Plant responses to grazing: a comparative evaluation of annual and perennial grasses*

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Summary

Differences in life history strategies among annual and perennial grasses influence the processes by which grazing modifies the persistence mechanisms of these two groups of grasses. Seed production constitutes an obligate persistence mechanism in annual grasses that represents an interruption of meristematic dependence in contrast to the regular replacement of longer lived tillers by perennial grasses. Early-season grazing in productive, semi-natural grasslands does not reduce survival, growth or reproduction of the dominant annual, *Triticum dicoccoides*, but late-season grazing directly removes inflorescences to reduce seed production by approximately 50% compared to ungrazed populations. In addition, grazing induces several indirect effects, including increased tiller initiation and reproduction of *T. dicoccoides* associated with mulch removal and defoliation of interspecific neighbors. Grazing appears to reduce the abundance of tall, dominant annuals by both direct and indirect mechanisms in a similar manner to that reported for perennial grasses, but the direct effect of late-season grazing exerts a substantially greater impact on the composition and structure of annual grasslands. Grazing deferment during the reproductive stage may be sufficient to maintain abundant populations of dominant annual grasses while grazing during the remainder of the year may limit their suppressive effects on associated annual species to maintain high species diversity.

Keywords: plant defoliation, grazing, population persistence, *Triticum dicoccoides*

Introduction

Livestock grazing has substantially modified the composition and structure of grasslands and savannas throughout the world. Relatively predictable patterns of compositional and structural change in response to long-term grazing have been documented in numerous perennial grasslands. Compositional changes most frequently involve the replacement of late-seral dominants by early or mid-seral species while structural changes frequently involve the replacement of tallgrasses by mid- or shortgrasses (Anderson & Briske, 1995). Grazing induced compositional and structural changes predominately occur in response to selective grazing and the subsequent modification of interspecific competitive interactions. Less severely grazed species gain a competitive advantage by preempting resources previously utilized by the dominant species in the absence of grazing (Caldwell et al., 1987). Long-term

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selective grazing can differentially affect population persistence among various species and thereby modify community composition and structure.

A central question to the ecology and management of Mediterranean grasslands is "Does grazing affect the composition and structure of annual grasslands by similar mechanisms as it does in perennial grasslands"? Related issues concern the relative persistence mechanisms of annual and perennial grasses and the extent to which managerial prescriptions may mitigate the detrimental effects of grazing between these contrasting life history strategies. Distinct differences in life history strategies between annual and perennial grasses may potentially influence the mechanisms by which grazing induces species composition changes. Sexual reproduction constitutes the exclusive persistence mechanism in annual grasses while perennial species rely on the frequent production of relatively longer lived tillers and only infrequent regeneration from seed. Grazing may disproportionately affect the persistence of these two contrasting life history strategies by differentially affecting the mechanisms contributing to population persistence. In this context, population persistence integrates developmental, physiological and demographic responses to grazing at the level of the species population.

The primary aims of this paper are to: 1) emphasize the developmental and demographic basis for life history differences between annual and perennial grasses, 2) determine how these life history differences interact with grazing to affect population persistence, and 3) draw both ecological and managerial implications from this comparative evaluation. The comparative approach contrasts our relatively limited knowledge of the responses of annual grasses to grazing with those of the more thoroughly understood responses of perennial grasses to grazing.

Hierarchical organization of grasslands

The ecological and managerial importance of population persistence within grasslands are readily illustrated by the ecological hierarchy theory. Hierarchy theory describes vegetation as a graded series of scales each of which is associated with overlapping temporal responses and spatial dimensions (Fig. 1). For example, individual grass plants are comprised of an assemblage of tillers, populations are defined by both plant density and tiller number per plant, and grassland communities are further composed of an aggregation of species populations. Physiological and developmental processes of individual plants respond in shorter time frames and at smaller spatial dimensions than do population or community dynamics. The gradation of scales within a hierarchy determines that the structure and function of lower hierarchical levels (i.e., tiller and plant) partially defines higher levels of vegetation organization. Higher hierarchical levels (i.e., communities and landscapes) constrain the structure and function of lower levels in ways that are not readily predicable from an evaluation of the lower levels in isolation (Brown & Allen, 1989). It is important to recognize that mechanisms regulating the persistence of species populations collectively scale-up through the various hierarchical levels to influence the structure and function of grassland ecosystems (e.g., biodiversity, stability and response to grazing). Therefore, several ecological scales must be considered simultaneously when evaluating vegetation responses to grazing to minimize incomplete or inaccurate conclusions.

