

Analysis of Environmental and Species Effects on the Magnitude of Biomass Investment in the Reproductive Effort of Annual Pasture Plants

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Summary. In annual pastures utilized for grazing, the amount and quality of the standing dry matter in the dry season is of importance for the performance of the animals. Often both characteristics decline at the end of the green season. It is shown, that dispersal of the reproductive structures of the vegetation may be the main reason for this phenomenon. Determination of the reproductive effort of the annuals indicates that the proportion of their total production invested in reproductive tissue may be as high as that of cultivated species. It is shown that the harvest index (or seed ratio) of annual species is closely related to nutrient (mainly nitrogen) transfer from vegetative organs to the reproductive organs in the period between flowering and maturity, when in most cases, additional uptake of nitrogen from the soil is negligible. The effect of environmental and genetic effects on these processes is discussed.

Introduction

Total biomass production of annual pastures in semi-arid regions has received considerable attention in recent years. The growth processes have been studied in fair detail, but the vegetation dynamics and the fate of the seed crop after maturity have received much less attention. That seems not fully justified, since in most semi-arid regions, including the mediterranean zone, the dry season is longer than the green season and the amount of biomass available at the beginning of the dry season and its quality will to a large extent determine the potential animal density that can be maintained.

It has often been reported, that the amount of dry matter and of plant nutrients in the pasture vegetation at the onset of the dry season is much lower than at peak growing season. Gutman (1978) found a decrease of about 30% in the standing crop, directly after drying, in a transitional mediterranean steppe in North-Israel. Van Keulen (1975) recorded losses of 35, 28 and 15% of the peak biomass, in three successive years in Migda, South-Israel (Fig. 1). Both, Van Keulen and Gutman suggest, that this decline in standing crop may be attributed to shedding of seeds and dead leaves.

The process is of great practical importance. When such a large proportion of the biomass consists of reproductive structures, which are inevitably lost at maturity, less material will

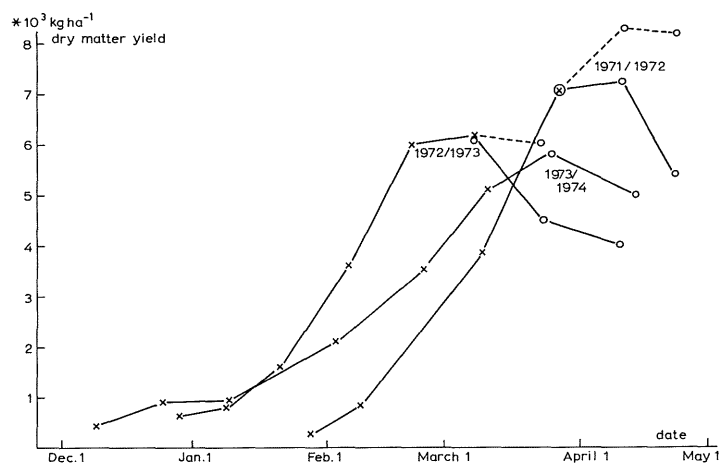


Fig. 1. Recorded losses of peak biomass of an annual pasture, in three successive years in Migda, South-Israel. (Source: Van Keulen 1975)

be available for intake by grazing animals in the dry season. Cattle especially, but also sheep and goats may have difficulties collecting the dispersed material some of which is buried in the soil and some blown away. Moreover, the competition for this material increases between the domesticated animals on the one hand and other animals as birds (Gaston 1976), insects (Green and Palmbald 1975; Janzen 1969) and rodents etc. on the other hand.

The effect of this decrease in quantity of available biomass is often aggravated by the very low quality of the remaining material. The reproductive organs are in general a strong sink for nutrients. Under limiting conditions by far the greatest part of especially nitrogen is accumulated in the seeds at maturity. Loss of this material therefore results in a sharp decrease in protein content and hence in digestibility of the standing crop.

This study concentrates on the question whether the amounts of dry matter involved may be partly or completely explained by seedfall or shedding of the total reproductive structure of plants, including those parts produced for seed protection and dispersal, such as awns, glumes etc. The harvest index (HI) which in seed crops is defined as the proportion of harvestable seed in relation to the total biomass produced, is a good reflection of the reproductive effort in crop plants. In dealing with wild species, where a large part of the reproductive effort is often invested in structures intended for protection and dispersal of the true seeds, it is useful to distinguish between the ratio of

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Table 1a. The seed ratio (SR) and reproductive ratio (RR) of some cultivated species

	SR	RR	Author
<i>Monocotyledons</i>			
<i>Hordeum vulgare</i>	0.13–0.57	0.33–0.66	Van Dobben (1965b); Donald and Hamblin (1976); Spitters (1979)
<i>Zea mays</i>	0.21–0.49	–	Donald and Hamblin (1976)
<i>Avena sativa</i>	0.29–0.53	0.43–0.56	Van Dobben (1962 and 1965a); Donald and Hamblin (1976)
<i>Oryza sativa</i>	0.13–0.56	–	Donald (1962); Donald and Hamblin (1976)
<i>Secale cereale</i>	0.31–0.36	–	Van Dobben (1962 and 1965a)
<i>Sorghum bicolor</i>	0.13–0.51	0.64	Anonymous (1968); Hodges et al. (1979); Donald and Hamblin (1976)
<i>Triticum vulgare</i>	0.15–0.54	0.35–0.50	Anonymous (1968); Kagan and Ephrat (1974); Campbell and Davidson (1979); Passioura (1977); Van Dobben (1965a); Donald and Hamblin (1976)
<i>Dicotyledons</i>			
<i>Carthamus tinctorius</i>	0.05–0.25	–	Beech and Norman (1963); Stern and Beech (1965)
<i>Cicer arietum</i>	0.67	–	Anonymous (1968)
<i>Helianthus annuus</i>	–	0.16–0.35	Gaines et al. (1974)
<i>Phaseolus vulgaris</i> (mean of 26 varieties)	–	0.46–	Rettig (1979)
<i>Arachis hypogea</i>	0.22–0.29	0.36–0.41	Goldin (1966 and unpublished data)

