ELSEVIER

Forestry Ecology and Management 99 (1997) 223–235

Forest Ecology and Management

The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands

Joseph M. Wunderle Jr.

International Institute of Tropical Forestry, USDA Forest Service, PO Box 490, Palmer, PR 00721, USA

Accepted 9 May 1997

Abstract

This paper reviews the characteristics of animal seed dispersal relevant to tropical forest restoration efforts and discusses their management implications. In many tropical regions seed dispersal by animals is the predominant form of dissemination of propagules and has the potential to facilitate recolonization of native vegetation on degraded sites. The site traits relevant for attracting seed dispersers include the availability of perches, the structural complexity of the vegetation and the presence of food resources, especially fruit, as an attractant. Tree plantations with these traits will be particularly attractive to animal seed dispersers and, therefore, will have higher rates of seed rain than plantations lacking these traits. The efficacy of animal seed dispersal to restoration sites can be limited by the degree of isolation from a seed source, absence of animal seed dispersers in the region and by large seed size. In highly degraded regions, where seed sources may be isolated and animal seed dispersers rare, restoration will require direct seeding or planting. However, even under the best of conditions with a full compliment of animal seed dispersers and a nearby seed source, large-seeded species, because of their relative immobility, should be planted if a full return to primary forest is desired. © 1997 Elsevier Science B.V.

Keywords: Animal seed dispersal; Forest restoration; Plantations; Seed dispersal; Wildlife

1. Introduction

Tree plantations established on degraded sites long devoid of natural forest can act as successional catalysts by facilitating the recolonization of native vegetation (e.g. Bhaskar and Dasappa, 1986; Lugo, 1988, 1992, 1993; Parrotta, 1992, 1993, 1995; Brown and Lugo, 1994; and papers in this volume). These plantations accelerate natural regeneration by influencing understory microclimate and soil fertility, suppressing dominant grasses and attracting animal seed dispersers. The factors that affect the rate of restoration include the initial site characteristics, plantation design and management practices. However, our understanding of how these factors influence succession within plantations is limited (e.g. Parrotta, 1992).

Seed dispersal is one of the processes potentially accelerated by tree plantations on degraded sites and is fundamental to biodiversity restoration. Seeds can be naturally dispersed to a site in many ways (van der Pijl, 1982), but wind, water and animals are the usual forms of transport. Animal seed dispersal is a predominant form of dispersal in the tropics (e.g. Howe and Smallwood, 1982), and because it involves an animal's behavior, it is the most complex. Although various aspects of animal seed dispersal have recently been summarized (e.g. Howe and Smallwood, 1982; Moermond and Denslow, 1985; Estrada and Fleming, 1986; Wheelwright, 1988; Stiles, 1989), no reviews have specifically focused on all the issues relevant to restoration efforts.

The purpose of this paper is to review the factors

PII S0378-1127(97)00208-9

affecting animal seed dispersal to tropical restoration sites. The geographic and ecological importance of animal seed dispersal are reviewed and the ecological consequences of animal and wind dispersal are summarized. To understand the nature of seed dispersal to restoration sites requires knowledge of both site and seed source traits and their effects on dispersers. The site characteristics relevant for attracting seed dispersers include the availability of perches, structural complexity and the role of fruit as an attractant. Plantations, as a special type of restoration site, are discussed in terms of their potential attractiveness to wildlife and particularly seed dispersers. Seed source traits are reviewed in terms of source isolation, characteristics of seed shadows and the effect of seed size on seed mobility. Finally, these factors are discussed in relation to the management considerations for enhancing animal seed dispersal to restoration sites.

This review includes animal dispersal based on endozoochory, in which the diaspores are carried inside the animal, and synzoochory, in which the diaspores are deliberately carried in the mouth (van der Pijl, 1982). In these instances, the animals feed on fruit and the seeds are simply a transported byproduct. The review ignores seed predation by animals, which under some circumstances can be a major factor inhibiting seed dispersal (e.g. Janzen, 1982a,b). Although a wide range of animal taxa are known to disperse seeds (van der Pijl, 1982), this review focuses on dispersal by vertebrates, principally birds and mammals, which are usually the most important seed dispersers in the wet tropics. Finally, this work is not intended to provide an exhaustive review of the subject, but rather focuses on relevant examples of factors which should be considered by restoration managers. Examples come primarily from the neotropics, representing the geographical bias of the author's own fieldwork, although examples from elsewhere in the tropics and temperate zone are used to help illustrate a process or principle.

2. Distribution and importance of animal seed dispersal

In many plant communities, seed dispersal by animals is often an important form of dissemination of propagules and in some sites over half the tree species have seeds dispersed by animals rather than wind, water, or other forms of dispersal. For example, in some neotropical forests more than 66% of the canopy tree species have seeds which are dispersed by animals (Howe and Smallwood, 1982). This contrasts with some temperate zone forests where wind is often the predominant form of dispersal, such as in eastern North America, where less than 33% of the forest trees have seeds dispersed by animals. Elsewhere or among different growth forms, the differences between the proportion of animal- versus wind-dispersed propagules is not as distinct. For instance, in tropical Asia and Africa a lower proportion of tree species produce seeds dispersed by animals, depending on habitat or region (35–46%, Howe and Smallwood, 1982).

Temperate–tropical differences in the proportion of plant species with animal-dispersed seeds are not as marked in understory plants in mature forests and in the early to middle stages of plant succession. Wind dispersal is not expected to be effective in forest understories and, therefore, it is not surprising that a large proportion of understory plant species have animal-dispersed seeds (48–90% of shrubs and vines in eastern NA, Willson, 1986; and 44–62% in southern Spain, Herrera, 1984). Similarly, in early to mid-stages of succession, plants with animal-dispersed seeds predominate in both temperate forests (e.g. Howe and Smallwood, 1982; Stapanian, 1986; Willson, 1986; Stiles, 1989; Robinson and Handel, 1993) and neotropical forests (Uhl et al., 1981; Uhl and Clark, 1983; Uhl and Jordan, 1984; de Foresta et al., 1984; Charles-Dominique, 1986; Foster et al., 1986).

Plants with wind- or ant-dispersed seeds tend to be more prevalent in dry habitats in contrast to plants with vertebrate-dispersed seeds, which tend to be more common in wet habitats. Howe and Smallwood (1982) found this trend in communities with comparable floras such as neotropical forests. They showed that there was a significant negative correlation between the percentage of wind-dispersed canopy trees and annual precipitation for six neotropical forests with samples of over 100 tree species. Similar trends have been documented elsewhere in the neotropics (Daubenmire, 1972). Even at the local level, the dispersal syndrome may be associated with a moisture gradient as demonstrated by a greater number and proportion of ant-dispersed herbs in damp than in dry sites within a mesic temperate forest (Handel et al., 1981). Finally, at the driest end of the rainfall/moisture continuum are deserts in which animal dispersal of seeds is very rare, such as the deserts of Israel in which only 3% of the plants are dispersed by animals (Ellner and Shmida, 1981).

