

Dispersal and growth form patterns of some zonal páramo vegetation types

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SUMMARY

In zonal vegetation of the páramo Boca Grande (Sumapaz), in the Colombian Cordillera Oriental, the dispersal and growth form spectra of the different vegetation zones are described. With increasing altitude the abundance of the zoochorous plant species decreased while anemochory increased. A possible relationship between the mode of dispersal and the growth forms was also investigated. The most important modes of dispersal were not restricted to a special growth form but appeared to prevail in the predominant growth forms of the successive zones. In addition a global distribution of the weight of the diaspores and of the phenological state of the species is given.

Key-words: diaspore, dispersal, growth form, páramo, zonation.

INTRODUCTION

Dispersal of seeds is an important process within the life cycle of a plant. A successful mode of dispersal is a pre-requisite for the survival of a species, both by maintaining existing stands and by establishing new areas. Until recently the study of dispersal biology has been focused on the modes of dispersal at the level of species. However, plant communities may also be characterized by means of spectra based on features of the dispersal units (Braun-Blanquet 1964). In every plant community there is usually a wide range of dispersal mechanisms to be found, although the proportion of species using the various agencies varies from one vegetation type to another (Fenner 1985). Only a few attempts have been made to investigate the dispersal spectra of whole plant communities (Müller 1933, Luftensteiner 1979, Gentry 1982, Hilger & Schultka 1988).

Little is known about dispersal in tropical alpine environments (Graf-Bock 1984). The aim of this study is to enlarge our knowledge on the dispersal of páramo species and to gain a better insight into the biological dispersal processes in páramo vegetation. The name páramo has been used, ever since the days of the Spanish conquest, for the high, more or less open, chilly areas of the northern Andes. They are located in the humid tropical Andean mountains, and occur as an altitudinal belt between the uppermost forest and the perennial snow (Cleef 1978; 1981). Geographically the páramos extend from Costa Rica at 11°N to northern Peru at 8°S, and reach from 3800 m (locally from 3200 m) up to 4800–5000 m altitude. The páramo belt mostly shows a clear altitudinal zonation. According to Cuatrecasas (1968), páramos can generally be divided into three regions.

This paper is dedicated to Professor Dr T. van der Hammen on the occasion of his 65th birthday.
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1. The sub-páramo, the lowest part of the páramo, which is dominated by shrubs; floristically it is a mixture of plants from the two adjacent belts.

2. The grass-páramo or páramo proper, in general an open bunch grass vegetation; the grass-páramo is associated with the caulirosetum of the Espeletiinae.

3. The super-páramo, the highest, subnival, region.

In the Colombian Cordillera Oriental these regions can be subdivided into a shrub- and a dwarf-shrub-páramo, a lower and an upper grass-páramo and a lower and an upper super-páramo (Cleef 1981). A similar gradient was found for the bryophyte flora (Gradstein *et al.* 1989).

In this study the different dispersal strategies of these zonal vegetations are described, as well as relations between the dispersal and growth form spectra within the different zonal páramo plant communities. The study was made within the scope of the ECOANDES-project (Perez *et al.* 1983; Van der Hammen & Ruiz 1984) which aimed after the first inventory phase, at inquiries to describe the processes better. Even the inclement páramos are being influenced by human activity for example by burning, in altitudinal transects, the bunch grass vegetation in order to get fresh grass for cattle which in turn affects the vegetation by trampling and grazing. These activities can have a great impact on the natural water-buffering capacity of the páramos and hence on the water supply of the lower areas (Guhl 1982). As the unaffected areas vanish rapidly it is of essential importance to study these tropical alpine ecosystems before they have disappeared.

MATERIALS AND METHODS

Research area and techniques

The study was carried out in the Cordillera Oriental of Colombia in the páramo Boca Grande (Sumapaz) located at 4°20'N and 74°05'E, about 30 km south of Bogotá, at an altitude between 3390 m and 3710 m in the period from May to October 1987.

A total of 40 relevées according to Braun-Blanquet (1964) with coverage in percentages, was recorded (for a species list see Table 1). The relevées belonged to five different (sub)regions or (sub)zones: I upper Andean dwarf-forest, II rivershore-forest, III shrub-páramo, IV dwarf-shrub-páramo, V (lower) grass-páramo. Except for zone II, which is more or less azonal, these zones belong to the zonal vegetation. The minimum area was 25 m² for the relevées made in zones III, IV and V, and 30 m² for the relevées in the zones I and II. The mean coverage of a species in a (sub)zone was calculated from the coverage percentages in all relevées of this zone. In the relevées all individual seed plants, from juveniles to specimens actually dispersing, were taken into account. In each relevée, the coverage, height, phenological state and growth form of the plants were recorded for each species.

Dried specimens were identified at the Herbarium of Utrecht (U), and by comparison with the reference collection of A.M. Cleef in Amsterdam (AMD). Nomenclature of species follows Cleef (1981).

For demonstrating structural adaptations to dispersal, most of the dried diaspores were, after ultrasonic treatment, gold/palladium sputtered for about 2.5 min and scanned with an ISI-DS130 scanning electron microscope.

Climate and soil

Climate data of the area have been gathered from the Empresa de Acueducto y Alcantarillado de Bogotá, which has one of their meteorological stations situated in the

research area at an altitude of 3450 m. The average annual precipitation at Boca Grande is 1388 mm. There is only one wet season (with more than 100 mm per month), with two peaks, which lasts from May to October. Concurrent with this rainfall there is also, especially in the wet season, a persistent state of fog. The wind direction is nearly always south-east with an average wind velocity of 6.3 km/h throughout the year. This frequent wind intensifies the effects of the cold and physiological dryness upon the plants of the páramo (Cuatrecasas 1968). The average annual temperature is 7.9°C and the average annual relative humidity 81%.

Páramo soils in general have the following features in common; a relatively high content of K and N, reduced uptake of these elements by plants, moderate to highly acid soils and correspondingly low Ca levels, a high water capacity, a low free P content, an organic content higher than 10% in the toplayer and hardly any podzolic features, or none at all (Sturm 1978).

Dispersal categories

As far as possible the type of dispersal was determined in the field. Apart from these field records structural adaptations of the diaspore to dispersal and data from literature were used to classify the species.

