

Seed dispersal syndromes in the rain forest of Chiloé: evidence for the importance of biotic dispersal in a temperate rain forest

J. J. ARMESTO and R. ROZZI *Laboratorio de Sistemática y Ecología Vegetal, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile*

Abstract. The dispersal syndromes of seventy-two species from the temperate rain forest of Chiloé (42°30' S) were analysed and compared with data for other temperate forests in New Zealand and New Jersey (eastern U.S.A.), and for dry, moist and wet neotropical forests. In Chiloé, ornithochory was the predominant dispersal syndrome for species of each growth form (70% of trees, 59% of shrubs, and 72% of vines and epiphytes). Only among the emergent trees anemochory was the most frequent syndrome. The overall distributions of dispersal syndromes were similar in Chiloé and New Zealand. In these forests, ornithochory was found in *c.* 70% and anemochory in 20–25% of the species. Mammalochory was rare in Chiloé and absent in New Zealand. In contrast, mammalochory was more prominent in all neotropical sites (22–34% of the species). In proportion, avian-disseminated propagules were more represented among forest taxa in Chiloé and New Zealand (67–70% of the species) than in the neotropics (35–53%). Deciduous forests of New Jersey, U.S.A., showed similar proportions (~33%) of mammalochory, anemochory and

ornithochory, having a distribution of syndromes that resembles that of dry neotropical forests. The contrasting array of dispersal syndromes in North and South temperate forests might be related to (1) the different ancestral pools for temperate forest taxa in each hemisphere, (2) the different relative isolation (past and present) of the areas compared, and (3) the different abundances of fruit-eating mammal species in each area. In all forests compared, with the exception of Chiloé, shrubs had the highest frequency of fleshy-fruited species. The higher incidence of ornithochory among shrubs seems to be related to the greater bird activity in forest clearings and margins, which would act to reinforce the association of ornithochorous shrubs with such habitats. Mutual dependence between fleshy-fruited plants and fruit-eating animals may be well developed in the temperate forests of Chiloé.

Key words. Chiloé, neotropical forests, temperate forests, seed-dispersal syndromes.

INTRODUCTION

The ecology and evolution of seed dispersal by animals continue to be the focus of many field studies in tropical (Snow, 1965, 1971; Howe & Primack, 1975; Howe & Estabrook, 1977; Janzen, 1983) and, more recently, in temperate forests (Thompson & Willson, 1979; Stiles, 1980; Herrera, 1981, 1984). Results of these investigations are a prime source of material for testing and refining current theories on the evolution of mutual dependence between animals and plants (McKey, 1975; Janzen, 1985; Howe, 1984a; Herrera, 1985a). While most studies of seed dispersal remain primarily descriptive (see Willson, 1986, for a review), they could reveal striking patterns or interactions that may be useful for developing new hypotheses or testing old ones. Ultimately, a general theory of the evolution of mutualistic seed dispersal by vertebrates should explain the patterns observed in both tropical and temperate regions.

In this light, new data on the importance of biotic disper-

sal in different types of communities around the world need to be analysed (Howe & Smallwood, 1982; Willson *et al.*, unpublished MS), and discussed from a broad perspective. Because of the paucity of data on the dispersal of plants in South American temperate forests, we made a survey of dispersal modes of plant species in the rain forests of Chiloé Island (42°30' S, in southern Chile). Our main purpose was to assess the importance of biotic (particularly avian) seed dispersal in this forest, and to make comparisons with available data for other temperate and tropical forests. We will stress the singularities, as well as the similarities to other temperate forests, of the array of dispersal syndromes of the species in the forest of Chiloé.

STUDY AREA

The forests of Chiloé are representative of the broad-leaved evergreen type characteristic of lowland and mid-elevation areas in the temperate region of South America (Veblen &

Schlegel, 1982); thus our results should apply to a broad geographic region. The forests are very humid (over 2000 mm of annual rainfall), with emergent trees reaching up to 40 m, an exuberant canopy very rich in epiphytic ferns (genus *Hymenophyllum*) and woody vines, and a species-poor understorey, where shrubs are conspicuously absent. The study area corresponds to a mosaic of forest communities, between 200 and 600 m elevation, in the Cordillera de Piuchué (42°30' S). In the lowlands (below 200 m) the forest has been intensely cut and burned to open farm and pasture land, but large tracts of undisturbed rain forest occur at mid and high elevations. Throughout the altitudinal range studied, forests are characterized by the importance of tree species in the family Myrtaceae (*Amomyrtus luma*,* *A. meli*, *Myrceugenia planipes*, *M. apiculata*, *M. ovata*), and by *Laurelia philippiana*. Different dominant tree species succeed each other through the altitudinal gradient (Villagrán, 1985; and unpublished data). From low to high elevation dominants are *Eucryphia cordifolia*, *Aextoxicon punctatum* and *Weinmannia trichosperma* (150–350 m), *Amomyrtus luma* and *Laurelia philippiana* (350–500 m), and *Podocarpus nubigena*–*Drimys winteri*–*Nothofagus dombeyi* (above 500 m). Many tree species, such as *Raphithamnus spinosus*, *Myrceugenia apiculata*, *Aristotelia chilensis*, *Embothrium coccineum* and *Drimys winteri*, are more often found in second-growth and early successional forests (Armesto & Figueroa, 1987, and unpublished data). Shrubs (species of *Fuchsia*, *Pernettya*, *Gaultheria*, *Berberis*) are almost exclusively found in forest margins, and also in open fields. The forest understorey is densely populated by woody vines (e.g. *Luzuriaga* spp., *Griselinia* spp.) and tree seedlings, mainly those of the dominant canopy trees (Armesto & Figueroa, 1987).

