

Strategies of Plant Survival in Grazed Systems: A Functional Interpretation

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INTRODUCTION

The concept of grazing resistance, within the context of grassland and pasture management, describes the relative ability of plants to survive and grow in grazed systems (Briske, 1991). Although a reasonable understanding of the major plant attributes that confer grazing resistance has been attained, the concept is largely based on empirical evidence with a limited theoretical base (e.g. Scogings, 1995). Consequently, the potential contribution of this critical concept toward understanding plant-herbivore interactions has not been fully realized.

Development of the grazing resistance concept has been constrained by two major phenomena. The first involves the development of philosophical differences between applied and theoretical scientists investigating plant-herbivore interactions, which limited interaction and information exchange (Scogings, 1995). For example, the ecological and entomological literature contains a substantially greater theoretical basis for the occurrence and evolution of grazing resistance, although it is largely based on experimentation with invertebrate herbivores (e.g. Herms and Mattson, 1992; Pollard, 1992). The second involves the conceptual approach employed to investigate plant-herbivore interactions. Initially, research emphasis focused on herbivores and herbivore population dynamics, based on the assumption that grazing had a minimal effect on individual plants and populations (Fox, 1981). It is only more recently that emphasis has shifted to investigation of the chemical and structural properties of individual plants that affect their resistance to herbivores (Fox, 1981). Investigation of unique components of grazed systems with disparate research objectives

and approaches has slowed development of a comprehensive theory of plant-herbivore interactions.

A functional interpretation of vegetation responses to grazing based on plant resistance mechanisms has yet to be developed. For example, documented patterns of herbivore-induced compositional changes in grasslands and pastures often cannot be anticipated or explained solely on the basis of the grazing resistance of plants which comprise the community. Progress toward a functional interpretation of grazing resistance will be required to address critical questions and issues associated with plant-herbivore interactions. Are late-successional dominants more susceptible to grazing than mid- or early-successional subordinate species? Can plants be organized into functional groups based on the relative expression and associated costs of grazing resistance mechanisms? Must threshold levels of grazing intensity be surpassed to induce shifts in species composition? Answers to these questions are required to develop a more thorough understanding of plant-herbivore interactions and to implement effective conservation and management prescriptions on grasslands and pastures.

The objective of this chapter is to extend our current perspective and understanding of grazing resistance by relating it to the much larger body of information that exists within the ecological and entomological literature. Although this approach is inherently speculative, it is intended to expedite development of a functional interpretation of the herbivore-induced patterns of vegetation change observed in grasslands throughout the world. The chapter begins with an overview of grazing resistance, proceeds with a functional interpretation of species composition change in response to grazing, addresses the resistance strategies that may potentially influence plant responses to grazing, and concludes with the presentation of several examples indicating how management may modify grazing resistance to induce desired vegetation responses.

GRAZING RESISTANCE CONCEPT

Grazing resistance describes the relative ability of plants to survive and grow in grazed plant communities. Resistant plants or species are those which are inherently less damaged than others under comparable environmental conditions (Painter, 1958). The level of resistance is often determined by qualitative and/or quantitative expression of the attribute(s) conferring resistance to the plant (e.g. specific trait approach) (Simms, 1992). The alternative approach to describing grazing resistance is to define the extent of herbivore damage or biomass removal (e.g. bioassay approach). Our limited knowledge of the relationship between the various attributes used to estimate resistance and their correlation with plant fitness represents a major constraint to our understanding of the function and evolution of grazing resistance (Pollard, 1992).

Grazing resistance can be divided into avoidance and tolerance components, based on the general mechanisms conferring resistance (Briske, 1986, 1991;

Rosenthal and Kotanen, 1994; Briske and Richards, 1995). Grazing avoidance involves mechanisms that reduce the probability and severity of grazing, while grazing tolerance consists of mechanisms that promote growth following defoliation (Fig. 2.1). Avoidance mechanisms are composed of architectural attributes, mechanical deterrents and biochemical compounds which reduce tissue accessibility and palatability. Tolerance mechanisms are composed of the availability and source of residual meristems and physiological processes capable of promoting growth following defoliation (Fig. 2.1). An evaluation of the specific mechanisms contributing to grazing avoidance and tolerance improves concept organization and clarity, but does little to enhance the functional interpretation of grazing resistance.

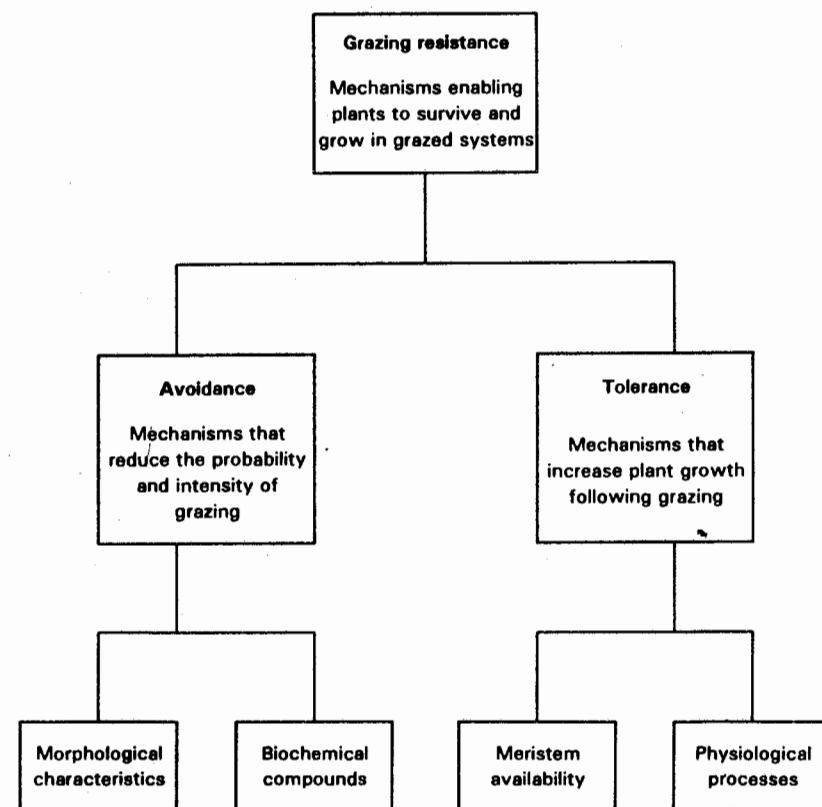


Fig. 2.1. Organization of grazing resistance into avoidance and tolerance strategies. The avoidance strategy decreases the probability and intensity of grazing while the tolerance strategy increases growth following grazing (from Briske, 1986, 1991).

