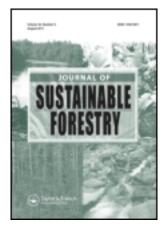
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Journal of Sustainable Forestry

Publication details, including instructions for authors and subscription information:

http://www.tandfonline.com/loi/wjsf20

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To cite this article: David Beaune , Loc Bollache , Musuyu D. Muganza , Franois Bretagnolle , Gottfried Hohmann & Barbara Fruth (2013) Artificial Germination Activation of Dialium corbisieri by Imitation of Ecological Process, Journal of Sustainable Forestry, 32:6, 565-575, DOI: 10.1080/10549811.2013.780199

To link to this article: http://dx.doi.org/10.1080/10549811.2013.780199

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ISSN: 1054-9811 print/1540-756X online DOI: 10.1080/10549811.2013.780199



Artificial Germination Activation of *Dialium* corbisieri by Imitation of Ecological Process

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Species of the gender Dialium commonly are trees found in Central African rainforests. They produce tasty sugary fruits, feeding numerous frugivores, but are, despite their valuable nutritional value, rarely exploited by humans. A potential reason for this could be the complexity of symbiotic dependence between trees and pollinators, germination activators, and dispersers causing problems in ancestral and contemporary domestication. We investigated Dialium corbisieri reproduction in the Democratic Republic of the Congo, Bandundu Province. Here we give a key for an artificial activation of germination of these trees ecologically adapted to the digestive system of their ape dispersers: By perforation of the impermeable seed coat protection, water assimilation and

The authors thank the Institut Congolais pour la Conservation de la Nature (ICCN) for granting permission to conduct research at Salonga National Park. Fieldwork at Lui Kotale was supported by la Région Bourgogne, France and the Max-Planck-Society, and the Federal Ministry of Education and Research, Germany. The methods used to collect data in the field are in compliance with the requirements and guidelines of the ICCN, and adhere to the legal requirements of the host country, the Democratic Republic of the Congo. Special thanks goes to Bas Van Der Veer, Sam Stubbs, Andrew Fowler, Constantin Lubini, Félicien Lukoki, Jean-Pierre Habari, and Llandu Lukebakio.

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subsequent activation of germination becomes possible. By this nicking, pretreatment germination increases from 0 to 96%, representing an inexpensive and simple treatment to be used under natural conditions and in developing countries. The use of this mechanical activation for forest management, conservation, and economic use is discussed.

KEYWORDS Dialium corbisieri, African velvet tamarind, seed pretreatment, germination activation, seed dormancy, endozoochory, domestication

INTRODUCTION

The family of the Leguminosae have an important ecological role in forests. Of particular interest are *Dialium* species belonging to the subfamily of Caesalpinioidae. They dominate parts of the tropical evergreen lowland rainforests of the Central Congo Basin, Democratic Republic of the Congo (DRC). Species of this gender are medium sized to very tall trees (up to 40 m) with a very hard wood, highly valued in timber, and fruit providing an edible pulp (Janick & Paull, 2008, p. 391). Some of them are considered of particular interest for their mono-lobed fruit consisting of a slightly flattened seed protected by a hard endocarp, embedded into a pithy and luscious sweetly sour edible mesocarp and enclosed by a black-brown velvety, thin, and brittle exocarp (capsule). Fruits stand erect at the end of branches and ripen over an extended period of the year, usually coinciding with dry seasons. Availability of fruit has been reported between February and May for Nigeria, and between November and July for Gabon (White & Abernethy, 1997). These fruits are important for a lot of frugivorous species in rainforest biocenoses and we can observe a strong interaction between plants and animals (Beaune et al., 2013a). To attract animals as seed dispersers, angiosperm fruit coevolved with fruit-predators adapting to the taste and digestive system of their partners (Thompson, 1991; Jordano, 1995). Partners include birds, ungulates, monkeys, and great apes including bonobo (Pan paniscus; Hohmann, Fowler, Sommer, & Ortmann, 2006; Beaune et al., 2013b), chimpanzee (Pan troglodytes), and gorilla (Gorilla gorilla; White & Abernethy, 1997; Kuroda, Nishihara, Suzuki, & Oko, 1996). Dialium seeds are adapted to endozoochory by their strong endocarp (i.e., seed coat dormancy) in order to survive through the frugivorous gut passage. This potentially avoids or inhibits the ability to self-germinate and thus may be considered as displaying dependency to endozoochory.

