T_{50}) was increased by GP. This was due to a delayed germination pulse observed only in the seed treated with GP (1:50) (Fig. 4). The germination process of *Cordia* can be divided into the following stages: (I) lag phase of approximately 13 d before protrusion of radicles; (II) germination in an S-shaped curve; (III) stagnation of the process over 34 d; and (IV) second germination pulse of seeds treated with GP (1:50) reaching 88%, which was significantly higher than in the control.

4. Discussion

Plant-derived smoke diluted in water can be considered as a natural stimulator for seed germination over a wide range of species occurring in ecosystems either regularly or rarely burnt (Light et al., 2009). The main germination stimulant in smoke has been identified as a low molecular weight organic compound active at very low concentrations (butenolide) (Flematti et al., 2004; Van Staden et al., 2004). The positive effects of smoke on seed germination have been shown for a wide variety of botanical families, on species which differ in reproductive strategy, seed size and seed morphology (Dixon and Roche, 1995). In this study, the ten selected Amazonian tree species occur in an unflooded terra firme forest, from a habitat which does not experience regular fires. Considering germination performance, the species differ in a number of seed characteristics and they also differed in their receptiveness to the smoke applications, depending on the plant material burned for its production and its dilution. In three species, *Jacaranda*, *Ochroma and Cordia*, smoke-water significantly improved the germination percentage. In six species, *Schizolobium*, *Tabebuia*, *Cariniana*, *Bellucia*, *Enterolobium* and *Bertholletia*, smoke-water did not influence final germination percentage. Finally in *Swietenia*, smoke-water reduced germination at all dilutions tested.

Varied responses in germination are common in the study of smoke, even in species of the same family (Brown, 1993) or genus (Kulkarni et al., 2007) or in the same species, depending on the dormancy status (Baker et al., 2005). The responses differed from strongly, moderately or slightly stimulated, not affected or inhibited by the smoke-water, in herbaceous dicotyledonous species from Australia (Adkins and Peters, 2001). In South African grasslands prone to fire, the degree of response varied from species to species; of the six Poaceae representatives studied, *Themeda triandra* Forssk. and *Tristachya leucothrix* Trin. ex Nees showed the greatest response, and with increasing temperature another three species responded positively to the smoke solutions (Ghebrehiwot et al., 2009). Of 18 woody species in central Chile, only three (*Acacia caven* (Molina) Molina, *Baccharis vernalis* Hellwig and *Trevoa quinquenervia* Gillies and Hook.) showed improved germination after smoke application (Gómez-González et al., 2008). Smoke-water and ash treatments were effective in 5 of 12 tree species from frequently burned areas in Mexico, another 6 species were only facilitated with an additional heat treatment (Zuloaga-Aguilar et al., 2011).

Even if the response to smoke-water was not measurable in the final germination percentage, other variables, especially those related to seedling vigour, may be significant, as was found in a previous study using *Albuca pachychlamys* Baker, *Merwilla natalensis* (Planch.) Speta and *Tulbaghia violacea* Harv. (Sparg et al., 2005). In this study, *Bertholletia* and *Bellucia* only showed a significant response to smoke in the germination rate (T_{50}) and not the final germination percentage. These species are slow to germinate. *Bertholletia* has large (13 g), recalcitrant seeds with mechanical dormancy caused by the woody integuments (Cunha et al., 1996; Kainer et al., 1999) and *Bellucia* is a small-seeded (0.2 mg), light-requiring pioneer species (Aud and Ferraz, 2012). *Jacaranda*, a small-seeded (12 mg) light-requiring pioneer species (6.5 mg) (Aud and Ferraz, 2012), was responsive both in germination percentage and germination rate (T_{50}).

The importance of the raw material used for smoke-water production has been tested previously, depending on the species, the only dilution which caused significant difference was 1:10 (*Acacia mearnsii* De Wild.); 1:100 (*Pinus patula* Schltdl. & Cham.; *Hypoxis colchicifolia* Baker) and 1:1000 (*Eucalyptus grandis* W. Hill ex Maiden) (Jäger et al., 1996). The active concentrations were also different when comparing four commercially available smoke solutions on *Avena fatua* L. and *Malva neglecta* Wallr. (Adkins and Peters, 2001).

