Journal of Applied Ecology 2002
39, 259–278

Response of wild wheat populations to grazing in Mediterranean grasslands: the relative influence of defoliation, competition, mulch and genotype

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Summary

1. Grassland management must be based on an understanding of key species' responses to various grazing regimes to achieve both production and conservation objectives. An experiment was designed to investigate several population processes that may potentially (i) contribute to the decline of *Triticum dicoccoides* (wild wheat) in intensively grazed grasslands, and (ii) promote the persistence of wild wheat in these grazing regimes.

2. The experiment was conducted in natural Mediterranean grassland on the Korazim Plateau in northern Israel in the 1991–92 growing season. Nursery-grown seed of two morphologically distinct wild wheat genotypes were sown in plots with defined mulch applications and clipping regimes.

3. Mulch application did not affect seedling emergence or establishment, but it did reduce tiller number per plant and ear size compared with plants grown without mulch. The detrimental effects of mulch on plant performance throughout the growing season indicated that both radiation and nitrogen limitations may have contributed to growth suppression. Mulch application reduced wheat biomass to a greater extent than that of interspecific competitors. The negative response indicated that mulch removal by intensive grazing during the dry season was unlikely to contribute to the decline of wild wheat in response to intensive livestock grazing.

4. Both vegetative and reproductive performance of wild wheat increased by 50% in response to a reduction of interspecific competition following defoliation of neighbouring plants. A single severe clipping of vegetative wheat plants in defoliated neighbourhoods did not affect plant survival or tiller number, but did reduce ear and spikelet numbers and vegetative and reproductive biomass, compared with unclipped wheat plants. The positive wheat response to the reduction of interspecific competition almost exactly compensated for the negative effect of direct clipping on wheat fitness, and may thus contribute to the persistence of wheat populations.

5. A second severe clipping of wheat plants in the reproductive growth phase severely reduced plant survival to reproduction, reproductive biomass, and seed quantity and quality in those plants that did become reproductive. One-half of the ears initiated following late-season clipping did not emerge from the flag leaf and produced mostly thin seed with reduced germinability.

6. Geniculate genotypes exhibited greater grazing tolerance and reproductive performance than the erect genotypes in response to the second severe clipping. An increase in the relative abundance of geniculate genotypes in intensively grazed communities may provide an important persistence mechanism for wild wheat populations.

7. An integrated estimate of wild wheat fitness, calculated as the mean reproductive output per seed sown, was < 1 in plants clipped during the later phase of reproductive

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growth. This indicates that wheat populations would experience local extinction if this defoliation regime were continued for several successive years.

8. Management prescriptions to conserve this key annual species must focus on the reduction or deferment of late-season grazing during the reproductive growth phase to ensure population persistence.

Key-words: annual grasslands, grassland ecology, herbivory, mulch accumulation, plant–animal interactions, population persistence, *Triticum dicoccoides*.

Journal of Applied Ecology (2002) **39**, 259–278

Introduction

Grasslands in the eastern Mediterranean have been grazed intensely since livestock domestication occurred in this region between 9000 and 8000 BP (Noy-Meir & Seligman 1979; Smith 1995). Consequently, plant populations and communities have been shaped, in both the ecological and evolutionary sense, by this long history of intensive grazing (Milchunas, Sala & Lauenroth 1988; Perevolotsky & Seligman 1998). The flora includes a rich assemblage of small annuals and geophytes that persist under intensive grazing and account for the high diversity of herbaceous communities in the region (Whittaker 1977; Noy-Meir, Gutman & Kaplan 1989). However, some tall grasses have survived millennia of intense livestock grazing, including the annual wild cereals, the progenitors of cultivated wheat (*Triticum*), barley (*Hordeum*) and oats (*Avena*). Greater insight into the ecological and evolutionary mechanisms regulating the response of the wild cereals to grazing are central to the management and conservation of these grasslands and for *in situ* conservation and utilization of the genetic diversity of these wild cereal populations (Harlan & Zohary 1966). Wild cereals also provide a valuable forage resource for livestock production systems in the eastern Mediterranean region. Ecological mechanisms contributing to the grazing tolerance and population persistence of perennial grasslands are relatively well established (Briske & Richards 1995), but these mechanisms are less well defined in annual grasslands (Briske & Noy-Meir 1998).

Wild emmer wheat *Triticum dicoccoides* (nomenclature of Zohary & Feinbrun-Dothan 1966–86) was the source for domestication of emmer wheat *T. dicoccum* about 9800 BP (Zohary & Hopf 1988; Smith 1995). Recent authors consider wild emmer to be a subspecies of hard wheat *T. turgidum* (Smith 1995). *Triticum dicoccoides* was apparently so rare in the 19th century that intensive botanical exploration failed to discover it, until it was identified in 1906 by Aaronsohn at Rosh-Pinna in Galilee. At this time, wild wheat populations were restricted to rocky outcrops and adjacent to spinescent shrubs (Aaronsohn 1909). However, Zohary & Brick (1961); Harlan & Zohary (1966) observed that wild wheat became more abundant and locally dominant in a wider range of habitats following reduced grazing pressure in the 1950s. They suggested that the rock and shrub microhabitats had provided refuges from the intensive grazing pressure prevailing in the region. The abundance of *T. dicoccoides* has since been documented consistently to decrease with an increasing intensity of cattle grazing in northern Israel (Noy-Meir, Gutman & Kaplan 1989; Noy-Meir 1990).

Previous investigations clearly indicate that grazing intensity is a major factor controlling the distribution and abundance of *T. dicoccoides* in eastern Mediterranean grasslands. The large seeds and erect habit of *T. dicoccoides* grant it a competitive advantage over associated annuals in communities with dense canopies, while the same attributes and its high palatability render it susceptible to grazing. Despite its apparent sensitivity to grazing, local populations of wild wheat have survived 8000 years of pastoralism in this region. These observations raise two important ecological questions. (i) What ecological processes and mechanisms have contributed to the decline of *T. dicoccoides* populations under intensive grazing? (ii) What population persistence mechanisms have prevented regional extinction of *T. dicoccoides* under intensive grazing?

We proposed several specific hypotheses relevant to each of these questions, which were tested in manipulative field experiments.

Hypotheses

GRAZING DAMAGE HYPOTHESES

Mulch germination/establishment hypothesis

Mulch removal by intensive grazing during the dry season reduces seed germination and seedling establishment of wild wheat early in the growing season.

Zohary & Brick (1961) suggested that dry plant remnants provided safe sites for spikelet burial, germination and establishment of wild wheat. Removal of the mulch layer by intensive grazing exposes bare soil and reduces the availability of safe sites, except near rocks (Noy-Meir 1990). The potential role of mulch in reducing evaporation and facilitating germination has long been recognized; however, mulch effects on grassland composition and production are complex and often contradictory (Ellison 1960; Seligman & Gutman 1979; Bartolome, Stroud & Heady 1980; Fowler 1988; Facelli & Pickett 1991; Foster & Gross 1998). Mulch affects soil water availability, temperature and light conditions, all of which are known to influence germination and seedling establishment (Briske & Wilson 1978; O'Connor 1996).

Mulch competition hypothesis

Mulch removal by intensive grazing during the dry season reduces the competitive advantage of the larger-seeded wild wheat compared with associated smaller-seeded annual species.

The wild cereals have larger seeds than most other annual grasses and dicots in the community. This may enable them to emerge rapidly through relatively thick layers of mulch and grant them a competitive advantage over associated small-seeded annuals in ungrazed grasslands (Noy-Meir, Gutman & Kaplan 1989; Noy-Meir, Agami & Anikster 1991a). Mulch removal by grazers may minimize this advantage and reduce the ability of wild wheat to compete successfully for resources.

Vegetative damage hypothesis

Severe grazing of wild wheat in the vegetative stage reduces plant fitness by suppressing leaf area and whole-plant photosynthesis.

Plant fitness and population persistence of wild wheat may be suppressed in intensely grazed areas by the direct removal of biomass during vegetative growth, which may critically reduce whole-plant photosynthesis and carbon availability to constrain subsequent plant growth (Noy-Meir 1975, 1978, 1990; Noy-Meir, Gutman & Kaplan 1989). The relatively tall and erect growth form of *T. dicoccoides* renders it more susceptible to defoliation than smaller annuals, even in response to non-selective grazers like cattle. The rock microhabitat with which wild wheat is frequently associated may provide refuges by reducing the ability of large grazers to access and prehend plants within close proximity to rocks (Noy-Meir, Agami & Anikster 1991a; Noy-Meir *et al.* 1991b; Noy-Meir 1996).

Reproductive damage hypothesis

Severe grazing of wild wheat plants in the reproductive stage reduces fitness by removing primary ears late in the growing season, when insufficient time and resources remain for the development of replacement ears.

Wild wheat is also highly vulnerable to direct grazing damage in the reproductive stage, because ears are located at the terminal end of tall erect culms that emerge and set seeds later than most other annual grasses. Results from a grazing experiment suggested that the removal of primary ears in the reproductive stage was the major mechanism contributing to a 50% reduction of fitness in grazed compared with protected wild wheat populations (Noy-Meir & Briske 1996). Soil water is typically depleted by early May in these eastern Mediterranean grasslands, which provides a limited growth period for the development of replacement ears from secondary tillers.

GRAZING PERSISTENCE HYPOTHESES

Reduced competition hypothesis

A reduction in interspecific competition resulting from non-selective grazing by cattle may limit the direct effects of defoliation on the growth and fitness of wild wheat.

