

Effect of seed passage through vertebrate frugivores' guts on germination: a review

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Abstract

The capacity of seeds to germinate after ingestion by frugivores is important for the population dynamics of some plant species and significant for the evolution of plant-frugivore interactions. In this paper the effects of different vertebrates on seed germination of nearly 200 plant species are reviewed, searching for patterns that predict the circumstances in which germination of seeds is enhanced, inhibited, or unaffected by the passage through the digestive tract of a seed disperser. It was found that seed dispersers commonly have an effect on the germinability of seeds, or on the rate of germination, or both, in about 50% of the plants they consume, although the diversity of animal species tested so far is still rather low (42 bird species, 28 non-flying mammals, 10–15 bats, 12 reptiles, 2 fishes). Enhancement of germination occurred about twice as often as inhibition.

In spite of the morphological and physiological differences in their digestive tracts, the different animal groups tested have similar effects on seed germination, although non-flying mammals tend to influence germination slightly more often than the other groups. Data on fishes are still too scarce for any generalization. Seed retention time in the dispersers' digestive tract is one factor affecting germination, and helps to explain the variation in seed responses observed among plant species, and even within a species. However other factors are also important; for example, the type of food ingested along with the fruits may affect germination through its influence on chemical or mechanical abrasion of the seed coat. Seed traits such as coat structure or thickness may themselves be responsible for some of the variation in seed retention times. Seeds of different sizes, which usually have different transit times through frugivores, and seeds of either fleshy or dry fruits, show often similar germination response to gut passage.

Seeds of different plants species differ strongly in their germination response after ingestion, even by the same frugivore species. Congeneric plants often show little consistency in their response. Even within a species variation is found which can be related to factors such as the environmental conditions under which germination takes place, seed morphology, seed age, and the season when the seeds are produced.

The effect of gut passage on germination differs between tropical and temperate zones. Seed germination of both shrubs and trees (data on herbaceous species are still scarce) in the temperate zone is more frequently enhanced than in the tropics. This result supports the hypothesis that enhanced germination may be more advantageous in unpredictable or less constant environments. Significant differences in frugivore-mediated germination are also found among different life forms. In both tropical and temperate zones, trees appear to be consistently more affected than shrubs or herbs. This might be due to an overall higher thickness of the seed coats, or to a higher frequency of seed-coat dormancy in tree species.

The influence of frugivory upon the population dynamics of a species has to be evaluated relative to other factors that influence germination and seedling recruitment

at a particular site. Whether seed ingestion by dispersers is really advantageous to a plant (as has commonly been assumed) can only be assessed if we also determine the fate of the ingested seeds under natural conditions, and compare it to the fate of seeds that have not been ingested.

Key words: frugivory, seed dispersal, seed ingestion, germination patterns

Introduction

In recent decades, there have been many studies of ecological and evolutionary aspects of frugivory and seed dispersal by animals, covering a range of latitudes and different habitats (e.g. Howe & Smallwood 1982; Janzen 1983; Estrada & Fleming 1986; Jordano 1992; Willson 1992; Fleming & Estrada 1993). However, the germination capacity of seeds after passing through the digestive tracts of an animal is one of those aspects that has received relatively little attention, although it is important to understand the evolution of plant-frugivore interactions. For example, the hypothesis that plants exert some kind of control over seed shadows produced by frugivores, by specific laxative and/or constipative chemicals in the fruit pulp which affect seed retention time in the dispersers' guts, has only recently been examined (Murray *et al.* 1994; Cipollini & Levey 1997; Wahaj *et al.*, in press).

Germination enhancement, i.e. an increased rate of germination or a higher final percentage germination or both, has been looked upon as one of the principal advantages of seed ingestion by frugivorous animals (Krefting & Roe 1949; van der Pijl 1982). However, the available data are often equivocal, and the number of animal species tested is small, especially in certain groups such as reptiles or fishes. In addition, there is often great variation in seed responses within a genus or even within the same plant species. Whether germination enhancement represents an advantage to a plant, and thus may be regarded as adaptive, probably depends on many factors, including the type of habitat where the seeds are deposited and the time of germination. Unless an increase in plant fitness can be shown, it is difficult to support the claim that germination enhancement is advantageous.

Few generalizations have been made as to how frequently and under what circumstances germination is influenced by fru-

givory, or how consistently the same frugivore affects seeds of different plant species (but see Lieberman & Lieberman 1986). The goal of this article is to review studies of different groups of frugivores (birds, mammals, reptiles and fishes) in the search for patterns that allow to assess the ecological and evolutionary importance of this aspect of plant-frugivore interactions. In particular, the following questions are addressed:

1. Do animal seed dispersers usually enhance the germination of the seeds they ingest? Frugivores can enhance germination in two ways: (a) by cleaning the seeds of pulp, which may contain germination inhibitors or be a potential source of infection by fungal or other pathogens, and/or (b) by having an abrasive effect on the seed coat, making it more rapidly permeable to water and gases.
2. Do different taxonomic groups of frugivores (differing in the morphology and physiology of their digestive tracts) affect seed germination differently? This could arise because of factors such as differences in the retention time of seeds in the gut, or from the presence of grit in gizzards (in some bird species, for example), which may have a mechanical and/or chemical effect on the seed coat.
3. Do seeds of different plant species respond similarly to ingestion by the same frugivore species? We might expect that the germination of closely related species, belonging to the same genus for instance, would be similarly affected by the same species of vertebrate. If not, what factors help to explain the differences (e.g. seed coat structure and thickness)?
4. Is there an interaction between seed size and the effect of a frugivore upon germination? For example, if small seeds are retained for a longer period within the animal's digestive tract than large seeds, as suggested in a number of studies, we may

- hypothesize that germination enhancement tends to decrease as seed size increases.
5. Do seeds of fleshy fruits and dry fruits respond similarly to frugivores' ingestion?
 6. Are there any differences between seed responses in the tropics and the temperate zones? If the effect of seed ingestion by frugivores on germination is adaptive in unpredictable or less constant environments, as Izhaki & Safriel (1990) suggest, we might expect that seeds in the temperate zones would be affected more often than seeds in the tropics.
 7. Do seeds of plants with different life forms differ in their response to ingestion by frugivores? If, for instance, trees have seed-coat dormancy more frequently than shrubs and herbs, a germination enhancement after ingestion might be more common in trees. Likewise, possible differences in seed traits such as coat thickness, among different life forms might well translate into differences in the effect that frugivores have on seed germination.
 8. Related to 7, do seed responses to frugivores' ingestion vary between habitats (e.g. grasslands, shrublands and woodlands)?
 9. How important is seed ingestion by frugivores for plant recruitment relative to other factors?

About 80 papers dealing with the effect of seed passage through vertebrate frugivores are reviewed here. They cover 182 plant

species belonging to 68 families, and 94–99 frugivore species belonging to 47 families (Table 1). A complete list of the plants and animals examined as well as a summary about how passage through the gut affects germination is given in the Appendix. The few controlled experiments performed prior to 1949 are mentioned in Krefting & Roe (1949) but are not included here as it was not possible to reexamine most of the data. These authors suggest that those data are often misleading due to small sample sizes and inadequate controls, and are thus not strictly comparable to later work. For example, it is not always clear whether ingested and control seeds came from the same plant population or the same individuals. Some other studies that examined the effect of seed passage through frugivores on germination have been reviewed but are not included in the Appendix (Alexandre 1978; Yan 1993; Wrangham *et al.* 1994), either because no information is available concerning samples sizes or the statistical tests performed, or because the authors do not say what kind of control was used in the comparison with ingested seeds.

In most studies, only the total percentage of seeds that germinated after a given period of time, often a few months, was measured. In less than half of the studies (see Table 1), both percentage of germination and germination rate are given, i.e. the time elapsed until the first germination and/or the time elapsed until 50% of the seeds have germinated. In some studies, the term germination rate is erroneously used as a synonym of the percent-

Table 1. Number of studies which showed enhancement, inhibition or a neutral effect on the two main characteristics of germination, i.e. *percent* germination and germination *rate*, after gut passage by different groups of vertebrate frugivores. For all plant species tested, ingested seeds have been compared with controls (uninged seeds). Based on data from the Appendix.

Frugivores (no. species/families)	Effect on germination	No. studies (families)	Plant species <i>N</i> (%)	Enhancement <i>N</i> (%)	Inhibition <i>N</i> (%)	Neutral
Birds (42/19)	percentage rate	153	80 (38)	55 (36)	25 (16)	73 (48)
		103		42 (41)	15 (14)	46 (45)
Non-flying mammals (28/18)	percentage rate	95	73 (40)	37 (39)	18 (19)	40 (42)
		46		14 (30)	6 (13)	26 (57)
Bats (10–15/2)	percentage rate	24	21 (16)	6 (25)	2 (8)	16 (67)
		17		0 (0)	5 (29)	12 (71)
Reptiles (12/6)	percentage rate	43	41 (23)	12 (28)	7 (16)	24 (56)
		19		9 (47)	3 (16)	7 (37)
Fishes (2/2)	percentage	2	2 (2)	2 (100)	0	0

age of germination. It is important to discriminate between these two components of germination performance, as they have quite different ecological consequences. The differences in germination rates between ingested and control seeds are often a few days, sometimes several weeks, and rarely a few months. Such differences are not examined in this review since their implications are completely unknown for the species examined.

The majority of germination experiments were carried out in the laboratory, usually in Petri dishes under controlled conditions of light, humidity and temperature; others were performed in glasshouses, and a very few investigated seed germination in potting soil placed in the natural habitat where the plants are usually found. In most experiments, depulped seeds were used as a control, i.e. manually cleaned from pulp. Thus, most studies did not test the effect that frugivores have in separating the pulp from the seeds, but rather the possible abrasive (scarifying) effect that ingestion by vertebrates has on seed coats (integuments). Intact fruits (fresh fruits with seeds inside) were used as controls in only eleven studies, eight of which took manually depulped seeds as additional controls.

The experimental data show that seed ingestion by dispersers may either increase or decrease the germinability of seeds. However, the large majority of studies did not examine the viability of the seeds that failed to germinate. Thus, it is unknown whether the remaining seeds could potentially germinate, or had died, or were already dead before the experiment began. The age of seeds must also be considered in any germination experiment, as it determines the degree of germinability in many species, and especially those that only remain viable for a short period. In most studies freshly collected seeds were used.

How common is enhanced germination due to passage through disperser guts?

About half of the data come from experiments with fruits consumed by birds, mostly passerines, and especially *Turdus merula*, *T. migratorius* and *Pycnonotus barbatus* (cf. Appen-

dix). The data suggest that birds have no consistent effect on *percent* germination: studies in which there was no effect on germination percentage are almost as frequent as those in which a significant effect (either positive or negative) occurred (Table 1). In 36% of cases germination was increased while it was reduced in only 16% of cases. On the other hand, birds had a significant effect on the *rate* of germination slightly more often (in 55% of all studies, and disregarding whether or not they had an effect on the final percent germination), accelerating the germination of ingested seeds much more commonly (40.5%) than delaying it (14.5%).

Non-flying mammals influence seed germination in 58% of all studies. Like birds, they enhanced germination (increasing both percent and rate of germination) more than twice as often as they inhibited it. However, in 57% of cases, the seed germination rate was not significantly affected by passage through the gut. Most data within this group of frugivores come from experiments performed with either primates or bears (see Appendix). Seed passage through the guts of primates either increased percent germination or had no effect on it in a similar number of cases (38% and 36%, respectively), and decreased it in 26%; they accelerated germination in 34% of cases, delayed it in 14%, but in more than half of cases (52%) had no effect on the rate of germination. The two species of frugivorous bears, in contrast, had no effect on the percent seed germination of most plant species, increasing it in only 29% of cases and decreasing it in none. Similarly, a neutral effect of seed passage through bears was found in all nine cases in which the rate of germination was examined.

The germination of most seed species ingested by frugivorous bats of the two families Pteropodidae and Phyllostomidae was not influenced by gut passage (Table 1). Neither the percentage nor the rate of germination was affected in the majority of studies (67% and 71% of the cases, respectively). In a quarter of cases, the percent germination was increased, but there were no cases of accelerated germination. In contrast, delays in germination were observed in 29% of cases, but decreases in percent germination only in 8%.

Fewer data have been published (in about ten papers) on the effects of reptiles on germination, turtles being more commonly

tested than lizards. The pattern that emerges from the 41 plant species is that percent germination is mostly (56% of cases) unaffected by seed ingestion by reptiles; when there was an effect it was more usually positive (28%) than negative (16%). In contrast, reptiles seems to modify the rate of germination in most cases (63%), accelerating it more often (47%) than delaying it (16%; Table 1). For the plant *Neochamalea pulverulenta* (Cneoraceae), whose fruit are consumed by the lacertid *Gallotia galloti* in the Canary Islands, seed germination was very low during the first year after planting, apparently due to inhibition by the reptile (Valido & Nogales 1994). Three years later, however, the total percentage of germination of treated and control seeds did not differ significantly (Valido & Nogales, pers. comm.). This suggests that, at least for some plants, apparent differences in the final percentage germination between control and ingested seeds depend on the duration of the germination experiment.

To my knowledge, the effect of fishes on seed germination has been tested with only two aquatic plants, both of which showed an increase in percent germination after ingestion by a cichlid and a cyprinid (Agami & Waisel 1988). More data on this group of vertebrates are needed, both from temperate zones and the tropics. In some tropical regions, especially in the Amazon and in Río Negro, large numbers of frugivore fishes have been reported (Gottsberger 1978; Gouling *et al.* 1988).