The occurrence of varying degrees of grazing resistance among plants is well established by the predictable patterns of species selection by herbivores (e.g. Heady, 1964; Jarman and Sinclair, 1979; Hanley and Hanley, 1982; Heitschmidt *et al.*, 1990) and species replacement in response to long-term grazing (e.g. Dyksterhuis, 1946; Ellison, 1960; Noy-Meir *et al.*, 1989). However, in most cases, it is uncertain whether grazing-induced species replacement occurs in response to the selective utilization of plant species (i.e. avoidance mechanisms) or the occurrence of unequal growth capabilities among species following grazing (i.e. tolerance mechanisms). Although both mechanisms are known to occur, the predominant mechanism or relative combination of mechanisms remains unknown for most species combinations and plant communities (e.g. Lawrey, 1983; van der Meijden *et al.*, 1988). Selective grazing of the late-successional dominant *Schizachyrium scoparium* has been recognized as the predominant mechanism contributing to species replacement in the southern true prairie of Texas (Brown and Stuth, 1993; Anderson and Briske, 1995). Frequent and intensive grazing appears to negate the greater competitive ability and equivalent grazing tolerance of the late-successional dominant compared with associated mid-successional species. Alternatively, the greater grazing resistance displayed by *Agropyron desertorum*, in comparison with *Pseudoroegneria spicata* (syn. *Agropyron spicatum*), in the intermountain west of North America, can be attributed to different degrees of grazing tolerance (Caldwell *et al.*, 1981; Richards and Caldwell, 1985; Caldwell *et al.*, 1987). In this comparison, the potential contribution of avoidance mechanisms is minimized by comparable canopy architectures, phenology and leaf nitrogen content between the two species and the imposition of equivalent defoliation intensities.

Species grazed less severely (i.e. avoidance mechanisms), capable of growing more rapidly following defoliation (i.e. tolerance mechanisms) or possessing a combination of these two mechanisms realize a competitive advantage within a community (Caldwell *et al.*, 1981; Richards, 1984; Briske, 1991). These species, through the possession of a greater canopy area, are able to intercept greater amounts of solar energy, assimilate greater amounts of carbon and further enhance their competitive ability. Consequently, grazing-resistant species are frequently able to pre-empt resources that may have been utilized by associated grazing-sensitive species prior to grazing (Mueggler, 1972; Caldwell *et al.*, 1987; Briske and Richards, 1995).

Recognition of grazing avoidance or tolerance as the predominant resistance strategy inducing species composition shifts has important implications for grassland and pasture management. It is especially important in cases where the reduction and/or local extinction of late-successional dominants in severely grazed grasslands may have been misinterpreted as a consequence of lesser grazing tolerance, as opposed to lesser grazing avoidance, in relation to the associated mid-successional species. If the late-successional dominants are perceived as being relatively intolerant of grazing, the only viable management strategy to maintain dominance of the late-successional species is to reduce the

intensity and/or frequency of grazing within the community. Alternatively, if a lesser expression of grazing avoidance by the late-successional dominants is the predominant mechanism inducing species replacement, then managerial decisions to regulate the uniformity of grazing among species may be implemented to maintain dominance of the late-successional species. Intensive grazing when the relative expression of avoidance mechanisms is lowest for subordinate, mid-successional species and highest for dominant, late-successional species can minimize, although not eliminate, selective grazing among grasses (e.g. Briske and Heitschmidt, 1991; Brown and Stuth, 1993).

FUNCTIONAL INTERPRETATION OF GRAZING RESISTANCE

Inferences drawn from herbivore-induced patterns of species replacement

Herbivore-induced shifts in species composition have been documented from native grasslands and savannas throughout the world (Ellison, 1960; Archer, 1989; Bosch, 1989; Noy-Meir *et al.*, 1989; Westoby *et al.*, 1989; Milton *et al.*, 1994). Compositional changes most frequently involve the replacement of late-successional dominants by early- or mid-successional species (Dyksterhuis, 1946; Canfield, 1957), while structural changes frequently involve the replacement of tallgrasses by mid- or shortgrasses (Arnold, 1955; Mitchley, 1988; Belsky, 1992). If species replacement continues, grassland communities may become vulnerable to an ingress of ruderals and herbaceous and woody perennials, which support fewer domestic herbivores and may eventually decrease the production potential of the site (Ellison, 1960; Archèr and Smeins, 1991; Milton *et al.*, 1994).

The compositional changes induced by grazing suggest that late-successional grassland dominants possess the least developed avoidance strategy and are therefore the most palatable or preferred species within the community (e.g. Sal *et al.*, 1986). This supposition is also inherent in the most current theory of plant defence, indicating that relatively rapidly growing, competitive plants express avoidance mechanisms to a lesser extent than slower-growing, less competitive plants (Coley *et al.*, 1985). However, little conclusive experimental evidence exists to support this interpretation and a majority of the information originates from research with invertebrate herbivores. Generalist herbivores have been documented to prefer early-successional species (Cates and Oriens, 1975), mid-successional species (Davidson, 1993) or late-successional species (Otte, 1975), or to possess no significant preference for plants of various successional stages (Rathcke, 1985). However, the survey of Davidson (1993) is the most comprehensive, including a broad range of plants and both vertebrate and invertebrate herbivores. The inconsistencies associated with herbivore preferences for plants

within various successional stages may reside in the fact that typical generalist herbivores do not exist (Crawley, 1983, pp. 207, 344). Generalist herbivores themselves are often characteristic of particular successional communities (Maiorana, 1978; Rathcke, 1985).

Are late-successional dominants more susceptible to grazing than subordinate species?

The concept of grazing resistance is at least partially based on the assumption that the possession of resistance mechanisms represents an associated cost to the plant (Simms and Rausher, 1987, 1989; Simms, 1992; Rosenthal and Kotanen, 1994). This assumption is most easily quantified in plants which produce secondary compounds to deter herbivores. For example, seedlings of the neotropical tree *Cecropia peltata*, possessing high tannin concentrations, experienced less grazing but displayed lower growth rates in the absence of grazing than did seedlings which possessed lower tannin concentrations (Coley, 1986). Slower growth rates in seedlings possessing high tannin concentrations were attributed to the cost of tannin production and can be interpreted as the cost of grazing avoidance. Similar conclusions have been drawn from other investigations in which secondary compounds were produced in various quantities by plants to deter herbivores (e.g. Windle and Franz, 1979; Dirzo and Harper, 1982).