An analysis of seed dispersal syndromes by Howe and Smallwood (1982) indicated that distinct differences exist in the syndrome types of different life forms in a forest. Most wind-dispersed plants are vines or canopy trees while few are small trees or shrubs. As found in a study of lianas, none of the five species which produced fruit below the canopy were wind-dispersed, whereas nearly half of the species (48%, $n = 25$) with fruits in the canopy were wind-dispersed (Keay, 1957). Howe and Smallwood (1982) concluded that consistent strong winds promote wind-dispersal, while mesic conditions promote animal-dispersal regardless of the level of analysis, i.e. communities, life forms within a community, or local differences within a life form.

Besides playing an important role in dispersing seeds from a host plant, animals can sometimes affect the germination probabilities of the seeds they defecate or regurgitate. For example, scarification in an animal gut can contribute to enhanced germination in some species (e.g. Olson and Blum, 1968; Hladik and Hladik, 1969; McDiarmid et al., 1977; Fleming and Heithaus, 1981). In other cases, seeds may rot if not processed by animal disperers (Howe and Vande Kerckhove, 1981) or fail to break dormancy (Rick and Bowman, 1961; Noble, 1975; Lieberman et al., 1979). However, most animal-dispersed seeds receive no advantage or only a slight increase in germination after handling by animals (Howe and Smallwood, 1982).

2.1. *Implications of wind versus animal seed dispersal*

Janzen (1988) has suggested that the predominant form of dispersal (i.e. wind versus animal) to a site can have substantial effects on the outcome of the community regeneration process and the composition of the plant community. Unfortunately, these observations were not quantified and were restricted only to dry forest. Furthermore, additional studies will be required to document the generality of these conclusions. Nevertheless, because of their potential management importance the conclusions will be summarized here. Janzen (1988) found that the two different dispersal syndromes contributed to the regeneration of very different forest types on abandoned pastures in the dry forest region of Costa Rica. Here, Janzen observed that wind-generated forest extended down-wind from existing forest fragments in a peninsula-like fashion out into pastures. These regenerating forest patches were composed mostly of wind-dispersed seeds and offered no food for frugivory, in contrast to fragments containing a more balanced mix of seed dispersal types. The absence of fruit makes the regenerating wind-dispersed forest unattractive to frugivores, thereby retarding the input of animal-dispersed seeds and limiting the tree diversity of the site. Because the wind-dispersed trees are first to colonize the site, they physically and numerically dominate it for many decades even as they die off from senescence.

In contrast to the wind-generated forests, Janzen (1988) observed that animals played a much more complex role in the initiation and growth of dry forest fragments. He attributed this to several factors including the fact that there were almost three times as many animal-dispersed as wind-dispersed trees and saplings in the area and that they brought with them more life forms and ways of occupying a site than found among the wind-dispersed species. Also, there are many more kinds of animal-generated than wind-generated seed shadows. Wind-generated seed shadows are often dense and very uniform in contrast to animal-generated seed shadows which are heterogeneous, depending on the location of perches, roosts, etc. (discussed below). Both the biology of the animal disperser and the biology of the plant contribute to the pattern of forest initiation. Seeds in an animal-generated patch can come from as far as many thousands of meters from the fragment and from any compass direction (in contrast to wind-generated patch which is derived from an adjacent forest). Because of this, Janzen argued that species in the fragment are, therefore, more likely to represent a much greater portion of their respective populations than is the case with a wind-generated patch. Finally, Janzen concluded that the species richness of trees and saplings was substantially greater in developing animal-generated habitat fragments than wind-generated habitat fragments due to the larger species pool (64% of the tree and sapling species there were animal-dispersed) and area from which the species are drawn.

3. Site traits which attract seed dispersers

3.1. Perches

Many avian seed dispersers are attracted to perches in open fields as frequently observed in the field (e.g. Ridley, 1930; McAtee, 1947; Livingston, 1972; Gleadow and Ashton, 1981; Glyphis et al., 1981; Debussche et al., 1982; Werner and Harbeck, 1982) and are documented in quantitative or experimental studies (McDonnell and Stiles, 1983; McDonnell, 1986; McClanahan and Wolfe, 1993). Seed rain beneath perches can be significantly higher than in nearby sites without perches. For example, seed fall beneath perches in Florida fields had both a higher diversity of seed genera and higher seed numbers (340 seeds m^2/year) and seed abundance was 150 times greater than in sites without perches (McClanahan and Wolfe, 1993). Similarly, Willson and Crome (1989) found that animal-dispersed seeds in a field bordering a Queensland rain forest were rarely found in seed traps in the open in contrast to seed traps under shrubs where seed fall rates were significantly higher.

A perch becomes attractive to avian seed dispersers when it projects above the existing level of herbaceous vegetation, although its attractiveness increases with its height, possibly because higher perches are better predator lookouts (McDonnell, 1986). The latter investigator found that seed rain under saplings increased proportionally with sapling height in open fields in New Jersey. Similarly, large isolated trees in pastures in southern Mexico played a role in attracting rain forest frugivores (birds and bats), thereby facilitating the establishment of animal dispersed plant species, which were common under the trees but rare or absent in the open pastures (Guevara et al., 1992). Emergent trees extending above a closed canopy in Brazilian Amazon forest restoration plots attracted several species of avian seed dispersers which were rare or absent from the closed canopy of the restoration plot (Wunderle, unpublished data). In addition, Robinson and Handel (1993) also found that restoration plots with high ratios of trees to shrubs had proportionately more dispersers.

3.2. Structural complexity

Structural complexity of the vegetation is known to affect the diversity of animals on a site as illustrated in mine reclamation studies (reviewed in Majer, 1989). For example, Karr (1968) concluded that the structural complexity of the vegetation already present in a regenerating surface mine in Illinois was important in determining bird diversity. Similarly, Reeders (1985) showed that bird recolonization of bauxite mines in northern Australia was associated with the existing vegetation structure on the site, and that islands of vegetation left undisturbed on the site facilitated bird invasions. Increased avian diversity associated with vegetation complexity is expected to result in increased seed input to the site.