Plants may benefit from defoliation of their neighbours coincident with their own defoliation in a process termed competitive fitness (Belsky 1986). Cattle grazing in these grasslands is non-selective, except for height, at high grazing intensity and most herbaceous species are clipped to a uniform height of 3–5 cm (Noy-Meir & Briske 1996). This reduction in diffuse competition may indirectly benefit wheat plants and at least partially counteract the detrimental effects of grazing. The expression of competitive fitness will then depend upon the relative herbivory tolerance of wild wheat relative to their interspecific neighbours (Anderson & Briske 1995; Augustine & McNaughton 1998). The experimental reduction of interspecific competition by clipping of neighbouring plants can disentangle the indirect positive effect of reduced competition from the direct negative effect of grazing on wild wheat plants.

Genotypic selection hypothesis

Natural selection under different grazing intensities has caused differentiation in growth form and developmental strategies between Triticum genotypes that are better competitors and genotypes that are better adapted to grazing.

Phenotypic variation among individuals of the same species in response to distinct grazing histories may involve both genetic differentiation and phenotypic plasticity (Detling & Painter 1983; Carman & Briske 1985; Archer & Tieszen 1986; Briske & Anderson 1992; Briske & Richards 1995). Long-term intensive grazing selects against tall, erect genotypes and favours genotypes characterized by a larger number of shorter, more prostrate tillers. These grazing morphotypes may be better adapted to intensive grazing than more erect morphotypes, based on greater expression of both grazing avoidance and grazing tolerance (Briske 1996). Grazing morphs are best documented in perennial grasses, but there is evidence to suggest that they occur also in wheat. Some genotypes of wild wheat expressed greater grazing tolerance than cultivated wheat (*T. turgidum*) in a common garden, indicating the occurrence of divergent selection since domestication (Waisel 1987). Wild wheat populations in northern Israel are genetically and morphologically diverse; 'robust' and 'slender' types have been distinguished (Poyarkova, Gerechter-Amitai & Genizi 1991).

The various hypothetical mechanisms by which wild wheat populations may be suppressed by intensive livestock grazing, and the mechanisms by which grazing damage may be mitigated, are not mutually exclusive. The important questions are, which mechanisms are most relevant, and what are the relative contributions of these mechanisms to the grazing response of *T. dicoccoides*? The objective of this study was to evaluate experimentally these non-exclusive hypotheses concerning the ecological mechanisms involved in the reduction of wild wheat populations in response to intensive livestock grazing. The experiment was designed to test each mechanism relative to the corresponding null hypothesis and to estimate the relative contribution of the hypotheses that would not be rejected.

Methods

PLANT AND SITE DESCRIPTION

Seeds were collected from populations of wild wheat *T. dicoccoides* with different growth morphology at two basalt grassland sites, 3 km distant from each other, on the Korazim Plateau in eastern Galilee, Israel. In the 'erect' population, collected from an ungrazed exclosure on a slope with large basalt rocks in the Karei-Deshe Experimental Range, most tillers tended to grow vertically from the soil and to elongate rapidly. In the 'geniculate' population, collected from an intensely grazed open range on a plateau near the Bedouin village Tuba-Zangharia, most tillers tended to be short and initially horizontal or inclined, bending upwards to grow vertically only in the reproductive stage. More than 50 plants were sampled from each population, and five spikelets of each plant were sown for propagation. In the nursery, progeny of the two populations showed pronounced differences in growth morphology similar to those observed in the field, indicating genetically based differences between an erect and a geniculate genotype. At maturity, ears from the progeny of each population were harvested and stored separately.

The experimental site was located in Mediterranean grassland on basaltic soil, in a heavily grazed cattle paddock 2 km west of Almagor, and about 2–5 km south of the sites of the source populations (32°55′ N, 35°35′ E). At this site, there was only a sparse natural population of wild wheat, which was concentrated mainly near rocks.

EXPERIMENTAL DESIGN

The experiment was carried out in the 1991–92 growing season. At the end of October 1991, after grazing cattle had removed most of the mulch, a 25 × 25-m area was fenced to exclude further grazing. Within the exclosure, 16 replicate blocks of the experiment were located in areas without rock outcrops. Each block was divided into 16 30 × 30-cm plots, the inner 20 × 20 cm of which was marked for sowing of *T. dicoccoides*. The plots were allocated to combinations of mulch and clipping treatments in an incomplete factorial design, and to seed source (genotype), as follows.

(a) Without addition of mulch; 2 seed sources × 4 clipping treatments:
  0, no clipping (control);
  1, wheat not clipped, all other plants clipped (reduced competition);
  2, wheat plants clipped once, all other plants clipped;
  3, wheat plants clipped twice, all other plants clipped.
(b) Mulch added at two levels; 2 seed sources × 4 mulch + clipping treatments:
  single mulch amount (120 g m^{-2}) × clipping treatments 0, 1 and 2;
  double mulch amount (240 g m^{-2}) – no clipping.

This design, with 16 treatment combinations, enabled us to test for the main effects of mulch, clipping and genotype as well as for the interaction effects genotype × mulch, genotype × clipping, and mulch treatments 0 and 1 × clipping treatments 0, 1 and 2. The clipping treatments imposed were relatively artificial compared with the defoliation patterns of livestock. However, these treatments were not intended to mimic livestock defoliation patterns, but to establish experimentally the basis for wild wheat responses to cattle grazing as documented in a companion experiment (Noy-Meir & Briske 1996). Clipping was imposed at two distinct growth phases, rather than continuously through the growing season, to compare the vegetative and reproductive damage hypotheses.

Wild wheat spikelets were separated into the two parts, each containing one seed, and only the part containing the terminal seed, which germinates more readily, was used in the experiment. On 6–7 November 1991, 16 terminal half-spikelets were sown, in four rows at 5-cm intervals, in the central (20 × 20-cm) portion of each plot. A total of 4096 (16 × 16 × 16) seeds was sown. The half-spikelets were inserted vertically into the soil, to a depth of about 1 cm. The soil surface was still moist from a prior rain (47 mm) at this time, but it was drying rapidly. Therefore, supplemental water equivalent to 6 mm of precipitation was added to each plot. An additional 7-mm precipitation event occurred 3 days following sowing.

Immediately after sowing, mulch that had been collected earlier in the vicinity, consisting mainly of stems and leaf sheaths of annual grasses, was spread over the appropriate plots at 120 g m^{-2} (single) and 240 g m^{-2} (double amount). The mulch was held in place by a coarse wire mesh, until subsequent rains pressed it into the soil.

In plots allocated to clipping treatments 1, 2 and 3, all plants other than the experimental wheat were clipped as close as possible to the surface on 15–17 February 1992. The regrowth was clipped again on two subsequent dates. In clipping treatments 2 and 3, wheat plants were clipped down to a length of 1 cm on all tillers on 1–2 March; in treatment 3, the regrowth was clipped again to 1 cm tiller length on 1 April. Clipping was imposed to a constant residual length, rather than to a constant height, so that both horizontal and vertical tillers received a similar clipping intensity. This was to enable us to compare the grazing tolerance of the erect and geniculate genotypes without confounding by grazing avoidance.

DATA COLLECTION

The emergence of individual seedlings, the survival of individual plants, and the number of tillers of each plant, were recorded on several dates during the growing season. Near the end of the growing season (26 April), the number of 'emerged' ears (those that had emerged from the flag leaf) and of 'enclosed' ears was recorded for each plant. Finally, all plant material in each plot was harvested and separated into wheat ears (emerged and enclosed separately), wheat vegetative material, and other plants. Each treatment was harvested when flag leaves and awns were dry in most plants, beginning with the unclipped treatment on 6 May, and ending with the twice-clipped treatment on 15 May 1992. The harvested material was weighed air-dry, and a subsample was weighed oven-dry; the difference was only about 5%, regardless of treatment. The number of harvested ears (emerged and enclosed separately) and of spikelets per ear of each type was counted for each plot.

Seeds were extracted from a subsample of 10 spikelets from each ear type in each plot. Seeds were classified and counted by position in the spikelet (basal or terminal) and by 'seed fullness' ('full' or 'thin'). A seed was defined as full when all sides were convex or planar, and as thin when one or more of its sides was visibly concave, wrinkled or shrivelled. Seed germinability was tested on samples of up to 100 seeds (or as many as were available), classified by grain position (basal or terminal), seed fullness (full or thin), ear stage (emerged or enclosed), genotype (geniculate or erect) and clipping treatments. Each of the 40 classified seed samples was placed in a Petri dishes containing wet filter paper, at approximately 20 °C in April 1992. Germination occurred after 2 days and the number of germinating seeds was recorded and removed daily for 8 days.

DATA ANALYSIS

The basic data analysed were means (for continuous and count variables) and frequencies (for binary variables) of plant variables in experimental plots ($n = 256$). Normalizing transformations were applied to some variables before analysis of variance. Frequencies varied widely and were a priori transformed to arcsine of the square root. Count variables and biomass variables that showed strongly left skewed distributions were transformed to square root and logarithm, respectively. The transformations produced more symmetric distributions that were similar to normal, in most cases.

