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Interactions Between Populations of Intermediate Wheatgrass and Western Wheatgrass as Influenced by Short-Duration Grazing and Moisture Availability

Gerrit B. Bartels
Utah State University

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INTERACTIONS BETWEEN POPULATIONS OF INTERMEDIATE WHEATGRASS AND WESTERN WHEATGRASS AS INFLUENCED BY SHORT-DURATION GRAZING AND MOISTURE AVAILABILITY

by

Gerrit B. Bartels

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of the requirements for the degree

of

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in

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Gerrit B. Bartels

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ABSTRACT

Interactions Between Populations of Intermediate Wheatgrass and Western Wheatgrass as Influenced by Short-duration Grazing and Moisture Availability

by

Gerrit B. Bartels, Doctor of Philosophy

Utah State University, 1992

Major Professor: Dr. Brien E. Norton
Department: Range Science

The effects of grazing and moisture availability on the competitive interactions of intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey) and western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love) were examined under a short-duration grazing system in central Utah. The fate of tiller cohorts was observed at approximately monthly intervals at the interface between patches of these two rhizomatous grasses and in monospecific stands. The effects of short-duration grazing, clipping of western wheatgrass following grazing to achieve levels of utilization equivalent to that of intermediate wheatgrass, irrigation, and removal of the competitor were assessed in terms of the recruitment, longevity, and mortality of ramets of both species. The effects of severance of clonal connections and defoliation on the performance of young shoots of both species were also studied.

The tiller dynamics of the two species differed greatly. Maximum life span of intermediate wheatgrass tillers was approximately 18 months, while that of western wheatgrass tillers exceeded the 3.5-year observation period. Tiller turnover was higher in intermediate wheatgrass than in western wheatgrass. Defoliation tended to increase the mortality risk of intermediate wheatgrass ramets but not that of western wheatgrass ramets. Supplemental water had the opposite effect. Irrigation increased the probability of ramet survival for intermediate wheatgrass during the growing season but led to higher winter mortality for western wheatgrass ramets.

During the four years of this study (1987-1990), western wheatgrass was the competitive dominant species. Recruitment of intermediate wheatgrass ramets at the interface was reduced compared to monospecific stands while that of western wheatgrass was enhanced. The mortality of intermediate wheatgrass tillers increased as a result of competition with western wheatgrass but only when plants were grazed. Competition had little effect on the mortality of western wheatgrass ramets. The competitive ability of intermediate wheatgrass versus western wheatgrass improved when both species were grazed heavily and when plants were irrigated.

(241 pages)

CHAPTER I

INTRODUCTION

The use of specialized grazing systems has often been advocated as an economically and ecologically attractive alternative to standard range improvement measures such as brush control and the seeding of improved forage grasses (Malechek and Dwyer 1983). A major objective of the use of a specialized grazing system on rangelands is increased livestock performance, but through time such an improvement can only be sustained if plant communities and soil stability improve or are at least maintained.

In a response to range degradation under continuous grazing, several forms of rotational grazing have been designed, particularly in southern Africa. These rotational grazing systems can be divided into two basic categories. One stresses moderate use of preferred plants with correspondingly little use of less desirable plants; the other emphasizes heavy use of all the plants present and little opportunity for selective grazing (Booysen and Tainton 1978). The first form of rotational grazing, called "high performance grazing," is based on the belief that the undefoliated plants will become moribund and thus will lose their competitive ability; the second one, called "high utilization grazing," is based on the assumption that defoliation of non-preferred species will make them less effective competitors. The premise is that moderate use of the less desirable plants is more detrimental to them than heavy short-term defoliation is to the preferred species.

Short-duration grazing

Short-duration grazing was introduced into the United States in 1978 (Savory 1978). This grazing system immediately produced considerable research interest because of claims that implementation of short-duration grazing would lead to an improvement in range condition concurrent with the use of higher stocking rates. This was contrary to one of the basic tenets of range management, viz., that range condition improves when livestock numbers are reduced.

Short-duration grazing as envisioned by Savory belongs in the category of "high performance grazing" systems because of the high degree of selectivity exhibited by the grazing animal (Savory 1978, 1983). However, as a consequence of higher stocking rates and declining forage availability as the grazing period progresses, this system may rapidly become a "high utilization grazing" system.

The main principles on which short-duration grazing (also called the Savory grazing method) is based are relatively short grazing and rest periods, concentration of animals into herds of considerable size, and managerial versatility (Savory and Parsons 1980). The theoretical basis for the benefits of short-duration grazing may be summarized as follows: (1) short grazing and adequate rest periods are needed to prevent repeated defoliation of plants that would otherwise occur under continuous grazing, and thus prevent deterioration of the forage's nutritive value and vigor; this should translate into increased forage production, (2) versatile management is required because on an almost day-to-day basis decisions must be made regarding time and location of grazing, and (3) concentration of animals creates a beneficial "herd effect" by hoof action that breaks up soil crusts, by more uniform utilization of available forage, and by more uniform distribution of dung and urine. Because of the purported range improvements, stocking rates can supposedly be increased almost immediately and in many cases doubled (Savory and Parsons 1980, Savory 1983).

As stated earlier, one of the major considerations when contemplating the introduction of a grazing method should be the sustainability or the improvement of the current carrying capacity of the resource. This encompasses maintenance of the forage plants' production capacity and the prevention of shifts towards plant communities dominated by less desirable species. A review of the literature reveals that, in general, short-duration grazing has had relatively little impact on range condition when compared to continuous grazing. Many of the studies cited, however, lasted only a few years.

After six years, Hart et al. (1986, 1988) in Wyoming found no difference in forage production or botanical composition between a short-duration grazing system and continuous grazing at two different stocking rates. Also, stocking rate did not affect forage production or species composition. During five of the six years, precipitation was above normal and at the higher stocking rate, which was 33 percent over the recommended rate, utilization may well have been too low (or too close to the control) to generate measurable vegetational responses.

Pitts and Bryant (1987) in west Texas found that changes in floristic composition were the same for continuous grazing and short-duration grazing in a four-year study, although stocking rates in the short-duration system were higher. They concluded that the observed botanical changes were more the result of precipitation patterns than of grazing system. Dahl (1986) and Bryant et al. (1989), in a review of their work in western Texas, reported no difference in herbage production and species composition between a moderately stocked, continuously grazed pasture and a short-duration grazing system with the same stocking rate. They found that differences in species composition were due to weather patterns rather than grazing treatments. In a study in northern Mexico, however, cover of desirable grasses decreased under short-duration grazing while it remained stable under continuous grazing. In that case, however, stocking rates were up to 33 percent higher in the rotationally grazed pasture (Bryant et al. 1989).

In a 20-month study in central Texas, Heitschmidt et al. (1987) found no difference in herbage growth dynamics nor in live standing crop biomass between a moderately stocked, continuously grazed pasture and a rotationally grazed pasture that was stocked 60 percent heavier. Total standing crop was higher in the continuously grazed pasture because of larger quantities of dead tissue, mainly due to the difference in stocking rates. For the same study site after four years, Heitschmidt (1986) found no evidence of a change in the botanical composition of the rotationally grazed pastures despite the higher stocking rate. In his opinion, a similar stocking rate under continuous grazing would have resulted in a degradation in species composition. Similarly, South African research has shown that by controlling competition between desirable and less desirable species, species composition could be maintained with rotational grazing but not with continuous grazing (Gammon 1978, Bransby 1984).

In southcentral New Mexico, White et al. (1991) found in a 5-year study that differences in vegetational response to short-duration grazing and continuous grazing on blue grama rangelands were small; stocking rates in the short-duration grazing system were consistently greater, though not by a fixed ratio.

Often, a shift in botanical composition towards more prostrate plants is reported but this apparently is more a function of increased stocking rates than of short-duration grazing per se. Thurow et al. (1988) reported a decline in bunchgrass cover under short-duration grazing compared to moderate continuous grazing in southwest Texas. However, stocking rate in the short-duration grazing system was 75 percent higher. When compared to continuous grazing at the same stocking rate, the decline in bunchgrass cover was much slower in the short-duration grazing treatment. The shift in species composition was towards an increase in the abundance of stoloniferous species and was associated with a decline in herbage production and increased runoff and erosion (Thurow et al. 1987, 1988, Taylor 1989).

In central Utah, Norton and Owens (1986) and Olson and Richards (1989) reported an expansion of the rhizomatous western wheatgrass in crested wheatgrass (Agropyron desertorum) pastures under short-duration grazing. However, such an increase was also observed in continuously grazed pastures of the same species (G.B. Bartels, personal observations). Gammon (1984) reported from Zimbabwe that comparisons between ranches using short-duration grazing and adjacent veld that was managed less intensively did not indicate any improvement in basal cover, litter cover nor species composition as a result of the implementation of short-duration grazing.

Most studies following the effects of short-duration grazing on botanical composition of pastures in North America were/are of relatively short duration, and this precludes an evaluation of long-term vegetation trends (Pieper and Heitschmidt 1988). In his review of experiments that compared rotational grazing and continuous grazing, Gammon (1978) concluded that a large number of these experiments were unable to detect potential differences between grazing treatments due to, among other things, insufficient duration of these studies. However, in long-term experiments rotational grazing frequently led either to pasture improvements or resulted in a deterioration that was less pronounced than under continuous grazing. Changes in botanical composition as a result of grazing treatments are usually slow, and considerable time may elapse before grazing management starts to affect the composition of plant communities in a measurable way (Booysen and Tainton 1978, Reece 1986).

In only a few cases changes in botanical composition under short-duration grazing are reported relative to undisturbed growth. In those cases, however, short-duration grazing at the stocking levels chosen was unable to maintain, let alone improve, range condition (Reece

1986, Dormaar et al. 1989).

General objectives

The present study is concerned with the impact of short-duration grazing on plant community changes in central Utah where a short-duration grazing system was initiated in 1983. Part of this system was an older intermediate wheatgrass pasture seeded in 1951. Within this pasture distinct patches of western wheatgrass are found. The question of interest, determining the overall objective of this study, was whether short-duration grazing had an effect on the persistence of the intermediate wheatgrass stand and, more particularly, on the rate of expansion or contraction of western wheatgrass patches.

While Olson and Richards (1989) reported a considerable increase of western wheatgrass in crested wheatgrass stands under short-duration grazing in the years 1983-1986, B.E. Norton (personal communications) noticed that such an invasion did not occur in stands of intermediate wheatgrass. Instead, intermediate wheatgrass appeared to outcompete western wheatgrass despite heavy grazing of intermediate wheatgrass and very light grazing of western wheatgrass. This observation would attest to the value of short-duration grazing as a "High Performance Grazing" system under these particular circumstances, bringing about a desirable change in the species composition of these pastures. The present study was designed to confirm or disprove this observation and to provide explanations for the observed interactions between these two grass species in terms of the plants' morphological, physiological and, especially, demographic traits.

Weaver (1942) has drawn attention to the consequences of a shift in botanical composition towards western wheatgrass, namely, lower forage values, reduced infiltration of precipitation and increased evaporation and runoff, when it replaces species with more abundant foliage. To determine whether this species increases with short-duration grazing under the conditions found in central Utah and whether it can be controlled by intermediate wheatgrass may, therefore, be of considerable ecological and economic importance.

The species

Intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey, syn. Agropyron intermedium (Host) Beauv. and Elytrigia intermedia (Host) Nevski) is a perennial cool-season rhizomatous grass native to the southern Commonwealth of Independent States, central Asia and eastern Mediterranean regions (Wagoner 1990). It was introduced into the USA in 1907 from Trans-Ural Siberia (Dewey 1978), but important material came from the

Caucasus region in the USSR in 1932 (Rogler 1973). Older literature separates intermediate wheatgrass from pubescent wheatgrass (Agropyron trichophorum (Link) Richt.) on the basis of pubescent or smooth glumes and lemmas. Dewey (1978) and Mariam and Ross (1972) suggested combining these two grasses into one species because both taxa do not differ in geographical distribution, ecological adaptation, mode of reproduction, or cytological behavior (see also Lawrence 1981).

Western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love, syn. Agropyron smithii Rydb.), which is also called bluestem wheatgrass (Holscher 1945) or blue joint wheatgrass (Latas and Nicholson 1976) in the older literature, is native to North America and is widely distributed from southern Ontario to Texas, California, and British Columbia. It is most abundant in the northern and central Great Plains where it often dominates in well-watered, broad or shallow ravines (Weaver and Albertson 1956), swales where it receives run-on water in addition to precipitation (Sala et al. 1982) and depressed microsites (Monson et al. 1986).

Western wheatgrass is a sod-forming perennial grass and usually forms streaks or patches (Weaver 1968). Individual shoots are connected by tough rhizomes 1 to 2 mm in diameter. Rhizome length varies from a few centimeters to more than one meter. These rhizomes exhibit great resistance to desiccation and stay alive for at least one year (Mueller 1941, Weaver 1942). Stems of western wheatgrass grow singly or in small numbers, arising from nodes of rhizomes that are usually spaced a few centimeters apart (Weaver 1942). Rhizome formation in this species may be promoted by increased soil water (Gardner 1942).

Numerous reports indicate that western wheatgrass is less productive than intermediate wheatgrass, especially when moisture conditions are favorable (Currie and White 1982, Lawrence 1978, Power 1985). The only report with results to the contrary is that by Cook et al. (1956) from central Utah. The yields reported in their study, however, were extremely low.

Intermediate wheatgrass exhibits earlier spring growth and matures at a faster rate than western wheatgrass (Cook et al. 1956, Frank et al. 1985). This earlier development was positively correlated with water use efficiency (Frank et al. 1985, Frank and Karn 1988). Frank and Barker (1976) demonstrated that under controlled conditions without water stress the transpiration rates of intermediate wheatgrass were appreciably lower than those of western wheatgrass. Relatively high transpiration rates for western wheatgrass have also been reported by Williams and Kemp (1978) and Monson et al. (1986). The "extravagant" (Monson et al. 1986) water use of western wheatgrass may restrict this species to sites where either water in addition to natural precipitation is available or where its extensive root system can explore deeper soil horizons. Sala et al. (1982) suggested that western wheatgrass is unable to respond very well to small rainfall events because of its stomatal behavior. They concluded that this grass is well adapted to sites with a frequent recharge of the soil profile and a less variable water supply. Weaver (1942) found that roots of western wheatgrass may penetrate as deep as 2.4 m, but its surface absorbing system is usually poorly developed in areas with moist soils (Weaver and Albertson 1956). Western wheatgrass extracted more soil water than intermediate wheatgrass from depths greater than 45 cm (Frank et al. 1985). This could be due to greater root density at these depths or to greater drought tolerance in general.

The drought tolerance of intermediate wheatgrass is apparently less than that of western wheatgrass (Frank 1981, Power 1985). Intermediate wheatgrass pastures completely deteriorated under drought (Currie and White 1982, Launchbaugh 1958). Contributing to western wheatgrass' drought tolerance are a waxy bloom on its foliage and its ability to exhibit leaf rolling (Weaver and Albertson 1956). However, intermediate wheatgrass is apparently more tolerant to early stress development than western wheatgrass. Western wheatgrass reduced photosynthesis more rapidly when soil moisture content decreased than did intermediate wheatgrass. Western wheatgrass apparently has a lower degree of osmotic adjustment than intermediate wheatgrass (Frank 1981). These findings suggest that intermediate wheatgrass has a higher potential for maintaining productivity during periods of moderate water deficit than western wheatgrass. This may partly explain why under most circumstances western wheatgrass has been less productive than intermediate wheatgrass, despite its substantially higher rates of net photosynthesis (Frank and Barker 1976). Another explanation for this difference may be that western wheatgrass might allocate a higher proportion of its photoassimilates to the growth and maintenance of its root system. A number of observations indicate that western wheatgrass produces more root biomass (Power 1985) and a deeper root system (Frank et al. 1985) than intermediate wheatgrass. A relatively low leaf area index (Frank and Karn 1988) may also contribute to its lower aboveground productivity.

Western wheatgrass has morphological features that are associated with high grazing resistance, such as few reproductive culms and rhizomes that keep many meristems belowground, and some associated with low grazing resistance such as early elevation of apical meristems (Branson 1953, Rechenthin 1956, Painter et al. 1989). The literature indicates that western wheatgrass does not withstand defoliation very well, especially when defoliation is uniform, as in clipping experiments. In virtually every experiment reviewed, clipping reduced herbage yield and plant vigor (Holscher 1945, Branson 1956, Everson 1966, Buwai and Trlica 1977, Santos and Trlica 1978, Painter and Detling 1981, Painter et al. 1989, Polley and Detling 1989, 1990). The negative effects of defoliation were much more pronounced on belowground biomass than on top growth (Branson 1956, Everson 1966, Santos and Trlica 1978, Bokhari and Singh 1974, Polley and Detling 1988, 1989, 1990, Painter et al. 1989). Tiller densities in the experiments of Holscher (1945), Branson (1956), Everson (1966), and Polley and Detling (1989, 1990) declined as a result of defoliation in line with aboveground biomass production.

Santos and Trlica (1978) concluded that western wheatgrass could tolerate only infrequent removal of its aerial parts and that removal of only a small portion of the foliage would reduce injury. Based on their study of the carbohydrate reserves in this species, Menke and Trlica (1981) characterized western wheatgrass as relatively drought tolerant but grazing intolerant. Virtually every clipping study has indicated that western wheatgrass will tolerate only light defoliation levels, and this has been confirmed by grazing studies. Several of these studies indicated that forage production of western wheatgrass declines rapidly when utilized between 20 and 40 percent (Klipple and Costello 1960, Reed and Peterson 1961, Launchbaugh 1967). Hart and Balla (1982), on the other hand, found in one year of their two-year study that in lightly stocked pastures grazed tillers produced more forage than ungrazed tillers. In heavily stocked pastures, however, the grazed tilers produced consistently less forage than their undefoliated counterparts. The effects of grazing on tiller density were not reported.