Mechanical deterrents may also convey large costs to plants, but the evidence is much less extensive than it is for secondary compounds (van der Meijden *et al.*, 1988; Björkman and Anderson, 1990; but see Ågren and Schemske, 1993). Although tolerance mechanisms require resources to replace biomass removed by herbivores (e.g. Wareing *et al.*, 1968; Ourry *et al.*, 1988), resource investment directly contributes to growth, rather than diverting resources from growth as in the case of avoidance mechanisms (e.g. Davidson, 1993). Therefore, avoidance mechanisms can be assumed to represent a greater production cost and a greater trade-off with competitive ability than tolerance mechanisms (van der Meijden *et al.*, 1988) (Fig. 2.2). However, the nature of this relationship is largely unexplored and is far from being quantified. Trade-offs between grazing resistance and competitive ability are assumed to be greatest in resource-rich environments (Coley *et al.*, 1985; Herms and Mattson, 1992). Alternatively, grazing resistance is assumed to be more compatible with competitive ability and therefore less costly in resource-limited environments. The potential trade-off between the costs and benefits of grazing resistance occurs because competition is the predominant selective agent constraining the evolution of grazing resistance (Herms and Mattson, 1992). In other words, plants do not become completely resistant to herbivores because the cost of grazing resistance must, at some point, exceed the benefit conveyed by resistance (Pimentel, 1988).

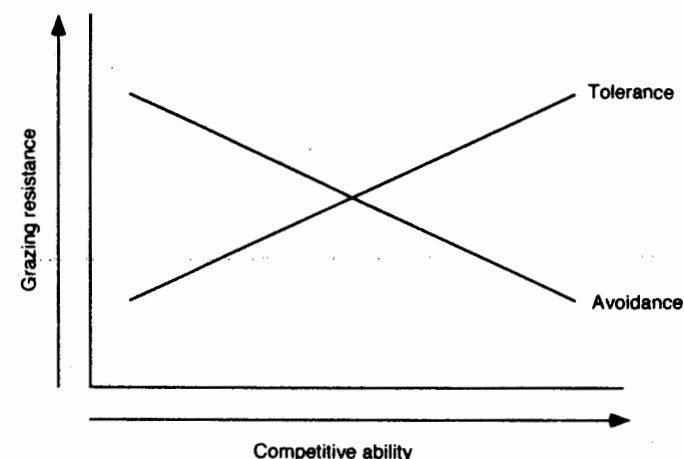


Fig. 2.2. Hypothesized relative contributions of tolerance and avoidance strategies to grazing resistance in plants possessing a range of competitive abilities. Avoidance mechanisms are assumed to represent a greater trade-off with competitive ability than tolerance mechanisms because they divert resources from plant growth. Therefore, late-successional dominants are proposed to rely on the tolerance strategy to a greater extent than early- or mid-successional species (see Fig. 2.4).

The resource availability hypothesis suggests that plants have adjusted their growth rates to match the level of resource availability in their habitats (Coley *et al.*, 1985; Coley, 1988; Yamamura and Tsuji, 1995) (Fig. 2.3). This hypothesis is based on the assumption that the realized growth rate represents the net effect of the growth reduction associated with the cost of grazing resistance and a growth increase associated with protection from herbivores. An optimal resource investment in grazing resistance is assumed to increase as the potential maximum growth rate decreases because: (i) it becomes more costly to replace resources removed by herbivores; (ii) a fixed proportion of biomass removal represents a larger fraction of net production; and (iii) a comparable reduction in growth rate resulting from the investment in plant defence represents a greater absolute growth reduction for fast-growing plants (Coley *et al.*, 1985). It can be inferred from this hypothesis that tolerance mechanisms comprise a greater proportion of herbivory resistance than avoidance mechanisms in late-successional dominants based on their relatively high maximal growth rates.

Mesic grasslands occupy relatively productive environments characterized by intermediate temperature and precipitation regimes (Walter, 1979). Consequently, many grassland dominants can be categorized as competitive strategists based on their relatively large stature, rapid growth rates and high rates of tissue turnover (Grime, 1979, p. 9). Effective competitive abilities are required

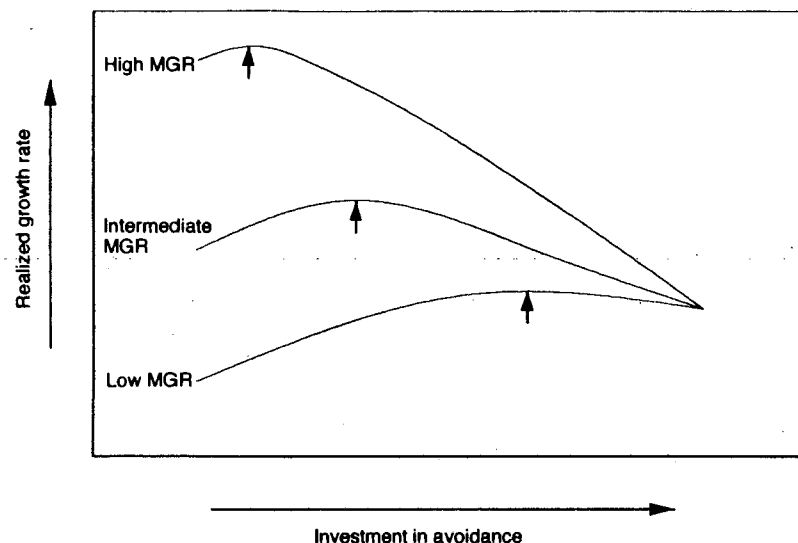


Fig. 2.3. Schematic representation of the resource availability hypothesis indicating that resource investment in avoidance mechanisms (i.e. plant defence) increases as the maximal growth rate (MGR) of plants decreases. Lines represent maximal growth rates for a broad range of plant species and arrows represent the point at which investment in avoidance mechanisms maximizes the realized growth rate (from Coley *et al.*, 1985).

for late-successional species to maintain their dominance within the community (Wilson and Keddy, 1986; Tilman and Wedin, 1991). However, a similar suite of attributes are also associated with the effective expression of herbivory tolerance (Herms and Mattson, 1992; Rosenthal and Kotanen, 1994). Competitive strategists generally possess nitrogen contents and palatability rankings intermediate to those of stress tolerators and ruderals (Cates and Orians, 1975; Southwood *et al.*, 1986; Van Arendonk and Poorter, 1994).