Each of the plant response variables was analysed by a general linear model for the main effects of mulch treatment, clipping treatment and wheat genotype, pairwise interactions between these treatments, and the block effect. Main effects, mulch × genotype and clipping × genotype interactions were evaluated over all plots ($n = 256$). Mulch × clipping interactions were evaluated in a restricted data set that included mulch treatments 0 and 1 and clipping treatments 0, 1 and 2 ($n = 192$). The clipping × genotype interaction was significant ($P < 0{\cdot}05$) for many variables. Means of all variables for the main treatments were calculated and compared by a multiple range test (Tukey; $P < 0{\cdot}05$) when three or more treatments were compared. Although mulch × clipping interactions were not significant, means for mulch treatments after the first clipping are presented for unclipped plots, where all mulch treatments were present ($n = 96$). Means for combinations of clipping treatment and wheat genotype are presented when the clipping × genotype interaction was significant.

Results

EFFECTS OF MULCH

Wheat germination, establishment and early survival

Adequate soil water at the time of sowing encouraged rapid and massive germination of annuals, including the experimentally sown wheat seeds. Within 10 days, 88% of the seeds had emerged successfully, and cumulative emergence reached 93% in early January. On the first sampling date, emergence was slightly higher (3–5%, $P < 0{\cdot}01$) in plots devoid of mulch than in plots with mulch (Table 1).

A very high percentage of seedlings survived through the winter. Only 8% of seedlings died in the first 2 months, another 1% in the third month, and 6% in the following 6 weeks prior to the end of March. In January, seedling survival was slightly higher (4%, $P < 0{\cdot}01$) in plots without mulch.

Vegetative growth

As early as 5 weeks after emergence, the frequency of plants that had initiated secondary tillers was 76% greater ($P < 0{\cdot}001$) in plots without mulch than in plots with added mulch (Table 1). The number of live tillers per plant was 10–17% greater ($P < 0{\cdot}005$) in plots without mulch throughout most of the vegetative growth phase. Live tiller number per plant reached a maximum in mid-February and then declined by 15% at the end of March, indicating that some tiller mortality had occurred. On the latter date, tiller number per plant was not significantly different ($P > 0{\cdot}05$) between plots with and without mulch.

Table 1. The effects of single (120 g m^{-2}) and double (240 g m^{-2}) mulch treatments on germination, survival and vegetative and reproductive growth variables of wild wheat plants. Significance refers to $P(F)$ of the main mulch effect in a general linear model analysis over all plots ($n = 256$) that included block, mulch, clipping and genotype main effects, clipping × genotype and mulch × genotype interactions; mulch × clipping interactions were not significant for any variable. Significance levels: NS, $P > 0{\cdot}05$; $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$. Means for mulch treatments are presented for unclipped plots ($n = 256$ until the first clipping, thereafter $n = 96$). In multiple comparisons, values with shared letters are not significantly different ($P > 0{\cdot}05$) as indicated by Tukey's multiple range test. Significantly higher values are in bold

		Mulch treatment			
	Significance	None	Single	Double	Single + double
Emergence and survival					
% cumulative emergence to date					
17.11.91	**	**90**a	87b	85b	
22.12.91	NS	93	92	89	
12.01.92	NS	94	93	91	
% cumulative survival of seedlings to date					
12.01.92	**	**94**a	90b	91ab	
18.02.92	NS	91	90	91	
30.03.92	NS	86	85	82	
Survival of plants established on 18.02.92–26.4.92					
% surviving	NS	86	84	76	
% with ears	NS	85	83	71	
% with emerged ears	NS	81	77	67	
Vegetative growth					
% of plants with > 1 live tiller on date					
22.12.91	***	**30**			17
12.01.92	***	**55**			41
18.02.92	***	**62**			50
30.03.92	NS	46			39
Number of live tillers per live plant on date					
22.12.91	***	**1·40**			1·27
12.01.92	***	**1·97**			1·68
18.02.92	***	**2·16**			1·84
30.03.92	NS	1·82			1·68
Reproduction					
Number of ears per reproductive plant, 26.04.92	NS	1·33			1·22
Number of ears per reproductive plant, final harvest	NS	1·41			1·35
Number of spikelets per ear	**	**6·5**			6
Number of spikelets per reproductive plant	**	**9·2**			8·3
Biomass					
Weight (g) per plot at final harvest					
Associated plants	NS	29			25
Wheat-total	**	**26**			18
Vegetative	**	**13**			9
Reproductive	**	**13**			9
% wheat reproductive/total	NS	51			49
Weight (g) per wheat plant					
Total	**	**2·08**			1.61
Vegetative	**	**1·03**			0.82
Reproductive	***	**1·07**			0.85
Weight (g) per emerged ear	***	**0·83**			0·7
Weight (g) per spikelet: emerged ears	**	**0·118**			0·109

Reproduction

Approximately 81% of the wheat plants in unclipped plots that were established on 18 February survived through most of the growing season (26 April). About 93% of the surviving plants or 75% of the established seedlings produced at least one mature, fully emerged, ear and another 5% produced only enclosed ears (Table 1). Plant survival to reproduction was not significantly affected by the mulch treatment ($P > 0{\cdot}05$).

The mean number of ears per reproductive plant was not significantly affected by the mulch treatment. However, the number of spikelets per ear and per reproductive plant was 9% lower in plots with mulch than in plots without mulch ($P < 0{\cdot}01$). The number of seeds per spikelet was not significantly affected by mulch treatment.

Biomass

The final biomass of associated vegetation was not significantly affected by mulch treatment (Table 1). However, wheat biomass per plot was reduced by 31% in unclipped plots that had either single or double amounts of mulch added to them ($P < 0{\cdot}01$). Both

Table 2. The effects of clipping treatments on survival and vegetative and reproductive growth variables of wild wheat plants. Significance refers to $P(F)$ of the main clipping effect in a general linear model analysis over all plots ($n = 256$) that included block, mulch, clipping, clipping × genotype and mulch × genotype interactions; mulch × clipping interactions were not significant for any variable. Significance levels: NS, $P > 0{\cdot}05$; *$P < 0{\cdot}05$; **$P < 0{\cdot}01$; ***$P < 0{\cdot}001$. Means for clipping treatments are presented for all plots ($n = 256$). In multiple comparisons, values with shared letters are not significantly different ($P > 0{\cdot}05$) as indicated by Tukey's multiple range test. Significantly higher values are in bold

	Significance	Clipping treatment			
		0	1	2	3
Neighbours clipped		**No**	**Yes**	**Yes**	**Yes**
Wheat clipped		**No**	**No**	**Once**	**Twice**
Vegetative growth					
% of plants with > 1 tiller, 30.03.92	***	41b	**79**a	**86**a	
Number of live tillers per plant, 30.03.92	***	1·70b	**3·01**a	**2·95**a	
Survival					
Survival of plants established on 18.02.92–26.04.92					
% plants surviving	***	**83**a	**84**a	**86**a	65b
% with ears	***	**82**a	**81**a	**84**a	35b
% with emerged ears	***	**75**a	**73**a	**74**a	5b
Reproduction					
Mean number of ears per reproductive plant on 26.04.92					
Emerged ears	***	1·10b	**1·52**a	1·14b	0·07c
Enclosed ears	***	0·13c	0·40b	0·35b	**1·04a**
All ears	***	1·24c	**1·92**a	1·49b	1·10c
Mean number of ears per reproductive plant, final harvest					
Emerged	***	1·24c	**1·81**a	1·51b	1·53b
Enclosed	***	0·15b	0·23b	0·19b	**1·25**a
Total	***	1·36d	2·04b	1·67c	**2·67**a
Mean number of spikelets per ear					
Emerged ears	***	**6·4**a	**6·3**a	5·5b	4·2c
Enclosed ears	***	**4·0**a	**3·7**a	**3·5**a	2·8b
All ears	***	**6·2**a	**5·9**a	5·2b	3·7b
Mean number of spikelets per reproductive plant					
Emerged ears	***	8·1b	**11·6**a	8·4b	6·4b
Enclosed ears	***	0·6b	0·9b	0·7b	**3·3**a
All ears	***	8·5b	**12·4**a	9·0b	9·2b
Biomass					
Weight (g) per plot: final harvest					
Associated plants	***	**26**a	7b	8b	1c
Wheat total	***	21b	**33**a	20b	5c
Vegetative	***	10b	**16**a	10b	3c
Reproductive	***	10b	**17**a	11b	2c
Weight (g) per plot: cumulative					
Wheat, total	***	21b	**33**a	22b	9c
% wheat reproductive/total: final harvest	***	50b	49b	**55**a	45c
Weight (g) per wheat plant					
Total	***	1·77b	**2·74**a	1·66b	0·48c
Vegetative	***	0·89b	**1·33**a	0·77b	0·26c
Reproductive	***	0·91b	**1·41**a	0·89b	0·23c
Weight (g) per ear: emerged ears	***	**0·74**a	**0·77**a	0·59b	0·26c
Weight (g) per ear: enclosed ears	**	0·18a	0·19a	0·19a	0·10b
Weight (g) per spikelet					
Emerged ears	***	0·114ab	**0·121**a	0·106b	0·063c
Enclosed ears	**	0·043bc	0·047ab	**0·053**a	0·034c

vegetative and reproductive biomass of wheat were reduced in mulch plots by similar amounts. The reproductive fraction of wheat biomass was 50%.

The total, vegetative and reproductive weight per wheat plant surviving at the final harvest was reduced by about 20% in mulched plots ($P < 0{\cdot}01$). Weight per emerged ear was reduced 16% by mulch addition ($P < 0{\cdot}001$), which was accounted for by reductions of 8% each in the number of spikelets per ear and in spikelet weight (both $P < 0{\cdot}05$).