Structural complexity of the vegetation has been demonstrated to be an important factor in attracting avian seed dispersers in studies of old field succession. For example, more seed rain was quantified in a 13-year-old field (structurally complex) than in a nearby 3-year-old field with a single layer of vegetation in New Jersey (McDonnell and Stiles, 1983). Here, the authors also found higher seed rain in a 2-year-old field in which they placed artificial structures, simulating saplings, than in an adjacent control field of similar age. However, they found that the shape of the individual structures (saplings) was not a significant factor affecting seed input, but evidently the overall complexity of the experimental field was important for attracting seed dispersers. They concluded that woody plants increase the structural diversity of old fields and function as recruitment foci for bird-disseminated seeds.

3.3. Fruit as an attractant to dispersers

It is well established that frugivores (i.e. potential seed dispersers) are especially responsive to spatial and temporal changes in fruit abundance at a variety of different scales (e.g. Leighton and Leighton, 1983; Terborgh, 1983; Wheelwright, 1983; Fleming, 1988; Levey, 1988; Blake and Loiselle, 1991; Loiselle and Blake, 1991). This was evident in an abandoned pasture in eastern Amazon where Silva et al. (1996)

observed that three species of avian seed dispersers were more common during the peak of fruiting of shrubs in the pastures than during the dry season when fruit was absent. Seed dispersers were observed feeding on the fleshy fruits of *Cordia multispictata* and Guimarães Vieira et al. (1994) found that the rain of bird- and bat-dispersed seeds of woody species was much greater in the zones of *Cordia* (92 seeds/m^2/year) than in the patches of grass (6 seeds/m^2/year). The seed rain also displayed a distinct seasonal component, with twice as many seeds captured per month during the rainy season as compared to dry months, a pattern which corresponds to the fruiting phenology of *Cordia* and the abundance of avian seed dispersers visiting *Cordia*.

Evidence that fruiting plants are attractants to seed dispersers that bring seeds of different species to the site come from other neotropical studies. For instance, Guevara et al. (1986) found that fruit-bearing remnant forest trees in abandoned pastures in southern Mexico had a higher mean number of species ($\bar{x} = 14.3$) underneath fruit-bearing than non-fruit-bearing trees ($\bar{x} = 8.4$) in the same area. Similarly, fruit trees appeared to be attracting seed dispersers in abandoned slash and burn plots in the Amazon region of Venezuela where Uhl et al. (1982) found that woody seeds were more abundant in soils under fruit trees (932 germinable woody seeds/m^2) as compared to slash (126 germinable woody seeds/m^2) and in bare soil plots (74 germinable woody seeds/m^2). Studies of frugivorous bats in Costa Rica indicate that bats are capable of bringing the seeds of a substantial diversity of species to the immediate vicinity of a fruiting tree (Fleming and Heithaus, 1981). This was also evident in fruit traps placed under fruiting *Tetragastris panamensis* visited by frugivorous birds and mammals (two monkey species and coatimundi) in which the seeds of numerous plant species were found (18 identified and 16 unidentified species) by Howe (1980).

In contrast to these findings, Willson and Crome (1989) unexpectedly found that seed deposition of animal-dispersed seeds was lower under fruiting bushes than non-fruiting bushes of *Solanum mauritanianum* in the same open field bordering a Queensland rain forest. They suggested that the effect of fruit on seed deposition patterns depends on the social, foraging and digestive behavior of the frugivores involved.

3.4. Plantations and their ability to attract seed-dispersers

The composition of a tree plantation makes certain types of plantations better suited than others for attracting animal seed-disperers. This is due to several factors, including the characteristics of the trees, which may lack pests, flowers, fruits, epiphytes and structural diversity, which are important for attracting wildlife. In the absence of these potential resources or foraging sites, many tree plantations are unattractive to wildlife and can retard or even prevent succession.

Plantations of pine have been established throughout the world. The attractiveness of pine plantations to native wildlife, where pine is an exotic, can vary depending on several factors. For example, the attractiveness of exotic pine plantations to birds can vary depending upon the specialization or generalization of the local avifauna. This was demonstrated by Cody (1985), who contrasted the use of pine plantations (*Pinus radiata*) by birds in South Africa and Chile to those used by birds in California, where pines are native. The South African pine plantations attracted very few birds, but the plantations in Chile were characterized by both densities and species numbers comparable to those in California. Cody attributed these differences to his earlier finding (Cody, 1975) that the South African avifauna is characterized by habitat-specific birds (i.e. use a restricted number of habitats) in contrast to Chile where the birds are habitat-generalists (i.e. use a variety of habitats).

Despite the degree of habitat-specificity of a region's fauna, monocultures of pine are unattractive to many organisms because they lack the requisite food resources for survival. For example, because pines lack nectar-producing flowers and fleshy fruits, they are unattractive to nectarivores and frugivores. In fact, avian foraging studies in pine plantations in Puerto Rico indicate that very few species of birds foraged in the exotic pine trees, but rather in the native understory shrubs, vines and the few retained native canopy trees in the plantations (Cruz, 1988). Here nectarivores and frugivores were common, but only because of the flower and fruit production of the native species. Similarly, Gepp (1976) and Suckling et al. (1976) observed more bird species in Australia where pine is an exotic when there was an understory of native vegetation; the least amount of species occurred in unthinned pine with virtually no understory.

Australian eucalypts, commonly used in plantation forestry around the world, are also unattractive to native wildlife when planted outside their normal range, despite the fact that they support a diverse fauna in Australia. In this case, eucalypts outside their homelands may lack their native insect fauna and, therefore, have little in the way of resources for insectivores (Cody, 1985). The absence of fleshy-fruits on eucalypts may also contribute to the paucity of frugivores in plantations. However, some eucalypts produce nectar used by avian nectarivores in some regions outside of Australia, and in Africa eucalypts primarily serve as nest sites (Cody, 1985). Similarly, Indian teak plantations which lacked nectar and fruit resources had a paucity of bird species requiring these resources and were visited only by flocks of wandering insectivorous birds (Beehler et al., 1987). Mahogany (*Swientenia* spp.) also lacks these resources and the presence of avian frugivores and nectarivores in a Puerto Rican plantation of hybrid mahogany was attributable to fruit and flower production of understory shrubs (Cruz, 1987).