Table 1b. The seed ratio (SR) and reproductive ratio (RR) of some annual wild species

	SR	RR	Author
1. Sahelian species:			
<i>Monocotyledons</i>			
<i>Aristida funiculata</i>	0.09	–	Bille (1977)
<i>Aristida mutabilis</i>	0.04	–	Bille (1977)
<i>Brachiaria ramosa</i>	0.02	–	Bille (1977)
<i>Cenchrus biflorus</i>	0.03	–	De Ridder (1976)
<i>Chloris prierii</i>	0.03	–	Bille (1977)
<i>Diheteropogon hagerupii</i>	0.01	–	Bille (1977)
<i>Diheteropogon hagerupii</i> –	–	0.19–0.34	Penning de Vries (pers. comm.)
<i>Echinochloa colona</i>	0.06	–	Bille (1977)
<i>Panicum leatum</i>	0.05	–	Bille (1977)
<i>Panicum humile</i>	0.02	–	Bille (1977)
<i>Pennisetum pedicellatum</i>	0.03	–	Bille (1977)
<i>Schoenefeldia gracilis</i>	0.01	–	Bille (1977)
<i>Schoenefeldia gracilis</i>	0.17	–	De Ridder (1976)
<i>Dicotyledons</i>			
<i>Zornia glochidiata</i>	0.05	–	Bille (1977)
<i>Blepharis linariifolia</i> (+ <i>Polycarpea</i>)	0.05	–	Bille (1977)
Annual Sahelian vegetation (Tsjad)	0.25–0.38	–	Gaston (1976)
2. Non-Sahelian species:			
<i>Dicotyledons</i>			
<i>Astragalus cibaricus</i>	0.22	0.67	Green and Palmbald (1975)
<i>Astragalus utahensis</i>	0.24	0.50	–
<i>Chenopodium rubrum</i>	0.47–0.54	–	Cook (1975)
<i>Polygonum cascadense</i>	–	0.38–0.58	Hickmann (1975)
<i>Polygonum cascadense</i>	0.55	–	Hickmann (1977)
<i>Polygonum douglasii</i>	0.15	–	Hickmann (1977)
<i>Polygonum kelloggii</i>	0.65	–	Hickmann (1977)
<i>Polygonum minimum</i>	0.10	–	Hickmann (1977)
<i>Senecio sylvaticus</i>	0.06–0.12	0.19–0.20	Van Andel and Vera (1977)
<i>Veronica peregrina</i>	0.38–0.43	–	Linhart (1974)

all reproductive tissues to the total biomass ('reproductive ratio' or RR) and the ratio of true seed to the total biomass ('seed ratio' or SR). The 'total biomass' term should in principle also include the root material. However in most studies, including

the present one, root weights have not been determined, because of the laborious methodology involved and the uncertainty in interpreting the data obtained.

Some values reported for RR and SR are presented in Tables 1a and 1b. These already give an indication of the magnitude of the reproductive effort in various annual species grown under widely varying conditions. These data show, that the SR of cultivated monocotyledons varies from 0.13 to 0.57 and the RR from 0.33 to 0.66. The SR of cultivated dicotyledons varies from 0.05 to 0.67 and the RR from 0.16 to 0.67. For the wild species the SR of monocotyledons varies from 0.05 to 0.54 and their RR from 0.19 to 0.67. The SR of Sahelian monocotyledons varies from 0.01 to 0.17. In one of the species (*Diheteropogon hagerupii*), the RR can be higher: 0.19 to 0.34. The SR for Sahelian vegetation found by Gaston (1976), is also quite high: 0.25–0.38. The RR would of course be considerably higher than that.

Estimation of the reproductive effort of wild species, growing in their natural habitat is difficult because flowering, fruit setting and seed dispersal continue simultaneously over prolonged periods. This in contrast to cultivated species which have been bred for resistance to seed shedding and for synchronized maturation.

The SR and RR values of wild species may be at the same level as those of their cultivated congeners. This could be inferred from data by Harper and Ogden (1970), who concluded that in that respect only small differences existed between *Avena fatua* (wild oats), *Avena sativa* (cultivated for grain) and *Avena strigosa* (cultivated for forage) (Table 2). Likewise, in a test with wild relatives of wheat, growing under low soil fertility conditions, harvest index values of 0.39 for *Triticum monococcum*, 0.43 for *Triticum spelta* and 0.44 for *Triticum dicoccum* were obtained (Zeven pers. comm.). In the long-term Broadbalk experiments (Garner and Dyke 1969) on the non-fertilized plots the harvest index does not show a consistent change and the values found in 1966/67 are identical to ten-year averages obtained at the end of last century (0.44). The general picture arising from these data is indeed that wild species or old varieties growing under conditions to which they are adapted, invest about the same proportion of their total production in reproductive tissue as do the modern varieties growing under present-day conditions.

The variability within one species can be considerable, due to environmental conditions during the growing cycle. The decisive influence of these conditions in determining seed yields

Table 2. The SR and RR of three *Avena* spp. (calculated from data by Harper and Ogden (1970), for above ground material assuming that 25% of the total biomass presented belongs to the root system)

	SR	RR
<i>Avena fatua</i>	0.34–0.37	0.56–0.61
<i>Avena sativa</i>	0.43–0.45	0.54–0.56
<i>Avena strigosa</i>	0.29–0.31	0.45–0.47

of cultivated crops is well-known (cf. Spiertz 1977). In the semi-arid northern Negev in Israel, where studies on annual pastures have been conducted since 1962 (Tadmor et al. 1974), biomass losses from seed dispersal and predation have been observed repeatedly, but no reliable information on actual seed yields, produced under grazing on fertilized and non-fertilized pastures under these conditions is available. It was considered worth-while therefore, to estimate the RR and SR under these conditions. This study is related to a more comprehensive study of seed production and seed survival in annual semi-arid pastures (Loria 1979).