Responses to grazing

Developmental morphology

The potential for canopy reestablishment in grasses following grazing is determined by the availability and activity of various types of meristems (Briske & Richards, 1995). This is a common characteristic of both annual and perennial grasses that has substantial implications for grazing resistance and population persistence. The interaction among meristem types, environmental variables and resource availability determines the rate of leaf area expansion in plants. Leaf growth occurs from cellular division and expansion of intercalary meristems located at the base of the blade, sheath and internode and collectively contribute to the growth of individual phytomers. Phytomers consist of a blade, sheath, node, internode and axillary bud and are recognized as the fundamental unit of grass growth (Briske, 1991). Growth from apical meristems is exhibited as the successive differentiation of phytomers to form an individual tiller. Axillary buds are rudimentary apical meristems that possess the capacity to develop into individual tillers. A single bud is differentiated from the apical meristem with each phytomer.

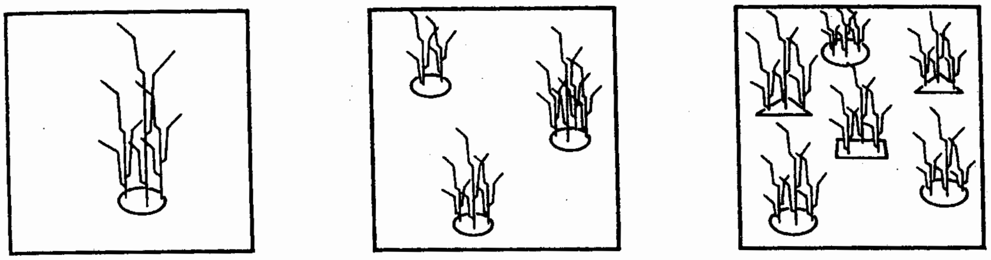

Figure 1. Hierarchical organization of grassland vegetation consisting of a series of graded scales possessing overlapping temporal processes and spatial dimensions (from Briske, 1991).

Growth is dependent on all three meristematic sources in grasses, but their relative contributions differ in magnitude and chronology (Briske, 1991). Although intercalary meristems form the basis for leaf growth, their contribution is limited to the relatively brief period of growth associated with the respective intercalary meristems of individual phytomers. Apical meristems play a central role in the meristematic potential of grasses because they are the source of phytomer and axillary bud production. Axillary buds may then develop into mature tillers that can produce successive axillary buds. Successive tiller production determines the persistence and sustainable productivity of perennial grasses.

Knowledge of the relative availability and activity of meristematic sources is necessary to accurately interpret and potentially anticipate the regrowth potential of grasses (Fig. 2). Canopy reestablishment proceeds most rapidly from intercalary meristems because cell division has previously occurred within leaf primordia (Olson & Richards, 1988; Briske, 1991). Leaf replacement from apical meristems occurs at a slower rate because of the time required for differentiation and cellular expansion within individual leaf primordia. Canopy reestablishment is slowest from axillary buds because of the time required for bud activation and leaf primordia differentiation. Although growth of these three meristematic sources can be considered independently, all three must occur simultaneously to promote leaf and canopy growth. The relative contribution of these meristematic sources to plant growth varies among species and is influenced by environmental variables and stage of phenological development (Olson & Richards, 1988; Briske& Richards, 1995).

The availability and source or meristematic potential forms the basis for many of the generalizations regarding the response of grasses to grazing. For example, the ability of grasses to regrow following defoliation is partially attributable to the basal location of the intercalary and apical meristems and axillary buds. Culm elongation makes a portion of these meristems, especially the apical and intercalary meristems, much more vulnerable to removal by grazing. In addition, floral induction halts the production of new phytomers from the apical meristem as inflorescence production proceeds from this structure (Briske, 1991; Briske & Richards, 1995). In both cases, regrowth must occur from axillary buds of existing tillers because a majority of the intercalary and apical meristems have been removed. Contrasting plant responses to grazing are often determined by meristematic availability at the time of defoliation.