Overall, seed dispersers appear to influence both the percentage and the rate of germination in a large fraction of plant species consumed (*c.* 52% and 50% of the studies, respectively). From these results, it seems that non-flying mammals have an effect on seed germination more frequently than other taxonomic groups, although the variability is quite high within each group of frugivores (see next section). Considering all dispersers together, the percentage germination is increased more often (35%) than reduced (17%), and an acceleration of germination after seed ingestion is more common (35% of the cases) than a delay (16%). Germination is either enhanced or inhibited in a wide variety of plant species belonging to different families (see Appendix). The seeds of such plants vary widely in size, shape and coat thickness. Therefore, by looking at seed traits

alone, it is not possible to predict whether germination will be affected after ingestion by a particular frugivore or not. It is possible that inhibition occurs in some species because the seeds are not completely mature when ingested. For example, Figueiredo & Longatti (1997) found that howler monkeys (*Alouatta fusca* ssp. *fusca*), which eat both mature and immature fruits of *Miconia cinnamomifolia*, inhibited germination, whereas marmosets (*Callithrix penicillata*), which feed only on mature fruits, did not.

A significant part of the variation in germination after ingestion appears to be related to plant species. This is consistent with the conclusions of Lieberman & Lieberman (1986), who also found that the effects of individual animal species are highly idiosyncratic and unpredictable from one plant species to the next. Using a total of 52 plant-animal combinations, these authors found that the majority of plants (73%) revealed no significant differences between ingested and uningested seeds, and concluded that "germination enhancement (and concomitant dependence upon ingestion) was neither inevitable nor even common".

How consistently does the same plant species respond to ingestion by different frugivores?

For a given plant species, the outcome of seed passage through a digestive tract may depend on the animal species that consumes it. The way in which seeds are 'treated' in the frugivore's gut is actually one of the components of dispersal quality that determine the effectiveness of a seed disperser (Schupp 1993). A rather long retention time in the vertebrate guts, for instance, and thus a prolonged exposure to digestive fluids, may result in the removal of much of the protective mesocarp and thus damage to the seed embryo, especially in seeds with soft seed coats (e.g. Gardener *et al.* 1993; Murphy *et al.* 1993). Likewise, an excessive mechanical grinding in a bird's gizzard may be detrimental, increasing the possibility of embryo desiccation and pathogenic attack. Since the digestive systems of frugivores such as mammals, birds and reptiles differ greatly, both morphologically and physiologically (e.g.

King 1996), it is scarcely surprising if there are differences in their influence upon germination.

Morphological and physiological traits of frugivores that can affect seed treatment

Just as the teeth of herbivorous mammals are modified in various ways, to crush, grind or shred plant matter, so also may the chemical environment of the digestive tract be modified to extract nutrients in an effective way, usually harbouring symbiotic bacteria and protozoa which can digest the structural polymers of the cell wall through fermentation. Ruminant artiodactyls (e.g. cows, deer, peccaries) have a refined stomach fermentation which takes place in the two compartments, rumen and reticulum, near the oesophagus (foregut fermentation). In contrast, hindgut fermentation (found in horses, rhinoceros, tapirs, for instance) takes place in the caecum, a much less complicated structure that allows a faster digestion (King 1996). Gut passage time for a ruminant such as a cow is usually 70–90 hours (Gardener *et al.* 1993), whereas food is processed in about 48 hours by a horse (Sibly 1981). Seeds of *Enterolobium cyclocarpum*, however, can be retained in horse guts for up to two months, and a large fraction will then be digested (Janzen 1982). Likewise, seeds of *Trewia* ingested by rhinoceros show peak passage times of 64–88 h, but ranging widely from 46 h to 172 h (Dinerstein & Wemmer 1988). Frugivorous bats also exhibit special modifications to their digestive tract: the oesophagus leads into a cardiac vestibule and the stomach is an elongated tube with a large, strongly-developed caecum (Jordano 1992). Transit times reported for bats are quite fast, ranging from 22 to 144 min (Laska 1990).

Jordano (1992) reviewed specific modifications of the digestive systems in frugivorous birds: (a) the crop and/or the proventriculus may be extremely reduced, or even absent in some species; (b) the gizzard may have thin, non-muscular walls; (c) the simplified gizzard is often in a lateral position, and thus the oesophagus is tightly connected with the duodenum; and (d) the intestine is short relative to body size. In strongly frugivorous birds, seeds are processed much more rapidly than pulp, presumably to maximize gut capacity for digestible pulp. Regurgitation

of seeds by passerine birds is very rapid, often within 5–20 min, while defaecated seeds are retained for much longer, usually 0.3–1.5 h (Sorensen 1981, 1984; Herrera 1984; Jordano 1992). Data for pigeons show gut passage times ranging from 55 to 140 min (Clout & Tilley 1992).

In herbivorous reptiles, the small and large intestines tend to be shorter and less coiled than in mammals and birds (King 1996); as a result, the rate of nutrient absorption is much greater in mammals and birds, which also have a much higher metabolic rate than reptiles. At the distal part of the large intestine there is usually a caecum, a prominent structure that can absorb nutrients and that houses symbiotic micro-organisms which ferment cell wall polymers. For lizards, in particular, the large intestine is much longer and the small intestine much shorter in herbivorous species than in their carnivorous counterparts (King 1996). Herbivorous lizards have long gut passage times (several days) compared to small herbivorous mammals (less than 10 h; Karasov *et al.* 1986), presumably because reptiles do not chew their food, and thus take more time to digest it. However, it is possible that some of them break up food mechanically in the stomach, as suggested by observations on Galápagos tortoises (*Testudo elephantopus* ssp. *porterii*), which produce faecal pellets containing sand, gravel and small pieces of wood (Rick & Bowman 1961), and on *Sauromalus* which ingests sand and gravel along with its food (Sylber 1988). Seed retention time in Galápagos tortoises ranges from 12 to 20 days (Rick & Bowman 1961), although much shorter ranges (24–48 h) are reported for turtles of the genus *Rhinoclemmys* (Moll & Jansen 1995). Geckos of the genus *Hoplodactylus* take 36–72 hours to defaecate seeds, being faster when temperatures are higher and the animals are more active (Whitaker 1987).

Studies performed with fishes show that only hard seeds pass through the intestines intact and that these can be retained in the digestive tracts for up to 65 hours (Agami & Waisel 1988). The mandibles of common carps (*Cyprinus carpio*), a species used in some tests, usually crush the seed coats of species such as *Najas marina* and *Ruppia maritima* completely, digesting the seed contents. Apparently, many other fish species consume some seeds but disperse and excrete the remainder (Agami & Waisel 1988).

Other factors that determine the time of seed passage within a frugivore

Food retention time within a digestive tract is not determined only by the intrinsic morphological and physiological traits of the particular animal. Factors such as nutritional levels (especially fat composition) of the diet, consistency, hardness, water content or amount of food are known to affect directly the speed at which a meal moves through the gut (e.g. Demment & van Soest 1985; Clench & Mathias 1992; Gardener *et al.* 1993). Mean gut passage time (*GPT*) can also vary depending on the amount of food consumed; for example, it has been found to decrease with an increasing number of fruits ingested (Murphy *et al.* 1993). In frugivorous birds, *GPT* tends to be short in order to increase the ingestion rate (Levey 1991), at the cost of a low digestive efficiency (Karasov & Levey 1990). The *GPT* can also change through the feeding season and even during the day, being short in the early morning as energy reserves are replenished, and in the late afternoon, presumably so as to build up sufficient energy for the night (Murphy *et al.* 1993).

Seed retention time within the same frugivore species can vary significantly depending on the fruit ingested, with high individual variability. Barnea *et al.* (1991) reported great variation in *GPT* in birds for 12 plant species, with values ranging from 9 to 33 min for bulbuls, and from 13 to 74 min for blackbirds. The size and weight of a seed usually determines the speed at which it passes through the digestive tract of a bird, large and heavy seeds being defaecated more quickly than small and light seeds (Garber 1986; Levey & Grajal 1991; Gardener *et al.* 1993). Seed size may also determine whether it will be defaecated or regurgitated, thus also affecting the time the seeds are kept in the digestive tract; this may translate into different germination patterns (Clergeau 1992; Izhaki *et al.* 1995). The texture of the fruit pulp is another trait that may influence seed retention time, as reported by Levey (1986), who found that seeds of fruits with a very firm texture were retained longer than those of watery fruits.

The effect of seed retention time in vertebrate guts on germination success can also differ among species of frugivores and plants. Barnea *et al.* (1991) found that blackbirds (*Turdus merula*), in general, show a stronger

enhancing effect on germination than bulbuls (*Pycnonotus xanthopygos*) because of the longer retention time. Not all plants responded equally, however; for example, very different retention times (a few minutes to 24 h) of *Solanum luteum* seeds in the two bird species had no effect on germination success (Barnea *et al.* 1992). In contrast, Murphy *et al.* (1993) found that spiny-cheeked honeyeaters (*Acanthagenys rufogularis*) retained the seeds of grey mistletoe, *Amyema quandang*, for much longer in their guts than mistletoebirds (*Dicaeum hirundinaceum*; 40 min vs. 13 min), which translated into lower seedling establishment after ingestion by honeyeaters. Apparently, the more gentle treatment in the guts of the specialized disperser was more beneficial to the seeds. A negative effect of seed retention time on germination success has also been reported for Galápagos tortoises (Rick & Bowman 1961), and for herbivorous mammals (Janzen *et al.* 1985).

Levey & Grajal (1991) proposed that rapid seed processing, e.g. by many frugivorous birds, has influenced the evolution of pulp composition and seed-packaging, with a selection for nutrients that are rapidly assimilated, e.g. simple sugars and free amino acids. In large-seeded fruits, which are often rich in lipids, this may be different as seeds are processed more rapidly and independently of pulp (Levey & Grajal 1991). Murray *et al.* (1994) have argued that the pulp of some fleshy fruits contains "laxative" chemicals that shorten seed retention time in the guts, thus reducing seed mortality. They found that, although percentage germination of *Witheringia solanacea* seeds was increased by passage through the gut of the bird *Myadestes melanops*, the germination success decreased with increasing time spent in the gut. While a mild abrasion probably enhances water imbibition or the perception of germination cues, a longer exposure to abrasion in the gut may be excessive and cause premature germination. However, Witmer (1996) has given an alternative explanation for the results of Murray *et al.* (1994), which concerns how nutrient concentration in food influences the digestive function of frugivorous birds. He found that for at least three species of birds (*Turdus migratorius*, *Hylocichla mustelina*, *Bombycilla cedrorum*) seed passage rates increased as sugar concentration in their diet declined. This result is not

true for all species; for example, starlings (*Sturnus vulgaris*) showed similar gut retention times regardless of the diet composition (insects vs fruits), whereas American robins (*Turdus migratorius*) showed a decrease in retention time when their diet was changed from insects to fruit (Levey & Karasov 1994). Recently, Cipollini & Levey (1997) have hypothesized that specific secondary metabolites found in the fruit pulp alter seed passage rates, either slowing them down (i.e. having a "constipating" effect on animals) or accelerating them (i.e. a "laxative" effects). Wahaj *et al.* (in press) show that glycoalkaloids in ripe fruits of *Solanum* can increase or decrease retention time and thereby influence seed deposition patterns (e.g. number of defaecations with seeds, number of seeds per defaecation, and presumably also dispersal distance). Future studies may shed more light on this subject, and allow us to determine whether the fruit chemicals that apparently influence the seed passage rate in certain frugivores have an adaptive function or not.

Patterns associated with different types of frugivore

Of the 34 plant species that were tested with more than one animal species of different classes or orders, 17 showed a consistent response to passage through the gut (Table 2). In 12 plant species the comparison was either between birds and bats or between birds and non-flying mammals. In at least two plant species, even though response to ingestion was consistent, one frugivore had a significantly stronger effect than the other. In *Spondias purpurea* seeds ingested by white-tailed deer (*Odocoileus virginianus*) germinated in a greater percentage than those ingested by the iguana *Ctenosaura pectinata* (Mandujano *et al.* 1994). Likewise, the germination of seeds of *Plocama pendula* ingested either by a lacertid or by birds did not differ from the control, yet a larger fraction of seeds ingested by the lizard germinated compared to those consumed by birds (Valido & Nogales, unpubl. data).

For the remaining plant species tested with frugivores belonging to different orders, there were significant differences in seed germination depending on the animal that had ingested the seeds (Table 3). The most

common comparisons were between birds and either non-flying mammals (ten plant species), bats (six plant species), or reptiles (four plant species); some species were tested with more than two groups. The longer seed retention times in mammals compared to those in birds might explain the enhancement of germination (either percentage or rate of germination, or both) in only six cases: *Azadirachta indica*, *Carissa edulis*, *Cornus stolonifera*, *Prunus virginiana*, *Premna quadrifolia* and *Securinega virosa*. At least three species (*Byrsocarpus coccineus*, *Clausena anisata* and *Plocama pendula*) seem to be negatively affected by the longer retention times within mammalian guts. In the case of *P. pendula*, rabbits have a negative effect on germination compared to birds. However, seed retention time is unlikely to be the reason, since lizards, although they have even longer retention times than rabbits, have a neutral effect on germination. When both birds and bats were tested with the same plant species, it was observed that bats had no effect on germination in three cases (*Carissa edulis*, *Ficus luschnathiana* and *Morus nigra*), enhanced germination in *Azadirachta indica* and *Ficus microcarpa*, and inhibited it in *Clausena anisata* compared to birds (Table 3). Reptiles had either no effect on seed germination tested against birds (with *Sambucus canadensis*, *Plocama pendula* and *Lycium intricatum*), and against mammals (with *Diospyros consolatae* and *P. pendula*), or inhibited germination (*Morus alba* and *L. intricatum*), while birds enhanced it (Table 3). Finally, in the three plant species in which non-flying mammals were compared with bats (*Securinega virosa*, *Azadirachta indica* and *Premna quadrifolia*), the non-flying mammals enhanced germination while bats had no effect.