It is hypothesized that late-successional dominants rely on tolerance mechanisms for grazing resistance to a greater extent than early- or mid-successional species because they are closely correlated with the life history attributes of the competitor strategy (e.g. Davidson, 1993). In contrast, large investments in avoidance mechanisms are considered to divert resources from growth and potentially decrease both competitive ability and the expression of tolerance mechanisms. However, tolerance mechanisms can be suppressed prior to avoidance mechanisms because a grazing intensity can be imposed which removes biomass more rapidly than tolerance mechanisms can replace it. The suppression of tolerance mechanisms will eventually reduce the grazing resistance of dominants to a level less than that of the associated mid- or early-successional species within the community. The grazing-induced suppression of tolerance

mechanisms within populations of late-successional dominants is proposed to be the predominant process contributing to species replacement within mesic grasslands. The physiological processes contributing to the decline in grazing tolerance with increasing grazing severity are reasonably well understood (Briske and Richards, 1994, 1995).

Does a threshold grazing intensity exist at which late-successional dominants are replaced by subordinate species?

The contribution of tolerance mechanisms to grazing resistance in late-successional dominants may potentially increase with increasing grazing intensities to some undefined point (Fig. 2.4). For example, compensatory photosynthesis, resource allocation, nutrient absorption and growth have been documented to increase at various defoliation intensities for numerous plant species (Briske and Richards, 1994, 1995). Although an increase in grazing tolerance may occur for subordinate species, it is assumed to occur to a lesser extent than for dominant species. However, the actual contribution of these compensatory processes to grazing tolerance has yet to be definitively established (e.g. Caldwell *et al.*, 1981; Nowak and Caldwell, 1984). Eventually, however, frequent, intensive grazing will suppress grazing tolerance mechanisms by chronic leaf removal. Although increases in the expression of avoidance mechanisms with increasing grazing intensities have also been demonstrated, they are much less frequent than for tolerance mechanisms (Abrahamson, 1975; Milewski *et al.*, 1991). Few examples of grazing-induced increases in avoidance mechanisms have been documented in grasses (see under Inducible Defences below). A notable exception is the development of decumbent canopies with frequent, intensive grazing (see under Architectural Plasticity below). However, this architectural response does not directly convey a cost associated with resource diversion from plant growth, but rather a potential loss in production (Briske and Richards, 1995). Therefore, the contribution of avoidance mechanisms is assumed to remain constant with increasing grazing intensity for both dominant and subordinate species (Fig. 2.4).

The grazing intensity at which the contribution of tolerance mechanisms is reduced to the point where grazing resistance of dominant plants equals grazing resistance of the subordinate species can be considered the resistance threshold (Fig. 2.4). If the resistance threshold is exceeded, the grazing resistance of the dominants is reduced to less than that of the subordinate species and the dominants will lose their competitive advantage and become locally extinct (O'Connor, 1991) or persist as small, scattered plants (Butler and Briske, 1988). The grazing intensity at which the contribution of tolerance mechanisms is eliminated represents the tolerance threshold (Fig. 2.4). Plant growth is entirely suppressed by

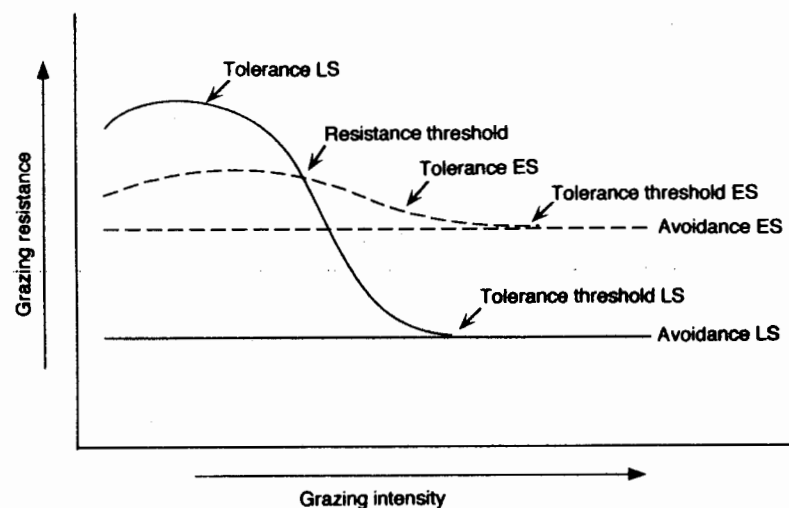


Fig. 2.4. Hypothesized functional interpretation of grazing induced species composition changes in mesic grasslands. Grazers initially suppress the expression of grazing tolerance in late-successional dominants (LS) because they can potentially remove biomass more rapidly than tolerance mechanisms can replace it. The grazing intensity at which the contribution of the tolerance strategy is reduced to the point where grazing resistance of dominant plants equals grazing resistance of the early- and mid-succession species (ES) represents the resistance threshold. Grazing resistance of the dominants is reduced to less than that of the subordinate species when the resistance threshold is exceeded and the dominants will lose their competitive advantage and decrease in abundance. The grazing intensity at which the contribution of the tolerance strategy is eliminated represents the tolerance threshold. At this grazing intensity, plant growth is suppressed by photosynthetic and/or meristematic limitations and plant death will result if this grazing intensity is maintained.

photosynthetic and/or meristematic limitations at this grazing intensity. Plant death will result if this grazing intensity is maintained.

Herbivores will begin to successively graze species with a progressively greater expression of avoidance mechanisms after the species relying on tolerance mechanisms have been reduced in abundance. Species with the most well developed avoidance strategy will be grazed to a lesser extent and their relative abundance will remain constant or increase in response to continued intensive grazing. Both the resistance and tolerance thresholds will vary among species in response to their relative expression of avoidance and tolerance strategies (see under Grazing Resistance Strategies below). In the context of this functional interpretation, communities can be envisioned as assemblages of plant species possessing a series of resistance and tolerance thresholds that vary in approximate proportion to their relative competitive abilities (Fig. 2.4).

GRAZING RESISTANCE STRATEGIES

Grazing resistance strategies are often organized into four general categories: (i) escape in time and space; (ii) confrontation (mechanical and biochemical defences); (iii) associative defence; and (iv) tolerance (Kennedy and Barbour, 1992). In this treatment, the first three categories will be presented as constitutive, spatial and temporal mechanisms of an avoidance strategy and the tolerance strategy will be divided into morphological and physiological mechanisms (Table 2.1). These strategies are capable of variously affecting the resistance and tolerance thresholds previously proposed. Resistance strategies also emphasize that frequently more than one plant attribute is involved in determining the relative grazing resistance within and among plant species (Pollard, 1992; Simms, 1992). The relative contribution of individual plant attributes to grazing resistance has been reviewed previously (Theron and Booysen, 1966; Pollard, 1992; Kennedy and Barbour, 1992; Briske and Richards, 1995). For purposes of brevity and continuity with previous sections, grazing resistance of grasses will be emphasized.