Dispersal can be classified on the basis of the dispersal agents, the vectors (Van der Pijl 1972) and on the basis of structural adaptations of the functional dispersal units, the diaspores (Luftensteiner 1979, 1982). In this study a combination has been made of both. The classification of the main categories is based on the dispersal agents and the sub-categories are based on the morphological adaptations. Five main categories can be distinguished:

1. Autochory, dispersal by the plant itself (only active ballists).
2. Barochory, dispersal by means of gravitation.
3. Zoochory, dispersal by animals divided into two subcategories, epi- and endozoochory (acanthochorous- and sarcochorous diaspores respectively).
4. Anemochory, dispersal by wind, divided into five subcategories, (a) balloons (sacchochorous diaspores), (b) plumes (pogonochorous and lophochorous diaspores), (c) winged (pterochorous) diaspores, (d) very small and light diaspores (<0.05 mg, weight class IV and less) are presumed to be wind-dispersed even if they lack any distinct morphological adaptation to anemochory (Fenner 1985), for example *Altensteinia fimbriata*; these species are referred to as wind-dispersed without adaptations (wwa), and (e) the last subcategory in anemochory, windballists, which is not based on morphological adaptations of the diaspore. Windballists, as recorded in this study, agree with the passive ballists of Van der Pijl (1972) and the semachorous species of Luftensteiner (1979). Luftensteiner's semachorous category also includes myxochorous species. In the páramos studied there are two myxochorous species, *Plantago australis* and *P. rigida*, of which the last one is an important element of the azonal vegetation types, but because of their low coverage (always less than 1%), myxochory is not taken into account in this study.
5. A last category of species of which no diaspores were observed during the field work period or which had seeds or fruits whose mode of dispersal could not be established. These species are referred to as 'unknown'.

Establishing the way of dispersal of a plant species is difficult owing to the fact that sometimes a species is dispersed by more than one vector. Most of the small diaspores, for example, can also be dispersed by rainwash or in mud sticking to animals. In such cases of diplo- or polychory the most important type of dispersal was chosen. Windballists, whose

Table 1. Alphabetical list of species

	Life form	Type of dispersal	Weight class
<i>Acaena cylindristachya</i> (Rosaceae)	H	epi	V
<i>A. elongata</i>	H	epi	VI
<i>Ageratina tinifolia</i> (Compositae)	T	pl	
<i>A. vaccinioides</i>	D	pl	
<i>Agrostis trichodes</i> (Gramineae)	G	ball	III
<i>A. turrialba</i>	G	ball	
<i>Alonsoa meridionalis</i> (Scrophulariaceae)	H	wwa	IV
<i>Altensteinia fimbriata</i> (Orchidaceae)	H	wwa	I
<i>Anthoxanthum odoratum</i> (Gramineae)	G	wwa	
<i>Arcytophyllum muticum</i> (Rubiaceae)	D	wing/wb	
<i>A. nitidum</i>	D	wing/wb	
<i>Arenaria</i> cf. <i>A. lanuginosa</i> (Caryophyllaceae)	H	wwa/wb	IV
<i>Azorella cuatrecasii</i> (Umbelliferae)	H	wwa/wb	IV
<i>Baccharis prunifolia</i> (Compositae)	S	pl	
<i>B. revoluta</i>	S	pl	III
<i>B. tricuneata</i>	D	pl	IV
<i>Bartsia santolinifolia</i> (Scrophulariaceae)	H	wwa/wb	III
<i>Berberis goudotii</i> (Berberidaceae)	T	endo	VII
<i>Bidens triplinerva</i> (Compositae)	H	epi	
<i>Bomarea</i> sp. (Liliaceae)	L	endo	
<i>Brachyotum lindenii</i> (Melastomataceae)	D	baro/wb	
<i>Calamagrostis bogotensis</i> (Gramineae)	G	pl	
<i>C. effusa</i>	G	pl	
<i>C. planifolia</i>	G	pl	
<i>Cardamine africana</i> (Cruciferae)	H	auto	V
<i>Carex amecta</i> (Cyperaceae)	G	wing	
<i>C. bonplandii</i>	G	wwa	IV
<i>C. jamesonii</i>	G	wwa	
<i>C. pichinchensis</i>	G	wwa	IV
<i>C. pygmaea</i>	G	wwa	
<i>Castilleja fissifolia</i> (Scrophulariaceae)	H	ball/wb	III
<i>C. integrifolia</i>	H	ball/wb	
<i>Castratella piloselloides</i> (Melastomataceae)	H	wwa/wb	III
<i>Cerastium subspicatum</i> (Caryophyllaceae)	H	wwa/wb	IV
<i>Cestrum parvifolium</i> (Solanaceae)	S	endo	VII
<i>Clethra fimbriata</i> (Clethraceae)	T	ball/wb	
<i>Digitalis purpurea</i> (Scrophulariaceae)	H	wwa/wb	III
<i>Diplostephium philicoides</i> (Compositae)	S	pl	IV
<i>D. revolutum</i>	S	pl	IV
<i>Disterigma empetrifolium</i> (Ericaceae)	D	endo	
<i>Ditassa</i> sp. (Asclepiadaceae)	L	pl	
<i>Epilobium meridense</i> (Onagraceae)	D	pl	
<i>Erigeron chionophilus</i> (Compositae)	H	pl	
<i>E. noticastrum</i>	H	pl	
<i>Eryngium humboldtii</i> (Umbelliferae)	H	epi	V
<i>E. humile</i>	H	epi	IV
<i>Escallonia myrtilloides</i> (Escalloniaceae)	T	wwa	
<i>Espeletia grandiflora</i> (Compositae)	T-D	baro	V
<i>Festuca dolichophylla</i> (Gramineae)	G	unknown	
<i>Galium ascendens</i> (Rubiaceae)	H	epi	
<i>G. canescens</i>	H	epi	V
<i>Gaultheria anastomosa</i> (Ericaceae)	D	wwa/wb	III
<i>G. rigida</i>	D	wwa/wb	III
<i>Gaylussacia buxifolia</i> (Ericaceae)	D	endo	VII

Table 1. (Continued)

