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# Fitness components of grazing-induced population reduction in a dominant annual, *Triticum dicoccoides* (wild wheat)

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## Summary

**1** Intensive cattle grazing reduces population density of the dominant annual *Triticum dicoccoides* (wild wheat) in Mediterranean grasslands in northern Israel. An experiment was designed to quantify the impact of grazing on various components of plant fitness in the growing season that may contribute to this reduction. Height, tiller number, survival and reproduction of marked plants were monitored throughout two growing seasons in paired grazed and protected plots and in recently defoliated and undefoliated plants in grazed plots.

**2** Plant survival in the vegetative stage was similarly high in grazed and protected plots in 1990–91, but in 1991–92 it was 14% higher in protected plots. Plants in protected plots were 60–172% taller than those in grazed plots, but plants in grazed plots had 44–107% more live tillers at the end of the vegetative stage. Tiller initiation was enhanced in undefoliated as well as defoliated plants within grazed plots, suggesting that the increase may have been a response to the modified radiation environment in the grazed community.

**3** The proportion of plants that produced mature inflorescences was 51–59% greater in protected than in grazed plots, and within grazed plots it was much lower among plants that had been grazed in the last month of the season. The number of mature inflorescences per fertile plant was not consistently different between treatments, but the number of immature inflorescences was greater in grazed plots. Apparently, following removal of inflorescences late in the growing season, insufficient resources remained for maturation of secondary inflorescences. Spikelet number per inflorescence was 21–42% greater in protected than in grazed plots, which may reflect effects of grazing in the vegetative stage on inflorescence development. Seed number and weight per spikelet were not significantly affected by grazing.

**4** The number of mature spikelets or seeds produced per seedling (an estimate of fitness throughout the growing season) was reduced by about 50% in grazed compared to protected plots in both years. The largest consistent components of reduction were due to removal of maturing inflorescences in the late reproductive stage.

**5** Deferment of grazing during the reproductive stage may be sufficient to maintain abundant populations of wild wheat, while grazing during the remainder of the year will limit their suppressive effects on other annual species.

*Keywords*: annual grass, defoliation, demography, herbivory, Mediterranean grassland, reproduction, tillering, *Triticum dicoccoides*

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## Introduction

In the absence of grazers, grassland communities are commonly dominated by a few tall, competitive species. These dominants form a closed green canopy and produce a dense mulch layer, both of which often inhibit regeneration of subordinate species. In general, grazing reduces canopy cover, biomass, and density of dominants (except where these are unpalatable), thereby facilitating regeneration of subordinate species, particularly in gaps created by grazing, and increasing species richness (Harper 1969, 1977; Grime 1979; Grubb 1986; Collins 1987; Milchunas *et al.* 1988; Bullock *et al.* 1995). The mechanisms by which herbivores reduce the abundance of dominants are critical to understanding vegetation dynamics in grassland ecosystems.

In temperate regions, the typical matrix forming (Grubb 1986) dominants of undisturbed grasslands are perennial tallgrass species. However, this role is assumed by tall, large-seeded, annual grasses in some grasslands in Mediterranean (Heady 1958) and monsoonal (Andrew & Mott 1983) climates. The mechanisms by which these tall annuals maintain dominance in the absence of grazing, and by which grazing reduces their abundance to create regeneration gaps, may differ from the corresponding mechanisms with perennial dominants (e.g. O'Connor 1991).

When grazers are excluded, the Mediterranean grasslands of northern Israel rapidly become dominated either by tall perennial grasses (mainly *Hordeum bulbosum*) and forbs (e.g. *Echinops* spp.), or by tall annual grasses, namely the wild cereals, wheat (*Triticum dicoccoides*), barley (*Hordeum spontaneum*) and oat (*Avena sterilis*) (Noy-Meir *et al.* 1989; botanical nomenclature follows Zohary & Feinbrun-Dothan 1966–86). The proportions of annual and perennial dominants apparently depend on site conditions and disturbance history.

*Triticum dicoccoides*, wild emmer wheat, has a more restricted distributional range than wild barley and oat, but within its range it is often the major dominant in ungrazed or leniently grazed sites, where the dominance of perennial species is limited. However, wild wheat density and cover decrease sharply under intensive cattle grazing (Noy-Meir *et al.* 1989; Noy-Meir 1990; Noy-Meir *et al.* 1991). In fact, when discovered early in this century, wild wheat was relatively rare and restricted to microhabitats among rocks or within spiny plants (Aaronsohn 1909). These microhabitats probably provided refuges from intensive grazing by domestic herbivores. Wild wheat has spread to large areas of less specialized habitats since the 1950s, apparently in response to a reduction in grazing intensity (Zohary & Brick 1961; Harlan & Zohary 1966).