Further data on the climate, topography and soils of Chiloé are given by Veblen (1985), Holdgate (1961), Donoso *et al.* (1985) and Armesto & Figueroa (1987). The vegetation is described concisely by Villagrán (1985) and by Holdgate (1961).

METHODS

For the comparisons of syndromes of temperate forests, published lists of species present in specific forest stands were preferred, rather than regional floral accounts. Thus, although some rare species may be missing in each locality, we ensured that no species from plant formations other than forests were included in the analysis. For Chiloé we relied on our own lists of forest species (Villagrán, Armesto & Leiva, 1986), based on the sampling of old-growth forests at different elevations in both flanks of the Cordillera de Piuchué. Nomenclatural authorities for all species are given in the Appendix.

Data for eastern North America were taken from lists published by Forman & Elfstrom (1975), derived from the sampling of trees and shrubs in eight old-growth deciduous woodlots in central New Jersey. Vines were not listed by these authors. New Zealand taxa were obtained from a study by Mark & Smith (1975) which lists all species in an old-growth, mixed *Nothofagus*–*Podocarpus* forest.

* All nomenclatural authorities are given in Appendix 1.

For comparative purposes we present the data on dispersal syndromes for several neotropical forests summarized by Gentry (1982). These are averages for four dry-forest, three moist-forest and two wet-forest sites from Venezuela, Costa Rica, Panama, Brazil and Ecuador. The geographical location and the average annual precipitation for each site are given by Gentry (1982).

All the data reported here are for woody taxa; data for herbs were only available for Chiloé.

To classify the species according to dispersal syndromes we checked the descriptions of fruit morphology given in local floras. For Chiloé, we based our assignments of species to syndromes on direct inspection of propagules, field observations of dispersal agents, and the presence of seeds in animal faeces (Armesto *et al.*, 1987). A similar method was used by Gentry (1982) to assign neotropical forest species to dispersal categories equivalent to ours.

RESULTS

Seed-dispersal syndromes in Chiloé

Most species in old-growth and successional forests in Chiloé (see Appendix) have brightly coloured berries or drupes, or seeds surrounded by fleshy arils (as in the case of *Saxe-gothaea conspicua*, *Podocarpus nubigena* and *Maytenus* spp.) which are characteristic of the syndrome of ornithochory (*sensu* van der Pijl, 1982). This syndrome is predominant in all the growth-forms and tree strata, with exception of the emergents (Table 1). Overall, almost 70% of the woody species and epiphytes have propagules that may be dispersed by avian frugivores. We are currently gathering data on stomach contents of birds of Chiloé which tend to confirm that seeds of these species are indeed bird disseminated (Armesto *et al.*, 1987, and unpublished). Only c. 19% of all the species have wind-dispersed propagules (winged, plumed or dust-like diaspores), although this is the most frequent syndrome among emergent trees (Table 1). Mammalochory and other syndromes (including hydrochory and balochory) are much less important among forest taxa.

The highest percentage of ornithochory was found in main canopy and subcanopy trees (86% and 92% of the species, respectively, Table 1); among shrubs and vines ornithochory was lower due to the increase in the number of anemochorous species and other syndromes (Table 1). Among the other syndromes, hydrochory is the most probable dispersal mechanism for one shrub species that has buoyant propagules (*Sophora microphylla*; see Murray, 1986), and for two species with small round seeds inside a dehiscent capsule, which would be carried away by rainfall. One shrub species and one epiphyte (see Appendix) have dust-like seeds (generally less than 1 mm in diameter) which could be dispersed in a number of ways, i.e. blown by wind, carried by water currents, or stuck to animal skins (Villagrán *et al.*, 1986). One case of epizoochory occurs in the epiphyte *Peperomia fernandeziana*, whose sticky propagules can travel on the body of birds (cf. Carlquist, 1974). Only one tree species (*Gevuina avellana*) has a dry nut, typical of the syndrome mammalochory according to van

TABLE 1. Dispersal syndromes of species in the temperate rain forest of Chiloé.