Materials and Methods

Plants were sampled at two sites in Israel: the Tadmor Experimental Farm in Migda (1978 and 1979) and Berurim seed farm (1978). The growing season in this mediterranean type climate extends from approximately November till April. The year 1978 refers here to the 1977/1978 growing season, 1979 to the 1978/1979 growing season. Migda is situated near Beersheva in the Northern Negev desert of Israel (34° 25' EL, 31° 22' NL). The average rainfall in the area is 250 mm·yr⁻¹. The region consists of slightly undulating plains composed of a 10–20 m thick mantle of löss overlying deposits of eocene chalk. Berurim is about 40 km south of Tel Aviv in an area with an average rainfall of 450–500 mm·yr⁻¹. The deep vertisol and an intensive crop rotation create very favourable growing conditions.

Because of the difficulties connected with the determination of the reproductive effort of wild species, special care was taken in this study to develop a consistent, although laborious, methodology. The methods used in the two years were different; both will be described in detail.

In 1978 individual plants were harvested carefully, on different dates to obtain plants at different degrees of maturity. To ensure that complete plants were obtained, only those individuals were chosen, that grew in relatively isolated positions, so that all the shedded leaves, seeds and/or fruits could be collected. At Migda, plants were sampled from relatively wet and relatively dry sites. The wet sites were, in general, depressions where run-on from surrounding areas created more favourable moisture conditions. The dry sites were areas from which run-off water was probably lost.

All plants were separated into fruits or ears and vegetative parts and dried in an oven for 48 h at 70° C. The individual samples of each plant were weighed: the mean weight of fruits or ears and the mean weight of vegetative parts provides the RR per species. Counting of the total number of fruits or ears per sample also enabled calculation of the mean fruit or ear weight. From the fruits or ears a subsample was taken and the seeds were separated from the rest. Both components were weighed and the fraction of seeds calculated. A relation was thus established between the total dry weight of the reproductive organ and the associated fraction of seeds in the sample. Using this relation the fraction of seeds was estimated from the main sample, which yielded the seed weight and hence the SR.

In 1979 randomly selected quadrats of 20 × 20 cm, were harvested, instead of individual plants. The treatments sampled and the number of samples collected are summarized in Table 3. The quadrats were harvested at the moment that the plants started to mature at the end of the growing season, about one week after the last rain. The samples were separated into the main-species present. All species samples were used for separation of vegetative and reproductive components, except those of *Schismus arabicus* of which only 2 or 3 of

Table 3. Summary of the samples collected in the 1978/1979 growing season (Field 1 continuous grazing; Field 11 and Field 12 deferred grazing; Field 13 ungrazed)

	Fertilizer application kg·ha ⁻¹			Stocking rate sheep·ha ⁻¹	No of samples
	N	P	K		
Field 1					
1977–1978	60	–	–	3.3	single plants
	60	–	–	0	single plants
1978–1979	–	18	–	3.3	10
	–	18	–	0	15
Field 11					
1977–1978	60	–	–	10.0	single plants
	60	–	–	0	single plants
1978–1979	–	18	–	10.0	10
	–	18	–	0	15
Field 12					
1977–1978	60	–	–	15.0	single plants
	60	–	–	0	single plants
1978–1979	–	18	–	15.0	10
	–	18	–	0	15
Field 13					
1977–1978	100	28	310	0	single plants
	–	28	310	0	single plants
1978–1979	100	28	310	0	30
	–	28	310	0	30

the samples of the fields 1, 11 and 12 were used for this purpose. The different components of the species were dried in an oven at 70° C for 24 h and the dry weight determined. The reproductive components were used for estimation of the potential SR and RR, under the assumption that all flowers present at the moment of harvest would produce seeds, that no more flowers would develop and that all unripe seeds present would mature.

Different methods of measuring and counting were applied for the various species, as described below. The species have been identified according to Zohary (1977).

A. Grasses

Phalaris minor

1. The total number of inflorescences per sample in all samples was counted.

2. The inflorescences of all samples were then pooled and 20 complete inflorescences (or as many as could reasonably be analysed) were collected at random.

3. For each of these inflorescences the total number of flowers was counted. All seeds and flowers were removed and the empty inflorescences were weighed.

4. A sample of 200 seeds was taken at random, including mature and immature seeds, and weighed. This was assumed to represent the situation of seed production at the date of sampling. Two hundred mature seeds (consisting of caryopsis and palea) were then counted and weighed.

Hordeum leporinum

1. and 2. Identical to *Phalaris minor*.

3. For each inflorescence the total number of dispersal units was counted: one dispersal unit has 3 spikelets, but only one spikelet produces a seed. Each inflorescence was weighed.

4. Samples of 200 mature seeds, 200 mature dispersal units without seeds and 200 mature and immature dispersal units were taken at random, counted and weighed.

Schismus arabicus

1. Identical to *Phalaris minor*.

2. The inflorescences of all samples were pooled and 10 complete inflorescences were taken at random.

3. For each inflorescence the total number of spikelets was counted, six spikelets were removed, two from the apex, two from the middle and two from the bottom position of the inflorescence, and the number of flowers per spikelet was counted.

4. The flowers and seeds from all spikelets of each inflorescence were collected. The empty inflorescences were then weighed.

5. A sample of 1,000 mature and immature seeds and a sample

of 1,000 mature seeds were taken at random. The samples were weighed. (From the quadrats taken from the grazed treatments of field 1 and 11 only 250 mature seeds were collected).

