

## Trait-based species selection

(photo - K. Naruangsri)



**Fig. 6.1 - Variation of seed size of five tree species native to Northern Thailand. From left to right: *Hovenia dulcis* Thunb., *Prunus cerasoides* Buch.-Ham. ex D.Don, *Alangium kurzii* Craib, *Choerospondias axillaris* (Roxb.) B.L.Burtt & A.W.Hill and *Horsfieldia amygdalina* (Wall.) Warb.**

(photo - K. Naruangsri)



**Fig. 6.2 - Seeds collected from mother trees to be sown in a tree**

## A TRAIT-BASED APPROACH FOR SELECTING TREE SPECIES FOR AERIAL SEEDING

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### ABSTRACT

We review recent ecological research on functional traits that can aid selection of tree species for restoration by aerial seeding. A major barrier in selecting species for restoration of hyperdiverse tropical forests is a lack of silvicultural and ecological information. Functional traits give insight into the potential performance of tree species in deforested sites and provide a mechanism to scale up from individual tree performance to ecosystem functions. Using relatively easy-to-measure functional traits may be an effective way to screen the suitability of tree species for aerial seeding for automated forest restoration. Aerial seeding would be particularly useful to restore forest in remote or isolated sites, where extirpation of vertebrate seed dispersers limits natural seed dispersal. Therefore, we focus on selecting tree species, based on fruit traits, to enhance restoration via aerial seeding.

**Key words:** functional traits, seed bombs, restoration, aerial seeding, stage of degradation, seed germination

### A TRAIT-BASED APPROACH FOR RESTORATION

Throughout their life cycle, plants undergo a multitude of interactions with other organisms, from mutualisms with seed dispersers and nutrient-foraging microorganisms, to antagonistic interactions with competitors, pathogens and seed predators (Fig. 6.4). In response to these interactions and the abiotic environment, plants have evolved a diversity of strategies to grow, survive and reproduce during their sedentary lives. These life history strategies are influenced

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by functional traits that mediate plant growth, survival, and reproduction (REICH et al., 2014). Such traits include the morphological, physiological and phenological traits (VIOLLE et al., 2007) that influence the ability of plants to acquire and conserve resources, disperse into new habitats, and defend themselves against herbivores and pathogens. Studies of variation in functional traits have revealed fundamental tradeoffs (e.g., WESTOBY et al., 2002; DIAZ et al., 2016) that relate to trade-offs in growth, survival, and reproduction (ADLER et al., 2014).

The burgeoning body of global databases and ecological studies on variation in functional traits and their relationships with plant performance and demography now enable the responses of unstudied plant species to be predicted in variable environments (e.g., KATTGE et al., 2011; SALGUERO-GÓMEZ et al., 2015). This is important in hyperdiverse tropical forests, where it is logistically impractical to conduct all the necessary ecological and silvicultural studies needed to develop conservation plans and management strategies. For most species, data on plant performance in different environments are lacking. Using easily measurable traits, which give insight into the germination, growth and survival requirements of species, may be an effective way to select plant species for restoration (OSTERTAG et al., 2015) and help foresters to select appropriate tree species for aerial seeding, to restore areas with different degradation stages. A functional trait-based approach can be used to incorporate aerial seeding into existing forest restoration strategies, including both the framework species and maximum diversity methods (ELLIOTT et al., 2013).

In 1994, Chiang Mai University's Forest Restoration Research Unit (FORRU-CMU) began adapting the framework species method to restore seasonally dry, upland, evergreen forest to degraded sites in northern Thailand. Originally conceived in Queensland, Australia (GOOSEM et al., 1995), the method involves selecting native tree species that are characteristic of the target forest type and enhance natural forest regeneration. Seedlings, 30-50 cm tall, of 20-30 framework tree species are planted out in degraded sites and nurtured for two rainy seasons by weeding and fertilizer application. FORRU-CMU has carried out both nursery and field research to determine which species meet the criteria of framework tree species for forest restoration. Such selection criteria include ease of propagation in the nursery, high seedling survival and growth after transplantation into exposed deforested sites, dense spreading crowns to shade out weeds, and attractiveness to seed-dispersing animals (through the early provision of fleshy fruits, nectar, nesting sites etc.) (BLAKESLEY et al., 2000). The latter is particularly important in the tropics, where most tree species depend on vertebrates for seed dispersal (BECKMAN & Rogers, 2013).