As a progenitor and close relative of cultivated hard wheat (*Triticum turgidum*), wild wheat is an economically valuable source of genetic material for wheat breeding programs. Some of the largest and genetically most diverse populations are found in the grasslands of Galilee and Golan, in northern Israel, and their *in situ* conservation and management is of considerable interest (Harlan & Zohary 1966; Anikster & Noy-Meir 1991). Although several recent studies have clearly documented the reduction in wild wheat abundance under intensive cattle grazing, they have not directly addressed the processes involved. A fundamental understanding of the response of plant communities to grazing is likely to be gained only from the analysis of the relevant demographic processes in important plant populations (Harper 1977; Crawley 1983; Dirzo 1984). Such an understanding can also provide rational guidelines for the management of grazing intensity and season to optimize conservation of grassland populations and communities.

This investigation was designed to identify and quantify some of the demographic mechanisms by which cattle grazing reduces wild wheat populations in Mediterranean grasslands. The initial assumption was that this reduction can be explained by the direct and indirect effects of leaf and tiller removal by grazers during the growing season on plant survival and reproduction. The possible effects of dry herbage and seed removal during the nongrowing season were not tested in this study. The questions asked were:

**1** To what extent does grazing reduce plant fitness during the growing season, i.e. the number of viable reproductive units produced at the end of a growing season, per individual seedling emerged at the beginning of the season?
**2** What are the quantitative contributions to grazing-induced reduction in fitness of various components, namely plant survival, tiller initiation and survival, inflorescence number, size and maturation, seed number and viability?
**3** What are the relative impacts of grazing in the vegetative and reproductive stages on plant fitness in the growing season?
**4** Can grazing management improve conservation of wild wheat populations and grassland communities?

## Materials and methods

### STUDY SITE

The grassland investigated represents a stable plant formation on stony, but fertile upland soils in a Mediterranean climate in northern Israel. These grasslands have been grazed by mixed livestock herds for thousands of years and are presently grazed mainly by cattle, at variable grazing intensities.

The research site was established in a Mediterranean grassland in eastern Galilee, 1 km west of Almagor (32°91′N, 35°35′E) on a south-east facing slope from the Korazim Plateau towards Lake Kinneret (Sea of Galilee), 10 m a.s.l. and 220 m above the lake. The soil is a dark heavy basaltic protogrumusol (Dan *et al.* 1970) or lithic xerochrept (Soil Survey Staff 1960), with basaltic rocks and stones on about 15% of the surface. Mean annual rainfall is about 490 mm, and is distributed from November to April (Table 1). Mean temperature ranges from 12 °C in January to 28 °C in July. Perennials comprise only about 5% of the foliar cover, and include *Echinops* spp., *Asphodelus aestivus*, *Hordeum bulbosum*, and *Prosopis farcta*. Most of the cover and biomass (150–500 g $m^{-2}$ peak standing crop in spring, depending on year and grazing regime) is produced by annual grasses (*Hordeum*, *Avena*, *Triticum*, *Bromus*, *Alopecurus*), legumes (*Trifolium*, *Medicago*), crucifers, composites, umbellifers and other dicots.

### EXPERIMENTAL DESIGN AND PROCEDURES

The study area was located within a paddock of the Karei-Deshe Experimental Range Station (Gutman & Seligman 1978), which is grazed by beef cattle during most of the year at a moderate to heavy density of about 50 cows $km^{-2}$ (2 ha for each cow). In October 1990, 12 5-m × 5-m plots were marked in a randomized block design including six blocks of two adjacent plots each. The blocks were placed randomly within a 100-m × 50-m rectangle, but locations which included large rock outcrops were rejected. One randomly selected plot in each block was fenced to exclose cattle grazing during the growing season, while the adjacent plot remained open to grazing. Experimental plots were located in a corner of the paddock far from the water and feeding points, so that the actual grazing pressure was relatively low.

At the beginning of the 1990–91 and 1991–92 growing seasons, 50 wild wheat seedlings within each of the 12 plots were marked with numbered plastic tags and rings and mapped with reference to a 1-m × 1-m grid. Seedlings were marked from the centre of each plot outwards, and included all seedlings identified as wild wheat that were more than 5 cm away from rocks. Marked seedlings were distributed over an area between 3 and 16 $m^2$ in the centre of the plot. Most of them were surrounded by neighbours of other species.