	Life form	Type of dispersal	Weight class
<i>Gentiana sedifolia</i> (Gentianaceae)	H	unknown	III
<i>Gentianella corymbosa</i>	H	wwa/wb	IV
<i>Geranium lindenianum</i> (Geraniaceae)	H	auto	
<i>G. multiceps</i>	H	auto	V
<i>G. multifida</i>	H	auto	
<i>G. sibbaldioides</i>	H	auto	
<i>Geranium</i> sp.	H	auto	
<i>Gnaphalium antennarioides</i> (Compositae)	H	pl	
<i>G. meridanum</i>	H	pl	
<i>G. spicatum</i>	H	pl	
<i>Gynoxys subhirsuta</i> (Compositae)	T	pl	
<i>G. trianae</i>	T	pl	
<i>Halenia asclepiadea</i> (Gentianaceae)	H	wwa/wb	IV
<i>H. brevicornis</i>	H	wwa/wb	IV
<i>Hesperomeles ferrugineus</i> (Rosaceae)	T	endo	VIII
<i>Hieracium avilae</i> (Compositae)	H	pl	
<i>Holodiscus argenteus</i> (Rosaceae)	S	pl	V
<i>Hydrocotyle ranunculoides</i> (Umbelliferae)	H	wwa/wb	
<i>Hypericum goyanesii</i> (Guttiferae)	S	wwa/wb	
<i>H. juniperum</i>	S	wwa/wb	
<i>H. lancioides</i>	S	wwa/wb	
<i>H. laricifolium</i>	S	wwa/wb	
<i>H. mexicanum</i>	S	wwa/wb	III
<i>H. strictum</i>	S	wwa/wb	III
<i>Hypochaeris</i> sp. (Compositae)	H	pl	
<i>Juncus</i> cf. <i>J. echinocephalus</i> (Juncaceae)	G	wwa	
<i>J. ecuadoriensis</i>	G	wwa	
<i>J. stipulatus</i>	G	wwa	
<i>Lachemilla andina</i> (Rosaceae)	H	unknown	
<i>L. aphanoides</i>	H	unknown	
<i>L. fulvescens</i>	H	unknown	
<i>L. galioides</i>	H	unknown	
<i>L. nivalis</i>	H	unknown	
<i>L. orbiculata</i>	H	unknown	
<i>Lachemilla</i> sp.	H	unknown	
<i>Lobelia tenera</i> (Lobeliaceae)	H	wwa/wb	
<i>Lourteigia gracile</i> (Compositae)	H	pl	
<i>Lupinus</i> sp. (Papilionaceae)	H	auto	VI
<i>Luzula gigantea</i> (Juncaceae)	G	baro	IV
<i>L. racemosa</i>	G	baro	
<i>Lysipomia sphagnophila</i> (Campanulaceae)	H	unknown	
<i>Miconia elaeoides</i> (Melastomataceae)	S	endo	
<i>Monnina salicifolia</i> (Polygalaceae)	T	endo	VI
<i>Muehlenbeckia thamnifolia</i> (Polygonaceae)	T	endo	VII
<i>Muehlenbergia fastigiata</i> (Gramineae)	G	wwa	
<i>Nertera granadensis</i> (Rubiaceae)	H	endo	VI
<i>Niphogeton glaucescens</i> (Umbelliferae)	H	wwa/wb	IV
<i>N. lingula</i>	H	wwa/wb	
<i>Oreobolus obtusangulus</i> (Cyperaceae)	G	unknown	V
<i>Oreopanax mutisianum</i> (Araliaceae)	T	endo	VII
<i>Oritrophium peruvianum</i> (Compositae)	H	pl	IV
<i>Orthrosanthus chimborasensis</i> (Iridaceae)	H	wing/wb	IV
<i>Oxalis</i> sp. (Oxalidaceae)	H	auto	IV

Table 1. (Continued)

	Life form	Type of dispersal	Weight class
<i>Paepalanthus karstenii</i> (Eriocaulaceae)	H	pl	IV
<i>P. lodiculoides</i>	H	pl	
<i>Paspalum bonplandianum</i> (Gramineae)	G	unknown	V
<i>Pentacalia abietina</i> (Compositae)	D	pl	IV
<i>P. andicola</i>	S	pl	
<i>P. ledifolia</i>	S	pl	IV
<i>P. nitida</i>	D	pl	
<i>P. reissiana</i>	S	pl	
<i>P. vaccinioides</i>	S	pl	IV
<i>Peperomia cuatrecasana</i> (Piperaceae)	H	epi	IV
<i>P. hispidula</i>	H	unknown	
<i>P. microphylla</i>	H	epi	IV
<i>Peperomia</i> sp.	H	epi	IV
<i>Pernettya prostrata</i> (Ericaceae)	D	endo	VII
<i>P. hirta</i>	D	endo	VII
<i>Pinguicula elongata</i> (Lentibulariaceae)	H	unknown	
<i>Plantago australis</i> (Plantaginaceae)	H	myxo	IV
<i>P. rigida</i>	H	myxo	IV
<i>Puya goudotiana</i> (Bromeliaceae)	D	wing/wb	
<i>P. santosii</i>	D	wing/wb	IV
<i>Ranunculus flagelliformis</i> (Ranunculaceae)	H	unknown	IV
<i>R. geranioides</i>	H	epi	
<i>R. limoselloides</i>	H	nauto	IV
<i>R. peruvianus</i>	H	epi	V
<i>Rapanea dependens</i> (Myrsinaceae)	T	endo	
<i>Relbunium hypocarpium</i> (Rubiaceae)	H	endo	VI
<i>Rhizocephalum candoleii</i> (Campanulaceae)	H	wwa/wb	
<i>Rhynchospora macrochaeta</i> (Cyperaceae)	G	pl	V
<i>R. paramorum</i>	G	pl	V
<i>Ribes</i> sp. (Saxifragaceae)	D	endo	
<i>Rubus</i> sp. (Rosaceae)	D	endo	VIII
<i>Rumex acetosella</i> (Polygonaceae)	H	wing	IV
<i>Scirpus inundatus</i> (Cyperaceae)	G	wwa	
<i>Senecio subbrunclatus</i> (Compositae)	H	pl	IV
<i>Siegesbeckia orientalis</i>	H	epi	IV
<i>Sisyrinchium pusillum</i> (Iridaceae)	H	wwa/wb	IV
<i>S. cf. trinerve</i>	H	wwa/wb	
<i>Stellaria cuspidata</i> (Caryophyllaceae)	H	wwa/wb	IV
<i>Symplocos theiformis</i> (Symplocaceae)	T	endo	
<i>Swallenochloa tessellata</i> (Gramineae)	G	unknown	
<i>Vaccinium floribundum</i> (Ericaceae)	D	endo	VII
<i>Valeriana longifolia</i> (Valerianaceae)	H	pl	IV
<i>V. pavonii</i>	L	pl	IV
<i>Vallea stipularis</i> (Elaeocarpaceae)	T	endo	VI
<i>Viola humilis</i> (Violaceae)	H	auto	
<i>Weinmannia microphylla</i> (Cunoniaceae)	T	pl	
<i>Werneria humile</i> (Compositae)	H	pl	IV
<i>Xyris acutifolia</i> (Xyridaceae)	H	wwa/wb	III

Abbreviations: endo = endozoochory, epi = epizoochory, ball = balloon, pl = plume, wing = winged, wwa = wind-dispersed without adaptations, wb = windballist, auto = autochory, baro = barochory, (myxo = myxochory and nauto = nautochory).

Weight classes: I = <0.001 mg, II = 0.001–0.01 mg, III = 0.01–0.1 mg, IV = 0.1–1 mg, V = 1–10 mg, VI = 10–100 mg, VII = 100–1000 mg, VIII = > 1000 mg.

diaspores also belong to one of the four morphological subcategories of anemochory, excepted.

Growth forms

Of all species the growth form was determined according to the following definitions:

1. Trees (T), woody species with a single stem and vegetative buds higher than 50 cm above the ground.
2. Shrubs (S), woody species, branched from near the base and with vegetative buds higher than 50 cm above the ground.
3. Dwarf-shrubs (D), woody species, branched from near the base and vegetative buds below 50 cm above the ground.
4. Herbs (H), herbaceous species (graminoids excepted) regardless of their height. In páramos therophytes do not occur or are extremely rare (Cuatrecasas 1968).
5. Graminoids (G), all members of the Graminae, Cyperaceae, and Juncaceae. Although lianas (L) do occur in the páramo up to the shrub-páramo, they are so low in coverage and in number of species that they are left out of consideration.