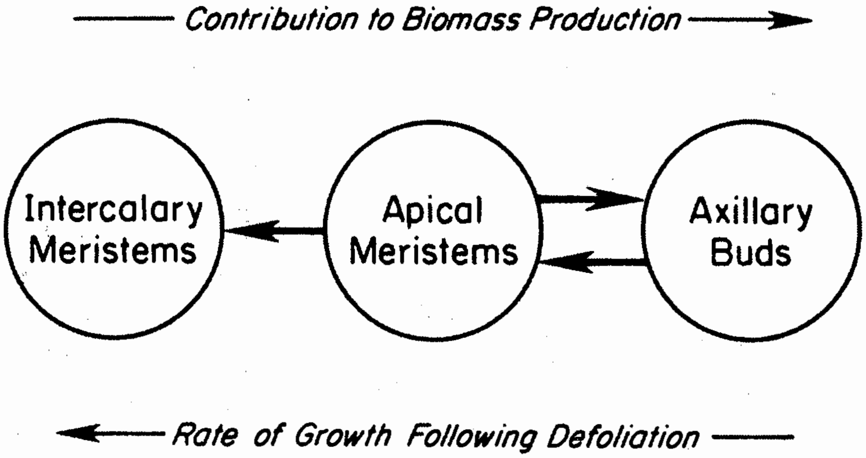

Figure 2. Relative contribution of various meristematic sources to the rate and duration of biomass production in grass plants (from Briske, 1991).

There does not appear to be any basis in developmental morphology to assume that the availability or relative proportion of meristems differs between annual and perennial grasses because these values are established on an individual tiller basis. Therefore, the potential for leaf replacement following grazing should be quantitatively similar. Perennials may accumulate a greater number of tillers per plant over the course of several growing seasons, but this may be more than compensated for by greater plant density in annual grasslands. Larger plant basal area in perennial grasses and associated accumulation of culms and dead leaf material may be more important as an avoidance mechanism to reduce the intensity of livestock grazing than as an increased source of meristems to promote regrowth (Briske & Richards, 1995).

Physiological response to grazing

Plant function is immediately disrupted by grazing in response to a substrate limitation imposed by a reduction in photosynthetic area. A reduction in whole-plant photosynthesis and preferential carbon allocation to rapid shoot growth reduces root growth and nutrient absorption as root carbohydrates are depleted. The extent to which these physiological processes are suppressed and their potential rates of recovery directly affect the grazing resistance, productivity, and competitive ability of defoliated plants. The physiological responses of perennial grasses to defoliation have been extensively reviewed and will not be repeated here (Briske & Richards, 1995).

Unfortunately, minimal information exists to compare physiological responses of annual and perennial grasses to grazing. However, it is reasonable to assume that the responses of annual grasses are at least qualitatively, if not quantitatively, similar to those of perennial grasses. This is especially true for relatively young perennial plants that progress through comparable developmental stages to those of annual plants. A notable exception between these two contrasting life history strategies is greater carbon allocation to shoots and less allocation to roots and juvenile tillers in annual compared to perennial grasses (Ryle, 1970).

An evaluation of the grazing resistance literature for perennial grasses indicates that architectural attributes and demographic processes are of greater importance than physiological processes (Briske & Richards, 1995; Hendon & Briske, 1997). For example, the ability to replace leaf area by rapid tiller initiation and development of leaves with low specific mass is often more important than compensatory photosynthesis or size of carbon reserve pools (Caldwell et al., 1981). Therefore, it may be most beneficial to compare and contrast differences in annual and perennial grasses with respect to meristematic and demographic processes that influence population persistence. Once these critical demographic mechanisms have been identified and evaluated, the underlying physiological processes can be investigated.

Seed versus meristematic dependence

Vegetative growth by successive tiller production is often assumed to be a more prevalent form of reproduction than plant establishment from seed in perennial grasses of both semiarid and mesic grasslands (Belsky, 1992). Investigations conducted in North America consistently demonstrate a lack of correspondence between the existing vegetation of late-successional grasslands and the species composition of the seed bank. Although seeds are frequently produced, few appear to retain their viability within the soil for longer than one year (Thompson & Grime, 1979; Pyke, 1990). In addition, the number of seedlings recruited within established grasslands is frequently low and recruitment only occurs sporadically during years of favorable precipitation and temperature conditions (Pyke 1990; Lauenroth et al., 1994). Tiller recruitment is generally more consistent than plant establishment from seed because juvenile tillers import resources from parental tillers to enhance establishment (Welker & Briske, 1992). Consequently, the initiation and growth of juvenile tillers is much less dependent upon immediate resource availability than is seedling establishment and growth.