Stipa capensis

1, 2 and 3. Identical to *Phalaris minor*.

4. Samples of 200 mature seeds and their awns and 200 mature

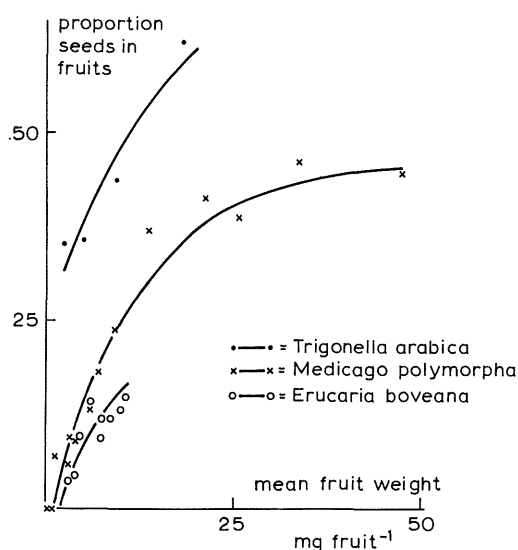


Fig. 2. The proportion of seeds in fruits in relation to the mean fruit weight

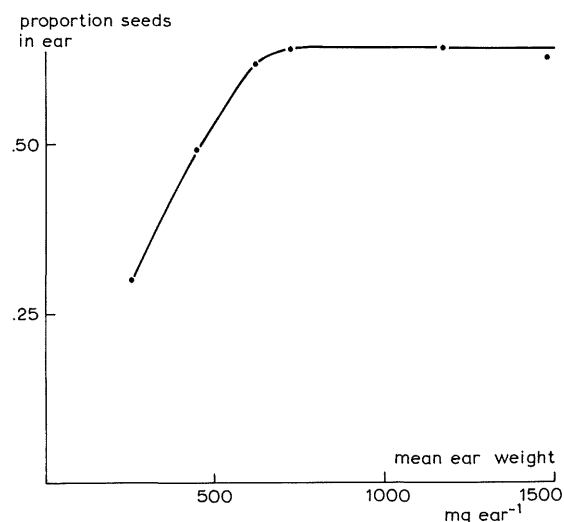


Fig. 3. The proportion of seeds in ears in relation to the mean ear weight

Table 4a. Vegetative and reproductive characteristics of the species sampled in 1978

Species	Site	Sampling date	No of plants	Plant dry wt (mg/plant)		Fruit or ear dry wt (mg/plant)		Mean fruit or ear wt (mg/fruit)	
				Mean	SE	Mean	SE	Mean	SE
Triticum sativum cv Miriam	Dry-3	April 5	5	1,020	67	458	69	458	68.9
	Wet-3	April 10	14	3,961	615	2,140	353	1,304	182.7
Erucaria boveana Coss.	Dry-221	April 10	4	1,852	240	795	88	9.4	0.13
	Dry-165	May 1	7	2,540	524	1,034	249	8.8	0.47
	Dry-4	May 1	6	1,913	332	953	177	8.8	1.10
	Wet-221	April 10	3	6,200	2,490	2,183	1,253	7.3	0.70
	Wet-165	April 18	2	7,629	2,766	1,812	1,037	4.3	0.48
	Wet-4	May 1	2	21,830	13,760	7,150	4,250	6.8	0.68
Glaucium corniculatum (L.) Rudolph	Dry-165	May 1	2	3,615	2,695	1,765	1,285	289.4	49.4
Medicago polymorpha L. (smooth bur)	Dry-8	April 10	3	603	273	197	145	19.6	8.6
	Dry-165	May 1	5	1,944	543	1,218	348	28.5	3.2
	Wet-8	April 10	4	685	121	303	49	24.0	2.4
	Wet-165	May 1	3	290	64	128	56	26.1	2.0
	Berurim	May 1	2	22,541	1,676	14,448	1,583	25.2	1.6
Medicago polymorpha L. (spring bur)	Dry-8	April 10	5	184	50	58	33	12.5	1.4
	Dry-165	May 1	8	841	134	448	87	27.2	4.3
	Wet-8	April 10	3	1,397	257	557	267	17.7	6.9
Medicago polymorpha L. cv 50/5	Berurim	May 1	2	47,022	12,903	32,503	8,413	96.0	5.5
Plantago lagopus L.	Dry-221	April 10	6	396	153	241	99	47.3	10.3
	Dry-165	May 1	5	2,790	1,614	1,460	767	55.1	13.0
	Wet-221	April 10	3	5,557	—	1,470	407	55.7	8.0
	Berurim	April 10	1	2,270	—	560	—	70.0	—
Trigonella arabica Del.	Dry-221	April 5	4	171	48	73	18	7.9	1.70
	Dry-165	May 1	5	876	439	710	354	12.3	1.25
	Wet-221	March 28	8	1,234	323	696	193	6.9	0.76