Phenological states of the species from May to October

As far as possible the phenological state of the species throughout the area was recorded, regardless of the altitude at which they occurred. Only a rough classification was used: vegetative, flowering, and fruit-bearing.

Weight classification of the diaspores

To determine the weight classes of the diaspores, samples of 100 fresh diaspores were weighed on a balance and classified according to the eight weight classes of Luftensteiner (1979). These decimal classes extended from less than 0.001 mg (class I) to more than 1000 mg (class VIII). The weight of the heaviest diaspore (*Hesperomeles ferrugineus*) amounted to 1511 mg. It was not possible to collect and weigh the diaspores of all species occurring in the studied area, but for 52% of the species a weight classification is presented.

RESULTS

Dispersal agents

The allochoric dispersal agents operative in the páramo are wind, water, gravitation and animals. In the open grass-páramo wind has free-play, and thus is an important dispersal agent. In the lower, more sheltered parts of the páramo it is of less importance. Next to the prevailing south-eastern wind direction there also is a daily shift in local 'up-slope' and 'down-slope' winds. Water is not an important dispersal agent in the zonal páramo vegetations, except for rainwash, which is of the greatest importance to small seeds because it has a secondary effect by carrying fallen seeds after their dispersal by wind or gravity (Ridley 1930). In the azonal páramo vegetation types, such as the *Sphagnum* bogs and the *Plantago rigida* cushion-bogs, however, water plays a more important role. The animals that participate in dispersal are neither large in number nor in amount of species. Most important are about 10 bird species (including snipes), rabbits and guinea-pigs. According to Sturm (1978) in earlier times two large species of deer, *Odocoileus virginianus goudotii* Gayl & Gervais and *Mazama rufina bricenii* Thomas and the bears *Tremarctos*

ornatus F. Cuvier and *Nasuella olivacea* Gray, may also have occurred in the area. Remarkably, no ants were observed. Beside these natural inhabitants dogs, cows, horses and men can also act as dispersal agents.

Adaptations of the diaspores

Páramo species show a great diversity in their diaspore morphology. Autochorous species, e.g. *Oxalis* sp., *Geranium* sp. and *Cardamine africana* eject their seeds in an active way. In general, it is the fruit that shows adaptations functional in this form of dispersal and not the seed. Oxalidaceae is the only taxon known in which the explosive mechanism is located in the seedcoat.

The diaspores of barochorous species encountered in this study, *Brachyotum lindenii*, *Espeletia grandiflora* (Fig. 1a and b), *Luzula gigantea* and *L. racemosa* also do not show structural adaptations.

In the category of plants with zoochorous dispersal a division based on adaptations of the diaspores can be made. The endozoochorous diaspores are in receipt of a fleshy cover, often coupled with a conspicuous colour of the fruit, as in *Cestrum parvifolium*, *Nertera granadensis* and *Relbunium hypocarpium*. The epizoochorous diaspores have adaptations to stick to animals such as hooks (*Acaena elongata* (Fig. 1c and d), *Galium canescens* (Fig. 1e and f)), or a sticky surface as in the *Peperomia* sp. Syn- and dysochorous species apparently do not occur among the species studied.

Adaptations to wind dispersal such as wings, loose covers, hairs, etc., are diverse. In our study the following adaptations were recorded: balloons which have a loose cover, plumes, diaspores bearing hairs in order to increase their air resistance (Fig. 2a) and also winged ones. Windballists, which have long, stiff fruit-stalks often have diaspores which do not show morphological adaptations to wind-dispersal (Fig. 2b and c), but sometimes the small and light diaspores do have such an adaptation, such as in *Castilleja fissifolia* (Fig. 2e and f) which has saccochorous diaspores, and in *Arcytophyllum nitidum* and *Puya santosii* (Fig. 2d) which have winged diaspores.

Description of the plots

A plot here represents the average of all relevées recorded in one (sub)zone. The plots II–V are situated in the páramo, which in this case can be divided into sub-páramo, containing the shrub- and dwarf-shrub-páramo, and the grass-páramo. Plot number I, representing the upper Andean dwarf-forest, is located in the region bounded by the páramo on top. Due to environmental factors the forest-line does not lie at the same altitude everywhere, nor do the limits between shrub- and dwarf-shrub-páramo and dwarf-shrub- and grass-páramo. As the relevées are not taken from a single altitudinal transect they cannot simply be put in a range of increasing altitude, but have to be ordered by region so that the classification is not based on the real altitude but on the successive (páramo) regions that show an altitudinal zonation.

For all plots two dispersal spectra were made, one based on coverage and one on a species basis (Fig. 3). Growth form spectra of all plots were also made on a coverage basis and on a species basis (Fig. 4).

Plot I, with an average number of 40 plant species, at an altitude of 3430 m, represents a relatively dry stand of upper Andean dwarf-forest of *Rapanea dependens* with *Gynoxys subhirsuta* and *Muehlenbeckia thamnifolia*. In plot I, the upper Andean dwarf-forest zoochory is the most important form of dispersal, 78% on coverage basis (percentages without brackets) and (46%) on a species basis (percentages between brackets), in which