However, grassland and pasture persistence is dependent upon plant recruitment from seed in numerous systems including both annual (Noy-Meir & Briske, 1996) and some perennial species populations (O'Connor, 1991). The greater commitment to reproduction in annual than in perennial grasses (Adams & Wallace, 1985) is also reflected in the larger contribution of annuals to the seed bank relative to perennial grasses even though perennials may be more abundant (Major & Pyott, 1966; McIvor & Gardener, 1991). Nevertheless, a poor correlation between the existing vegetation and the composition of the seed bank has been documented for both annual and perennial grasses (Russi et al., 1992). This response may be based in part on the transient or short-lived seed bank in annual grasses. The transient nature of the seed bank is largely a function of a high proportion of seed germination immediately following the occurrence of favorable environmental conditions (Hulbert, 1955; McIvor & Gardener, 1991), rather than of a physiological restriction to seed longevity (Miller & Nalewaja, 1990). The occurrence of a transient seed bank in annual grasses constrains a critical persistence mechanism that is well-recognized in annual plant communities (Pagnotta et al., 1997).

Tiller demography

Tiller recruitment may occur throughout the growing season in both cool-season and warm-season perennial grasses, but maximum recruitment frequently occurs in the autumn and/or spring (Briske & Richards, 1995). Some species recruit a single tiller cohort in the spring or autumn, while others recruit two tiller cohorts during the growing season. Tillers recruited early in the growing season frequently become florally induced and terminate their life cycle during the same growing season while tillers recruited later in the season frequently over-winter and resume growth the subsequent growing season. This pattern of tiller development results in greater tiller longevity, but longevity does not generally exceed two complete growing seasons in temperate perennial grasses (Langer, 1956; Briske & Richards, 1995).

Mortality of vegetative tillers is frequently associated with reproductive development of parental tillers. Young vegetative tillers succumb to shading by the taller reproductive tillers and/or the cessation of resource allocation from parental tillers because of the additional resource demand created by culm and inflorescence development (Ong, 1978). Apparently the smallest tillers within the plant, which are partially dependent upon parental tillers for resources, are unable to effectively compete for resources when the plant encounters stress and are the first to undergo mortality (Ong, 1978). The mortality of reproductive tillers is initiated by the transition of the apical meristem from a vegetative structure to a reproductive structure. At this point, the tiller has lost the capacity to produce new phytomers and will die following senescence of the existing phytomers.

It is difficult to make similar generalizations concerning tiller demography of annual grasses based on the limited information available. However, information for wild (*Triticum dicoccoides*) (Noy-Meir & Briske, 1996) and domestic wheat (*T. aestivum*) (Peterson et al., 1982) suggest the occurrence of comparable demographic patterns to those observed in perennial grasses. Tillers of many annual and perennial grasses are initiated throughout the growing season rather than synchronously at a specific season. However, defoliation and grazing may stimulate tiller initiation more consistently in annual than in perennial grasses (Murphy & Briske, 1992; Noy-Meir and Briske, 1996).

Persistence mechanisms

Population persistence in annual grasses involves the annual regeneration of plants from seed while annual tiller replacement from axillary buds is required for population persistence in perennial grasses. Several parallel responses exist between persistence mechanisms of annual and perennial grasses, but sufficient differences occur to suggest that grazing may disproportionately affect persistence in these two contrasting life history strategies. For example, in annual grasses seed availability generally equates to bud availability, seed viability with bud viability and seed germinability with bud initiation (Fig. 3). Grazing can modify population persistence by affecting one or more of these critical demographic states or processes. However, it appears that a grazing induced reduction in seed availability (Noy-Meir & Briske, 1996) and axillary bud production and activation (Hendrickson & Briske, 1997) are the primary mechanisms by which livestock grazing decreases the persistence of annual and perennial grasses, respectively. Therefore, knowledge of the effects of grazing on the availability and demography of seed for annuals and bud dynamics for perennials will have the greatest consequences to understanding population persistence and community stability.

Grazing can reduce seed production in both annual and perennial grasses by affecting resource availability for reproduction, alteration of the microenvironment for seed germination and seedling establishment, and the direct removal of flowers and seeds (O'Connor, 1991; Noy-Meir & Briske, 1996). In addition, large seeded species may be preferentially selected to confer a survival advantage to associated small seeded species (O'Connor, 1991; Russi et al., 1992).