EFFECTS OF CLIPPING TREATMENTS

Vegetative growth

On 30 March, the proportion of wheat plants with > 1 tiller in plots in which associated vegetation had been clipped was twice that in unclipped plots ($P < 0{\cdot}001$) (Table 2). The mean number of tillers per plant was 75% greater ($P < 0{\cdot}001$) in plots where associated plants had been clipped compared with control plots.

The number of live tillers increased after 18 February in response to clipping of associated vegetation, while it declined in unclipped plots. This indicated that clipping of interspecific competitors both reduced tiller mortality and increased tiller initiation in wheat plants. However, clipping of wheat plants at the beginning of March had no further effect on the number of tillers per plant at the end of March.

Reproduction

Clipping of both wheat plants and associated neighbours in early March had no effect on survival of established wheat plants to the reproductive phase or on the proportion of plants producing emerged ears (Table 2). However, a second clipping in early April significantly ($P < 0{\cdot}001$) reduced the survival of wheat plants (by 24%) and drastically (by 93%) reduced the proportion of plants producing emerged ears by the end of April. Although 75% of the plants clipped a second time did regrow vegetatively, only one-half of them produced ears.

The number of ears per reproductive wheat plant on 26 April was 55% greater ($P < 0{\cdot}001$) where associated plants had been clipped than in control plots. The first clipping of wheat reduced ear number by 22% ($P < 0{\cdot}05$), but it was still 20% greater ($P < 0{\cdot}05$) than in control plots where neither wheat nor neighbours had been clipped. The second clipping caused an additional 26% reduction ($P < 0{\cdot}05$) in the total number of ears per reproductive plant. More than 90% of the ears in the plots clipped twice were still enclosed within the flag leaf on 26 April, compared with only 10–23% of the ears in plots that were unclipped or clipped only once.

A substantial increase in the number of emerged ears and total ears per reproductive plant occurred between 26 April and the final harvest (6–15 May), particularly in wheat plants clipped twice. At the final harvest, plants clipped twice had a similar number of emerged ears and significantly ($P < 0{\cdot}001$) more enclosed (and hence more total) ears than plants clipped once. Approximately 47% of the ears remained enclosed in plants that were clipped twice compared with 10% in the other clipping treatments. Otherwise, effects at the final harvest were similar to those observed on 26 April: a 50% increase in ear number per plant in response to clipping of associated vegetation ($P < 0{\cdot}001$), and a 20% reduction in response to early season clipping of wheat ($P < 0{\cdot}01$).

Wheat plants that had been clipped once produced ears with 13% fewer spikelets ($P < 0{\cdot}05$) than unclipped plants. The second clipping caused an additional 29% reduction ($P < 0{\cdot}001$) in the number of spikelets per ear. Clipping of interspecific neighbours did not significantly affect ear size.

Clipping of associated vegetation increased spikelet number per plant by 46% ($P < 0{\cdot}001$), but early season clipping of wheat negated this response by reducing spikelet number to a level similar to that of the control plants. The second clipping did not affect the total yield of spikelets per reproductive plant, but it did reduce the proportion of spikelets produced in emerged (vs. enclosed) ears from 93% to 70%.

Each spikelet of wild wheat can potentially produce two grains (basal and terminal), although the uppermost spikelet usually produces only one grain. Over all treatments, 88% of spikelets in emerged ears had a basal grain and 78% had a terminal grain. In ears that ended their development while still enclosed in the flag leaf, only about 25% of spikelets had a basal grain and only 12% a terminal grain. Moreover, 90% of the seeds produced in enclosed ears were classified as 'thin' compared with 54% of the seeds produced in emerged ears (data not shown).

Clipping treatments had highly significant ($P < 0{\cdot}01$ or $P < 0{\cdot}001$) effects on the number of seeds per spikelet in most seed positions and fullness categories (Table 3). Clipping of neighbours only and a single clipping of wheat plants had no significant effect on the number of seeds per spikelet in emerged ears. The second clipping of wheat reduced the number of both basal (by 19%) and terminal (by 26%) seeds per spikelet in emerged ears, and drastically reduced the number of full seeds in both positions, compared with plants clipped once. The total number of seeds per spikelet in enclosed ears was significantly ($P < 0{\cdot}001$) increased by clipping of associated plants, but was not further affected by one or two clippings of wheat.

Biomass

Clipping of associated plants drastically reduced their biomass at the final harvest and released experimental wheat plants from interspecific competition (Table 2). Clipping of associated plants alone increased wheat biomass per plot at the final harvest by 57% ($P < 0{\cdot}001$); both vegetative and reproductive components increased similarly. However, a single clipping of wheat in early March reduced final wheat biomass by 40%, to a value similar to that of the control plants. The second clipping of wheat, in early April, further reduced wheat biomass at the final harvest to 25% of the biomass in the plots clipped once ($P < 0{\cdot}001$). When biomass removed in the two clippings was included into the total biomass production, cumulative wheat biomass harvested from plots clipped twice was only 40% of biomass in plots clipped once.

The reproductive fraction of wheat biomass was 50% in unclipped wheat plants, regardless of the clipping of associated plants. A single early season clipping of wheat increased the reproductive biomass fraction to 55% at the final harvest. However, this response was negated when the clipped biomass was included in the total biomass estimate. The second clipping reduced the reproductive biomass fraction to 45% at the final harvest ($P < 0{\cdot}001$).

Mean total, vegetative and reproductive biomass per plant surviving to final harvest showed similar

Table 3. The effects of clipping treatments on the percentage of wild wheat spikelets that produced seeds of various types. Notation as in Table 2

		Clipping treatment			
	Significance	0	1	2	3
Neighbours clipped		**No**		**Yes**	**Yes**
Wheat clipped		**No**	**No**	**Once**	**Twice**
Emerged ears					
Basal grain					
Total	**	**93**a	**93**a	**89**a	72b
Full seeds	***	**35**a	**39**a	**40**a	6b
Thin seeds	NS	58	54	49	69
Terminal grain					
Total	***	**83**a	**83**a	**77**a	57b
Full seed	***	**49**a	**49**a	**49**a	3b
Thin seeds	***	34b	34b	28b	**54**a

responses to clipping, as did biomass per plot. The mean weight of ears enclosed in the flag leaf was only 25% that of emerged ears, due to fewer spikelets which had 42% of the mean weight per spikelet in emerged ears. The mean weights per ear and per spikelet were not significantly affected by clipping of neighbours alone. A single clipping of wheat reduced weight per ear by 23% and per spikelet by 12% ($P < 0·05$) in emerged ears, compared with unclipped plants. The second clipping caused further reductions in weight per ear (56%) and per spikelet (41%) in emerged ears ($P < 0·001$), compared with plants clipped once. The weight of enclosed ears and spikelets was also reduced by a second clipping.

EFFECTS OF GENOTYPE AND GENOTYPE × CLIPPING INTERACTION

Wheat germination, establishment and early survival

There was no difference ($P > 0·05$) in seedling, establishment and survival between the two genotypes. Seedling emergence and survival were 94% and 92%, and 86% and 84%, for the geniculate and erect genotypes, respectively, at the end of the vegetative growth phase on 30 March. Seedlings of both genotypes showed 91% seedling establishment at this time.

Vegetative growth

During the entire vegetative growth phase the frequency of tillering plants and the mean number of tillers per plant were substantially greater ($P < 0·001$) in plants from the geniculate population than in those from the erect population (Table 4). At the first sampling date in December there was a significant ($P < 0·001$) genotype × mulch interaction. Genotypes expressed a greater difference in initial tiller number in the bare plots than in the mulched plots.

On 30 March, the proportion of plants that developed tillers, and the mean number of tillers per plant, were still significantly ($P < 0·001$) greater, over all clipping treatments, in the geniculate than in the erect genotype. However, clipping of associated plants reduced the advantage of the geniculate over the erect genotype in the percentage of plants that developed tillers (genotype × clipping interaction, $P < 0·01$; Table 5).

Reproduction

There was no difference between genotypes in survival to reproduction in unclipped plots or averaged over clipping treatments. Geniculate plants appeared to survive the second clipping better than erect plants, but the interaction was not significant ($P = 0·16$).

The number of emerged ears per reproductive plant on 26 April was significantly greater in the erect than in the geniculate genotypes, in plots where interspecific neighbours had been clipped and wheat had been clipped once (interaction $P < 0·05$; Table 5). In contrast, the number of enclosed ears per plant on this date was considerably greater in the geniculate than in the erect genotype, for the same clipping treatments (interaction $P < 0·001$). The total number of ears on 26 April did not show a significant genotype × clipping interaction. However, the total number of ears was 11% greater in the geniculate than in the erect genotype ($P < 0·01$) over all clipping treatments at this date.