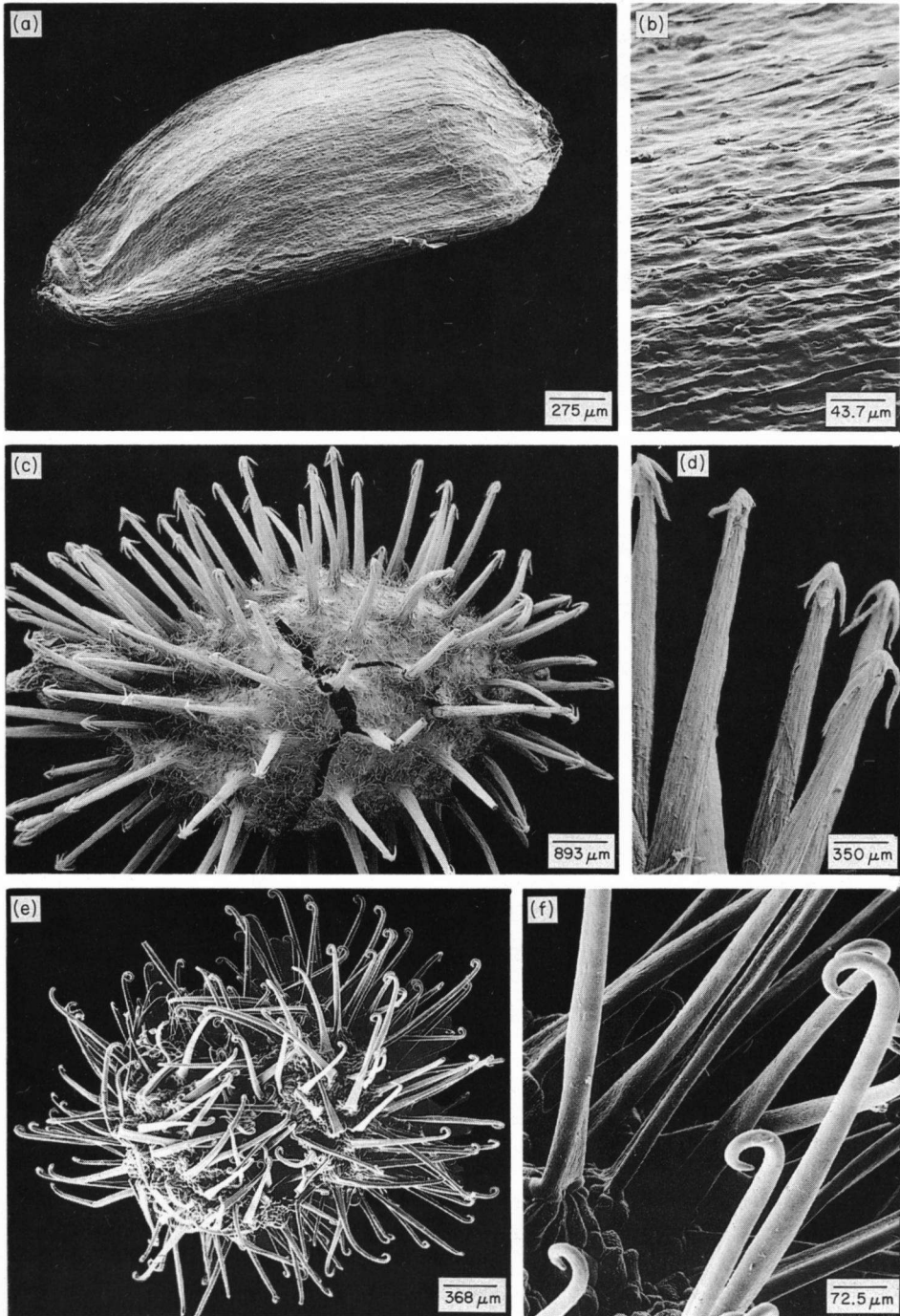


Fig. 1. Scanning photographs of (a) *Espeletia grandiflora* (barochory), (b) *E. grandiflora* detail of fruit wall, (c) *Acaena elongata* (epizoochory), (d) *A. elongata* detail of the barbs, (e) *Galium canescens* (epizoochory) and (f) *G. canescens* detail of the hooks.

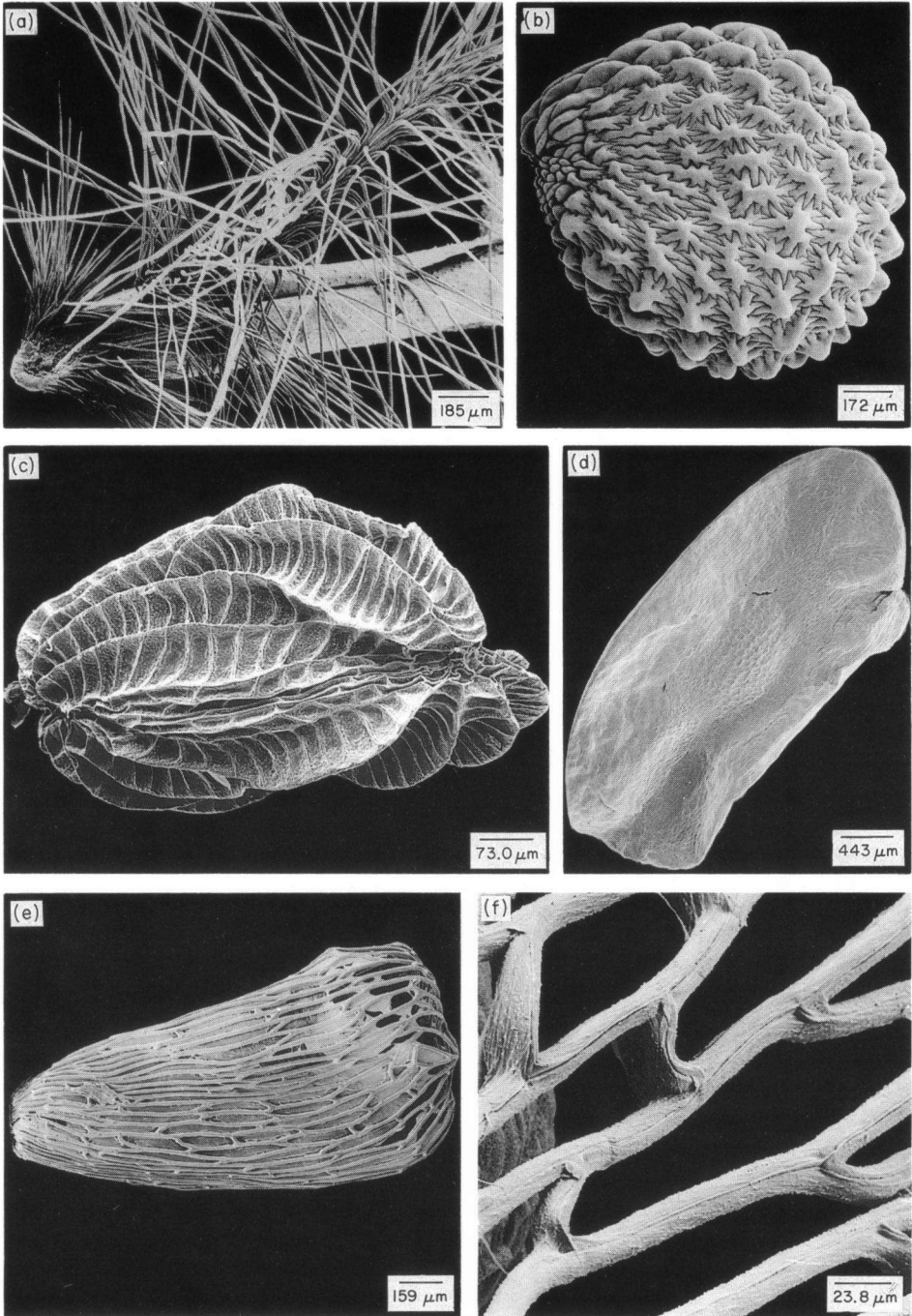


Fig. 2. Scanning photographs of (a) *Calamagrostis effusa* (anemochory) plumed diaspore, (b) *Cerastium subspicatum* (anemochory, windballist) diaspore without adaptation, (c) *Bartsia santolinifolia* (anemochory, windballist) diaspore without adaptation, (d) *Puya santosii* (anemochory, windballist) winged diaspore, (e) *Castilleja fissifolia* (anemochory, windballist) balloon and (f) *C. fissifolia* detail of balloon.