In contrast to the abundance of information regarding the effects of defoliation on western wheatgrass, very little detailed information is available on intermediate wheatgrass' response to foliage removal. Several clipping experiments under dryland conditions have shown deterioration of stands of intermediate wheatgrass, especially when defoliated repeatedly (Heinrichs and Clark 1961, Whitman et al. 1961, 1962). The same defoliation impact was found when plants were irrigated. Lawrence and Ashford (1966) concluded that long recovery periods between successive cuttings were necessary for stand maintenance. Ogden and Loomis (1972), in southern Utah, compared irrigated intermediate wheatgrass that was clipped to a 2.5 cm-stubble height three times during summer at six-week intervals to unclipped plants. Clipping reduced root weight, but not nearly to the same extent as reported for western wheatgrass (cf. Everson 1966). Only small differences between the carbohydrate contents of the roots of clipped and unclipped plants were reported.

Studies on the nutritive value of these wheatgrasses indicate that at comparable early phenological stages, the feeding value of intermediate wheatgrass is higher than that of western wheatgrass (Lawrence 1978, Frank and Karn 1988). Intermediate wheatgrass is also much more palatable to both sheep and cattle than western wheatgrass (Cook et al. 1956, Launchbaugh 1958).

The demographic approach

The effects of grazing can be assessed and evaluated at different scales and levels of organization (Brown and Allen 1989). The impact of grazing at higher levels of organization such as plant communities is in some way a reflection of phenomena that have occurred at lower hierarchical levels such as that of the individual plant. In our assessment of the effects of short-duration grazing on the performance of intermediate wheatgrass and western wheatgrass we used a demographic approach. This approach was used because changes in plant communities due to grazing or other environmental factors are, in aggregate, the result of differences in the natality, longevity, and mortality of the individual plants making up these communities (Archer and Tieszen 1986). Studies of these population dynamics have two important advantages compared to typical vegetational and growth studies: they are capable of documenting how certain processes evolved rather than just giving their end results, and they are non-destructive (Harper 1967, 1980, Bazzaz and Harper 1977). In the context of grazing management, knowledge obtained from such demographic studies may help explain the results of grazing experiments, suggest modifications of grazing practices, and emphasize plant characteristics that merit consideration in plant introduction and breeding programs (Jones and Mott 1980). Moreover, responses to defoliation at the community level may be noticed much sooner at the higher resolution of individual plants or plant modules. As such, plant demography may have an important future role to play in the monitoring of rangelands.

Clonal plants, including many perennial grasses, distinguish themselves from their non-clonal counterparts by an ability to produce ramets that have the potential to become ecologically independent units. This attribute causes several complications for the demographic study of these plants because population dynamics occur at two levels, namely that of the genet and that of its constituent ramets (Harper and White 1974). From an evolutionary point of view, it would be preferable to study population dynamics on the basis of genets. The longevity of genets, however, may be such that birth and death of the same individual cannot be observed within the time-span of a typical ecological study (see Canfield 1957, Williams 1970, Wright and Van Dyne 1976, West et al. 1979). For certain grass species, life spans of 40 years or more have been observed. Also, in many clonal plants, especially rhizomatous ones, the identification of these genetic individuals under natural growing conditions is often impossible (Hutchings and Barkham 1976, Harper 1977, 1980, Bell and Tomlinson 1980). Consequently, many studies of clonal plants have followed the dynamics of ramets, the functional units (sensu Sarukhan and Harper 1973) in vegetatively reproducing species. This makes sense not only from a pragmatic point of view but from an ecological perspective as well because these basic units are more sensitive to environmental variation than the overall genet (White 1980). A plant may be viewed as a metapopulation of its parts and by studying these parts a plant's ecological status can be clarified (White 1979).

In the special case of grassland studies, the tiller (ramet) is frequently considered the basic unit of growth. The rate of appearance and loss of these tillers together with their individual performance determine the productivity of swards (Garwood 1969). Under circumstances where productivity aspects are important, the study of ramets rather than genets is justified (White 1979, Harper 1980). Counts of ramets and ramet performance are good indicators of a plant's vitality, and following the fate of tillers rather than of genets has often been of value in assessing the performance of grass species (White 1980).

Following the dynamics of ramets, especially those of rhizomatous species, has two drawbacks, however. It is often not known whether or not a ramet may be considered an ecological individual (Harper 1967) and, second, the clonal identity of ramets is frequently unknown. Members of a population of tillers may be integrated modules of one clone (genet) or may belong to different clonal fractions or even different genets. A ramet's growth, development, and fate are influenced by the number of its neighbors and their performance, neighbors to which it may still be connected (Harper 1967, 1977, 1978, Hutchings and Barkham 1976, Abrahamson 1980, Cook 1983). Tillers and shoots are physiologically interdependent in many grass species (Cook 1983, 1985, Pitelka and Ashmun 1985), and such integration among ramets has demographic consequences. One cannot assume that the performance, birth, and death of a ramet are independent of clonal identity. Physiologically integrated genets may be capable of regulating the density, position, and performance of their ramets (Hutchings and Barkham 1976, Cook 1985, Hartnett and Bazzaz 1985a). This may result in reduced sensitivity to resource limitations, competitors, and herbivores (Hutchings and Bradbury 1986) and, consequently, an increase in the probability of a ramet's survival. Ecologically, a physiologically integrated ramet is not an individual, and its response to environmental variation differs from that of single plants (Kays and Harper 1974, Hutchings and Barkham 1976, Hutchings 1979, Hartnett and Bazzaz 1985b, Dickerman and Wetzel 1985). Without complete knowledge of clonal identity and degree of functional integration, as is usually the case in grassland studies, the interpretation of demographic data based on ramets has certain limitations.

Organization of the dissertation

In Chapters II, III, and IV the tiller dynamics of intermediate wheatgrass and western wheatgrass were followed during several growing seasons. The objective was to collect life history and demographic information on ramets that would provide insight into the effects of short-duration grazing and moisture availability on the growth of these two species and on their competitive interactions.

The basic dynamics of ramet populations of these two species during the years 1987-1990 and how short-duration grazing impacted the recruitment, longevity, and mortality of these ramets are described in Chapter II.

The tiller dynamics at the interface of the two species are the focus of Chapter III. A phenomenological approach to studying the competitive interactions between these two species was used. The influence of short-duration grazing on the relative competitive abilities of these two species is described as well.

Although the study of population dynamics may reveal processes that will have an impact on plant communities, such studies are often deficient because the underlying biological causes for the observed changes in the populations remain obscure. Therefore, a more mechanistic approach to examine the competitive interactions between intermediate wheatgrass and western wheatgrass was taken in an experiment described in Chapter IV. In this experiment two additional perturbations were introduced, viz., supplemental moisture and the removal of the companion species.

In Chapter V the effects of various defoliation regimes on the performance of recently emerged shoots of both species were examined to assess the relative importance of intraclonal resource sharing and intraspecific competition in these two grasses and to evaluate their defoliation tolerance.

Finally, in Chapter VI the competition between intermediate wheatgrass and western wheatgrass under short-duration grazing is discussed in relation to their growth form and tiller life histories. The implications of the results for grazing management as well as future research directions are addressed also.

CHAPTER II

TILLER DYNAMICS OF THINOPYRUM INTERMEDIUM AND PASCOPYRUM SMITHII AS INFLUENCED BY SHORT-DURATION GRAZING

Abstract. The objectives of this four-year field study in central Utah were to investigate the tiller dynamics of two co-occurring rhizomatous grasses, intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey) and western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love) and to determine if these dynamics are altered by short-duration grazing. Demographic methods were used to monitor birth and death of tiller cohorts. Tiller longevity in western wheatgrass was more affected by environmental conditions than in intermediate wheatgrass, which apparently is under strict genetic control. Despite a pronounced drought during this study (1987-1990), ramet density of intermediate wheatgrass in enclosures increased eight percent but declined 63 percent under short-duration grazing. Grazing had little effect on the ramet density of western wheatgrass with a decline of only 18 and 22 percent for protected and grazed plots, respectively. In contrast to intermediate wheatgrass, tiller life span in western wheatgrass is indeterminate and, as a result, tiller turnover was higher in intermediate wheatgrass than western wheatgrass. Tiller recruitment and death in both species were seasonal. Recruitment generally peaked in

late fall for intermediate wheatgrass and in early spring for western wheatgrass. The risk of mortality in both species was highest during the summer months, whereas winter mortality of newly established ramets was extremely low in both species. In most cohorts, grazing increased the mortality risk of intermediate wheatgrass ramets but not of western wheatgrass ramets. Defoliation and drought increased the life span of western wheatgrass ramets. It appeared that reduced survival and recruitment of intermediate wheatgrass ramets as a result of grazing was not due to grazing *per se* but a consequence of asymmetric competition between the two species following differential defoliation.

Introduction

Defoliation of plants usually, though not always, results in declining biomass production and loss of vigor (Jameson 1963, Hyder 1972, Hart and Norton 1988). Plants differ, however, in their ability to tolerate or avoid defoliation due to specific morphological and physiological characteristics (Branson 1953, Rechenthin 1956, Briske 1986). Differences among plant community members in the degree of herbivory tolerance and avoidance and levels of defoliation experienced may eventually lead to changes in species composition of the community.

One of the goals of grazing management often is to prevent shifts in botanical composition towards communities dominated by less desirable species. The range manager does this by judicial use of animal numbers and by control over time, location, frequency, and severity of defoliation (Heady 1975). Grazing systems differ greatly with respect to the degree of control they offer, and it is frequently assumed that those systems providing most control have the greatest potential for maintaining favorable plant composition of grazing lands (Heitschmidt and Walker 1983, Bransby 1984). One such intensive grazing system proposed for rangelands in the western United States is short-duration grazing (Savory 1978, Savory and Parsons 1980).

The relative importance of grazing and grazing systems in determining sward dynamics and the botanical composition of grazing lands, particularly in arid environments, has been questioned recently. Westoby (1980), Walker (1988) and Walker et al. (1986) emphasized the role of weather sequences, the effects of which were found to override those of grazing in defining these dynamics. Several long-term demographic studies on the effects of grazing on plant survival, the ultimate measure of plant vigor, indicated that grazing per se may not be as important as often assumed. Grazing increases plant longevity (Canfield 1957, Williams 1970, West et al. 1979) as well as decreases plant longevity (Canfield 1957, Williams 1970). Other authors found either no or little effect of grazing on the survival of grasses (Williams and Roe 1975, Wright and Van Dyne 1976).

Studying the demographic effects of grazing on individual grass plants (genets) is time consuming and feasible only when the genetic individuals can be recognized. In sward situations, especially when species are rhizomatous, this level of plant discrimination is seldom possible, and the fate of plant modules must be studied (Harper 1977, 1980, Bell and Tomlinson 1980, White 1980). A plant may be viewed as a population of its parts (White 1979) whose performance, in the case of a grass, is the integral of tiller appearance and tiller death, and the growth and development of individual ramets (Garwood 1969).

Few studies have recorded the recruitment of tillers in graminoids and followed their fate under actual grazing conditions. Effects of grazing on the longevity of ramets apparently are as ambiguous as those on the longevity of genets. Chapman et al. (1984) compared set-stocking and rotational grazing in New Zealand. They found that defoliation by sheep significantly contributed to the death rate of Lolium perenne tillers but was less important than other, unknown, causes of death in the mortality of tillers of Agrostis spp. Grazing by lesser snow geese appeared to reduce tiller mortality in the stoloniferous grass Puccinellia phryganodes, but the results were inconclusive because of the short observation period. Grazing stimulated tillering in this grass (Bazely and Jefferies 1989). In the same habitat, however, grazing did not encourage shoot production in the rhizomatous sedge Carex subspathacea, and mortality of grazed shoots was higher than of ungrazed shoots (Kotanen and Jefferies 1987). Fetcher and Shaver (1983) found that mechanical disturbance of the tundra sedge Eriophorum vaginatum increased tiller mortality and led to earlier production of daughter tillers as compared to undisturbed plants. Noble et al. (1979) produced survivorship curves of shoot cohorts of the sedge Carex arenaria from two different sites, one of which was grazed by sheep and cattle. Differences between the survivorship curves of ramets from these two sites apparently were only minor.

A better understanding of the autecology of grassland species is a prerequisite for better grazing management practices (Jones and Mott 1980, Walker 1988). The purpose of this study was to compare the ramet demography of two co-occurring rhizomatous grasses, intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey) and western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love) and to establish if and how short-duration grazing affects the demographic attributes of these two species. Intermediate wheatgrass is a very palatable species introduced from the Caucasus region in 1932. Western wheatgrass is a widely distributed native species which is of only limited forage value in the Great Basin, although a desirable species in the central and northern Great Plains of the United States (Rogler 1973).

Materials and methods

The study was conducted from May 1987 to September 1990 at the Tintic Range Experiment Area in Juab County, Utah (39° 51' N, 112° 08' W). The elevation at Tintic is 1750 m and the long-term (23 years) average annual precipitation is 373 mm, 37 per cent of which falls during the months November through February (Fig. 2.1). During 1983-1990, the area experienced a steady decline in annual precipitation (Fig. 2.1) and the final three years of this study were remarkably, and uniformly, dry (Fig. 2.2), except for above-average rainfall in July 1989.

The pasture used in this study was seeded in 1951 to monocultures of intermediate wheatgrass and crested wheatgrass (*Agropyron desertorum* (Fischer ex Link) Schultes) after mechanical removal of big sagebrush (*Artemisia tridentata* ssp. *tridentata* Nutt.) and juniper trees (*Juniperus osteosperma* (Torr.) Little.). The soils of the study site are coarse-loamy, mixed (calcareous), mesic, Torrifluventic Haploxerolls (Jensen 1983).

In 1983, a short-duration grazing cell was established with 10 radially arranged paddocks of 8.5 ha each (Malechek and Dwyer 1983). The paddock in which the

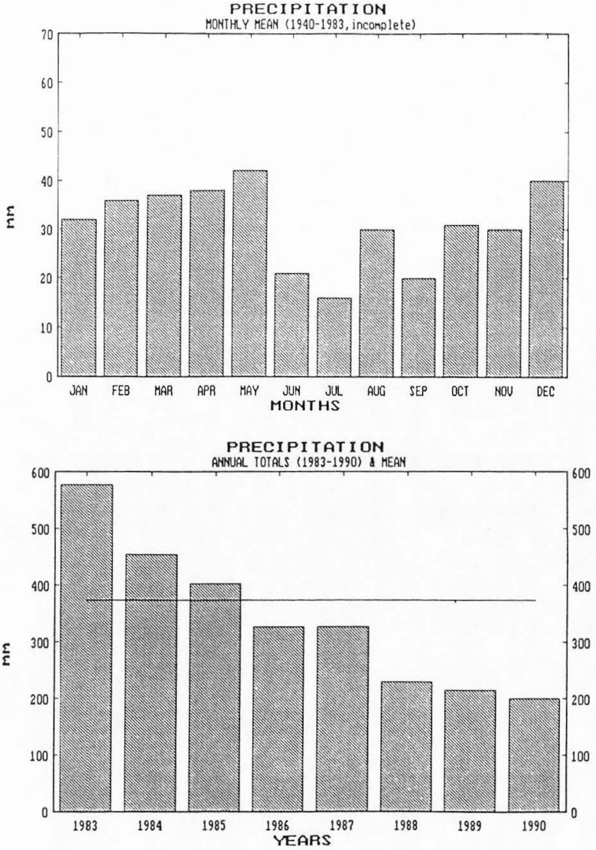

Fig. 2.1. Precipitation at Tintic, Utah. Monthly means based on 23 years of data between 1940 and 1983 (top). Annual totals of 1983 to 1990 relative to long-term annual mean (373 mm)(bottom).

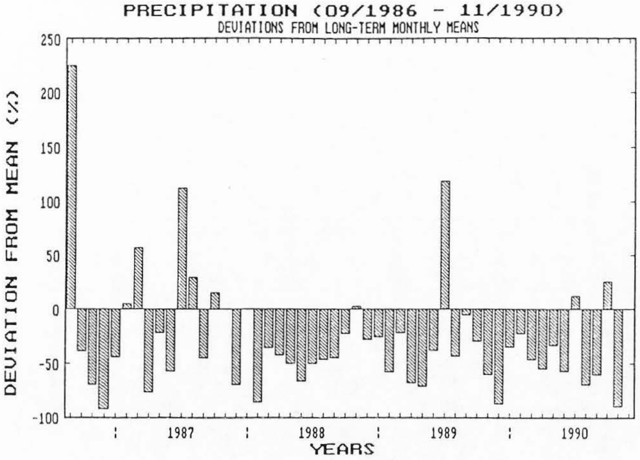

Fig. 2.2. Monthly precipitation at Tintic, Utah for the period September 1986 to November 1990, expressed as deviations from long-term monthly means.

present study was conducted consisted of one-fourth of crested wheatgrass; the remainder was originally dominated by intermediate wheatgrass. However, big sagebrush has since re-occupied about half of the intermediate wheatgrass area (paddock number 8). Within both the crested wheatgrass and intermediate wheatgrass swards distinct patches of western wheatgrass are found.

Ten triplets of belt-transects, 25 cm x 300 cm, were placed perpendicularly across the sharp boundary interface of intermediate wheatgrass and western wheatgrass populations in April 1987. In each case, one transect was protected from grazing (further referred to as "control"), and one transect was grazed ("grazed"). The third transect was also grazed, but immediately after grazing the unconsumed western wheatgrass was clipped to simulate grazing at the same level of utilization as observed in the more heavily grazed intermediate wheatgrass ("clipped"). Clipped material was discarded. Thus, for intermediate wheatgrass the "clipped" treatment was equal to the "grazed" treatment as far as defoliation is concerned.

Each belt-transect was subdivided into twelve, 25 cm x 25 cm contiguous permanent plots; six of these plots were allocated initially to each species. Biomass in each plot was estimated using a non-destructive, double sampling technique (Tadmor et al. 1975) just before grazing, and after grazing in the grazed and clipped transects. This allowed estimation of herbage consumption.