	Ornithochory	Anemochory	Mammalochory	Others*
(a) Trees ($N=27$)	19 (70.4%)	7 (25.9%)	1 (3.7%)	–
Emergents ($N=7$)	1 (14.3)	6 (85.7)	–	–
Main canopy ($N=7$)	6 (85.7)	–	1 (4.3)	–
Subcanopy ($N=13$)	12 (92.3)	1 (7.7)	–	–
(b) Shrubs ($N=27$)	16 (59.2)	4 (14.8)	3 (11.1)	4 (14.8)
(c) Epiphytes and vines ($N=18$)	13 (72.2)	3 (16.3)	–	2 (11.1)
Total ($N=72$)	48 (66.7)	14 (19.4)	4 (5.6)	6 (8.3)

* Other syndromes include hydrochory, balochory and epizoochory.

der Pijl (1982). The other three possible cases of mammalochory correspond to the bamboos (*Chusquea* spp.), all of which have propagules that fall directly underneath the plants. These propagules could be carried away, and dispersed by seed-harvesting rodents, as in the case of other species of bamboo cited by Janzen (1976). There is some evidence that native mammals feed on *Chusquea* seeds (see Armesto *et al.*, 1987). It is possible that rodents may also eat and disperse some of the fleshy fruits (see Murua & Gonzales, 1985) classified here as ornithochorous. The 'real' importance of multiple dispersal agents for a given plant species can only be assessed in field studies. Although the relative importance of different seed vectors for a particular plant species may vary once such field studies are carried out, the overall importance of biotic dispersal in the rain forest of Chiloé will remain unchanged.

There were only nine species of understory herbs in the forests of Chiloé. Among these herbs epizoochory is the most frequent (44%) dispersal syndrome (see Appendix). We have noted that the hairy propagules of *Uncinia* species adhere strongly to the fur of local deer (*Pudu pudu*), and to the feathers of birds. The two ornithochorous species grow very often as epiphytes on standing or fallen tree trunks. Because of their small size, berries of these two species, and those *Gunnera magellanica*, are likely to be eaten also by lizards (*Liolaemus* spp.; H. Núñez, personal communication).

Comparison with neotropical forests

The overall importance of vertebrate (mammal and bird) dispersal in the forest of Chiloé appears to be somewhat lower than in moist or wet neotropical forests, and comparable to dry neotropical forests (Table 2). In comparison to neotropical forests where 26–34% of the tree species have mammal-dispersed propagules (Table 2), mammalochory is clearly underrepresented in the rain forest of Chiloé (Table 1). The overall distribution of dispersal syndromes in Chiloé is significantly different from that of dry, moist or wet neotropical forests ($\chi^2 \geq 11.6$; $P \leq 0.003$), when mammal, wind and bird-dispersed fruits are considered. If only the frequencies of wind and bird-dispersed propagules are used in the comparison, moist and wet neotropical sites are not significantly different from Chiloé ($\chi^2 \leq 2.0$; $P \geq 0.16$).

Proportionally, however, more ornithochorous species

(66.7%) are found in the temperate forest of Chiloé than in any neotropical forest, from dry to wet sites (35–53%). Bird-disseminated propagules are especially important (72%) among vines and epiphytes in Chiloé, whereas in the neotropics species with this growth-form are predominantly wind-dispersed (50–81%, Table 2).

The relative importance of anemochory in Chiloé is lower than that of dry neotropical forests (Table 2), and it is greater than that of moist or wet forests where over 70% of the species have propagules dispersed by vertebrates.

Comparison with other temperate forests

The distribution of seed dispersal syndromes in the rain forest of Chiloé (Table 1) is similar, and does not differ statistically ($\chi^2=1.06$; $P=0.59$, NS) from that of a mixed *Nothofagus–Podocarpus* dominated forest in New Zealand (Table 2). In these two forests, species with ornithochorous fruits correspond approximately to 70%, and anemochory to 20–26% of the total. Despite this overall similarity, New Zealand has a higher incidence of ornithochory among shrubs and trees (Table 2). In New Zealand, anemochory is a characteristic syndrome for vines and epiphytes (Table 2). This group shows a different distribution of syndromes than species of the same growth form in Chiloé, where ornithochory is more frequent (Table 1). This difference may be due in part to the richness of epiphytic orchids (*Earina* spp.) in New Zealand, which are lacking in Chiloé. With regard to mammalochory, this syndrome is absent in New Zealand and very rare in Chiloé. Thus, most of animal-dispersed propagules in both forests are related to avian frugivores.

