南日本の付着散布植物の生態的特徴

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Hiroki Nakanishi : **Ecological characteristics of epizoochorous plants in southern Japan**

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Abstract

Epizoochorous plant ecology, plant form and their disseminules were investigated in southern Japan. Most epizoochorous plants are perennial herbs which grow on forest margins. The potential dispersal season was chiefly from autumn to winter with three or four months duration. The height of disseminule positions on the plant body is comparatively high, usually from 40 to 80 cm. Some species have disseminules whose highest position is more than 100 cm. The infructescences of these plants are mainly elongate and branching type, and are clearly advantageous to attachment to animals. The disseminules of the plants are fruits or fruits with persistent organs such as calyx or bract, with disseminule weights being comparatively heavy among herbaceous plants. Disseminules attaching by burrs are usually heavier than those attached by mucilage. These ecological characteristics of epizoochorous plants were discussed.

Key words : attachment, disseminule, epizoochory, infructescence, seed dispersal.

Seed dispersal by animals has been frequently studied as one of the most interesting aspects of dispersal ecology, especially seed dispersal by birds and by ants. Epizoochory, seed dispersal by attaching animal fur and human clothes has been described in general (e.g. Ulbrich 1928 ; Ridley 1930 ; Müller 1955 ; van der Pijl 1972). There are, however, still relatively few empirical studies on the epizoochorous dispersal (Carlquist and Pauly 1985 ; Sorensen 1986 ; Nakanishi 1989 ; Kiviniemi 1996).

Epizoochorous plants do not provide any food rewards to the disseminators unlike endozoochory and myrmecochory, and do not have any means of attraction like brightness and fragrance. This is not to say that there is no relationship between these plants and their disseminators. One of the most interesting subjects in epizoochory is certainly the morphology of disseminules with their spines, hooks and viscid exudates. Some efforts to explain the subject have been done (Ridley 1930 ; Sorensen 1986 ; Nakanishi 1989). Sorensen (1986) and Kiviniemi (1996) suggested that the location of the diaspores on an animal's body affect their retention. In order to understand fully the plant and animal relationship, plant form such as plant height and shape of infructescence must be studied as well as disseminule morphology, because these characters influence the position of attachiment on an animal's body.

The present study aims to examine the general ecological characteristics of epizoochorous plants, plant form for and disseminule morphology in relation to dispersal, and to discuss their adaptations for attaching dispersal in southern Japan.

Methods

For this study, epizoochorous plants were regarded as plants whose disseminules have some kinds of apparatus for attachment to animal fur or human clothes. Data on growth habits, habitats, dispersal season, plant form and attaching methods were collected in the field. Most field observations were done in Nagasaki Prefecture, western Kyushu and the others were done in Hiroshima Prefecture, western Honshu. The habi-

tats were classified into four categories: ruderal sites such as roadside and paddy field margins, forest margins, forest floor and grassland. The potential dispersal season was indicated by the month of the dispersal beginning and ending. Dispersal season was referred from when plants had dispersed more than about 10% of their disseminules, to when the individuals had dispersed almost more than about 90% of all disseminules. These percentages were roughly estimated in several localities. Based on the data for the dispersal season of each species, percentage frequency of every ten days, the number of species which were in the dispersal season to the total number of species observed, was accounted. Two aspects of plant morphology were recorded, the height of the disseminule position on plants and infructescence types. The highest and lowest of disseminule position height was measured from the ground level on ten individual plants of each species. This height varied on the same species plants depending on the growing conditions. Consequently, the average range of height was given. Infructescence types were classified into six by the extension of disseminules on plantbody: elongate, branching, short branching, branching-elongate, brushy and separate type (Fig. 1). Elongate type has infructescences that elongate during or after flowering. Branching type has infructescences that are well branched and short branching type has those shortly branched. Branching-elongate type possesses both branching and elongate characteristics. Brushy type has short infructescences where disseminules concentrate on top of the plant. Separate type has separate heads. In elongate type, special attention was also paid to the length of infructescence. Three hundred disseminules of each species were collected in the field and dried for about a month in the laboratory. They were weighed in lots of 100 with a Sartorius analytical balance. Attaching methods were divided into adhesion by burrs, spines and mucilage that the disseminules exuded. Based on these data, per-