In five randomly chosen blocks, each containing a triplet of belt-transects, the tiller dynamics of the two species were assessed by tagging newly emerged tillers at regular, approximately monthly, intervals with color-coded wire loops in the two innermost and two outermost plots of the transects (see Appendix A for a diagrammatic representation of the layout). Their fates were followed not as individuals but as members of a cohort. Death was considered the time when a ramet had lost all green color. Differently shaped loops were used for the two species. [Loss of loops was only minor in the defoliated plots: 0.3 % of the loops could not be accounted for.] A ramet was also considered dead when a loop could not be recovered during the census immediately following grazing. Most censuses took several days to complete, and the dates used in this chapter correspond to the midpoints of the census periods. No observations were made during winter because of the presence of snow.

In the years preceding this study, paddocks were grazed twice or three times during the season (Olson et al. 1989). Because of below-average precipitation, the study site was grazed only twice in 1987 (for 48 hours starting on 14 May and for 24 hours starting on 21 June) and only once for 48 hours in the other three years (starting 11 June 1988, 13 May 1989, and 18 May 1990). In 1987, the short-duration grazing system was stocked with 90 yearling Angus heifers and four bulls and in the following years with 60 cow-calf pairs and three or four bulls. This resulted in a stocking density of approximately 7.5 AU (animal unit) per ha. Defoliation of intermediate wheatgrass was always uniform, but that of western wheatgrass varied, especially in the first two years. In these first two years, utilization of western wheatgrass was markedly lower than that of intermediate wheatgrass. Only in the last two years of this study did the utilization of the two species reach comparable levels.

This chapter reports on the observations made in the outermost plots of the transects, which were monospecific stands of the two grasses. [After the start of the study, one grazed plot of western wheatgrass was found to contain a clump of intermediate wheatgrass ramets, and in a clipped transect one intermediate wheatgrass plot was partly occupied by western wheatgrass ramets. The data from these two plots were omitted from the analysis.] The initial census was taken in July 1987 after the first year's grazing, but all experimental units had received their respective treatments.

The design of this experiment was a randomized block, analyzed as a split-split plot design with defoliation as the mainplot factor, species as the subplot factor and time as the sub-subplot factor (Steel and Torrie 1960). Differences among treatment means were examined using Fischer's protected LSD.

Survivorship curves were constructed by combining the number of surviving ramets for all four or five replicates in life table form. Differences between survivorship curves resulting from different treatments within the same cohort were assessed using Mantel and Haenszel's chi-square test (Mantel and Haenszel 1959, Lee 1980); only sample sizes of 30 or more were tested using this procedure. Differences in mortality patterns that were significant at the five percent level are reported.

Results

Number of cohorts and life history of ramets

Following the initial census on 8 July 1987, an additional 21 censuses were taken during the study. In 14 of these 21 censuses, new recruits were detected in the control plots of both intermediate wheatgrass and western wheatgrass; in 18 and 13 for the grazed plots of intermediate and western wheatgrass, respectively; and in 18 and 17 censuses for the clipped treatment of intermediate and western wheatgrass, respectively (Figs. 2.3 and 2.4). Some of these cohorts, however, consisted of only a few ramets.

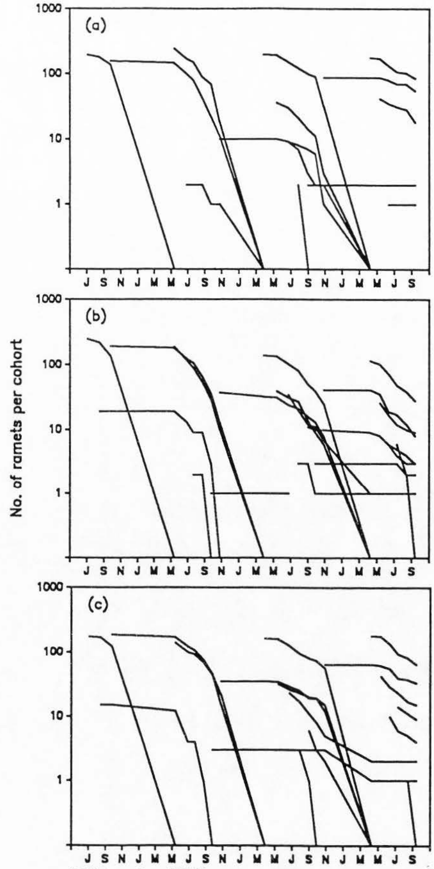

Fig. 2.3. Depletion and survivorship curves for successive cohorts of intermediate wheatgrass ramets. (a) control, (b) grazed, (c) clipped. Number of ramets is the total from five 0.0625 m^2 plots in the case of (a) and (b), and from four plots in the case of (c).

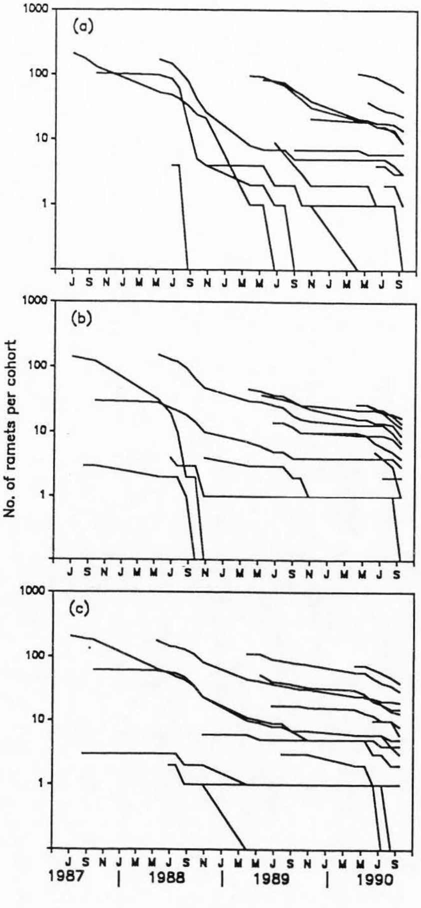

Fig. 2.4. Depletion and survivorship curves for successive cohorts of western wheatgrass ramets. (a) control, (b) grazed, (c) clipped. Number of ramets is the total from five 0.0625 m^2 plots in the case of (a) and (c), and from four plots in the case of (b).

Life history of the ramets of these two species differed greatly. Whereas ramets of western wheatgrass apparently were indeterminate (Fig. 2.4), those of intermediate wheatgrass had only a limited life span (Fig. 2.3). The potential life span of intermediate wheatgrass ramets depended on time of origin and was maximum for tillers emerging in June. Intermediate wheatgrass ramets produced before June did not survive beyond the following winter; those originating after June were able to survive the winter and had the potential to remain alive until the winter of the following year. The ramets of intermediate wheatgrass, therefore, have annual and biennial characteristics. In contrast, western wheatgrass ramets apparently do not have a predetermined life span. Three and a half years after the start of this study, some ramets that had been members of the initial population were still alive.

Ramet density

Live ramet densities fluctuated seasonally, more so in intermediate wheatgrass than in western wheatgrass (Fig. 2.5). Each year, ramet density was maximum in May and reached its minimum between September and November, depending on the advent of sufficient precipitation to stimulate the formation of new ramets. The sharp decline in tiller density in 1988 was the result of an extremely dry summer and autumn when virtually no recruitment

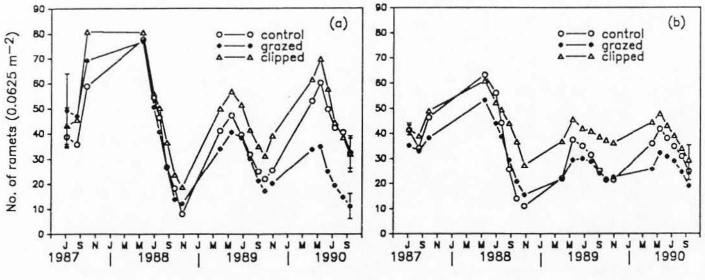

Fig. 2.5. Mean number of live ramets per 0.0625 m^2 (± 1 SE) from July 1987 to September 1990 under three defoliation regimes. (a) intermediate wheatgrass (b) western wheatgrass. (n=5, except for intermediate wheatgrass, clipped and western wheatgrass, grazed, where n=4).

occurred. In that year ramet density declined on average 85 percent for intermediate wheatgrass and approximately 70 percent for western wheatgrass from their respective peaks in May. For western wheatgrass this decline was steeper in the control plots than in the defoliated plots.

During the course of this four-year experiment, ramet density generally declined for both species. This decline, however, started not immediately but only in the second year when drought conditions became more pronounced (Fig. 2.1). Compared to the first census date, density increased in the first year for both intermediate wheatgrass ($p<0.100$) and western wheatgrass ($p<0.050$) when protected from grazing as well as for western wheatgrass in the clipped treatments ($p<0.050$). Two years after the first census, however, tiller density in intermediate wheatgrass was 11 percent lower in the control plots and 33 percent lower in the grazed plots ($p<0.050$), but still 4 percent higher in the clipped treatments than at the start of the experiment. In western wheatgrass density was reduced by 21 ($p<0.050$), 17, and 1 percent for the control, grazed, and clipped treatments, respectively. This decline continued during the final year in intermediate wheatgrass, except when protected from grazing. Three years after the first census, ramet density for the control was 8 percent higher than at the start of the study, while that for the grazed and clipped treatments declined 63 ($p<0.001$) and 1 percent, respectively. Ramet density of western wheatgrass seemed to stabilize somewhat after the second year. In three years, ramet densities for western wheatgrass declined 18 ($p<0.050$), 22 ($p<0.050$), and 10 percent for the control, grazed, and clipped treatments, respectively.

Defoliation did not greatly affect overall ramet density in western wheatgrass, but did affect tiller dynamics of this species (Fig. 2.5b). The absence of defoliation favored tiller turnover, as indicated by the precipitous declines in ramet density of control plots during the summer and fall periods and the steeper increases during winter and early spring. In intermediate wheatgrass grazing significantly reduced ramet density only in the final year of this study (Fig 2.5a). The difference in tiller density between the grazed and control treatments for intermediate wheatgrass three years after the start of this experiment was statistically significant ($p<0.050$).

Flux of ramets

The fluctuations in tiller density over the course of this study do not adequately reflect the substantial turnover of ramets in these two species. This turnover was greater for intermediate wheatgrass than for western wheatgrass (Fig. 2.6); many more ramets of intermediate wheatgrass were recruited during the course of this study

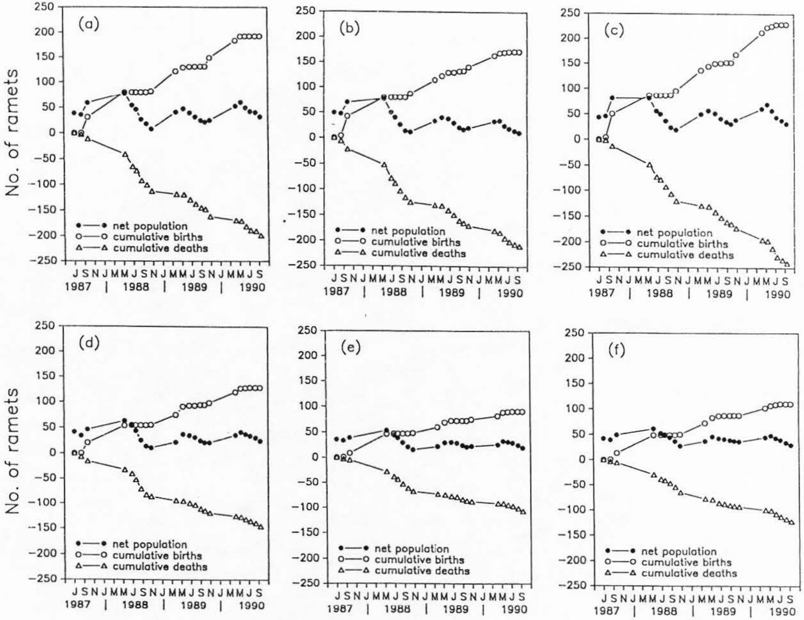

Fig. 2.6. Flux of ramets and changes in net population size. Number of ramets are means per 0.0625 m^2. (a), (b), (c) are intermediate wheatgrass, (d), (e), (f) are western wheatgrass control, grazed, and clipped, respectively.

than of western wheatgrass ($F_{1,10}=16.47$, $p=0.002$).

For every live tiller present at the first census, 5.0, 3.5, and 5.3 ramets appeared in the following three years for the control, grazed, and clipped plots of intermediate wheatgrass, respectively. Recruitment of intermediate wheatgrass ramets under grazing was markedly reduced over the course of this study compared to the control ($p<0.100$) and the clipped treatment ($p<0.050$).

Recruitment of new ramets in western wheatgrass was not statistically different among treatments. For each original live ramet about three new ramets appeared during the study.

Reproductive efforts

Reproductive performance of both species was recorded in the last three years of this study, but not in 1987.

No sexual reproduction occurred in the last three years of the study. Western wheatgrass did not exsert inflorescences at all, while intermediate wheatgrass in the protected plots produced five inflorescences in 1988 and four in 1990. This corresponded to only 1.3 and 1.4 percent, respectively, of all the ramets present during peak tiller density in early May of the respective year. In the grazed plots of intermediate wheatgrass, four tillers or 2.3 percent of all live tillers present in early May, exserted inflorescences in 1990 and only one out of 278 tillers present in that year produced an inflorescence in the clipped treatment. Of the 14 intermediate wheatgrass tillers exserting inflorescences in this study, 12 belonged to summer or fall cohorts, while the other two were members of the first spring cohort. Anthesis was seldom observed, and no viable seed was ever produced.

Birth and death rate

Ramet birth and ramet death were seasonal in both species (Fig. 2.7). Generally, recruitment of new ramets was somewhat earlier in intermediate wheatgrass than in western wheatgrass. Only in 1987 did the tiller appearance rate for both species peak in early fall with relatively little recruitment in winter and the following spring. Because almost no precipitation was received in the summer and fall of 1988, this peak shifted to late fall and early winter for intermediate wheatgrass and to the spring of 1989 for western wheatgrass. A year later recruitment of new ramets of intermediate wheatgrass took place in fall, winter, and spring with a peak in fall, whereas in western wheatgrass the recruitment rate again was highest in spring.

Only minor differences were observed between the defoliation treatments concerning the temporal effects on recruitment and mortality, except for the somewhat extended periods of recruitment in the grazed and clipped plots of intermediate wheatgrass. Recruitment in these

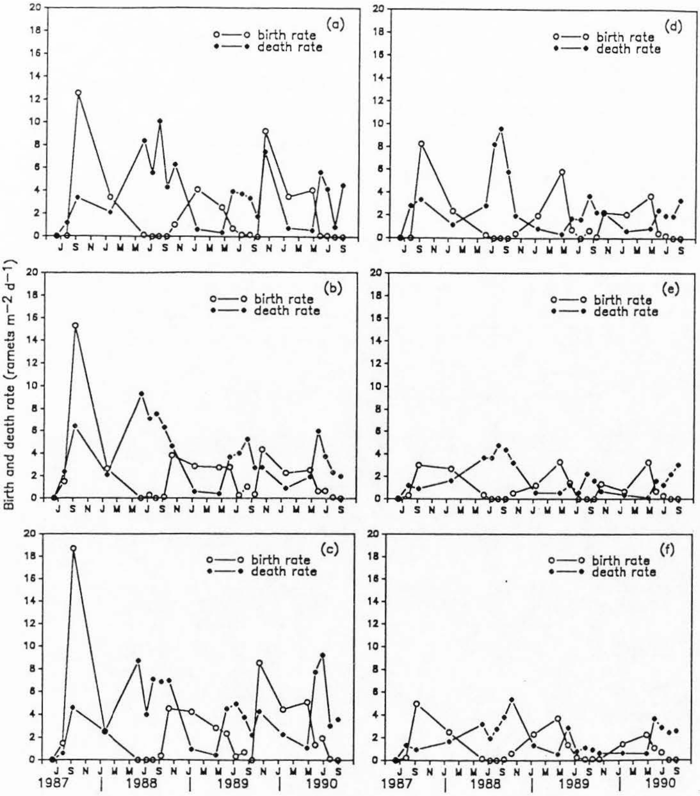

Fig. 2.7. Tiller appearance and mortality rates of intermediate wheatgrass and western wheatgrass, scaled to 1 m^2. (a), (b), and (c) are intermediate wheatgrass, (d), (e), (f) are western wheatgrass control, grazed, and clipped, respectively.

defoliated plots tended to start slightly earlier and last a little longer into summer.

Recruitment for both species was higher in the first year (July 1987-June 1988) than in the second ($p<0.001$). In intermediate wheatgrass recruitment did not change significantly after the second year, whereas in western wheatgrass recruitment continued to decline with the number of recruits in the third year significantly lower than in the second year ($p<0.001$).

Defoliation had no significant effect on the recruitment of new ramets of intermediate wheatgrass in each year separately and only in the final year was the recruitment of new western wheatgrass ramets significantly higher in the control plots than in the grazed ($p<0.010$) and clipped ($p<0.050$) plots.

Ramets of both species die year-round, but mortality was concentrated in the summer months; lowest mortality rates were found during winter. Defoliation treatments did not appear to have much of an effect on the mortality rate of intermediate wheatgrass tillers, although there is some indication that the peaks in mortality rate occurred later in the control plots than in the defoliated plots.

The birth and death rates of intermediate wheatgrass ramets were generally higher than those of western wheatgrass. This was more pronounced under defoliation.

Ramet survival

The initial population and eight cohorts of intermediate wheatgrass ramets were of sufficient size to permit a statistical comparison of the survivorship curves under the three defoliation regimes (Table 2.1). The risk of mortality for grazed ramets was higher than for ungrazed ramets in the initial population (depletion curve) and in three additional cohorts. In the remaining cohorts (09/26/87, 03/22/89, 05/06/89, 05/01/90) the patterns of mortality of protected and grazed tillers were not statistically different. Clipping of western wheatgrass immediately following grazing reduced the risk of mortality of intermediate wheatgrass tillers. This was the case in the initial ramet population and in five of the eight major cohorts. Compared to ramets protected from grazing, clipping of western wheatgrass even tended to reduce the risk of mortality for grazed intermediate wheatgrass ramets; in the two spring cohorts of 1989 this effect was statistically significant. In only one case (cohort of 03/30/90) was the survival of protected ramets significantly better than that of ramets in the clipped treatment. This was towards the end of the study, however, and the survival data were right censored. The life expectancy of fall-produced ramets was markedly higher than that of ramets originating in spring because of low winter mortality of young ramets (see Fig. 2.3). The

Table 2.1. Life expectancy (e_x)[1] in days and the results of Mantel-Haenszel's chi-square test for the major ramet cohorts of intermediate wheatgrass (P = protected, G = grazed, C = clipped).