A limitation of the framework species method is that it requires nearby remnant forest to provide a diversity of seed sources and habitat for seed-dispersing animals for natural regeneration. Globally, vertebrates are declining rapidly due to hunting, habitat destruction, climate-change and invasive species (DIRZO et al., 2014). Larger-bodied vertebrates are more susceptible to extirpation, due to hunting and habitat loss, than are smaller-bodied animals. Furthermore, large-seeded species rely on these large-bodied vertebrates for dispersal (STONER et al., 2007; BRODIE et al., 2012 & MARKL et al., 2012). Decline in vertebrate abundance creates another major challenge for restoration approaches that rely on vertebrate seed-dispersal – a challenge being addressed by “maximum diversity methods” of restoration. These involve planting saplings of all (or as many as possible) species that meet restoration objectives (ELLIOTT et al., 2013), together with intensive site preparation, to ensure their survival. Plantings can be done in one or several stages, sometimes by planting pioneers first, followed by late-successional species afterwards (ELLIOTT et al., 2013).

Where vertebrates have been extirpated, seeding by unmanned aerial vehicles (UAV's), planes, or helicopters could be implemented. While seedling performance, in the nursery and in the field, are primary criteria when selecting species for both methods, other characteristics must also be considered when substituting tree planting with aerial seeding. Plant mortality, due to abiotic environmental filters, predation (Fig. 6.4) and diseases, is highest during the seed-to-seedling transition. Therefore, selection criteria for aerial seeding should include a set of seed traits that promote seed germination, desiccation tolerance, predator deterrence, pathogen resistance, and the ability to outcompete weeds.

The optimal strategy for restoring forest ecosystems, depends how degraded the restoration site is. ELLIOTT et al., (2013) provided a concise classification of degradation stages, based on critical shifts in regeneration potential that require fundamental changes in restoration approaches. They classified five stages of degradation, based on remaining vegetation, seed sources for natural regeneration, soil conditions, nearby natural forest remnants, animal dispersal agents and fire risk (ELLIOTT et al., 2013). Stage 1 is the least degraded, with trees dominant over herbaceous weeds, and soils mostly fertile. Protecting Stage-1-degradation sites from cattle, fire and other disturbances is usually sufficient to facilitate natural regeneration. A mix of trees and weeds, rarity of large seed-dispersing animals, and medium to high fire risk characterize Stage-2 degradation. In Stage-3, weeds are dominant, fire risk is high, and small seed-dispersing animals remain present. In Stages 4 & 5, seed-dispersing animals have mostly been extirpated, forest remnants are too distant or too sparse to serve as seed sources and soils are at higher risk of erosion. Additionally, poor soil conditions in Stage-5 can limit the growth of herbaceous weeds and establishment of trees.

**SPECIES SELECTION FOR AERIAL SEEDING, BASED ON FUNCTIONAL TRAITS**

In selecting species for aerial seeding, practitioners should consider which values of seeds traits are most suitable for each degradation stage. In Table 1, we highlight seed traits to consider when selecting native species for aerial seeding to restore sites at various degradation stages, including seed size (Fig. 6.1), seed defense, seed germination and desiccation tolerance.

**Table 1. Recommendations for Aerial Seeding. Degradation stages described in Elliott et al. (2013) and summarized in the text**

<b>Degradation Stage</b>	<b>Vegetation</b>	<b>Traits</b>
<b>Stage 1</b>	Trees dominate	Aerial seeding not necessary, unless forest remnants are too far to provide seed sources or vertebrates locally extirpated
<b>Stage 2</b>	Mixed trees and herbaceous weeds	Large seeds preferable Seeds with high investment in seed defence
<b>Stage 3</b>	Herbaceous weeds dominate	Mixture of large and small seeded species Desiccation tolerance Rapid germination
<b>Stage 4</b>	Herbaceous weeds dominate	High proportion of species with small seeds Desiccation tolerance Rapid germination
<b>Stage 5</b>	No tree cover and few weeds	Aerial seeding not recommended without intensive site preparation e.g. provision of shade soil/substrate amelioration