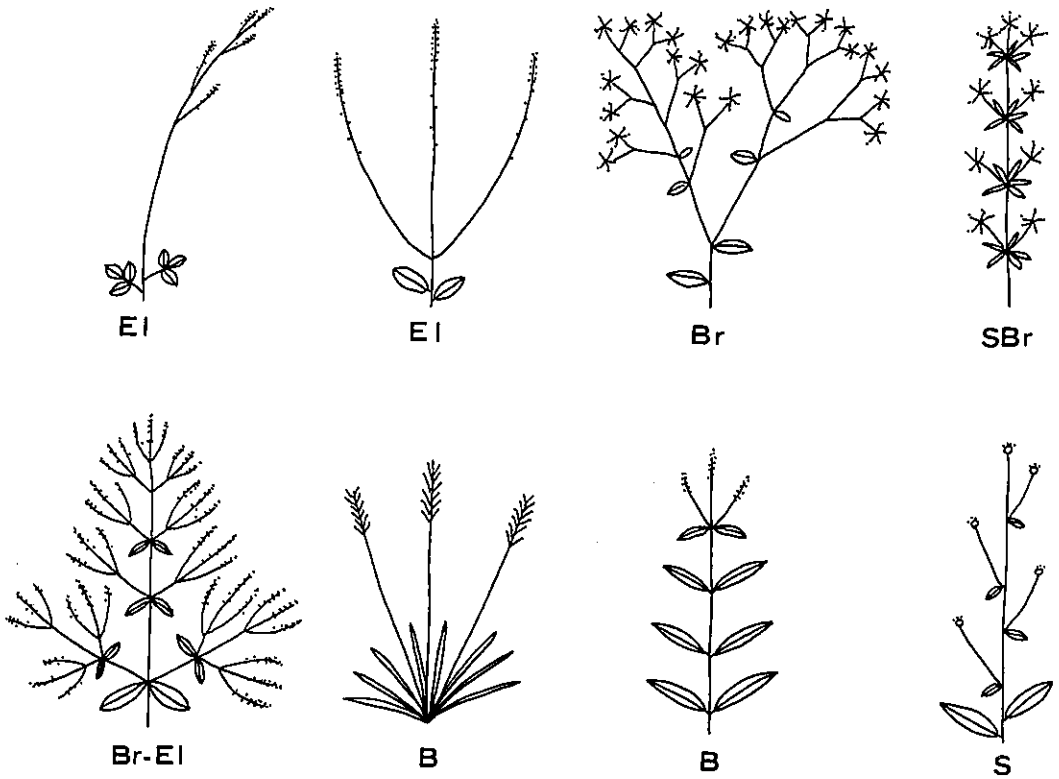

Fig. 1. Infructescence type. El: elongate type; Br: branching type; SBr: short branching type; Br-El: branching-elongate type; B: brushy type; S: separate type.

centage frequency of number of species in the weight class of Baker (1972) which was constructed on a logarithmic basis are accounted in differences of adhesive method. Nomenclature follows Ohwi and Kitagawa (1983).

