ENVIRONMENTAL EFFECTS ON THE SEX RATIO OF *RUMEX ACETOSELLA* L.

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INTRODUCTION

Löve (1944) concluded that there were no cytological reasons to expect a deviation from a 1:1 sex ratio in *Rumex acetosella* L. *s. lat.* His observations of 14 sources supported this conclusion (Table 1).

Recently Harper (1967), in citing unpublished studies by Putwain who investigated the competitive adjustment of the sex ratio of *R. acetosella*, stated that "natural populations have been shown by Löve and many others to have a sex ratio not departing significantly from equality". This was connected with Putwain's results that populations with either sex in excess, readjusted, through a process of vegetative growth, the sex ratio towards 1:1.

Löve presented data for the mean height of staminate and pistillate plants separately for each of the populations of diploid, tetraploid or hexaploid chromosome number. The females were consistently taller than the males for all three ploidies, although this difference was not significant.

METHODS

The observations recorded in this study were made during an examination of the phenotypic and genotypic components of variability of *R. acetosella, s. lat.* Counts were made of staminate and pistillate plants from three sources:

(a) Herbarium specimens covering the greater part of the range of the species *s. lat.*

(b) A random sampling of individuals at forty-four sites in the South Island, New Zealand. Sampling points were spaced to avoid including shoots of the same plant more than once, although in some situations, particularly in recently developed pastures which had been disced and harrowed, the vegetative dispersal of particular genetic individuals over a wide area was likely and complicated the sampling technique.

(c) Plants from sowings of seed samples collected throughout the world. Seedlings were transplanted from seedling flats before deaths from intra-specific competition could occur. Plants were grown until they flowered, in non-competitive layouts at the Botany Department's Experimental Garden, University of Canterbury, Christchurch. There were three separate plantings.

For the samples at each of forty-three South Island sites, the height of matured, intact panicles was measured for staminate and pistillate individuals separately.

RESULTS AND DISCUSSION

The numbers of plants of each sex from the different sources are presented in Table 1.

For the total of all observations, including both Löve's data and mine, the ratio shows a significant deviation from the 1:1 expected because of a greater number of staminate plants. The ratios of material recorded from the herbarium collection, Löve's collection and that recorded from plants cultivated in the glasshouse conform to the 1:1 ratio. For the natural populations a significant overall preponderance of staminate plants is shown. Of the 44 sites for which counts were recorded six had significantly greater numbers of male plants whereas the converse applied to the counts from two sites.

Some bias may have been involved in the collection of staminate as opposed to pistillate individuals, for the following reasons:

(a) In the natural populations, because of differences in the colour or structure (i.e. height, see Table 3) of the staminate as compared to the pistillate panicles, one may have been more conspicuous than the other and accordingly sampled more frequently. In sampling natural populations an attempt was made to randomise the sampling as much as possible. This randomness of choice would not apply to the herbarium collections.

(b) In collecting specimens for herbaria selection of representative individuals of both staminate and pistillate plants may have been made, and this

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TABLE 1. *Numbers of staminate and pistillate individuals of* R. acetosella *in natural populations, South Island, New Zealand.*

SOURCE OF SAMPLE				
LOCALITY	HABITAT	♀	♂	χ^2
Murchison, flats	Roadside	11	9	—
Motupiko, flats	Roadside	12	11	—
Rakaia River	Roadside	14	9	—
Lumsden–Gore	Roadside	14	14	—
Waianakarua	Roadside	15	7	—
Hermitage	Rough scree	10	11	—
Motupiko River	Riverbed	10	10	—
Jacksons	Roadside	10	10	—
Fairlie	Road bank	10	11	—
Rapahoe	Roadside	3	15	**
Clifton	Weedy fallow	10	10	—
Spooner Mountains	Roadside	6	15	(*)
Greymouth, camping grounds	Rough pasture	8	12	—
South Fox River	Old pasture	17	4	**
Westport	Roadside	3	17	**
Five Rivers–Mossburn	Weedy fallow	9	14	—
Lake Rotoiti	Lake foreshore	14	9	—
Mid Dome	Waste, fallow land	11	10	—
Alford Forest	Roadside	13	8	—
Eglinton Valley	New pasture	8	13	—
Homer Tunnel	Roadside	9	10	—
Tekapo–Pukaki	Roadside	18	5	*
Kingston	Roadside	12	9	—
Grassmere–Cass	New pasture	9	16	—
Queenstown–Arrowtown	Roadside	12	10	—
Rotoiti airstrip	New pasture	10	12	—
Rakaia Gorge	Roadside	10	10	—
Lake Wakatipu	Lake foreshore	12	13	—
Te Anau–Mossburn	Roadside	9	11	—
Geraldine	Riverbed pasture	10	14	—
Orari	Riverbed pasture	8	12	—
Manapouri	New pasture	13	6	—
Burkes Pass	Roadside	3	18	**
Lake Wanaka	Waste ground	8	12	—
Tarras	Lucerne–tussock	19	11	—
Bealey	Low tussock roadside turf	9	12	—
Pukaki–Omarama	Low tussock	12	9	—
Lake Tekapo	Low tussock	10	13	—
Crown Range	Tall tussock	6	29	**
Pukaki–Hermitage	Low tussock	15	10	—
Lindis Pass	Low–tall tussock	5	22	**
Cass	Low tussock	9	16	—
Lyndon	Low tussock	4	12	*
Tekapo–Pukaki	Low tussock	6	8	—
All natural populations		447	517	*
Cultivated populations		167	177	—
Observations from Löve (1944) in total (from Table 9, p. 99)		511	528	—
Herbarium observations		1123	1168	—
Total of all observations		2248	2390	*