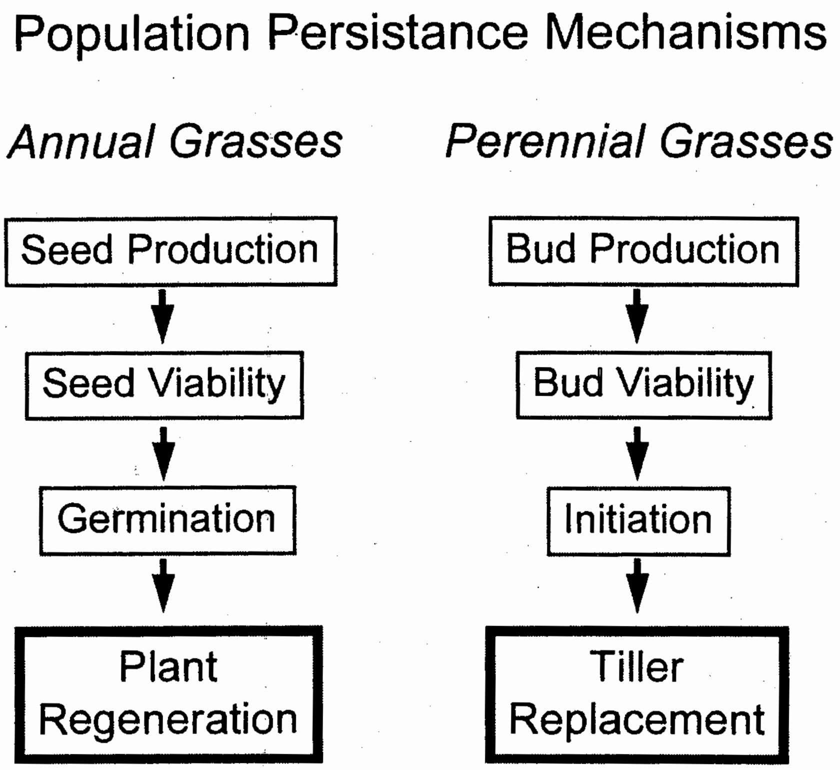

Figure 3. Illustration of the major processes contributing to population persistence in annual and perennial grasses.

Seedlings of annual grasses appear to be equally, or even more, resistant to grazing than seedlings of perennial grasses (Pyke, 1987). Even in cases where grazing does contribute to seedling mortality, seed production of the remaining plants is increased in a density-dependent manner. Similarly, seed production of annual grasses is tolerant of defoliation especially early in the growing season. Negative impacts of grazing on reproductive output can be induced by a reduction in seed weight per plant and/or seed number per plant (Mutikainen et al., 1993; Noy-Meir & Briske, 1996). The effect of defoliation on plant phenology and seed production is more pronounced as it occurs during the later stages of tiller development. In addition, the effect of defoliation is magnified by increased plant density and shading (Pierson et al., 1990; Mutikainen et al., 1993).

In contrast to seed production in annual grasses, bud availability, viability and longevity are relatively insensitive to grazing on an individual tiller basis in temperate perennial grasses (Hendrickson & Briske, 1997). Tiller growth occurs primarily from the most recently developed mature buds on parental tillers. Older basal buds may remain viable for 2-3 years, but less than 10% grow out to produce new tillers. However, long-term grazing can affect bud availability per unit area by modifying plant and tiller densities. Therefore, it must be concluded that while bud banks (sensu Harper 1977, p. 108) exist in perennial grasses, they appear to be of a transient nature similar to those of seed banks. Severe grazing appears to be required to constrain tiller replacement from axillary buds in perennial grasses, but the specific mechanisms are poorly defined.

Direct versus indirect plant responses to grazing

Grazing can contribute to increased plant mortality, reduced recruitment and an overall reduction in population persistence by both direct and indirect effects (Table 1). Direct effects or intrinsic mechanisms are associated with grazing induced physiological plant function and may potentially be positive or negative (McNaughton, 1983; Archer & Smeins, 1991). Negative direct effects are associated with a carbon limitation imposed by a reduction in photosynthetic area and low photosynthetic efficiency of the remaining canopy following defoliation. Positive direct effects are generally associated with compensatory processes including photosynthesis and carbon allocation patterns (Briske & Richards, 1995; Briske et al., 1996). Seed consumption from plants or soil represents an important direct effect in annual plant communities (Russi et al., 1992; Noy-Meir & Briske, 1996).