Results

Epizoochorous plants of 11 families, 20 genera and 44 species including 2 varieties which were counted as a species respectively were observed. They are almost all of the epizoochorous species in southern Japan. The list including growth habits, habitats and potential dispersal season is arranged in Appendix 1. All epizoochores observed except *Desmodium caudatum* which is a small shrub are herbs; 82.2% of which are perennial and 15.6% annual. Most species are found on the forest margins (57.8%), followed by ruderal sites (22.2%) and forest floor (13.3%). Only three species (6.7%) grow on grasslands. Species found on forest margins usually composed the skirt or sleeve plant communities close to secondary forests or afforestations with other herbaceous species. The change of percentage frequency of every ten days in species which were actively dispersing seeds is shown in Fig. 2. There were only a few species (less than 20%) whose dispersal season was from spring to summer. Some *Galium* species and *Torilis scabra* dispersed from May and June. More than 70% of species are dispersed from October to December. There were a number of species which were dispersed through winter time. Most species had long dispersal durations, of about three or four months (Appendix 1). Even after withered, the stems and infructescences with disseminules were still upright during winter.

The data on disseminules position height and infructescence type are summarized in Appendix 2. Disseminule positions height greatly varied according to species and individuals. The highest disseminules occurred in *Desmodium oldhamii* while the lowest was *Circaea alpina*. The percentage frequency of the height classes is shown in Fig. 3. Most species investigated had disseminules whose position was higher than 60 cm (80.1%) and whose lowest was higher than 40 cm (62.2%). Some species disseminules (15.6%) were higher than 100 cm. Frequent infructescence types were the branching (35.6%) and elongate type (24.4%) (Table 1). Species with higher disseminule positions were dominated by the elon-

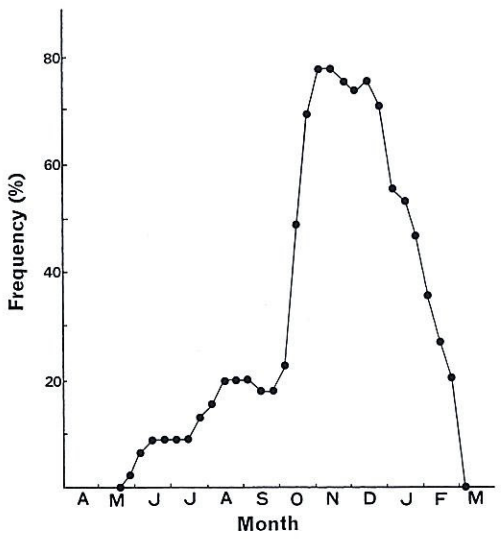

Fig. 2. Change of percentage frequency of every ten days in epizoochorous species which are actively dispersing seeds.

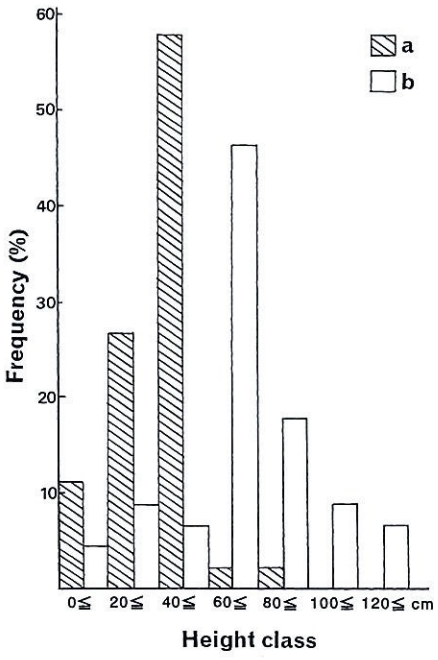

Fig. 3. Percentage frequency of the height classes in epizoochorous species. a: lowest height; b: highest height.

Table 1. Frequency of infructescence type

Infructescence type	No. of species (%)
branching type	16 (35.6)
elongate type	11 (24.4)
separate type	6 (13.3)
brushy type	5 (11.1)
branching-elongate type	4 (8.8)
short branching type	3 (6.7)

gate, branching and branching-elongate type. Elongate type infructescences were very long in proportion to plant height and occupied from one -half to two thirds of plant height (Appendix 2).