Not all plantations of exotic trees are unattractive to wildlife as observed in plantations of *Albizia falcataria* (1, 3, 5, and 7 years old) in Sabah, East Malaysia where 64% of the 162 bird species known from primary forest were recorded (Mitra and Sheldon, 1993). The authors attributed the attractiveness of their *Albizia* plantations to four factors, i.e. (1) the rapid growth and thin canopy of *Albizia* provided the space and light for the development of a substantial secondary forest with the appropriate food resources, (2) the *Albizia* trees were infested with caterpillars which attracted birds (including many frugivores), (3) the plantation was adjacent to primary forest and near to areas of active logging and, therefore, had a ready source of birds and (4) the plantation was young and thus there may not have been enough time for birds displaced by logging to be depleted, and there was still microhabitat structure present (e.g. stumps and logs) from clearing primary forest. The authors concluded that the attractiveness of plantations to forest species depends upon many factors including the types, ages and mixtures of cultivated trees, crop rotation, proximity of primary forest, plantation physiognomy (e.g. streams, cliffs, etc.) and timing and complexity of pest infestations.

4. Seed source characteristics

4.1. The nature of seed shadows

Studies of the dispersion of seeds from a host plant, or seed shadow, indicate that seed shadows include two basic components, i.e. the 'best-fit' function of seed density versus distance from the seed source, and the heterogeneity around this function. The density–distance function is commonly a leptokurtic distribution with a peak at the source plant (Harper, 1977; Levin, 1979; Fleming and Heithaus, 1981). This leptokurtic distribution is characteristic of all dispersal systems and not just those based on animals. However, the degree of kurtosis of the seed shadow is affected by the type of dispersal which influences the probability that seeds will be deposited at great distances from the parent (Hubbell, 1979). Animal dispersers affect the leptokurtic function by their foraging and food processing behavior, which includes the time spent near the fruiting plant, distances moved from the plant, travel speed and the time for which the seeds are retained (Fleming and Heithaus, 1981).

Deviation from the expected leptokurtic dispersion pattern of seeds can result from the behavior of animal seed dispersers, particularly when they consume and digest food in one or only a few special localities (Fleming and Heithaus, 1981). These sites include nest sites, display sites and perches of birds (e.g. Snow, 1962a,b,c, 1970, 1976; Silva et al., 1996), and day and/or night roosts of bats (e.g. Vásquez-Yanes et al., 1975; Janzen et al., 1976; Heithaus and Fleming, 1978; Morrison, 1978, 1983; Fleming and Heithaus, 1981; Fleming, 1988). Deviation from a leptokurtic dispersion pattern of seeds dispersed by *Artibeus* bats was documented in a seed shadow around two Costa Rican trees (Janzen et al., 1976). At one of the trees, approximately 48% of the seed crop remained under the parent, while 0.02–35% of the seed crop was found under several roost trees up to 100 m or more from the parent tree.

Most seeds are deposited by seed dispersers around fruiting plants and it is likely that most seeds handled by birds, bats and primates move less than 100 m before being regurgitated, dropped, defecated or spat out (Fleming, 1988). However, a small fraction of seeds can be moved considerable distances from the parent plant, particularly by pteropodid bats and certain birds (Ridley, 1930). Seed dispersal distances of several hundreds of meters to several kilometers are not unusual as documented in several species of birds (e.g. Snow, 1962c, 1976), bats (e.g. Williams and Williams, 1970; Heithaus and Fleming, 1978; Morrison, 1978) and primates (e.g. MacKinnon and MacKinnon, 1978).

4.2. Isolation and its effect on seed dispersal

An important factor affecting the distance over which seeds are dispersed by animals are the habitat types visited by the forager, as many species will not cross certain habitat boundaries or venture too far into a foreign habitat (Weins, 1992). In other words, habitat specialists provide more limited dispersal in heterogeneous habitats than habitat generalists which are not limited to only one or a few habitat types. For example, many forest-dwelling animals will not enter forest openings (e.g. MacArthur, 1972) and others may venture only a short distance from the forest edge out into adjacent fields or pastures.

In many instances, only a few animal seed dispersers actually make inter-habitat movements required for plants to colonize new sites and they frequently venture only short distances into foreign habitats. A good example comes from the work of Silva et al. (1996) on the movements of second-growth forest birds into adjacent pastures in the eastern Amazon region of Brazil. Although they found 47 frugivorous birds (potential seed dispersers) in a second-growth forest, only 18 species (38%) entered an adjacent abandoned pasture and even fewer (three species, 6%) also moved into the adjacent active pasture.

To document the potential for birds to disperse seeds onto Amazonian pastures, Silva et al. (1996) observed bird movements from a second-growth forest into the pastures. They found that the maximum distance moved by three frugivorous species (all tanagers) out into the abandoned pasture from the second-growth forest edge varied from 2 to 254 m, but most movements were between 1 and 80 m. The birds spent from 0.5 to 23 min in the abandoned pastures where they moved from 0.5 to 225 m before returning to the second-growth forest. Thus, the resulting seed shadow in the abandoned pasture exhibited two characteristics, i.e. a general decrease in seed density from the source plant and a localized increase in seed density in relation to the existing shrubs/small trees in the pasture closely linked with the perching and defecating behavior of the birds.

Colonization of a site can be limited because it is distant from a potential seed source (McClanahan, 1986a, 1986b; Hughes and Fahey, 1988). For example, studies of isolated woodlots in Europe indicated that plants with animal-dispersed seeds were negatively affected by woodlot isolation (van Ruremonde and Kalkhoven, 1991). In this case, the total area of broad-leaved forest within a radius of 500 m, as well as the distance to the nearest connecting landscape element, were found to be good indicators of woodlot isolation.

The actual distance for effective dispersal onto a site varies with the traits of the dispersers and the intervening habitats through which the dispersers must move. For example, when working in the Peruvian Amazon, Gorchov et al. (1993) showed that seed rain from primary forest across a newly cleared strip of 25 m indicated that bird-dispersed plant species showed a substantial decline with distance, compared with bat-dispersed species which showed only a slight decline, while wind-dispersed species did not decline with distance across the strip. The authors attributed the differences between bird and bat dispersal to the fact that birds defecate from perches, which were absent in the strip cut and that relatively few forest-dwelling bird species entered the cut. In contrast, forest bats, which are known to defecate on the wing as well as from roosts and perches, entered the cut. Thus, perch availability is the primary factor influencing the numbers of bird-dispersed seedlings on an open site (e.g. Campbell et al., 1990), while distance from a seed source is of secondary importance (e.g. McClanahan and Wolfe, 1987).