It is important to recognize that the grazing resistance strategies expressed by plants vary greatly between native and introduced and/or intensively managed systems (Kennedy and Barbour, 1992). The most obvious distinction is that resistance strategies in native systems are not influenced as greatly by anthropogenic considerations. For example, the mechanism of escape in time and space in intensively managed grazing systems is constrained by limited herbivore movement and managerially imposed grazing periods. Therefore, caution is

Table 2.1. Categories of mechanisms within the avoidance and tolerance strategies of grazing resistance. Resistance strategies imply that more than one plant attribute is frequently involved in determining the relative grazing resistance within and among plant species. These resistance strategies are capable of variously affecting the resistance and tolerance thresholds proposed in the functional interpretation (see Fig. 2.4).

Avoidance strategy	Tolerance strategy
<i>Constitutive mechanisms</i>	<i>Morphological mechanisms</i>
Mechanical deterrents	Meristem source/number
Biochemical compounds	Seed availability
Defensive symbiosis	
<i>Spatial mechanisms</i>	<i>Physiological mechanisms</i>
Growth form	Compensatory process
Architectural plasticity	Compensatory growth
Species associations	
<i>Temporal mechanisms</i>	
Inducible defences	
Asynchronous growth	
Developmental resistance	

required when attempting to draw inferences or extrapolate data concerning grazing resistance between these two diverse systems.

Avoidance strategy

Constitutive mechanisms

Constitutive mechanisms remain relatively constant in space and time (Feeny, 1976; Rhoades, 1983). These mechanisms can be considered to form the 'background' resistance level of plants (Ernest, 1994).

Mechanical

Although mechanical attributes of plants are widely assumed to function as deterrents to grazing by vertebrate herbivores, their influence is not well documented. For example, experimental evidence to verify that awns and sharpened calluses of caryopses influence livestock preferences is non-existent. Trichomes and epidermal waxes are known to be important deterrents to insect herbivores (Becerra and Ezcurra, 1986; Woodman and Fernandes, 1991), but they appear to have only limited influence on mammalian herbivores (Theron and Booyesen, 1966). Similarly, the presence of vascular bundles within the Kranz leaf anatomy of C₄ grasses has been demonstrated to reduced palatability to insect herbivores (Caswell *et al.*, 1973; Heidorn and Joern, 1984), but this anatomical attribute is only known to reduce tissue digestibility in livestock (Wilson *et al.*, 1983; Akin, 1989). Leaf toughness is regarded as among the most important mechanical attributes influencing grazing by both vertebrate and invertebrate herbivores (Theron and Booyesen, 1966; Coley, 1983).

Cattle have been demonstrated to graze caespitose grasses with intermediate basal areas to a greater extent than plants with larger or smaller basal areas (Norton and Johnson, 1983). Animal preference and/or accessibility to live biomass within large plants is restricted by the accumulation of culms and senescent leaf material (Norton and Johnson, 1983; Ganskopp *et al.*, 1992). When these deterrents are removed, grazing intensity becomes proportional to the canopy volume of plants. Small plants may not be grazed proportionately because herbivores are less likely to locate them within the community (Feeny, 1976; Norton and Johnson, 1983).

Biochemical compounds

Grasses are generally considered to be relatively depauperated with regard to biochemical compounds capable of deterring herbivores (McNaughton, 1983; Briske, 1991). Although this may be an accurate generalization relative to all other angiosperms, grasses are known to possess a broad array of secondary compounds

(Redak, 1987; Vicari and Bazely, 1993). Although relatively little is known about the ecological function of secondary compounds in grasses, their occurrence has been demonstrated to deter grazers. For example, alkaloids in *Phalaris arundinacea* have been shown to reduce sheep (Simons and Marten, 1971) and cattle preference (Marten *et al.*, 1976) and the occurrence of phenolics deterred grazing by voles (*Microtus* spp.) (Kendall and Sherwood, 1975; Lindroth and Batzli, 1984) and geese (Buchsbaum *et al.*, 1984). Grasses are also known to contain cyanide and cyanogenic glycosides (Georgiadis and McNaughton, 1988) as well as condensed tannins (Redak, 1987; du Toit *et al.*, 1991; Chesselet *et al.*, 1992), but the relative contribution of these compounds to grazing resistance has yet to be determined.

Defensive symbiosis

Ergot alkaloids produced by systemic fungi within infected grasses and sedges may protect plants against grazers and seed predators (Cheplick and Clay, 1988). Most endophytic fungi are distributed intercellularly throughout above-ground plant tissues including leaves, stems, flowers and seeds. Alkaloids produced in this symbiotic relationship are known to deter grazing by both insect and mammalian grazers and are potentially toxic to livestock and humans (Clay, 1990; Towers and Siegel, 1993; Latch, 1994). This symbiotic association has been interpreted as a defence mechanism in which fungi defend host plants from grazers, thereby defending their own resources (Clay, 1988; Vicari and Bazely, 1993). For example, infected *Festuca arundinacea* plants had higher survival, tiller production, biomass production and flowering than non-infected plants in a 3-year field study (Clay, 1990). Endophytes induced similar responses in *Sporobolus poiretii*, but flowering was suppressed in comparison with non-infected plants. Although the known distribution of this symbiotic interaction is currently limited (Cheplick and Clay, 1988), it has been suggested that endophytic fungi are as common among plants as are mycorrhizae (Carroll, 1988).

Spatial mechanisms

Spatial avoidance mechanisms influence the vertical and horizontal distribution of plant canopies to limit herbivore accessibility.

Growth form

Species replacement in grasslands frequently involves the replacement of tall-grasses by midgrasses and of midgrasses by shortgrasses (Arnold, 1955; Mitchley, 1988; Belsky, 1992). This pattern of grazing induced replacement is partially based upon the relative accessibility and relative amount of biomass or canopy volume removed from these various growth forms. The accessibility of plant tissues within close proximity of the soil surface varies with the anatomical

structure and prehensile abilities of specific herbivores (Stobbs, 1973; Hofmann, 1988). Therefore, large-statured grasses may potentially encounter greater biomass removal than small-statured grasses when defoliated to a comparable height.