The weight, disseminules morphology, and attaching methods are shown in Appendix 3. The disseminule weights varied from 5029.1 mg for *Desmodium oldhamii* to 32.3 mg for *Carpesium abrotanoides*. But there were only two other species whose disseminule weight was less than 100 mg besides the genus *Carpesium*. The frequency number of species of weight class are shown in Fig. 4. The disseminules attached by viscidity were most frequent in weight class 6 and those by burrs in weight class 8. The viscid disseminules were generally lighter than those with burrs. The average weights of 100 disseminules were 300.6 mg and 764.1 mg, respectively. The

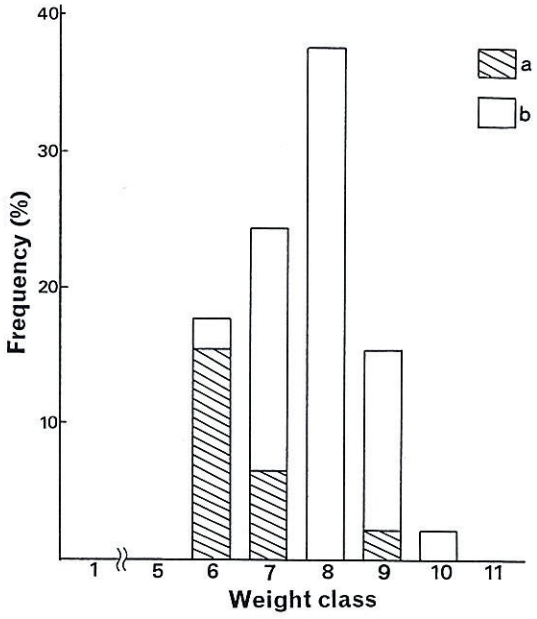

Fig. 4. Percentage frequency of the seed weight classes (Baker 1972) in epizoochorous species. a: by viscidity; b: by burrs.

Table 2. Frequency of disseminule type

Type	No. of species (%)
fruitlet	16 (35.6)
fruit	11 (24.4)
fruit + glume	5 (11.1)
fruit + calyx	5 (11.1)
fruit + bract	3 (6.7)
fruit + style	2 (4.4)
fruit + calyx + bract	2 (4.4)
fruitlet + style	1 (2.2)

difference between them was statistically significant from results of t-test ($T=4.41$, $p<0.001$).

No epizoochorous disseminules consisted of only seeds. They were all fruits, fruitlets or fruits with persistent organs such as calyx and bract (Table 2).

Discussion

The epizoochorous species are frequently found on forest margins and among an abundant component species of skirt or sleeve plant communities (Müller 1962; Dierschke 1974; Nishimura and Toyohara 1985). The forest margin is area where large mammals including man can pass easily and thereby the chance of attachment might be increased in humid climate zone such as Japan where there is in general ample precipitation for the development of forest. Some epizoochorous species are also found at ruderal sites such as roadside and paddy field margins where human activities are evident. Nowadays the human is an important disseminator for epizoochores.

Epizoochory is a seed dispersal way of plants which directly touch animals passing through. Then, the height of the disseminule positions may be very important. Epizoochores being all herbs except *Desmodium caudatum* are low plants (Ridley 1930; Harper et al. 1970; Gentry 1983; Sorensen 1986; Hughes et al. 1994). But the height of the epizoochores disseminule positions may be comparatively high for herbaceous plants. If frequency of attachment is related to both dissemnule height on plants and mammals height, most epizoochorous species would be adapted to attachment not to small or medium size mammals but to large mammals such as bears and deer. Most mammals are active, often

running and jumping so that higher positioned disseminules can attach to animal body. I have often experienced disseminules of higher positions attaching themselves to my socks and shoe strings. So in many cases the higher positions of disseminules may be more advantageous than the lower ones.