(*) = $p<0.10$
* = $p<0.05$
** = $p<0.01$

is emphasised by the inclusion of both sexes on the same herbarium sheet in many instances. Furthermore, the importance of the character *angiocarpus contra gymnocarpus* in the taxonomy of the sub-genus may have resulted in the greater sampling of pistillate plants because the character applies to seed.

(c) The ratio of pistillate to staminate plants may be influenced by different capacities for vegetative spread. The observed shoot numbers per container of 82 staminate plants of 49.7 ± 3.1 and of 72 pistillate plants of 52.4 ± 3.4 does not confirm this possibility, as the numbers for each sex do not differ significantly. However, these data do not give a measure of the rate of lateral spread of plants, which may be independent of the capacity for the production of shoots from the thickened root system.

Löve stated that, on the basis of the described sex mechanisms, "if no differences occur in germination percentage, nor in the death rate of males and females, nor a high frequency of agamospermous seed formation, the mature male and female plants will be found in about 1:1 ratio in nature and by experiment". Discussing each of Löve's preconditions for a 1:1 ratio in turn:

(a) There is no indication of difference in germination percentage, as the ratio of staminate to pistillate plants of cultivated material conforms closely to the 1:1 ratio. The system of establishing seedlings was such that no loss of individuals because of intra-specific competition was possible.

(b) Löve referred to the possibility of the occurrence of agamospermy in *R. acetosella*. Agamospermy would result in a preponderance of pistillate individuals, which is the converse of the result shown in Table 1.

(c) Löve's statement of differential death rate of male and females could imply either differences in the capacity for perennation between the sexes or differences of competitive ability. Putwain's observations on intra-specific, inter-sex interactions are difficult to extrapolate to field situations where, although *R. acetosella* may occur in relatively pure stands, e.g. Moore (1954), Wace and Holdgate (1958), it more frequently occurs interspersed with other species.

I consider that the significantly deviating numbers of staminate and pistillate plants in the natural populations may be explained by differences in the survival of the sexes resulting from interspecific competition. To investigate this possibility sites have been classified into three categories each representing different competitive situations. These are:

(1) Relatively closed communities in which *R. acetosella* has been established for several years

and is likely to persist in association with the other species indefinitely as long as the current environmental situation prevails. In this category, counts from tussock sites and sites on stabilised, closely vegetated old river beds are included. Here a competitive balance between *R. acetosella* and the other species has probably been attained and is being maintained.

(2) All sites of recently sown pastures or weedy fallows. On these, the establishment of *R. acetosella* was regarded as having been comparatively recent, generally less than one year, and competitive equilibrium had probably not been attained. Included in this category were three sites where competition was at a minimum. These were from (a) the Motupiko River where the species occurred as isolated plants in pockets of silt amongst river bed boulders; (b) the foreshore of Lake Rotoiti where discrete plants were growing amongst large pebbles; and (c) a roadbank near Fairlie where *R. acetosella* occurred as isolated plants in pockets of soil in rock crevices.

(3) Roadsides. Here *R. acetosella* is maintained by periodic disturbance by grading and other road maintenance.

TABLE 2. *Numbers of staminate and pistillate individuals in three community types.*

COMMUNITY TYPE	♀	♂	χ^2
Tussock, etc.	86	143	p=.001
New pastures, etc.	153	158	—
Roadside	183	200	—

The results derived from this classification are presented in Table 2. These indicate a highly significant (p=0.001) deviation from the 1:1 ratio for the samplings from the tussock communities because of a preponderance of staminate plants; whereas for the other two categories the deviation is not significant.