The distribution of dispersal syndromes in the temperate forests of Chiloé (Table 1) and New Zealand (Table 2) differs significantly ($\chi^2=19.86$; $P \leq 0.001$) from the pattern found in deciduous temperate forests of eastern North America (Table 2), where mammalochory is as important as anemochory and ornithochory. In woodlots of New Jersey, a majority of trees have indehiscent dry nuts dispersed by mammals (58% of the canopy and 16% of the subcanopy species), or wind-dispersed propagules (42% of the canopy and 37% of the subcanopy species). The overall distribution of dispersal syndromes in New Jersey woods is equivalent to that of dry neotropical forests ($\chi^2=0.89$; $P=0.64$), but differs significantly ($\chi^2=9.02$; $P=0.011$) from that of wet neotropical sites (Table 2). Ornithochory

TABLE 2. Dispersal syndromes in some temperate and tropical forests (see text for data sources).

	Ornithochory	Anemochory	Mammalochory	Others*
Neotropical†				
1. Dry forests				
(a) Trees (N=51)	21 (41.2)	15 (29.4)	13 (25.5)	2 (3.9)
(b) Vines (N=12)	1 (8.3)	8 (66.7)	1 (8.3)	2 (16.7)
Total (N=63)	22 (34.9)	23 (36.5)	14 (22.2)	4 (6.3)
2. Moist forests				
(a) Trees (N=79)	41 (51.9)	12 (15.2)	23 (29.1)	3 (3.8)
(b) Vines (N=26)	9 (34.6)	15 (57.7)	1 (3.9)	1 (3.9)
Total (N=105)	50 (47.6)	27 (25.7)	24 (22.9)	4 (3.8)
3. Wet forests				
(a) Trees (N=109)	63 (57.8)	6 (5.5)	37 (33.9)	3 (2.7)
(b) Vines (N=31)	11 (35.5)	15 (48.4)	4 (12.9)	1 (3.2)
Total (N=140)	74 (52.8)	21 (15.0)	41 (29.3)	4 (2.9)
Temperate forests				
1. New Jersey, U.S.A.				
(a) Trees (N=38)	8 (21.1)	15 (39.5)	14 (36.8)	1 (2.6)
Main canopy (N=19)	–	8 (42.1)	11 (57.9)	–
Subcanopy (N=19)	8 (42.1)	7 (36.8)	3 (15.8)	1 (5.3)
(b) Shrubs (N=12)	8 (66.7)	1 (8.3)	1 (8.3)	2 (16.7)
Total (N=50)	16 (32.0)	16 (32.0)	15 (30.0)	3 (6.0)
2. New Zealand				
(a) Trees (N=14)	11 (78.6)	3 (21.4)	–	–
(b) Shrubs (N=15)	15 (100.0)	–	–	–
(c) Epiphytes and vines (N=12)	3 (25.0)	8 (66.7)	–	1 (8.3)
Total (N=41)	29 (70.7)	11 (26.8)	–	1 (2.4)

* Other syndromes include hydrochory, balochory, epizoochory.

† Recalculated from data in Gentry (1982).

appears as the predominant mode of dispersal among shrubs (67% of the species), and subcanopy trees (42% of the species).

DISCUSSION

The frequency of ornithochory is higher than that of any other syndrome among tree species of the temperate forests of Chiloé and New Zealand. The frequency of species with ornithochorous propagules in these forests is higher than the relative importance of this syndrome in neotropical forest sites (Gentry, 1982). Values for ornithochory in Chiloé and New Zealand are similar to those reported by Willson (unpublished MS) for four tropical rain forests in Australia.

On the other hand, fleshy-fruited trees are clearly more common in temperate forests of the southern hemisphere than in New Jersey woods, and other deciduous forests of North America. The frequencies of bird-dispersal among tree species in eight North American temperate forests reported by Willson (1986) range from 9% to 30%. Howe & Smallwood (1982) report values of 10–25% for the proportion of tree species with fleshy fruits in temperate deciduous forests of Indiana and Ohio, U.S.A. This difference results from the higher percentages of mammalochory and anemochory for North American trees. Some ecological and historical reasons may account for the difference in dispersal characteristics between North and South America

temperate forests. On the one hand, there seems to be a greater diversity and activity of fruit-eating mammals in North American temperate forests (Martin, Zim & Nelson, 1951), than in Chilean temperate forests (Armesto *et al.*, 1987) in the present times. On the other hand, tree species of eastern North America are likely derived from dry-deciduous subtropical taxa (Axelrod, 1966), whereas trees of Southern Chile belong to families (e.g. Monimiaceae, Flacourtiaceae, Myrtaceae) that have their close relatives among evergreen species of wet tropical forests (Raven, 1973; Landrum, 1981; Troncoso, Villagrán & Muñoz, 1980). Species of dry-season deciduous forests have a large proportion of wind-dispersed taxa (Howe & Smallwood, 1982), whereas species with fleshy fruits are increasingly found in wet forests (Gentry, 1982). Tropical areas in South America are very rich in avian frugivores (Janson, 1983), and if the tree flora of Chiloé had an important component of neotropical species, these are likely to be conservative with regard to their original dispersal syndromes (cf. Herrera, 1986). In the case of New Zealand, the predominance of ornithochory might be related to the fact that this syndrome is most frequent in the flora of oceanic islands (Carlquist, 1974), and also to the conspicuous absence of native mammals that could act as dispersers.