Most species investigated have elongate infructescences. They are much longer compared to plant height. Some species of elongate type have infructescences which are slender and bent by the weight of disseminules. They straighten slowly as disseminules disperse. Consequently, the position of remaining disseminules becomes higher. The branch and branch-elongate type infructescences allow omnidirectional disseminule attachment. The infructescences of elongate, branch and branch-elongate type may be suited to attachment to animal bodies.

Only few species had dispersal seasons from spring to summer. During this time plant growth is quick. The dense vegetation may be obstructive to contact between disseminules and animals. However, in late autumn and winter most herbaceous plants wither and easily make dispersers contact epizoochorous plants with disseminules.

Epizoochore disseminules are not seeds but dry fruits (fruitlets) or fruits with other persistent organs. This may be owing to the fact that the disseminules are accompanied with attaching mechanisms. This reflects the disseminule weight. Tateda and Ishikawa (1968) reported that more than half of disseminules of 450 wild species were lighter than 1 mg. The most frequent class of disseminule weight in herbaceous plants is class 6 (0.316–0.919 mg) in California (Baker 1972) and 0.316–1mg in the alpine zone of Mt. Shirouma in Japan (Nakagoshi and Soga 1981). From these results the mean weight of one disseminule can be estimated at most 1 mg. Most epizoochous plants have heavy disseminules, the viscid disseminules were 3.0mg on average and the those with burrs were 7.6mg. Epizoochorous dispersal is chiefly by mammals, so that disseminule weight may not be an important limiting factor as with ants in myrmecochory (Nakanishi 1988). The viscid disseminules were generally lighter than those with burrs. The attachment to animal body by mucilege could not supporte the heavier disseminules than those by burrs.

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中西弘樹：南日本の付着散布植物の生態的特徴

南日本に分布する付着散布植物11科20属44種2変種について，生態，散布のための形態，散布体について調べ，論議した。ほとんどの付着散布植物は多年生草本で，林縁に生育していた。林縁部は他の生育環境に比べ動物がより頻繁に通過する所であり，付着散布に適した場所と言える。散布季節は主として秋から冬の間で，3〜4カ月と長い。この季節は他の植物が枯れるため，付着の妨げになるものが少なくなり，しかも散布期間が長いことはそれだけ動物に付着する可能性が高くなると考えられる。植物体における散布体の位置は比較的高く，多くが40〜80センチの間にあり，中には100センチを越えるものもあった。また果序は特徴的で植物体に比べて長かったり，頻繁に枝分かれしているものが多かった。これらの形態的特徴は，明らかに動物に付着しやすくなっていると考えられる。散布体は種子だけのものはなく，果実または萼とか苞などが付属した果実であり，その重量は草本植物としては重かった。付着散布は多くが哺乳類によって散布されるため，運搬の重量はそれほど妨げとならないであろう。また棘で付着するものの方が粘液で付着するものよりも重かったが，粘液による付着方法は，棘による方法より，より重い散布体を支えられることができないためと考えられる。

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Appendix 1

Epizoochorous species in the warm temperate zone of Japan, with their growth habits, habitats and dispersal season. Nomenclature follows Ohwi and Kitagawa (1983). Growth habit: P: perennial; A: annual; S: small shrub. Habitats: Rs: ruderal site; Fm: forest margin; Ff: forest floor; Gr: grassland. Dispersal season: e: early; m: middle; l: late.

Family and species	Growth habit	Habitat	Dispersal season
Amaranthaceae			
Achyranthes fauriei	P	Rs	mOct.-lFeb.
A. japonica	P	Fm	mOct.-lFeb.
Boraginaceae			
Cynoglossum zeylanicum var. *villosulum*	A	Fm	mAug.-eOct.
Compositae			
Adenocaulon himalaicum	P	Fm	lOct.-lDec.
Adenostemma lavenia	P	Fm, Ff	lOct.-lFeb.
Bidens biternata	A	Rs	lOct.-eJan.
B. pilosa	A	Rs	lOct.-eFeb.
B. tripartita	A	Rs	mOct.-lDec.
Carpesium abrotanoides	P	Fm	eNov.-lFeb.
C. cernuum	P	Fm	eNov.-lFeb.
C. divaricatum	P	Fm	eNov.-lFeb.
C. glossophyllum	P	Fm	eNov.-lFeb.
C. rosulatum	P	Fm	eNov.-lFeb.
C. triste	P	Fm	eNov.-lFeb.