### Desiccation tolerance of seeds in storage

The ability to store seeds should be considered when selecting species for aerial seeding. Storing seeds after seed collection (Fig. 6.2) is necessary when (1) seeds are collected when immediate aerial seeding is not suitable, (2) seeds must be transported to areas where seeds are unavailable and (3) seeds are not available every year (FOREST RESTORATION RESEARCH UNIT, 2005). Desiccation tolerance determines whether seeds can be stored dry. Species can be categorized into three groups, according to their degree of desiccation tolerance. Orthodox seeds tolerate dry conditions without physiological damage. Intermediate seeds tolerate being dried to approximately eight percent of initial moisture, but cannot withstand low storage-temperatures. Recalcitrant seeds are sensitive to desiccation and therefore cannot be stored dry. About 10 – 45% of tropical tree species have recalcitrant seeds, depending on habitat and location (TWEDDLE et al., 2003), so sensitivity to desiccation limits seed storage of a very large number of tree species and consequently limits their potential use for aerial seeding. Storage tolerance, or the lack of it, plays a major role in determining which species can be used for aerial seeding and at what times of the year aerial seeding can be carried out.

Several seed traits are correlated with desiccation tolerance during seed storage. However, the correlations between traits and desiccation tolerance are complex and one trait alone is not a good indicator. Several studies have shown that desiccation tolerance depends on seed size, covering structures (endocarp and testa), dormancy, and species' successional status (see TWEDDLE et al., 2003; PRITCHARD et al., 2004; DAWS et al., 2005; LAN et al., 2014). Desiccation tolerance decreases with seed size, as larger seeds (>3000 mg) lose viability quickly after being dried compared with smaller seeds (PRITCHARD et al., 2004; DAWS et al., 2005; DAWS et al., 2006). However, within desiccation tolerant and desiccation sensitive species, seed size varies across five orders of magnitude (PRITCHARD et al., 2004). Therefore, seed size alone is not a useful indicator of likely desiccation tolerance. The second correlative trait is investment in seed covering structures. Desiccation tolerance increases with thickness of covering structures (DAW et al., 2006). The mass ratio of seed covering structures to total seed mass (SCR) is used in predictive models of desiccation tolerance. These models show that species with low SCR are more likely to be sensitive to desiccation (DAWS et al., 2006; LAN et al., 2014). Low SCR indicates a thin seed covering structure in relation to total seed size. Large seeds with "thin" seed covering structures are therefore less likely to survive drying.

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Seed dormancy also appears to be linked with desiccation tolerance. Non-dormant seeds are those able to germinate when seeds are placed under suitable conditions (BASKIN et al., 2004), whereas dormant seeds are those that do not germinate, even when conditions appear suitable for germination. Seed dormancy may be caused by physical, physiological, morphological or morphophysiological factors (BASKIN et al., 2004). Desiccation-sensitive seeds (recalcitrant) can be found more frequently among non-dormant than dormant species. However, not all dormant seeds are orthodox because of different types of seed dormancy. It is likely that species with water-impermeable seed or fruit coats (physical dormancy) have orthodox seeds. However, exceptions exist for species with other dormancy types (TWEDDLE et al., 2003).

The successional status of species is another factor that relates to desiccation tolerance. Species can be classified as either pioneer or late successional species. Pioneer species require full sunlight for seed germination (Fig. 6.3) and rapid seedling growth. They can therefore colonize open areas, after disturbance (SWAINE et al., 1988). In contrast, late successional species establish after canopy closure and can tolerate shade. Seeds of late successional species are commonly desiccation-sensitive, whilst those pioneer species are split equally between recalcitrant and orthodox species (TWEDDLE et al., 2003).