Cohort	Treatment	e_x	M-H chi-square test
07/08/87		initial population	C=P (p=0.936)
			C>G (p<0.001)
			P>G (p=0.001)
09/26/87	P	295	C=G (p=0.360)
	G	300	C=P (p=0.076)
	C	302	G=P (p=0.333)
05/12/88	P	91	C=P (p=0.066)
	G	75	C>G (p<0.001)
	C	104	P>G (p=0.003)
10/22/88	P	--	
	G	285	C=G (p=0.099)
	C	336	
03/22/89	P	157	C>P (p=0.027)
	G	147	C>G (p=0.006)
	C	173	P=G (p=0.190)
05/06/89	P	99	C>G (p=0.008)
	G	105	C>P (p=0.002)
	C	155	G=P (p=0.745)
10/18/89		*	P=C (p=0.077)
		*	P>G (p<0.001)
		*	C>G (p=0.001)
03/30/90		*	P>C (p=0.029)
		*	P>G (p<0.001)
		*	C>G (p=0.014)
05/01/90		*	P=C (p=0.194)
		*	P=G (p=0.170)
		*	C=G (p=0.809)

*	life span of cohort exceeded observation period.
> and =	denote that mean survival time of ramets under one defoliation regime was significantly greater than or equal to that of ramets under another defoliation regime.

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[1] Values for e_x may be somewhat high in some cases as the winter was regarded as one interval.

mortality pattern of the fall-produced ramets that survived the winter differed very little from that of spring-produced ramets.

For western wheatgrass ramets the depletion curve and the survivorship curves of six major cohorts were compared, five of which are presented in Fig. 2.8. No significant differences in mortality pattern were observed between grazed and protected western wheatgrass ramets belonging to the initial population, but in three later cohorts the risk of mortality was significantly higher for ramets protected from grazing (09/26/87 ($p<0.001$); 05/12/88 ($p<0.001$); 03/22/89 ($p=0.006$)). Clipping after grazing apparently increased the survival of ramets. This was significant for the initial population of ramets ($p<0.001$) and the cohorts of 05/12/88 ($p=0.016$) and 05/01/90 ($p=0.029$). In three cohorts (09/26/87, 05/12/88, 03/22/89) as well as the initial ramet population, the mortality risk of clipped western wheatgrass ramets was significantly lower than that of protected ramets ($p<0.001$ in all four cases).

The shapes of the survivorship curves for western wheatgrass ramets apparently changed through time, indicating that the average life span of later-produced ramets was higher than that of ramets that were observed earlier in the study. This is particularly evident for ramets that were protected from grazing but is also

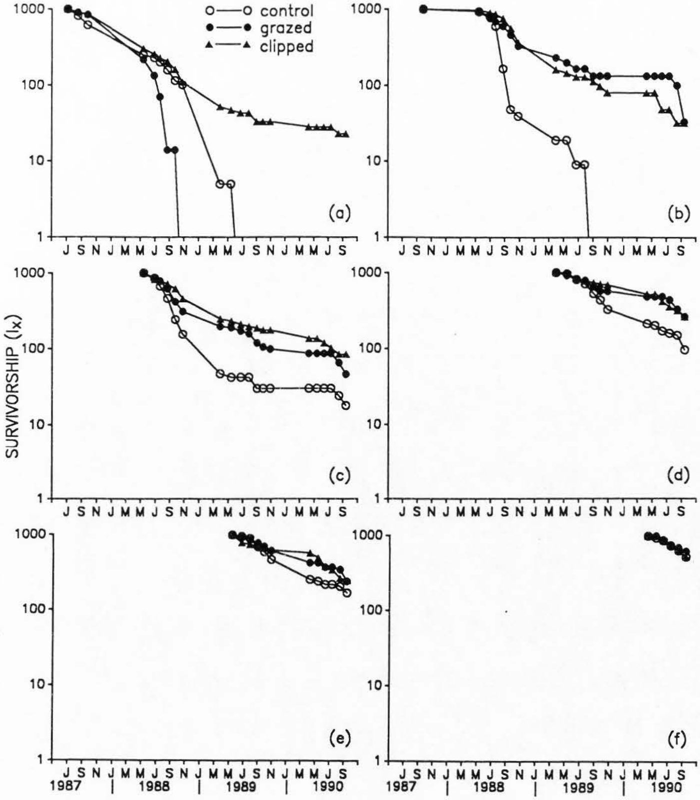

Fig. 2.8. Depletion curve and survivorship curves of five major cohorts of western wheatgrass ramets subjected to various defoliation regimes. (a) initial population, (b) cohort of 09/26/87, (c) cohort of 05/12/88, (d) cohort of 03/22/89, (e) cohort of 05/06/89, and (f) cohort of 03/30/90.

noticeable in the other two defoliation regimes (see Fig. 2.8).

Discussion

Intermediate wheatgrass and western wheatgrass differed greatly in their tiller dynamics, and these differences explain to a large extent the performance of these two species during the years of this study. Although sexual reproduction did not take place, developmental processes in individual ramets apparently were the primary determinants of the observed tiller dynamics. These dynamics are markedly influenced by environmental conditions in the case of western wheatgrass but less so in the case of intermediate wheatgrass.

Mean life spans of intermediate wheatgrass ramets depended on their time of origin (Table 2.1). The ramets behaved as either annual or biennial modules of a perennial plant, which apparently is a consequence of the induction of apical meristems and rudimentary tiller initials by low temperatures and short photoperiods (Elliott 1966). Though very few tillers of intermediate wheatgrass actually exserted inflorescences at our site, virtually all fall- and spring-produced ramets exhibited internode elongation during the month of May. Elliott (1966) found almost no blind tillers in this species and suggested the existence of a close link between the stimuli for flowering and stem elongation. Drought and possibly other stresses may have prevented the proper development and exsertion of inflorescences; devernalization of induced tillers may have been a factor as well (Elliott 1966). In the present study, apices were not dissected to confirm whether initiation of floral primordia had actually occurred in spring. However, for the life span of individual ramets of intermediate wheatgrass, the actual transition of the apical meristem from the vegetative to the reproductive phase is probably inconsequential. Elliott (1966) found that the few blind tillers in his study produced the same number of leaves as reproductive tillers and subsequently died.

Ramets of western wheatgrass cannot be as easily categorized based on longevity as those of intermediate wheatgrass. Their life span apparently is indeterminate, and some ramets in this study lived more than 3.5 years. Western wheatgrass does not have a requirement for low temperature vernalization but has an absolute requirement for long photoperiods to produce inflorescences (Benedict 1940, Spector 1956, Vince-Prue 1975). Following shoot emergence, internodes reportedly quickly elongate, and this is independent of the apex transitioning to the reproductive phase (Branson 1953). However, stem elongation in this species is influenced by defoliation and growing conditions (Enevoldsen and Lewis 1978).

As illustrated by Fig. 2.5, precipitation was the main factor determining ramet density in both species but particularly in intermediate wheatgrass. The effects of reduced precipitation on ramet survival and recruitment were greatest in 1988, the year in which drought intensified (Fig. 2.1). This represented a sudden reduction in the carrying capacity for intermediate wheatgrass ramets and, to a lesser extent, western wheatgrass ramets, as illustrated by the high mortality and reduced birth rates in that year (see Fig. 2.7). The absence of late-summer and fall rains postponed and possibly reduced recruitment of a new generation of ramets. Intermediate wheatgrass, whose ramets start to senesce in June, requires the formation of a new generation of ramets in the fall for perennation. Rudimentary tillers in the form of basal axillary buds will become new ramets when the inhibiting influence of stem meristems diminishes and environmental conditions become favorable (Booysen et al. 1963, Langer 1963, Jewiss 1966, 1972, Marshall 1987). Environmental conditions only marginally affect the formation of axillary buds but greatly influence their development and subsequent emergence as tillers (Langer 1963, Jewiss 1966, Marshall 1987). A delay in the occurrence of conditions conducive to axillary bud development could lead to a reduction in recruitment (Mitchell 1953, Busso et al. 1989). Earlier mortality of parent tillers and the failure of late-summer rains in 1988 may have combined to reduce the proportion of buds in intermediate wheatgrass that eventually developed into new ramets.

Demographically, western wheatgrass appears to be better adapted to withstand sustained drought than intermediate wheatgrass. Ramet life span is indeterminate, which in the absence of floral initiation may have postponed death of many elongated stems to the winter (e.g., Lamp 1952, Robson 1968, Hyder 1972). This may partly explain the late recruitment of western wheatgrass ramets in these dry years. In addition, many western wheatgrass ramets remained culmless with their apical meristems below the soil surface where they were protected from desiccation and winterkill. Once sufficient water became available after drought, these tillers resumed growth by re-activating intercalary meristems and forming new leaves. For perennation then, western wheatgrass is far less dependent on summer and fall rains than intermediate wheatgrass.

Though precipitation did not increase in the two years following 1988, ramet density of intermediate wheatgrass tended to recover in those two years, except in the grazed plots. This was due to improved ramet survival in 1989 compared to 1988, presumably a result of lower ramet densities, followed by a somewhat better recruitment in the fall of that year.

These observations allude to the importance of summer rains for intermediate wheatgrass swards. Our data on tiller recruitment would indicate that winter and spring precipitation affect productivity of these swards mainly by influencing the growth of individual tillers. The number of ramets in the sward, on the other hand, is often determined by light rains in summer and fall.

Survivorship curves of the major cohorts of intermediate wheatgrass ramets (see Fig. 2.3) reflect the dominant role of the reproductive process in the tiller dynamics of this grass. They belong predominantly to the Deevey Type I category, which is characteristic of populations whose members die more or less simultaneously after a certain life span (Deevey 1947). With few exceptions, survivorship curves of western wheatgrass, though with seasonal influences on mortality superimposed, more closely resemble a Deevey Type II curve, representative of populations experiencing an age-independent mortality rate.

Of particular interest are the three depletion/survivorship curves of western wheatgrass ramets that form exceptions to this general pattern (see Fig. 2.8). These curves suggest that severe defoliation of western wheatgrass increases the life span of its ramets, a phenomenon that was also reported by Jewiss (1966) for

Festuca pratensis. Initially, the mortality patterns of protected and grazed ramets did not differ (Fig. 2.8a), which concurs with the fact that western wheatgrass was hardly grazed during the first year. Due to reduced availability of the more palatable intermediate wheatgrass and crested wheatgrass in the paddock and, possibly, the change to more experienced animals, utilization of western wheatgrass in the following three grazing seasons reached levels comparable to those of intermediate wheatgrass. [For a more detailed discussion of forage utilization, see Chapter III.] From that time onwards, survivorship of grazed ramets closely resembled the pattern exhibited by ramets that were clipped following grazing.

As the present study progressed, an increasing proportion of western wheatgrass ramets remained small and kept their apical meristem below ground level. This was at first evident in the defoliated treatments but became apparent later in plots that were protected from grazing. Defoliation combined with unfavorable growing conditions may have prevented the apical meristem of many ramets from receiving the photoperiodic stimulus to initiate the transition to the reproductive mode (Jameson 1963, Dahl and Hyder 1977) or allowed insufficient energy substrate to start internode elongation (Hyder 1972). Menke and Trlica (1981) observed that while most western wheatgrass plants in their study remained vegetative during a dry year, many became reproductive a year later when soil moisture conditions returned to normal. Enevoldsen and Lewis (1978) showed that the degree of stem elongation in western wheatgrass was a function of growing conditions and, possibly, defoliation. In their study, heights of apices were markedly reduced on poorer range sites with a history of severe grazing. These authors did not speculate on whether this behavior of western wheatgrass was a phenotypic response to 22 years of heavy grazing or represented a change in genotypes.

Our data indicate that western wheatgrass is capable of prompt plastic adjustments to changes in its environment by reducing the size of its shoots and controlling the elevation of growing points. These observations agree with the conclusion of many studies that western wheatgrass is not very tolerant of severe defoliation when plant vigor, non-structural carbohydrate levels, and biomass production are used as criteria (Holscher 1945, Branson 1956, Everson 1966, Buwai and Trlica 1977, Santos and Trlica 1978, Polley and Detling 1989). But at the same time, these adjustments give western wheatgrass a measure of grazing resistance and reduce ramet mortality as a result of monocarpic flowering, defoliation, and climatic stress. Our study, however, was too short to conclude that density of western wheatgrass ramets had already reached a new equilibrium.

Continued defoliation of this species conceivably could lead to further deterioration.

Western wheatgrass grows in distinct patches within the intermediate wheatgrass sward, and we did not expect the influence of western wheatgrass on the growth of intermediate wheatgrass to extend far beyond the edges of these patches. However, a greater influence was evident, as demonstrated by the positive effect of clipping of western wheatgrass ramets on the survival and recruitment of intermediate wheatgrass tillers that were approximately 1.50 m removed from the interface of the two species. Belowground proliferation of western wheatgrass probably made it a strong competitor for soil water and nutrients, even to intermediate wheatgrass modules which were far removed. At our study site, intermediate wheatgrass had a history of heavy grazing whereas western wheatgrass in the three years prior to the start of this study had hardly been defoliated (B.E. Norton, personal observations). Previous experiments investigating the effects of defoliation indicated that biomass production of western wheatgrass was more negatively affected belowground than aboveground (Branson 1956, Everson 1966, Santos and Trlica 1978, Polley and Detling 1988, 1989). Thus, the interaction between the two species under grazing probably had a distinct asymmetric character, at least until 1989 when animals consumed western wheatgrass to a degree comparable to that of intermediate wheatgrass. When western wheatgrass was clipped following grazing, grazed intermediate wheatgrass ramets displayed levels of recruitment and patterns of mortality that did not differ greatly from those of non-defoliated ramets. It seems unlikely that a high degree of physiological integration within intermediate wheatgrass clones could have contributed to the extension of the competitive influence of western wheatgrass as a result of resource sharing between stressed and less stressed ramets within clones. Intermediate wheatgrass rhizomes in a sward are short and determinate and do not appear to be physiologically functional beyond one year, although they may be physically intact much longer (G.B. Bartels, personal observations).

The basic patterns of tiller birth and death in intermediate wheatgrass and western wheatgrass are similar to those described for several other species (e.g., Lamp 1952, Langer et al. 1964, Robson 1968), but they are modified substantially by climatic influences. In contrast to Langer (1956) with Phleum pratense, Robson (1968) with Festuca arundinacea, Huiskes and Harper (1979) with Ammophila arenaria, and Noble et al. (1979) with Carex arenaria, we found no synchrony of tiller death and birth in either species. In both species, recruitment occurred during fall and winter with relatively little tiller formation in spring, while mortality of tillers and shoots occurred throughout the year with distinct peaks in summer. Langer (1956), Robson (1968), Huiskes and Harper (1979), and Noble et al. (1979) found that high tiller mortality coincided with the period of maximum growth in late spring or early summer. This period of high ramet mortality coincided with, or was preceded by, strong recruitment of new tillers. This synchrony of mortality and birth is usually assumed to be the result of density-dependent mortality of older ramets due to the birth of new tillers. This density-dependent process is purportedly responsible for the relative constancy of ramet numbers through time despite considerable turnover (Sarukhan and Harper 1973, Huiskes and Harper 1979, Noble et al. 1979).

These explanations were challenged by Cook (1983, 1985) on the grounds that individual ramets are not necessarily independent. In addition, it is unlikely that intraclonal competition between established ramets and young developing ramets results in the death of established ramets. Ong (1978), Ong et al. (1978), and Colvill and Marshall (1984) showed that young tillers are more likely to die during the period of maximum growth in grass swards than older tillers. After flowering, however, young developing ramets may be supported by carbohydrates stored in the bases of senescing tillers (Colvill and Marshall 1984).

Our results with intermediate wheatgrass, in the dry years especially, confirm Cook's (1983) interpretation of the reported synchrony of ramet death and birth in temperate climates, viz. the emergence of a new generation of ramets coinciding with the genetically programmed senescence and death of parent tillers. In our study, peaks in mortality usually preceded those in recruitment. Regulation of population size in our study was based on the replacement of dying tillers by new ones, the degree of which apparently depended primarily on the time elapsed between the senescence of parent tillers and the re-occurrence of favorable growing conditions in late summer or fall. Death may have been partly density-dependent as ramets of either the same or a different clone, or clonal fraction, competed for water during late spring. This resulted in earlier deaths and probably affected the scale of recruitment.

Density-dependent ramet mortality is an important component of total deaths during the period of maximum growth in temperate climates where grasses have fully developed canopies and smaller tillers die because of self-shading or other stresses (Langer et al. 1964, Kays and Harper 1974, Ong 1978). The sward structure in our study was such that light probably was never a limiting factor. Contrary to our expectations, we were unable to show significant differences between the survival patterns of fall-produced ramets of intermediate wheatgrass that had survived the winter and ramets originating in April and May. Because our plots were small, the likelihood of all ramets in a plot belonging to the same clone is rather large. Thus, little intraclonal competition for limited resources, particularly water, probably occurred between different-aged ramets. It may be that plants, as far as the physiological integration and resource-sharing of their modules is concerned, exhibit different reactions to light or moisture stress.