**Table 1** Mean monthly rainfall (mm) at Almagor (about 1 km from study site) for the 1990–92 seasons, and the long term mean

| | 1967–91 | 1990–91 | 1991–92 |
|---|---|---|---|
| October | 16 | 5 | 0 |
| November | 57 | 0 | 105 |
| December | 101 | 29 | 301 |
| January | 120 | 146 | 206 |
| February | 90 | 49 | 250 |
| March | 77 | 85 | 32 |
| April | 30 | 31 | 2 |
| May | 0 | 1 | 0 |
| Total | 491 | 346 | 896 |

Sufficient precipitation for wild wheat germination did not occur in the 1990–91 season (Table 1) until late December and early January. As a consequence, wild wheat seedlings were marked during January 1991, and observed at five dates, from late January until the end of April, by which time inflorescences were mature (Tables 2 and 3). Precipitation occurred at regular intervals during that period, but the season total was only 77% of the long term average. In the 1991–92 season, precipitation occurred in early November (Table 1) and wild wheat seedlings were marked during the third week of November. The marked plants were monitored at four dates, until the final sampling on April 30 in protected plots and May 10 in grazed plots. Total seasonal precipitation during the 1991–92 growing season was approximately double the long term mean.

Survival, height and number of tillers of each labelled plant were recorded at each of the sampling dates during the growing season. Signs of recent grazing were recorded for individual plants in the grazed plots. The number of emerged, mature inflorescences, of spikelets per inflorescence, and of inflorescences remaining enclosed in the flag leaf, were recorded for each plant at the end of the growing season.

In 1991–92, every fifth plant with an emerged inflorescence was harvested for measurements of inflorescence weight and seed number. Seeds extracted from harvested plants within grazed and protected plots were sorted by position in the spikelet (basal and terminal) and by seed fullness. A seed was defined as 'full' when its surfaces were convex or planar, and as 'thin' when one or more surfaces were concave or wrinkled. Germination percentage of seeds classified by grazing treatment, position and fullness was tested on moist filter paper in uncovered Petri dishes at 20 °C for 10 days in November 1992.

In the summer of 1991, exclosures were opened to cattle grazing to reduce litter and standing dead biomass. The remaining dry biomass both inside and outside the exclosures, was estimated by harvesting five 25-cm × 25-cm quadrats systematically placed within each plot, in October 1991, prior to the second growing season. Although summer grazing had removed a portion of the dry herbage that had accumulated in the exclosures, litter and dead standing biomass in them was still twice that in grazed plots at the beginning of the 1991–92 growing season (262 vs. 128 g $m^{-2}$, respectively). Consequently, differences in plant responses between grazed and protected plots in 1991–92, but not in 1990–91, may reflect the effects of greater initial litter mass, in addition to direct grazing effects.

The data were recorded in the field on a palmtop computer and transferred to a PC for editing and statistical analysis with SAS-PC. Significance of grazing treatment effects on quantitative measures of plant

**Table 2** Morphological development, survival and reproductive performance of wild wheat plants in grazed and protected plots during two growing seasons. Significances of differences due to the grazing treatment were evaluated by the paired *t*-test for quantitative measures, and by a logit response categorical model for survival and fertility.

| | 1990–91 | | | | 1991–92 | | | |
|---|---|---|---|---|---|---|---|---|
| | date | protected | grazed | *P* | date | protected | grazed | *P* |
| height (cm) | 11/2 | 6 | 5 | | 23/12 | 12 | 5 | *** |
| | 10/3 | 22 | 12 | *** | 3/3 | 30 | 11 | *** |
| | 26/3 | 40 | 25 | ** | 5/4 | 60 | 23 | *** |
| | 29/4 | 64 | 38 | ** | 30/4 | 57 | 31 | *** |
| # tillers/plant | 27/12 | 2.8 | 3.4 | | 23/12 | 2.1 | 3.3 | * |
| | 11/2 | 4.4 | 4.4 | | | | | |
| | 10/3 | 6.2 | 7.7 | | 3/3 | 2.0 | 3.2 | ** |
| | 26/3 | 4.3 | 6.2 | * | 5/4 | 1.4 | 2.9 | ** |
| % survival of marked plants | 10/3 | 97 | 96 | | 3/3 | 97 | 85 | *** |
| | 26/3 | 95 | 94 | | 5/4 | 92 | 73 | *** |
| | 29/4 | 93 | 88 | * | 10/5 | 88 | 64 | *** |
| % fertile/surviving plants | 29/4 | 96 | 67 | *** | 10/5 | 97 | 83 | *** |
| % with only enclosed ears/surviving plants | 29/4 | 2 | 13 | ** | 10/5 | 2 | 5 | |
| % fertile/marked plants | 29/4 | 89 | 60 | *** | 10/5 | 86 | 54 | *** |
| # emerged inflorescences/plant with inflorescence | 29/4 | 2.0 | 1.4 | * | 10/5 | 1.1 | 1.2 | |
| # enclosed inflorescences/plant with inflorescence | 29/4 | 0.2 | 0.5 | * | 10/5 | 0.0 | 0.2 | * |
| # emerged inflorescences/fertile plant | 29/4 | 2.1 | 1.7 | | 10/5 | 1.1 | 1.3 | |
| # spikelets/emerged inflorescence | 29/4 | 7.5 | 6.2 | * | 10/5 | 7.1 | 5.0 | * |
| # spikelets/fertile plant | 29/4 | 16.2 | 10.4 | * | 10/5 | 8.1 | 6.7 | |
| # spikelets/marked plant | 29/4 | 14.4 | 6.5 | † | 10/5 | 7.0 | 3.7 | † |
| # full seeds/marked plant | | | | | 10/5 | 6.1 | 2.6 | † |