Table 4b. The reproductive ratio and seed ratio of species sampled in 1978

Species	Site	RR		Seed fraction in ears/fruits	SR
		Mean	SE		
Triticum sativum cv Miriam	Dry-3	0.45	0.04	0.50	0.32
	Wet-3	0.50	0.03	0.64	0.32
Erucaria boveana Coss.	Dry-221	0.43	0.03	0.14	0.06
	Dry-165	0.41	0.02	0.13	0.05
	Dry-4	0.50	0.04	0.13	0.06
	Wet-221	0.35	0.08	0.11	0.04
	Wet-165	0.24	0.06	0.05	0.01
	Wet-4	0.35	0.02	0.11	0.04
Glaucium corniculatum (L.) Rudolph	Dry-165	0.50	0.02	0.24	0.12
Medicago polymorpha L. (smooth bur)	Dry-8	0.33	0.14	0.37	0.12
	Dry-165	0.61	0.03	0.41	0.25
	Wet-8	0.46	0.05	0.40	0.18
	Wet-165	0.44	0.09	0.40	0.18
	Berurium	0.64	0.02	0.40	0.26
Medicago polymorpha L. (spring bur)	Dry-8	0.32	0.10	0.30	0.10
	Dry-165	0.52	0.03	0.41	0.21
	Wet-8	0.40	0.12	0.35	0.14
Medicago polymorpha L. cv 50/5	Berurium	0.69	0.01	—	—
Plantago lagopus L.	Dry-221	0.58	0.02	—	—
	Dry-165	0.52	0.02	—	—
	Wet-221	0.26	0.02	—	—
	Berurium	0.25	—	—	—
	—	—	—	—	—
Trigonella arabica Del.	Dry-221	0.45	0.03	0.46	0.21
	Dry-165	0.80	0.02	0.52	0.42
	Wet-221	0.55	0.02	0.43	0.24

and immature seeds (consisting of caryopsis and palea) and their awns were taken at random, counted and weighed.

B. *Dicotyledons*

Erucaria boveana

1. The number of fruits and flowers per quadrat sample was counted.

2. All fruits from all quadrat samples were pooled and 20 fruits were collected at random. From each fruit the number of seeds was counted.

3. Samples of 200 fruits, 200 mature seeds and 200 mature and immature seeds collected at random, were counted and weighed.

Asphodelus tenuifolius

1. Identical to *Erucaria boveana*.

2. Every pod contains 6 seeds.

3. Samples of 200 mature seeds and 200 empty pods were counted and weighed. The plants were almost completely mature, therefore immature seeds were not taken into consideration.

Trigonella arabica

1, 2 and 3. Identical to *Erucaria boveana*.

The originally oven-dried samples were stored for two months before processing. The weights given are those obtained after the storage period on an analytical balance with an accuracy of 0.001 g. Using for seed weight the weight of mature seeds and the weight of a mixture of mature and immature seeds respectively, potential and actual SR and RR are calculated as follows:

1. actual (or potential) seed weight \times total number of seeds per m^2 = total actual (or potential) weight of seeds per m^2 (S)

2. weight of empty inflorescence or fruit \times total number of inflorescences or fruits per m^2 = total weight of empty inflorescences or fruits per m^2 (E)

3. weight of above ground vegetative components per m^2 + total actual (or potential) weight of seeds per m^2 + total weight of empty inflorescences or fruits per m^2 = total biomass per m^2 (B)

$$4.a. SR = \frac{S}{B}$$

$$b. RR = \frac{(S+E)}{B}$$

Results

Results of the year 1978 are presented in Figs. 2 and 3 and Tables 4a and b. Figures 2 and 3 show, that the proportion of seeds in ears or fruits increases as their weights increase, up to maximum value, which varies per species. This relationship reflects the process of seed maturation, as the lighter fruits are generally immature.

Differences between species are evident with respect to the SR, but less so for the RR (Table 4a and b): the lowest SR is found for *Erucaria* (0.01) and the highest for *Trigonella* (0.42); the RR of all species may reach a value of 0.50 or more up to an exceptionally high value of 0.80 for *Trigonella*, under certain conditions (single, widely spaced plants growing and maturing over a short period late in the season).

The dry and wet sites distinguished do not show a significant difference in RR or SR, although there is a tendency for higher values of the two indices in the dry sites for *Erucaria* and *Plantago*, which may be partly due to the fact that towards the end of the growing season, the plants on the wet sites were still green in parts and had more immature pods and seeds than those growing on the dry sites. Hence, the effect of moisture availability on the SR and RR values is not too clear. The variation of SR and RR within one species can also be great (e.g. the SR of *Erucaria* varies from 0.01–0.06 and the RR from 0.24–0.50). In 1978 only individual plants were collected, many of them in very sparse stands. When plant density is low, SR is generally higher.

Results for 1979 are presented in Tables 5a and b. In these tables both potential and actual values for the RR and the SR are given. In reality, the real harvest indices will be situated between the potential and actual values.

The SR and RR values of *Erucaria* which were determined in both years are reasonably consistent. In the 1979 data there were large differences in SR between species: the lowest potential SR is found for *Erucaria* (0.02) and the highest for *Schismus* (0.46). The value for *Schismus* is similar to that obtained for the same species in a much drier environment (0.4; Loria and Noy-Meir, 1980). The potential RR varies from low (0.10) for *Erucaria* to high (0.65) for *Schismus*.

Differences between the treatments with and without nitrogen supply and between grazed and non-grazed are small, but the values tend to be higher without nitrogen (compared to nitrogen supply) and without grazing (compared to grazing). Exceptions are *Phalaris*, where nitrogen fertilization does not affect the SR and *Hordeum*, where grazing affects the SR in the fields 12 and 1 differently; field 12 with a lower and field 1 with higher SR than in the non-grazed plots. The treatment effects (nitrogen fertilizer and grazing) are statistically significant ($F=4.9$, $P=0.001$) when measured as inflorescences or fruits per unit of vegetative biomass (Table 5a). The differences persist as SR and RR but are not significant due to the additional variation accumulated during the seed ripening and dispersal period.