Significant differences in seed responses can also be observed in frugivores belonging to the same order, usually birds, since these are the most commonly studied group (Table 3). This suggests that seed retention time alone cannot explain the high variability found in seed responses to avian ingestion. The differences in the effect of two primate species on *Miconia cinnamomifolia* can also not be attributed to differences in seed retention time in their guts but, as already noted, to the consumption of immature fruits by howler monkeys but not by marmosets (Figueiredo & Longatti 1997).

Table 2. Plant species tested with vertebrate frugivores belonging to different orders which show a *consistent* seed germination response to ingestion: enhancement (+), inhibition (-), or neutral (0). The first symbol refers to total *percent* germination and the second one to germination *rate*.

Plant species	Frugivores	Effect on germination		Reference
		percent	rate	
<i>Carissa edulis</i>	1 sp. of bird	0	0	Lieberman & Lieberman (1986)
	1 sp. of bat	0	0	
<i>Clausena anisata</i>	1 sp. of bird	-	-	Lieberman & Lieberman (1986)
	1 sp. of bat	-	-	Lieberman & Lieberman (1986)
	1 sp. of primate	-	-	Lieberman & Lieberman (1986)
<i>Ehretia cymosa</i>	2 spp. of birds	0	0	Lieberman & Lieberman (1986)
	2 spp. of bats	0	0	Lieberman & Lieberman (1986)
<i>Ficus carica</i>	1 sp. of bird	0	.†	Lisci & Pacini (1994)
	1 sp. of bat	0	0	
<i>Ficus microcarpa</i>	1 sp. of bird	+	+	Guerrero & Figueiredo (1997) Figueiredo <i>et al.</i> (1995)
	Unid. spp. of bats	+	.	
<i>Flacourtia flavescens</i>	2 spp. of birds	-	-	Lieberman & Lieberman (1986)
	1 sp. of primate	-	-	Lieberman & Lieberman (1986)
	1 sp. of bat	-	-	Lieberman & Lieberman (1986)
<i>Najas marina</i>	1 sp. of bird	+	+	Agami & Waisel (1988)
	2 spp. of fish	+	.	Agami & Waisel (1986)
<i>Oplopanax horridus</i>	2 spp. of birds	0	0	Traveset & Willson (1997)
	2 spp. of bears	0	0	Traveset & Willson (1997)
<i>Premna quadrifolia</i>	1 sp. of bat	0	0	Lieberman & Lieberman (1986)
	1 sp. of bird	0	0	Lieberman & Lieberman (1986)
<i>Prunus serotina</i>	1 sp. of bird	+	.	Krefting & Roe (1949)
	Unid. spp. of birds	+	.	Smith (1975)
	1 sp. of turtle	+	.	Braun & Brooks (1987)
<i>Ribes bracteosum</i>	2 spp. of birds	0	0	Traveset & Willson (1997)
	2 spp. of bears	0	0	Traveset & Willson (1997)
<i>Rubus procerus</i>	1 sp. of bird	0	.	Brunner <i>et al.</i> (1976)
	1 sp. of fox	0	.	Brunner <i>et al.</i> (1976)
<i>Rubus spectabilis</i>	2 spp. of birds	0	+	Traveset & Willson (1997)
	2 spp. of bears	0	+	Traveset & Willson (1997)
<i>Securinega virosa</i>	3 spp. of birds	0	0	Lieberman & Lieberman (1986)
	2 spp. of bats	0	0	Lieberman & Lieberman (1986)
<i>Spondias purpurea</i>	1 sp. of deer	+	.	Mandujano <i>et al.</i> (1994)
	1 sp. of iguana	+	.	Mandujano <i>et al.</i> (1994)
<i>Spreptopus amplexifolius</i>	2 spp. of birds	0	0	Traveset & Willson (1997)
	2 spp. of bears	0	0	Traveset & Willson (1997)
<i>Vaccinium alaskaense</i> , <i>V. ovalifolium</i>	2 spp. of birds	0	0	Traveset & Willson (1997)
	2 spp. of bears	0	0	Traveset & Willson (1997)

† No results.

Table 3. Plant species tested with frugivore species belonging to the same or different orders which showed an *inconsistent* seed germination response to ingestion: enhancement (+), inhibition (–), or neutral (0). The first symbol refers to total *percent* germination and the second one to germination *rate*.

Plant species	Frugivores	Effect on germination		Reference
		percent	rate	
<i>Azadirachta indica</i>	2 spp. of birds	0	+	Lieberman & Lieberman (1986)
	1 sp. of bird	+	+	Lieberman & Lieberman (1986)
	1 sp. of primate	+	+	Lieberman <i>et al.</i> (1979)
	1 sp. of primate	+	0	Lieberman & Lieberman (1986)
	1 sp. of bat	0	0	Lieberman & Lieberman (1986)
	1 sp. of bat	+	–	Lieberman & Lieberman (1986)
<i>Byrsocarpus coccineus</i>	3 spp. of birds	0	0	Lieberman & Lieberman (1986)
	1 sp. of primate	–	–	Lieberman & Lieberman (1986)
<i>Capparis erythrocarpos</i>	1 sp. of bird	0	0	Lieberman & Lieberman (1986)
	2 spp. of birds	0	+	Lieberman & Lieberman (1986)
	1 sp. of primate	0	+	Lieberman & Lieberman (1986)
<i>Carissa edulis</i>	1 sp. of bird	–	–	Lieberman & Lieberman (1986)
	1 sp. of bird	0	0	Lieberman & Lieberman (1986)
	1 sp. of bat	0	0	Lieberman & Lieberman (1986)
<i>Clausena anisata</i>	1 sp. of bird	0	–	Lieberman & Lieberman (1986)
	1 sp. of bird	–	–	Lieberman & Lieberman (1986)
	1 sp. of primate	–	–	Lieberman & Lieberman (1986)
	1 sp. of bat	–	–	Lieberman & Lieberman (1986)
<i>Cornus racemosa</i>	2 spp. of birds	–	.†	Krefting & Roe (1949)
	Unid. spp. of birds	+	.	Smith (1975)
<i>Cornus stolonifera</i>	2 spp. of birds	–	.	Krefting & Roe (1949)
	1 sp. of bear	+	.	Rogers & Applegate (1983)
<i>Diospyros consolatae</i>	1 sp. of primate	+	.	Engel (1997)
	1 sp. of snake	0	.	Engel (1997)
<i>Ficus luschnathiana</i>	1 sp. of bird	+	.	Figueiredo & Perin (1995)
	1 sp. of bat	0	.	Figueiredo & Perin (1995)
<i>Ficus microcarpa</i>	Unid. spp. of birds	0	.	Figueiredo <i>et al.</i> (1995)
	1 sp. of bird	+	+	Guerrero & Figueiredo (1997)
	Unid. spp. of bats	+	.	Figueiredo <i>et al.</i> (1995)
<i>Juniperus virginiana</i>	3 spp. of birds	–	.	Livingston (1972)
	2 spp. of bird	+	.	Holthuijzen & Sharik (1985)
<i>Lonicera tatarica</i>	1 sp. of bird	+	.	Krefting & Roe (1949)
	1 sp. of bird	0	.	Krefting & Roe (1949)
<i>Lycium intricatum</i>	1 sp. of bird	+	+	Nogales <i>et al.</i> (1998)
	1 sp. of lizard	0	0	Valido & Nogales (1994)
	1 sp. of lizard	–	–	Nogales <i>et al.</i> (1998)
<i>Miconia cinnamomifolia</i>	1 sp. of primate	–	.	Figueiredo & Longatti (1997)
	1 sp. of primate	0	.	Figueiredo & Longatti (1997)

Table 3. (continued).

Plant species	Frugivores	Effect on germination		Reference
		percent	rate	
<i>Morus alba</i>	1 sp. of bird	+	.	Krefting & Roe (1949)
	1 sp. of turtle	-	.	Braun & Brooks (1987)
<i>Morus nigra</i>	2 spp. of birds	+	+	Barnea <i>et al.</i> (1991)
	1 sp. of bat	0	0	Izhaki <i>et al.</i> (1995)
<i>Neochamaelea pulverulenta</i>	1 sp. of lizard	-	+	Valido & Nogales (1994)
	1 sp. of lizard	+	+	Valido & Nogales (unpubl.)
<i>Plocama pendula</i>	2 spp. of birds	0	+	Valido & Nogales (unpubl.)
	1 sp. of rabbit	-	-	Nogales <i>et al.</i> (1995)
	1 sp. of lizard	0	0	Valido & Nogales (unpubl.)
<i>Premna quadrifolia</i>	1 sp. of bird	0	0	Lieberman & Lieberman (1986)
	1 sp. of primate	0	+	Lieberman & Lieberman (1986)
	1 sp. of bat	0	0	Lieberman & Lieberman (1986)
<i>Prunus virginiana</i>	1 sp. of bird	-	.	Krefting & Roe (1949)
	1 sp. of bear	+	.	Rogers & Applegate (1983)
<i>Rosa</i> sp.	1 sp. of bird	-	.	Krefting & Roe (1949)
	1 sp. of bird	+	.	Krefting & Roe (1949)
<i>Rubus</i> sp.	1 sp. of bird	0	.	Krefting & Roe (1949)
	2 spp. of birds	+	.	Krefting & Roe (1949)
<i>Rubia tenuifolia</i>	5 spp. of birds	0	-	Izhaki & Safriel (1990)
	2 spp. of birds [†]	0	+	Barnea <i>et al.</i> (1991)
<i>Smilax aspera</i>	1 sp. of bird	+	0	Izhaki & Safriel (1990)
	2 spp. of birds	0	0	Izhaki & Safriel (1990)
<i>Solanum nigrum</i>	2 spp. of birds	0	.	Barnea <i>et al.</i> (1990)
		0	0	Mas & Traveset (unpubl.)
	2 spp. of birds	+	+	Clergeau (1992)
<i>Rhamnus palaestinus</i>	1 sp. of bird	+	+	Izhaki & Safriel (1990)
		+	-	Barnea <i>et al.</i> (1991)
	1 sp. of bird	+	0	Barnea <i>et al.</i> (1991)
	4 spp. of birds	0	0	Izhaki & Safriel (1990)
<i>Sambucus canadensis</i>	1 sp. of bird	-	.	Krefting & Roe (1949)
	2 spp. of birds	+	.	Krefting & Roe (1949)
	1 sp. of turtle	0	.	Braun & Brooks (1987)
<i>Sambucus racemosa</i>	2 spp. of birds	0	.	Traveset & Willson (1997)
	1 sp. of bear	0	0	Traveset & Willson (1997)
<i>Securinega virosa</i>	3 spp. of birds	0	0	Lieberman & Lieberman (1986)
	1 sp. of primate	+	+	Lieberman & Lieberman (1986)
	2 spp. of bats	0	0	Lieberman & Lieberman (1986)

[†]No results.

[‡]One of these species is the same as used by Izhaki & Safriel (1990).

In short, the great variation observed in the effect of seed ingestion on germination, even when comparing congeneric frugivores, suggests that differences in retention time (at least within a limited range of hours or days) is not the only important factor. For most species, an effect on germination is not associated, either positively or negatively, with the time that seeds remain in the digestive tract of dispersers. Other factors, such as the type of food ingested along with the fruits (with variable acidity, water content, etc.), may even be more relevant in determining the extent to which the seeds are mechanically and/or chemically abraded.

Responses of different seed species ingested by the same frugivores

A particular animal species can have significantly different effects on seed germination depending on a variety of traits (seed size, coat thickness, sculpture, etc.) which are intrinsic to the plants it consumes. Many studies show that pulp (aril) removal may be sufficient to enhance germination, as germination inhibitors present in these tissues are eliminated (e.g. Evenari 1949; Mayer & Poljakoff-Mayber 1975; McDiarmid *et al.* 1977; Izhaki & Safriel 1990; Barnea *et al.* 1991; Clergeau 1992; Bustamante *et al.* 1993; Lisci & Pacini 1994) and the possibility of microbial or fungal attack is reduced (Ng 1983; Jackson *et al.* 1988). At least three studies confirm that, in addition, some frugivores enhance germination by abrading the seed coats (Izhaki & Safriel 1990; Barnea *et al.* 1991; Clergeau 1992).

For other species, the ingestion implies a chemical or mechanical abrasion of the seed coat that may or may not enhance germination, depending on the extent to which seeds are abraded. For a long time it has been assumed that the fruits of some plants, especially those believed to have "coevolved" with their animal dispersers, obligatorily need to be ingested by them for seeds to germinate (the case of the dodo and the tambalacoque tree from Mauritius Island is probably the most famous example; Temple 1977). Nevertheless, evidence that contradicts this assumption is accumulating (e.g. Witmer & Cheke 1991). In some species, there is cor-

relative evidence for a dramatic reduction in plant populations, associated with extinction or decline of a specific disperser (e.g. Temple 1977; Janzen & Martin 1982; Given 1995; Traveset 1995). However, little evidence exists that such reduction has been due to the requirement for seed ingestion by a particular frugivore. Probably the reduction in plant population densities is more related to the limited dispersal of seeds, with the consequence of higher seed/seedling mortality due to predators and pathogens. Nonetheless, there are a few cases where ingestion seems to be essential; for example, Rick & Bowman (1961) reported that the only natural way of breaking seed dormancy in the native Galápagos tomatoes (*Lycopersicon esculentum* var. *minor*) was through ingestion by giant tortoises.