5. Source traits

5.1. The immobility of large seeds

Large seeds are more likely to be dispersed shorter distances than small seeds and, therefore, are expected to have a lower rate or likelihood of colonizing sites. Evidence for the limited dispersal of large seeds comes from several sources. For instance, studies of the distribution patterns of juvenile plants indicate that large-seeded plants have limited dispersal from the parents relative to small-seeded plants (e.g. Hubbell, 1979). In addition, large-seeded species tend to be rare relative to small-seeded species in seed banks (e.g. Uhl and Clark, 1983; McClanahan and Wolfe, 1993). Measurement of seedfall at different distances from host plants in an Illinois woodland demonstrated that small seeds were dispersed further than large seeds (Hoppes, 1988). The lower mobility of large seeds was also evident in a 10-year-old restoration plot in the Brazilian Amazon, where large-seeded trees were slow to arrive. Here the average seed size of tree species which were naturally dispersed onto the site was significantly smaller than the seeds of tree species absent from the plot but found in the surrounding primary forest (Parrotta et al., 1997).

Behavioral studies of seed dispersers also indicate that large seeds have limited dispersal potential relative to small seeds. For example, differences in the handling behavior of large and small seeds by avian frugivores suggested to Levey (1986) that small seeds are likely to be dispersed more widely than large seeds. According to Levey, such differential dispersal is likely because small seeds are more frequently ingested and defecated than large seeds, which tend to be regurgitated shortly after ingestion. Similarly, field observations of monkeys and birds indicate that they dropped about 89% of the large seeds (14 mm long) of *Tetragastris panamensis* under the parent crown (Howe, 1980). Animals often prefer smaller seeded fruits when given a choice as documented by Howe and Vande Kerckhove (1981), who found that fruit-eating birds and mammals in Panama preferentially depleted trees of *Virola surinamensis* with small seeds and coincidentally favored trees with high aril-to-seed ratios. Moreover, only a small proportion of the fruit-eating animals visited *Virola* and of these only three of seven bird species which consumed the fruit dispersed the seeds at least 40 m from the parent tree. Finally, even agoutis (*Dasyprocta* spp. , Rodentia), the largest scatterhoarders of seeds which surpass all other extant neotropical mammals in dispersing large seeds, are unlikely to travel more than 200 m with a large (30–150 g) pod of *Hymenaea courbaril* and the mean distance is likely to be well under 100 m (Hallawachs, 1986).

Often animals capable of dispersing large seeds will not cross certain habitats (e.g. forest openings) or when they do they are unlikely to carry large seeds. For instance, Janzen (1988) noted that forest-dwelling agoutis and monkeys were unlikely to carry the large seeds of several tree species across pastures and as a result these tree species are likely to be absent from isolated regenerating dry forest fragments. Many arboreal primates, which feed on large-seeded fruits, rarely come to the ground (Terborgh, 1983) and thus are unlikely to cross large forest openings or visit sites in the early stages of succession. Finally, many of the larger frugivores (e.g. curasows, guans, primates, ungulates, etc.) which are potentially capable of transporting large seeds may be rare or absent in appropriate tropical habitats due to overexploitation by humans (e.g. Terborgh, 1983; Fragoso, 1991; Mittermeier, 1991; Silva and Strahl, 1991).

The limited dispersal of large-seeded relative to small-seeded plant species suggests that many restoration sites will result in retarded or even arrested successional development in which the sites are overwhelmingly composed of small-seeded pioneer plant species. Studies of natural succession in neotropical forests have found that the pioneer plant species are characterized by small seeds that are dispersed mostly by abundant, but relatively small, bats and birds (e.g. Uhl et al., 1981; Uhl and Clark, 1983; de Foresta et al., 1984; Uhl and Jordan, 1984; Charles-Dominique, 1986). However, as a natural forest ages, generalized competition for seedling establishment is expected to increase, which Foster et al. (1986) argued selects for trees with large seeds dispersed by arboreal mammals and large birds. Indeed, seed masses of mature forest species have been found to be significantly larger than those of pioneer species, even when the effects of tree height, dispersal syndrome and growth form are statistically controlled (Foster and Janson, 1985). Even in the best of natural conditions, when primary forest plants might also invade disturbed sites shortly after disturbance, they do so in a more stochastic fashion due to their limited mobility relative to small-seeded pioneer species (Swaine and Hall, 1983). Finally, even if large seeds make it to a site they are more likely to be found and consumed by seed predators than small seeds (e.g. Janzen, 1986).

6. Implications for forest restoration

As the preceding review indicates, seed dispersal by animals has the potential to help restore forest plant diversity on degraded sites in a reasonable period of time, thereby helping to defray restoration costs. However, reliance on animal seed dispersal is not without its limitations, some of which can be overcome by management intervention, while others are less tractable to management. Much of the potential for animals to contribute seeds to a site is dependent on characteristics of the region or landscape in which a site is situated. These include the availability of a nearby seed source and animal seed dispersers, both of which are likely to be limited in highly degraded landscapes. Although under these conditions supplemental planting or seeding will surely be required, a number of management strategies exist which may facilitate animal dispersal of seeds to restoration sites.

The degree of isolation of the restoration site in relation to the seed source is a major factor influencing natural dispersal to the site. Admittedly, the exact definition of isolation depends on the type of animal seed disperser(s) and the intervening habitat. However, it is reasonable to expect that seeds of forest plant species will be dispersed greater distances from their source through continuous forest than through open fields or pasture. Therefore, restoration sites should ideally be contiguous with the native forest seed source. If this is not possible, consideration should be given to the development of forest or plantation corridors (e.g. hedgerows) through which forest-dwelling seed dispersers might pass to the restoration site. Another option might be to consider an 'archipelago' of small restoration patches scattered with intervening open areas less than 50 m across. Thus, the important management concern here is to reduce the site's isolation from seed sources to ensure adequate seed rain.

Several options are available for making tree plantations attractive to seed dispersers. It is evident from the preceding review that just simply providing a perching or roosting site in pastures or grasslands has the potential to attract at least some seed dispersers. Increasing the vegetation complexity of the site increases the attractiveness to more animal species, thereby improving the likelihood of seed dispersal by generalist or opportunistic frugivores. Thus, even age monocultures will usually be less attractive to wildlife than plantations of mixed ages and species.

The effect of plantation size on animal diversity is currently unknown and it is likely to vary depending on the tree species involved. Although it is well established from studies of species–area relationships that large natural habitat patches harbor more species than small patches (e.g. MacArthur and Wilson, 1967), it is unknown how this relates to plantations, particularly in even-age monocultures. It is likely that monoculture plantations of certain tree species (e.g. teak, casuarina) lacking appropriate food resources may be less attractive to forest wildlife in large patches than in small patches. In these instances, smaller plantations with a higher ratio of edge to interior than larger plantations may actually be more attractive to wildlife due to increased edge habitat. Indeed, studies of seedling colonization indicate higher colonization rates on the periphery of plantations than in the interior, suggesting a differential use of plantation edges by some seed dispersers (Parrotta, 1995).