Table 5a. Some characteristics of the reproductive organs of the species sampled in 1979

Species	Treatment	1000-seedweight (mg)		Number of seeds ($10^3/m^2$)	Number of fruits or ears per m^2	Weight of empty fruits or ears per m^2	\bar{x} of (number of fruits or ears/weight of vegetative components) \pm SE of \bar{x}
		potential	actual				
<i>Schismus arabicus</i> Nees.	NPK	72	17	117.4	418	10	35 ± 5
	PK	79	20	68.0	300	8	53 ± 4
	F ₁ -grazed	69	55	826.4	3,545	6	49 ± 12
	F ₁ -ungrazed	76	49	1,409.9	6,791	5	35 ± 5
	F ₁₁ -grazed	62	64	1,220.2	6,048	8	42 ± 1
	F ₁₁ -ungrazed	76	67	1,691.4	10,443	8	35 ± 5
	F ₁₂ -grazed	68	64	570.3	2,628	9	41 ± 12
	F ₁₂ -ungrazed	76	76	2,172.5	8,324	9	35 ± 5
<i>Hordeum leporinum</i> Link (formerly <i>Hordeum murinum</i>)	NPK	2,380	2,250	1.1	40	12	8 ± 2
	F ₁ -grazed	1,700	136	3.4	163	38	13 ± 3
	F ₁ -ungrazed	1,979	292	1.6	87	35	8 ± 2
	F ₁₂ -grazed	2,700	2,700	0.8	70	54	6 ± 2
	F ₁₂ -ungrazed	2,476	2,476	0.7	28	69	8 ± 2
<i>Phalaris minor</i> Retz	NPK	1,560	340	19.3	143	47	8 ± 3
	PK	1,310	270	3.1	47	25	9 ± 1
	F ₁ -ungrazed	1,700	630	6.1	48	45	8 ± 3
	F ₁₂ -ungrazed	1,800	1,350	4.2	32	65	8 ± 3
<i>Stipa capensis</i> Thunb.	F ₁₁ -ungrazed	300 ^a	300	7.3	183	10	22 ± 7
		+ awns: 1,560	+ awns: 2,410				
<i>Erucaria boveana</i> Coss.	NPK	200	172	18.4	2,149	4	$(58 \pm 12)^b$
	PK	289	339	7.6	805	4	- ^c
	F ₁ -grazed	170	160	6.5	878	6	- ^c
	F ₁ -ungrazed	230	190	7.3	1,094	5	$(58 \pm 12)^b$
	F ₁₂ -ungrazed	240	270	2.0	267	6	$(58 \pm 12)^b$
<i>Asphodelus tenuifolius</i> Cav.	NPK	1,310	1,310	11.4	1,904	4	74 ± 9
	PK	1,210	1,210	17.8	2,963	3	110 ± 8
<i>Trigonella arabica</i> Del.	PK	1,070	890	1.5	272	3	135 ± 26

^a This is about $4 \times$ lower than other data on *Stipa capensis* and may be due to the fact that the dispersal units weighed may have consisted of empty glumes.

^b Values from one bulked sample

^c Not determined

Discussion

The results obtained in this study indicate that in annual wild species 10–80% of the total biomass produced during the growing period is eventually invested in the reproductive organs that include seeds as well as subsidiary protection and dispersal structures. Mean values, taken over all treatments and over two years of observations, range between 26 and 60% (Table 6) and cover the range for annual cultivated species. Such behaviour is appropriate for species that have to rely on their seed stock for survival from year to year. In some cases, the major part of the total effort is invested in subsidiary structures for protection and dispersal, rather than in true seeds (e.g. *Stipa*, *Erucaria*). These include thickened seed-coats (e.g. *Asphodelus*) which have a protective or other (germination inhibition) function. In *Erucaria* the seeds remain on the skeleton of the dead plant which protects them till they become detached by mechanical disturbance. In that sense, the whole dead plant participates in the protection and dispersal of the seed.

The magnitude of the losses of biomass towards the end of the growing season, reported for natural vegetation could thus well be explained by dispersal of part or all of the reproductive structures produced. As is shown in Fig. 1, the losses may

vary from year to year, due to variations in the botanical composition and/or different environmental conditions from one year to another. As the SR and RR vary for different species (Tables 1, 4, 5), variations in botanical composition may thus change the SR and RR of the total canopy. The amount of standing biomass lost may then be further modified since the proportion of the produced dry matter of seeds and reproductive structures that is shed, differs from species to species: almost no shedding of seeds and reproductive structure from *Erucaria* until late in the dry season, only seed fall from *Phalaris* and *Asphodelus* whereas from *Schismus*, *Hordeum* and *Stipa* most of the reproductive parts are dispersed.

The wide range of year to year SR values can be represented as a function of the mineral, mainly nitrogen (and phosphorus?) translocation to the seeds. It has often been noted that uptake of nitrogen after flowering is negligible, unless extra nitrogen is applied as a late top-dressing (Anonymous 1968; Van Dobben 1962; Gmelig-Meyling and Van Dobben 1965). Nitrogen for the developing seeds, S , and associated reproductive structures has to be supplied mainly by translocation from the vegetative tissue, V (Sinclair and de Wit 1976). The SR is then dependent on the concentration of nitrogen in the seeds, N_s , and the difference in the nitrogen concentration of the vegetative tissue be-

tween flowering, N_f and maturity, N_m . Thus, $V(N_f - N_m) = SN_s$ and $SR = \frac{S}{V+S} = \frac{N_f - N_m}{N_s + N_f - N_m} = \frac{D_{fm}}{N_s + D_{fm}}$ where D_{fm} is the difference (or depletion) in nitrogen concentration of the vegetative tissue between flowering and maturity. The response surface of this function is given in Figure 4. As N_s values generally