Architectural plasticity

Many species of tall- and midgrasses are capable of developing a prostrate or decumbent architecture in response to frequent, intensive defoliation. Examples include *Hordeum bulbosum* (Noy-Meir *et al.*, 1989), *Cynodon plectostachyus* (Georgiadis and McNaughton, 1988) and *Cenchrus ciliaris* (Hodgkinson *et al.*, 1989). Decumbent canopies are better able to resist grazing because less biomass is accessible to herbivores (Stobbs, 1973; Hofmann, 1988) and a greater amount of photosynthetic and meristematic tissues remain to facilitate growth following grazing (Detling and Painter, 1983; Carman and Briske, 1985).

Long-term herbivory of several perennial grass populations is known to have selected against morphotypes possessing an erect canopy architecture (Painter *et al.*, 1989; Briske and Richards, 1995). The plant morphotypes remaining in the population are characterized by a large number of small tillers with reduced leaf numbers and blade areas (Alexander and Thompson, 1982; Detling and Painter, 1983). A majority of the evidence suggests that grazing-induced selection of morphotypes is genetically based, but developmental plasticity also appears to be involved (Briske and Richards, 1994). Although the concept of biotic selection by herbivores was recognized early in this century (Gregor and Sansome, 1926; Kemp, 1937), its potential ecological significance to plant-herbivore interactions has only recently been appreciated (Detling and Painter, 1983).

It is generally assumed that grazing-induced selection primarily affects architectural attributes of plants, rather than physiological processes (Detling and Painter, 1983; Jaramillo and Detling, 1988). Consequently, the inference drawn from morphotypic selection in grazed populations is that the avoidance strategy, rather than the tolerance strategy, makes the greatest contribution to grazing resistance (Detling and Painter, 1983; Jaramillo and Detling, 1988). However, root systems of grazing morphotypes in *Pascophyllum smithii* populations had a three-fold greater rate of nitrogen accumulation (Poley and Detling, 1988) and tillers of grazing morphotypes of *P. smithii* were more productive following defoliation than were populations with no history of grazing (Painter *et al.*, 1989). Therefore, it must be concluded that both the avoidance and tolerance strategies of grazing resistance can be affected by grazing-induced morphotypic selection.

Species associations

The association of less palatable species with more palatable species may also influence the relative frequency and intensity of grazing (McNaughton, 1978; Hay, 1986; Tuomi and Augner, 1993). The protection afforded to grasses growing

within the canopy of low-growing shrubs is a widely observed example (Davis and Bonham, 1979; Jaks and Fuentes, 1980). Although this phenomenon is not well documented in grasslands or pastures, there is no reason to suspect that it does not occur among herbaceous plant assemblages (McNaughton, 1978). For example, association of a palatable grass, *Bouteloua gracilis*, with an unpalatable grass, *Aristida* spp., reduced the probability of grasshoppers grazing the more palatable species in one of two years, but increased the grazing intensity of the more palatable species when they were located by grasshoppers (Holmes and Jepson-Innes, 1989). The benefits derived from associative defences is based on the assumption that the growth reduction resulting from competition with unpalatable plants is less than the growth reduction resulting from severe grazing (Hay, 1986).

Temporal mechanisms

Temporal mechanisms influence the extent to which the expression of grazing avoidance varies throughout the growing season and with time following plant defoliation.

Inducible defences

Avoidance mechanisms which increase with increasing grazing intensity are termed inducible defences (Rhoades, 1985). The vast majority of cases involve qualitative biochemical compounds, but a few examples of increasing mechanical deterrents have also been identified (Karban and Myers, 1989). For example, browsed *Acacia* shrubs have been documented to produce a greater density of longer thorns than unbrowsed branches (Young, 1987; Milewski *et al.*, 1991). Inducible defences may have evolved to minimize the cost of avoidance when herbivores are not present (Karban and Myers, 1989). However, minimal evidence exists to demonstrate that grazing-induced responses actually increase grazing resistance and plant fitness.

Silica (SiO_2), within the epidermal cells of grasses, has been proposed as an inducible avoidance mechanism. Grasses subjected to long-term grazing often possess higher silica concentrations than do grasses with a limited history of grazing (McNaughton and Tarrants, 1983; McNaughton *et al.*, 1985; Brizuela *et al.*, 1986). However, the short-term responsiveness of silica to defoliation is less definitive (Brizuela *et al.*, 1986) and the ability of silica to deter a broad range of mammalian herbivores has not been well established (Theron and Booysen, 1966; Shewmaker *et al.*, 1989; but see Gali-Muhtasib *et al.*, 1992). Current evidence indicates that silica in grasses is a more effective deterrent to invertebrate than vertebrate herbivores (Vicari and Bazely, 1993).

Cyanide has also been documented to increase within 18 hours of defoliation in potted plants of *C. plectostachyus* relative to undefoliated plants (Georgiadis and McNaughton, 1988). Although cyanide levels in plant shoots varied within

and among collection sites, it was not significantly correlated with previous grazing history, soil nitrogen content or plant water potential. The authors concluded that cyanogenesis functioned as a deterrent to grazers and suggested that cyanide levels may become sufficiently high to become lethal to cattle.

Grasshopper grazing has been demonstrated to increase phenolic concentrations by 47% in foliage of *Pascopyrum smithii* (Redak and Capinera, 1994). The increase in phenolics and associated reductions in foliage quality contributed to a decrease in consumption rate and weight gains of grasshoppers.

Asynchronous growth and development

The concept of phenological escape (*sensu* Kinsman and Platt, 1984) has been studied extensively by comparing seed production and predation among years (Evans *et al.*, 1989; Wright, 1994). Periodicity of various phenological events, including bud break and flowering, has also been interpreted as temporal avoidance in relation to herbivorous insects (Evans *et al.*, 1989; Tuomi *et al.*, 1989). Phenological development is known to influence the relative degree of grazing avoidance expressed by plant species to mammalian herbivores. For example, reproductive culm development and the accumulation of dead leaves are known to reduce animal preference for grasses (Willms *et al.*, 1980; Norton and Johnson, 1983; Ganskopp *et al.*, 1992). However, 12 years of livestock grazing did not significantly modify the periodicity of flowering or fruiting in a montane grassland in Argentina (Diaz *et al.*, 1994).

Asynchronous growth periods among plant species can also influence the frequency and intensity of grazing. Plants which are intensively grazed throughout their entire growing season are placed at a competitive disadvantage with plants that are dormant or quiescent throughout a portion of the grazing period. For example, the maintenance of green biomass by perennial grasses following senescence of annual grasses increases their susceptibility to livestock grazing in Mediterranean grasslands (I. Noy-Meir, personal communication). Alternatively, ephemeral annuals may encounter minimal grazing based on their short life history and inconspicuous nature relative to perennial plants (Feeny, 1976).