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; †significance not tested.

**Table 3** Morphology, survival and reproductive performance of recently grazed and ungrazed wild wheat plants within grazed plots, during two growing seasons. Statistical tests and notation – as in Table 2.

| | 1990–91 | | | | | 1991–92 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | date | | defoliated | | | date | | defoliated | | |
| | def. | meas. | yes | no | *P* | def. | meas. | yes | no | *P* |
| height(cm) | 11/2 | 11/2 | 5 | 5 | | | | | | |
| | 10/3 | 10/3 | 11 | 15 | * | | | | | |
| | 26/3 | 26/3 | 23 | 27 | | 5/4 | 5/4 | 23 | 31 | * |
| | 29/4 | 29/4 | 29 | 48 | *** | 10/5 | 10/5 | 19 | 34 | *** |
| # tillers/plant | 11/2 | 11/2 | 4.5 | 4.4 | | | | | | |
| | 10/3 | 10/3 | 8.0 | 6.7 | | | | | | |
| | 26/3 | 26/3 | 6.4 | 6.2 | | 5/4 | 5/4 | 3.1 | 2.0 | ** |
| % fertile/surviving plants | 11/2 | 29/4 | 70 | 65 | | | | | | |
| | 10/3 | 29/4 | 60 | 78 | * | | | | | |
| | 26/3 | 29/4 | 63 | 73 | | 5/4 | 10/5 | 86 | 86 | |
| | 29/4 | 29/4 | 35 | 93 | *** | 10/5 | 10/5 | 43 | 93 | *** |
| # emerged inflorescence/fertile plant | 29/4 | 29/4 | 1.3 | 1.9 | | 10/5 | 10/5 | 1.4 | 1.3 | |
| # spikelets/emerged inflorescence | 29/4 | 29/4 | 5.9 | 6.2 | | 10/5 | 10/5 | 4.7 | 5.0 | |
| # spikelets/fertile plant | 29/4 | 29/4 | 8.1 | 11.9 | | 10/5 | 10/5 | 7.0 | 6.6 | |

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.
def., date when defoliation was observed; meas., date when variable was measured

performance was evaluated with a paired *t*-test applied to the difference of means of treatment plots within blocks ($n = 6$). Significance of the effects of recent defoliation was evaluated similarly, using the differences between means of grazed and ungrazed plants within grazed plots. Significance of grazing treatment and recent defoliation effects on plant survival was evaluated with a categorical model (CATMOD) using a logit response to block, grazing and block × grazing effects.

## Results

### GRAZING, GROWTH AND SURVIVAL

In 1990–91, the percentage of plants in grazed sites that showed signs of recent defoliation increased from

26% in early February to 67% and 63% in March, then decreased to 46% in late April. Large differences between plots indicated that cattle grazing was patchy at the scale of the experiment. In 1991–92, the percentage of recently grazed plants was high (about 80%) in all plots in early April, but was much lower (mean 18%) and more variable at the end of the season.

Plant height in protected plots was 60–172% greater than for plants in grazed plots at almost all sampling dates in both years ($P < 0.01$; Table 2). Undefoliated plants in grazed plots were 36–78% taller than plants that had been recently defoliated ($P < 0.05$; Table 3), but still 25–49% ($P < 0.05$) shorter than plants in protected plots.