Table 5b. The reproductive ratio and seed ratio of the species sampled in 1979

Species	Treatment	Total yield (g/m ²)		RR		SR	
		po- ten- tial	ac- tual	po- ten- tial	ac- tual	po- ten- tial	ac- tual
Schismus arabicus Nees.	NPK	32.6	26.1	0.39	0.24	0.26	0.08
	PK	15.2	11.2	0.51	0.34	0.35	0.12
	F ₁ -grazed	150.6	139.1	0.52	0.48	0.38	0.33
	F ₁ -ungrazed	232.9	194.8	0.65	0.53	0.46	0.35
	F ₁₁ -grazed	269.7	272.2	0.46	0.47	0.28	0.29
	F ₁₁ -ungrazed	386.1	370.9	0.55	0.53	0.33	0.31
	F ₁₂ -grazed	131.6	129.3	0.47	0.47	0.30	0.28
Hordeum leporinum Link (formerly murinum)	NPK	23.9	23.8	0.13	0.13	0.11	0.11
	F ₁ -grazed	23.4	18.1	0.51	0.37	0.25	0.03
	F ₁ -ungrazed	16.3	13.5	0.39	0.26	0.20	0.04
	F ₁₂ -grazed	41.7	41.7	0.14	0.14	0.05	0.05
Phalaris minor Retz	NPK	87.2	63.7	0.42	0.21	0.34	0.10
	PK	11.7	8.5	0.45	0.24	0.35	0.10
	F ₁ -ungrazed	35.7	29.2	0.35	0.21	0.29	0.14
Stipa capensis Thunb.	F ₁₂ -ungrazed	21.1	19.2	0.46	0.41	0.36	0.30
	F ₁₁ -ungrazed	24.0	29.7	0.55	0.66	0.09	0.07
Erucaria boveana Coss.	NPK	49.0	48.4	0.25	0.24	0.08	0.07
	PK	17.8	18.2	0.31	0.32	0.12	0.14
	F ₁ -grazed	21.1	21.0	0.30	0.30	0.05	0.05
	F ₁ -ungrazed	20.8	20.5	0.34	0.34	0.08	0.07
	F ₁₂ -ungrazed	20.8	20.9	0.10	0.10	0.02	0.03
Asphodelus tenuifolius Cav.	NPK	52.9	52.9	0.43	0.43	0.28	0.28
	PK	62.3	62.3	0.49	0.49	0.35	0.35
Trigonella arabica Del.	PK	5.0	4.7	0.48	0.45	0.31	0.28

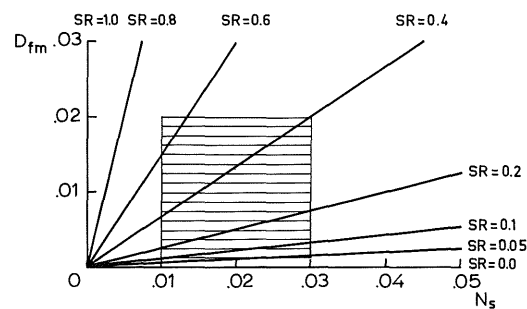


Fig. 4. The response surface of seed ratio, SR, as a function of nitrogen concentration of the seed, N_s , and the dilution of nitrogen in the vegetative pools, D_{fm} , between flowering and maturity. The shaded area indicates the main range of variation in most of the species studied

fall between 0.01 and 0.03 and D_{fm} values between 0.002 and 0.02, it is possible to obtain SR values anywhere between 0.05 and 0.67. The actual values achieved will depend on genetic characteristics that strongly affect N_s and environmental factors, mainly nitrogen economy that largely affect D_{fm} . These effects were reflected in this study but can be traced in the literature as will be discussed below.

1. Nitrogen application generally results in a decrease in SR (Van An del and Vera 1977; Campbell and Davidson 1979; Kagan and Ephrat 1974; Anonymous 1968; Donald and Hamblin 1976). On the other hand increasing values have also been reported (Van Dobben 1962; Gmelig-Meyling and Van Dobben 1965; Anonymous 1968).

Decrease would occur if $\frac{D_{fm}}{N_s}$ decreases and indeed, in non-depleted agricultural fields, N_s in grain can increase considerably with increasing fertilizer application in relation to D_{fm} . In wheat, N_s can increase from 0.018 to 0.025, whereas N_f and N_m tend to increase together, thus diminishing the effect of added nitrogen on D_{fm} (Ellen and Spiertz 1980).

The harvest index should increase if D_{fm} increases in relation to N_s . This is possible under two different circumstances: 1) If there is added uptake of nitrogen during seed-fill and ripening conditions are favourable long enough for seed fill to utilize the extra assimilate. This could occur as senescence of vegetative parts is delayed by more available nitrogen (Van Dobben 1962; Spiertz 1977); and 2) under conditions of severe nitrogen defi-

Table 6. Mean values (\pm SE) of the reproductive ratio (RR) and seed ratio (SR) of annual pasture species in Israël

Species	RR		SR	
	1978	1979	1978	1979
Erucaria boveana	0.38 \pm 0.09	0.26 \pm 0.10	0.04 \pm 0.02	0.07 \pm 0.04
Trigonella arabica	0.60 \pm 0.18	0.47	0.29 \pm 0.11	0.30
Medicago polymorpha	0.47 \pm 0.12		0.18 \pm 0.06	
Plantago lagopus	0.40 \pm 0.17		—	
Glaucium corniculatum	0.50		0.12	
Schismus arabicus		0.48 \pm 0.09		0.31 \pm 0.08
Hordeum leporinum		0.26 \pm 0.13		0.11 \pm 0.03
Phalaris minor		0.35 \pm 0.07		0.16 \pm 0.10 ^a
Asphodelus tenuifolius		0.46 \pm 0.04		0.32 \pm 0.05
Stipa capensis		0.61		0.08 ^b

^a True seed ratio about 77% of SR as dispersal unit contains seed and a tightly fitting palea

^b Low compared to other data, possibly due to empty glumes

ciency where N_f can be as low as 0.006 and N_m and N_s are around 0.003 and 0.010 respectively (Penning de Vries et al. 1980). Under such conditions, moderate application of nitrogen could increase the SR mainly by increasing D_{fm} . Deviations from this pattern can occur as seed-set and seed-fill can be strongly affected by environmental conditions including pollination disturbances, grazing, plant disease, drought and other depredations.