Different seed coat sculptures, which may be found even in closely related species such as *Solanum luteum* and *S. nigrum* (Barnea *et al.* 1990), or different seed coat thickness (Gardener *et al.* 1993) can sometimes account for the different effects of a frugivore on germination. Amongst congeneric plant species, seed responses to ingestion show a great variability (see Appendix). The genera *Rubus*, *Ficus*, *Vaccinium*, *Solanum* and *Vitis* have been most often studied (although data of at least three species also exist for *Cornus*, *Juniperus*, *Prunus*, *Acacia* and *Sambucus*); none of them shows a consistent result response to ingestion, even when the frugivores belong to the same order. The results for the ten species of *Rubus* tested so far show that seed germination may be: (a) enhanced (in three species tested with several frugivores including bears and birds), (b) inhibited (in three species ingested by either rodents or birds), and (c) unaffected (in the other four species ingested by foxes, turtles or birds). Within the genus *Ficus*, the effect of seed passage through various vertebrates (primates, bats and birds) has been examined in nine species, the results being a consistent germination enhancement in five of them, and variable in four (*F. carica*, *F. glabrata*, *F. insipida* and *F. microcarpa*). Of the *Vaccinium* species studied, seeds were unaffected by frugivore ingestion (by bears, turtles or birds) in three species, but germination was inhibited in two (ingested by either rodents or birds) and enhanced in one (ingested by martens). In the case of *Solanum*, seeds of

two of six species are enhanced by mammals, three are not affected by either birds or a mammal, and the sixth (*S. nigrum*) is either enhanced or not affected, depending on the species of bird used in the test. Finally, while two species of *Vitis* are not affected by ingestion by a species of turtle, the germination of another species is enhanced after passing through the same reptile, and a fourth (*V. riparia*) is either enhanced or inhibited depending on the bird consuming it.

Even the same plant species can respond differently to the same frugivore, depending on factors such as environmental conditions, plant population and/or seed age. Seeds of *Solanum luteum*, for instance, were differently influenced by avian ingestion in summer and in winter, suggesting that seeds with different qualities of seed coats are produced by the same plant throughout the year (Barnea *et al.* 1990); the seed coat might be thicker in summer than in winter in order to withstand desiccation. Similar findings have been reported by Howe (1986) and by Agami & Waisel (1988). Lombardi & Motta (1995) show different results for *Rhipsalis baccifera* seeds ingested by birds according to the plant population which produced the seeds. Salomonson (1978) found that six-month-old seeds of *Juniperus monosperma* were unaffected by avian ingestion but the germination of one-year-old seeds was inhibited by the same bird species. These variable seed responses may partly be the contradictory results found by different authors working on the same plant and testing it with the same species of frugivore. Examples of such inconsistencies include: (1) germination of *Rubia angustifolia* was found to be either accelerated (Barnea *et al.* 1991) or delayed (Izhaki & Safriel 1990) after seeds were fed to blackbirds; (2) the seeds of *Solanum nigrum* were unaffected by blackbirds (Barnea *et al.* 1990; Mas & Traveset, unpubl. data), although Clergeau (1992) reports that their germination is enhanced by this species; and (3) the percentage of germination of *Aralia nudicaulis* seeds was either not affected (Krefting & Roe 1949) or enhanced (Rogers & Applegate 1983) by black bears. There are other factors, however, which might also explain the equivocal results. Krefting & Roe (1949) found that, depending on the treatment applied to break seed dormancy, the response to seed ingestion by frugivores can vary significantly. Rogers & Applegate (1983) also

obtained different results in their experiments when they compared seeds placed in the refrigerator with seeds not refrigerated prior to the germination tests. The conditions under which such germination tests are performed may also affect the results. Bustamante *et al.* (1992) found a significant effect of seed passage through foxes on germination in the laboratory but not in the field, where germination varied depending on habitats. Similar results were found by Figueiredo *et al.* (1995) working with *Ficus microcarpa*. Likewise, Figueiredo & Perin (1995) found a significant effect of ingestion by bats on germination under laboratory conditions but not in the field; they attributed this to factors such as variation in temperature, chemical characteristics of the soil, and soil-borne pathogens that kill the embryos. Other conditions, such as the amount of illumination per day or the degree of humidity, might also be a source of variation in seed responses.

The same plant species may also be affected differently by the same frugivore if seeds are polymorphic. This has been shown in at least two studies, where the effect of frugivores on seed germination was studied comparing different fruit colour morphs. In one species, *Rhagodia parabolica*, seeds of the white morph show a greater response to passage through silvereyes' (*Zosterops lateralis*) guts than the red or the yellow morph (Willson & O'Dowd 1989). In another species, *Rubus spectabilis*, seeds of the orange morph showed a slight shift in germination patterns compared to the red morph after passing through the digestive tract of birds (Traveset & Willson 1998), and also through an invertebrate seed disperser, the banana slug *Ariolimax columbianus* (Gervais *et al.* 1998). Differences in responses of the two type of seeds to ingestion do not seem to be attributable to differences in seed coats, as both morphs are equally thick and have a similar coat structure. In a variety of species, mainly Compositae, Chenopodiaceae and Gramineae, the germination of seeds from the same parent plant is correlated with their position in the inflorescence. These species usually produce two types of seeds, which differ in size, shape and germinability. In *Bidens pilosa*, for instance, Forsyth & Brown (1982) found that the smaller ray seeds have a higher degree of dormancy than the larger disk seeds produced by the plant.

Does the effect of frugivores on germination vary with seed size and with the type of fruit?

As mentioned above, the size of a seed may determine the time it remains in an animal's digestive tract (Levey & Grajal 1991; Izhaki *et al.* 1995) and, ultimately, the degree to which its coat is mechanically and/or chemically abraded. In order to test the hypothesis that the germination of large seeds is less affected by ingestion than that of small seeds, the species in the compiled data set were sorted into three groups (*small* seeds: those in which the largest dimension (l.d.) was < 5 mm; *medium* seeds: l.d. 5–10 mm; and *large* seeds: l.d. > 10 mm) and examined for differences in germination. Even though sample sizes for the medium and large categories are much lower than for the small one (Table 4), results showed no significant association between seed size and either effect on germination percentage (chi-square test of independence; $\chi^2 = 4.8$, $P > 0.05$) or on the rate of

germination ($\chi^2 = 3.0$, $P > 0.05$). This result is in accordance with the finding that seed retention time in the digestive tract often has no effect on germination; smaller seeds which tend to be longer in the digestive tract are not necessarily more often affected than large ones. Seed size, however, as well as seed retention time in the frugivore guts, are important for some species in determining their germination success.

If the texture of the fruit pulp influences seed retention time, as reported by Levey (1986), we might find some differences in seed responses to ingestion between fleshy and dry fruits. To test this, the data set was divided into fleshy and dry fruits and the effects of frugivores on seed germination examined. Fleshy fruits have been tested much more often than dry ones (by a factor of ten), but no significant differences were found between the two categories (Table 5), either in the frugivore's effect on percentage of germination ($\chi^2 = 3.7$, $P > 0.05$), or on germination rate ($\chi^2 = 1.2$, $P > 0.05$). Although dry fruits have

Table 4. Number and percentage (in brackets) of study cases (not species, as some are tested in several studies) for three seed size categories where germination was enhanced, inhibited or not affected by passage through frugivore's guts. Both components of germination performance (*percentage* and *rate* germination) are given. Only species for which seed size was known (see Appendix) were included.

Seed size	Enhancement		Inhibition		Neutral effect	
	percent	rate	percent	rate	percent	rate
Small (<5 mm)	72 (34)	45 (38)	37 (18)	16 (13)	100 (48)	58 (49)
Medium (5–10 mm)	17 (40)	6 (27)	6 (14)	5 (23)	20 (46)	11 (50)
Large (>10 mm)	14 (45)	8 (44)	1 (3)	1 (6)	16 (52)	9 (50)

Table 5. Number and proportion (in brackets) of study cases for each fruit type category that are enhanced, inhibited or not affected by passage through frugivore's guts. Both components of germination performance (*percentage* of germination and *germination rate*) are given.

Fruit type	Enhancement		Inhibition		Neutral effect	
	percent	rate	percent	rate	percent	rate
Dry fruits	15 (52)	5 (31)	4 (14)	4 (25)	10 (34)	7 (44)
Fleshy fruits	99 (34)	60 (35)	48 (16)	25 (15)	145 (50)	84 (50)

been tested most frequently with non-flying mammals and fleshy fruits with birds, the effect of each of these groups of frugivores on seed germination is found to be similar for both type of fruits.

Influences of region, life form and habitat on the effect of frugivores on seed germination

The effect that ingestion by frugivores has both on the percentage germination and on the speed of germination differs significantly between tropical and temperate zones ($\chi^2 = 7.1$ and $\chi^2 = 6.2$, $P < 0.05$, respectively), germination enhancement being more frequently in the temperate zone (Fig. 1). To determine if such differences can be attributed to the unequal representation of life forms of the species studied (mostly trees in the tropics and mostly shrubs in the temperate zone), I tested the possibility that different plant life forms vary in their seed responses to passage through frugivores. The species in the data set were divided into three categories: herbs, shrubs, and trees. The percentage of germination of ingested seeds appeared to be more frequently increased in tree species than in either herbs or shrubs ($\chi^2 = 22.0$, $P < 0.01$); the effect on germination rate, in contrast, did not differ among life forms ($\chi^2 = 7.3$, $P > 0.05$). The germination of most herbs and shrubs was not significantly affected after passing through an animal's digestive tract, although shrubs were more frequently inhibited than either herbs or trees. Such differences among life forms were consistent in the two regions (Fig. 1): both percentage and speed of germination were enhanced more frequently in trees than in the other life forms in the temperate zones ($\chi^2 = 24.2$ and $\chi^2 = 16.0$, $P < 0.01$, respectively) and in the tropics ($\chi^2 = 10.6$ and $\chi^2 = 19.0$, $P < 0.01$, respectively). Therefore, the greater frequency of germination enhancement after gut passage in the temperate zone compared to the tropics is not due to the different frequency of plant life forms tested in the two zones. The different distribution of seed sizes (see above) between tropical and temperate zones (a greater proportion of large seeds in the tropics) is also not responsible for the difference, as all seed sizes were found to re-

spond similarly to ingestion by frugivores in both regions.

In order to know if the differences between tropics and temperate zones were consistent among life forms, the analyses were performed for each of the three categories. While no differences in the effect on seed germination performance were observed between tropical and temperate herbs ($\chi^2 = 0.74$

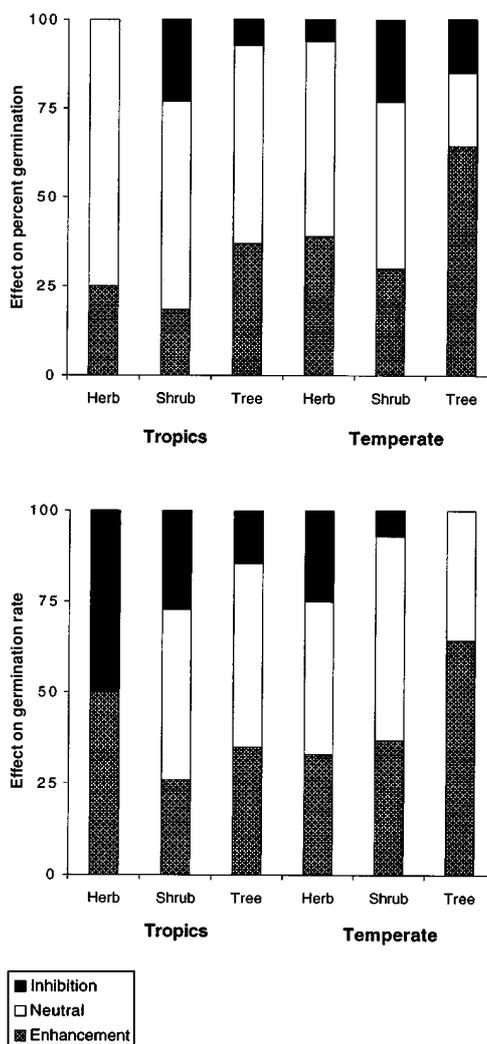


Fig. 1. Proportion of studies for each *life form* and *region* that showed enhancement, inhibition or a neutral effect on (a) percent and (b) rate of germination after seeds have passed through frugivore guts.

and $\chi^2 = 1.3$, $P > 0.05$, for percentage and rate of germination, respectively), shrubs and trees were more frequently affected in the temperate zones. Seed germination of temperate shrubs was accelerated much more often than that of tropical shrubs ($\chi^2 = 9.8$, $P < 0.01$), although the majority of shrubs in both regions were unaffected by passage through

frugivores, and the final percentage of germination is also similar ($\chi^2 = 3.1$, $P > 0.05$). Temperate trees, on the other hand, showed a more frequent enhancement in both components of seed germination performance ($\chi^2 = 17.1$ and $\chi^2 = 7.1$, $P < 0.01$, respectively) than tropical trees; moreover, while in the tropics most tree seeds are unaffected in either their germination potential or rate, in the temperate zones the opposite occurs (Fig. 1).

These results, therefore, support two of the hypotheses presented in the Introduction: (1) that an effect of seed passage through the dispersers' guts might be more adaptive in less constant environments, such as those usually found in temperate regions, and (2) that trees are more likely to be affected than other life forms (perhaps due to a larger frequency of species with seed-coat dormancy). The effect of seed ingestion by frugivores on germination appears also to be influenced by the habitat where the plant species is most common (Fig. 2). A germination enhancement of seeds passed through vertebrate frugivores occurs more commonly in grasslands than in the other two habitats ($\chi^2 = 10.0$ and $\chi^2 = 11.6$, $P < 0.05$, for percentage and rate of germination, respectively; Fig. 2). In both shrublands and woodlands, most of the species show a neutral effect of seed ingestion, although a much larger fraction of species of shrublands are inhibited compared to species of woodlands. In analyses for each region separately, significant differences are only found when the percentage of seed germination is compared and only in the temperate zone ($\chi^2 = 11.1$, $P < 0.05$; Fig. 2). The possibility exists, however, that the "grassland" results are biased due to the much smaller sample size of species tested compared to those of the other two habitats. The reason for the greater proportion of shrubland species that show an inhibition effect in their germination when ingested compared to woodland species, especially in the temperate zone, is unknown.