Indirect effects or extrinsic mechanisms are associated with grazing induced competitive interactions and environmental modifications and include modifications of microclimatic variables which include modifications of microclimatic variables, hydrological processes, and nutrient cycling.

Table 1. Summary of several documented direct and indirect effects of grazing on plant growth and function (modified from McNaughton, 1983).

Direct - modification of plant function and development
  - Increased photosynthetic rates
  - Increased allocation to shoots rather than roots
  - Enhanced meristem activation
  - Consumption of flowers and seeds

Indirect - modification of environmental variables
  - Increased photosynthetically active radiation
  - Enhanced ratio of red:far-red radiation
  - Altered resource competition
  - Modified hydrological cycle
  - Increased nutrient cycling

The accumulation of a mulch or litter layer on the soil surface has received special attention as an indirect mechanism capable of maintaining dominance of large erect annuals (Biswell, 1956; Zohary & Brick, 1961). A thick mulch layer may maintain dominance of large annuals by suppressing vegetative growth and minimizing seedling emergence of smaller associated annual species (Noy-Meir, 1990). In addition, mulch may conserve soil water and promote successful seedling establishment of larger annuals capable of growing through the mulch layer. Additional indirect mechanisms that are known to modify the structure and composition of perennial grasslands include grazing mediated competitive interactions (Anderson & Briske, 1995) and drought-grazing interactions (O'Connor & Roux, 1995). Indirect effects are often difficult to recognize and interpret because they occur over long time periods and may be expressed at various scales of vegetation organization. Nevertheless, the cumulative consequences of indirect effects may often equal or exceed those of direct effects in grazed systems (Archer & Smeins, 1991; Hendon & Briske, 1997).

A case study with *Triticum dicoccoides* (wild wheat)

Research with native populations of *T. dicoccoides* in productive, semi-natural grasslands of northern Israel indicates that both direct and indirect effects of grazing influence the population dynamics of this dominant annual grass. Grazing reduced seed production by decreasing the number of surviving plants that produced inflorescences and spikelet number per inflorescence, but seed number and spikelet weight were unaffected by grazing (Table 2) (Noy-Meir & Briske, 1996). This direct effect reduced reproductive fitness by 50% compared to ungrazed populations and can solely account for substantial reductions in the abundance of *T. dicoccoides*. Additional inflorescences developed from secondary tiller cohorts, but insufficient time and resources remained within the growing season for inflorescence production and seed maturation. Consequently, many of the inflorescences did not successfully emerge from the enclosing leaf sheaths when these secondary tillers senesced at the end of the growing season. Therefore, grazing had the greatest detrimental effect on seed production when it occurred in the latter portion of the growing season (Table 3). Indirect, as well as direct, effects of grazing on *T. dicoccoides* populations were documented in this investigation.

Table 2. Several variables describing the reproductive performance of *Triticum dicoccoides* plants in grazed (G) and protected (P) populations (modified from Noy-Meir & Briske, 1996).

Plant variable	1990-91		1991-92	
	G	P	G	P
% fertile plants	67	96	83	97
# emerged ears	1.4	2.0	1.2	1.1
# enclosed ears	0.5	0.2	0.2	0.0
# spiklets	10.4	16.2	6.7	8.1
# full seed	-	-	2.6	6.1

While grazing early in the growing season had no significant effects on plant survival, 50 - 100% more tillers were initiated in the grazed plots than in the ungrazed plots (Noy-Meir & Briske, 1996). Even individual plants in grazed plots that had not been grazed had up to 40% more tillers than did plants in ungrazed plots. This builds a very strong case for the occurrence of an indirect grazing effect at a scale higher than that of the individual plant. Grazing very likely reduced the plant canopy and mulch layer to increase both the amount of photosynthetically active radiation and the ratio of red:far-red solar radiation reaching seedlings near the soil surface. Both components of the radiation environment have been demonstrated to increase tiller initiation in grasses (Murphy & Briske, 1992, 1994). However, additional indirect effects associated with hydrological and nutrient cycles may also have been operating.