If restoration efforts are designed to rely heavily on natural seed dispersal, then careful consideration should be given to the species composition of the tree plantation. As demonstrated by Parrotta (1995), the species composition of the plantation overstory can have substantial effects on the recruitment rate in the understory. As the preceding review indicated, attractiveness to potential animal seed dispersers is based on the availability of resources (usually food) and the wildlife diversity and abundance in monoculture plantations lacking such resources can be exceptionally low. Often exotic trees, because they may lack their normal insect pests of their homeland, are unattractive to wildlife, particularly if they also do not provide nectar or fruit resources. However, in the instances where the exotic plant provides an appropriate resource, they can be equivalent or better than native species.

Consideration should be given to planting some fruit-bearing plants to attract seed dispersers into plantations to accelerate seed dispersal and enrich diversity. This recommendation follows from previous studies which indicate that fruiting plants attract frugivores to a site and that seeds which they deposit beneath fruiting plants represent a diversity of plant species. Obviously care should be given in selecting appropriate plant species because the seeds of an attractant plant are likely to be well dispersed throughout the plantation, and if aggressive, the species has the potential to dominate the plantation. However, with this consideration in mind, thought should be given to planting species which bear fruit over a considerable period of time and attract a variety of generalist seed dispersers, which will be likely to contribute new species to the site.

There is a growing recognition among tropical ecologists and conservationists of the importance of small (<100 ha) isolated fragments of tropical forests as refuges for re-establishing native forests on degraded landscapes (Turner and Corlett, 1996). Although these isolated fragments are too small for the long-term survival of viable populations of many forest species, they may serve as refugia from which re-colonization can occur once a deforestation phase has ended (Janzen, 1988). However, as previously reviewed here and noted by Turner and Corlett (1996), many primary forest species possess limited dispersal abilities and re-establishment of primary species in secondary forests may be very difficult, if not impossible, unless a source is located very near the site. In fact, Turner and Corlett (1996) argued that even if the restoration site (i.e. secondary forest) is contiguous with primary forest, lack of dispersal may prevent the arrival of many primary forest species.

The relative immobility of primary forest plant species, characterized by large seeds, has been recognized by numerous workers, as previously reviewed. Even under the best of conditions in intact primary forest with a full compliment of native seed dispersers, dispersal rates of large-seeded species can be very low. In this instance, managers can not rely on animal seed dispersers to provide adequate dispersal. Therefore, managers should consider planting or seeding large-seeded species on restoration sites, if a full return to primary forest diversity is desired. Indeed, several workers in this volume have recognized this need and made such recommendations (Parrotta et al., 1997; Tucker and Murphy, 1997). In the absence of such management intervention, it is likely that many tropical forest restoration efforts will result in a preponderance of small-seeded pioneer species with an absence of large-seeded primary forest species.

Restoration ecology in the tropics is in its early stages of development, with some basic studies available to provide guidance for restoration of degraded landscapes. At this stage, there are many generalized guidelines for restoration, but we currently need more specific studies to adapt management to local conditions. Studies on the effects of plantation size, composition, age and isolation on animal seed dispersal are needed to evaluate the potential for animal dispersers to enhance diversity on degraded sites. These studies will enable us to better evaluate the potential and limitations of natural seed dispersal on specific sites.

Acknowledgements

This work benefited from the critical constructive comments of several colleagues, who do not necessarily share all of the views expressed in this paper. The author thanks T. Mitchell Aide, Ariel E. Lugo, Richard R. Bierregaard, Jr., John Francis, Carolina Murcia, Juan Torres, Nigel J. Tucker and Peter Weaver for their assistance.

References

Beehler, B.M., Krishna Raju, K.S.R. and Ali, S., 1987. Avian use of man-disturbed forest habitats in the eastern Ghats, India. Ibis, 129: 197–211.

Bhaskar, V. and Dasappa, 1986. Ground flora in Eucalyptus plantations of different ages. In: J.K. Sharma, C.T.S. Nair, S. Kedharnath and S. Kondas (Editors), Eucalypts in India: Past, Present and Future. Kerala Forest Research Institute, Peechi, Kerala, pp. 213–224.

Blake, J.G. and Loiselle, B.A., 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Cost Rica. Auk, 108: 114–130.

Brown, S. and Lugo, A.E., 1994. Rehabilitation of tropical lands: a key to sustaining development. Rest. Ecol., 2: 97–111.

Campbell, B.M., Lynman, T. and Hatton, J.C., 1990. Small-scale patterning in the recruitment of forest species during succession in tropical dry forest, Mozambique. Vegetatio, 87: 51–57.

Charles-Dominique, P., 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds, and bats in French Guyana. In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 119–135.

Cody, M.L., 1975. Towards a theory of continental species diversity: bird distributions over Mediterranean habitat gradients. In: M.L. Cody and J.M. Diamond (Editors), Ecology and Evolution of Communities. Harvard University Press (Belknap), Cambridge, MA, pp. 214–257.

Cody, M.L., 1985. An introduction to habitat selection in birds. In: M.L. Cody (Editor), Habitat selection in birds. Academic Press, New York, pp. 3–56.

Cruz, A., 1987. Avian community organization in a mahogany plantation on a neotropical island. Carib. J. Sci., 23: 286–296.

Cruz, A., 1988. Avian resource use in a Caribbean pine plantation. J. Wildlife Manage., 52: 274–279.

Daubenmire, R., 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. J. Ecol., 60: 147–170.

Debussche, M.J., Escarre, J. and Lepart, J., 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. Vegetatio, 48: 255–266.

de Foresta, H., Charles-Dominique, P., Erard, C. and Prevost, M.F., 1984. Zoocorie et premiers stades de la régénération naturelle après coupe en forêt guyanaise. Rev. Ecol., 39: 369–400.

Ellner, S. and Shmida, A., 1981. Why are adaptations for long-range seed dispersal rare in desert plants? Oecologia, 51: 133–144.

Estrada, A. and Fleming, T.H. (Editors), 1986. Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, 392 pp.

Fleming, T.H., 1988. The Short-Tailed Fruit Bat. University of Chicago Press, Chicago, IL, 365 pp.

Fleming, T.H. and Heithaus, E.R., 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropica, 13 (Suppl.): 45–53.

Foster, S.A. and Janson, C.H., 1985. The relationship between seed size, gap dependence, and successional status of tropical rain forest woody species. Ecology, 66: 773–780.

Foster, R.B., Arce, J. and Wachter, T.S., 1986. Dispersal and the sequential plant communities in Amazonian Peru floodplain. In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 357–370.