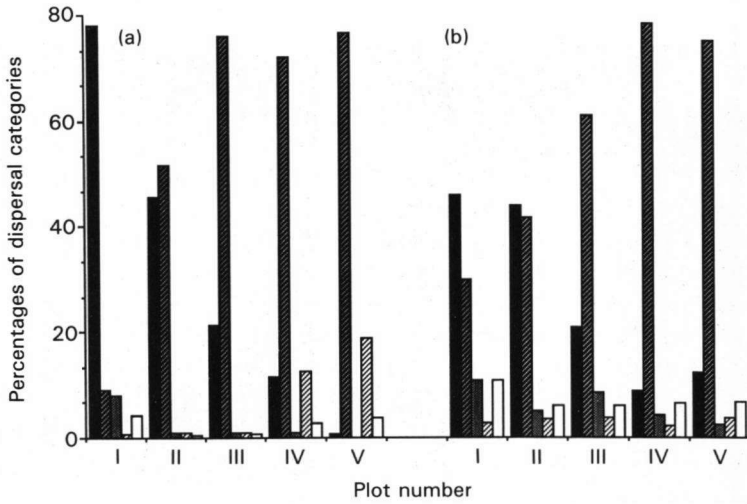


Fig. 3. Dispersal spectra. Percentages of the dispersal categories per plot, on coverage basis (a) and on species basis (b). Plot I-V arranged according to the altitudinal zonation. (■) Zoochory, (▨) anemochory; (▩) autochory, (▧) barochory and (□) unknown.

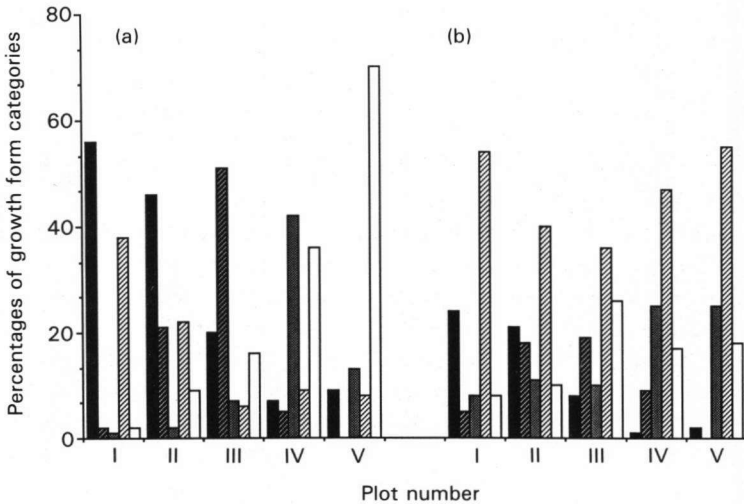


Fig. 4. Growth form spectra. Percentages of the growth form categories per plot, on coverage basis (a) and on species basis (b). (■) Trees, (▨) shrubs, (▩) dwarf-shrubs, (▧) herbs and (□) graminoids.

endozoochory takes the greatest part 56% (27%). The most abundant growth forms are trees 56% (24%) and herbs 38% (54%). In the growth form spectra the differences between the spectra based on coverage and on a species basis (Fig. 4) are marked. On a coverage basis trees are the most important growth form, followed by the herbs. In the spectrum on species basis it is the other way around, but in both spectra these growth forms are dominant.

Plot II, at an altitude between 3400 m and 3420 m, with an average number of 32 plant species, is located in the shrub-páramo along little brooks and is therefore humid. These dwarf-forests can be considered as azonal continuations of the upper Andean dwarf forest-line. They are described as an azonal *Escallonia myrtilloides* dwarf-forest with *Hesperomeles ferrugineus* and *Symplocos theiformis* and a more zonal *Ageratina tinifolia* forest with *Weinmannia microphylla* and *Miconia elaeoides*. In this humid rivershore-forest trees are the most important growth form in percentage cover. Shrubs, which are virtually absent in the upper Andean dwarf-forest 2% (5%) represent 21% (18%) here. The dispersal shows a swing towards anemochory and a decrease in zoochory. This is not due to the increase of shrubs, which are for about 80% endozoochorous (*Miconia elaeoides*, *Vaccinium floribundum*), but to the replacement of the endozoochorous trees by anemochorous ones such as *Ageratina tinifolia*, *Escallonia myrtilloides* and *Weinmannia microphylla*.

Plot III, representing the shrub-páramo, at an altitude between 3390 m and 3560 m, has an average number of 33 plant species and belongs to the community of *Escallonia myrtilloides*. In plot III shrubs are the most important growth form 51% (19%). Trees have decreased both in percentage cover and in species number. Herbs, 6% (36%), also decreased but graminoids take up a large part, 16% (26%). In the dispersal spectra, wind dispersal again increased while zoochory declined.

Plot IV, at an altitude between 3500 m and 3620 m, has an average number of 22 plant species, represents the dwarf-shrub-páramo, and belongs to the community of *Arcytophyllum nitidum* with *Calamagrostis effusa*. The spectra of the dwarf-shrub-páramo, plot IV, resemble the spectra of the shrub-páramo, but in the dwarf-shrub-páramo there is a rise of barochory (that is almost lacking in the shrub-páramo) and a replacement of shrubs by dwarf-shrubs as the most important growth form 43% (25%).

Plot V, at an altitude between 3530 m and 3720 m contains an average number of 22 plant species, and represents an open grass-páramo. There are two plant communities in this plot, one of *Azorella cuatrecasii*, and one of *Baccharis tricuneata*, both with *Calamagrostis effusa* and *Espeletia grandiflora*. There is almost no zoochory in coverage. Anemochory 77% (79%), and barochory, 19% (4%), are the most important dispersal strategies. The barochory percentage is based on *Espeletia grandiflora* alone (*Brachyotum lindenii*, *Luzula gigantea* and *L. racemosa* do not attain coverage percentages > 1%), which, especially in the grass-páramo, can reach high percentages of coverage. *E. grandiflora* is considered to be barochorous, in spite of observations of birds active on *E. grandiflora*, because the seeds are relatively heavy and do not show any adaptation to one of the dispersal strategies; the flowering heads bend down when the seeds are mature, and around the somewhat older *E. grandiflora* individuals a circle of younger plants is nearly always present.

Relations between dispersal types and growth forms

In order to determine a possible relation between the dispersal types and the growth forms one needs to know which mode of dispersal the growth forms use in each plot and of which growth forms the different dispersal types consist.

Except for epizoo- and autochory, which are restricted to herbs, the remainder of the dispersal types occur in more than one growth form. Both epizoo- and autochory have their optimum in plot I, the upper Andean dwarf-forest: 21% (14%) and 8% (11%) respectively, and decline in coverage and number of species with increasing altitude to <1% (7%) and <1% (2%) respectively in plot V, the grass-páramo. In Fig. 5 the percentages to the different dispersal types for each growth form, per plot, is given.