CHAPTER III

COMPETITIVE INTERACTIONS BETWEEN *THINOPYRUM INTERMEDIUM* AND *PASCOPYRUM SMITHII* UNDER SHORT-DURATION GRAZING

Abstract. The objective of this four-year field study in central Utah was to investigate how competitive interactions between intermediate wheatgrass (*Thinopyrum intermedium*) and western wheatgrass (*Pascopyrum smithii*) are influenced by short-duration grazing. The basic patterns of tiller dynamics in these two species in response to competitive interactions, with and without accompanying defoliation, were investigated. Short-duration grazing had no significant effects on the annual recruitment of new ramets in either intermediate wheatgrass or western wheatgrass. Competition, however, decreased total recruitment in intermediate wheatgrass and increased that in western wheatgrass compared to monospecific stands. Competition also affected the mortality risk of ramets, but the response differed depending on defoliation regime. When intermediate wheatgrass was defoliated, the longevity of its ramets was significantly reduced when in competition with western wheatgrass, particularly in the first two years of this four-year study. When protected from grazing, competition with western wheatgrass did not affect the mortality pattern of intermediate wheatgrass ramets. Competition initially had little influence on the mortality risk of

western wheatgrass ramets under defoliation. In the last year, however, competition reduced the longevity of grazed western wheatgrass ramets. These different responses are explained by the recent grazing history of the study site and by differences in forage utilization during the initial phases of this experiment. Because of the impact of competition on ramet survival and recruitment, ramet density of western wheatgrass increased at the interface of the two species while that of intermediate wheatgrass declined, irrespective of defoliation regime. In the dry years of this study western wheatgrass had a competitive advantage over intermediate wheatgrass based on differences in physiological and morphological characteristics as well as genetically determined differences in ramet life histories.

Introduction

Competitive interactions between primary producers play an important role in structuring plant communities (Risser 1969, Harper 1977). The direction and outcome of these interactions are determined by the competitive abilities of the species involved, whereby competitive ability may be viewed as a suite of morphological, phenological, and physiological characteristics. Consequently, competitive ability may fluctuate greatly in response to changes in the plant's biotic and abiotic environment (Fowler 1981, Berendse 1982, Law and Watkinson

1987).

Herbivory can greatly modify the nature of interference among plant species (Crawley 1983). Plants differ markedly in their grazing resistance (Briske 1986). Species that are not as palatable or accessible as others and species which have a greater tolerance to defoliation are less likely to have their competitive ability curtailed as a result of grazing than species without these traits. Defoliation alters competitive relationships between and even within plants. Mueggler (1972) and Archer and Detling (1984) demonstrated that the adverse effects of defoliation on the growth of plants or plant parts can be reduced or even offset by clipping the surrounding vegetation. These results imply that grazing systems in which animals are forced to defoliate less palatable plants may benefit the vigor and productivity of the preferred species.

In the four years prior to this study (1983-1986), it appeared that intermediate wheatgrass was outcompeting western wheatgrass under short-duration grazing (B.E. Norton, personal observations). This was unusual because intermediate wheatgrass was highly preferred by the grazing animals while western wheatgrass was hardly defoliated. We hypothesized that this better performance of intermediate wheatgrass could be due to the greater grazing tolerance of intermediate wheatgrass. In addition, western wheatgrass may experience substantial defoliation at the interface between patches of the two grasses because of the inability of cattle to selectively exclude it from their bites. Several reports have alluded to the poor defoliation tolerance of western wheatgrass (Holscher 1945, Branson 1956, Everson 1966, Buwai and Trlica 1977, Santos and Trlica 1978, Polley and Detling 1989).

An alternative hypothesis is that the performance of intermediate wheatgrass was the result of favorable growing conditions during the first three years in which the short-duration grazing system was implemented and was not related to the grazing system per se. Precipitation in those three years was well above average (see Chapter II). Intermediate wheatgrass is considered less drought tolerant than western wheatgrass (Launchbaugh 1958, Frank 1981, Power 1985, Frank and Karn 1988) but produces more forage than western wheatgrass under favorable growing conditions (Lawrence 1978, Currie and White 1982, Power 1985).

To test the hypothesis that the performance of intermediate wheatgrass was due to the implementation of short-duration grazing, an experiment was designed in which the effects of competition on the tiller dynamics of the two species were examined. This was done both under short-duration grazing and under exclusion of grazing. It was expected that intermediate wheatgrass would exhibit greater production and exclude western wheatgrass from the interface under short-duration grazing but not under protection from grazing.

In the previous chapter the basic tiller dynamics of intermediate wheatgrass and western wheatgrass in monospecific stands were described. How defoliation influenced these dynamics was reported as well. Defoliation was found to affect the mortality risk of western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love) ramets, but it had relatively little influence on that of ramets of intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey). This was explained by differences in the ramet life history of these two species. It was also noted that competitive interactions between the two species may play an important role in governing the tiller dynamics of intermediate wheatgrass particularly. In this chapter, the effects of interspecific competition on the tiller dynamics of intermediate wheatgrass and western wheatgrass are further examined.

The outcome of competitive interactions between two grasses can be measured by the relative changes in ramet density of the two species (e.g., van den Bergh and Elberse 1962). Changes in the abundance of grass species under conditions of interspecific competition are the result of differences in recruitment, mortality, and longevity of both genets and ramets. Rhodes (1970) cites several sources that indicate that tiller production is a very sensitive indicator of competitive stress in grass species. However, we are not aware of studies that have examined the effects of competitive interactions on the risk of ramet mortality in sympatric grasses.

Materials and methods

Site, climatic characteristics, design, and execution of the study are described in Chapter II. In the present chapter, the observations made in the two outermost plots of the transects, representing monospecific stands, were compared to those made in the two plots straddling the visually-estimated interface of the two species (see Appendix A). Data on tiller density and tiller recruitment were analyzed for the two species separately using a split-split plot design with defoliation regimes as the mainplot factor, competition as the subplot factor, and time as the sub-subplot factor (Steel and Torrie 1960). Before subjecting the tiller density data to analysis of variance, they were log-transformed to achieve homoscedasticity.

Based on the tiller life histories described in Chapter II, annual tiller recruitment represented the number of new tillers produced in the period July to June. The annual number of recruits of western wheatgrass, but not of intermediate wheatgrass, was log-transformed before analysis of variance. Forage utilization was estimated as a percentage of standing biomass before the start of the respective grazing period and was arcsin-transformed prior to analysis of variance[1]. Reported means and confidence limits in the tables are values transformed back to their original scales. Survivorship curves were constructed by combining the number of surviving ramets for all four or five replicates in life table form. Differences between survivorship curves resulting from different treatments within the same cohort were assessed using Mantel and Haenszel's chi-square test (Mantel and Haenszel 1959, Lee 1980). This test was only used when group sizes were 30 or larger. Differences in mortality patterns are reported when significant at the five percent level.

Results

Utilization

Except for western wheatgrass in the first year (1987), we were unable to detect significant spatial heterogeneity concerning where animals grazed within the 1.5 m transect. In that first year, however, animals

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[1] The paddock containing this experiment was grazed once for 48 hours in the years 1988-1990. It was grazed twice in 1987, the second time for only 24 hours. The utilization for the first grazing period is reported; we were unable to quantify utilization during the second grazing period due to low forage availability.

grazed significantly more of the western wheatgrass within 25 cm of the visually estimated interface with intermediate wheatgrass. Within this 25 cm, utilization of western wheatgrass was 34 percent compared to an average of 12 percent for the remainder of the western wheatgrass in the transect. This contrast in utilization of western wheatgrass was significant (t_{99}=2.04, p=0.044) and suggests that when intermediate wheatgrass and western wheatgrass intermingle, the heifers were unable to discriminate between the two. In the next three years defoliation of western wheatgrass was more severe and more uniform and reached levels in 1989 and 1990 comparable to those measured for intermediate wheatgrass (Table 3.1).

Table 3.1. Utilization (%) of intermediate wheatgrass and western wheatgrass under short-duration grazing in four successive years.

Year	IWG	WWG	Difference
	%	%	
1987	36 a	15 a	*
1988	47 b	37 b	*
1989	46 b	55 d	ns
1990	52 b	48 c	ns

Means within a column followed by the same letter did not differ significantly at the 0.05 level. * = difference between species within a year, significant at the 0.05 level (Fisher's protected LSD).

Recruitment of ramets

Annual recruitment of intermediate wheatgrass ramets was affected by year as well as by competition with western wheatgrass, but defoliation regime had very little influence on the level of recruitment (Fig. 3.1). Recruitment was higher in monospecific stands than at the interface, and the effect of competition on recruitment became more pronounced through time (interaction between time and competition $F_{2,36}=3.53$, $p=0.040$) (Table 3.2).

Table 3.2. Annual recruitment of intermediate wheatgrass ramets per 0.0625 m^2 in three seasons as influenced by the presence of western wheatgrass.

Years	Interface	Monospecific	Difference
1987-1988	80.2 a	86.5 a	ns
1988-1989	41.9 b	57.2 b	ns
1989-1990	35.2 c	64.2 b	*

Means within a column followed by the same letter did not differ significantly at the 0.05 level. * = difference between locations within a year, significant at the 0.05 level (Fisher's protected LSD).

Recruitment was much greater in the first than in the second year when its level dropped nearly 40 percent on average. Annual tiller recruitment stabilized at that lower level, particularly in monospecific stands. The effects of competition on the recruitment of intermediate wheatgrass tillers were identical for the three defoliation regimes. No significant interaction was found between defoliation regime and competition ($F_{2,9}=1.03$, $p=0.396$).

Recruitment of ramets in western wheatgrass also was not significantly affected by defoliation treatment, but

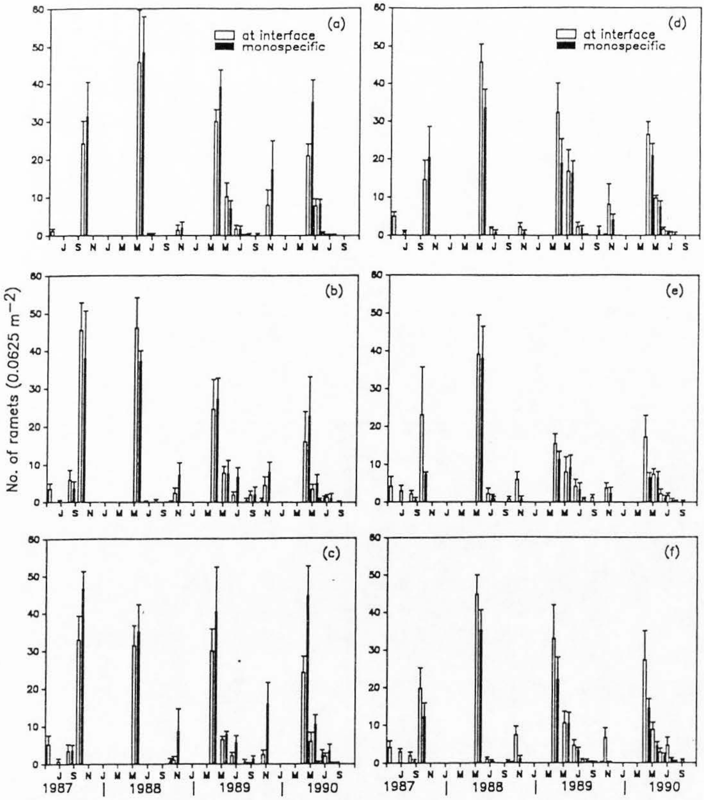

Fig 3.1. Recruitment of ramets over a three-year period. Each bar represents the mean number (+ 1 SE) of recruits per 0.0625 m^2 at a particular census. Open bars represent recruitment at the interface, filled bars represent recruitment in monospecific stands. (a), (b), (c) are intermediate wheatgrass, (d), (e), (f) are western wheatgrass control, grazed and clipped, respectively. (n=5, except for intermediate wheatgrass, clipped and western wheatgrass, grazed, where n=4).

both competition and year significantly affected recruitment. In contrast to intermediate wheatgrass, recruitment of western wheatgrass ramets was significantly higher at the interface than in monospecific stands ($F_{1,9}$=21.51, p=0.001) (Table 3.3).

Table 3.3. Effect of competition on annual ramet recruitment per 0.0625 m^2 in western wheatgrass (geometric means and 95% confidence intervals).

Location	No. of new ramets
Interface	46.1 (52.4 - 40.4)
Monospecific	31.4 (35.9 - 27.5)

This effect of competition on the recruitment of western wheatgrass ramets was unaffected by both defoliation regime (interaction $F_{2,9}$=1.06, p=0.386) and time (interaction $F_{2,36}$=1.04, p=0.362). Annual recruitment of western wheatgrass ramets was significantly lower in the second year than in the first year and was further reduced in the third year (Table 3.4).

Table 3.4. Annual recruitment of western wheatgrass ramets per 0.0625 m^2 in three years, July-June (geometric means and 95% confidence intervals).

Years	No. of new ramets
1987-1988	53.4 (60.0 - 47.4)
1988-1989	35.8 (40.3 - 31.8)
1989-1990	28.8 (32.5 - 25.6)

Proportional recruitment

No significant differences were detected in the proportional recruitment (new ramets/live ramets present) between ramet populations of intermediate wheatgrass and western wheatgrass growing at the interface and those in monospecific stands.

Ramet survival

Competition with western wheatgrass at the interface did not affect the mortality pattern of intermediate wheatgrass ramets when protected from grazing. In none of the seven major cohorts was there a change in the mortality risk of intermediate wheatgrass tillers as a result of competition. Conversely, in protected western wheatgrass the chance of ramet survival was significantly higher ($p<0.050$) under competition than in monospecific stands in all but the last (05/01/90) of the six major cohorts of this species (Fig. 3.2).

When plots were grazed, survival of intermediate wheatgrass ramets was significantly reduced by competition with western wheatgrass in the first two years of this experiment. In three (09/26/87 ($p<0.001$), 05/12/88 ($p=0.006$), 05/06/89 ($p=0.017$)) of the first four major cohorts the risk of mortality was significantly higher at the interface than in monospecific stands; in the last three cohorts of this experiment competition did not significantly affect mortality pattern. The effect of

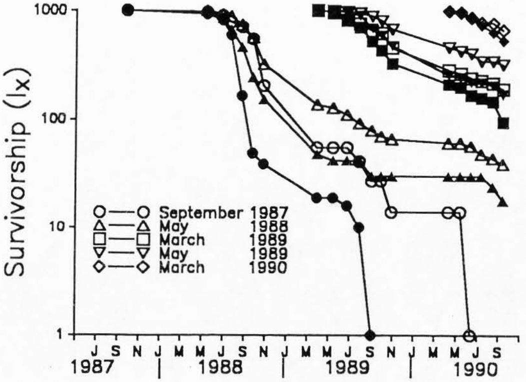

Fig. 3.2. The effect of interspecific competition on the survivorship of five major cohorts of western wheatgrass ramets that were protected from grazing. Open symbols represent ramets at the interface, filled symbols represent ramets in monospecific stands.

competition on survival of western wheatgrass ramets under grazing was only minor; ramets of just one cohort (05/12/88) showed greater longevity (p=0.045) when competing with intermediate wheatgrass.

When western wheatgrass ramets were clipped following grazing, survival of intermediate wheatgrass ramets was still significantly reduced by competition in three (05/12/88 (p=0.011), 05/06/89 (p=0.003), 10/18/89 (p=0.014)) of the seven major cohorts. Competition did not affect the survival rate of clipped western wheatgrass ramets until the last year. The probability of ramet survival was significantly reduced by competition with intermediate wheatgrass in the last two major cohorts (03/30/90 (p=0.005) and 05/01/90 (p=0.007)).

In monospecific stands, the survival pattern of intermediate wheatgrass tillers in the clipped treatment was the same or somewhat better than that of ungrazed tillers. This was just the opposite under competition from western wheatgrass when the mortality risk of intermediate wheatgrass tillers was less when they were protected from grazing in the initial population (p<0.001) and in two further cohorts (10/18/89 (p=0.002) and 05/01/90 (p=0.007). In monospecific stands, the average life span of grazed tillers of intermediate wheatgrass was significantly increased when grazing was followed by the clipping of western wheatgrass ramets. This was evident in the initial ramet population and in five additional cohorts (see Chapter II). Under direct competition with western wheatgrass, the beneficial effect of the clipping of western wheatgrass on the survival of grazed intermediate wheatgrass tillers was still present but less pronounced. It was found in the first three major cohorts, those of 09/26/87 (p=0.006), 05/12/88 (p=0.001), and 03/22/89 (p=0.027).

In monospecific stands of western wheatgrass the mortality risk of protected ramets was frequently higher than that of grazed or clipped ramets. Under competition with intermediate wheatgrass, however, a lower risk of mortality was observed for the protected rather than the defoliated ramets. This lower mortality risk for protected ramets was found in the initial population and in the last three major cohorts of this study. This may signify a loss of vigor of western wheatgrass when severely and uniformly defoliated under competition with intermediate wheatgrass. Under competition, little difference was observed between the survival patterns of grazed and clipped western wheatgrass ramets; only the clipped ramets belonging to the initial population exhibited lower mortality rates than the grazed ramets (p<0.001).

Ramet density

Because of its effects on the recruitment and survival of ramets, competition had a strong negative impact on the tiller density of intermediate wheatgrass ($F_{1,9}$=11.54, p=0.008) and a less pronounced but positive effect on ramet density of western wheatgrass ($F_{1,9}$=3.53, p=0.093) (Fig. 3.3). These effects of competition on the tiller density of intermediate wheatgrass and western wheatgrass were similar for all three defoliation treatments (interaction between defoliation and competition $F_{2,9}$=0.42, p=0.669 and $F_{2,9}$=0.63, p=0.554 for intermediate wheatgrass and western wheatgrass, respectively). Defoliation regime affected the tiller density in intermediate wheatgrass ($F_{2,6}$=6.24, p=0.034) but did not affect that of western wheatgrass ($F_{2,6}$=1.10, p=0.393).