For aerial seeding, it is easier to handle seeds of desiccation-tolerant species (orthodox seeds) than desiccation-sensitive species (intermediate or recalcitrant seeds). However, practitioners should not omit entirely those species with desiccation-sensitive seeds from aerial seeding, because some of them may provide important ecological functions (e.g. food sources for animals, shade to impede weeds, etc.). Therefore, the seed storage behaviour of species should be determined before planning seed-handling techniques and aerial seeding. As described above, desiccation tolerance can be inferred from a combination of traits, including seed size, mass ratio of seed covering structures to total seed (SCR), seed dormancy, and successional status. With aerial seeding, it is possible to overcome seed-storage limitations by using seed containers and/or seed pelleting (see Chapter 8).

### **Germination response to desiccation**

While information on the desiccation tolerance of seeds can guide the selection of species that can be stored before aerial seeding, information on the germination response of different species to desiccation can aid the selection of species that have an increased chance of survival and establishment in degraded areas. Seed germination depends on site conditions, such as light availability, gas

exchange and soil-moisture availability (Fig 6.3). In particular, soil dryness can limit seed germination, because imbibition of water is an essential germination trigger. In large, open, degraded sites (e.g. Stage-3-degradation or higher), surface soil can dry to the permanent wilting point after only six days without rain (ENGELBRECHT et al., 2006). Therefore, species selection for aerial seeding should consider trait values that indicate high survival and germination at particular degradation stages. In addition, germination success can be modified with seed enablement technologies (see Chapter 8).

Information on seed traits can help guide the selection of species that can tolerate dry conditions. In dry areas, selecting a species mixture that includes a large proportion of drought-tolerant species could increase the chances of success. For example, in seasonally dry tropical forests, larger tree seeds tend to germinate better than smaller ones do under drier conditions (KHURANA et al., 2004; DAWS et al., 2008). However, the relationship between seed size and germination response to desiccation is not universal. In the aseasonal humid tropics, seed size is not correlated with the ability to germinate under dry conditions. Smaller seeds can also germinate under dry conditions and can germinate faster than larger seeds do (TIANSAWAT, 2013). The ability of smaller-seeded species to germinate under dry conditions is determined by their successional status (TIANSAWAT, 2013). Small seeded pioneer species that can regenerate in desiccation-prone environments can germinate under drier conditions than shade-tolerant species can (i.e. late successional species) (TIANSAWAT, 2013). Seed size and plant successional status can indicate germination success under unpredictable, dry site conditions. We suggest selecting a mixture of large and small seeded where drought is likely, such as Stages-3-4 degradation, and selecting a higher proportion of smaller-seeded pioneer species for Stage 4 (Table 1).

### **Predation and Herbivory**

Seed predation (Fig. 6.4) and seedling herbivory (Fig. 6.5) can be high in the tropics (COLEY et al., 1996; HULME 1998). Seed predation and herbivory vary with degradation stage. Less degraded areas tend to have more animals (BLACKHAM et al., 2015), with potentially higher risk of seed predation and herbivory in Stages-1-2 degradation compared to Stages-3-4. Less degraded areas are more prone to higher seed predation and herbivory (BLACKHAM et al., 2015), so species should be selected with trait values that deter or tolerate seed predation and herbivory. Functional traits are correlated with seed predation by vertebrates and insects and susceptibility to disease. Smaller seeds may escape predation by being more



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easily buried (LEISHMAN et al., 2000). LEISHMAN et al., (1994) predicted that larger seeds are more attractive to seed predators, because they have larger energy reserves, but they are also more tolerant to predator attacks (DALLING et al., 1997). Larger seeds also take longer to germinate because of a long imbibition time until radicle emergence, compared to smaller seeds. Remaining in the seed stage on the soil surface for longer allows more time for seed predation and pathogen infection to occur. Larger seeds produce larger seedlings, which may be more tolerant of herbivory (ARMSTRONG et al., 1993). In species whose seeds contain multiple embryos (e.g. *Antirhea tricantha*, *Choreospondias axillaris*), the number of locules (embryos) within a propagule also increases the probability of escaping insect seed predation (BECKMAN et al., 2011). In addition to size, seed defense mechanisms can help protect seeds from predation. Seeds with more physical and chemical defenses may be less susceptible to predation (MOHAMMED-YASSEEN et al., 1994) and pathogen attack (WHITEHEAD et al., 2014). For example, thicker seed coats may protect seeds from pathogens (BECKMAN et al., 2011) and insects (THEIRY 1984; KITCH et al. 1991). However, there may be tradeoffs between physical and chemical defenses (TEWKSBURY et al., 2008). Where seed predators and herbivores are abundant, we suggest selecting species that have higher physical or chemical defenses, to deter seed predators and pathogens (Table 1).