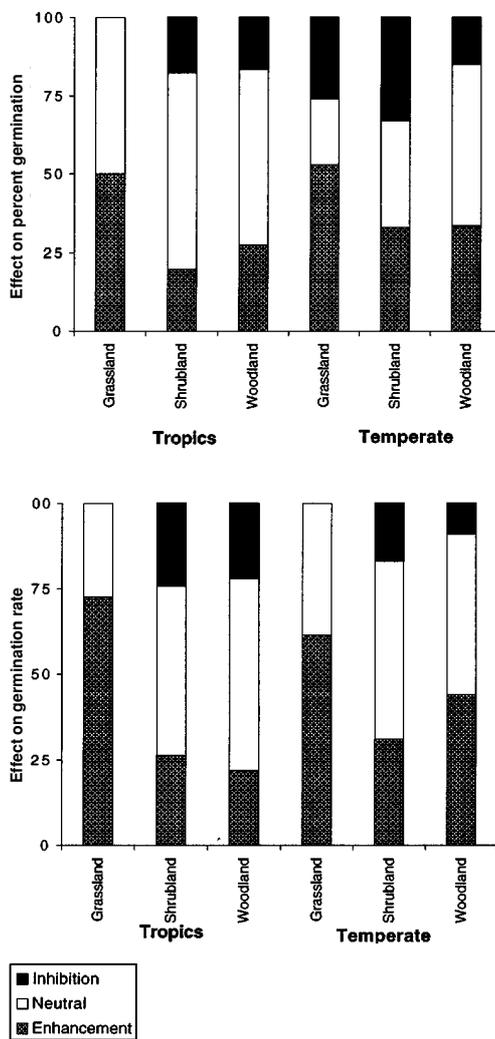


Fig. 2. Proportion of studies for each type of *habitat* and *region* that showed enhancement, inhibition or a neutral effect on (a) percent and (b) rate of germination after seeds have passed through frugivore guts.

Other ways in which frugivores influence establishment success

Besides having the potential to affect percentage and rate of germination of the seeds they ingest, vertebrate frugivores can determine germination success and seedling es-

establishment in various other ways. These include: (1) the site and microsite where they regurgitate or defaecate seeds; (2) the time when seed ingestion and dispersal takes place, (3) how clean of pulp (or aril) they leave the seeds; (4) the amount of seeds defaecated in a dropping, (5) the diversity of seed species found in a defaecation; (6) the frugivore's selection for particular fruit traits within a species (fruit size – which may be correlated with seed size in certain species and, thus, with germination – level of seed infestation by insects); and (7) the plant nutrient content of the frugivore's faeces, which may be important, especially for seedling establishment and growth.

(1) The environmental conditions of the microhabitat where seeds are "released" may be crucial for successful establishment. Numerous studies have shown the effects of distance from the parent plant, the type of habitat where the seeds are deposited, the probability of seed predation by animals, or seedling survival to herbivores or pathogens. Likewise, many studies have demonstrated the effects of competition for nutrients in sites where seedlings are found in great densities. Hence, a frugivore may enhance the germination of seeds by passing them through its digestive tract but this enhancement may be insignificant if the animal is inefficient as a seed disperser and regurgitates or defaecates most seeds at high densities under the parent plant, or in places (e.g. within caves, in intertidal zones, on rocky outcrops) where the necessary conditions (light, temperature, humidity, nutrient availability) for germination and/or growth of that plant are not found (e.g. Bustamante *et al.* 1992). By defaecating seeds free of pulp, frugivores may enhance germination, but simultaneously may increase seed predation by rodents, as found by Bustamante *et al.* (1993). Chemical traits of the soil where seeds are deposited are also known to affect seed germination, modifying osmotic pressure (e.g. Evenari 1949; Mayer & Poljakoff-Mayber 1975; Debussche 1985) and even affecting metabolic processes secondarily related to flower and fruit pigments (Chenery 1948; Horowitz 1976). In a recent study on *Rubus spectabilis*, some unknown (physical or chemical) soil traits were shown to affect the germination behaviour of the two seed morphs of this species (Traveset & Willson 1998). Moreover, soil-borne pathogens can kill the em-

bryo (e.g. Titus *et al.* 1990). More information is needed to find out which soil components and pathogens affect seed germination in general. In future studies on the effect on germination of seed passage through vertebrates, it is important to realize that the results of the experiments may vary significantly, depending on the type of soil in which the seeds are planted. Also, as already mentioned, the outcome of tests performed in Petri dishes is not always the same as that of tests performed by planting the seeds in 'more natural' conditions.

(2) The time in the season when a fruit is consumed and dispersed may be crucial for germination and seedling establishment. This may be especially important for plant species with long fruiting periods that can encompass a whole season. A seed that is dispersed early in the season may have a higher or lower probability of establishment than a later dispersed seed depending on the environmental conditions, both physical (water availability, temperature, etc.) and biological (seed predators, pathogens, etc.) prevalent at the moment of dispersal. Seed predation, for instance, can either be smaller (Schupp 1988) or greater (Traveset 1990) for early dispersed seeds than for seeds dispersed late in the season. Earlier seedlings may also out-compete the next emerging ones (Loiselle 1990).

(3) The pulp that remains around the seeds once these leave the digestive tract of the frugivore may still contain germination inhibitors. Seeds that are regurgitated, especially by birds, are usually completely cleaned; in contrast, it is not unusual to find more or less pulp still attached to seeds which have been defaecated, and in some cases, most or even all apparently intact pulp is expelled with the seeds (e.g. in the dung of bears, fruits of blueberries, *Vaccinium*, may survive almost entire and with all seeds inside; pers. obs.). Therefore, if defaecated seeds are still partially or totally surrounded by pulp, and such pulp still contains active germination inhibitors after passing through the vertebrate's guts, the possible enhancing effect of the frugivore on germination may be masked. Even if the defaecated pulp does not contain any germination inhibitor, it can become infested with fungi or bacteria which may prevent germination (Witmer & Cheke 1991; Crossland & Vander Kloet 1996). This should be taken into account when designing the seed germina-

tion experiments in future studies, especially if plant species are investigated whose seeds are not completely depulped during ingestion; in these cases, the suitable controls might be seeds extracted from uningested fruits but with some pulp still attached to them, and not the absolutely clean, usually rinsed, seeds often used.

(4) The number of seeds defaecated in a dropping is also relevant to the future establishment success of a plant. Barnea *et al.* (1992) reported that the number of seeds in a defaecation is inversely correlated with germination success, suggesting that the mechanism might operate at the seed level (e.g. autotoxicity). They found that for multi-seeded fruits, birds reduce the number of seeds per group and that this enhances germination. However, this was only found in Petri dishes and needs to be confirmed in natural conditions. The presence of a large quantity of seeds in a dropping can also influence both post-dispersal seed predation (e.g. Janzen 1982, 1986; Schupp 1988; Traveset 1990; Willson & Whelan 1990; Hulme 1994; Bermejo *et al.* 1998) and intra- and interspecific competition for resources among seedlings (e.g. Loiselle 1990). The importance of seed predation can vary (Hulme 1998) depending on factors such as the habitat in which the droppings have been left (within the forest, in a gap, below plants or far away from them, etc.), the time when seeds have been dropped, the predator species (rodents, insects, birds), seed density, and even the amount of dung; these findings seem to be true for all vertebrate seed disperser species. Seedling competition, in contrast, is presumably much more important in droppings left by big mammals, such as bears, cattle, elephants and primates, than in scats of reptiles, bats or birds. In droppings of big mammals, we can easily find several thousand seeds (especially small seeds such as those of *Vaccinium*) whereas in scats, the number of seeds rarely reaches several hundreds and low densities are usual. Indeed, the laxative chemicals (Murray *et al.* 1994) or secondary metabolites (Cipollini & Levey 1997) present in the pulp of some fruits might serve not only to decrease seed retention time in the guts of dispersers but also to cause frugivores to defaecate more often so that lower numbers of seeds are expelled together, thus decreasing seedling competition.

(5) As pointed out above, animal seed dispersers may affect plant fitness by depositing seeds in different densities, but they can also affect it by defaecating seeds in different species combinations. This was demonstrated by Loiselle (1990), who showed that seed composition in bird droppings determined the survival of certain species. Using different seed combinations in pairwise growth experiments, she found that some plant species were competitively superior to others. At least in the case of frugivorous birds, most species consume a variety of fruits in a short period of time with the result that seed mixtures are commonly observed in bird droppings, both in the tropics and in the temperate zones. The composition of seeds in droppings, however, varies among frugivore groups, for instance between birds that swallow whole fruits and birds that mandibulate them (Loiselle 1990, and references therein). The composition can also vary during the season, being more diverse when birds are more dependent on fruit (White & Stiles 1990). Certain species combinations in droppings are more common than others, as frugivores do not choose fruits randomly, and this has direct consequences for plant establishment. If a plant species is always outcompeted by others in the droppings, we might expect that birds that swallow entire fruits are attracted, as they probably deposit seeds in monocultures (Loiselle 1990). More experimental data on intra- and interspecific seedling competition in droppings of birds as well as of mammals and reptiles are required. The fate of seeds and seedlings in such defaecations may actually be crucial for offspring survival, and for the composition of plant communities (Loiselle 1990, and references therein).

(6) Frugivores are known to select their food on the basis of different traits such as size, shape, colour, accessibility, nutrient composition, presence of insect larvae inside the fruits, etc. Such fruit selection is another factor that can influence seed germination patterns. By choosing large fruits (either within a species or among species), for example, a frugivore may ingest larger seeds, which in turn may be competitively superior to smaller seeds (possibly because the larger seed may be more viable or have higher germination rates, e.g. Banovetz & Scheiner 1994). Similarly, a frugivore's preferences concerning nutritional (e.g. for simple sugars;

Martínez del Río *et al.* 1989) and water content in the pulp could also influence seed passage rates, and ultimately determine whether seeds are abraded or not and thus whether germination is enhanced, inhibited or unaffected. The presence of insect larvae within fruits may either foster or inhibit selection of infested fruits (Traveset *et al.* 1995, and references therein) with consequences for seed germination success. A frugivore that chooses berries containing attacked seeds, even if not all of them are killed, is obviously dispersing some inviable seeds; thus germination success will be lower than with another frugivore that rejects the infested fruits and defaecates a larger proportion of viable seeds. Seeds attacked by insects, even if the larvae have not killed the embryo, presumably are less likely to survive the passage through a vertebrate gut. However, seeds of *Acacia* infested, but not killed, by bruchid beetles actually showed enhanced germination after passing through the gut of a browser where the insect larvae died (Halevy 1974; Lamprey *et al.* 1974; Coe & Coe 1987). More data from other species will allow us to determine how frequently this occurs.

(7) Depending on the other materials ingested with the fruits, the composition of the faeces will change, and so will the potential effect on seedling establishment. Many frugivores consume a mixed diet, which results in a variable composition of their excrement. This is evident in birds, which excrete relatively high amounts of white urates when eating invertebrates, and watery material often colored with fruit pigments when eating fruits. In carnivorous mammals that seasonally consume high volumes of fruits (Herrera 1989; Willson 1993), such variation in composition is even more evident, and a single defaecation may contain bones, feathers, leaves, stems, roots and seeds. Little experimental data exist on the effect of such dung composition on seed germination and seedling growth, though a few studies show that such effect is significant for some species (Archer & Pyke 1991; Jones *et al.* 1991; Quinn *et al.* 1994; Malo & Suárez 1995; Traveset *et al.*, unpubl.) but not for others (Izhaki & Ne'eman 1997). The type of substrate in which seeds germinate has also been shown to influence the effect of seed passage through frugivores' guts on germination. Quinn *et al.* (1994) found that cattle increased both percentage and rate of seed germination, but

that this effect was obscured by the temporal inhibition produced by the substrate in which seeds were planted, consisting of soil and dung. Fresh dung often kills or suppresses vegetation, but once this dung has partially decomposed, it represents a more favorable microhabitat, as it has a greater capacity of humidity and nutrients. Seedlings grow better in such microhabitats, even though germination has been temporally inhibited.

Are differences in seed germination rates adaptive?

In environments with unpredictable climatic conditions, selection is expected to favour those species that show asynchronous germination, as the risk of seedling mortality is spread over a longer time (Harper 1977). Variation in temporal patterns of germination of uningested seeds can often be found among individuals and among populations within a species (e.g. Lieberman *et al.* 1979; Zimmerman & Weis 1984; Miller *et al.* 1994). According to Izhaki & Safriel (1990) and Izhaki *et al.* (1995), when fruits are consumed by a variety of seed dispersers, such variation in germination patterns may become even more pronounced. These authors interpret asynchronous germination as an adaptation of the species they study to eastern Mediterranean habitats where rainfall patterns are rather unpredictable. Such an explanation, however, is not valid for other environments where climatic conditions are more predictable, such as rainforests of temperate zones (Traveset & Willson 1997).

A variety of frugivore species modify the length of seed dormancy, but not necessarily increasing the final germination percentage. That an early germination and establishment may represent an advantage for a particular species has been shown in a number of studies (e.g. Ross & Harper 1972; Halevy 1974; Weaver & Cavers 1979; Cook 1980; Garwood 1983, 1986; Zimmerman & Weis 1984; Waller 1985). A difference in germination time of only a few days may lead to differences in seedling fates (growth rate, probability of death), later seedlings being at a disadvantage (Symonides 1977). According to Cook (1980), differences in mortality risks in *Viola blanda* may even persist for several years. Selection, however, does not always favour

prompt high germination (Janzen 1981) and, in fact, the probability of predation, or pathogen attack, might be greater for early than for late seedlings (Traveset 1990), depending on the time of season, etc. Also, for example, a large number of species (e.g. many shrubs and trees in the Northern Hemisphere; Burrows 1994) have developed mechanisms for delaying seed germination over winter. If passage of these seeds through frugivores breaks this inherent dormancy, seeds will germinate under unfavourable conditions. We would thus expect that selection acts on these species to preclude any enhancement effect on germination rate after seeds are ingested by dispersers. Probably seed passage through a frugivore's guts only breaks seed-coat dormancy (so-called functional dormancy), and not the physiological (internal or embryological) dormancy. If this proves true, differences in germination time between ingested and uningested seeds will only be a matter of days or weeks (this was found in most species studied so far). Whether dispersers benefit the plant by advancing seed germination time, even by a few days, will depend ultimately on each species and on the quality of the conditions for establishment provided by the prevailing environment.