Three years after the July 1987 census, ramet density of intermediate wheatgrass not competing with western wheatgrass declined only when grazed (Fig. 3.3). In the presence of western wheatgrass, however, tiller density after three years was lower under the two defoliation regimes and under protection from grazing. The extent of this decline was almost identical for the grazed and clipped treatments (approximately 65 percent) but tiller density decreased 43 percent in intermediate wheatgrass protected from grazing. In monospecific stands tiller density of intermediate wheatgrass in the protected and clipped plots somewhat recovered in the final year, but this did not occur when in competition with western

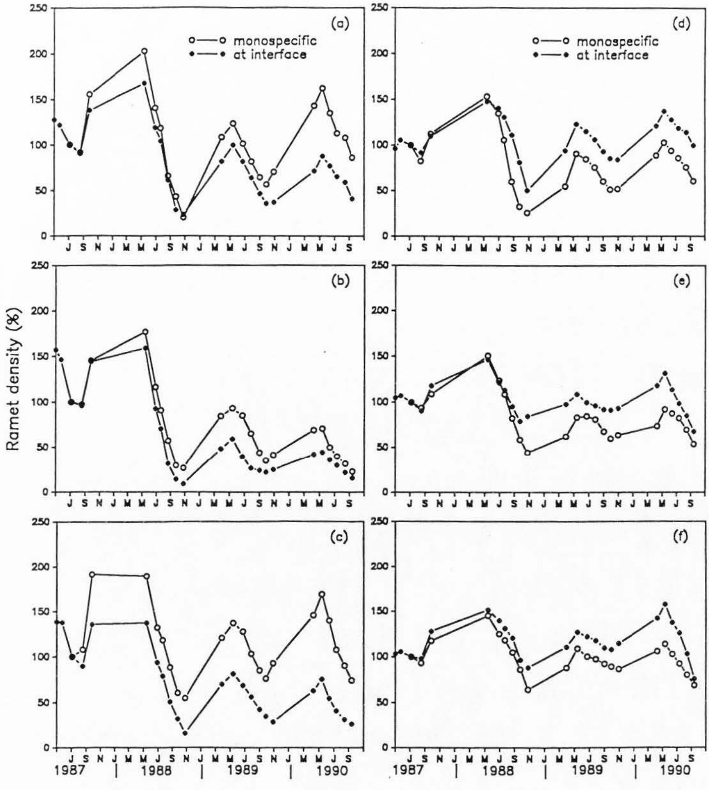

Fig. 3.3. Ramet density over a three-year period. Values are relative to the live ramet density of the July 1987 census (=100). (a), (b), (c) are intermediate wheatgrass, (d), (e), (f) are western wheatgrass control, grazed and clipped, respectively. (n=5, except for intermediate wheatgrass clipped and western wheatgrass grazed where n=4).

wheatgrass.

Comparison of the tiller ratios (intermediate wheatgrass:western wheatgrass) at the interface with the ratios of the number of tillers in the respective monospecific stands demonstrates the effects of competition over the three-year study period (Fig. 3.4). The effects of competition were essentially the same for the three defoliation treatments, but when plants were protected from grazing the tiller ratio widened significantly (t_8=2.055, p=0.074) from 0.94:1 in July 1987 to 1.22:1 exactly three years later when there was no competition between the two species. In the same period the tiller ratio narrowed from 0.86:1 to 0.46:1 when the two species were competing. Consequently, although the two ratios did not differ significantly in July 1987, they differed greatly in July 1990 (t_{10}=5.622, p<0.001).

Similar effects were observed when western wheatgrass was clipped following grazing (Fig. 3.4c). Three years after the initial census of July 1987, the tiller ratio was essentially unchanged when the two species were not competing, but declined from 0.91:1 to 0.27:1 during the same period when under competition (t_6=4.779, p=0.003). The two ratios differed significantly in July 1990 (t_9=6.894, p<0.001).

When the transects were grazed, both tiller ratios declined (Fig. 3.4b). Although the decline was somewhat

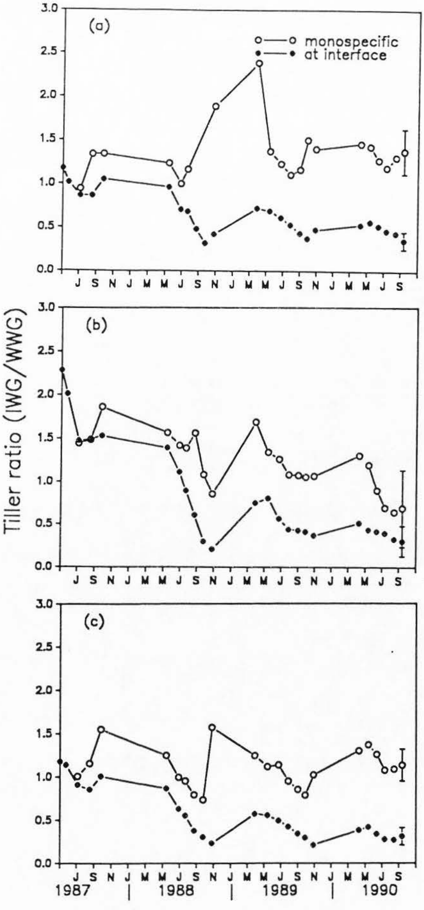

Fig. 3.4. Ratio (IWG/WWG) of the number of live ramets growing at the interface and in monospecific stands (± 1 SE) over a three-year period. (a) protected (n=5), (b) grazed (n=4), (c) clipped (n=4).

steeper in the plots at the interface, the difference between the two tiller ratios at the end of the study was not statistically significant.

Reproductive efforts

Reproductive performance of both species was recorded during the last three years of this study but not in 1987.

Whereas intermediate wheatgrass produced some inflorescences in monospecific stands during these three years (see Chapter II), no inflorescences were produced when in competition with western wheatgrass, irrespective of defoliation regime.

Western wheatgrass did not exsert inflorescences in monospecific stands (see Chapter II) but produced two spikes at the interface with intermediate wheatgrass in 1989 in the grazed treatment and another two in the same defoliation treatment in 1990. This represented only a small fraction of all ramets present under that treatment during peak tiller density in May of the respective years; only 0.8 percent of these ramets became reproductive in 1989 and 0.5 percent in 1990. At the time of anthesis in 1989 the two reproductive ramets were 7 and 13 months old, while in 1990 they were 15 and 26 months old. None of the inflorescences produced seed.

Discussion

The data on utilization in 1987 confirmed earlier observations that western wheatgrass is not preferred by grazing animals; but this low grazing pressure did not continue. Utilization of both species increased significantly in the three years that followed. This may be attributed to a combination of less available forage in those three years and a grazing period that was fixed at 48 hours throughout the study. It is perhaps also significant that in the last three years more mature and experienced animals were used than the yearling heifers of 1987. The mature cows grazed with more intensity, were less averse to consumption of western wheatgrass, and did not seem to anticipate the changes to fresh paddocks in the short-duration grazing cell as well as the younger animals. Our initial assumption that western wheatgrass might be more severely defoliated at the interface was confirmed in 1987 but, possibly because of the reasons above, not in the next three years. The more severe defoliation of western wheatgrass at the interface in the first year apparently did not seriously affect its tiller dynamics, nor did it hamper its competitive ability with intermediate wheatgrass during the following years.

Nondefoliated ramets have the ability to share resources with defoliated ramets of the same clone (Nyahoza et al. 1973, 1974, Rogan and Smith 1974).

Physiological integration among ramets of western wheatgrass whereby an abundance of undefoliated or only marginally defoliated ramets in the hinterland supported relatively few defoliated ramets at the leading edge of the clone may explain the absence of a clear demographic effect of defoliation on these ramets.

Our study showed that competition may markedly affect a plant's response to defoliation as reported by Mueggler (1972). While in monospecific stands defoliated intermediate wheatgrass had tiller densities equal to those of protected intermediate wheatgrass, tiller densities were reduced under interspecific competition with western wheatgrass. This was especially the case when defoliation pressures were not equal, as in the grazed treatments where intermediate wheatgrass experienced heavier grazing pressure.

If ramet density three years after the start of this study is used as a criterion, intermediate wheatgrass apparently performed as well as western wheatgrass in monospecific stands when plants were protected from grazing and when the two species were defoliated nearly equally (Figs. 3.4a and 3.4c). Tiller density of the two species changed, though not in synchrony, to approximately the same extent when not competing. At the interface, however, where the two species probably were competing for limited resources, western wheatgrass performed much better than intermediate wheatgrass, irrespective of the defoliation regime (Figs. 3.3 and 3.4). Disregarding seasonal fluctuations, ramet density of western wheatgrass at the interface remained fairly constant under all three defoliation regimes while that of intermediate wheatgrass showed a steady decline (Fig. 3.3).

In the grazed and clipped treatments, the poorer performance of intermediate wheatgrass at the interface was the result of both a reduction in ramet life span, particularly in the first two years, and lower recruitment. Under protection from grazing, however, only the recruitment of new ramets was reduced; the risk of mortality of intermediate wheatgrass ramets was not significantly affected by the presence of western wheatgrass. In contrast, competition with intermediate wheatgrass hardly affected ramet longevity in western wheatgrass when the plants were defoliated, except for a higher mortality risk in the last two cohorts. However, under protection from grazing the average life span of ramets was greater at the interface than in monospecific stands (Fig. 3.2).

These differences in ramet mortality risk could be related to resource availability. The acquisition of resources, particularly water, by western wheatgrass may have been less difficult at the interface than in monospecific stands because of its deep root system

(Appendix B) and its "guerilla" type clonal morphology (Fitter 1986, Hutchings and Bradbury 1986). This may have postponed ramet death due to desiccation. In this study we followed ramets as cohorts rather than as individuals and this precluded the determination of the probable cause of death (e.g., removal of apex, desiccation, frost, monocarpic flowering, pests, or diseases) for each ramet individually.

The differences in ramet mortality rates at the interface and in monospecific stands could also be a consequence of phasic clonal development and expansion in western wheatgrass. Data for the rhizomatous sedge _Carex arenaria_ indicated that the risk of tiller mortality tended to be higher in older sections of a clone, farther removed from its leading edge. A higher respiratory load as a consequence of the accumulation of older rhizomes may have been one possible reason for the higher mortality risk of ramets in these older clonal segments (Noble et al. 1979). The disintegration of clonal connections among individual ramets or ramet groups may be another explanation. Once these connections decay, genetically identical individuals will compete with each other without any regulatory mechanisms that clonal integration could provide. Under such circumstances a higher mortality risk for ramets would not be unexpected.

Through the years, recruitment of new ramets at the interface declined in both species but this decline was not as steep in western wheatgrass as compared to intermediate wheatgrass. Because ramets of intermediate wheatgrass are basically annual modules, tiller density of this species was, consequently, greatly reduced. Western wheatgrass ramets, on the other hand, apparently had an indeterminate life span (see Chapter II). Consequently, this species does not have the same requirement as intermediate wheatgrass to replace every tiller each year in order to maintain tiller density. Decreasing annual tiller recruitment in western wheatgrass during this study may be as much a reflection of reduced ramet mortality as it was a consequence of less favorable growing conditions. Whatever the cause, lower ramet recruitment in western wheatgrass during this study coincided with lower ramet mortality, resulting in only minor deviations from initial tiller densities. This suggests that western wheatgrass, by virtue of clonal integration, is capable of maintaining tiller densities within narrow bounds by coordinating ramet death and recruitment through internal hormonal regulation and redistribution of metabolites (Cook 1983, 1985). The apparent ability to adjust the life span of its ramets in response to factors such as defoliation and availability of resources (see Chapter II) greatly facilitates the maintenance of ramet densities.

Gross recruitment (sensu Thomas 1980) of western wheatgrass ramets was higher at the interface than in monospecific stands for all three defoliation treatments, despite the lack of significant differences between proportional recruitment at the interface with intermediate wheatgrass and in monospecific stands. Recruitment at the interface was higher because, even though very few statistically significant differences were found in cohort survivorship under defoliation, ramets growing under competition with intermediate wheatgrass survived somewhat better, up to the last year of this experiment. Small but consistent differences in mortality rate and/or proportional recruitment of ramets can result in significant differences in recruitment and, thus, in ramet density after a number of years. Proportional recruitment of western wheatgrass at the interface may have been underestimated. This species has a "guerilla" type clonal structure (L. Clegg, in Harper 1978), a growth form that enables it to quickly invade stands of other species. In this study, it invaded intermediate wheatgrass beyond the two central plots of the transects in which the demographic data were collected.

No significant differences were found between the proportional recruitment of intermediate wheatgrass ramets at the interface and those in monospecific stands. This suggests that the reduced ramet recruitment due to competition with western wheatgrass is not only the result of a negative effect of the presence of western wheatgrass on recruitment proper but also a consequence of earlier death among intermediate wheatgrass ramets growing at the interface as compared to those growing in monospecific stands. Only in the case of intermediate wheatgrass protected from grazing, where no effect of competition on the risk of ramet mortality was detected, did the tendency of a slightly better proportional recruitment in monospecific stands contribute to a greater recruitment in this species when not under competition with western wheatgrass. This lower proportional recruitment at the interface under protection from grazing was due mainly to reduced proportional recruitment among the fall cohorts. In the spring cohorts, proportional recruitment of intermediate wheatgrass ramets at the interface was generally as high as that in monospecific stands. This may suggest that western wheatgrass had little impact on the recruitment of tillers in intermediate wheatgrass when soil moisture was not limiting, such as in spring, but negatively affected the recruitment of intermediate wheatgrass tillers when competition for water was intense, such as in fall.

Survival of intermediate wheatgrass ramets under grazing and clipping was significantly reduced by the presence of western wheatgrass in the first two years of this study but not in the last year. This may have arisen because prior to the initiation of this experiment intermediate wheatgrass had been grazed severely and western wheatgrass had been grazed very little. Thus, in the case of the clipped treatment and, particularly, the grazed treatment, considerable time may have been required to approach conditions which would approximate symmetry of competition between the two grasses. This is supported by the relatively poor performance of western wheatgrass in the last year at the interface under grazing and grazing followed by clipping (see Figs. 3.3e and 3.3f). Severe, uniform defoliation of western wheatgrass over a number of years apparently weakened its ability to compete with intermediate wheatgrass. This is the only indication from this study, that short-duration grazing may have a desirable effect on the plant composition of this particular pasture. Unfortunately, additional time would be required to confirm this reversal in trend. Other studies showed that periodic uniform defoliation is more detrimental to western wheatgrass than identical levels of utilization under continuous grazing (Stroud et al. 1985)

Populations of western wheatgrass and intermediate wheatgrass are generally spatially segregated, occurring in monospecific patches, strongly suggesting a process of competitive exclusion between two species with similar resource demands. Our data indicate that during this study western wheatgrass was the competitive dominant. This does not eliminate the possibility that some form of coexistence between the two species exists because of shifts in the competitive balance due to climatic variability, or that on a longer time scale western wheatgrass is the subordinate species. However, environmental fluctuations alone can not explain coexistence unless these fluctuations are exactly around a mean value where the competitive abilities of the species are equivalent. Functional differences between species are also necessary to explain their coexistence (Braakhekke 1980).

Root systems of different species often intermingle and while it is not fully understood which characteristics of root systems make one species a superior competitor for water and nutrients (Caldwell and Richards 1986), similarities in root distribution enhance the competition for water between sympatric species due to overlap of resource exploration (Veresoglou and Fitter 1984, Franco and Nobel 1990). The somewhat poorer performance of intermediate wheatgrass at the interface under grazing and clipping than in enclosures can probably be attributed to the negative effects that defoliation generally has on root growth and metabolic functions (Crider 1955, Jameson 1963, Milthorpe and Davidson 1966). Reductions in size of the root system may have limited the capacity of intermediate wheatgrass to compete with western wheatgrass for water and nutrients.

Data from two trenches (Appendix B) in areas that had not been grazed for two years indicated that western wheatgrass has more prolific root growth deeper in the soil profile than intermediate wheatgrass. Intermediate wheatgrass, on the other hand, maintains higher root densities in soil layers close to the surface. In environments in which plant growth relies heavily on winter precipitation, species with a large proportion of their root system in contact with deep soil layers very likely have a competitive edge over more shallow-rooted ones, especially when precipitation during the growing season is low.

The contrast in root distribution between these two species (Appendix B) must have given western wheatgrass a competitive advantage over intermediate wheatgrass, particularly in years when spring rains were below normal. The dissimilar history of defoliation of these two grasses during the early stages of this study may have contributed to the competitive dominance of western wheatgrass. The competitive advantage of western wheatgrass in this study was lowest under protection from grazing. This may be related to intermediate wheatgrass having had the opportunity to restore at least partially the volume of its belowground biomass.

The results of this study do not support our hypothesis that intermediate wheatgrass will outcompete western wheatgrass under short-duration grazing. In fact, it appears that this grazing system, or defoliation in general, has had relatively little influence on the competitive balance between the two species, at least in the three years of this study. Under the two defoliation regimes and under protection from grazing, western wheatgrass eliminated intermediate wheatgrass from the interface. The effect of competition may have been mediated somewhat by defoliation because the decline in tiller density of intermediate wheatgrass at the interface was slightly less steep when plants were protected from grazing.

The overriding factor influencing the botanical composition of the pasture during our study was the droughty conditions. These dry conditions have affected both species to similar degrees in monospecific stands. However, at the interface western wheatgrass obtained a competitive edge which was not unexpected because of known or observed physiological and morphological differences between the two species (Risser 1969, Gaudet and Keddy 1988). These characteristics include leaf rolling (Latas and Nicholson 1976) and glaucousness in western wheatgrass, more rapid conditioning to drought in western wheatgrass than in intermediate wheatgrass (Frank 1981), greater allocation of photosynthates to growth and maintenance of the root system in western wheatgrass (Power 1985), extraction of more water from deeper soil depths (Frank et al. 1985), and deeper root penetration in western wheatgrass (Appendix B). This study indicates that besides these physiological and morphological differences between the two species, dissimilar, genetically programmed tiller dynamics also may have contributed to the superior competitive ability of western wheatgrass.