In 1990–91, the number of live tillers per plant in grazed plots was not significantly greater than that in protected plots until the late vegetative stage, when it was 44% greater ($P < 0.05$; Table 2). In contrast, in 1991–92, tiller number per plant was 57% greater in grazed than in protected plots as early as one month after germination ($P < 0.05$). This difference in tiller number per plant remained significant ($P < 0.01$) and increased to twice as many live tillers per plant in grazed compared to protected plots at the end of the vegetative stage in early April 1992. At this time, recently defoliated plants had 55% more live tillers than did undefoliated plants in grazed plots ($P < 0.01$; Table 3), but the latter still had 43% more tillers than plants in protected plots.

In 1990–91, plant survival during the vegetative stage exceeded 90% and was similar in both grazed and protected plots (Table 2). At the end of the season, cumulative plant survival was only 6% greater in protected than in grazed plots ($P < 0.05$). In 1991–92, a difference in plant survival occurred earlier during vegetative growth, with 14% greater plant survival in protected than in grazed plots in early March ($P < 0.001$). Differences in plant survival became more pronounced as the season progressed, with cumulative plant survival in protected exceeding that in grazed plots by 37% at the end of the 1991–92 growing season ($P < 0.001$).

### REPRODUCTION

The proportion of fertile plants, defined as those with an emerged inflorescence, among plants which survived to the end of the growing season, was greater in protected than in grazed plots (43 and 17% in 1990–91 and 1991–92, respectively, $P < 0.001$; Table 2). Within grazed plots, the percentage of fertile plants among survivors was greater in plants that had not been recently grazed compared to those that had been grazed (165 and 116%, respectively, in the two years, $P < 0.05$; Table 3). The effects of defoliation during vegetative growth were smaller and in most cases not significant (Table 3).

Plants in protected plots flowered and matured inflorescences earlier than those in grazed plots. In protected plots, almost 100% of the eventually fertile inflorescences had already begun to emerge on 5 April 1992, compared to only 10% in grazed plots. At the end of April 1992, virtually all inflorescences in protected plots were dry and mature. Most inflorescences in grazed plots did not dry up until 10 days later, and even then many of them were still enclosed in the flag leaf.

The number of emerged inflorescences per plant, among plants possessing inflorescences at the end of the growing season, was 43% ($P < 0.05$) greater in protected than in grazed plots in 1990–91, but no significant difference was observed in 1991–92 (Table 2). In both treatments most plants had only one emerged inflorescence. The number of enclosed and apparently immature inflorescences per plant was significantly greater in grazed than in protected plots in both years ($P < 0.05$, Table 2).

Spikelet number per emerged inflorescence was greater in protected than in grazed plots (21 and 42% in 1990–91 and 1991–92, respectively, $P < 0.05$; Table 2). No significant ($P > 0.05$) difference occurred between recently defoliated and undefoliated plants in grazed plots (Table 3).

Spikelet number per fertile plant was 56% greater in protected than in grazed plots in 1990–91 ($P < 0.05$), but in 1991–92 the difference (21%) was not significant (Table 2). Spikelet number per fertile plant did not differ significantly ($P > 0.05$) between recently defoliated and undefoliated plants in grazed plots (Table 3).

The total number of seeds per spikelet in emerged inflorescences did not differ between protected and grazed plots. Its mean was 1.34, compared to the maximum morphological potential of 2 seeds per spikelet. The number of full seeds per spikelet, and percentage of full seeds, appeared to be greater in protected (0.87 and 63%) than in grazed plots (0.70 and 54%), particularly in the terminal position within the spikelet (0.49 and 86% vs. 0.37 and 70%). However, these differences were not significant (maximum $P = 0.072$ for the terminal position). Weight per spikelet in emerged inflorescences did not differ significantly ($P > 0.05$) between protected and grazed plots.

Germinability of seeds from emerged inflorescences depended on seed position and fullness, but was not consistently different between grazed and protected plots. Almost all full terminal seeds (97%) germinated within 10 days, compared to 60% of full basal seeds, which apparently have some dormancy, and only 37% of thin seeds from both positions.

### FITNESS

We calculated the number of mature spikelets (in both years), and of full seeds in 1991–92, produced per emerged seedling. These values represent measures of