Fragoso, J.M.V., 1991. The effects of hunting on tapirs in Belize. In: J.G. Robinson and K.H. Redford (Editors), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, IL, pp. 154–162.

Gepp, B.C., 1976. Bird species distribution and habitat diversity in an exotic forest in southern Australia. Aust. For., 39: 269–287.

Gleadow, R.M. and Ashton, D.H., 1981. Invasion by *Pittosporum undulatum* of the forests of central Victoria. I. Invasion patterns and plant morphology. Aust. J. Bot., 29: 705–720.

Glyphis, J.P., Milton, S.J. and Siegfried, W.R., 1981. Dispersal of *Acacia cyclops* by birds. Oecologia, 48: 138–141.

Gorchov, D.L., Cornejo, F., Ascorra, C. and Jaramillo, M., 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio, 107/108: 339–349.

Guevara, S., Purata, S.E., and Vand der Maarel, E., 1986. The role of remnant forest trees in tropical secondary succession. Vegetatio, 66: 77–84.

Guevara, S., Meave, J., Moreno-Casasola, P. and Laborde, J., 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. J. Veg. Sci., 3: 655–664.

Guimarães Vieira, I.C., Uhl, C. and Nepstad, D., 1994. The role of the shrub *Cordia multispicata* Cham. as a 'succession facilitator' in an abandoned pasture, Paragominas, Amazonia. Vegetatio, 115: 91–99.

Hallawachs, W., 1986. Agoutis (*Dasyprocta punctata*), the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 285–304.

Handel, S.M., Fisch, S.B. and Schatz, G.E., 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. Bull. Torrey Bot. Club, 108: 430–437.

Harper, J.L., 1977. The Population Biology of Plants. Academic Press, London, 245 pp.

Heithaus, E.R. and Fleming, T.H., 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomidae). Ecol. Monogr., 48: 127–143.

Herrera, C.M., 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. Ecol. Monogr., 54: 1–23.

Hoppes, W.G., 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. Ecology, 69: 320–329.

Hladik, A. and Hladik, C.M., 1969. Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado (Panama). Terre Vie, 116: 25–117.

Howe, H.F., 1980. Monkey dispersal and waste of a neotropical fruit. Ecology, 61: 944–959.

Howe, H.F. and Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst., 13: 201–228.

Howe, H.F. and Vande Kerckhove, G.A., 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology, 62: 1093–1106.

Hubbell, S.P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science, 203: 1299–1309.

Hughes, J.H. and Fahey, T.J., 1988. Seed dispersal and colonization in a disturbed northern hardwood forest. Bull Torrey Bot. Club, 115: 89–99.

Janzen, D.H., 1982a. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. Ecology, 63: 1887–1900.

Janzen, D.H., 1982b. Seed removal from fallen guanacaste fruits (*Enterlobium cyclocarpum*) by spiny pocket mice (*Liomys salvini*). Brenesia, 19/20: 425–429.

Janzen, D.H., 1986. Mice, big mammals, and seeds: it matters who defecates what where. In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 251–273.

Janzen, D.H., 1988. Management of habitat fragments in a tropical dry forest: growth. Ann. Missoui Bot. Gard., 75: 105–116.

Janzen, D.H., Miller, G.A., Hackforth-Jones, J., Pond, C.M., Hooper, K. and Janos, D.P., 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). Ecology, 57: 1068–1075.

Karr, J., 1968. Habitat and avian diversity on strip-mined land in east-central Illinois. Condor, 70: 348–357.

Keay, R.W.J., 1957. Wind-dispersed species in a Nigerian forest. J. Ecol., 45: 471–478.

Leighton, M. and Leighton, D.R., 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick (Editors), Tropical Rain

Forest: Ecology and Management. Blackwell Scientific, Oxford, pp. 181–196.

Levin, D.A., 1979. The nature of plant species. Science, 204: 381–384.

Levey, D.J., 1986. Methods of seed processing by birds and seed deposition patterns. In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 147–158.

Levey, D.J., 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecol. Monogr., 58: 251–269.

Lieberman, D., Hall, J.B., Swaine, M.D. and Lieberman, M., 1979. Seed dispersal by baboons in the Shai Hills, Ghana. Ecology, 60: 65–75.

Livingston, R.B., 1972. Influence of birds, stones and soil on the establishment of pasture juniper, *Juniperus communis*, and red cedar, *Juniperus virginiana*, in New England pastures. Ecology, 53: 1141–1147.

Loiselle, B.A. and Blake, J.G., 1991. Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. Auk, 108: 114–130.

Lugo, A.E., 1988. The future of the forest. Environment, 30: 17–45.

Lugo, A.E., 1992. Tree plantations for rehabilitating damaged lands in the tropics. In: M.K. Wali (Editor), Environmental Rehabilitation, Vol. 2. SPB Academic, The Hague, pp. 247–255.

Lugo, A., Parrotta, J.A. and Brown, S., 1993. Loss of species caused by tropical deforestation and their recovery through management. Ambio, 22: 106–109.

MacArthur, R.H., 1972. Geographical Ecology: Patterns in the Distribution of Species. Harper and Row, New York, 277 pp.

MacArthur, R.H. and Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ, 203 pp.

MacKinnon, J.R. and MacKinnon, K.S., 1978. Comparative feeding ecology of six primates in West Malaysia. In: D.J. Chivers and J. Herbert (Editors), Recent Advances in Primatology, Vol. 1. Academic Press, London, pp. 305–321.

Majer, J.D., 1989. Animals in Primary Succession. Cambridge University Press, Cambridge, 547 pp.

McAtee, W.L., 1947. Distribution of seeds by birds. Am. Midland Nat., 38: 214–223.

McClanahan, T.R., 1986a. The effect of a seed source on primary succession in a forest ecosystem. Vegetatio, 65: 175–178.

McClanahan, T.R., 1986b. Seed dispersal from vegetation islands. Ecol. Model., 32: 301–309.

McClanahan, T.R. and Wolfe, R.W., 1987. Dispersal of ornithochorous seeds from forest edges in central Florida. Vegetatio, 71: 107–112.

McClanahan, T.R. and Wolfe, R.W., 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Cons. Biol., 7: 279–288.

McDiarmid, R.W., Ricklefs, R.E. and Foster, M.S., 1977. Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. Biotropica, 9: 9–25.

McDonnell, M.J., 1986. Old field vegetation height and the dispersal pattern of bird-disseminated woody plants. Bull. Torrey Bot. Club, 113: 6–11.

McDonnell, M.J. and Stiles, E.W., 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia, 56: 109–116.