CHAPTER IV

COMPETITION BETWEEN THINOPYRUM INTERMEDIUM AND PASCOPYRUM SMITHII AS AFFECTED BY SHORT-DURATION GRAZING AND SUPPLEMENTAL WATER

Abstract. The effects of grazing, supplemental water, and competition on the tiller dynamics and aboveground biomass production of intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey) and western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love) were examined in a short-duration grazing system in central Utah. Compared to competition and especially irrigation, grazing had little effect on the phytomass production of intermediate wheatgrass, but stimulated that of western wheatgrass. Grazing decreased the average life span of intermediate wheatgrass ramets but had comparatively little effect on that of western wheatgrass up to the last major cohort of this study. The probability of survival of ramets of this cohort was significantly reduced by grazing, irrespective of moisture availability and interference from intermediate wheatgrass. Grazing stimulated recruitment of ramets in both species and markedly changed the pattern of tiller recruitment in intermediate wheatgrass. Supplemental water increased forage production in both species, the result of improved tillering and greater ramet size. The probability of ramet survival increased as a result of irrigation in intermediate wheatgrass but not in western wheatgrass. In the latter species, improved growing conditions due to irrigation led to higher ramet mortality rates in winter. Phytomass production, tiller recruitment, and number of fertile tillers increased for intermediate wheatgrass when western wheatgrass was removed; this treatment had little effect on ramet survival. Western wheatgrass, on the other hand, responded to the removal of associated intermediate wheatgrass tillers with improved phytomass production only when grazed. It was concluded that defoliation of western wheatgrass will gradually lead to considerable niche overlap between the two species because of reduction in root penetration at depth for western wheatgrass.

Introduction

Plant competition in arid and semi-arid regions is thought by some not to be very important (Grime 1977). In a review of pertinent literature, however, Fowler (1986a:104) demonstrated that competition among plants does occur in these habitats and that it is often "strong enough to be readily detected." In the previous chapter we reported that during the dry years 1987 to 1990 western wheatgrass (Pascopyrum smithii (Rhydb.) A. Love) was competitively superior to intermediate wheatgrass (Thinopyrum intermedium (Host) Barkw. & D.R. Dewey) under short-duration grazing and when protected from grazing.

This contrasted with earlier observations in which western wheatgrass was apparently the competitive subordinate in a short-duration grazing system. These conflicting results are believed due, at least partially, to the greatly dissimilar weather patterns that occurred during the years in which the respective observations were made. However, experimental proof for this assumption is lacking.

The presence of competition between individuals is suggested when a negative relationship can be established between the performance of individuals and the abundance of their neighbors (Keddy 1989). Evidence that two or more plants of the same or different species influence each other's activities in the field can be obtained by the selective removal of neighbors and then measuring the performance of the remaining plants. A large number of these experiments are reported in the literature using many different performance traits to assess the effects of removal on the remaining plants. These include: counts of individuals (Sagar and Harper 1961), standing crop biomass (Pinder 1975), a combination of standing crop biomass and number of individuals (Putwain and Harper 1970), cover (Fowler 1981) and cover and biomass (Allen and Forman 1976).

These removal experiments, however, can only demonstrate the existence of mutual interference; they are unable to provide insights into its exact nature and the underlying mechanisms (Harper 1977) unless, perhaps, when they are accompanied by measurements of the physiological status of plants (e.g., Fonteyn and Mahall 1981, Ehleringer 1984, Fetcher 1985, Manning and Barbour 1988) and morphological parameters (Tilman 1987).

The results of the previous chapter were acquired using a largely phenomenological approach to the study of competition. On the assumption that competition in arid and semi-arid regions is primarily for water (Walter 1973), a more mechanistic approach would require the use of different levels of water availability (Tilman 1987).

The relationship between the performance of target individuals and the abundance of neighbors may vary among habitats (Keddy 1989). Both defoliation and environmental fluctuations affect the competitive ability of grassland species (Mueggler 1972, Fowler 1981, 1982, Archer and Detling 1984, Archer and Tieszen 1986), but little is known about the relative importance of herbivory and competition in shaping plant communities (Parker and Salzman 1985). The significance of defoliation in general and grazing systems in particular in affecting species composition of grazing lands has been questioned recently, particularly for areas characterized by great environmental variability (Norton 1978, Walker et al. 1986, Walker 1988).

With a few notable exceptions such as the studies by Robberecht et al.(1983), Fetcher (1985), and Nobel and Franco (1986) relatively little is known about how changes in biomass production as a result of alterations in a plant's competitive environment are expressions of modifications of a plant's morphological traits. How the removal of supposedly competing species affects the dynamics of tiller recruitment and tiller death in the remaining species has, as far as we were able to ascertain, not been examined.

In this chapter we report the results of a study in which the effects of defoliation (short-duration grazing) and water on the competitive balance between intermediate wheatgrass and western wheatgrass were investigated. The response of the two species to changes in interspecific competition was measured in terms of aboveground biomass production, ramet recruitment and survival, and reproductive efforts. We hypothesized that supplemental water would enhance the performance of both species, especially that of intermediate wheatgrass. We expected intermediate wheatgrass to outcompete western wheatgrass under irrigation in protected and, particularly, in grazed plots but, based on previous information (see Chapter III), not under drier conditions. We further postulated that the removal of western wheatgrass in the competitive environment would result in an improvement of all of the selected performance traits in intermediate wheatgrass and vice versa. Finally, the question of whether intensity of competition is negatively or positively correlated with resource level has long been debated (cf. Welden and Slauson 1986). We hoped that our data would enable us to answer this question in the special case of two rhizomatous grass species in a semi-arid grassland in central Utah.

Materials and methods

Site and climatic characteristics for this study, which started in June 1988 and lasted until September 1990, are described in Chapter II. The present study was conducted in paddock 9 of the short-duration grazing cell. Soil type of the experimental area was the same as in the study reported on in Chapters II and III: a coarse-loamy, mixed (calcareous), mesic, Torrifluventic Haploxeroll (Jensen 1983).

The paddock in which the experiment was located was grazed three times for 48 hours on each occasion: 25-27 June 1988, 19-21 May 1989, and 23-25 May 1990. Grazing was done with 60 cow-calf pairs plus three or four bulls. This resulted in a stocking density of approximately 7.5 AU (animal unit) per ha.

Three plots (25 x 50 cm) were established perpendicular to and across the interface between apparently homogeneous patches of intermediate wheatgrass and western wheatgrass. From one of these plots intermediate wheatgrass shoots were removed and from another western wheatgrass shoots were removed, using the herbicide Roundup (glyphosate). The remaining plot was the control where the two species were allowed to grow together. Roundup was applied to individual shoots and tillers with a small brush to make certain that only the intended sympatric species was affected. The total plot area treated in this way was 75 x 100 cm, the experimental plot and a 25 cm border. Because of the dry conditions during the summer and fall of 1988 which precluded active growth of the grasses, the application of Roundup was postponed until early April 1989. [It was repeated a year later in those plots where the removed species tried to re-establish itself.]

In these three interface plots, births and deaths of ramets were recorded by marking newly emerged tillers with color-coded wire loops at approximately monthly intervals, except during the winter, and following their fates until death. Aboveground biomass in these plots was estimated before and after grazing in 1989 and 1990 using a non-destructive double sampling technique (Tadmor et al. 1975). In the vicinity of each triplet of interface plots, two additional plots were randomly selected; one contained a pure stand of intermediate wheatgrass, the other a stand of western wheatgrass. In these two additional pure-stand plots only estimates of forage biomass were made.

The experiment had five blocks (replicates). Each block consisted of four "clusters," each cluster containing a quintet of plots as described above (three interface plots plus two pure-stand plots, see Appendix C). Within each block one cluster was grazed and irrigated, a second one was grazed but remained unirrigated, a third was protected from grazing and was given additional water, while the fourth cluster was also protected from grazing but received only natural precipitation.

Irrigation was used to simulate the wettest year on record (1983) which had an annual total of 577 mm. This is 55 percent higher than the long-term average for this site. The volume of supplemental water was based on the difference between the actually received monthly precipitation and the amount of precipitation that the month in question would have received if the total were to be 577 mm and the rainfall distribution reflected the long-term monthly precipitation data for this site. These monthly deficits were erased by applying water once every two weeks. The deficit accumulated through winter was added by irrigation in April using more frequent applications.

Irrigation was carried out with four lawn sprinklers connected to a pump (Honda WB20X) mounted on a truck with a water tank. The system was tested before the start of irrigation in September 1988 and again a year later after replacement of the pump. Application rates were 0.34 mm per minute in 1988 and 0.37 mm per minute in 1989. Distribution uniformity (DU) was calculated using the method of Merriam and Keller (1978) and was approximately 74 percent in both years.

For each species separately, the design of this experiment was a randomized block, analyzed as a split-split plot design with defoliation and irrigation as mainplot factors, competition as the subplot factor and time as the sub-subplot factor (Steel and Torrie 1960). Before analysis of variance, the estimated percentage utilization data were arcsin-transformed and estimated biomass data were log-transformed. Reported means in the tables are values transformed back to their original scales. Survivorship curves were constructed by combining the number of surviving ramets for the five replicates in life table form. Differences in survival distributions resulting from different treatments within the same cohort were assessed using Mantel and Haenszel's chi-square test (Mantel and Haenszel 1959, Lee 1980). Differences in these distributions that were significant at the ten percent level are reported.

Results

Forage utilization

Removal of the sympatric species did not affect the utilization of intermediate wheatgrass or western wheatgrass ($F_{2,32}=1.45$, $p=0.250$). The interaction between irrigation, species and year was significant ($F_{1,48}=5.06$, $p=0.029$). Cattle removed a greater portion of the available forage in 1990 than in 1989, except in the case of unirrigated western wheatgrass (Table 4.1). More than a year of supplemental water apparently improved the acceptability of western wheatgrass as a forage. While in 1989 the utilization of irrigated intermediate wheatgrass was much higher than that of western wheatgrass, no difference in utilization was detected between the two species a year later. Without the extra moisture, no such increase in the consumption rate of western wheatgrass was observed.

Table 4.1. Estimated forage utilization (%) of intermediate wheatgrass and western wheatgrass in 1989 and 1990 as affected by supplemental moisture.

	Irrigation		No irrigation	
	IWG	WWG	IWG	WWG
1989	51	37	33	42
1990	59	60	48	38

IWG = intermediate wheatgrass
WWG = western wheatgrass

Phytomass production

The amount of forage produced in 1989 and 1990 was more affected by the amount of water received than by defoliation. Significant interactions were found between grazing, irrigation, species, and time ($F_{1,96}$=24.33, p<0.001) and irrigation, species, competition, and time ($F_{2,96}$=9.41, p<0.001). Irrigation increased forage production of intermediate wheatgrass and western wheatgrass in both years, independent of defoliation regime (Table 4.2). However, the difference between irrigated and non-irrigated plots was much greater in 1990. Without supplemental water western wheatgrass produced more phytomass than intermediate wheatgrass in both years under grazing as well as under protection from grazing. Western wheatgrass also produced more forage than intermediate wheatgrass when plots were irrigated, with the exception of the protected plots in 1990 (Table 4.2).

The phytomass production of western wheatgrass in 1989 was as high in protected plots as in grazed plots, but in 1990 grazed plots produced significantly more aboveground biomass than protected plots (interaction between grazing and time $F_{1,48}$=19.61, p<0.001). This indicates that in the time period covered by this study grazing stimulated forage production in this previously poorly utilized species under dry as well as more moist conditions (Table 4.2). A similar stimulating effect of grazing on the

Table 4.2. Estimated forage production ($g.m^{-2}$) of intermediate wheatgrass and western wheatgrass in 1989 and 1990 as affected by supplemental water and short-duration grazing.

	Protected				Grazed			
	Irrigation		No irrigation		Irrigation		No irrigation	
	IWG	WWG	IWG	WWG	IWG	WWG	IWG	WWG
1989	20	31	10	24	19	27	12	24
1990	57	46	14	26	40	66	18	34

IWG = intermediate wheatgrass
WWG = western wheatgrass

forage production of intermediate wheatgrass was not detected (interaction $F_{1,48}$=1.14, p=0.291).

Fig. 4.1 depicts the phytomass produced by the two species in 1990. Both water availability and competitive interactions were important factors affecting the forage production of these two species. Irrigation explained 33 percent of the variation in growth in intermediate wheatgrass and 28 percent in western wheatgrass, while competition explained 28 and 18 percent of the variation in phytomass production in intermediate wheatgrass and western wheatgrass, respectively (Table 4.3). Aboveground biomass production of western wheatgrass in 1990 was significantly higher under short-duration grazing ($F_{1,12}$=11.87, p=0.005) than in the exclosures. The effect of grazing on growth of western wheatgrass, however, was smaller than that of irrigation or competition, explaining

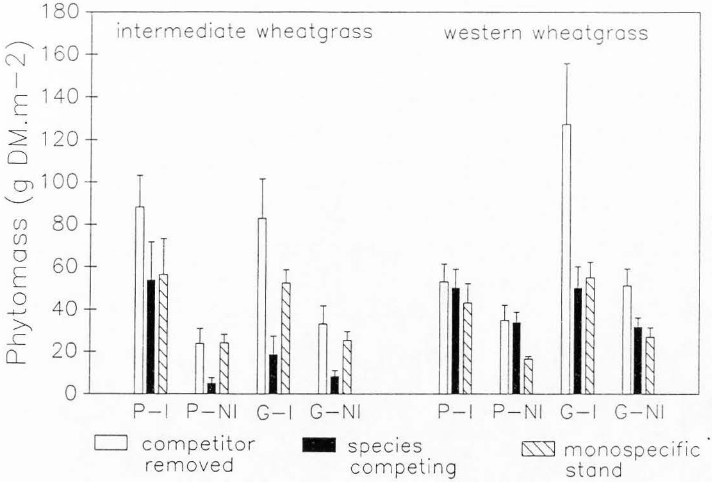

Fig. 4.1. The effects of grazing and supplemental moisture on the aboveground biomass produced in May 1990 by intermediate wheatgrass and western wheatgrass growing at different levels of intra- and interspecific competition (means + 1 SE, n=5) (P = protected from grazing, G = grazed, I = irrigated, NI = not irrigated).

Table 4.3 Analysis of variance: aboveground dry matter production of (a) intermediate wheatgrass and (b) western wheatgrass in May 1990 (log-transformed).

(a) Source	DF	Sum-Squares	Mean Square	F	Prob>F
BLOCK	4	.6435465	.1608866		
GRAZING	1	.06650	.06650	.17	0.687
IRRIGATION	1	10.49006	10.49006	26.94	<0.001
G * I	1	.8895646	.8895646	2.28	0.157
ERROR (a)	12	4.672333	.38936		
COMPETITION	2	8.852121	4.426061	29.85	<0.001
G * C	2	.5041533	.2520766	1.70	0.199
I * C	2	.4246762	.2123381	1.43	0.254
G * I * C	2	.8587859	.429393	2.90	0.070
ERROR (b)	32	4.74409	.14825		
TOTAL (adj)	59	32.14584			

(b) Source	DF	Sum-Squares	Mean Square	F	Prob>F
BLOCK	4	.2356904	.05892		
GRAZING	1	1.040861	1.040861	11.87	0.005
IRRIGATION	1	3.881037	3.881037	44.28	<0.001
G * I	1	.04567	.04567	.52	0.485
ERROR (a)	12	1.051843	.087654		
COMPETITION	2	2.437991	1.218996	9.31	<0.001
G * C	2	.8431363	.4215681	3.22	0.053
I * C	2	.3081524	.1540762	1.18	0.320
G * I * C	2	.1724968	.08624	.66	0.524
ERROR (b)	32	4.19065	.13096		
TOTAL (adj)	59	14.20753			

only 7 percent of the variation in the 1990 phytomass production. Grazing did not affect the amount of phytomass produced in 1990 by intermediate wheatgrass ($F_{1,12}$=0.17, p=0.687). In both species the effect of defoliation was independent of moisture availability (interaction

$F_{1,12}=2.28$, $p=0.157$ and $F_{1,12}=0.52$, $p=0.485$ for intermediate wheatgrass and western wheatgrass, respectively). In intermediate wheatgrass the effect of defoliation was independent of competitive environment (interaction $F_{2,32}=1.70$, $p=0.199$). In western wheatgrass, however, the positive effect of removing intermediate wheatgrass from the interface was more pronounced when grazing took place than when plants were protected from grazing (interaction $F_{2,32}=3.22$, $p=0.053$).

In monospecific stands both species produced approximately the same amount of aboveground biomass under short-duration grazing as when protected from grazing (Fig. 4.1). This was true regardless of the amount of water applied. However, intermediate wheatgrass produced significantly less forage than western wheatgrass when the two species grew together. Compared to monospecific stands, phytomass production of intermediate wheatgrass was considerably reduced when in competition with western wheatgrass ($p<0.010$), except when protected from grazing with irrigation. In contrast, forage production of western wheatgrass was little affected by the presence of intermediate wheatgrass. Only in the enclosures that did not receive supplemental irrigation did western wheatgrass produce significantly less phytomass in monospecific stands than when growing with intermediate wheatgrass ($t_{32}=2.28$, $p=0.029$).

Aboveground biomass generally increased for both species when the competitor was removed. This was particularly true for intermediate wheatgrass where the removal of western wheatgrass led to a significant improvement in forage production under all four treatment combinations of irrigation and defoliation ($p<0.050$). Western wheatgrass responded favorably to the removal of intermediate wheatgrass only when grazed ($t_{32}=3.64$, $p<0.001$ and $t_{32}=1.68$, $p=0.102$ with and without supplemental water, respectively).

Mean tiller size

Irrigation had a highly significant positive effect on the mean ramet size of intermediate wheatgrass ($F_{1,12}=17.64$, $p=0.001$) but increased the size of western wheatgrass ramets only when this species was grazed (interaction between irrigation and grazing $F_{1,12}=3.44$, $p=0.088$).

Grazing reduced the tiller size of intermediate wheatgrass ($F_{1,12}=5.21$, $p=0.041$). In May 1989, the average tiller weighed 59 mg (dry matter) in the protected and 47 mg in the grazed plots. In May 1990 the average weights were 79 and 56 mg per tiller in the protected and grazed plots, respectively. In western wheatgrass the opposite was observed. In 1989, tiller weights averaged 67 and 65 mg in the grazed and protected plots, respectively. One year later the average weight of tillers in the grazed plots was 103 mg while that of tillers in the protected plots was 82 mg (interaction between grazing and time $F_{1,32}$=4.62, p=0.039).