Mean germination time was a very sensitive variable and exhibited inhibitory effects at high concentrations (1:10) of smoke-water, as seen in *Jacaranda*, *Cariniana* and *Bellucia* seeds. A series of herbs were inhibited with high concentrations of smoke-water as found with *Syncarpha vestita* (L.) B. Nord., inhibited with a dilution of 1:2 (Brown, 1993; Brown and Van Staden, 1997), and *Senecio grandiflorus* P.J. Bergius, *Restio similis* Pillans (Brown, 1993) and *Lamium purpureum* L. (Adkins and Peters, 2001) were inhibited with smoke-water dilutions of 1:10 similar to those tested in this study. Agronomic species seem to be even more sensitive, such as tomato was inhibited with a dilution of 1:50 (Taylor and Van Staden, 1998) and corn with 1:250 (Sparg et al., 2006).

The negative effect of high concentrations of smoke-water on germination had been shown earlier and was attributed to inhibitory compounds present in smoke other than butenolide (Adkins and Peters, 2001; Daws et al., 2007). Recently a second butenolide was identified in smoke-water which inhibits germination and significantly reduces the effects of the stimulatory compounds (Light et al., 2010).

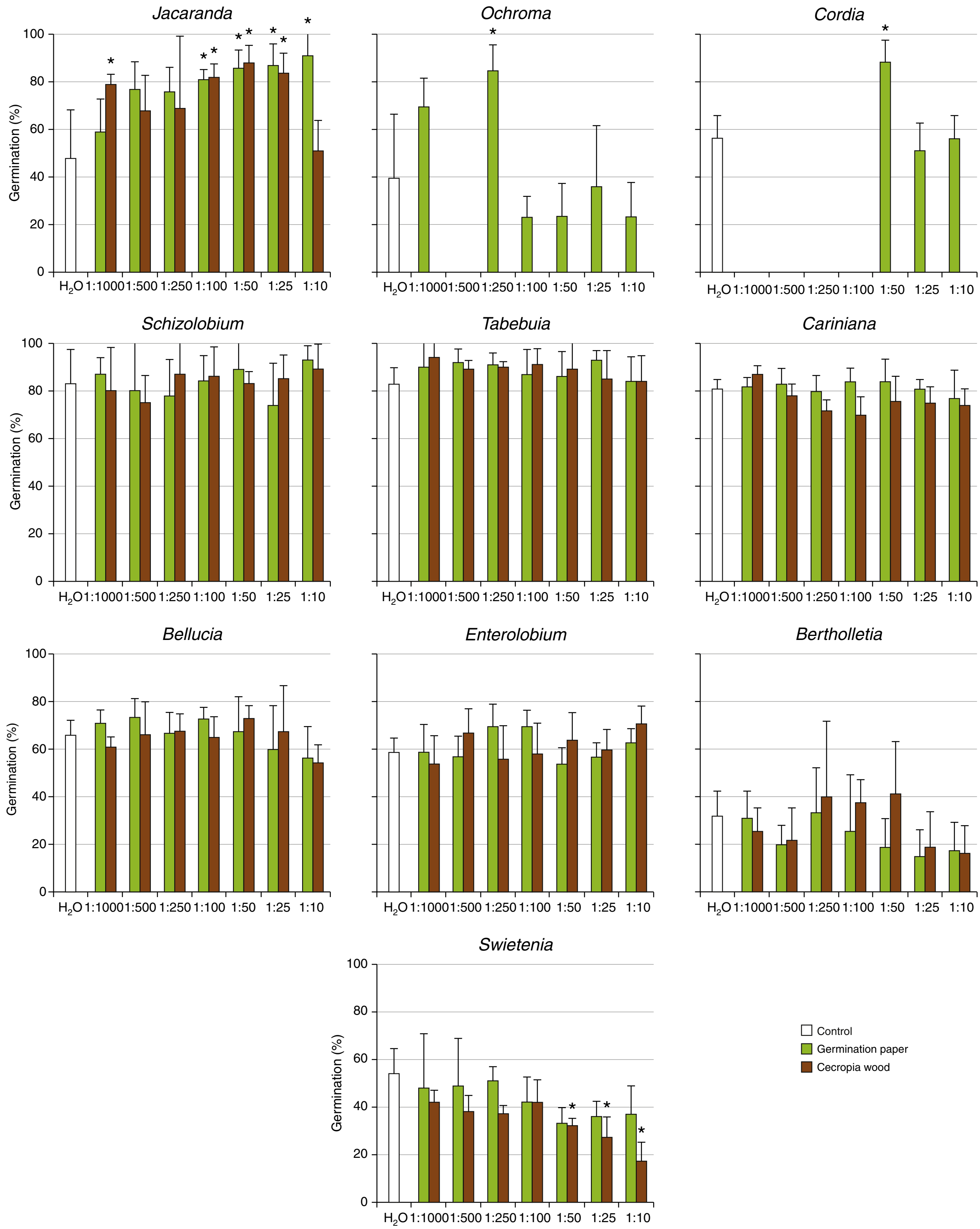

Fig. 1. Seed germination of ten Amazonian tree species (listed in Table 1) with different dilutions of smoke-water, produced from burning germination paper (GP — green column) or *Cecropia* wood (CW — brown column). Standard deviation is shown with bars and statistically significant difference to control (white column) of each species by Wilcoxon Test (5% probability) is indicated by *.

5. Conclusions

Positive responses to smoke-water were shown in the germination pattern of five of ten Amazonian trees, which do not experience regular fire in their natural habitats. In one species final germination percentage and germination rate were increased (*Jacaranda*); in two species final germination percentage was increased (*Ochroma* and *Cordia*) and in two more species the germination rate was increased (*Bellucia* and *Bertholletia*). Responsiveness to smoke was found in small- to middle-sized, wind-dispersed, desiccation-tolerant, and