Chiloé was the only area where shrubs did not have a higher proportion of fleshy-fruited species than the other growth-forms. In the other three forests compared here, as well as in other North American temperate woodlands

(Willson, 1986), and in the tropics of Australia (Willson *et al.*, unpublished MS), fleshy fruits were most common among shrubs (range 48–90% for North American shrubs and vines; 75–100% for Australian shrubs). Howe & Smallwood also report 85–100% of fleshy fruits among shrubs in temperate deciduous forests. Shrubs are also predominantly (>80%) bird-dispersed in neotropical forests (Gentry, 1982). The lower relative frequency of ornithochory in the shrubs of Chiloé is related in part to the presence of three species of bamboo (*Chusquea* spp.), which is presumably mammal-dispersed. If these three species are excluded, the frequency of bird-dispersal rises to 67%, still lower than the values for the other growth-forms. In Chiloé, shrub species are typically found in open areas (both natural and man-made clearings) and in forest margins, but seldom in the forest understorey. Because anemochory is the most common dispersal system in open habitats (Howe & Smallwood, 1982), this could explain in part the frequency of anemochory among shrubs in Chiloé. The high proportion of wind-dispersed species found among emergent trees in Chiloé is also consistent with the idea that this mode of dispersal is associated with exposure to wind (Howe & Smallwood, 1982; van der Pijl, 1982). Forests of Chiloé Island extend often to the shore, so that shrub species growing at forest margins are sometimes restricted to the coastal areas (e.g. *Sophora microphylla*). Hydrochory (probably related to ocean dispersal; see Murray, 1986) is then another dispersal syndrome found among shrubs of Chiloé, which also contributes to the reduction of the relative importance of ornithochory.

The high frequencies of ornithochory found among forest shrubs do not have a clear explanation in the literature (cf. Willson, 1986; Howe & Smallwood, 1982). We propose that the predominance of this syndrome among shrubs might be related to the patterns of habitat selection of avian frugivores. It has been widely documented (Thompson & Willson, 1978; Murray, 1985; Leck, 1987) that bird species richness and abundance are greater in forest margins, clearings, and second-growth forests, where shrub species are most common. Leck (1987) attributes the birds' preference for open habitats to the greater abundance of species with fleshy fruits, which are important food items, especially for migrants. It seems, therefore, that the distribution and abundance of species with fleshy fruits and the activity patterns of fruit-eating birds are closely associated (Herrera, 1985b). Data on dispersal syndromes in the forest of Chiloé point to the conclusion that mutual dependence between plant and animal (particularly bird) populations may be well developed in South American temperate areas. Plant–animal interactions related to seed dispersal need to be addressed in field studies, and their results should have important implications for the design and management of forest reserves in the South American temperate region (see Howe, 1984b).

ACKNOWLEDGMENTS

We are grateful to Dr Mary Willson for providing the stimulus for writing this paper, and for sending us her unpublished manuscripts and reprints. We thank Dr

S. T. A. Pickett and two anonymous reviewers for making useful comments on the manuscript. This research was supported by the Universidad de Chile (DIB, project N-2210-8735) and Fondecyt through grants 1461, and 860. The senior author acknowledges the hospitality of the Institute of Ecosystem Studies of the New York Botanical Garden during the revision of the manuscript.