Subsequent experiments in this grassland indicate that mulch plays a less important role in the dominance of *T. dicoccoides* than generally assumed (Noy-Meir & Briske, unpubl. manu.). Experimentally applied mulch applications of 120 and 240 g m^{-2} did not benefit germination, survival or growth of this dominant annual grass in either year of the 2-year investigation. However, in both years substantial rains occurred early in the growing season which may have negated the potentially beneficial effects of a mulch cover. Experimental mulch application actually reduced tiller number and final inflorescence weight compared to non-mulched plants and the suppressive effect of mulch was greater for *T. dicoccoides* than for associated interspecific neighbors. These data strongly suggest that excessive removal of mulch by livestock during the dry season is not a major factor contributing to the decline of this dominant annual in response to grazing.

Appropriate paradigm for evaluating plant responses to grazing

The 'specific trait approach' (Simms, 1992) was initially adopted as the predominant paradigm for investigating and evaluating grazing resistance in North American grassland ecology and management during the middle of the 20th century. This approach is based on the assumption that a relatively small number of traits, or even a single trait, associated with the developmental morphology or physiological function of individual species are responsible for their inherent grazing resistance. However, an interpretation of grazing resistance based on the partial involvement of indirect mechanisms, rather than solely on direct mechanisms, challenges this paradigm. Species do not necessarily have to possess obvious physiological or morphological traits for grazing to induce a decrease in tiller and plant density and potentially contribute to species replacement. Indirect mechanisms may be of equal or greater importance than direct mechanisms in determining species responses in grazed systems (Archer & Smeins, 1991). Assessment of grazing resistance based on the specific trait approach fails to recognize and address the importance of indirect mechanisms associated with grazing induced processes at higher ecological scales (Hendon & Briske, 1997).

Table 3. Percentage of reproductive *Triticum dicoccoides* plants in relation to grazing (G) at progressively later dates in the growing season compared to ungrazed (U) plants in the same population (from Noy-Meir & Briske, 1996).

	1990-91		1991-92	
Defoliation date	G	U	G	U
February 11	70	65	-	-
March 10	60	78	-	-
March 26	63	73	86	86
April 29	35	93	43	93

The ineffectiveness of the specific trait approach to explain species responses to grazing is first illustrated with dominant annuals from Mediterranean grasslands and second with a dominant perennial from temperate, semi-arid grasslands. Species responses to long-term livestock grazing in productive, semi-natural annual grassland in northern Israel were not associated with general palatability attributes, including spinescence (Noy-Meir et al., 1989). Instead, the response of species abundance to grazing was most strongly associated with plant growth form. Species that increased with protection from grazing were mostly tall, erect plants, species that increased with grazing were mostly small prostrate or rosette plants, and species with intermediate responses were erect plants with intermediate height. In this case, growth form had a greater influence on relative grazing resistance than did specific attributes associated with palatability.

The grazing sensitive perennial grass, *Eriochloa sericea,* was once dominant in temperate, semi-arid grasslands of the southern mixed prairie of North America (Hendon & Briske, 1997). However, its abundance has been substantially reduced by 125 years of intensive livestock grazing. A demographic evaluation of the species did not reveal morphological attributes traditionally associated with grazing sensitive grasses. The reproductive:vegetative tiller ratio did not exceed 10%, apical meristem elevation above the soil surface did not exceed 5 mm in vegetative tillers, and tiller initiation was not synchronous, but rather occurred throughout the growing season. The absence of a specific trait contributing to the defoliation-induced meristematic limitation in *E. sericea* makes it difficult to explain the significant reduction in cumulative tiller recruitment and basal area and increased rate of tiller mortality in plants subjected to multiple defoliations.

The explanation for decreasing species abundance in the absence of recognized traits that are associated with grazing sensitivity may lie beyond the inherent ability of individual species to replace leaf area following defoliation. An alternative interpretation of herbivory-sensitivity, within comparable grass growth forms, is based on the involvement of more subtle indirect mechanisms and their interaction with direct mechanisms, rather than on the exclusive contribution of direct mechanisms. *E. sericea* was apparently placed at a competitive disadvantage with associated perennial grasses by selective grazing induced by early growth initiation, rapid growth and a relatively high tissue nitrogen content.

Ecological and managerial implications

Contrasting life history strategies between annual and perennial grasses is associated with a significant distinction in the predominant mechanisms of population persistence. Maintenance of annual grass populations is dependent upon the annual production of abundant seed while maintenance of perennial grass populations is dependent upon annual tiller replacement from axillary buds. Grazing may disproportionately modify these persistence mechanisms to produce several important ecological and managerial distinctions between annual and perennial grasses.