2. Species and varietal effects. Differences in SR between species can be partially related to differences in the N_s , where seeds with high N_s tend to have low SR (H. Breman, pers. communication). However, where the seeds are only a small part of the dispersal unit (e.g. *Hordeum leporinum* and *Stipa capensis*) then, in order to compare reproductive efforts, it is more appropriate to use the RR. In these cases morphological differences in dispersal units over-ride translocation limitations in determining seed ratios. But as the nitrogen concentration in the dispersal and protective structures is low, the nitrogen concentration of the dispersal unit is also low, generally around 0.01. If this is taken as N_s , then RR (instead of SR) rises steeply to 0.6 as D_{fm} increases to 0.015 (see Fig. 4). This covers the range of values found in this study. Varietal differences in harvest index of cultivated crops appear to be inversely related to N_s (Kramer 1979; 1980). These varietal differences are generally maintained at different nitrogen availability levels. Thus the data of Warren and Johnston (1967) describing a change in variety in the continuous barley experiment in the Rothamsted Hoosfield, show that the harvest index of Plumage Archer, grown from 1917 onwards is equal to that of Maris Badger, a modern variety, at all levels of nitrogen availability. At the low soil fertility level the total yield of the older variety is higher, which seems to be the result of a higher nitrogen uptake. A similar result was obtained by Hiltner and Lang (1912) who compared an improved rye variety (Petkuser) with a traditional one at different fertility levels. At the low fertility level the traditional variety yielded more, but the harvest index is identical for both. At the higher fertility levels, total production is higher for the improved variety, but the harvest index changes for both in the same way.

The results of Sandfaehr et al. (1965) for a number of barley varieties, ranging in year of introduction between 1904 and 1954 are different only in that the newer varieties have a higher harvest index at all N levels tested. A similar conclusion was reached by van Dobben (1962) for wheat. Under high fertility levels the harvest index ranged from 0.34 to 0.40 for varieties introduced between 1900 and 1950, the modern varieties maintaining a higher harvest index at higher N-levels than the older varieties. At lower nitrogen levels, the harvest indices are higher for all varieties.

Generally it may be concluded, that the influence of plant breeding in small grains has mainly been in counteracting the deleterious effects of high nutrient availability on the seed/straw ratio. This, however, has been achieved at the cost of lower N_s (Kramer 1980). This value appears to be genetically determined, as the higher harvest indices are maintained in relation to older varieties even under low fertility conditions.

3. Plant density influences the harvest index: the lower the plant density, the higher the harvest index will be (Linhart 1974; Stern and Beech 1965; Goldin 1966; Hickmann 1975; Donald and Hamblin 1976), although the latter describe, that for maize the harvest index decreases again when the plant density is very low. Darwinkel (1978 and 1979) describes such an optimum-curve also for wheat. This is apparently due to poor seed production on tillers that are produced late under very low density conditions.

4. Water stress generally increases the harvest index (Pasioura 1977; Hodges et al. 1979; Gaston 1976; Donald and Hamblin 1976). This could be related to the fact that water stressed plants tend to have higher N_f -values. If subsequent growth is relatively unstressed, N_m and N_s would hardly be affected and consequently SR would increase. However, water stress after flowering would cause the harvest index to fall, and N_s is then invariably higher. A striking example was observed in wheat growing at the Migda site in the '79/'80 growing season. Abundant rain early in the season resulted in luxurious vegetative growth (10–12 tons dry matter per ha). From early on in the reproductive phase a prolonged dry period together with hot dry winds from the desert ("chamsien") caused rapid drying of vegetation and soil, resulting in shrunken seeds and low grain yields (± 3 ton ha⁻¹) with HI around 0.2. The N_s of such shrunken seed can typically be well above 0.03.

5. Beech and Norman (1963) found that the harvest index of short-day plants strongly decreases at long days.

6. Light intensity affects the harvest index. Donald and Hamblin (1976) recorded that lower levels of irradiance decrease the harvest index.

7. The effects of multiple stress conditions may counteract each other or they may work in the same direction, as illustrated by the results of Campbell and Davidson (1979). Water stress in an early stage of development of wheat well supplied with nitrogen tended to counteract the negative effect of nitrogen supply on the harvest index, whereas waterstress in a later stage enhanced the unfavourable effect.

These effects may in general be understood on the basis of dry matter production in the different phases. There are also indications however, that stresses during flowering and fertilization may have strongly adverse effects on seed setting. In the later stages of development the capacity of these seeds to store reserve substances may be the limiting factor. Under such conditions a low harvest index may be found, which is not correlated to the dry matter production in the two major growth phases.

The indicated influences of especially moisture availability, nitrogen supply and plant density on the SR and RR are also noted in the results obtained in this study on semi-arid annuals in field conditions. The environmental differences here are not statistically significant because the sample size was too small in relation to the large degree of heterogeneity in both soil properties and plant characteristics under field conditions in the study area.

Conclusions

The results of this study and those of related work show that the magnitude of the reproductive effort in many wild annual pasture species is similar to that of cultivated annual crop plants. It is proposed that the ratio of seed to total biomass is closely related to nutrient translocation processes from the vegetative parts to the reproductive parts. An analysis based on the nitrogen content of the vegetation at flowering and maturity and on the nitrogen concentration of the seeds appears to apply equally well to both wild and cultivated, including highly bred species. Most of the environmental effects on harvest indices (or seed ratios) can also be interpreted in terms of their effect on the above nitrogen concentrations. In view of these conclusions, it is clear that the reproductive effort of annual pasture species is a major factor in determining the availability and quality of the available biomass for grazing, especially after plant maturity. Understanding these relationships can contribute to more rational management of such pastures.

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