

SEED DISPERSAL AND FOREST RESTORATION

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ABSTRACT

Most trees in the tropics reach their place of growth via the gut of an animal. Thus the fruit choices of local disperser fauna can have a major influence on which tree species arrive at a site and how quickly. In degraded landscapes, the major dispersers of large seeds and large-seeded fruits (such as, in Asia, large fruits bats, gibbons, elephants, rhinoceroses, hornbills and imperial pigeons) have usually been eliminated. Small frugivorous birds (such as bulbuls) and small fruit bats (often *Cynopterus* spp.) ensure that both small fruits and larger, soft fruits with many small seeds are still dispersed. However, the absence of food and suitable perches greatly reduces the movements of these tolerant dispersal agents into treeless grassland sites. In such situations, active planting of trees or shrubs may greatly speed the early stages of forest succession, and the resulting enhancement of seed dispersal can lead to diversification of initially low-diversity plantings. In theory, tree species that provide suitable fruits would be expected to attract more seed dispersal agents and thus more seeds than tree species with unattractive, non-fleshy, fruits. However, all the more tolerant fruit-eating birds are at least partly insectivorous and fruit bats use non-fruiting trees as feeding roosts, under which they drop seeds, so the choice of trees for planting may not be crucial. Whether or not some trees are initially planted, tree species with large-seeded fruits are unlikely to arrive at degraded sites of their own accord. Including some of these species in the planting mix will both ensure their survival in the landscape and provide food for their dispersal agents if these later re-invade or are reintroduced to the area.

INTRODUCTION

Tropical deforestation is not a one-way process. Most of the uses for which forest is cleared are not sustainable and the majority of the cleared area is sooner or later abandoned. Unless succession is prevented by continued disturbance such as fire, most of this abandoned land will eventually revert to secondary forest (CORLETT, 1995). The rate at which woody vegetation develops on cleared sites is related to the frequency, duration and intensity of disturbance (NEPSTAD *et al.*, 1996; HUGHES *et al.*, 1999). On highly degraded sites, such as most non-forest areas in Hong Kong, succession can be very slow. In places with a distinct dry season, there is a long period of vulnerability to fire in grassland sites (over 10 years in Hong Kong), before a closed, woody canopy suppresses the fire-promoting grasses. In addition, most of the various biotic and abiotic processes, which control the rate

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of succession, are highly selective. As a result, only a subset of the mature forest flora occurs in secondary forests even after several decades of succession (FINEGAN, 1996; TURNER *et al.*, 1997; FERREIRA & PRANCE, 1999). This is particularly apparent in Hong Kong, where most of the original forest remnants are confined to remote upland ravines and the dispersal agents of forest dominant species, such as the Fagaceae, are apparently lacking (DUDGEON and CORLETT, 1994). Forest succession is thus more successful at restoring forest biomass than floristic diversity, and is more successful on less degraded sites.

Despite massive planting efforts in the last century, plantation cover in the tropics as a whole was only 0.8 % of the natural forest cover in 1990 (WORLD RESOURCES INSTITUTE, 1999). It seems generally agreed that we will have to rely on succession as the main means of forest restoration in the tropics (ALIAS *et al.*, 1998; ELLIOTT *et al.*, 1995; FOREST RESTORATION RESEARCH UNIT, 1998; GOOSEM & TUCKER, 1995; GOMEZ-POMPA & BAMBRIDGE, 1995; KARTAWINATA, 1994; KOLB, 1993; MOLINE, 1999; PONE, 1997). Thus, it is important that we understand the factors, which limit its rate and control the species composition of the resulting secondary forest. If these barriers – or, more accurately, filters – to succession can be understood, it may be possible to accelerate and diversify succession over large areas at a much smaller cost than that required for artificial planting. Even if this does prove possible, understanding the factors that control natural succession will help formulate strategies for the use of native tree species in reforestation.

Whilst the intensity and duration of disturbance will influence on-site survival of tree propagules as seeds, seedlings, stumps and roots, through changes in the microclimate and fauna, the first and the major problem of forest succession on highly degraded sites is recruitment by post-disturbance dispersal (CORLETT, 1995). However, one should not overlook the fact that dispersal, while necessary for succession to take place, is not by itself sufficient. Prolonged cultivation or frequent fires can degrade the soil to such an extent that succession is slow irrespective of the availability of seeds. Nevertheless, we now attempt to summarise the characteristics of post-disturbance seed dispersal on degraded tropical forestlands in tropical Asia and make suggestions to overcome this initial filter-barrier to forest succession.