Dialium fruit is not only of importance to forest dwelling animals, particularly non-human primates, but also to humans. Particularly Dialium guineense, known in Africa as black velvet tamarind, is used by people

in West and Central Africa. The fruit is popular and traded in Benin and of regular use in Nigeria (Arogba, Ajiboro, & Odukwe, 1994). It is known to contain high levels of Vitamin C, sugars, essential oils, and other nutritive components (Achoba, Lori, Elegbede, & Kagbu, 1992; Ude et al., 2002; Essien, Ogunwande, Ogunbinu, Flamini, & Cioni, 2007; Arogba et al., 1994; Onwuka & Nwokorie, 2006).

However, traditional use of Dialium fruits across Africa is not widespread, and attempts to enhance cultivation or incite industrialization so far were constrained by their ecology. In addition, certain Dialium species are at risk by habitat loss and registered on the International Union for Conservation of Nature (IUCN, 2010) red list as follows: D. bipindense (lower risk/near threatened); D. cochinchinense (lower risk/near threatened); D. excelsum (endangered); D. holtzii (vulnerable); D. lopense (lower risk/near threatened); D. orientale (lower risk/near threatened); and D. travancoricum (critically endangered). An increasing risk that has been so far underestimated is the loss of seed dispersers. Commercial hunting and the bush meat trade cause a considerable decline in seed dispersers. Overhunted forests, stigmatized by the empty forest syndrome, become disturbed in the reproduction and dynamic of their current vegetation (Terborgh et al., 2008). To conserve and support Dialium progeny, therefore, is not only of interest for the purpose of agriculture but also for the purpose of habitat conservation.

In this study, we propose an artificial activation of the Dialium corbisieri seeds, with regard to the natural activation in great apes, trying to mechanically replace what is chemically happening in the apes' digestive tract. Dialium seeds recovered from apes' dung are either intact or swollen and show coat removal. The major hypothesis is that strong seed protection (i.e., endocarp or seed coat dormancy) is perforated by mechanical or chemical digestive processes. Consequently, seeds become porous and absorb water. Previous studies tried different chemical (Razanamandranto, Tigabu, Neya, & Oden, 2004; Tanaka-Oda, Kenzo, & Fukuda, 2009) or chemical as well as mechanical methods (Razanamandranto et al., 2004; Tanaka-Oda et al., 2009; Vari, Jethani, Sharma, Khanna, & Barnwal, 2007; Todd-Bockarie & Duryea, 1993; Sozzi & Chiesa, 1995; Nwaoguala & Osaigbovo, 2009). Both sulphuric acid bath (H₂SO₄) and nicking of seeds appear to be the most effective pretreatments. However, the chemical effects seem to be similar to the mechanical treatment in that they cause perforation of the seed coat tissue improving water absorption by the embryo. While chemical incitement is expensive, dangerous, and needs peculiar equipment for usage in nurseries (Olufunke & Gbadamosi, 2009; Todd-Bockarie & Duryea, 1993); mechanical treatments are simple, harmless, and available to all. Here we apply a mechanical treatment as a simple and cheap way to test the potential of Dialium reproduction in artificial nurseries as a replicable procedure for countries containing tropical rainforests.

MATERIALS AND METHODS

Study Area

The study was carried out from April to May 2009 within the Lui Kotale research site (2° 47' S; 20° 21' E), located within the equatorial rainforest, southwest of Salonga National Park, Bandundu Province, DRC (Hohmann & Fruth, 2003). The climate is equatorial with abundant rainfall (2,016 mm for the year 2008; 448 mm for April and May 2009) and a relatively dry season from February to July. Mean temperature at Lui Kotale ranges between 21 to 28°C with a minimum of 17°C and a maximum of 38°C (n = 360 days for 2008). For April and May the range was 21 to 29.3°C with a minimum of 20°C and a maximum of 33°C (Beaune, Fruth, Bollache, Hohmann, & Bretagnolle, 2013c).

Sample Collection and Measurements

We used one species only: Dialium corbisieri. For genetic similarity, fruits were collected from the same branch at a 25-m height. Collection was done on April 8, 2009, when seeds were fully ripe. The entire fruits were taken back to Lui Kotale camp field laboratory where they were manually opened by breaking the brittle exocarp. Seeds were isolated by manually removing the mesocarp. Seeds were separated into three groups (see below) to undergo a different treatment each. Seed transformation was measured before and after 48 hr of immersion in water (see below) in order to test the coat permeability and potential water assimilation. For this, seed weight was taken in milligrams using an electronic balance (KERN-Taschenwaage 0–300 mg \pm 10 μ g), seed diameters (length and breadth) were taken in millimeters using a slide caliper (0–10 cm \pm 1 μ m).