Developmental resistance

Developmental resistance refers to changes in plant tissues with increasing age that can alter the behaviour, growth and survival of herbivores that consume them (Kearsley and Whitham, 1989). Greater palatability and digestibility of younger tissues, in comparison with older mature tissues, is widely recognized (Georgiadis and McNaughton, 1990; Fryxell, 1991). Structural carbohydrates often increase and nitrogen often decreases with ageing in grass tissues (Mattson, 1980; Van Soest, 1982). Consequently, plants at various developmental stages may possess various degrees of avoidance resulting from developmental resistance. Developmental resistance may be an important mechanism contributing to the

development of patch grazing (Bakker *et al.*, 1983; Kellner and Bosch, 1992) and the occurrence of 'grazing lawns' (McNaughton, 1984; Georgiadis and McNaughton, 1990).

Tolerance strategy

Morphological mechanisms

Number and source of meristems

Grass growth is dependent upon the availability and activity of intercalary meristems, apical meristems and axillary buds, but their relative contribution differs in magnitude and chronology (Briske and Richards, 1995). Leaf extension proceeds most rapidly from intercalary meristems because cell division has previously occurred within leaf primordia and growth occurs rapidly from cell expansion (Cook and Stoddart, 1953; Hyder, 1972; Briske, 1991). Leaf growth from apical meristems occurs at a slower rate because of the time required for cell differentiation prior to cell expansion (Skinner and Nelson, 1994). Leaf growth is slowest from axillary buds because of the time required for bud activation and leaf primordium differentiation. The relative contribution of these meristematic sources to plant growth varies among species and is influenced by environmental variables and stage of phenological development (Coughenour *et al.*, 1985; Olson and Richards, 1988). For example, species producing a large proportion of reproductive or culmed vegetative tillers are best suited to intermittent defoliation rather than continuous grazing (Branson, 1953; Hyder, 1972). Intermittent defoliation provides a sufficient period of time for tillers to express maximum vegetative production prior to the termination of growth following floral induction or apical meristem removal by grazers.

Differences in grazing tolerance between rhizomatous and caespitose grasses and among species within each group is largely a function of meristem availability at the time of defoliation. Rhizomatous species frequently possess large numbers of active meristems throughout the growing season and are most sensitive to defoliation when tiller densities are at a seasonal low (Hull, 1987). Synchronous tiller development increases the susceptibility of caespitose grasses to a greater loss of active shoot meristems when grazed after internode elongation (Branson, 1953; Westoby, 1980; Olson and Richards, 1988). Synchronous tiller development also contributes to wide fluctuations in grazing tolerance with the progression of phenological plant development. For example, the grazing-sensitive *P. spicata* is quite tolerant of defoliation in the early spring when culmless, because active intercalary and apical meristems are located at or near ground level. However, defoliation tolerance decreases rapidly following internode elongation (Richards and Caldwell, 1985; Busso *et al.*, 1990). Height of apical meristems among vegetative tillers of temperate perennial grasses

varies appreciably (Branson, 1953; Wilman *et al.*, 1994). Seasonal variation in defoliation tolerance is much less pronounced in species with asynchronous tiller development. The most grazing tolerant caespitose grasses frequently possess asynchronous tiller development, producing a situation similar to that described for rhizomatous grasses (e.g. Hodgkinson *et al.*, 1989; Mott *et al.*, 1992).

Number and viability of seed

Seed production and development of a seed bank can be interpreted as either a tolerance or an avoidance strategy to grazing. Although the short vegetative life cycle of annuals may function as a temporal avoidance mechanism in some cases (e.g. Feeny, 1976), the production of seed and a seed bank will be treated as a mechanism to promote plant establishment and growth following severe grazing (e.g. Noble and Slatyer, 1980).

Vegetative growth (i.e. tillering) is often assumed to be a more prevalent form of reproduction than plant establishment from seed in both semiarid and mesic grasslands (e.g. Belsky, 1992). Investigations conducted in the tallgrass (Rabinowitz, 1981; Johnson and Anderson, 1986), midgrass (Kinucan and Smeins 1992) and shortgrass (Coffin and Lauenroth, 1989) prairies of North America consistently demonstrate a lack of correspondence between the existing vegetation of late-successional grassland communities and the species composition of the seed bank. Although caryopses are frequently produced, few appear to retain their viability within the soil for greater than 1 year (Thompson and Grime, 1979; Pyke, 1990). In addition, the number of seedlings recruited within established grasslands is frequently low and this occurs only sporadically during years of favourable moisture and temperature conditions (Salihi and Norton, 1987; Pyke, 1990; Jonsdottir, 1991). However, infrequent sexual reproduction may be sufficient to maintain genetic diversity and contribute to population regeneration following plant mortality associated with large-scale disturbances.

However, grassland and pasture persistence is dependent upon plant recruitment from seed in numerous systems, including both annual (Andrew and Mott, 1983; Noy-Meir *et al.*, 1989) and perennial species populations (O'Connor, 1991). The greater commitment to reproduction in annual than in perennial grasses (Adams and 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 and Pyott, 1966; McIvor and Gardener, 1991). Nevertheless, the seed bank of annual grasses is relatively short lived, similar to that of perennial species (Russi *et al.*, 1992). 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 and Briske, 1996).

Physiological mechanisms

Compensatory processes

Several physiological and morphological mechanisms potentially capable of increasing plant growth following defoliation have been identified. Compensatory photosynthesis, resource allocation, nutrient absorption and shoot growth have been documented in a variety of species by numerous investigators (Briske and Richards, 1994, 1995). However, the expression of a single compensatory process does not explain the differential responses of grazing-tolerant and grazing-sensitive grasses (e.g. Caldwell *et al.*, 1981; Hodgkinson *et al.*, 1989). For example, both the grazing-tolerant and the grazing-sensitive caespitose grasses, *A. desertorum* and *P. spicata* respectively, display comparable rates of compensatory photosynthesis (Nowak and Caldwell, 1984).

Compensatory growth

The frequency of occurrence and the magnitude and significance of these compensatory processes to individual plant growth and community productivity following grazing are less clearly understood (Briske and Richards, 1995). These compensatory mechanisms may frequently prevent plant growth from being suppressed in direct proportion to the frequency and intensity of defoliation (McNaughton, 1983, 1985), but only infrequently increase total growth beyond that of undefoliated plants (Belsky, 1986; Milchunas and Lauenroth, 1993). Although the available data substantiate the occurrence of compensatory growth, they also demonstrate the specific and ill-defined conditions necessary to induce this response (Briske and Richards, 1995). For example, compensatory growth in *Ipomopsis arizonica* decreased in response to increasing competition, decreasing resource availability and grazing during the latter portions of the growing season (Maschinski and Whitham, 1989).