SEED DISPERSERS

The probability of a particular species arriving at the site will depend on the number and proximity of adult fruiting trees, and the mode of dispersal. Most of the tree species in the tropics are dispersed by animals rather than wind, water, or other forms of dispersal (WUNDERLE, 1997). Seed dispersal by vertebrates is a key process in the dynamics of natural vegetation and in forest succession on degraded tropical forestland (CORLETT, 1998a). Studies of frugivory and seed dispersal in tropical Asia have concentrated on primates, fruit bats and a few families of birds, but many other vertebrates consume some fruits and disperse some seeds. Degraded landscapes in the tropics typically lack many of the best-studied dispersal agents, such as gibbons and hornbills. The detailed behaviour of individual animal species and the impact of hunting, which typically concentrates on larger animals, become crucial in determining what tree species are dispersed. Few forest birds and

mammals are willing to enter open areas. The open country fauna in previously forested areas is usually dominated by small animal species. In deforested Asian landscapes, the relative importance of vertebrate seed dispersers can be ranked as birds, bats and then non-flying mammals.

Birds

The relative importance of different frugivorous bird families varies with the stage of forest succession or restoration. Frugivorous birds that can tolerate degraded landscapes are more important at the initial stage of forest succession or reforestation (CORLETT, 1998a). They include passerine birds belonging to the Corvidae (magpies, jays, orioles etc.), Muscicapidae-Turdinae (thrushes), Muscicapidae-Saxicolini (robins and chats), Sturnidae (starlings and mynas), Pycnonotidae (bulbuls), Zosteropidae (white-eyes) and Sylviidae-Garrulacinae (laughingthrushes). Note that none of these birds are strict frugivores and all depend on insects for a significant part of their diet. Other bird families, which are tolerant of fragmentation and disturbance and could make use of secondary and disturbed habitats, will become increasingly important as forest succession or reforestation proceed, notably the highly frugivorous non-passerines Megalaimidae (barbets) and some Columbidae (fruit-pigeons). The more tolerant species of Bucerotidae (hornbills) may also appear if there is primary forest nearby and no hunting. These birds vary in gape width and therefore the largest fruits they can utilise: from less than 1 cm in the white-eyes to greater than 3 cm in the larger hornbills and fruit pigeons.

Bats

Old World fruit bats (Pteropodidae) are not only abundant and diverse in the Oriental Region, but also extremely varied ecologically (FLANNERY, 1975). All species are largely or entirely frugivorous. Fruit bats feed on very large, soft fruits *in situ*. For smaller fruits, the treatment depends on bat size (CORLETT, 1998a). With small bat species, either a single large fruit is plucked or several small fruits. The bat then usually flies away to a feeding roost where the fruit or fruits are processed, 20-200 m from the fruiting tree, (MARSHALL, 1983; PHUA & CORLETT, 1989; BHAT, 1994). Small fruit bats can fly with more than their own weight in fruit. The larger species can carry more than 200 g (VAN DER PIJL, 1982). However, they seem more likely to process fruit in the fruiting tree, dropping seeds underneath (ROBERTS, 1977; RICHARDS, 1990; UTZURRUM, 1995).

Fruit processing can be complex and the fate of the seeds depends on bat, fruit and seed characteristics. For fruits which are removed from the parent plant, seed fate seems to be influenced by both seed size and pulp texture (CORLETT, 1998a). Most large seeds are dropped under feeding roosts by all species, although some may also be dropped, apparently by accident, in flight. Some or all of the smallest seeds may be ejected from the mouth in a fibrous wad, but others may be swallowed with the juice and defecated in flight. Although gut passage is normally rapid, a proportion of the seeds may be retained in the gut for much longer, so long distance seed dispersal is possible (SHILTON *et al.*, 1999). The threshold for seed swallowing is reported as less than 4 mg for *Rousettus* in Israel (IZHAKI *et al.*, 1995), less than 2.4 mm diameter for 35 g *Cynopterus* in Singapore (PHUA & CORLETT, 1989), and

less than 3.2 mm diameter for a 600 g *Pteropus conspicillatus* in Australia (RICHARDS, 1990). The proportions of seeds swallowed seem to be greatest for fruits with semi-fluid interiors (PHUA & CORLETT, 1989) or very slippery seeds (UTZURRUM & HEIDEMAN, 1991). Although the pteropodids as a whole consume a wide variety of fruits, there is a distinct 'bat fruit' syndrome: medium to large, drab colour, strong odour, held away from the foliage (MARSHALL, 1983).