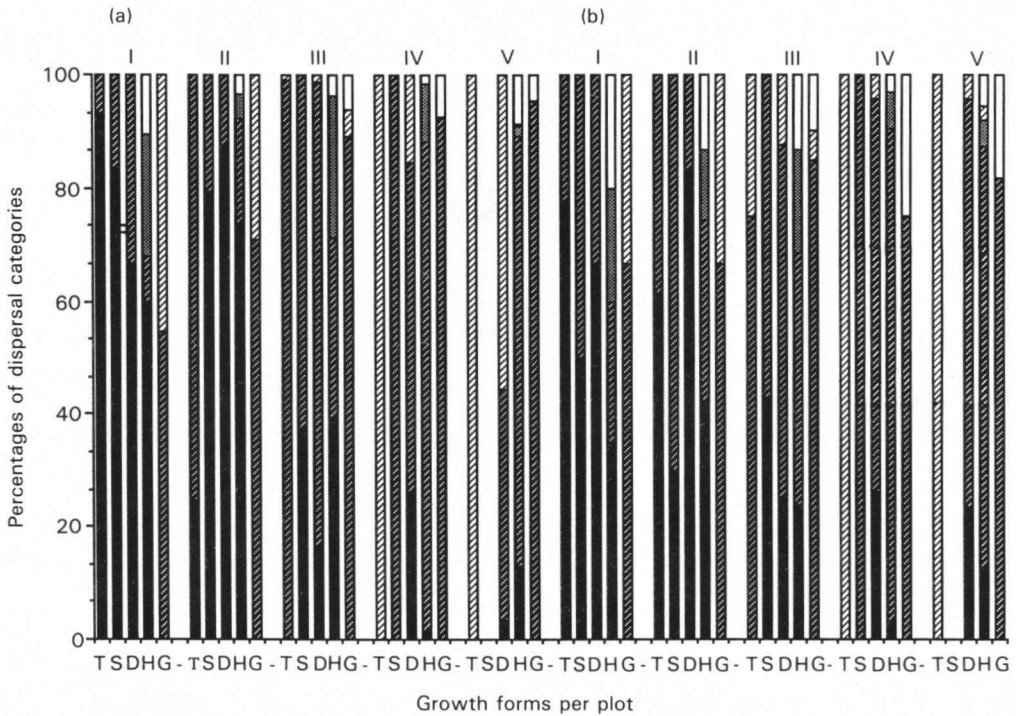


Fig. 5. Percentages of the dispersal categories divided over the growth forms, per plot, on coverage basis (a) and on species basis (b). Growth form categories: T=trees, S=shrubs, D=dwarfshrubs, H=herbs, G=graminoids. (■) Zoochory, (▨) anemochory, (▩) autochory, (▧) barochory and (□) unknown.

Trees show a decrease in endozoochory in the successive plots from 93% (78%) in the upper Andean dwarf-forest, to 25% (62%) in the rivershore-forest, to a total absence of zoochory in plot III, IV and V. The opposite trend is visible in wind-dispersal, which rises from 7% (22%) in plot I to 99% (75%) in plot III. In the dwarf-shrub- and grass-páramo of plot IV and V *Espeletia grandiflora* is the only 'tree'.

Shrubs exhibit the same tendency. In the upper Andean dwarf-forest 83% (50%) of the shrubs are endozoochorous, this falls to 79% (30%) and 37% (43%) in plot II and III, respectively. Wind-dispersed shrubs increase from 17% (50%) in plot I to 100% (100%) in plot IV, the dwarf-shrub-páramo. Shrubs are absent in the grass-páramo.

Dwarf-shrubs are less predictable in the way they exploit the dispersal agents. Again there is a strong decrease in endozoochory from 67% (67%) in plot I to 3% (24%) in plot V, and an increase in wind-dispersal from 33% (33%) to 41% (72%) in the same plots. The reduced increase in wind-dispersal is caused by the strong increase in barochory (*Espeletia grandiflora* individuals below 50 cm) in plot IV and V with 15% (4%) and 56% (4%), respectively. Only in the plot of the rivershore-forest do the values of endozoochory and anemochory in the dwarfshrubs not conform, with percentages of 88% (83%) endozoochory and 12% (17%) anemochory.

Herbs, as already stated, constitute the only growth form category which exploit epizoochory. After a remarkable shift (apart from an increase in zoochory from 60% (35%) to 73% (42%)) from epi- to endozoochory from plot I to plot II, zoochory decreases with increasing altitude. Anemochory, also in herbs, increases from 8% (25%) in plot I to 76% (75%) in plot V.

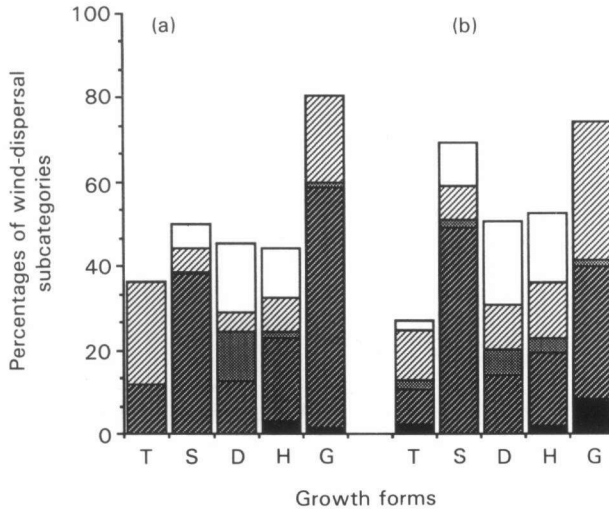


Fig. 6. Percentages of the wind-dispersal subcategories divided over the growth forms, irrespective of the plots, on coverage basis (a) and on species (b). For abbreviation of growth forms see Fig. 5. (■) Balloons, (■) plumes, (■) winged diaspores, (■) wind wa and (□) windballistics.

In graminoids wind is the chief dispersal agent in all plots and its importance increases from 55% (67%) in plot I to 95% (82%) in plot V. Barochory, the other dispersal strategy decreases from 45% (33%) in plot I to 0% (0%) in the plots IV and V. We have to bear in mind that graminoids only account for 2% and 9% of the coverage and for 8% and 10% of the species in the plots I and II.

Irrespective of the location of the plots, among the wind-dispersed diaspores, plumed diaspores account for more than 10% (8%) of the diaspores in all growth forms (Fig. 6). In the shrubs, herbs and graminoids, plumed diaspores are the most important with 38% (49%), 20% (18%) and 57% (32%) of the diaspores, respectively. Balloons and winged diaspores represent the lowest percentages in the growth forms, with the exception of winged diaspores in the dwarf-shrubs which account for 12% (6%) of the diaspores. Diaspores without distinct adaptations are most common in trees 24% (12%) and graminoids 21% (33%). Windballistics, which is not a morphological adaptation of the diaspore but a special method of wind-dispersal, occurs mostly in dwarf-shrubs (mainly because of the share of *Arcytophyllum nitidum*) 16% (20%) and herbs 12% (17%).

Phenological state

In order to ascertain the distribution of the phenology of the species, the phenological state of the species in the relevés supplemented by field observations outside the plots, was recorded (unpublished data). In general, flowering and fruiting occurs somewhat earlier down-slope than it does up-slope (Cleef, personal communication). Although the data are not complete the ratio between flowering, fruiting and vegetative individuals of the recorded species is fixed. In the rainy season one-third of the individuals are flowering, one-third fruiting and one-third vegetative.