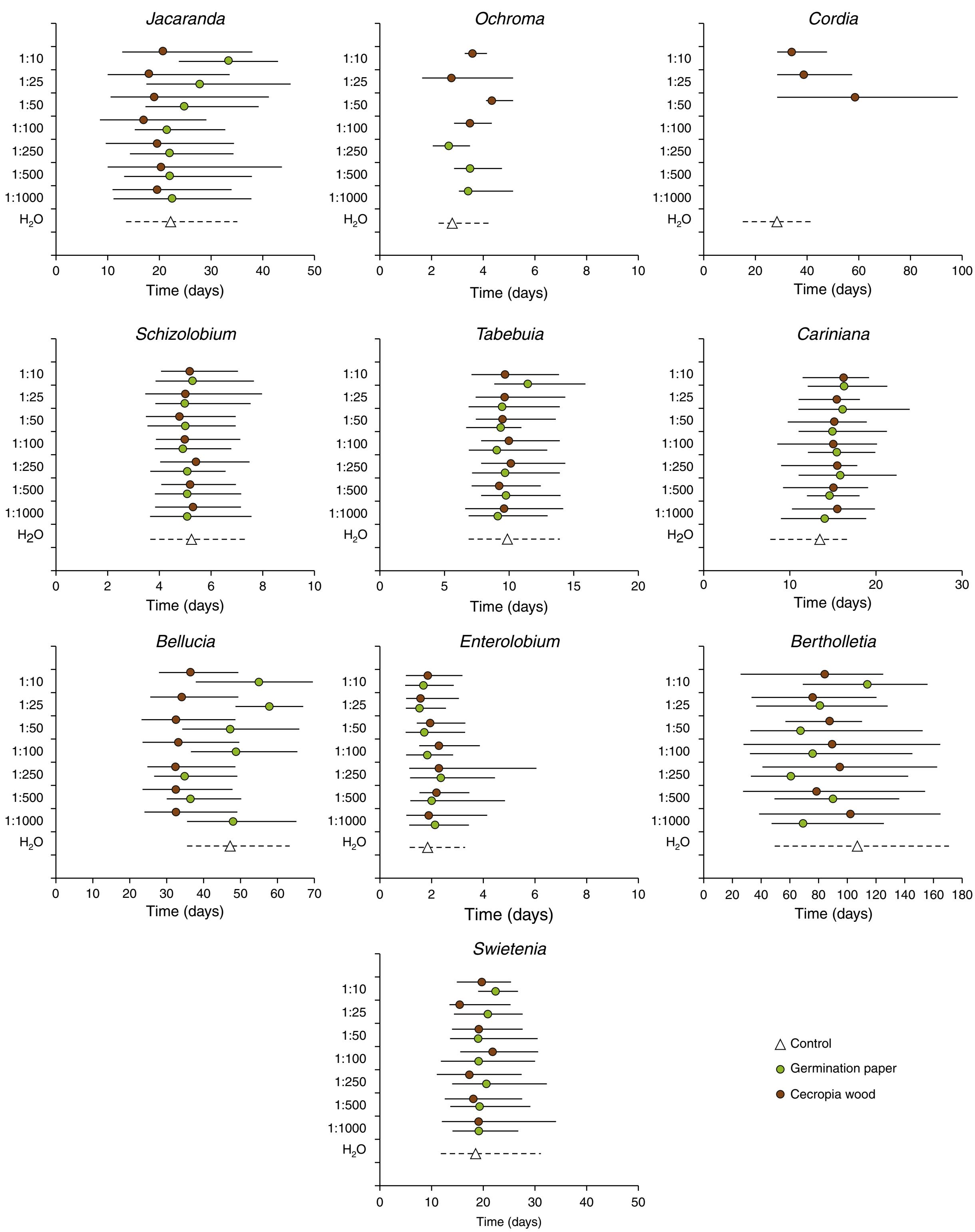

Fig. 2. Germination time: mean (triangle), initial and final (line) of ten Amazonian tree species after application of different dilutions of smoke-water produced from burning germination paper (GP — green circle) or *Cecropia* wood (CW — brown circle) compared with the respective control (triangle and dotted line).

photoblastic-positive or -neutral seeds, and also in *Bertholletia* which has large, desiccation-sensitive seeds with mechanical dormancy.

The smoke-receptive species had seed lots with low vigour (*Cordia*, *Jacaranda* and *Ochroma*) or with long germination periods (*Bertholletia* and *Bellucia*). For future studies we suggest comparing different quality seed lots of these species to verify if smoke susceptibility can be influenced by seed vigour and to look for smoke-receptive seeds in other species with a long germination period.

Smoke responsiveness varied between species and also smoke concentration. Therefore it is not possible to indicate a specific dilution effective in all smoke-receptive seeds.