MANAGEMENT IMPLICATIONS

Development and implementation of successful management prescriptions require at least a partial understanding of the tolerance and avoidance strategies utilized by the major species and/or functional plant groups within grasslands and pastures. The existence of various resistance and tolerance thresholds among species presents management opportunities to influence plant utilization and growth responses among species populations within plant communities. Several examples of how management strategies may influence the resistance and tolerance thresholds of plants are presented below.

Stocking rate

Stocking rate directly influences plant utilization and the relative expression of grazing resistance among species. Late-successional dominants are frequently grazed more severely than subordinate species because they have the most rapid growth rate and a lesser expression of avoidance mechanisms (see Functional Interpretation of Grazing Resistance above). Although increasing grazing intensity can minimize selective grazing by reducing the opportunity for expression of herbivore preference, it is difficult to eliminate selective grazing entirely. For example, stocking rates required to achieve comparable utilization among two perennial grasses in a Texas grassland exceeded stocking rates required to maintain adequate forage intake by cattle (Brown and Stuth, 1993).

Season of grazing

Recognition that both avoidance and tolerance strategies vary throughout the growing season presents opportunities to differentially impact species populations in grazed systems. Grazing at a time when dominant plants express tolerance and/or avoidance strategies to the greatest extent would increase the grazing intensity at which the resistance and tolerance thresholds would be attained. Intensively grazing caespitose grasses following culm elongation represents a good example of how grazing at an inappropriate time can detrimentally influence plant growth and population persistence (e.g. Olson and Richards, 1988; Mott *et al.*, 1992).

In communities where species growth patterns are asynchronous, season of grazing will determine which species are grazed most severely during the growth period. Species grazed less intensively during the growth period or grazed when dormant will attain their resistance and tolerance thresholds at higher grazing intensities than those species grazed throughout the growing season (e.g. West *et al.*, 1979). Season of grazing is also an important consideration in species that are dependent on seed production for persistence (O'Connor, 1991; Noy-Meir and Briske, 1996).

Species of herbivore

Herbivores possess unique preferences for various plant species or plant groups within communities (Heady, 1964; Theron and Booyesen, 1966). Therefore, specific herbivores will have a different impact on species populations and plant communities by utilizing various proportions of the available species. Incorporation of two or more species of herbivores will potentially utilize a greater portion of plant species within the community. A more uniform pattern of herbivore

utilization between late-successional dominants and subordinate species will increase the grazing intensity at which the resistance and tolerance thresholds of the late-successional dominants will be attained.

Prescribed burning

Burning can modify the relative expression of grazing resistance among species in two distinct ways. First, fire can temporarily eliminate the expression of various avoidance mechanisms (e.g. culms and senescent leaves) and increase herbivore accessibility to younger tissues. This can minimize selective grazing among species until plants avoidance mechanisms are re-established. For example, bison were observed to more intensively graze caespitose, as opposed to rhizomatous grasses in recently burned grasslands (Vinton *et al.*, 1993; Pfeiffer and Steuter, 1994). Second, fire may modify relative species abundance and thereby alter the relative expression of avoidance and tolerance strategies among species within a community. For example, frequent burning is known to increase abundance of the late-successional dominants, *S. scoparium* and *Andropogon gerardii*, in the mixed and tallgrass prairies of North America respectively (Collins, 1987, 1992). A greater abundance of late-successional dominants would imply a greater dependence on tolerance, rather than on avoidance strategies, for population maintenance in response to grazing.

SUMMARY AND CONCLUSIONS

The concept of grazing resistance, within the context of grassland and pasture management, describes the relative ability of plants to survive and grow in grazed systems. Although a reasonable understanding of the major plant attributes that confer grazing resistance has been achieved, the concept is largely based on empirical evidence with a limited theoretical base. Consequently, the potential contribution of this critical concept towards understanding plant-herbivore interactions has not been fully realized. Progress toward a greater functional interpretation of grazing resistance will be required to address critical questions and issues associated with plant-herbivore interactions.

A functional interpretation of widely documented herbivore-induced shifts in species composition is proposed. The concept is based on the relative expression of resistance mechanisms and their associated costs in various ecological plant groups. It hypothesizes that late-successional dominants rely on the tolerance strategy to a greater extent than early- or mid-successional species because they are closely correlated with life history attributes of the competitor strategy. Although tolerance mechanisms require resources to replace biomass removed by herbivores, they do not represent a diversion of resources from growth, but rather directly contribute to plant growth. Therefore, avoidance mechanisms can

be assumed to represent a greater production cost and a greater trade-off with competitive ability than can tolerance mechanisms.

However, the contribution of tolerance mechanisms to grazing resistance can be suppressed prior to those of avoidance mechanisms because grazers can potentially remove biomass more rapidly than tolerance mechanisms can replace it. The grazing intensity at which the contribution of tolerance mechanisms is reduced to the point where the grazing resistance of dominant plants equals the grazing resistance of the subordinate species represents the resistance threshold. If the resistance threshold is exceeded, the grazing resistance of the dominants is reduced to less than that of the subordinate species and the dominants will lose their competitive advantage and become locally extinct or persist only as small, scattered plants. The grazing intensity at which the expression of tolerance mechanisms is eliminated represents the tolerance threshold. Plant growth is entirely suppressed by photosynthetic and/or meristematic limitations at this grazing intensity, and plant death will result if grazing intensity is maintained. Herbivores will begin to successively graze species with progressively greater expressions of avoidance mechanisms after species relying on tolerance mechanisms have decreased in abundance.

Grazing resistance is categorized into constitutive, spatial and temporal mechanisms of avoidance strategy, while tolerance strategy is divided into morphological and physiological mechanisms. The concept of resistance strategies emphasizes that frequently more than one plant attribute is involved in determining the relative grazing resistance within and among plant species. These strategies are capable of variously affecting the resistance and tolerance thresholds proposed in the functional interpretation of grazing resistance. The existence of various resistance and tolerance thresholds among species presents management opportunities to influence plant utilization and growth responses among species populations within plant communities. Development and implementation of successful management prescriptions requires at least a partial understanding of the tolerance and avoidance strategies utilized by the major species and/or functional plant groups within grasslands and pastures.

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