REFERENCES

- Armesto, J.J. & Figueroa, J. (1987) Stand structure and dynamics in the rain forests of Chiloé Archipelago. *J. Biogeogr.* **14**, 367–376.
- Armesto, J.J., Rozzi, R., Miranda, P. & Sabag, C. (1987) Plant/frugivore interaction in South American temperate forests. *Rev. Chilena Hist. Nat.* **60**, 321–336.
- Axelrod, D.I. (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution*, **30**, 1–15.
- Carlquist, S. (1974) *Island biology*. Columbia University Press, New York.
- Donoso, C., Escobar, B. & Urrutia, J. (1985) Estructura de un bosque virgen de ulmo (*Eucryphia cordifolia* Cav.) – tepa (*Laurelia philippiana* Phil.) Looser en Chiloé, Chile. *Rev. Chilena Hist. Nat.* **58**, 171–186.
- Forman, R.T.T. & Elfstrom, B.A. (1975) Forest structure comparison of Hutcheson Memorial Forest and eight old woods on the New Jersey Piedmont. *The W. L. Hutcheson Memorial Forest Bull.* **3**, 44–51.
- Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biol.* **15**, 1–84.
- Herrera, C.M. (1981) Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. *Oikos*, **36**, 51–58.
- Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants and their interaction in mediterranean scrublands. *Ecol. Monogr.* **54**, 1–23.
- Herrera, C.M. (1985a) Determinants of plant–animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos*, **44**, 132–141.
- Herrera, C.M. (1985b) Habitat–consumer interactions in frugivorous birds. *Habitat selection in birds* (ed. by M. L. Cody), pp. 341–365. Academic Press, New York.
- Herrera, C.M. (1986) Vertebrate-dispersed plants: why they don't behave the way they should. *Frugivores and seed dispersal* (ed. by A. Estrada and T. H. Fleming), pp. 5–18. Junk, The Hague.
- Holdgate, M.W. (1961) Vegetation and soils in the south Chilean islands. *J. Ecol.* **49**, 359–380.
- Howe, H.F. (1984a) Constraints on the evolution of mutualisms. *Am. Nat.* **123**, 764–777.
- Howe, H.F. (1984b) Implications of seed dispersal by animals for tropical reserve management. *Biol. Conserv.* **30**, 261–181.
- Howe, H.F. & Estabrook, G.F. (1977) On intraspecific competition for avian dispersers in tropical trees. *Am. Nat.* **111**, 817–832.
- Howe, H.F. & Primack, R.B. (1975) Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica*, **7**, 278–283.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* **13**, 201–228.
- Janson, C.H. (1983) Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science*, **219**, 187–189.
- Janzen, D.H. (1976) Why bamboos wait so long to flower. *Ann. Rev. Ecol. Syst.* **7**, 347–391.
- Janzen, D.H. (1983) Dispersal of seeds by vertebrate guts. *Coevolution* (ed. by D. J. Futuyama and M. Slatkin), pp. 232–262. Sinauer, Sunderland, Mass.

- Janzen, D.H. (1985) The natural history of mutualisms. *The biology of mutualism. Ecology and evolution* (ed. by D. G. Boucher), pp. 40–99. Oxford University Press, New York.
- Landrum, L. (1981) The phylogeny and geography of *Myrceugenia* (Myrtaceae). *Brittonia*, **33**, 105–129.
- Leck, C.F. (1987) Habitat selection in migrant birds: seductive fruits. *Trends Ecol. Evol.* **2**, (2), 33.
- Mark, A.F. & Smith, P.M.F. (1975) A lowland vegetation sequence in south westland: Pakihi bog to mixed beech-podocarp forest. Part 1: The principal strata. *Proc. N.Z. Ecol. Soc.* **22**, 76–92.
- Martin, A.C., Zim H.S. & Nelson, A.L. (1951) *American wildlife and plants: A guide to wildlife food habits*. Dover, New York.
- McKey, D. (1975) The ecology of coevolved seed dispersal systems. *Coevolution of animals and plants* (ed. by L. D. Gilbert and P. H. Raven), pp. 159–191. University of Texas Press, Austin.
- Murray, D.R. (1986) Seed dispersal by water. *Seed dispersal* (ed. by D. G. Murray), pp. 49–85. Academic Press, Sidney.
- Murray, K.G. (1985) Avian seed dispersal of neotropical gap-dependent plants. Ph.D. dissertation, University of Florida, Gainesville, Florida.
- Murua, R. & Gonzales, L. (1985) Producción de semillas de especies arbóreas en la pluviselva Valdiviana. *Bosque*, **6**, 15–23.
- Raven, P.H. (1973) The evolution of mediterranean floras. *Mediterranean-type ecosystems. Origin and structure* (ed. by F. di Castri and H. A. Mooney), pp. 213–224. Springer, Berlin.
- Snow, D.W. (1965) A possible selective factor in the evolution of fruiting seasons in tropical forests. *Oikos*, **15**, 274–281.
- Snow, D.W. (1971) Evolutionary aspects of fruit eating by birds. *Ibis*, **113**, 194–202.
- Stiles, E.W. (1980) Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the Eastern deciduous forest. *Am. Nat.* **116**, 670–688.
- Thompson, J.N. & Willson, M.F. (1979) Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution*, **33**, 973–982.
- Troncoso, A., Villagrán, C. & Muñoz, M. (1980) Una nueva hipótesis acerca del origen y edad del bosque de Fray Jorge (Coquimbo, Chile). *Bol. Mus. Nac. Hist. Nat. Chile*, **37**, 117–152.
- van der Pijl, L. (1982) *Principles of dispersal in higher plants*. Springer, Berlin.
- Veblen, T.T. (1985) Forest development in tree-fall gaps in the temperate rain forest of Chiloé. *Natl. Geogr. Res.* **1**, 162–183.
- Veblen, T.T. & Schlegel, F.M. (1982) Reseña ecológica de los bosques del sur de Chile. *Bosque*, **4**, 73–115.
- Villagrán, C. (1985) Análisis palinológico de los cambios vegetacionales durante el Tardiglacial y Postglacial en Chiloé, Chile. *Rev. Chilena Hist. Nat.* **58**, 57–69.
- Villagrán, C., Armesto, J.J. & Leiva, R. (1986) Recolonización postglacial de Chiloé insular: evidencias basadas en la distribución geográfica y modos de dispersión de la flora. *Rev. Chilena Hist. Nat.* **59**, 19–39.
- Willson, M.F. (1986) Avian frugivory and seed dispersal in eastern North America. *Current Ornithol.* **3**, 223–279.