### Abiotic Environmental Filters

Functional traits, related to the acquisition and conservation of resources, can indicate whether a plant can survive and grow under prevailing environmental conditions. Several studies show that plant species with traits that enable resource conservation when resources are limiting, tend to have low growth rates and high survival rates, compared with species with traits for rapid resource acquisition when resources are more abundant (REICH et al., 2014). For example, plants with higher wood density tend to have higher survival (KRAFT et al., 2010; WRIGHT et al., 2010) and, in some cases, slower growth rates (CHAVE et al., 2009). Wood requires a lot of carbon for its synthesis, but it provides trees with biomechanical support needed to grow above competing plants. Higher wood density (dry mass divided by green volume) correlates with a tree's ability to resist mechanical breakage, drought-induced embolism, and pathogens (CHAVE et al., 2009; KRAFT et al., 2010). Investing carbon and energy in higher wood density is therefore a conservative strategy that enables plants to conserve limited resources through increased protection and survival.

Several studies have shown that seedlings from larger seeds have higher establishment rates (TUNJAI et al., 2012; VISSER et al., 2016), lower seedling growth rates, and survival rates that depend on seedling size (VISSER et al., 2016). Larger

seeds produce larger seedlings, making them better able to tolerate hazards. As larger seedlings have deeper roots, they are less susceptible to dry conditions and disturbance by animals (COOMES et al., 2003). KHURANA et al. (2004) showed that, under water-stress, seedlings from larger-seeded tree species suffer lower mortality compared with those of smaller-seeded tree species. Seed size is loosely related to shade-tolerance (COOMES et al., 2003), although a few small-seeded species can persist under shade (GRUBB, 1998).

### **Competition**

Competition among young plants for limited resources is a key ecological process in forest restoration and strongly influences successional dynamics. As environmental conditions change with degradation stage and succession, so does the competitive hierarchy within the plant community. Under moderate degradation stages (Stages 3-4), tree species selected for aerial seeding must be able to outcompete weeds at the seed and seedling stage.

Time of germination and seed morphology are important in determining the success of competition. Small-seeded species may germinate rapidly but their resultant small seedlings may not be able to compete well for resources, particularly where water and light are severely limited. Larger seeds tend to be better competitors (TURNBULL et al., 1999; COOMES et al., 2003). DIAZ et al. (2016) showed that species with larger seeds tend to have taller maximum adult heights, a measure of plant size that indicates the competitive ability of plants to preempt light resources as taller plants display leaves over smaller plants.

At higher degradation levels (Stage 4), we suggest selecting small-seeded, light-demanding species that have high seedling growth rates, to capture light and space before herbaceous weeds become dominant and subsequently planting larger-seeded species that have slower growth rates, but larger maximum heights that can outcompete weeds long-term.

### **Trade-offs among traits**

Trade-offs in functional traits occur when one trait value increases whilst another one decreases. They can be inferred from a negative correlation between two traits. For example, species may trade the ability to compete for one limited resource for the ability to compete for another limited resource (GRIME 2002; FORTUNEL et al., 2012) or trade the ability to colonize new areas with the ability to compete for a limited resource (TILMAN, 1994; LEVINE et al., 2002) or tolerate environmental stresses (MULLER-LANDAU, 2010). Trade-offs in functional trait

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values relate to trade-offs in plant performance (ADLER et al., 2014). These trade-offs among traits and plant performance constitute a challenge when selecting species that meet all species criteria for aerial seeding and restoration. For example, there is a trade-off between seed size and the numbers of seeds produced (MULLER-LANDAU, 2008; VISSER et al., 2016). Species with large seeds (e.g. *Azizica xylocarpa*) produce fewer seeds compared with small-seeded species (e.g. *Ficus* spp.). Therefore, it may be easier to obtain smaller seeds. However, small seeds tend to be less competitive (TURNBULL et al., 1999; COOMES et al., 2003) and have lower tolerance to environmental stresses (COOMES et al., 2003). Hence, collecting a sufficient number of seeds of species with trait values that reflect optimal survival, establishment, and competitive ability for the purpose of restoring degraded areas may be challenging. Selecting a range of species that have a mixture of functional trait values may be the best approach.