**Table 4** Fitness components of wild wheat plants in protected plots relative to plants in grazed plots, during two growing season. Values are the ratios of means for each component (Fig. 1) in protected to grazed plots

| | 1990–91 | 1991–92 |
|---|---|---|
| Basic fitness components | | |
| $k_1$: plant survival: early March/seedlings | 1.01 | 1.14 |
| $k_2$: plant survival: end of season/early March | 1.04 | 1.21 |
| $k_3$: fertile plants/plants surviving at end of season | 1.43 | 1.17 |
| $k_4$: maximum number of tillers/plant | 0.80 | 0.64 |
| $k_5$: tiller survival: live at end of March/maximum number | 0.85 | 0.76 |
| $k_6$: mature inflorescences/live tillers at end of March | 1.85 | 1.76 |
| $k_7$: number of spikelets/mature inflorescence | 1.21 | 1.42 |
| $k_8$: full seeds/spikelet | – | 1.24 |
| Major fitness components | | |
| $k_9$: plant survival: end of season/seedlings | 1.06 | 1.37 |
| $k_{10}$: fertile plants/seedlings | 1.41 | 1.59 |
| $k_{11}$: live tillers at end of March/plant | 0.69 | 0.48 |
| $k_{12}$: mature inflorescences/fertile plant | 1.28 | 0.85 |
| $k_{13}$: mature spikelets/fertile plant | 1.55 | 1.21 |
| $k_{14}$: full seeds/fertile plant | – | 1.49 |
| Overall growing season fitness | | |
| $k_{15}$: number of mature spikelets/seedling | 2.32 | 1.92 |
| $k_{16}$: number of full seeds/seedling | – | 2.36 |

fitness, integrating survival and reproductive success, of a population of plants over the entire growing season.

All measures were much greater in protected than in grazed plots, 132% and 92% for spikelets in the two seasons, respectively, and 136% for seeds in 1991–92. (Tables 2 and 4).

The ratio of overall growing season fitness in protected to grazed plots is the product of fitness components at several levels (Fig. 1, table 4). Two major components contributed approximately equally to the doubling of fitness in protected plots, namely survival of seedlings to fertile plants ($k_{10}$) and fecundity, represented by the number of mature spikelets ($k_{13}$) in 1990–91, or full seeds ($k_{14}$) in 1991–92, produced per fertile plant.

A finer analysis of the survival component of relative fitness shows that in 1990–91 it was almost entirely due to the final reproductive stage ($k_3$). In 1991–92 the effect was more equitably distributed between the vegetative ($k_1$), transitional ($k_2$) and reproductive ($k_3$) stages.

The fecundity component of relative fitness ($k_{13}$, $k_{14}$) was in both years largely a function of spikelet number per mature inflorescence ($k_7$). The number of mature inflorescences per fertile plant ($k_{12}$) did not

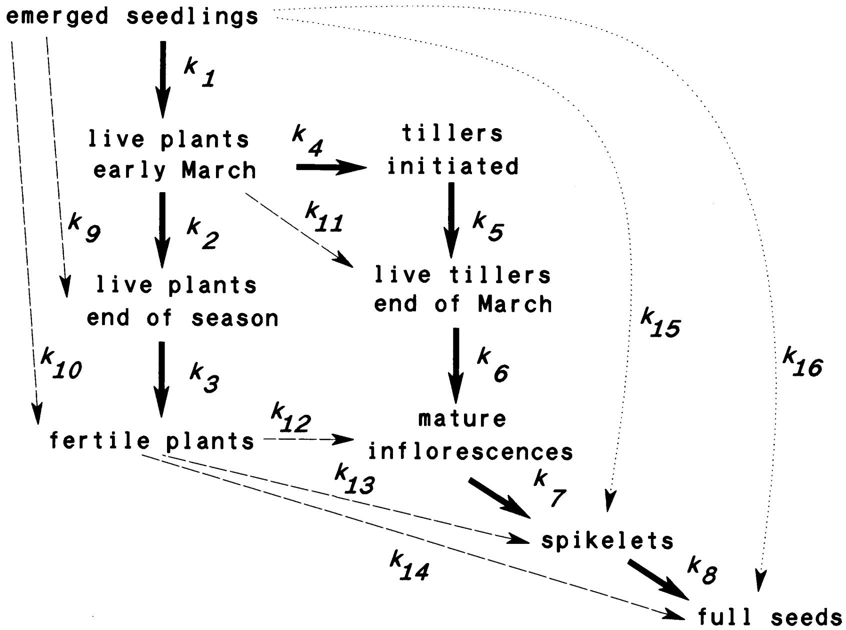

**Fig. 1** Components of fitness during the growing season, from seedling to seed, measured in this study and expressed as relative fitness in Table 4. (——) Basic fitness components; (– – –) major fitness components; (· · ·) overall growing season fitness.

make a consistent or significant contribution to relative fitness, because of counteracting effects. Increased tiller production ($k_4$) and tiller survival ($k_5$, $k_{11}$) in grazed plots was approximately offset by the greater proportion, in protected plots, of surviving tillers that developed into mature inflorescences ($k_6$).