The number of emerged ears per reproductive plant at the final harvest (5–15 May) was similar to the number of total ears per plant on 26 April, for both genotypes and for most genotype × clipping combinations. This correspondence indicates that an additional 10–15 days was sufficient for enclosed ears present on 26 April to emerge by the final harvest. As the number of late emerging ears was greatest in the geniculate genotype, this genotype had 12% more emerged ears than the erect genotype at the final harvest over all clipping treatments ($P < 0·01$; Table 4). However, in twice-clipped plots, an additional late cohort of ears appeared after 26 April that remained enclosed in the flag leaf until they senesced prior to 15 May. The number of late-developing enclosed ears was considerable greater in erect than in geniculate genotypes

Table 4. The effects of genotype on survival, vegetative and reproductive growth variables of wild wheat plants. Significance refers to $P(F)$ of the main genotype effect in a general linear model analysis over all plots ($n = 256$) that included block, mulch, clipping, clipping × genotype and mulch × genotype interactions; mulch × clipping interactions were not significant for any variable. Significance levels: NS, $P > 0·05$; $^{*}P < 0·05$; $^{**}P < 0·01$; $^{***}P < 0·001$. Means for genotypes are presented for all plots ($n = 256$). In multiple comparisons, values with shared letters are not significantly different ($P > 0·05$) as indicated by Tukey's multiple range test. Significantly higher values are in bold

		Genotype	
	Significance	Geniculate	Erect
Vegetative growth			
% of plants with > 1 tiller on date			
11.12.91	***	**34**	14
12.01.92	***	**61**	37
18.02.92	***	**70**	38
30.03.92	***	**75**	59
Mean number of live tillers per live plant			
11.12.91	***	**1·50**	1·17
12.01.92	***	**1·99**	1·55
18.02.92	***	**2·41**	1·59
30.03.92	***	**2·93**	2·06
Survival			
Survival of plants established on 18.02.92–26.04.92			
% surviving	NS	83	80
% with ears	NS	77	75
% with emerged ears	NS	63	68
Reproduction			
Mean number of ears per reproductive plant on 26.04.92			
Emerged	NS	1·08	1·15
Enclosed	***	**0·46**	0·24
Total	**	**1·53**	1·39
Mean number of ears per reproductive plant: final harvest			
Emerged	**	**1·57**	1·40
Enclosed	NS	0·32	0·28
Total	*	**1·86**	1·65
Mean number of spikelets per ear			
Emerged	NS	5·8	6·0
Enclosed	NS	3·8	3·4
Total	NS	5·4	5·7
Mean number of spikelets per reproductive plant			
Emerged ears	NS	9·3	8·5
Enclosed ears	NS	1·2	0·8
Total	*	**10·3**	9·1
Biomass			
Weight (g) per plot: final harvest			
Wheat: total	NS	21	23
Vegetative	NS	11	10
Reproductive	**	10	**13**
% wheat reproductive/total: final harvest	***	47	**54**
Weight(g) per wheat plant			
Total	NS	1·74	1·93
Vegetative	NS	0·94	0·85
Reproductive	***	0·82	**1·08**
Weight (g) per ear: emerged	*	0·53	**0·79**
Weight (g) per spikelet: emerged ears	***	0·09	**0·126**

(genotype × clipping interaction $P < 0·01$; Table 5). Therefore, the total number of ears (emerged and enclosed) at the final harvest was 15–23% greater for geniculate than erect genotypes for all treatments, except when wheat plants were clipped twice. In this treatment, the total number of ears was 24% greater for erect than for geniculate genotypes (interaction $P < 0·05$).

The number of spikelets per emerged or enclosed ears was not significantly different between genotypes. However, the mean number of spikelets per ear in plots clipped twice was 20% greater for geniculate than for erect genotypes, while in plots where wheat had not been clipped it was 10% greater for erect genotypes (interaction $P < 0·05$). The total number of spikelets per reproductive plant was 13% greater in geniculate genotypes, over all treatments ($P < 0·05$).

Over all clipping treatments, emerged ears of the erect genotype had 7% more total (full + thin) seeds per spikelet ($P < 0·01$) than those of the geniculate genotype (Table 6). The proportion of full seeds in emerged

Table 5. Significant effects of genotype × clipping interaction on some vegetative and reproductive variables of wild wheat plants. In all other variables there was no significant genotype × clipping interaction. Notation similar to Table 2, but significance refers to the clipping × genotype interaction. In each cell the first value is for the geniculate type and the second for the erect type. Bold: cells where the difference in favour of the geniculate type is greatest (or the difference in favour of the erect type is least); bold italic: cells where the difference in favour of the erect type is greatest (or the difference in favour of the geniculate type is least)

		Clipping treatment			
	Significance	0	1	2	3
Neighbours clipped		**No**	**Yes**	**Yes**	**Yes**
Wheat clipped		**No**	**No**	**Once**	**Twice**
Vegetative growth					
% of plants with > 1 tiller on date 30.03.92	**	**54/27**	***88/78***		
Reproduction					
Mean number of ears per reproductive plant on 26.04.92					
Emerged	*	**1·15/1·10**	1·46/1·59	***1·01/1·27***	0·03/0·10
Enclosed	***	***0·15/0·12***	0·53/0·25	**0·56/0·14**	1·13/0·94
Mean number of ears per reproductive plant at final harvest					
Enclosed	**	0·21/0·10	0·29/0·17	**0·27/0·11**	***0·94/1·56***
Total	*	1·49/1·23	2·18/1·89	**1·85/1·50**	***2·38/2·95***
Mean number of spikelets per ear					
All ears	*	**5·9/6·5**	5·7/6·2	5·1/5·3	**4·0/3·3**
Biomass					
% wheat reproductive/total: final harvest	*	46/54	***45/56***	45/51	**23/19**
Weight (g) per wheat plant					
Reproductive	**	0·79/1·02	***1·13/1·70***	0·81/0·97	**0·23/0·23**
Emerged ears	*	0·78/1·02	***1·09/1·67***	0·79/0·96	**0·21/0·22**
Weight (g) per ear: emerged	**	0·60/0·89	***0·59/0·97***	0·50/0·67	**0·23/0·29**
Weight (g) per spikelet: emerged ears	***	0·10/0·13	***0·10/0·15***	0·09/0·12	**0·05/0·07**

Table 6. The effects of genotype on the percentage of wild wheat spikelets that produced seeds of various categories. Notation as in Table 4

		Genotype	
	Significance	Geniculate	Erect
Emerged ears			
Basal grain			
Total	**	87	**92**
Full seeds	***	21	**48**
Thin seeds	***	**67**	44
Terminal grain			
Total	**	75	**82**
Full seeds	***	28	**60**
Thin seeds	***	**48**	22

ears was much greater in the erect than in the geniculate genotype (51% vs. 26% in basal grains, and 72% vs. 37% in terminal grains, respectively). In the basal and terminal positions, respectively, there were 128% and 114% more full seeds per spikelet in the erect genotype, but 52% and 118% more thin seeds in the geniculate genotype ($P < 0{\cdot}001$). The total number of seeds per spikelet in enclosed ears was 86% higher ($P < 0{\cdot}01$) in the geniculate than in the erect genotype. There were no significant clipping × genotype interactions in numbers of seeds per spikelet.

Biomass

Reproductive wheat biomass per plot was 25–30% higher ($P < 0{\cdot}001$) in the erect than in the geniculate genotype, in unclipped plots as well as over all clipping treatments (Table 4). This was partly offset by a non-significant trend of greater vegetative biomass in the geniculate genotype, so that total biomass was not significantly different between genotypes. The reproductive biomass fraction was generally greater in the erect than in the geniculate genotype ($P < 0{\cdot}001$). However, the reproductive biomass fraction of the geniculate genotype was less depressed by the second clipping (interaction $P < 0{\cdot}05$).

The erect genotype had significantly greater reproductive weight per plant (by 32%, $P < 0{\cdot}001$) over all clipping treatments, despite its smaller number of ears. This resulted from a substantially greater weight per emerged ear (by 49%, $P < 0{\cdot}05$) and per spikelet in emerged ear (by 40%, $P < 0{\cdot}001$) than in plants of the geniculate genotype. The advantage of the erect genotype in these three measures was enhanced by clipping of associated plants only, but it was reduced by the second clipping of wheat (clipping × genotype interaction, $P < 0{\cdot}01$).

EFFECTS ON SEED GERMINABILITY

Percentage germination was analysed by a general linear model, using clipping treatment, genotype, ear stage (emerged/enclosed), seed position (basal/terminal) and seed fullness (full/thin) as factors. Seed position and seed fullness were the only factors that contributed significantly ($P < 0{\cdot}05$) to the model. These two factors accounted for 75% of variation in germinability. Germinability of terminal seeds was much higher than

Table 7. Effects of mulch and clipping treatments and genotype on three measures of per capita reproductive output of wild wheat seeds sown. Means for mulch treatments are over unclipped plots ($n = 96$) and means for clipping treatments and genotype are over all plots ($n = 256$). Significance of main effects was determined by non-parametric analysis of variance (Kruskal–Wallis). Significance levels are as in Table 1

Measures of per capita reproductive output	Spikelets (emerged) per seed sown	Full seeds (emerged) per seed sown	Ear weight (emerged) per seed sown
Mulch treatments			
No mulch	6·6	5·2	0·81
Single or double mulch	5·2	3·9	0·55
Mulch effect	*	NS	*
Clipping treatments			
No clipping	5·7	4·3	0·64
Only neighbours clipped	8·4	7·0	1·02
Wheat clipped once	6·1	5·3	0·66
Wheat clipped twice	2·0	0·2	0·12
Clipping effect	***	***	***
Genotypes			
Geniculate	6·3	2·9	0·58
Erect	5·7	6·5	0·78
Genotype effect	NS	***	**

of basal seeds, and germinability of full seeds was considerably higher than that of thin seeds. In fact, virtually all full terminal seeds (98%) germinated within 8 days, compared with only 29% of full basal seeds. This was consistent with the results of field trials and is probably associated with the occurrence of dormancy or some other mechanism of inhibition in basal seeds (Horovitz 1998). Surprisingly, even the seeds classified as thin showed fairly high germinability (64%), insofar as they came from the terminal position in the spikelet.