Groups of Seed Treatment for Activation and Monitoring of Artificial Germination

Group 1 consisted of artificial seed coat perforation. In accordance to the seed enhancement technique (Taylor et al., 2008), seed protection was interrupted in 92 seeds by scratching with a knife a piece of endocarp (<1 mm) until the endosperm appeared. These nicked seeds were immersed in rainwater for 48 hr. Group 2 included intact seed coats. A total of 92 seeds were left with intact endocarp. These intact seeds were immersed in rainwater for 48 hr and served as a control for Pw. In Group 3, a total of 100 seeds neither underwent mechanical treatment nor was immersed in rainwater. These seeds were considered being similar to dropped seeds *in natura* such as seeds spread by seed spitting of monkeys (personal observation) and served overall as a control group.

All seeds were randomly positioned on a sieve with absorbent paper. For distinction between treatments, each seed was flagged with a bamboo stick next to it. Sieves were kept under the canopy with a grid protection against predators, under *in situ* climatic conditions.

Every day at 6:00 a.m., all seeds were monitored in order to detect the emergence of the radicle and subsequently hydrated with rainwater. Radicle emergence was used rather than flushing of the cotyledons because radicle emergence is considered to be the first sign of germination and thus demonstrates the viability of seeds (Knogge, Herrera, & Heymann, 2003; Heß, 1999).

Statistical Analysis

After testing the data's normality (Shapiro-Wilk normality test), parametric data of the size and weight were tested by Student's *t*-test. The germination rate between groups was compared using the binomial test. The power analysis of the tests is specified when a difference is detected. Analyses were performed using R 2.11R (R Development Core Team, 2005).

RESULTS

Seed Transformation

Already after the first hours of immersion, all perforated seeds started to swell. Figure 1A–C shows weight and size dimensions of perforated (n = 92) and intact seeds (n = 92) before and after 48 hr of immersion in rainwater.

In terms of weight, perforated seeds were on average twice (\times 2.21) as heavy as were intact seeds of the control group. While they weighed 0.27 \pm 0.01 mg on average before, they weighed 0.59 \pm 0.01 mg on average after immersion, resulting in a highly significant difference (Figure 1A: t=-31, df=112, p<.001, power analysis = 100%).

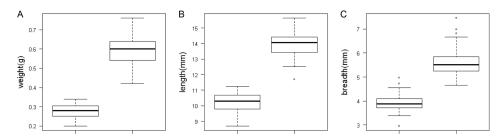


FIGURE 1 (A–C). Seed transformation of intact (left) versus perforated seed coat (right), after 48 h of immersion in water.

In terms of size, perforated seeds were significantly larger than intact seeds of the control group: This was reflected by an increase in length by 1.35 times of perforated seeds in comparison to intact seeds. While the length measured 10.28 ± 0.09 mm on average before immersion, they measured 13.93 ± 0.09 mm on average after immersion (Figure 1B: t = -28, df = 132, p < .001, power analysis = 100%), as well as by an increase in breadth by 1.39 times between these two groups of seed treatment. While the breadth measured 4.02 ± 0.06 mm on average before immersion, they weighed 5.63 ± 0.07 mm on average after immersion (Figure 1C: t = -17, df = 128, p < .001, power analysis = 100%).

In summary, all 92 perforated seeds were swollen after 60 hr, there was neither an effect on intact seeds immersed for 48 hr in rainwater as shown by the control group nor was there any measurable effect on the overall control group without any treatment (weight: t = -0.7, df = 132, p = 0.5; length: t = 1.5, df = 132, p = 0.1; breadth: t = 0.2, df = 128, df = 0.9).

Artificial Germination Activation

Figure 2 shows the results of the monitoring of radicle emergence in 284 seeds divided according to the treatments described above, into three test-groups: Perforated (n=92), Intact (n=92), and Control (n=100). After 24 h in the nursery, 27% of the treated seeds showed appearance of their radicle. After 4 days, 96% of the perforated seeds germinated whereas all other seeds did not. The proportion of germinated perforated seed is significantly different since the first day (p < .001).

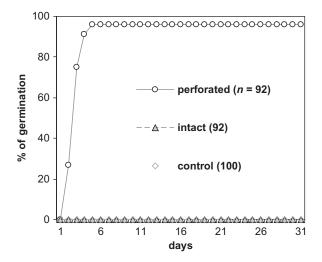


FIGURE 2 Radicle emergence in relation to time in *Dialium corbisieri* seeds according to treatment.