Further research on germination patterns of uningested (fresh) seeds compared with those of seeds ingested by their natural dispersers is required for more species of the same community, to improve our knowledge about establishment success in the field. We also need more information on the type of seed dormancy of the plant species tested, on how often and in what cases frugivores can break inherent seed dormancy, and about the consequences for fate of seeds and seedlings.

Concluding remarks

In addition to moving seeds from the parent plant to sites that can be suitable for recruitment and seedling growth, frugivore seed dispersers have the capacity to modify the germination patterns of many plants by varying the potential germinability of seeds, the rate of germination, or both. They can enhance germination by abrading the seed coats, which become more rapidly permeable to gases and water, or just by removing the

pulp (or other structures that may contain germination inhibitors) in their digestive tracts. Frugivores can also inhibit seed germination by reducing the number of seeds that are able to germinate, probably by excessive abrasion, or by delaying their time of germination (the mechanism for this is unknown). Presumably, this inhibitory effect must occur only rarely if the frugivore is to be an effective disperser of the plant, and if the plant-animal interaction has evolved over a long time. On the other hand, seed passage through frugivores' guts can have no effect on germination; in such cases frugivores only act as disseminators of the seeds.

If the plants and frugivores tested so far are representative of what happens in nature, it can be concluded that overall they significantly influence the germination patterns of nearly half the species they consume, enhancing germination – increasing either the germinability of seeds or the speed of germination – twice as often as they inhibit it. The different groups of frugivores tested, regardless of the morphological and physiological differences in their digestive tracts, have similar effects, although non-flying mammals tend to influence germination patterns of the seeds slightly more often than other groups. The effect of a particular frugivore species is largely unpredictable, varying from one plant to the next and presumably depending on seed traits, intrinsic to the plant species. These traits may determine the extent of seed coat abrasion in the digestive tract. In turn, only about half of the plant species tested, belonging to many different families, show a consistent response to seed passage through the guts of different frugivores. Congeneric plants also show little consistency in their seed responses to ingestion. Even the same plant species can be found to respond differently to the same frugivore, depending on factors such as environmental conditions under which germination takes place, the plant population, the individual plant, the seed morph, seed age, or even time of the season when seeds are produced.

Seed retention time in frugivore guts is a significant factor influencing the degree of abrasion in some species, but is certainly not the only one. Despite the possible advantage that a long retention time may have in terms of seed dispersal, the time seeds remain within the digestive tract of dispersers is not associated for most species with a particular

effect on germination; indeed, factors like the type of food ingested may actually be more important. Seeds of different sizes, which usually have different transit times through frugivores, and seeds of either fleshy or dry fruits show similar responses to gut passage. Seed coat thickness might perhaps be a more important factor determining whether germination patterns will be affected by seed ingestion; presumably seeds with a thick coat might be less abraded than seeds with a thin one, although this also depends on the time spent within the anaerobic conditions of the digestive tract. Species having seed-coat dormancy might also be more affected than those which do not. So far, however, we do not have the necessary information to test such possibilities.

The hypothesis that an effect of seed passage through the dispersers' guts might be more adaptive in unpredictable or less constant environments, such as those in temperate regions, appears to be confirmed. Except for herbaceous species, for which little data exist yet, seed germination of both shrubs and trees in the temperate zones is more frequently enhanced after passage through frugivores than in the tropics. This finding is consistent with the idea that germination enhancement is especially advantageous in habitats like those found in the eastern Mediterranean, where the risk of seed mortality needs to be spread with time, as climatic conditions, mainly rain, are rather unpredictable (Izhaki & Safriel 1990; Barnea *et al.* 1991; Izhaki *et al.* 1995). Likewise, trees are found to be more often affected than shrubs or herbs. This may reflect a generally greater coat thickness in tree seeds, or a higher frequency of seed-coat dormancy in tree species. Future studies may help to elucidate these assumptions.

Whether germination enhancement in a particular species, regardless of life form, habitat or region, translates into an advantage for the plant can only be determined by studying the fate of ingested seeds and compare it with that of uningested ones. That such enhancement increases plant fitness depends on many factors: for example, on the particular plant species and on whether it forms a seed bank, and on the environmental conditions (temperature, rain, nutrient availability, intra- and interspecific competition, herbivory, pathogen attack, etc.) prevalent in the population or in the community at the time of seed emergence.

Finally, the importance of this aspect of plant-frugivore interactions, namely the role of seed dispersers as "modifiers" of germination patterns, can only be assessed when evaluated together with other factors (e.g. site where seeds are deposited, time when they are dispersed, quantity and diversity of seeds in a defaecation, frugivores' selection for particular fruit traits, quality of nutrient conditions where seeds are found) that also can influence germination and establishment success.

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Appendix. List of plant species that have been tested for an effect of seed ingestion by frugivores on germination performance. The first symbol in the "Effect" column represents *percentage of germination* while the second symbol refers to *germination rate* (+, enhancement; -, inhibition; 0, neutral). Except for the studies by Rogers & Applegate (1983) and Clout & Tilley (1992), who use intact fresh fruits as the only controls, and Figueiredo (1997), who uses arillate seeds as controls, all others compare seeds that have been manually depulped with those ingested by frugivores. Eight studies (indicated by the symbol ϕ) use both kind of controls, although only the result of comparing ingested *vs.* depulped seeds is given in the table (see text for the effect of pulp removal). The scientific names in the original articles have been maintained here, even though some of them have changed since publication. For each species, the following variables are also given: fruit type (F; fleshy; D; dry), seed size (S; small; largest dimension < 5 mm; M; medium, l.d. 5–10 mm; L; large, l.d. > 10 mm), life form (H; herb; S; shrub; T; tree), habitat (G; grassland; S; shrubland; W; woodland) and zone (Temp; temperate; Trop; tropics).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
Fish									
NAJADACEAE									
<i>Najas marina</i>	<i>Oreochromis</i> sp.	Cichlidae	+	Agami & Waisel (1988)	D	S	H	A	Temp
<i>Najas marina</i>	<i>Ctenopharyngodon idella</i>	Cyprinidae	+	Agami & Waisel (1988)	D	S	H	A	Temp
RUPPIACEAE									
<i>Ruppia maritima</i>	<i>Oreochromis</i> sp.	Cichlidae	+	Agami & Waisel (1988)	D	S	H	A	Temp
<i>Ruppia maritima</i>	<i>Ctenopharyngodon idella</i>	Cyprinidae	+	Agami & Waisel (1988)	D	S	H	A	Temp
Reptiles									
ANACARDIACEAE									
<i>Spondias purpurea</i>	<i>Ctenosaura pectinata</i>	Iguanidae	0	Mandujano <i>et al.</i> (1994)	F	M	T	W	Trop
ARACEAE									
<i>Arisaema triphyllum</i>	<i>Terrapene carolina</i>	Testudinidae	+	Braun & Brooks (1987)	F	M	H	W	Temp
<i>Dieffenbachia longispatha</i>	<i>Rhinoclemmys funerea</i>	Emydidae	0	Moll & Jansen (1995)	F	S?	H	W	Trop
BERBERIDACEAE									
<i>Podophyllum peltatum</i>	<i>Terrapene carolina</i>	Testudinidae	++	Rust & Roth (1981), Braun & Brooks (1987)	F	M	H	W	Temp
CACTACEAE									
<i>Melocactus violaceus</i>	<i>Tropidurus torquatus</i>	Tropiduridae	++	Côrtes Figueira <i>et al.</i> (1994)	F	L	S	S	Trop
<i>Opuntia dilleanii</i>	<i>Gallotia galloti</i>	Lacertidae	00	Valido & Nogales (1994)	F	S	S	S	Temp
CAPRIFOLIACEAE									
<i>Sambucus canadensis</i>	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	S	S	W	Temp

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
ROSACEAE									
<i>Duchesnea indica</i>	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	S	H	W	Temp
<i>Fragaria virginiana</i>	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	S	H	W	Temp
<i>Prunus serotina</i>	<i>Terrapene carolina</i>	Testudinidae	+	Braun & Brooks (1987)	F	M	T	W	Temp
<i>Rubus phoenicolasius</i>	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	S	S	W	Temp
<i>Rubus</i> sp.	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	S	S	W	Temp
RUBIACEAE									
<i>Faramea suerrensii</i>	<i>Rhinoclemmys annulata</i>	Emydidae	0	Moll & Jansen (1995)	F	M?	T	W	Trop
<i>Nertera granadensis</i>	<i>Liolaemus pictus</i>	Tropiduridae	++	Wilson <i>et al.</i> (1996)	F	S	H	W	Temp
<i>Plocama pendula</i>	<i>Gallotia galloti</i>	Lacertidae	00	Valido & Nogates (unpubl.)	F	S	S	S	Temp
<i>Relbunium hypocarpium</i>	<i>Liolaemus pictus</i>	Tropiduridae	00	Wilson <i>et al.</i> (1996)	F	S	H	W	Temp
<i>Rubia fruticosa</i>	<i>Gallotia galloti</i>	Lacertidae	-0	Valido & Nogates (1994)	F	S	S	S	Temp
SANTALACEAE									
<i>Kunkelella retamoides</i>	<i>Gallotia galloti</i>	Lacertidae	++	Valido & Nogates (unpubl.)	F	S	S	S	Temp
SOLANACEAE									
<i>Lycium intricatum</i>	<i>Gallotia atlantica</i>	Lacertidae	--	Nogales <i>et al.</i> (1998)	F	S	S	S	Temp
<i>Lycium intricatum</i>	<i>Gallotia galloti</i>	Lacertidae	00	Valido & Nogates (1994)	F	S	S	S	Temp
<i>Lycopersicon esculentum</i>	<i>Testudo elephantopus</i>	Testudinidae	++	Rick & Bowman (1961)	F	S	H	S	Trop
<i>Solanum ochraceo-ferrugineum</i>	<i>Rhinoclemmys annulata</i>	Emydidae	0	Moll & Jansen (1995)	F	S	S	W	Trop
<i>Solanum siparunoides</i>	<i>Rhinoclemmys annulata</i>	Emydidae	0	Moll & Jansen (1995)	F	S	S	W	Trop
<i>Withania aristata</i>	<i>Gallotia galloti</i>	Lacertidae	++	Valido & Nogates (1994)	F	S	S	S	Temp
VITACEAE									
<i>Vitis aestivalis</i>	<i>Terrapene carolina</i>	Testudinidae	+	Braun & Brooks (1987)	F	M	S	W	Temp
<i>Vitis rotundifolia</i>	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	M	S	W	Temp
<i>Vitis vulpina</i>	<i>Terrapene carolina</i>	Testudinidae	0	Braun & Brooks (1987)	F	M	S	W	Temp
Birds									
ANACARDIACEAE									
<i>ϕ Pistacia palaestina</i>	<i>Phoenicurus phoenicurus</i>	Muscicapidae	++	Izhaki & Safrieli (1990)	F	S	T	W	Temp
<i>ϕ Pistacia palaestina</i>	<i>Turdus merula</i>	Muscicapidae	++	Izhaki & Safrieli (1990)	F	S	T	W	Temp
<i>ϕ Pistacia palaestina</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	++	Izhaki & Safrieli (1990)	F	S	T	W	Temp