The results conform to a hypothesis of differences in the competitive characteristics or the ability to perennate of staminate and pistillate plants. For the recently established pastures sampling was done at a time when death of plants established in these associations would not have occurred. On these sites *R. acetosella* behaves essentially as a biennial, becoming established in spring- and autumn-sown pastures when competition from the sown species is at a minimum. After spreading vegetatively in the first season and overwintering, it flowers and produces a seed crop. If growth of the associated pasture species is not markedly limited by low availability of nutrients, overgrazing, etc., *R. acetosella* is eliminated and the seed crop of the species is produced at the expense of root reserves. In the tussock communities where *R. acetosella* occurs, inter-specific competition for light is moderated by climatic and soil factors and the species perennates. However, some loss of individuals during the flowering and seeding period could be expected in the tussock communities. The apparent difference of the competitive or perennating ability between male and female could be attributed to a greater loss of reserves by the pistillate plants producing a seed crop under "competitive stress" when compared to the staminate plants whose reproductive activity is more restricted. Dore (1953) reported that it was "apparent that the antagonism between regenerating capacity and flowering is quite widespread and, apart from possible biochemical complications, may have an important bearing on competition and survival of such plants". Also Raju, Steeves and Coupland (1964) consider that the nutritional strain associated with the maturation of seed of *Euphorbia esula* is greater than that associated with the occurrence of flowering. Thus, in the new pasture, plant competition is ultimately of such a severity that all plants of *R. acetosella* are killed. In the tussock communities an equilibrium is attained favouring the staminate plants, which, because of a smaller reproductive activity are able to proceed more favourably to a late summer–autumn period of vegetative growth, and so accumulate reserves to initiate and maintain growth and flowering in the subsequent season. Populations from roadsides would be expected, from this hypothesis, to maintain a sex ratio close to that at germination because of the frequent disturbance of the habitat and consequent re-initiation of the succession both from new seedlings or regeneration of the fragmented root systems of established plants.

Means, standard errors and coefficients of variation for panicle height of staminate and pistillate samples at each of forty-three sites are presented in Table 3. The table shows that for most of the sites the panicles of the pistillate plants were taller than those of the staminate plants. This difference was emphasised the greater the mean plant height for a site. This relationship was expressed as a regression of the ratio of female panicle height relative to male panicle height upon mean plant height. The calculated regression,

$$\text{Female/male height ratio} = +0.9298 + (.00072 \pm .00027)\ \text{mean height at site}$$

plotted in Figure 1 is significant at p=0.02, and records that as the mean plant height for each site decreased from 40.0 cm. to 10.0 cm., the female/male height ratio decreased from 1.217 to 1.002.

TABLE 3. *Panicle height of staminate and pistillate plants of* R. acetosella *in cm.*

	Pistillate			Staminate		
	n	Mean and standard error	Coefficient of variation	n	Mean and standard error	Coefficient of variation
Murchison, flats	10	42.7 ± 3.6	26.7	9	46.6 ± 3.6	22.9
Motupiko, flats	10	45.9 2.9	19.9	5	36.4 3.8	23.7
Rakaia River	10	42.4 3.7	27.7	9	34.1 1.9	16.6
Lumsden–Gore	10	33.7 1.5	14.1	10	30.9 1.1	11.0
Waianakarua	13	34.1 2.2	23.8	7	26.4 1.2	12.0
Hermitage	10	32.0 2.3	22.8	10	30.6 2.0	21.0
Motupiko R.	10	32.8 2.0	19.3	10	27.0 1.9	21.9
Jacksons	10	31.2 3.1	31.4	10	28.5 2.1	23.1
Fairlie	10	32.5 3.3	31.7	10	26.6 1.7	19.9
Rapahoe	3	31.5 0.8	4.2	11	26.5 1.2	15.5
Clifton	10	26.5 1.6	19.6	10	24.9 1.0	12.4
Spooner Mts.	6	28.5 1.5	12.9	10	24.3 1.9	24.9
Greymouth	8	26.1 2.1	23.0	10	24.8 1.9	24.1
South Fox R.	17	26.3 1.4	21.8	4	16.4 1.2	15.2
Westport	3	30.5 2.5	14.2	10	24.7 1.5	19.8
Five Rivers–Mossburn	9	25.8 2.2	25.2	10	23.0 0.9	12.3
Lake Rotoiti	10	25.1 1.3	15.7	9	22.6 1.8	22.9
Mid Dome	10	23.6 1.0	13.0	10	23.5 1.5	20.4
Alford Forest	12	21.9 1.6	25.7	8	20.3 1.2	17.0
Tophouse	8	20.0 0.7	10.1	12	21.4 1.2	20.6
Eglinton Val.	8	20.3 2.0	27.9	10	20.2 1.2	19.2
Tekapo–Pukaki	10	22.1 1.2	17.0	5	18.8 1.6	19.5
Kingston	10	20.2 1.5	23.5	9	20.2 0.9	13.8
Cass, Grassmere	9	19.1 1.0	16.3	11	18.4 1.1	20.0
Queenstown–Arrowtown	10	19.2 1.4	22.3	10	18.2 1.5	25.9
Rotoiti, airstrip	10	19.3 1.2	19.3	10	16.0 1.0	20.7
Rakaia Gorge	10	19.2 1.3	22.0	10	16.1 1.4	28.0
L. Wakatipu	10	18.2 1.6	27.8	10	17.0 1.0	18.5
Te Anau–Mossburn	9	19.1 1.2	19.4	10	16.6 0.9	17.2
Geraldine	10	17.2 1.8	32.9	11	17.1 0.9	17.5
Orari	8	17.3 1.1	17.9	12	16.7 0.8	16.8
Manapouri	10	17.7 1.0	18.3	6	14.8 0.9	15.1
Burkes Pass	3	13.2 0.7	27.0	10	16.9 1.1	7.4
L. Wanaka	8	14.9 1.5	28.9	12	15.1 1.0	22.1
Tarras	10	15.9 1.5	29.9	10	13.0 0.8	20.0
Bealey	9	13.4 1.0	22.8	10	15.3 0.9	19.5
L. Tekapo	10	11.2 0.7	19.7	10	11.9 0.4	11.3
Crown Range	6	8.8 1.2	34.6	14	11.6 0.8	26.8
Pukaki–Hermitage	10	11.7 1.0	27.3	10	8.6 0.6	20.3
Lindis Pass	5	9.1 1.0	23.8	10	10.1 0.7	21.4
Cass	10	8.2 0.8	32.0	10	10.1 0.7	21.6
Lyndon	4	9.1 1.7	36.5	10	9.2 0.4	15.3
Tekapo–Pukaki	7	5.6 0.6	30.8	8	6.4 0.7	28.6