## RECOMMENDATIONS

Selecting species for aerial seeding depends on the degradation stage, as discussed above. Combining knowledge of framework tree species and maximum diversity methods with trait data is useful for preliminary screening of potential species that are suitable for aerial seeding. This relies on availability of trait data for species in the study system from floras, target forest surveys, indigenous local knowledge, and research conducted on species within the area of interest (ELLIOTT et al., 2013). If species-level information is not available, information from closely related species can be used, because they tend to be more functionally similar than distantly related species (SWENSON et al., 2007). Surveying relevant traits that are quick and inexpensive to measure could be integrated into forest surveys, if little information is available from previous research, floras, or indigenous local knowledge. A trait-based approach can help prioritize whether an unstudied species may meet the criteria for restoration by aerial seeding and merit further investigation with experiments.

We suggest that aerial seeding could be used to replace or complement tree planting for sites at degradation Stages-2-4. Depending on the availability of seed sources and abundance of vertebrate seed-dispersers, aerial seeding could be useful for remote sites, where conventional tree planting is more difficult. Restoring forest to sites at Stages-1-2 degradation relies on manipulating natural regeneration, to bring about canopy closure (no tree planting necessary). Consequently, aerial seeding would only be necessary if seed sources (forest remnants or scattered remnant trees) are too distant to provide seed inputs into the restoration sites or if vertebrate seed dispersers have been locally extirpated.

For the most severely degraded sites (Stage-5), aerial seeding would not be effective, unless soil remediation measures are also implemented.

Seeds, representing the full functional diversity needed to attain restoration objectives, could be dropped all at once or with different species added in stages. Many tropical seeds are recalcitrant and germinate at the beginning of the wet season, so a challenge will be time of seed collection and dropping seeds before they desiccate. If dropping mixtures of species, all at once, proves to be impractical, different species may be dropped at different times of the year (depending on fruiting times). We recommend dropping large seeds in either the first stage or second stage of restoration, across all degradation stages, as large-seeded tree species are more likely to have lost their seed dispersers (STONER et al., 2007; BRODIE et al., 2012; MARKL et al., 2012). Species that are heavily defended with thick seed coats or chemicals are good choices for restoration, where vertebrate seed predators are present.

### **OTHER CONSIDERATIONS**

Though not discussed here, the spatial arrangement of seeds and seed bombs (Chapter 8) should also be considered, as this can affect interspecific competition (BOLKER et al., 2003), as well as seed predation and infection by pathogens (BECKMAN et al., 2012). Models can be used to simulate different restoration strategies to explore the influence of the spatial arrangement of seeds and seed bombs on growth and survival of selected species and help choose a spatial distribution of seeds with a diverse set of functional traits to achieve restoration objectives.

Finally, a trait-based approach can be used to select species that meet overall ecological and social restoration objectives and achieve a self-sustaining system (ELLIOTT et al., 2013) and reduce future interventions. Integrating empirical information on functional traits with quantitative ecological models, practitioners can explore the expected community and ecosystem dynamics under different restoration scenarios and whether model predictions meet restoration objectives (LAUGHLIN, 2014). Theoretical underpinnings of restoration are discussed in more detail by LAUGHLIN (2014), and a practical example is provided by OSTERTAG et al. (2015).

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(photo - K. Naruangsri)



**Fig. 6.3 - Germination of *Alangium kurzii* after seed sowing in a direct seeding experimental plot in Chiang Mai, Thailand**

(photo - K. Naruangsri)



**Fig. 6.4 - Seed covering structures of *Prunus cerasoides* left behind by seed predators.**

(photo - K. Naruangsri)



**Fig 6.5 - Herbivory of a young seedling**