<i>φ Pistacia palaestina</i>	<i>Sylvia atricapilla</i>	Sylviidae	++	Izhaki & Safriel (1990)	F	S	T	W	Temp
<i>φ Pistacia palaestina</i>	<i>Sylvia curruca</i>	Sylviidae	++	Izhaki & Safriel (1990)	F	S	T	W	Temp
<i>φ Pistacia palaestina</i>	<i>Sylvia hortensis</i>	Sylviidae	++	Izhaki & Safriel (1990)	F	S	T	W	Temp
<i>Rhus glabra</i>	<i>Colinus virginianus</i>	Phasianidae	+	Krefting & Roe (1949)	F	S	T	W	Temp
<i>Toxicodendron vernix</i>	<i>Colinus virginianus</i>	Phasianidae	+	Krefting & Roe (1949)	F	S	T	W	Temp
<i>Toxicodendron vernix</i>	<i>Phasianus colchicus</i> <i>ssp. torquatus</i>	Phasianidae	+	Krefting & Roe (1949)	F	S	T	W	Temp
APOCYNACEAE									
<i>Carissa edulis</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	00	Lieberman & Lieberman (1986)	F	S?	ST	SW	Trop
<i>Carissa edulis</i>	<i>Lamprotornis</i> sp.	Sturnidae	--	Lieberman & Lieberman (1986)	F	S?	ST	SW	Trop
<i>φ Stermadienia donnell-smithii</i>	<i>Vireo flavoviridis</i>	Vireonidae	0 -	McDiarmid <i>et al.</i> (1977)	D	M	T	W	Trop
ARACEAE									
<i>φ Arum hygrophilum</i>	<i>Turdus merula</i>	Muscicapidae	0 -	Barnea <i>et al.</i> (1991)	F	S	H	W	Temp
ARALIACEAE									
<i>φ Hedera helix</i>	Unidentified passerines	Muscicapidae,	00	Debussche (1985)	F	M	S	S	Temp
<i>φ Hedera helix</i>	<i>T. merula</i> , <i>Sturnus vulgaris</i>	Sturnidae	00	Clergeau (1992)	F	M	S	W	Temp
<i>Oplonax horridus</i>	<i>Ixoreus naevius</i>	Muscicapidae	00	Traveset & Willson (1997)	F	M	S	W	Temp
<i>Oplonax horridus</i>	<i>Turdus migratorius</i>	Muscicapidae	00	Traveset & Willson (1997)	F	M	S	W	Temp
BORAGINACEAE									
<i>Ehretia cymosa</i>	<i>Poicephalus senegalus</i>	Psittacidae	00	Lieberman & Lieberman (1986)	F	S	ST	S	Trop
<i>Ehretia cymosa</i>	<i>Lamprotornis</i> sp.	Sturnidae	00	Lieberman & Lieberman (1986)	F	S	ST	S	Trop
CACTACEAE									
<i>Rhipsalis baccifera</i>	<i>Turdus leucomelas</i>	Muscicapidae	+, -	Lombardi & Motta (1995) different results in two populations	F	S	S	W?	Trop
<i>Rhipsalis puniceo-discus</i>	<i>Turdus leucomelas</i>	Muscicapidae	+	Lombardi & Motta (1995)	F	S	S	W?	Trop
CAPPARACEAE									
<i>Capparis erythrocarpos</i>	<i>Poicephalus senegalus</i>	Psittacidae	00	Lieberman & Lieberman (1986)	F	S?	S	SW	Trop
<i>Capparis erythrocarpos</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	0+	Lieberman & Lieberman (1986)	F	S?	S	SW	Trop
<i>Capparis erythrocarpos</i>	<i>Lamprotornis</i> sp.	Sturnidae	0+	Lieberman & Lieberman (1986)	F	S?	S	SW	Trop
CAPRIFOLIACEAE									
<i>Lonicera tatarica</i>	<i>Dumetella carolinensis</i>	Mimidae	0	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Lonicera tatarica</i>	<i>Turdus migratorius</i>	Muscicapidae	+	Krefting & Roe (1949), inconsistent among pre-seed treatments	F	S	S	W	Temp

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
<i>Sambucus canadensis</i>	<i>Dumetella carolinensis</i>	Mimidae	+	Krefting & Roe (1949)	F	S	ST	W	Temp
<i>Sambucus canadensis</i>	<i>Turdus migratorius</i>	Muscicapidae	+	Krefting & Roe (1949)	F	S	ST	W	Temp
<i>Sambucus canadensis</i>	<i>Phasianus colchicus</i> <i>ssp. torquatus</i>	Phasianidae	-	Krefting & Roe (1949)	F	S	ST	W	Temp
φ <i>Sambucus nigra</i>	<i>T. merula</i> , <i>Sturnus vulgaris</i>	Muscicapidae, Sturnidae	- +	Clergeau (1992)	F	S	S	W	Temp
<i>Sambucus racemosa</i>	<i>Ixoreus naevius</i>	Muscicapidae	0+	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Sambucus racemosa</i>	<i>Turdus migratorius</i>	Muscicapidae	0+	Traveset & Willson (1997)	F	S	S	W	Temp
CENOPODIACEAE									
<i>Rhagodia parabolica</i>	<i>Zosterops lateralis</i>	Zosteropidae	++	Willson & O'Dowd (1989)	F	S	S	W	Temp
CONNARACEAE									
<i>Byrsocarpus coccineus</i>	<i>Poicephalus senegalus</i>	Psittacidae	00	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
<i>Byrsocarpus coccineus</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	00	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
<i>Byrsocarpus coccineus</i>	<i>Lamprolornis</i> sp.	Sturnidae	00	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
CORNACEAE									
<i>Cornus racemosa</i>	Unidentified passerines		+	Smith (1975)	F	S	S	W	Temp
<i>Cornus racemosa</i>	<i>Colinus virginianus</i>	Phasianidae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Cornus racemosa</i>	<i>Phasianus colchicus</i> <i>ssp. torquatus</i>	Phasianidae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Cornus stolonifera</i>	<i>Colinus virginianus</i>	Phasianidae	-	Krefting & Roe (1949), inconsistent among pre-seed treatments	F	S	T	W	Temp
<i>Cornus stolonifera</i>	<i>Phasianus colchicus</i> <i>ssp. torquatus</i>	Phasianidae	-	Krefting & Roe (1949), inconsistent among pre-seed treatments	F	S	T	W	Temp
CUPRESSACEAE									
<i>Juniperus monosperma</i>	<i>Myadestes townsendi</i>	Muscicapidae	00	Salomonson (1978), inconsistent results among seed ages	F	S	ST	W	Temp
<i>Juniperus virginiana</i>	<i>Bombycilla cedrorum</i> , <i>Dendroica coronata</i>	Bombycillidae, Emberizidae	+	Holthuijzen & Sharik (1985)	F	S	T	G	Temp
<i>Juniperus virginiana</i>	<i>Cyanocitta cristata</i>	Corvidae	-	Livingston (1972)	F	S	T	G	Temp
<i>Juniperus virginiana</i>	<i>Lophortyx californica</i>	Phasianidae	-	Livingston (1972)	F	S	T	G	Temp
<i>Juniperus virginiana</i>	<i>Sturnus vulgaris</i>	Sturnidae	-	Livingston (1972)	F	S	T	G	Temp

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
<i>Miconia affinis</i>	<i>Pipra mentalis</i>	Tyrannidae	- +	Elison <i>et al.</i> (1993)	F	S	T	W	Trop
<i>Miconia simplex</i>	<i>Pipra mentalis</i>	Tyrannidae	+ -	Elison <i>et al.</i> (1993)	F	S	T	W	Trop
<i>Ossaea macrophylla</i>	<i>Pipra mentalis</i>	Tyrannidae	+ -	Elison <i>et al.</i> (1993)	F	S	T	W	Trop
MELIACEAE									
<i>Azadirachta indica</i>	<i>Poicephalus senegalus</i>	Psittacidae	0+	Lieberman & Lieberman (1986)	F	L	T	SG	Trop
<i>Azadirachta indica</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	++	Lieberman & Lieberman (1986)	F	L	T	SG	Trop
<i>Azadirachta indica</i>	<i>Lamprolornis</i> sp.	Sturnidae	0+	Lieberman & Lieberman (1986)	F	L	T	SG	Trop
MORACEAE									
<i>Ficus bengalensis</i>	<i>Acridotheres tristis</i> , <i>A. fuscus</i>	Sturnidae	++	Midya & Brahmachary (1991)	F	S	T	W	Trop
<i>Ficus carica</i>	<i>Sylvia borin</i>	Sylviidae	0	Lisci & Pacini (1994)	F	S	T	C	Temp
<i>Ficus luschnathiana</i>	<i>Turdus leucomelas</i>	Muscicapidae	+	Figueiredo & Perin (1995)	F	S	T	W	Trop
<i>Ficus microcarpa</i>	Unidentified species	Muscicapidae	0	Figueiredo <i>et al.</i> (1995)	F	S	T	C	Trop
<i>Ficus microcarpa</i>	<i>Turdus rufigenis</i>	Muscicapidae	++	Guerrero & Figueiredo (1997)	F	S	T	C	Trop
<i>Morus alba</i>	<i>Turdus migratorius</i>	Muscicapidae	+	Kreffing & Roe (1949)	F	S	T	C	Temp
<i>Morus nigra</i>	<i>Turdus merula</i>	Muscicapidae	++	Barnea <i>et al.</i> (1991, 1992)	F	S	T	C	Temp
<i>Morus nigra</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	++	Barnea <i>et al.</i> (1991, 1992)	F	S	T	C	Temp
MYRTACEAE									
<i>Myrtus communis</i>	<i>Turdus merula</i>	Muscicapidae	0+	Barnea <i>et al.</i> (1991)	F	S	S	W	Temp
<i>Myrtus communis</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	0+	Barnea <i>et al.</i> (1991)	F	S	S	W	Temp
NAJADACEAE									
<i>Najas marina</i>	<i>Anas platyrhynchos</i>	Anatidae	++	Agami & Waisel (1986)	D	S	H	A	Temp
PODOCARPACEAE									
<i>Prumnopitys ferruginea</i>	<i>Hemiphaga novaeseelandiae</i>	Columbidae	00	Clout & Tilley (1992)	F	L	T	W	Temp
RHAMNACEAE									
<i>Rhamnus alaternus</i>	<i>Turdus merula</i>	Muscicapidae	++	Barnea <i>et al.</i> (1991)	F	S	ST	SW	Temp
<i>Rhamnus alaternus</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	++	Barnea <i>et al.</i> (1991)	F	S	ST	SW	Temp
<i>Rhamnus palaestinus</i>	<i>Turdus merula</i>	Muscicapidae	++	Izhaki & Safriel (1990)	F	S	S	S	Temp
<i>Rhamnus palaestinus</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	+ -	Barnea <i>et al.</i> (1991)	F	S	S	S	Temp
<i>Rhamnus palaestinus</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	00	Izhaki & Safriel (1990)	F	S	S	S	Temp
<i>Rhamnus palaestinus</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	+0	Barnea <i>et al.</i> (1991)	F	S	S	S	Temp

<i>Rhamnus palaestinus</i>	<i>Sylvia atricapilla</i>	Sylviidae	00	Izhaki & Safriel (1990)	F	S	S	S	Temp
<i>Rhamnus palaestinus</i>	<i>Sylvia curruca</i>	Sylviidae	00	Izhaki & Safriel (1990)	F	S	S	S	Temp
<i>Rhamnus palaestinus</i>	<i>Sylvia hortensis</i>	Sylviidae	00	Izhaki & Safriel (1990)	F	S	S	S	Temp
ROSACEAE									
<i>Prunus serotina</i>	Unidentified passerines		+	Smith (1975)	F	M	T	W	Temp
<i>Prunus serotina</i>	<i>Turdus migratorius</i>	Muscicapidae	+	Krefling & Roe (1949)	F	M	T	W	Temp
<i>Prunus virginiana</i>	<i>Phasianus colchicus</i>	Phasianidae	-	Krefling & Roe (1949)	F	M	T	W	Temp
	ssp. <i>torquatus</i>								
<i>Pyracantha coccinea</i>	Unidentified passerines		0+	Debussche (1985)	F	S	S	S	Temp
<i>Rosa blanda</i>	<i>Colinus virginianus</i>	Phasianidae	-	Krefling & Roe (1949), inconsistent among pre-seed treatments	F	S	S	SW	Temp
	<i>Phasianus colchicus</i>	Phasianidae	-	Krefling & Roe (1949), inconsistent among pre-seed treatments	F	S	S	SW	Temp
	ssp. <i>torquatus</i>								
<i>Rosa</i> sp.	<i>Pediocetes phasianellus</i>	Phasianidae	-	Krefling & Roe (1949)	F	S	S	SW	Temp
<i>Rosa</i> sp.	<i>Phasianus colchicus</i>	Phasianidae	+	Krefling & Roe (1949)	F	S	S	SW	Temp
	ssp. <i>torquatus</i>								
φ <i>Rubus fruticosus</i>	<i>Turdus merula</i>	Muscicapidae,	00	Clergeau (1992)	F	S	S	G	Temp
	<i>Sturnus vulgaris</i>	Sturnidae							
<i>Rubus occidentalis</i>	<i>Bombycilla cedrorum</i>	Bombycillidae	-	Krefling & Roe (1949), inconsistent among pre-seed treatments	F	S	S	SW	Temp
<i>Rubus procerus</i>	<i>Dromaius novaehollandiae</i>	Casuaridae	0	Brunner <i>et al.</i> (1976)	F	S	S	SW	Temp
<i>Rubus sanctus</i>	<i>Turdus merula</i>	Muscicapidae	- 0	Barnea <i>et al.</i> (1991)	F	S	S	S	Temp
<i>Rubus sanctus</i>	<i>Pycnonotus xanthopygos</i>	Pycnonotidae	- 0	Barnea <i>et al.</i> (1991)	F	S	S	S	Temp
<i>Rubus</i> sp.	<i>Bombycilla cedrorum</i>	Bombycillidae	0	Krefling & Roe (1949)	F	S	S	SW	Temp
<i>Rubus</i> sp.	<i>Dumetella carolinensis</i>	Mimidae	+	Krefling & Roe (1949)	F	S	S	SW	Temp
<i>Rubus</i> sp.	<i>Turdus migratorius</i>	Muscicapidae	0+	Krefling & Roe (1949)	F	S	S	SW	Temp
<i>Rubus spectabilis</i>	<i>Ixoreus naevius</i>	Muscicapidae	0+	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Rubus spectabilis</i>	<i>Turdus migratorius</i>	Muscicapidae	0+	Traveset & Willson (1997)	F	S	S	W	Temp
RUBIACEAE									
<i>Plocama pendula</i>	<i>Sylvia melanocephala</i> ,	Sylviidae	0+	Valido & Nogales (unpubl.)	F	S	S	S	Temp
	S. <i>conspicillata</i>								
<i>Rubia tenuifolia</i>	<i>Turdus merula</i>	Muscicapidae	0 -	Izhaki & Safriel (1990)	F	S	H	W	Temp
φ <i>Rubia tenuifolia</i>	<i>Turdus merula</i>	Muscicapidae	0+	Barnea <i>et al.</i> (1991)	F	S	H	W	Temp
<i>Rubia tenuifolia</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	0 -	Izhaki & Safriel (1990)	F	S	H	W	Temp
φ <i>Rubia tenuifolia</i>	<i>Pycnonotus xanthopygos</i>	Pycnonotidae	0+	Barnea <i>et al.</i> (1991)	F	S	H	W	Temp
<i>Rubia tenuifolia</i>	<i>Sylvia atricapilla</i>	Sylviidae	0 -	Izhaki & Safriel (1990)	F	S	H	W	Temp
<i>Rubia tenuifolia</i>	<i>Sylvia curruca</i>	Sylviidae	0 -	Izhaki & Safriel (1990)	F	S	H	W	Temp
<i>Rubia tenuifolia</i>	<i>Sylvia hortensis</i>	Sylviidae	0 -	Izhaki & Safriel (1990)	F	S	H	W	Temp