(continued)

Family and species	Growth habit	Habitat	Dispersal season
Sigesbeckia glabrescens	P	Rs	lOct.-lDec.
S. orientalis	P	Rs	lOct.-lDec.
S. pubscens	P	Rs	lOct.-lJan.
Gramineae			
Lophatherum gracile	P	Fm	mOct.-lDec.
L. sinense	P	Ff	mOct.-lDec.
Oplismenus compositus	P	Ff, Fm	mOct.-mDec.
O. undulatifolius	P	Ff, Fm	mOct.-mDec.
Pennisetum alopecuroides	P	Rs	lOct.-lJan.
Leguminosae			
Desmodium caudatum	S	Fm	mDec.-lFeb.
D. fallax	P	Fm	mOct.-mJan.
D. heterocarpon	P	Gr	mOct.-mNov.
D. laxum	P	Ff	eOct.-lJan.
D. oldhamii	P	Fm	lOct.-mJan.
D. oxyphyllum	P	Fm	eOct.-mFeb.
D. podocarpum	P	Fm	mOct.-lJan.
Onagraceae			
Circaea alpina	P	Fm	eAug.-eSept.
C. erubescens	P	Ff, Fm	mAug.-lOct.
C. mollis	P	Fm	mOct.-lJan.
Phrymaceae			
Phryma leptostachya var. *asiatica*	P	Ff, Fm	lAug.-mNov.
Polygonaceae			
Polygonum filiforme var. *filiforme*	P	Fm	mOct.-mFeb.
var. *neofiliforme*	P	Fm	lOct.-lFeb.
Rosaceae			
Agrimonia pilosa	P	Fm	mOct.-eFeb.
A. nipponica	P	Fm	mOct.-lDec.
Geum japonicum	P	Fm	lSept.-eFeb.
Rubiaceae			
Galium japonicum	P	Ff	eJune-mOct.
G. pogonanthum	P	Gr	eJune-eOct.
G. spurium var. *echinospermon*	A	Rs	lMay-lJuly
Umbelliferae			
Osmorhiza aristata	P	Ff, Fm	lJuly-lOct.
Sanicula chinensis	P	Fm	mOct.-mJan.
Torilis japonica	A	Gr	lJuly-eOct.
T. scabra	A	Rs	mMay-mSept.

Appendix 2

Height of disseminules position and infructescence type. Average height is indicated with the 95% confidence limit in parentheses. Infructescence type: El: elongate type; Br: branching type; Br-El: branching-elongate type; S: separate type; B: brushy type; SBr: short branching type, average length of infructescence in parentheses.

Species	Highest height (cm)	Lowest height (cm)	Infructescence type (cm)
Desmodium oldhamii	137.8 (116.0–159.6)	90.8 (75.3–106.3)	El (78.6±22.7)
Bidens pilosa	137.7 (119.5–155.9)	85.3 (67.1–103.5)	Br
Sigesbeckia pubescens	136.6 (113.1–160.2)	52.0 (44.5– 59.5)	Br
Cynoglossum zeylanicum var. *villosulum*	107.3 (103.8–110.8)	48.8 (43.4– 54.2)	Br-El
Carpesium abrotanoides	104.9 (77.7–132.1)	51.4 (36.3– 66.6)	Br
Achyranthes japonica	103.2 (88.4–118.1)	56.9 (49.8– 63.9)	Br-El
Lophatherum sinense	101.6 (85.5–117.4)	51.4 (49.1– 53.7)	El (53.3±2.1)
Achyranthes fauriei	96.3 (86.3–106.2)	32.9 (29.0– 36.9)	Br-El