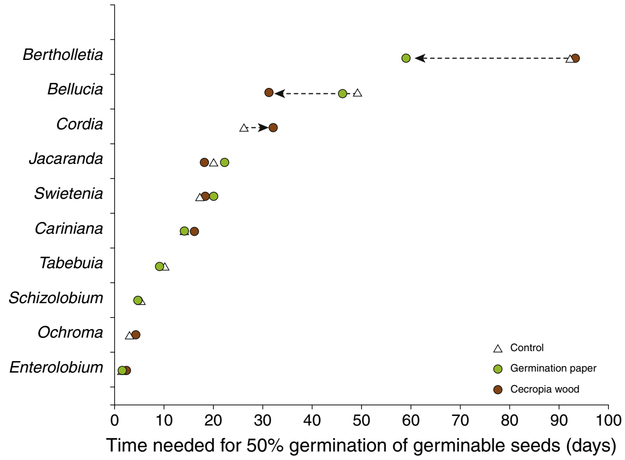

Fig. 3. Time needed for 50% germination of germinable seeds (T_{50}) of ten Amazonian tree species. Comparing T_{50} of the control (triangle) with the best results obtained with smoke-water produced from burning germination paper (GP — green circle) or *Cecropia* wood (CW — brown circle). Arrows indicate positive or negative effects on T_{50} by smoke-water.

No consistent difference was observed in smoke-water response comparing GP and CW, which allows the use of the latter, as it is an inexpensive and readily obtainable raw material for future studies. The ease of production and its wide applicability could be very useful for local producers even in remote communities.

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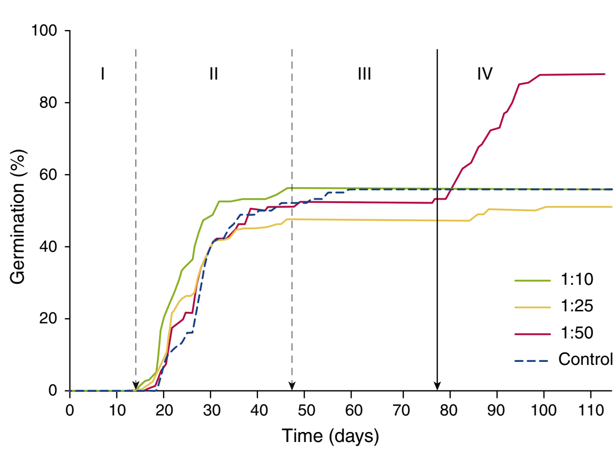

Fig. 4. Germination curves of *Cordia goeldiana* seeds at 25 °C (±2 °C), constant temperature, moistened with water (dotted line) or with smoke-water produced from burning germination paper (GP, continuous line) diluted at 1:10, 1:25, and 1:50.

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