After accounting for the effects of seed position and fullness, additional differences in germinability between clipping treatments were neither significant nor consistent. The only significant ($P < 0{\cdot}05$) genotype effect was a higher fraction of germinable seeds in the first 2 days of the experiment in the geniculate (83%) than in the erect genotype (68%).

GROWING SEASON FITNESS AND ITS COMPONENTS

An integrated estimate of fitness throughout the growing season was calculated as the mean reproductive output per seed sown, using the number of spikelets in emerged ears, the number of full seeds, and the weight of emerged ears as measures of reproductive output. Mulch addition caused a moderate reduction in two of these measures (Table 7) and the erect genotype was superior to the geniculate genotype in two of the three measures. All three measures were substantially affected by clipping treatment (Table 7). The reproductive output of plants in the twice-clipped treatment was far less than in the other treatments. The number of full seeds produced per seed sown, a maximum estimate of the per capita population growth rate, was < 1 in the twice-clipped treatment, indicating that a population would decline to extinction under such treatment. In all other treatments, this estimate was considerably and significantly > 1, indicating population persistence.

The ratio of per capita reproductive output between the two genotypes or two treatments is an overall measure of relative 'fitness' during the growing season. Overall fitness is the product of 'fitness components' (Noy-Meir & Briske 1996), i.e. between-genotype or between-treatment ratios of demographic variables expressing relative survival or performance at different phases or processes within the growth cycle (Table 8 and Fig. 1). Treatment responses at successive growth phases may amplify or, in some cases, counteract each other partially or completely.

The negative effect of mulch on tiller initiation was compensated for by greater tiller survival to reproduction; thus, the suppression of overall fitness (–22% to –32%) in the mulch treatments was mainly the result of lower ear size and weight (Table 8 and Fig. 1). The large (+49% to +59%) positive effect of clipping interspecific neighbours on the reproductive success of wheat plants resulted largely from a substantial increase in tiller density during the vegetative phase that was partially negated by a reduction in the proportion of tillers that became reproductive.

Clipping of wheat plants in the vegetative stage did not have a negative effect on plant survival and growth in the vegetative growth stage (Table 8 and Fig. 1). The negative effect (–27% to –35%) of clipping in the vegetative phase on overall fitness resulted from the accumulation of small negative after-effects in the reproductive stage (proportion of reproductive tillers, ear and spikelet size). The drastic (–68% to –97%) reduction of fitness caused by clipping wheat plants in the reproductive stage resulted from a peculiar combination of effects. Late-season clipping was associated with a large reduction in the proportion of plants producing mature ears, but within those few fertile plants there was no effect on tiller survival to reproduction. A

Table 8. Effects of mulch treatment, clipping treatment and genotype on 'fitness components' of wild wheat. The values are between-treatment ratios of means of demographic variables at various growth phases. The symbols k1, k2, etc., associate each variable and fitness component with a specific process or phase within the growing season as shown in Fig. 1. Intermediate and overall fitness components are related to basic components as indicated by the equations in terms of k. Ratios that are significantly ($P < 0{\cdot}05$) different from 1 are shown in bold

Fitness of treatment	Mulch (single + double)	Clip only other plants	Clip wheat in vegetat. stage	Clip wheat also in reprod. stage	Geniculate type
Compared to reference treatment	No mulch	No clipping	Clip only other plants	Clip wheat only in vegetat. stage	Erect type
Basic fitness components					
k1: germination + establishment: plants 18·02/seeds	0·99	1·00	1·00	1·00	1·00
k2: plant survival: end of season/18·02	0·95	1·01	1·02	0·76	1·04
k3: fertile plants/plants surviving end of season	0·97	0·96	0·99	0·09	0·89
k4: maximum number of tillers/plant	**0·85**	**1·77**	0·98	1·00	**1·42**
k5: tiller survival: live end of March/maximum number	1·08	1·00	1·00	1·00	1·00
k6: emerged ears/live tillers at end of March	1·04	**0·82**	**0·85**	1·01	**0·79**
k7: number of spikelets/emerged ear	**0·92**	0·98	**0·87**	**0·76**	0·97
k8: full seeds/spikelet in emerged ear	0·99	1·05	1·01	0·10	**0·45**
k9: weight per emerged spikelet	**0·92**	1·06	**0·88**	**0·59**	**0·71**
Intermediate fitness components					
k10 = k1 × k2: plants surviving end of season/seed	0·94	1·01	1·02	0·76	1·04
k11 = k3 × k10: fertile plants/seed	0·91	0·97	1·01	0·07	0·93
k12 = k4 × k5: live tillers at end of March/plant	0·92	**1·77**	0·98	1·00	**1·42**
k13 = k6 × k12: emerged ears/fertile plant	0·96	**1·46**	**0·83**	1·01	**1·12**
k14 = k7 × k13: emerged spikelets/fertile plant	**0·88**	**1·43**	**0·72**	**0·76**	1·09
k15 = k8 × k14: full seeds/fertile plant	**0·87**	**1·50**	**0·73**	**0·08**	**0·49**
k16 = k9 × k14: weight emerged ears/fertile plant	**0·81**	**1·52**	**0·63**	**0·45**	**0·77**
Overall growing season fitness					
k17 = k11 × k14: emerged spikelets/seed sown	**0·78**	**1·49**	**0·73**	**0·32**	1·11
k18 = k11 × k15: number of full seeds/seed sown	0·75	1·61	0·76	**0·03**	**0·45**
k19 = k11 × k16: weight emerged ears/seed sown	**0·68**	**1·59**	**0·65**	**0·18**	**0·74**

further reduction in the size and quality of the ears following the second clipping further contributed to the extremely low overall fitness in plants subjected to two intensive clippings.

The fitness of geniculate and erect genotypes was similar when measured by number of spikelets, because opposing responses in various fitness components partially cancelled each other (Table 8 and Fig. 1). However, the lower quality of spikelets in the geniculate genotype reduced fitness, as measured by reproductive biomass and by number of full seeds, (–26% and –55%, respectively) compared with the erect genotype.

Discussion

MULCH GERMINATION/ESTABLISHMENT HYPOTHESIS

The minimal effect of mulch application on seedling emergence and early survival of wheat plants in this investigation may have been a response to the prevailing precipitation patterns. Rainfall events were frequent early in the growing season and the soil remained moist for long periods in both plots with and without mulch. Consequently, the potentially beneficial effect of mulch associated with the conservation of water near the soil surface was minimized. Mulch may have a more positive effect on seedling emergence and survival when partial germination is induced by a small rain event (15–20 mm) early in the season, followed by an extended dry period (Noy-Meir, Agami & Anikster 1991a). This precipitation pattern occurred in only four seasons out of 10 in the period 1983–93. The variable timing and amount of early season precipitation probably contributes to the inconsistent effects of mulch on seedling emergence and establishment among years and investigations.

REDUCTION OF TILLER NUMBER AND EAR SIZE BY MULCH

Mulch accumulation had unexpected negative effects on tiller number per wheat plant throughout the vegetative phase. The effect was initially observed within 1 week following seedling emergence from the soil and shortly after wheat seedlings had overtopped the mulch layer. A similar delay in tiller initiation of wheat plants in ungrazed compared with grazed plots was documented in a companion grazing experiment (Noy-Meir & Briske 1996). Several mechanisms may have contributed to the detrimental influence of mulch on wheat growth in the vegetative phase. First, a reduction in light intensity at the soil surface may have initially retarded seedling growth and tiller initiation (Kays &

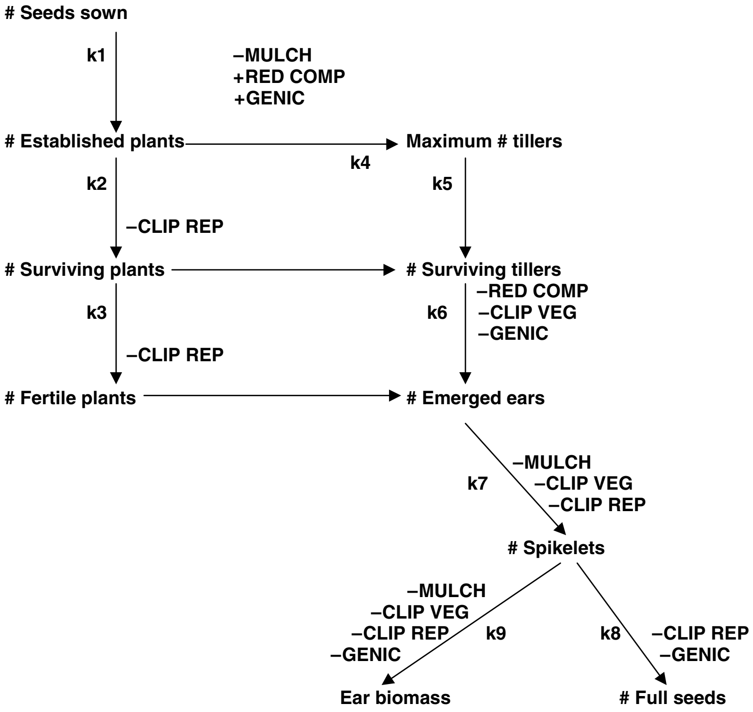

Fig. 1. Schematic model of several growth phases and processes in a wild wheat population. The fitness component associated with each phase or process is designated by k1 to k9 and corresponds with those presented in Table 8. The factors that had significant ($P < 0\cdot05$) effects on each phase or process are indicated by an abbreviation of the factor name (MULCH, mulch application; RED COMP, reduction of competitors; CLIP VEG, clipping in the vegetative phase; CLIP REP, clipping in the reproductive phase; and GENIC, geniculate vs. erect genotype). Sign denotes whether each factor had a positive or negative effect.