## Discussion

Changing the mean reproductive success of individuals during each growing season by a factor of two can potentially induce rapid decreases or increases in plant density. Thus, the doubling in growing season fitness in protected vs. grazed plots, measured in this study (Table 4), is sufficient to explain the reduction in population density and cover of wild wheat in response to intensive cattle grazing, which has been observed in previous studies (Noy-Meir *et al.* 1989; Noy-Meir 1990; Noy-Meir *et al.* 1991). The result is consistent with the initial assumption that this reduction is mainly due to effects of defoliation during the growing season However, the possibility of an additional contribution due to effects of grazing during the dry season, such as litter removal, can not be excluded. In previous studies, litter cover has been found to have positive, negative, or no influence on germination and establishment of annuals (Heady 1975; Bartolome *et al.* 1980; Fowler 1988; Facelli & Pickett 1991). Observations in the study site in the 1992–93 season indicated that establishment of the earliest cohort of seedlings was 16% greater in the litter-covered exclosures than in the relatively bare grazed plots. However, in experiments in the two previous years no effect of litter cover on germination and establishment was found (Noy-Meir & Briske, unpublished). Possibly, this effect occurs only with certain patterns of rainfall early in the season.

The effects of grazing on the various components of growing season fitness (Table 4) can be attributed to different mechanisms of response to grazing in the vegetative and reproductive stages, some of which have been documented or suggested in the literature.

### EFFECTS OF GRAZING IN THE VEGETATIVE STAGE

Chronic plant defoliation during the vegetative stage can retard the rate and total amount of leaf area and biomass production, particularly when defoliation begins early in the growing season (Noy-Meir 1978, 1992; Ungar 1990). Potential demographic consequences of restricted plant growth and photosynthetic capacity are mortality and reduced seed production. In this investigation, increased plant mortality during the vegetative stage proper contributed to reduced fitness in grazed plots in only one of the two seasons (Table 4), although some later mortality may have been a delayed response. Plants in grazed plots flowered later and produced fewer spikelets per inflorescence than did plants in protected plots. This response has previously been documented in various species (e.g. Cook *et al.* 1958; Stechman & Laude 1962; Hill & Watkin 1975; Crawley & Weiner 1991). Inflorescences may differentiate later and produce fewer floral primordia in response to leaf area and photosynthate limitations following defoliation in the vegetative stage. However, the reduction in spikelet number in this study may have partially resulted from the effects of grazing in the late reproductive stage (below).

During the vegetative stage, the number of live tillers per plant tended to be greater in grazed compared to protected plots (Tables 2 and 4). Grazing-induced increases in tiller initiation and longevity is a commonly observed response in grasses of mesic, fertile environments (e.g. Jones *et al.* 1982; Grant *et al.* 1983), but it is not as consistent a response in other temperate grasslands (Murphy & Briske 1992; Briske & Richards 1994). Stimulation of tiller initiation from axillary buds has been traditionally interpreted as release from apical dominance following removal of the apical meristem region by grazing (apical dominance hypothesis; Branson 1953; Richards *et al.* 1988; Murphy & Briske 1992). However, in this investigation, increased tiller initiation was not restricted to plants that had been recently grazed, although the response was further enhanced in those plants (Table 3). Undefoliated plants within grazed plots also initiated a greater number of tillers than did plants in protected plots. In the 1991–92 season, increased tiller initiation in grazed plots was measured within a few weeks following germination, before any signs of cattle grazing on the small wheat plants were observed.

Increased tiller initiation in undefoliated plants within grazed plots suggests that livestock grazing stimulated tiller production by an extrinsic mechanism. Extrinsic mechanisms are associated with herbivore-mediated environmental modifications while intrinsic mechanisms result from herbivore-induced modifications of plant growth and function (McNaughton 1983). High radiation intensities and a high red/far-red ratio have both been reported to enhance tiller initiation in grasses (Mitchell 1953; Langer 1963; Davies *et al.* 1983; Deregibus *et al.* 1985; Kasperbauer & Karlen 1986; McNaughton 1992; but see Murphy & Briske 1994). Similar mechanisms are probably involved in the plastic morphogenetic responses of plants to both density of neighbours and defoliation. (e.g. Schmitt & Wulff 1993; Novoplansky *et al.* 1994; Bullock *et al.* 1994b, 1994c). In this experiment, light at the soil surface was apparently reduced in intensity and modified its spectral composition earlier and to a greater extent in the exclosed plots compared to the continuously grazed plots. At the beginning of the 1990–91 growing season, leaf area and litter mass were similarly low in grazed and in recently exclosed plots. Thus, differences between treatments in canopy structure and radiation conditions developed later in the growing season, as grazing retarded the accumulation of leaf area. Consequently, tiller initiation was not significantly altered until late March in 1990–91 (Table 2). In the second season, initial litter mass and seedling density were greater in the exclosures, hence the presumed difference in the radiation environment and the observed tiller initiation response developed within the first month of the growing season. The early suppression in tiller height of undefoliated plants in grazed plots compared to those in protected plots (Tables 2 and 3) may also have partially resulted from canopy induced alterations in the radiation microenvironment. Grasses grown in high red:far-red radiation ratios are known to produce shorter leaves and lesser cumulative tiller heights than plants grown in low red:far-red ratios (Casal *et al.* 1985, 1987; Skinner & Simmons 1993).