APPENDIX 1. Plant species of the temperate rain forests of Chiloé and their dispersal syndromes (according to van der Pijl, 1982).

Species§	Family	Stratum*	Syndrome
(a) Trees			
<i>Aextoxicon punctatum</i> R. et P.	Aextoxicaceae	C	O
<i>Amomyrtus luma</i> (Mol.) Legr. et Kaus.	Myrtaceae	C	O
<i>Amomyrtus meli</i> (Phil.) Legr. et Kaus.	Myrtaceae	C	O
<i>Aristotelia chilensis</i> (Mol.) Stuntz	Elaeocarpaceae	SC	O
<i>Caldcluvia paniculata</i> (Cav.) D. Don	Cunoniaceae	SC	A
<i>Dasyphyllum diacanthoides</i> (Less.) Cabr.	Asteraceae	E	A
<i>Drimys winteri</i> Phil.	Winteraceae	C	O
<i>Eucryphia cordifolia</i> Cav.	Eucryphiaceae	E	A
<i>Gevuina avellana</i> Mol.	Proteaceae	C	M
<i>Laurelia philippiana</i> Looser	Monimiaceae	E	A
<i>Luma apiculata</i> (DC.) Burret	Myrtaceae	SC	O
<i>Maytenus boaria</i> Mol.	Celastraceae	SC	O
<i>Maytenus magellanica</i> (Lam.) Hook. f.	Celastraceae	SC	O
<i>Myrceugenia chrysocarpa</i> (Berg) Kaus.	Myrtaceae	SC	O
<i>Myrceugenia exsucca</i> (DC.) Berg	Myrtaceae	SC	O
<i>Myrceugenia ovata</i> (H. et A.) Berg	Myrtaceae	C	O
<i>Myrceugenia parvifolia</i> (DC.) Kaus.	Myrtaceae	SC	O
<i>Myrceugenia planipes</i> (H. et A.) Berg	Myrtaceae	SC	O
<i>Nothofagus dombeyi</i> (Mirb.) Oerst.	Fagaceae	E	A
<i>Nothofagus nitida</i> (Phil.) Krasser	Fagaceae	E	A
<i>Ovidia pillopollo</i> (Gay) Meisn.	Thymeliaceae	SC	O
<i>Podocarpus nubigena</i> Lindl.	Podocarpaceae	E	O
<i>Pseudopanax laetevirens</i> (Gay) Franchet	Araliaceae	SC	O
<i>Pseudopanax valdiviense</i> (Gay) Seem.	Araliaceae	SC	O

APPENDIX 1 (continued)