(continued)

Species	Highest height (cm)	Lowest height (cm)	Infructescence type (cm)
Sigesbeckia orientalis	96.0 (87.4–104.6)	39.5 (32.6– 46.4)	Br
Desmodium oxyphyllum	93.8 (63.3–124.3)	58.6 (49.7– 67.5)	El (68.4±19.7)
D. podocarpum	89.8 (85.2– 94.5)	56.5 (52.5– 60.6)	El (52.3±11.8)
Adenostemma lavenia	89.4 (80.6– 98.3)	55.4 (45.9– 64.9)	Br
Desmodium laxum	87.6 (71.7–103.4)	56.4 (45.3– 71.6)	El (76.4±10.1)
Sigesbeckia glabrescens	83.8 (80.2– 97.4)	43.2 (31.1– 55.3)	Br
Geum japonicum	82.0 (72.4– 91.6)	48.3 (38.7– 57.9)	Br
Torilis scabra	80.5 (70.7– 92.6)	58.4 (42.2– 63.3)	Br
Polygonum filiforme var. *filiforme*	79.5 (68.2– 90.8)	43.1 (37.9– 48.4)	El (39.7±7.8)
Circaea mollis	78.0 (64.2– 91.9)	43.9 (37.2– 50.7)	Br
Torilis japonica	76.8 (69.5– 84.1)	52.0 (45.0– 59.0)	Br
Polygonum filiforme var. *neofiliforme*	76.7 (61.1– 92.4)	44.3 (36.9– 51.7)	El (40.7±5.9)
Carpesium cernuum	76.6 (66.4– 86.9)	44.0 (36.4– 51.6)	S
Osmorhiza aristata	74.3 (65.3– 83.3)	51.3 (40.2– 62.3)	Br
Bidens biternata	73.8 (63.7– 83.9)	49.3 (39.5– 59.1)	Br
Lophatherum gracile	73.6 (67.0– 80.1)	42.3 (34.2– 50.3)	El (52.2±2.1)
Desmodium fallax var. *mandshuricum*	71.9 (44.2– 99.5)	56.8 (42.3– 71.2)	El (44.9±17.7)
Sanicula chinensis	69.4 (61.4– 77.4)	44.6 (37.2– 52.0)	Br
Phryma leptostachya var. *asiatica*	69.3 (58.3– 80.5)	31.7 (24.9– 38.4)	El (38.7±0.9)
Desmodium caudatum	68.4 (63.7– 73.1)	48.4 (38.2– 58.6)	B
Agrimonia pilosa	68.3 (64.0– 72.5)	39.3 (32.5– 46.0)	Br-El
Carpesium triste	68.3 (62.7– 74.0)	28.3 (25.1– 31.6)	S
C. divaricatum	67.9 (63.5– 73.3)	36.1 (29.4– 42.9)	S
Adenocaulon himalaicum	67.0 (58.3– 75.7)	34.2 (27.8– 40.6)	S
Pennisetum alopecuroides	66.5 (61.7– 71.3)	46.0 (37.2– 54.8)	B
Galium spuricum var. *echinospermon*	65.5 (53.4– 81.6)	14.5 (10.2– 18.8)	SBr
Desmodium fallax	62.9 (49.9– 76.2)	52.5 (48.3– 56.7)	El (52.0±20.0)
Bidens tripartita	61.2 (53.5– 68.9)	18.8 (15.6– 22.0)	S
Oplismenus compositus	56.7 (47.1– 66.2)	49.0 (40.6– 57.4)	B
O. undulatifolius	52.5 (47.4– 57.6)	42.5 (38.2– 46.9)	B
Agrimonia nipponica	45.3 (42.2– 48.3)	22.0 (19.0– 25.0)	Br
Carpesium rosulatum	38.6 (34.4– 42.7)	14.3 (10.1– 18.4)	S
Circaea erubescens	33.0 (31.0– 35.0)	25.1 (23.9– 26.3)	Br
Galium japonicum	23.5 (20.6– 26.4)	21.2 (18.6– 23.8)	SBr
G. pogonanthum	23.0 (18.9– 27.0)	21.9 (17.9– 25.8)	SBr
Desmodium heterocarpon	13.0 (10.7– 15.3)	7.9 (6.5– 9.2)	Br
Circaea alpina	8.5(7.7– 9.3)	7.2 (6.5– 7.9)	B