Dispersal categories and the weight classification

The weight classes with the heaviest diaspores (> 100 mg), VII and VIII (Fig. 7), only occur in endozoochorous species with berries, such as *Hesperomeles ferrugineus*, *Pernettya pro-*

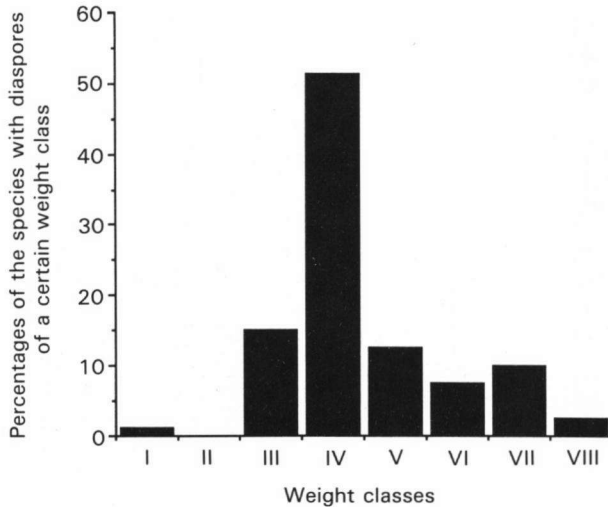


Fig. 7. Percentages of the species with diaspores of a certain weight class. Weight classes: I = <0.001 mg, II = 0.001–0.01 mg, III = 0.01–0.1 mg, IV = 0.1–1 mg, V = 1–10 mg, VI = 10–100 mg, VII = 100–1000 mg, VIII = > 1000 mg.

strata and *Vaccinium floribundum*. In weight class VI (10–100 mg), epi-, endozoochorous and autochorous species are to be found. In weight class V (1–10 mg) endozoochorous species disappear and wind-dispersed species such as *Holodiscus argenteus* and *Rhynchospora* div. sp. appear. The barochorous diaspores of *Espeletia grandiflora* also belong to this class. Weight class IV (0.1–1 mg) comprises 51% of the total number of species of all plots combined (of which the weight was determined). Apart from some epizoochorous species (only those with sticky surfaces) and *Oxalis* sp, which is autochorous, these are mainly wind-dispersed species. To this class the myxochorous species of *Plantago* also belong. Weight class III (0.01–0.1 mg) only contains wind-dispersed diaspores and the weight classes I and II are not represented, except for *Altensteinia fimbriata*, with dust diaspores in class I.

DISCUSSION

From the data presented, it is clear that the dispersal and growth form spectra differ between the subsequent páramo regions. With regard to the modes of dispersal this change follows an obvious trend. With increasing altitude zoochory declines and anemochory increases. The growth form spectra also change. Most of the growth forms have their optimum in a different region which is not surprising because the growth form was a criterion on which the different páramo regions were distinguished (Cleef 1981). One region can contain several plant communities (Cleef 1981), plot V for instance, consists of two communities, one of *Baccharis tricuneata* and one of *Azorella cuatrecasii*, both with *Calamagrostis effusa* and *Espeletia grandiflora*, which slightly differ in dispersal and growth-form spectra. The changes between the spectra of zonal communities in one (sub)zone are markedly smaller as compared to the changes in spectra between such communities in different altitudinal zones. It is worthwhile investigating whether this also holds for other zonal páramo communities.

With increasing altitude both the coverage and the number of the zoochorous species decrease. Zoochory is unimportant in the grass-páramo. Going from the upper Andean

dwarf-forest to the grass-páramo the main growth form of the endozoochorous species (epizoochory is restricted in its occurrence to herbs) changes, from trees in the upper Andean dwarf-forest to mainly shrubs in the rivershore-forest, shrubs in the shrub-páramo and to dwarf-shrubs in the dwarf-shrub- and grass-páramo. Although shrubs constitute the main growth form in endozoochory in the shrub-páramo, 63% of the shrubs turn out to be anemochorous, which accounts for 44% of the anemochory in the shrub-páramo. In the dwarf-shrub-páramo where dwarf-shrubs account for all the endozoochory, 58% of the dwarf-shrubs are anemochorous.

More or less the same happens in the anemochorous species. Their growth form also changes with increasing altitude, but both number and coverage of the anemochorous species also increases. In the upper Andean dwarf-forest there is hardly any wind dispersal, trees and herbs being the growth forms with the highest percentages of anemochory. This feature shifts to trees in the rivershore-forest and to shrubs in the shrub-páramo (when *E. grandiflora* is disregarded, all trees in the shrub-páramo are anemochorous, while 37% of the shrubs are still endozoochorous, accounting for 90% of the endozoochory in the shrub-páramo). In the dwarf-shrub-páramo it shifts to dwarf-shrubs and graminoids. By now trees do not occur, *E. grandiflora* excepted, and all the shrubs are anemochorous while dwarf-shrubs are still endozoochorous (26%) which accounts for all of the endozoochory. In the grass-páramo graminoids exhibit the highest percentages of anemochory. Trees and shrubs are absent from the grass-páramo and 3% of the dwarf-shrubs are still endozoochorous which again accounts for all of the endozoochory. This tendency of increasing anemochory and decreasing endozoochory with increasing altitude is not only due to the differences between the growth form spectra in the subsequent plots but also to the changes in dispersal strategy within the same growth form category.

Except for auto- and epizoochory, the dispersal strategies are not restricted to, or even show a relation to, one special growth form. These results supplement the observations of Gentry (1982) who worked only in one zone, the neo-tropical lowland forest below 300 m altitude. His data suggested a tendency of the growth forms of the rainforest towards a specialization in dispersal (Fenner 1985), even in a gradient of increasing precipitation.

Barochory records, as already stated, are mainly based on the contribution of just one species, *Espeletia grandiflora*, which is aspect-determining in the grass-páramo. With increasing altitude the coverage of the barochorous species also increases while the barochory on a species basis remains almost constant. Barochory is not of great importance except in the dwarf-shrub- and grass-páramo. As *E. grandiflora* is classified into the growth forms 'tree' and 'dwarf-shrub', and because it can attain a high coverage, it strongly influences the numerical dispersal spectra of trees and dwarf-shrubs.

Within anemochory, balloons can be neglected, and plumed diaspores occur most frequently. The plumed diaspores have an optimum in coverage in the grass-páramo because of *Calamagrostis effusa*, the most abundant grass. Winged diaspores which, except for *Rumex acetosella*, also belong to windballists represent a very small group in the studied area on a species basis. Winged diaspores and diaspores without adaptations, which also nearly always belong to windballistic species, have their coverages in the shrub- and dwarf-shrub-páramo. There is no trend visible of a concentration of a special morphological adaptation in one growth form or of passing through a series of growth forms.

Owing to the absence of relevant data from other tropical alpine environments a comparison cannot be made. The assumption that páramos do not show special adaptations to dispersal also cannot be tested.

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