Mittermeier, R.A., 1991. Hunting and its effect on wild primate populations in Suriname. In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 93–107.

Mitra, S.S. and Sheldon, F.H., 1993. Use of an exotic tree plantation by Bornean lowland forest birds. Auk, 110: 529–540.

Moermond, T.C. and Denslow, J.S., 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithol. Monogr., 36: 865–897.

Morrison, D.W., 1978. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. Ecology, 59: 716–723.

Morrison, D.W., 1983. *Artibeus jamaicensis*. In: D.H. Janzen (Editor), Costa Rican Natural History. University of Chicago Press, Chicago, IL, pp. 449–450.

Noble, J.C., 1975. The effects of emus (*Dromaius novae-hollandiae* Latham) on the distribution of the nitre bush (*Nitraria billardieri*). J. Ecol., 63: 979–984.

Olson, S.L. and Blum, K.E., 1968. Avian dispersal of plants in Panama. Ecology, 49: 565–566.

Parrotta, J.A., 1992. The role of plantation forests in rehabilitating degraded ecosystems. Agric. Ecosyst. Environ., 41: 115–133.

Parrotta, J.A., 1993. Secondary forest regeneration on degraded tropical lands: the role of plantations as 'foster ecosystems'. In: H. Lieth and M. Lohmann (Editors), Restoration of Tropical Forest Ecosystems. Kluwer, Dordrecht, pp. 63–73.

Parrotta, J.A., 1995. The influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. J. Veg. Sci., 6: 627–636.

Parrotta, J.A., Knowles, O.H. and Wunderle, J.M., Jr., 1997. Floristic diversity development in a 10-year-old restoration forest on a bauxite mined site in Amazonia. For. Ecol. Manage., this issue.

Reeders, A.P., 1985. Vertebrate fauna in regenerated mines at Weipa, north Queensland. In: J.W. Lawrie (Editor), North Australian Mine Rehabilitation Workshop No. 9. Comalco Aluminum, Weipa, pp. 105–118.

Rick, C.M. and Bowman, R.I., 1961. Galapagos tomatoes and tortoises. Evolution, 15: 407–417.

Ridley, H.N., 1930. The Dispersal of Plants Throughout the World. I. Reeve and Co., Kent, 277 pp.

Robinson, G.R. and Handel, S.N., 1993. Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. Cons. Biol., 7: 271–278.

Silva, J.L. and Strahl, S.D., 1991. Human impacts on populations of chachalacas, guans, and curassows (Galliformes: Cracidae) in Venezuela. In: J.G. Robinson and K.H. Redford (Editors), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, IL, pp. 37–52.

Silva, J.M.C., Uhl, C. and Murray, G., 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Cons. Biol., 10: 491–503.

Snow, B.K., 1970. A field study of the bearded bellbird in Trinidad. Ibis, 112: 299–329.

Snow, D.W., 1962a. A field study of the black-and-white manakin, *Manacus manacus*, in Trinidad. Zoologica, 47: 65–104.

Snow, D.W., 1962b. A field study of the golden-headed manakin, *Pipra erythrocephala*, in Trinidad. Zoologica, 47: 183–198.

Snow, D.W., 1962c. The natural history of the oil bird *Steatornis caripensis*, in Trinidad, W.I. Part 2. Population, breeding ecology and food. Zoologica, 47: 199–221.

Snow, D.W., 1976. The Web of Adaptation. Collins, London, 196 pp.

Stapanian, M.A., 1986. Seed dispersal by birds and squirrels in the deciduous forests of the United States. In: A. Estrada and T.H. Fleming (Editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht, pp. 225–236.

Stiles, E.W., 1989. Fruits, seeds, and dispersal agents. In: W. Abrahamson (Editor), Plant Animal Interactions. McGraw Hill, New York, pp. 87–122.

Suckling, G.C., Backen, E., Heisler, A. and Neumann, F.G., 1976. The flora and fauna of *Pinus radiata* plantations in north-eastern Victoria. For. Comm. Victoria Bull., 24, 58 pp.

Swaine, M.D. and Hall, J.B., 1983. Early succession on cleared forest land in Ghana. J. Ecol., 71: 601–627.

Terborgh, J., 1983. Five New World Primates. Princeton University Press, Princeton, NJ, 260 pp.

Tucker, N.I.J. and Murphy, T.M., 1997. The effects of ecological rehabilitation on vegetation recruitment: some observations from the wet tropics of north Queensland. For. Ecol. Manage., 99: 133–152.

Turner, I.M. and Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol. Evol., 11: 330–333.

Uhl, C. and Clark, K., 1983. Seed ecology of selected Amazon basin successional species. Bot. Gazette, 144: 419–425.

Uhl, C. and Jordan, C.F., 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology, 65: 1476–1490.

Uhl, C., Clark, K., Clark, H. and Murphy, P., 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. J. Ecol., 69: 631–649.

Uhl, C., Clark, H. and Clark, K., 1982. Successional patterns associated with slash-and-burn agriculture in the upper Río Negro region of the Amazon basin. Biotropica, 14: 249–254.

van der Pijl, L., 1982. Principles of Dispersal in Higher Plants, 3rd edn. Springer-Verlag, New York, 214 pp.

van Ruremonde, R.H.A.C. and Kalkhoven, J.T.R., 1991. Effects of woodland isolation on the dispersion of plants with fleshy fruits. J. Veg. Sci., 2: 377–384.

Vásquez-Yanes, A., Orozco, G., Francios, G. and Trejo, L., 1975. Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. Biotropica, 7: 73–76.

Weins, J.A., 1992. Ecological flows across landscape boundaries: a conceptual overview. In: A.J. Hansen and F. di Castri (Editors), Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, Berlin, pp. 218–235.

Werner, P.A. and Harbeck, A.I., 1982. The pattern of tree seedling establishment relative to staghorn sumac cover in Michigan old fields. Am. Midland Nat., 108: 124–132.

Wheelwright, N.T., 1983. Fruits and ecology of the resplendent quetzals. Auk, 100: 286–301.

Wheelwright, N.T., 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. Trends Ecol. Evol., 3: 270–274.

Williams, T.C. and Williams, J.M., 1970. Radio-tracking of homing and feeding flights of a neotropical bat *Phyllostomus hastatus*, with evidence for visual orientation. Anim. Behav., 14: 468–473.

Willson, M.F., 1986. Avian frugivory and seed dispersal in eastern North America. Curr. Ornithol., 3: 223–279.

Willson, M.F. and Crome, F.H.J., 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. J. Trop. Ecol., 5: 301–308.