Harper 1974; Gautier, Varlet-Grancher & Hazard 1999). Secondly, tiller initiation may have been suppressed by a reduction of the red : far-red radiation ratio (R : FR) (Kasperbauer & Karlen 1986; Casal 1988; Skinner & Simmons 1993) in light transmitted through or reflected by the mulch layer, relative to that of ambient radiation. However, senescent plant tissues often function as neutral filters with respect to R : FR (Ballare *et al.* 1987; Kasperbauer & Hunt 1987; Hunt, Kasperbauer & Matheny 1989; Masoni *et al.* 1994) and some may even enhance the R : FR in reflected light (Kasperbauer 1999). Thirdly, reflection of radiation by the mulch layer may have reduced soil temperatures in the Mediterranean winter growing season. This could reduce tillering, both directly by reduced root growth and nutrient absorption and indirectly by slowing nitrogen mineralization and reducing nitrogen availability (Knapp & Seastedt 1986). Although the precise mechanism requires further investigation, the suppression of tiller initiation in response to moderate mulch accumulation may be an important, but often ignored, process in the response of plant populations and communities to various grazing regimes.

The greater number of tillers in the vegetative phase in the plots without mulch was not expressed as a greater number of reproductive tillers. Competition for light and carbohydrates between primary and secondary tillers may have contributed to tiller mortality prior to the reproductive phase in non-mulched, non-clipped plots (Ong, Marshall & Sagar 1978; Del Moral & Del Moral 1995). However, plants in mulched plots had fewer spikelets per ear and lower reproductive biomass per plant than plants in plots without mulch. This suggests a lower availability of soil resources, possibly nitrogen, in the mulched plots at the time when the apical meristem became reproductive and the number of floral primordia was determined.

The negative effect of mulch on the growth of wild wheat is consistent with the observed increases in wild wheat cover the season following mulch removal by fire (Noy-Meir 2001). Evidence for a mulch-induced resource limitation on wheat growth in this annual grassland is consistent with the transient maxima hypothesis described for mesic C_4 perennial grasslands in North America (Seastedt & Knapp 1993). This hypothesis suggests that infrequent fires optimize the availability of both soil nitrogen and light the season following burning to maximize primary production. In subsequent years without fire, litter accumulation decreases primary production by shading and soil nitrogen correspondingly increases. Non-selective grazing by cattle may mimic the effect of fire on mulch removal (Knapp *et al.* 1998). A similar set of multiple resource limitations mediated by fire and grazing may be regulating primary production in Mediterranean annual grasslands.

MULCH COMPETITION HYPOTHESIS

Wheat biomass was reduced to a greater extent than that of associated species by mulch accumulation. This contradicts the hypothesis that wheat abundance increases in ungrazed grasslands because mulch disproportionately suppresses competitors with smaller seeds and seedlings.

The results of this experiment did not support the two hypotheses involving removal of dry plant remnants during the dry season as a major and consistent mechanism contributing to the decline of wild wheat populations under intense grazing. On the contrary, they suggest that removal of the natural mulch may actually enhance vegetative and reproductive growth of wild wheat plants in Mediterranean grassland, by mechanisms that as yet can only be speculated upon.

REDUCED COMPETITION HYPOTHESIS

The reduction of interspecific competition induced by severe clipping of interspecific neighbours increased the performance of wheat plants in both the vegetative and the reproductive growth phase by at least 50% compared with plants grown with unclipped neighbours. The initial increase in tiller number in the vegetative phase, like that observed in a parallel grazing experiment (Noy-Meir & Briske 1996), can be partially explained by reduced competition for light. An increase in the intensity and R : FR ratio of light within plant canopies has been documented to increase tiller development in wheat and related annual grasses (Kasperbauer & Karlen 1986; Casal 1988; Skinner & Simmons 1993).

However, the positive effect of reduced interspecific competition persisted throughout the reproductive growth phase of wheat, leading to a 50% increase in the number and weight of ears, spikelets and seeds per plant. This implies that clipping of interspecific neighbours increased resource availability to wheat plants not only early in the season, but throughout the entire growing season. Additional resources would have been necessary to support the survival and growth of the greater number of secondary tillers through the end of the vegetative phase and in the reproductive phase when spikelet number was determined and seed filling occurred. The reduction in interspecific competition probably increased the availability of soil water and nutrients, as well as light, during the latter portions of the growing season. Competition has been shown to have a strong influence on tiller initiation, growth and survival by mediating resource availability in grasses (Kays & Harper 1974; Briske & Butler 1989; Derner & Briske 1999) and on plant size and seed weight in annual dicots (Sheppard, Smyth & Swirepik 2001). An increase in tiller density in response to greater resource availability conforms to the reserve meristem hypothesis as an ecological interpretation for the role of apical dominance (Aarssen 1995). The plastic developmental responses exhibited by tiller initiation is anticipated to be of adaptive value in environments where individuals experience large fluctuations in resource availability and interspecific competition at various spatial and temporal scales associated with variable grazing and variable rainfall patterns (Bullock, Clear & Silvertown 1994b; Bullock, Mortimer & Begon 1994).

VEGETATIVE DAMAGE HYPOTHESIS

Wheat plants were tolerant of a single severe clipping in the vegetative growth phase that removed all photosynthetic tissue from plants. Clipping at this phase apparently did not damage the apical meristems located at or near the soil surface; or, if it did, there was an exact numerical replacement by juvenile tillers. Therefore, clipping did not reduce live tiller number per plant or tiller survival compared with unclipped plants grown with clipped neighbours; but neither did clipping stimulate an increase in the number of tillers in clipped plants. These results contrast with those from controlled experiments with containerized *T. dicoccoides* plants, where clipping plants twice during the vegetative phase to heights of 1 and 2·5 cm did significantly increase tiller numbers per plant (Gutman *et al.* 2001). The inconsistent response of tiller number per plant between the two experiments may be partially explained by the difference in clipping treatments and the greater abundance of soil resources in the container experiments. Contrasting plant responses in these two experimental approaches supports the interpretation that tiller initiation in grazed systems may be influenced to an equal or greater extent by extrinsic or indirect mechanisms (McNaughton 1983; Noy-Meir & Briske 1996) than by intrinsic or direct mechanisms, e.g. apical dominance (Richards, Mueller & Mott 1988; Murphy & Briske 1992; Hendon & Briske 1997).

Although a severe clipping in the vegetative phase did not affect plant or tiller numbers, it substantially reduced reproductive performance as measured by numbers of ears and spikelets, and ear weight. Clipped tillers had to replace their entire leaf area in the remaining 2 months of the growing season. Even though regrowth was relatively rapid, because light and soil resources were abundant following clipping, this time period was not sufficient for the clipped plants to compensate fully for either reproductive or total shoot production compared with unclipped plants. A reduction in biomass per tiller following clipping probably limited leaf area and reduced carbohydrate availability for spikelet and ear development. The ears and flag leaves of clipped plants remained green for up to a week longer than those of unclipped plants, presumably by utilizing the soil water that remained in response to reduced transpiration associated with clipping (Wraith *et al.* 1987).

Seed and biomass production of wheat plants that were clipped once and grown with clipped interspecific neighbours was similar to that of unclipped wheat plants grown with unclipped neighbours. The negative effects of severely clipping wheat plants and the positive effects of clipping their neighbours were nearly balanced when clipping occurred at mid-growing season when wheat plants had an opportunity for substantial regrowth. These counteracting responses indicate that the competitive fitness of wild wheat was neither increased nor reduced by non-selective clipping relative to its interspecific neighbours (McNaughton 1979; Belsky 1986).

These experimental results do not support the hypothesis that grazing in the vegetative growth phase is an important mechanism contributing to the decline of wild wheat populations, as long as cattle graze non-selectively, on the basis of sward height. Wheat may respond differently if it was selectively grazed by sheep or other small ruminants in the vegetative phase.

REPRODUCTIVE DAMAGE HYPOTHESIS

A second severe clipping, 1 month following the first clipping, substantially magnified the detrimental effects on wheat plants. The primary tiller in each plant, and possibly one or more secondary tillers, had elevated their apical meristems beyond the 1-cm clipping length by this point in the growing season. Consequently, many plants did not regrow at all following the second defoliation, because all active meristems had been removed and soil resources may have been insufficient to support juvenile tiller initiation from axillary buds. Many of the plants that did regrow vegetatively, did not accumulate sufficient resources to develop reproductive tillers in the remaining 5–6 weeks of the growing season, and only a few plants completed the development of reproductive tillers after the second clipping. Although the total number of ears per plant in those few survivors was similar to or greater than in unclipped plants, approximately 50% of the ears initiated following the late season clipping did not develop sufficiently to emerge from the flag leaf before desiccation. Even those ears that did emerge were not fully developed and had fewer spikelets, less weight per spikelet and per ear, and fewer, smaller seeds compared with unclipped plants. Tillers that regrew after clipping in the reproductive phase apparently had neither sufficient time, nor sufficient leaf area and carbohydrate supply, to develop the normal number of reproductive primordia and to complete seed filling. In experiments conducted with *T. dicoccoides* grown in containers, repeated clipping had little or no effect on vegetative biomass production, but even a single moderate clipping in the reproductive phase greatly reduced reproductive biomass and its proportion of total production (Gutman *et al.* 2001). Previous investigations have reported that grazing delayed reproduction, and reduced the proportion of plants setting seeds (Bullock, Clear Hill & Silvertown 1994a; Bastrenta, Lebreton & Thompson 1995; Ehrlén 1995) and the number of seeds set per inflorescence (Stechman & Laude 1962; Hill & Watkin 1975).