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
RUTACEAE									
<i>Clausena anisata</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	0 –	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
<i>Clausena anisata</i>	<i>Lamprolornis</i> sp.	Sturnidae	--	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
SANTALACEAE									
<i>Osyris alba</i>	<i>Turdus merula</i>	Muscicapidae	++	Izhaki & Safriel (1990)	F	M	S	W	Temp
<i>Osyris alba</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	++	Izhaki & Safriel (1990)	F	M	S	W	Temp
SAXIFRAGACEAE									
<i>Ribes bracteosum</i>	<i>Ixoreus naevius</i>	Muscicapidae	00	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Ribes bracteosum</i>	<i>Turdus migratorius</i>	Muscicapidae	00	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Ribes missouriense</i>	<i>Bombycilla cedrorum</i>	Bombycillidae	+	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Ribes missouriense</i>	<i>Dumetella carolinensis</i>	Mimidae	+	Krefting & Roe (1949)	F	S	S	W	Temp
SMILACACEAE									
ϕ <i>Smilax aspera</i>	<i>Turdus merula</i>	Muscicapidae	+0	Izhaki & Safriel (1990)	F	S	S	SW	Temp
ϕ <i>Smilax aspera</i>	<i>Turdus philomelos</i>	Muscicapidae	00	Izhaki & Safriel (1990)	F	S	S	SW	Temp
ϕ <i>Smilax aspera</i>	<i>Pycnonotus barbatus</i>	Pycnonotidae	00	Izhaki & Safriel (1990)	F	S	S	SW	Temp
SOLANACEAE									
<i>Lycium intricatum</i>	<i>Lanius excubitor</i>	Laniidae	++	Nogales <i>et al.</i> (unpubl.)	F	S	S	S	Temp
<i>Solanum dulcamara</i>	Unidentified passerines		0	Smith (1975)	F	S	H	W	Temp
<i>Solanum luteum</i>	<i>Turdus merula</i>	Muscicapidae	+	Barnea <i>et al.</i> (1990),	F	S	H	C	Temp
<i>Solanum luteum</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	++	Mas & Traveset (unpubl.)	F	S	H	C	Temp
<i>Solanum luteum</i>	<i>Sylvia melanocephala</i>	Sylviidae	+	Barnea <i>et al.</i> (1990)	F	S	H	C	Temp
ϕ <i>Solanum nigrum</i>	<i>Turdus merula</i> ,	Muscicapidae,	++	Mas & Traveset (unpubl.)	F	S	H	C	Temp
<i>Solanum nigrum</i>	<i>Sturnus vulgaris</i>	Sturnidae	++	Clergeau (1992)	F	S	H	C	Temp
<i>Solanum nigrum</i>	<i>Turdus merula</i>	Muscicapidae	0	Barnea <i>et al.</i> (1990),	F	S	H	C	Temp
<i>Solanum nigrum</i>	<i>Pycnonotus xanthopygus</i>	Pycnonotidae	00	Mas & Traveset (unpubl.)	F	S	H	C	Temp
<i>Solanum nigrum</i>	<i>Sylvia melanocephala</i>	Sylviidae	00	Barnea <i>et al.</i> (1990)	F	S	H	C	Temp
<i>Witheringia solanaceae</i>	<i>Myadestes melanops</i>	Muscicapidae	+	Mas & Traveset (unpubl.)	F	S?	S	W	Trop
URTICACEAE									
<i>Urtica caracasana</i>	<i>Arremon aurantirrostris</i>	Emberizidae	0	Levey (1986), only viability tested	F	S	S?	W	Trop

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
MORACEAE									
<i>Chlorophora tinctoria</i>	<i>Carollia perspicillata</i>	Phyllostomidae	0	Fleming (1988)	F	S	T	W	Trop
<i>Ficus carica</i>	<i>Rousetus aegyptiacus</i>	Pteropodidae	00	Izhaki <i>et al.</i> (1995)	F	S	T	C	Temp
<i>Ficus chrysolepis</i>	5–10 species	Pteropodidae	+0	Utzurrum & Heideman (1991)	F	S	T	W	Trop
<i>Ficus luschnathiana</i>	<i>Platyrrhinus lineatus</i>	Phyllostomidae	0	Figueiredo & Perin (1995)	F	S	T	C	Trop
<i>Ficus microcarpa</i>	Unidentified species	Phyllostomidae	+	Figueiredo <i>et al.</i> (1995), in laboratory not field	F	S	T	W	Trop
<i>Morus nigra</i>	<i>Rousetus aegyptiacus</i>	Pteropodidae	00	Izhaki <i>et al.</i> (1995)	F	S	T	C	Temp
PIPERACEAE									
<i>Piper amalago</i>	<i>Carollia perspicillata</i>	Phyllostomidae	0	Fleming (1988)	F	S	ST	W	Trop
RHAMNACEAE									
<i>Zizyphus spina-christi</i>	<i>Rousetus aegyptiacus</i>	Pteropodidae	00	Izhaki <i>et al.</i> (1995)	F	L	T	S	Temp
ROSACEAE									
<i>Eriobotrya japonica</i>	<i>Rousetus aegyptiacus</i>	Pteropodidae	+0	Izhaki <i>et al.</i> (1995)	F	L	T	C	Temp
RUTACEAE									
<i>Clausena anisata</i>	<i>Epomophorus gambianus</i>	Pteropodidae	--	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
SOLANACEAE									
<i>Solanum hazenii</i>	<i>Carollia perspicillata</i>	Phyllostomidae	+	Fleming (1988)	F	S	?	SG?	Trop
VERBENACEAE									
<i>Premna quadrifolia</i>	<i>Epomophorus gambianus</i>	Pteropodidae	00	Lieberman & Lieberman (1986)	F	S	S	SW	Trop
Non-flying mammals									

ANACARDIACEAE									
<i>Pseudospondias microcarpa</i>	<i>Pan troglodytes</i>	Pongidae	0	Takasaki (1983)	F	L	T	W	Trop
<i>Sclerocarya caffra</i>	<i>Loxodonta africana</i>	Elephantidae	+	Lewis (1987)	F	L	T	W	Trop
<i>Spondias purpurea</i>	<i>Odocoileus virginianus</i>	Cervidae	0	Mandujano <i>et al.</i> (1994)	F	L	T	W	Trop
ANNONACEAE									
<i>Rollinia jimenezii</i>	<i>Alouatta palliata</i>	Cebidae	0	Estrada & Coates-Estrada (1986)	F	?	T	W	Trop

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
EBENACEAE									
<i>Diospyros consolatae</i>	<i>Otolemur garnetti</i>	Galagonidae	+	Engel (1997)	F	M	T	W	Trop
<i>Diospyros mespiliformis</i>	<i>Papio anubis</i>	Cercopithecidae	0+	Lieberman <i>et al.</i> (1979)	F	L	T	SW	Trop
<i>Diospyros</i> sp.	<i>Loxodonta africana</i>	Elephantidae	+	Lieberman <i>et al.</i> (1987)	F	L	T	W	Trop
ERICACEAE									
<i>Vaccinium ovalifolium</i>	<i>Martes americana</i>	Mustelidae	0	Hickey <i>et al.</i> (in press)	F	S	S	W	Temp
<i>Vaccinium alaskaense</i>	<i>Martes americana</i>	Mustelidae	+	Hickey <i>et al.</i> (in press), only in old growth	F	S	S	W	Temp
<i>Vaccinium alaskaense</i> , <i>V. ovalifolium</i>	<i>Ursus americanus</i>	Ursidae	00	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Vaccinium alaskaense</i> , <i>V. ovalifolium</i>	<i>Ursus arctos</i>	Ursidae	00	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Vaccinium</i> sp.	<i>Peromyscus maniculatus</i>	Muridae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Vaccinium</i> sp.	<i>Eutamias minimus</i>	Sciuridae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Vaccinium</i> sp.	<i>Tamias striatus</i>	Sciuridae	-	Krefting & Roe (1949)	F	S	S	W	Temp
ϕ <i>Vaccinium</i> spp.	<i>Ursus americanus</i>	Ursidae	0	Rogers & Applegate (1983)	F	S	S	W	Temp
EUPHORBIACEAE									
<i>Drypetes variabilis</i>	<i>Alouatta seniculus</i>	Cebidae	00	Julliot (1996)	F	?	?	W	Trop
<i>Securinega virosa</i>	<i>Erythrocebus patas</i>	Cercopithecidae	++	Lieberman & Lieberman (1986)	F	S	S	SG	Trop
<i>Securinega virosa</i>	<i>Papio anubis</i>	Cercopithecidae	++	Lieberman <i>et al.</i> (1979)	F	S	S	SG	Trop
<i>Trewia nudiflora</i>	<i>Rhinoceros unicornis</i>	Rhinocerotidae	00	Dinerstein & Wemmer (1988)	F	M	T	W	Trop
FLACOURTIACEAE									
<i>Flacourtia flavescens</i>	<i>Erythrocebus patas</i>	Cercopithecidae	--	Lieberman & Lieberman (1986)	F	M	S	SW	Trop
LURACEAE									
ϕ <i>Cryptocarya alba</i>	<i>Dusicyon culpaeus</i>	Canidae	++	Bustamante <i>et al.</i> (1992, 1993)	F	L	T	W	Temp
LEGUMINOSAE									
<i>Acacia caven</i>	<i>Bos taurus</i>	Bovidae,	+	Gutiérrez & Armesto (1981)	D	M	ST	G	Temp
	<i>Equus caballus</i>	Equidae							
<i>Acacia raddiana</i>	<i>Gazelle dorcas</i>	Bovidae	++	Haley (1974)	D	M	ST	G	Temp
<i>Enterolobium cyclocarpum</i>	<i>Equus caballus</i>	Equidae	0	Janzen (1981)	D	L	T	G	Trop
<i>Enterolobium cyclocarpum</i>	<i>Homo sapiens</i>	Hominidae	0	Hunter (1989)	D	L	T	G	Trop
<i>Fetima raetam</i>	<i>Lepus</i> spp.	Leporidae	00	Izhaki & Ne'eman (1997)	D	M	S	G	Temp

Appendix. (continued).

Plant species (FAMILY)	Disperser species	Disperser family	Effect	Reference	Fruit type	Seed size	Life form	Habitat	Zone
<i>Prunus pennsylvanicus</i>	<i>Ursus americanus</i>	Ursidae	0	Rogers & Applegate (1983)	F	M	T	W	Temp
<i>Prunus virginiana</i>	<i>Ursus americanus</i>	Ursidae	+	Rogers & Applegate (1983)	F	M	T	W	Temp
<i>Rubus idaeus</i>	<i>Peromyscus maniculatus</i>	Muridae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Rubus idaeus</i>	<i>Eutamias minimus</i>	Sciuridae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Rubus idaeus</i>	<i>Tamias striatus</i>	Sciuridae	-	Krefting & Roe (1949)	F	S	S	W	Temp
<i>Rubus procerus</i>	<i>Vulpes vulpes</i>	Canidae	0	Brunner <i>et al.</i> (1976)	F	S	S	SW	Temp
<i>Rubus spectabilis</i>	<i>Ursus americanus</i>	Ursidae	0+	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Rubus spectabilis</i>	<i>Ursus arctos</i>	Ursidae	0+	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Rubus strigosus</i>	<i>Ursus americanus</i>	Ursidae	+	Rogers & Applegate (1983)	F	S	S	W	Temp
RUBIACEAE									
<i>Nauclea latifolia</i>	<i>Papio anubis</i>	Cercopithecidae	++	Lieberman <i>et al.</i> (1979)	F	S	ST	G	Trop
<i>Plocama pendula</i>	<i>Oryctolagus cuniculus</i>	Leporidae	--	Nogales <i>et al.</i> (1995)	F	S	S	S	Temp
<i>Psychotria cf. carthaginensis</i>	<i>Alouatta seniculus</i>	Cebidae	-0	Julliot (1996)	F	S?	S?	W	Trop
RUTACEAE									
<i>Clausena anisata</i>	<i>Erythrocebus patas</i>	Cercopithecidae	--	Lieberman & Lieberman (1986)	F	M?	S	S	Trop
SAPOTACEAE									
<i>Chrysophyllum lucentifolium</i>	<i>Alouatta seniculus</i>	Cebidae	00	Julliot (1996)	F	L	T	W	Trop
<i>Chrysophyllum prieurii</i>	<i>Alouatta seniculus</i>	Cebidae	-0	Julliot (1996)	F	L	T	W	Trop
SAXIFRAGACEAE									
<i>Ribes bracteosum</i>	<i>Ursus americanus</i>	Ursidae	00	Traveset & Willson (1997)	F	S	S	W	Temp
<i>Ribes bracteosum</i>	<i>Ursus arctos</i>	Ursidae	00	Traveset & Willson (1997)	F	S	S	W	Temp
SOLANACEAE									
<i>Solanum lycocarpum</i>	<i>Chrysocyon brachyurus</i>	Canidae	+	Lombardi & Motta (1993)	F	M	S	S	Trop
<i>Solanum sp.</i>	<i>Alouatta seniculus</i>	Cebidae	00	Julliot (1996)	F	S?	?	W	Trop
UMBELLIFERAE									
<i>Heracleum lanatum</i>	<i>Ursus arctos</i>	Ursidae	+	Applegate <i>et al.</i> (1979)	D	M	H	W	Temp
VERBENACEAE									
<i>Premna quadrifolia</i>	<i>Erythrocebus patas</i>	Cercopithecidae	0+	Lieberman & Lieberman (1986)	F	S	S	SW	Trop