### EFFECTS OF GRAZING IN THE REPRODUCTIVE STAGE

Two large and consistent components of differential fitness were the proportions of those plants and tillers surviving at the end of March that were eventually fertile. Both proportions were substantially lower in grazed plots than in exclosures (Tables 2 and 4), and the reduction was closely associated with grazing of individual plants during April (Table 3). The failure of grazed plants and tillers to produce mature inflorescences was most likely a result of inflorescence removal in the last few weeks of the growing season. Apparently, removal of maturing primary inflorescences late in the season left insufficient soil moisture and/or assimilates available for inflorescence maturation in any one of the competing secondary tillers. This interpretation is supported by the greater number and percentage of enclosed, immature inflorescences in grazed compared to ungrazed plots (Table 2). Similar reductions in the proportion of plants setting seeds in grazed populations have been documented (e.g. Sarukhan 1974; Bullock *et al.* 1994a; Bastrenta *et al.* 1995; Ehrlén 1995).

A further consistent component of relative fitness which may be related to grazing in the reproductive stage is the smaller number of spikelets per mature inflorescence in grazed plots (Tables 2 and 4). This may have resulted from the selective removal of inflorescences on the larger primary tillers, which left a larger proportion of the smaller inflorescences on secondary tillers (Stechman & Laude 1962; Hill & Watkin 1975). However, the size of inflorescences may also have been restricted by photosynthetic limitation associated with grazing in the vegetative stage (see above).

The number of emerged inflorescences per fertile plant was not an consistent component of relative fitness, since the balance between stimulation of tiller initiation by grazing in the vegetative stage and damage to inflorescence development by grazing in the reproductive stage, was different in the two years of the study (Tables 2 and 4). Variable plant responses between years may have been associated with differences in tiller dynamics due to weather (Table 1), length of the growing season and initial plant cover (Langer 1956; Butler & Briske 1988; Bullock *et al.* 1994b). The number of mature seeds per spikelet in mature inflorescences, and spikelet weight were not significantly reduced by grazing in this study, indicating that seed filling had a high priority for carbon allocation, if sufficient resources existed for inflorescence development and maturation following grazing (but see Cook *et al.* 1958; Stechman & Laude 1962; Mutikainen *et al.* 1993).

Of the components of reduced fitness in grazed plots, the large and consistent reductions in the proportions of fertile plants and fertile tillers can definitely be attributed to the detrimental effects of grazing in the late reproductive stage. Direct evidence for a negative effect of grazing in the vegetative stage on survival was found in one of two years. The consistent reduction in spikelet number may be attributed to grazing in either or both vegetative and reproductive stages.

### IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

The detrimental effect of intensive cattle grazing on the reproductive success of wild wheat can thus, to a large extent, be attributed to grazing in a period of four to six weeks (late March to early May) during which reproductive culms elongate, flower and set seed. The potential detrimental effects of grazing in the vegetative stage on tiller and inflorescence size may be largely offset by increased tiller initiation and longevity within the sparser canopies characteristic of grazed communities.

It is hypothesized that moderate to intensive cattle grazing during 10 or 11 months of the year, followed by grazing deferment during the reproductive stage, will not cause serious reductions in the density of wild wheat. In fact, this grazing regime may eventually maintain a higher density of wild wheat than complete protection from grazing, particularly in habitats were perennials are capable of replacing wild wheat in the absence of grazing (Noy-Meir 1990).

In grasslands managed primarily for conservation of biological diversity, grazing deferment during the reproductive stage is likely to serve two important conservation goals. First, grazing throughout much of the year will limit the accumulation of biomass from dominant annual grasses (wild wheat, barley and oat) and so allow regeneration of subordinate annuals and maintain a rich flora within the community. Secondly, grazing deferment during the reproductive stage will conserve large, and potentially genetically diverse, populations of wild cereals. Deferment during the reproductive stage of wild wheat development will also contribute to maintenance of productive swards of high forage quality. Consequently, where this management regime is logistically feasible, it will also be compatible with livestock production goals.

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