In cultivated wheat, barley and other annual cereals, grain yield is progressively reduced as mowing or grazing is imposed later into the period of reproductive growth (Ramos *et al.* 1996; Redmon *et al.* 1996; Young, Chilcote & Youngberg 1996; Royo 1999). The sensitivity of seed production to defoliation during the reproductive phase is a critical factor in the management of dual-purpose winter cereal crops for both forage and grain production (Bonachela, Orgaz & Fereres 1995; Royo 1997; Gooding *et al.* 1998). The results of this investigation and a companion grazing experiment (Noy-Meir & Briske 1996) indicate that the sensitivity of seed production to defoliation in the reproductive phase is strongly expressed in a wild ancestor of wheat, *T. dicoccoides*, and it is not necessarily a by-product of selection during domestication.

Most seeds produced by plants clipped twice, as well as most seeds in enclosed ears and one-half the seeds in emerged ears in other treatments, were classified as thin. Despite the shrivelled and immature appearance of these seeds, the germinability of seeds in the terminal position was only 34% less than that of full seeds. This indicates that the embryo had fully developed, but that the size of the endosperm was compromised in thin compared with full seeds. Although thin seeds were capable of germination, they may result in lower rates of seedling emergence and survival in the field compared with full seeds (Mutikainen, Walls & Ojala 1993; Bockus & Shroyer 1996; Kidson & Westoby 2000).

The results from this experiment support and explain the results obtained in a grazing experiment with natural wheat populations (Noy-Meir & Briske 1996). The combined results from both experiments demonstrate that a drastic reduction of viable seed production per plant, caused by grazing of wheat plants in the reproductive phase, is the principal mechanism contributing to the observed reductions in wild wheat abundance. Plants that were clipped at both the middle and latter portions of the growing season had per capita seed production << 1, which is well below that required for population maintenance. Although cattle rarely graze wheat plants as severely as the clipping treatments (1 cm tiller length) imposed in this investigation, clipping of tillers to heights of 3–4 cm is common under intensive grazing (Noy-Meir & Briske 1996). This defoliation intensity would be sufficient to remove most developing ears as well as most photosynthetic tissue from wheat plants in the reproductive phase.

GENOTYPE SELECTION HYPOTHESIS

Plants of the geniculate genotype initially produced more tillers than plants of the erect genotype, in all treatments including the most shaded conditions (no clipping, double mulch). This indicates a weaker expression of apical dominance in the geniculate compared with the erect genotype, which pre-adapts the two genotypes for competition in intensively grazed and ungrazed or lightly grazed grasslands, respectively. The strong tendency to initiate secondary tillers provides the geniculate genotype with an advantage in capturing horizontal space and light in open grassland communities. In contrast, the tendency of the erect genotype to concentrate resources into rapid vertical growth of the primary tiller favours it in grasslands with a dense leaf canopy. Contrasting genotypes of both annual and perennial grasses have shown different degrees of success in distinct competitive environments (Bullock, Mortimer & Begon 1994; Hazard & Ghesquiere 1995; Finck & Mundt 1996; Huel & Huel 1996). However, both genotypes expressed considerable phenotypic plasticity in response to defoliation of interspecific neighbours.

Ear development occurred earlier and more biomass was allocated to reproduction in the erect than in the geniculate genotype. Greater tiller production in geniculate genotypes eventually enabled them to produce slightly more ears, but the ears of the erect type were heavier and more of the seeds were fully developed. A greater commitment to reproductive effort would probably pre-adapt the erect genotype to greater fitness in dense grasslands characterized by intense competition for resources. The extended vegetative growth phase of the geniculate genotype would have an advantage only in intensively grazed grasslands characterized by less competition, where the period of available soil moisture for growth and seed filling is extended. However, both genotypes were capable of extending the period of reproduction following severe clipping. In all but the most extreme clipping treatments, the number of emerged spikelets per plant did not differ between genotypes, but the number of full seed and ear weight were significantly greater in plants of the erect compared with the geniculate genotype.

A prostrate or geniculate growth form, with low tiller height and angles, obviously confers greater structural grazing avoidance (Briske 1996) by reducing the amount of photosynthetic and meristematic tissue removed at a given grazing height (Hodgkinson *et al.* 1989). It is less obvious whether prostrate genotypes also possess greater grazing tolerance, i.e. greater capacity for regrowth after a given intensity of defoliation (Briske 1996). In this experiment we were able to evaluate the relative expression of herbivory tolerance, because all tillers were clipped to a constant length (1 cm), rather than a constant height, thus negating the expression of structural grazing avoidance in the geniculate genotype. Following a severe clipping during the vegetative growth phase there were differences in regrowth tiller dynamics between the two genotypes, but the final effect on reproductive biomass and fitness was negligible. The second clipping, during the reproductive phase, severely reduced plant survival, biomass, seed production and fitness in both genotypes. Among plants that survived and regrew, those of the erect type actually produced more reproductive tillers, but the regrowth ears of the geniculate type compensated with a greater number and weight of spikelets. Plants of the geniculate genotype may have possessed a greater number of juvenile tillers at various stages of development that were immediately available to replace the damaged reproductive tillers. On the other hand, stronger apical dominance in plants of the erect genotype may have required a greater time interval for the development of replacement tillers (Olson & Richards 1988; Pierson, Mack & Black 1990).

The imposition of two intensive clippings significantly reduced and negated the advantage of the erect genotype in reproductive biomass per plant compared with the geniculate genotype. Thus, the more equitable pattern of meristem activation and resource allocation among tillers in plants of the geniculate genotype provided them with an advantage over the erect genotype in production of reproductive biomass following intense late season grazing. Although the effect was significant for biomass, but not for seed number, it indicates a greater expression of grazing tolerance in the geniculate genotype, in addition to the greater grazing avoidance naturally associated with the decumbent growth form. Greater grazing tolerance in plants that possess a larger number of active meristems following defoliation conforms to the 'meristem model' of herbivory tolerance (Briske & Richards 1995).

CONCLUSIONS

We conclude from this extensive data set that the direct, detrimental, effect of late season grazing on plant fitness is the primary mechanism contributing to the decline in wild wheat populations in response to intensive livestock grazing. Wheat plants exhibited substantial grazing tolerance to defoliation early in the growing season to minimize the detrimental consequences to fitness. The indirect grazing effect of mulch removal had a stimulatory, rather than a detrimental, effect on wild wheat, so it is unlikely to contribute to a decline in wild wheat abundance. Two distinct mechanisms contribute to the population persistence of wild wheat in grazed systems, in addition to refuges provided by rocks on the soil surface. The reduction of interspecific competition associated with non-selective grazing in the vegetative growth phase effectively negated the direct detrimental effects of grazing on wheat plants. A potentially more important persistence mechanism is an increase in the relative abundance of geniculate wheat genotypes, which possess both greater grazing avoidance and tolerance than the erect genotypes in intensively grazed communities.

IMPLICATIONS FOR MANAGEMENT

The conclusions from this series of manipulative experiments strengthen the recommendations for sustainable grazing management of wild wheat populations that were based on an actual grazing experiment (Noy-Meir & Briske 1996). Grazing of plant remnants during the dry season and grazing during the vegetative phase can be quite intensive without endangering the persistence of wild wheat populations. However, in the case of intensive grazing, a reduction of grazing intensity or deferment of grazing during the last 4–6 weeks of the reproductive phase is necessary to ensure viable seed production at a rate sufficient for population persistence.

These data also possess broader implications for the selection and development of genetic materials for both wild and domestic wheat. The occurrence of similar defoliation responses between wild wheat populations and those reported for domesticated wheat indicate that morphological and physiological mechanisms have not been fundamentally altered by thousands of years of divergent selection. However, we did find substantial quantitative differences between genotypes of *T. dicoccoides* in their response to competition and defoliation that may be utilized in the selection and development of genetic materials. The domestication of cereals for grain production has often been associated with an increase in apical dominance and a reduction in secondary tiller development (Doebley, Stec & Hubbard 1997) and in grazing tolerance (Waisel 1987) compared with the wild ancestors. We found that the erect genotype expressed these traits to a similar extent as domestic wheat cultivars, while the geniculate genotype expressed greater tillering and defoliation tolerance. These latter traits may be of value in the development of cereal cultivars for forage or for dual-purpose forage and grain production.

Acknowledgements

We thank Michal Ramati-Amitai, Mark Rubin and Judith Canetti for efficient technical assistance in both the field and laboratory and two anonymous referees for constructive comments on the manuscript. The research was supported by a grant from the US-Israel Binational Science Foundation (89–14/1), which is gratefully acknowledged.

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Received 11 September 2000; final copy received 4 December 2001