Grazing induced species composition changes in annual grasslands appear to be driven by selective grazing of the larger more erect species similar to the process described for species replacement in perennial grasslands. However, contrasting mechanisms of population persistence in annual and perennial grasses determines that they are differentially affected by grazing at various time frames and scales of vegetation organization. Annual grasses are most detrimentally impacted by the direct effects of grazing late in the season at the level of individual plants while perennial grasses are most detrimentally impacted by the indirect effect of grazing mediated by competitive interactions and environmental stress at the community level of vegetation organization.

Direct effects of grazing appear to be more important than indirect effects to population persistence in annual grasses based on their dependence on seed production and the direct accessability of inflorescences and seed to herbivores both during and following the reproductive stage. In contrast, indirect effects of grazing appear to be more significant for perennial grasses based on their dependence on tiller initiation from axillary buds and the relative inaccessibility of these buds located at or near the soil surface. Therefore, grazing influences the population persistence of perennial grasses indirectly by modifying competitive interactions and abiotic stresses to influence tiller and plant demography.

Late season grazing during or shortly following plant reproduction is of sufficient impact to directly compromise the persistence of annual species populations. Seed production can be reduced by approximately 50% by the direct removal of inflorescences and associated seed by herbivores. The reduction of seed production is a function of a decrease in the number of plants producing mature inflorescences and spikelet number per inflorescence while seed and spikelet weight per plant are relatively unaffected.

The significant impact of direct grazing effects on the persistence of annual species populations also indicates that these detrimental impacts can be minimized by grazing management decisions. Grazing deferment during the reproductive stage in the latter 4 - 6 weeks of the growing season may be sufficient to maintain abundant populations of dominant annual grasses while grazing during the remainder of the year may limit their suppressive effects on associated annual species to maintain high species diversity.

Assessment of grazing resistance based on the specific trait approach fails to recognize and address the importance of indirect mechanisms associated with grazing induced processes at higher ecological scales. Indirect effects of grazing may be equally or more important than direct effects in determining vegetation responses to grazing. This may be partially accounted for by evaluating vegetation responses at higher ecological scales rather than just the individual plant level.

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Effects of grazing on Mediterranean grasslands: the community level*

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Summary

The grasslands of the Mediterranean Region can be classified as sub-humid (productive) ecosystems with a long history of grazing according to the model of Milchunas et al. (1988). Theoretically, this models predicts that grasslands of this type will, at zero or low grazing intensity, be dominated by species which are the most successful competitors for space, light and soil resources, and that with increasing grazing intensity there will be large changes in community composition in favour of species that are better adapted to survive intense grazing. Species diversity is predicted to increase to a maximum at intermediate grazing intensity before decreasing at high intensity. Empirical evidence from studies in Mediterranean grasslands, in particular in Central Spain and Northern Israel, shows responses of community structure and diversity to grazing that mostly confirm the predictions of this and related theoretical models. However, some phenomena observed are unexpected, indicating that the ecological mechanisms of grassland response to grazing may be more complex. The individual characteristics of key species of herbivores or of plants can significantly modify the response. Livestock grazing intensity may affect grassland communities indirectly, through interaction with fire intensity and small mammals' activity. On some Mediterranean soils of very low fertility, the herbaceous communities are of relatively low productivity and high diversity even in the absence of grazing and are easily invaded by woody plants. Spatial patchiness caused by herbivore behaviour or by habitat micro-structure has an important role in some grasslands. The grasslands and other herbaceous communities of the Mediterranean Region are highly valuable for conservation of floristic biodiversity and of landscape diversity, in addition to their value for livestock production. Fortunately, due to the history and characteristics of these communities, these two management goals are not in strong conflict and can be complementary, if management is based on an understanding of ecological responses to grazing.

Keywords: biodiversity, community structure, conservation, livestock, Israel.

Introduction

How does grazing by domestic herbivores affect species composition, structure and biodiversity of natural plant communities? Scientifically, this question is central to our understanding of the ecological processes that create, maintain or modify plant communities. It is particularly interesting in biomes that have a long history of grazing, such as those of the Mediterranean region. Practically, the question is critical to the compatibility of two major land uses with distinct management goals, namely livestock production and the conservation

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* Invited paper

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