Fruit bats are often the most important dispersers of seeds to abandoned pastures in the Neotropics but their role in the Asian tropics has been relatively little studied. On highly degraded sites in Singapore, forest succession is dominated by the exclusively bat-dispersed *Adinandra dumosa* (Theaceae), which has greenish fruits with a semi-fluid interior, and tiny seeds which are defecated in flight by *Cynopterus brachyotis* (PHUA & CORLETT, 1989). However, birds disperse the majority of tropical Asian pioneer trees, including the many species in the important pioneer genus *Macaranga*. The role of fruit bats in forest restoration is still unclear.

Non-flying Mammals

While large mammals, especially primates, are very important seed dispersers in intact forests, they are usually rare or absent in deforested landscapes. Macaques are the most disturbance-tolerant primates, and several species can survive in partly deforested areas (LUCAS & CORLETT, 1998). The most tolerant, medium-sized, partial frugivores are the civets (Viverridae), several species of which can persist in largely deforested landscapes, if they are not hunted. They are potentially important dispersal agents for large seeds (DUDGEON & CORLETT, 1994).

Even the most degraded tropical landscapes support one or more species of rat (Muridae). These have been regarded more as seed predators than dispersers, but seed dispersal may occur via ingestion and defecation. Many intact small seeds are found in the faeces of all three non-urban rat species in Hong Kong (CORLETT, 1996). In the Neotropics, scatter-hoarding caviomorph rodents are also very important dispersal agents for large seeds, but there have been no reports of such behaviour in tropical Asia (CORLETT, 1998a). However, at least one Old World rat species caches large numbers of big seeds in Australian rainforests (HARRINGTON *et al.*, 1997) and it is possible that such behaviour has simply been overlooked in tropical Asia. Squirrels (Sciuridae) may also cache seeds in places suitable for subsequent germination and growth, but again, there is very little evidence for this behaviour in tropical Asia.

SEED/FRUIT SPECIES

Fruits differ in many ways that might be expected to influence their interactions with potential dispersal agents (CORLETT, 1998a). The most obvious of these are: seasonality of production, protection (i.e. the presence of an inedible rind which must be removed to get at the flesh), colour, the amount and nutritional value of the fruit flesh, and the size of the fruit and the seeds it contains. Small fruits tend to be better dispersed than larger ones in most

situations because they have more potential dispersal agents, although the attractiveness of small fruits to animals is influenced by many factors other than size. Large soft fruits with many seeds may also attract a wide array of dispersal agents. Large-seeded, large fruits are dispersed by a small number of relatively large birds and mammals, and the presence of a protective outer rind reduces this number even further.

SITE CHARACTERISTICS

The attractiveness of a site to tree seed dispersers determines the quantity and quality of seeds dispersed into it. The availability of perch sites and fleshy fruits and the structural complexity of the vegetation tend to affect the attractiveness of a site to animal seed dispersers, especially avian seed dispersers (HOLL, 1998; STILES, 1992; WUNDERLE, 1997). Many studies have demonstrated that the seed rain beneath perches is significantly higher than in nearby sites without perches (DEBUSCHE & ISENMANN, 1994; GUEVARA *et al.*, 1992; KOLB, 1993; McCLANAHAN & WOLFE, 1993; NEPSTAD *et al.*, 1991; WILLSON & CROME, 1989). Abundant seed input under perches can be related to the observation that most regurgitation and defecation of seeds by avian frugivores occurs when birds perch or immediately after they take off, rather than during flight (GUEVARA & LABORDE, 1993).

The presence of fleshy fruits in a site tends to attract more avian seed dispersers, which in turn bring in other seeds. Seeds carried into abandoned pastures in the Amazon are concentrated beneath fruiting treelets (NEPSTAD, 1989). The observations of NEPSTAD *et al.* (1990) show that seeds are concentrated beneath shrub-like lianas and trees that produce fruits throughout the year. LEVEY (1988) found that the abundance of fruit-eating birds in lowland Costa Rican rain forest followed the same general patterns of spatial and temporal variation in fleshy fruit abundance. KOLB (1993) found that seed flow was positively correlated with fruit availability on island vegetation and negatively correlated with spatial isolation in abandoned pasture in tropical America. However, TOH *et al.* (1999) show that whether or not a tree offers a fruit reward appears less important than its structure and suitability as a bird perch. In a bird perching study in abandoned pasture in Costa Rica, artificial perches baited with banana did not increase either bird visitation rates or seed rain (HOLL, 1998).