Appendix 3

Weight and morphology of disseminule, and adhesive methods. Morphology : fr : fruit ; fr.let : fruitlet. Method : B : by burrs ; V : by viscidity.

Species	Weight (mg/100 gr.)	Morphology	Method
Desmodium oldhamii	5029.8±319.2	fr.let	B
Adenocaulon himalaicum	2315.7±14.5	fr	V
Agrimonia pilosa	2055.4±60.0	fr	B
Desmodium laxum	1998.4±145.5	fr.let	B
D. caudatum	1966.1±47.1	fr.let	B

(continued)

Species	Weight (mg/100 gr.)	Morphology	Method
D. oxyphyllum	1637.8±68.9	fr.let	B
D. podocarpum	1307.2±52.9	fr.let	B
D. fallax	1201.0±39.1	fr.let	B
Bidens biternata	1108.4±29.0	fr+calyx	B
Lophatherum sinense	733.4±6.9	fr+glume	B
Osmorhiza aristata	717.9±30.9	fr.let	B
Agrimonia nipponica	709.3±21.9	fr+calyx	B
Torilis scabra	529.9±17.4	fr.let	B
Sanicula chinensis	514.2±11.5	fr.let	B
Polygonum filiforme var. *neo-filiforme*	508.3±28.1	fr+style	B
Achyranthes japonica	506.8±11.5	fr+calyx+bract	B
Lophatherum gracile	467.4±43.8	fr+glume	B
Galium japonicum	460.1±60.8	fr.let	B
Pennisetum alopecuroides	456.9±28.4	fr+glume	B
Circaea mollis	387.3±3.2	fr	B
Phryma leptostachya var. *asiatica*	377.8±9.8	fr+calyx	B
Achyranthes fauriei	370.6±5.4	fr+calyx+bract	B
Galium spurium var. *echinospermon*	337.3±9.2	fr.let	B
Polygonum filiforme	336.7±5.4	fr+style	B
Bidens tripartita	318.1±5.6	fr+calyx	B
Cynoglossum zeylanicum var. *villosulum*	317.2±11.5	fr.let	B
Galium spuricum var. *echinospermon*	303.4±2.1	fr.let	B
Sigesbeckia pubescens	245.4±19.9	fr+bract	V
Bidens pilosa	227.9±25.6	fr+calyx	B
Sigesbeckia glabrescens	227.0±10.6	fr+bract	V
Torilis japonica	224.5±4.9	fr.let	B
Circaea erubescens	176.8±8.5	fr	B
Desmodium heterocarpon	168.9±12.0	fr.let	B
Oplismenus undulatifolius	161.4±3.4	fr+glume	B
O. compositus	144.9±2.9	fr+glume	B
Geium japonicum	142.4±3.1	fr.let+style	B
Sigesbeckia orientalis	125.8±23.4	fr+bract	V
Adenostemma lavenia	84.7±1.3	fr	V
Galium pogonanthum	75.0±0.8	fr.let	B
Carpesium triste	64.1±4.8	fr	V
C. glossophyllum	62.4±5.6	fr	V
C. cernuum	59.4±1.5	fr	V
C. triste	50.0±1.1	fr	V
C. divaricatum	40.5±1.1	fr	V
C. abrotanoides	32.3±1.5	fr	V