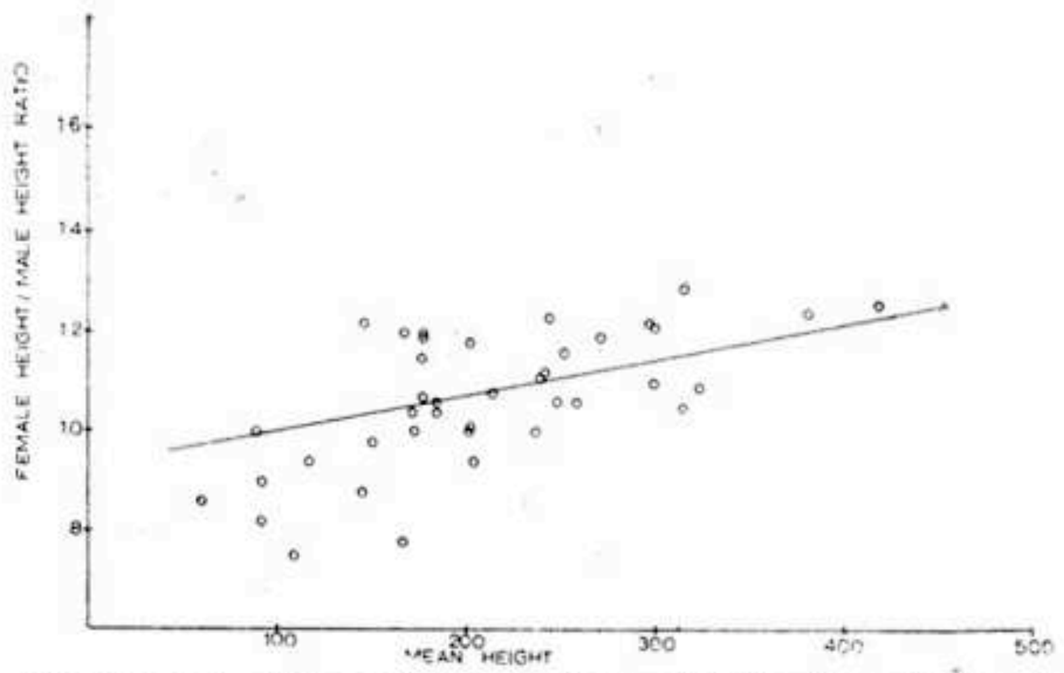

FIGURE 1. *Plotted regression of the female/male height ratio on mean panicle height at site.*

This result is cited as evidence that there is a reduction of the vigour of pistillate palnts relative to staminate plants, with increasing limitation of plant growth by the environment. The indication of decrease of vigour is related to the previously stated explanations of the predominance of staminate *R. acetosella* individuals in the tussock grasslands communities.

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SUMMARY

Observations on the ratio of staminate to pistillate individuals of *Rumex acetosella* from a variety of sources indicate the predominance of males. Results from forty-four sites in the South Island of New Zealand suggest the sex ratio is affected by the environment, and this is related to differences in the intensity of competition at roadside, new pasture and tussock grassland sites. Results for the sex ratio are related to the height differences between staminate and pistillate individuals.

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