Species§	Family	Stratum*	Syndrome
<i>Raphithamnus spinosus</i> (A. L. Juss.) Mold.	Verbenaceae	SC	O
<i>Saxe-gothaea conspicua</i> Lindl.	Podocarpaceae	C	O
<i>Weinmannia trichosperma</i> Cav.	Cunoniaceae	E	A
(b) Shrubs			
<i>Azara lanceolata</i> Hook. f.	Flacourtiaceae		O
<i>Berberis buxifolia</i> Lam.	Berberidaceae		O
<i>Berberis darwini</i> Hook.	Berberidaceae		O
<i>Berberis serrato-dentata</i> Lechler	Berberidaceae		O
<i>Chusquea palenae</i> Phil.	Gramineae		M?
<i>Chusquea quila</i> Kunth	Gramineae		M?
<i>Chusquea uliginosa</i> Phil.	Gramineae		M?
<i>Coriaria ruscifolia</i> L.	Coriariaceae		H
<i>Crinodendron hookerianum</i> Gay	Elaeocarpaceae		H
<i>Desfontainea spinosa</i> R. et P.	Desfontaineaceae		O
<i>Embothrium coccineum</i> J. R. et G. Forst.	Proteaceae		A
<i>Empetrum rubrum</i> Vahl ex Willd.	Empetraceae		O
<i>Escallonia rubra</i> (R. et P.) Pers.	Saxifragaceae		Multiple†
<i>Fuchsia magellanica</i> Lam.	Onagraceae		O
<i>Gaultheria antarctica</i> Hook. f.	Ericaceae		O
<i>Gaultheria phillyreifolia</i> (Pers.) Sleu.	Ericaceae		O
<i>Lomatia ferruginea</i> (Cav.) R.Br.	Proteaceae		A
<i>Lomatia hirsuta</i> (Lam.) Diels	Proteaceae		A
<i>Myoschilos oblonga</i> R. et P.	Santalaceae		O
<i>Myrteola numularia</i> (Poir.) Berg	Myrtaceae		O
<i>Pernettya insana</i> (Mol.) Gunckel	Ericaceae		O
<i>Pernettya mucronata</i> (L.f.) Gaud.	Ericaceae		O
<i>Pernettya myrtilloides</i> Zucc. ex Steudel	Ericaceae		O
<i>Ribes magellanicum</i> Poir.	Saxifragaceae		O
<i>Sophora microphylla</i> Aiton	Papilionaceae		H
<i>Tepualia stipularis</i> (H. et A.) Griseb.	Myrtaceae		A
<i>Ugni molinae</i> Turcz.	Myrtaceae		O
(c) Epiphytes and vines			
<i>Asteranthera ovata</i> (Cav.) Hanst.	Gesneriaceae		O
<i>Boquila trifoliolata</i> (DC.) Dcne.	Lardizabalaceae		O
<i>Cissus striata</i> R. et P.	Vitaceae		O
<i>Campsidium valdivianum</i> (Phil.) Skottsb.	Bignoniaceae		A
<i>Elytropus chilensis</i> (A.DC.) Muell.-Arg.	Apocynaceae		A
<i>Ercilla syncarpellata</i> Nowicke	Phytolaccaceae		O
<i>Greigia landbeckii</i> (Lechler ex Phil.)	Bromeliaceae		O
<i>Griselinia racemosa</i> (Phil.) Taub.	Cornaceae		O
<i>Griselinia ruscifolia</i> (Clos) Taub.	Cornaceae		O
<i>Hydrangea serratifolia</i> (H. et A.) F. Phil.	Hydrangeaceae		Multiple†
<i>Luzuriaga marginata</i> (Banks et Soland. ex Gaertn.) Benth.	Philesiaceae		O
<i>Luzuriaga polyphylla</i> (Hook.) Macbr.	Philesiaceae		O
<i>Luzuriaga radicans</i> R. et P.	Philesiaceae		O
<i>Mitraria coccinea</i> Cav.	Gesneriaceae		O
<i>Peperomia fernandeziana</i> Miq.	Piperaceae		E
<i>Philesia magellanica</i> J. F. Gmel.	Philesiaceae		O
<i>Sarmienta repens</i> R. et P.	Gesneriaceae		A
<i>Tropaeolum speciosum</i> P. et E.	Tropaeolaceae		O
(d) Herbs			
<i>Chrysosplenium valdivicum</i> Hook.	Saxifragaceae		Multiple†
<i>Gunnera magellanica</i> Lam.	Gunneraceae		S?
<i>Nertera granadensis</i> ‡ (Mutis ex L.f.) Druce	Rubiaceae		O

APPENDIX 1 (continued)

Species§	Family	Stratum*	Syndrome
<i>Osmorhiza chilensis</i> H. et A.	Umbelliferae		E
<i>Uncinia erinaceae</i> (Cav.) Pers.	Cyperaceae		E
<i>Uncinia multifaria</i> Nees ex Boott	Cyperaceae		E
<i>Uncinia phleoides</i> (Cav.) Pers.	Cyperaceae		E
<i>Dysopsis glechomoides</i> (A. Rich.) Muell.-Arg.	Euphorbiaceae		B
<i>Relbunium hypocarpium</i> ‡ (L.) Hemsl.	Rubiaceae		O

Syndromes: A=anemochory, B=balochory, E=epizoochory, H=hydrochory, M=mammalochory, O=ornithochory, S=saurochory.

* Tree strata: C=canopy, SC=subcanopy (including trees from forest margins and second-growth areas), E=emergent.

† Multiple: dust-like diaspores that may be carried by wind, water, or on animal bodies (see Villagrán *et al.*, 1986).

‡ Also grow as epiphytes.

§ Nomenclature follows Marticorena, C. & Quezada, M. (1985) Catálogo de la flora vascular de Chile. *Gayana*, **42**, 1–157.