DISCUSSION

As shown in our results, only *Dialium* seeds with seed coat perforation were able to swell and germinate. These results may illustrate a clear adaptation of the seed coat impermeable to rainwater on endozoochory. By coat perforation the seeds absorb water and the germination rate is triggered by 0 to 96%. Dialium corbisieri recruitment shows dependence of seeds passing a partner's gut to be not condemned to everlasting dormancy in the forest (Beaune et al., 2013a). In the absence of natural seed dispersers, seed dormancy can be broken by imitation of the natural process, allowing the seed to absorb water, to swell, and activate germination. This is what happens with endozoochoric partners as apes: the digestive acid nicks the coat and induces germination. Seeds found in bonobo dung are similar in size and shape to transformed seeds as obtained by artificial seed coat perforation and water immersion (Pw; personal observation). However, not all frugivores can act as partners for this effect. Cheek pouch monkeys such as crested black mangabeys (Lophocebus aterrimus) spit the Dialium seeds apparently unharmed onto the ground (personal observation). The teeth may scratch the coat, but whether or not this is enough to induce water absorption needs to be investigated by focusing on seeds dispersed by ectozoochoric partners. In addition, transit time across the dispersers' gut passage may affect perforation. While bonobo's gut passage time appears to be appropriate, we do not know if the transit time of birds or bats is long enough to perforate *Dialium* seed coats. Moreover, the question remains, whether or not after spitting the seed on the ground, the ambient moisture absorption (versus: digestive bath) is rapid enough to avoid pathogen infection of the dormant seeds. Indeed, fast germination can help to skip seed predators and start the race against seedling pathogens.

This result is a good example for application of ecological processes to ecological and economic management. Pretreatment for tree breeding of *Dialium* species could be of use for both the (a) restoration and conservation of natural forests and the (b) potential for future nutritional use.

Restoration and Conservation

Tree nurseries are used for forest restoration and conservation (Dumroese & Riley, 2009). In the restoration of forest impacted by logging or other ecological catastrophes, fruiting trees are important resources for maintaining or restoring frugivorous populations such as primates, birds, or bats (Dew & Boubli, 2005) that consequently may regain their keystone role in the ecosystem (Terborgh, 1986). However, in a disturbed system, natural colonization of these dependent trees could be difficult if populations of animal partners have decreased or partners are already exterminated (Chapman,

1995; Chapman & Onderdonk, 1998). Human interventions may be the last solution with *Dialium* nurseries becoming now possible with this artificial method for the breeding of shoots.

Potential for Future Nutritional Use

Focusing on the larger environments of our study site, indigenous people of the Bolongo area in Bandundu Province, southwest of the Salonga National Park in DRC, have a profound knowledge of the trees species of their surroundings. Among 56 local people asked during visits to adjacent villages, all knew the "Maku" which is the vernacular name for all Dialium trees. The majority of these people distinguishes between the two ethnospecies "Maku rouge" and "Maku pembe," comprising seven species taxonomically described for the Lui Kotale study area (Beaune, 2012): the "Maku rouge" (Dialium corbisieri and D. zenkeri) and "Maku pembe" (D. gossweileri, D. kasaiense, D. pachyphyllum, D. angolensis, and D. tessmannii) with reddish and clear bark, respectively. With their large naturalist knowledge, "Maku rouge" stays for the consumption of caterpillars feeding on *Dialium* leaves, as well as for the use of wood in construction or tree sap in medicine; fruits of "Maku rouge," however, despite their highly nutritive value, are not on their menu. In our study area, this lack of consumption of Dialium fruit by local people can be easily explained by the availability of fruits of other species that are much easier to access. In contrast, explanations may differ for areas where Dialium is part of the human diet such as in Benin. Here, the symbiotic dependence between tree and dispersers, which is a barrier for domestication, may explain the difficulty of this fruit becoming a diet widespread among people inhabiting tropical zones of sub-Saharian Africa. The system, however, is even more complex: in addition to great apes and dung beetles as dispersers (Beaune, Bollache, Bretagnolle, & Fruth, 2012), Dialium trees are highly symbiotic with a lot of partners such as nitrogenfixing bacteria for nitrogen absorption, insects for pollination (Kato et al., 2008), or apes for germination activation. All these dependencies could be an obstacle for domestication.

There are two potential ways to successfully domesticate plants: either randomly by trial and error of seed recruitment or by detailed understanding of the complex ecological processes such as shown for *Ficus* requesting a specific wasp for pollination (Murray, 1985) and specific manipulations for horticulture thereafter (Kjellberg & Valdeyron, 1984).

This example may show the high ecological interdependence of rainforest-species and the problem of domestication of species in these areas despite their great potential for nutritional or economic use. Increase in overall population size of *Homo sapiens* and the related challenge to face nutritional requirements for all, asks for the domestication of new plants by help of modern agriculture paired with scientific knowledge. As we have

shown here, the problem of the activation of germination of *Dialium* seeds can be overcome artificially. Will we find the luscious *Dialium* fruit in our organic supermarket from the African agriculture in 50 yr?

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