Structurally complex vegetation has been demonstrated to be attractive to avian seed dispersers in studies of old field succession (Wunderle, 1997). Structurally complex vegetation cover would have either or both of the above two site traits that attracts avian seed dispersers. In addition, it provides more refuges from predators for avian seed dispersers and alternative food resources for partial frugivores. In Puerto Rico, PARROTTA (1992) attributed much higher species richness of woody seedlings and vines in a 4.5-year-old *Albizia lebbek* plantation, compared with an adjacent control area with no tree cover, to increased propagule availability by provision of roosting and nesting sites for bird species. KOLLMANN (1995) reported an increasing gradient of seed rain with progressive shrub development and successional time in dry grassland with interspersed shrubs in central Europe. HOLL (1998) showed that branch perches had significantly higher bird visitation rates and seed rains than crossbar perches placed in abandoned pasture in Costa Rica.

5. DISCUSSION

There is no doubt that animal seed dispersal has the potential to speed up the succession- restoration process and enrich the resulting forests. This is clearly shown by the diversity of native tree and shrub species that appear spontaneously in exotic plantation monocultures throughout the tropics. If restoration efforts are designed to rely mainly on natural seed dispersal, careful consideration should be given to the tree species that are planted at different stages of the restoration process. Studies in Hong Kong suggest that the apparent matching of bird and fruit characteristics in the secondary shrub-land community is probably a result of “selection” by the bird fauna from the regional species pool (CORLETT, 1998b). Only species that can be dispersed by the surviving avifauna (or by wind or other less important vertebrate seed dispersers) have been able to participate in secondary succession. (Note that almost all forests in Hong Kong are secondary and most of the true forest fauna is locally extinct). This hypothesis is supported by the presence of a much wider range of fruit sizes and types in the flora as a whole than in the secondary shrub-land and forest in Hong Kong. Much of the tree flora may no longer be effectively dispersed and is thus not represented in succession.

Assuming that covering the whole restoration site (especially large and rugged ones) with tree seedlings by planting is not cost-effective or is financially impossible in some cases, the crucial point in the initial stage of forest succession-restoration is to maximise tree seeds dispersed into the site. The site conditions at this stage normally favour pioneer trees. These pioneers come from few genera and share some or all the following characteristics: rapid height growth, low density wood, sparse branching, indeterminate growth, often large, simple leaves, flowering while young, producing abundant, small fruits, well dispersed by birds, bats or wind, and seeds usually with dormancy (CORLETT, 1995). Pioneers on the most degraded sites, however, may be relatively slow growing and have high-density wood. The provision of perch sites, either as artificial perches or by planting tree islands, the planting of trees, which produce fleshy fruits, and increasing the structural complexity of the vegetation, could all raise the attractiveness of the site to animal seed dispersers. Most woody pioneers in tropical East Asia have bird-dispersed fruits with sizes within the gape-limits of all the common frugivorous birds, while a minority are dispersed largely or entirely by small fruit bats, so the species composition of the disperser fauna is probably not an important factor at this stage.

Pioneer trees are typically short-lived with maximum life spans in the range 7-25 years. Life spans are longer on highly degraded sites and shorter on less degraded sites. Subsequent to the establishment of a pioneer tree cover, the site conditions will gradually become more suitable for the more shade-tolerant mature forest tree species. The poorly dispersed primary forest plant species are normally characterised by large seeds (WUNDERLE, 1997). At this stage the species composition of the disperser fauna becomes crucial. The provision of wildlife corridors linking the restoration site with nearby forests is desirable, especially for non-flying mammal seed dispersers but also for the many forest bird species which are unwilling to cross large open spaces. However, the effectiveness of such measures depends on the availability of both nearby forest and suitable seed dispersers. In unfavourable sites – including all those in Hong Kong - planting seedlings of large-

seeded species or direct seeding (with precautions against seed predation) may be necessary (GOOSEM & TUCKER, 1995). In the longer term, the reintroduction of locally extinct dispersers of large seeds may be necessary. Such reintroductions are likely to be easier if restoration of a species-rich forest cover has already started and local support for such conservation initiatives has been built up.

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