Competition with western wheatgrass reduced the size of intermediate wheatgrass tillers under normal growing conditions but not when plots were irrigated (interaction between competition and irrigation $F_{1,16}$=5.51, p=0.032). In western wheatgrass, on the other hand, tiller size was reduced by competition regardless of whether supplemental moisture was provided or whether plants were grazed or not ($F_{1,16}$=5.71, p=0.030).

The average size of western wheatgrass tillers was higher in 1990 (92 mg) than in 1989 (66 mg). The same was true for intermediate wheatgrass, but only when western wheatgrass was absent (79 mg vs. 53 mg). When intermediate wheatgrass competed with western wheatgrass, the difference in weight between the two years was small (interaction between competition and year $F_{1,32}$=5.70, p=0.023).

Ramet recruitment

The recruitment of intermediate wheatgrass ramets increased with the removal of western wheatgrass (Fig. 4.2). This was particularly evident in plots with no supplemental moisture. Ramet recruitment increased with the removal of western wheatgrass when plants were grazed and received extra water. However, these data are somewhat

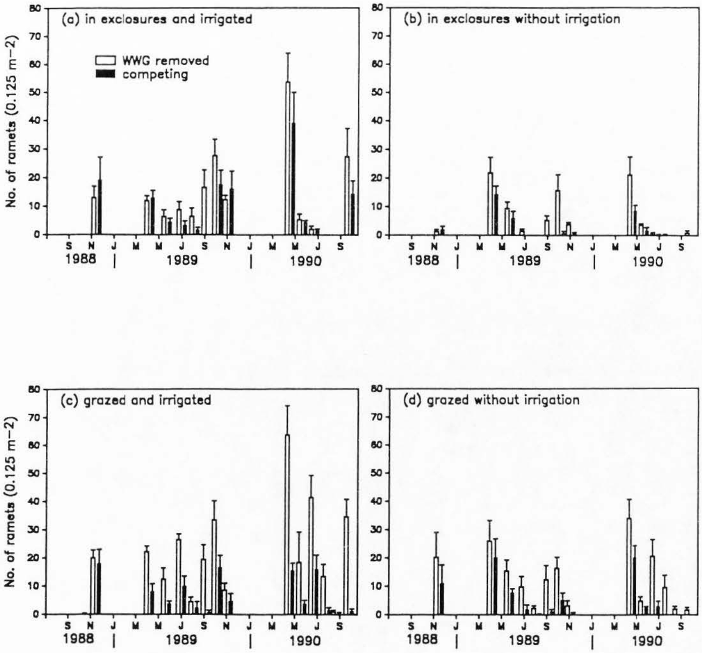

Fig. 4.2. Recruitment of intermediate wheatgrass ramets from June 1989 to September 1990 as affected by short-duration grazing, supplemental moisture, and competition with western wheatgrass (means + 1 SE, n=5).

distorted by the lower number of live tillers present at the start of this study in the plots from which western wheatgrass was not removed. The effects of the removal of western wheatgrass on ramet recruitment of intermediate wheatgrass were the least in the enclosures that received additional water; only during the summer of 1989 did ramet recruitement increase. Without western wheatgrass there was considerable recruitment in intermediate wheatgrass in August, whereas not a single new ramet was produced during this month in the presence of western wheatgrass. In the other treatments also the effect of the presence of western wheatgrass on the recruitment of intermediate wheatgrass ramets was most evident during the summer months and early fall, the period of the most acute water shortages.

Supplemental water stimulated tillering, particularly immediately following the summer months but also during the winter of 1989/1990. Grazing not only stimulated tiller formation but also markedly changed the pattern of tiller recruitment in intermediate wheatgrass (Fig. 4.3). In the grazed plots, peaks in the rate of tillering were found in the first half of June 1989 as well as June 1990. There was virtually no tiller formation during that month in plants that were protected from grazing. The rate of tillering in grazed plants was especially high in plots that received supplemental water and from which western

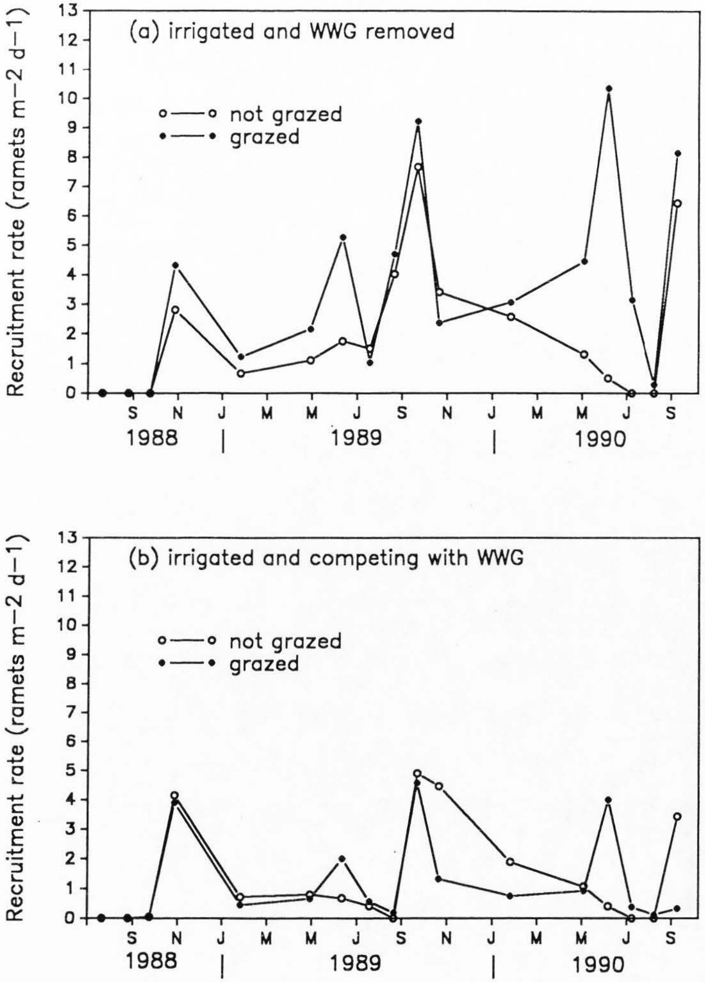

Fig. 4.3. The rate of ramet recruitment in intermediate wheatgrass between June 1988 and September 1990 as influenced by short-duration grazing and competition with western wheatgrass.

wheatgrass was removed. Under dry conditions grazing enhanced the recruitment of tillers in the fall of 1988 and during June/July 1990.

The removal of intermediate wheatgrass had only limited impact on the recruitment of western wheatgrass ramets in the enclosures; only in the fall of 1989 was the rate of recruitment higher on plots where intermediate wheatgrass was eliminated (Fig. 4.4). Under grazing, recruitment was generally better in plots from which intermediate wheatgrass had been removed, especially when they were irrigated. This was true, particularly, in the fall of 1989 and in June 1990. Recruitment of western wheatgrass ramets increased with supplemental water, especially in the second half of this study, but was little affected by grazing. However, levels of recruitment were generally somewhat higher in plants that were subjected to grazing, and this difference became more apparent during the latter part of the study.

Recruitment of new tillers in fall is generally earlier in intermediate wheatgrass than in western wheatgrass. The unusual dry fall of 1988 was an exception. The two species also differed with respect to the time period in which tillering was most dynamic. In undisturbed intermediate wheatgrass the highest rates of ramet production occurred in early fall, whereas in western wheatgrass the recruitment rates were highest during

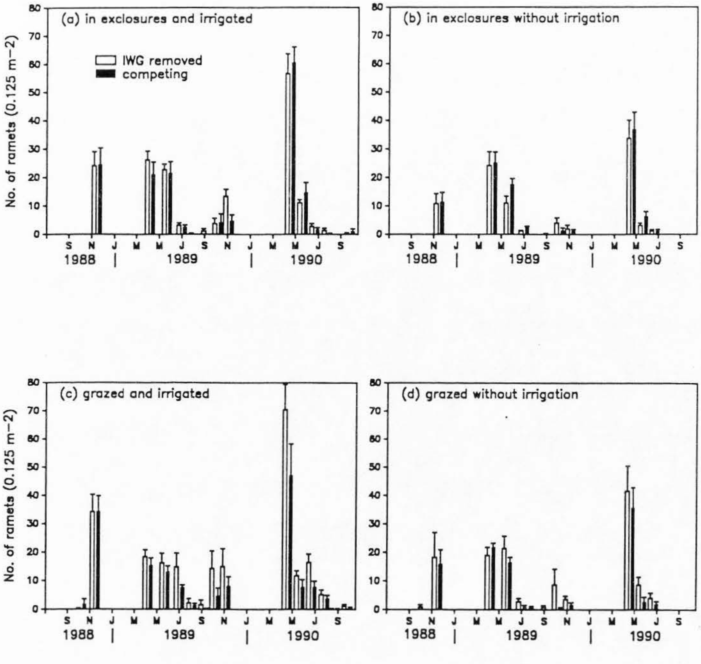

Fig. 4.4. Recruitment of western wheatgrass ramets from June 1989 to September 1990 as affected by short-duration grazing, supplemental moisture, and competition with intermediate wheatgrass (means + 1 SE, n=5).

late fall, winter, and early spring.

Ramet mortality

The effect of grazing on the probability of survival of intermediate wheatgrass tillers apparently depended on both water application and the presence of western wheatgrass (Table 4.4). When western wheatgrass was absent, grazing had a statistically significant negative effect on the survival of intermediate wheatgrass tillers in seven out of the ten larger cohorts when plants were irrigated. When plants grew under natural precipitation, grazing reduced ramet survival in two out of the four larger cohorts. The smaller cohorts also displayed this increase in ramet mortality under grazing. When plants competed with western wheatgrass and received supplemental water, grazing reduced the average life span of intermediate wheatgrass tillers in three out of five large cohorts. The smaller cohorts responded similarly. With natural rainfall and under interspecific competition, grazing did not affect the longevity of intermediate wheatgrass tillers. In fact, grazing increased ramet longevity in the cohort of 03/29/89.

Supplemental water, as expected, markedly reduced the risk of early mortality for ramets of intermediate wheatgrass (Table 4.5). Of the 19 comparisons made, 14 showed significantly improved survival distributions with irrigation. The great majority of the smaller cohorts in

Table 4.4. Results of the Mantel-Haenszel test for consistent differences in ramet mortality in intermediate wheatgrass due to grazing (p-values).

Cohort	Irrigated	Irrigated competing	Dry	Dry competing
11/05/88	0.001	<0.001	-	-
03/29/89	0.010	0.006	0.001	0.006 *
05/14/89	ns	-	ns	ns
06/23/89	0.056	-	-	-
07/27/89	0.019	-	-	-
08/29/89	<0.001	-	-	-
09/27/89	0.001	0.003	<0.001	-
10/26/89	0.003	-	-	-
04/10/90	ns	ns	ns	ns
05/13/90	ns	ns	-	-
06/14/90	-	-	-	-
07/18/90	-	-	-	-

* positive effect of grazing on ramet survival

Table 4.5. Results of the Mantel-Haenszel test for consistent differences in ramet mortality in intermediate wheatgrass due to irrigation (p-values).

Cohort	Grazed	Grazed competing	Not grazed	Not grazed competing
11/05/88	0.077*	ns	-	-
03/29/89	0.001	ns	<0.001	<0.001
05/14/89	0.007	-	0.030	-
06/23/89	ns	-	-	-
07/27/89	-	-	-	-
08/29/89	0.002	-	-	-
09/27/89	<0.001	<0.001	0.047	-
10/26/89	-	-	-	-
04/10/90	0.012	0.024	ns	0.067
05/13/90	-	-	-	-
06/14/90	<0.001	-	-	-
07/18/90	ns	-	-	-

* all significant effects of irrigation on ramet survival were positive

this study showed similar trends.

The effect of competition from western wheatgrass on the survival of intermediate wheatgrass tillers was relatively minor (Table 4.6). When plants were irrigated and grazed, the presence of western wheatgrass increased the risk of mortality in only two of the six major cohorts. Both cohorts originated in June when interference from western wheatgrass is believed most severe. When plants were protected from grazing and irrigated, interspecific competition did not influence ramet survival. In fact, survival of tillers increased with competition for the 04/10/1990 cohort. With natural precipitation and grazing, competition did not affect the longevity of intermediate wheatgrass tillers. The presence of western wheatgrass improved the survival distribution of tillers belonging to the 03/29/89 cohort. In the enclosures, on the other hand, that same cohort was the only one to show a significant decrease in survival due to the presence of western wheatgrass.

The effects of grazing on ramet mortality were not as consistent in western wheatgrass as in intermediate wheatgrass. When western wheatgrass was irrigated, grazing generally decreased tiller longevity whether in competition with intermediate wheatgrass or not (Table 4.7). This was almost invariably due to a direct impact of the grazing animal on the mortality of tillers during the grazing period. Only in the May and June cohorts when

Table 4.6. Results of the Mantel-Haenszel test for consistent differences in ramet mortality in intermediate wheatgrass due to competition (p-values).

Cohort	Grazed irrigated	Grazed dry	Not grazed irrigated	Not grazed dry
11/05/88	ns	ns	ns	-
03/29/89	ns	0.010 *	ns	<0.001
05/14/89	-	ns	-	ns
06/23/89	0.074	-	-	-
07/27/89	-	-	-	-
08/29/89	-	-	-	-
09/27/89	ns	ns	ns	-
10/26/89	-	-	ns	-
04/10/90	ns	ns	0.001 *	ns
05/13/90	-	-	-	-
06/14/90	<0.001	-	-	-
07/18/90	-	-	-	-

* positive effect of competition on ramet survival

Table 4.7. Results of the Mantel-Haenszel test for consistent differences in ramet mortality in western wheatgrass due to grazing (p-values).

Cohort	Irrigated	Irrigated competing	Dry	Dry competing
11/05/88	ns	ns	ns	0.062
03/29/89	ns	0.086	ns	ns
05/14/89	0.029 *	0.031	ns	ns
06/23/89	-	-	-	-
07/27/89	-	-	-	-
08/29/89	-	-	-	-
09/27/89	-	-	-	-
10/26/89	ns	-	-	-
04/10/90	0.001	0.007	0.005	0.002
05/13/90	ns	ns	-	-
06/14/90	-	-	-	-
07/18/90	-	-	-	-

* positive effect of grazing on ramet survival

intermediate wheatgrass was not present did grazing increase the survival rate of ramets during the following summer. This effect of grazing was statistically significant for the May 1989 cohort. The negative effects of grazing on the survival of western wheatgrass ramets was apparently magnified by competitive interference from intermediate wheatgrass. The response of western wheatgrass tillers' survival to grazing without competition from intermediate wheatgrass was significant only in the 04/10/1990 cohort, but was significant in the 03/29/89, 05/14/89 and 04/10/90 cohorts of western wheatgrass when in competition with intermediate wheatgrass. When plants did not receive supplemental water, grazing tended to reduce ramet longevity as well. The negative effects of grazing on ramet survival of western wheatgrass became more pronounced as the study progressed, possibly indicating a gradual weakening of western wheatgrass as a result of several, relatively heavy defoliations (see Table 4.1).

In contrast to the response of intermediate wheatgrass to supplemental water, western wheatgrass apparently reduced average tiller life span with increased water (Table 4.8). In none of the cohorts was ramet survival significantly improved by additional water.

Figure 4.5 shows that much of the negative effect of supplemental water on ramet longevity was attributable to high mortality rates during late fall and winter.

Table 4.8. Results of the Mantel-Haenszel test for consistent differences in ramet mortality in western wheatgrass due to irrigation (p-values).

Cohort	Grazed	Grazed competing	Not grazed	Not grazed competing
11/05/88	ns	ns	ns	ns
03/29/89	0.084 *	0.011 *	ns	0.032 *
05/14/89	ns	0.003 *	<0.001 *	ns
06/23/89	-	-	-	-
07/27/89	-	-	-	-
08/29/89	-	-	-	-
09/27/89	ns	-	-	-
10/26/89	-	-	-	-
04/10/90	ns	ns	0.100 *	0.081 *
05/13/90	ns	-	-	ns
06/14/90	-	-	-	-
07/18/90	-	-	-	-

* effect of irrigation on ramet survival was negative

The effects of competition from intermediate wheatgrass on the survival of western wheatgrass were relatively minor and not always consistent (Table 4.9). Only the cohort of 05/14/1989 showed a significant, though somewhat weak, reduction in tiller survival with competition when plots were irrigated and protected from grazing. In none of the other cohorts could a significant negative effect of competition on the survival of western wheatgrass ramets be established.

The negative effect of the removal of intermediate wheatgrass on the survival of western wheatgrass tillers when plants were grazed and received supplemental water was due to an infestation of snow mold (Typhula spp.) in one of the plots from which intermediate wheatgrass was

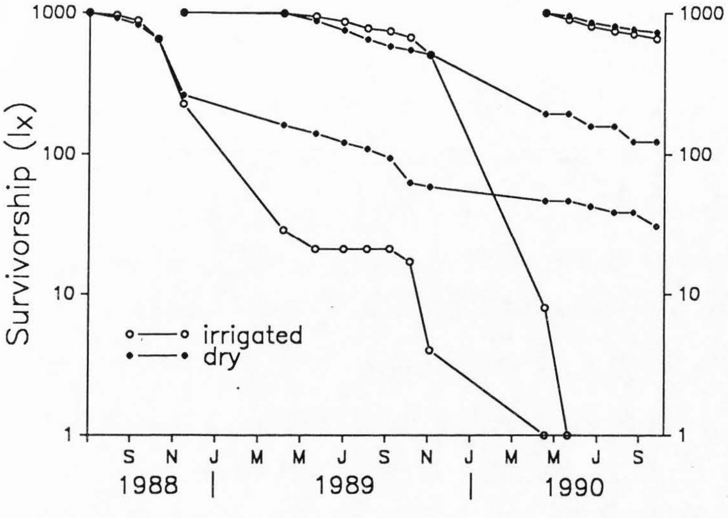

Fig. 4.5. The depletion curve and survivorship curves of two cohorts of western wheatgrass ramets growing in exclosures and competing with intermediate wheatgrass. Note that the Mantel-Haenszel test indicated that the two survivorship curves of the April 1990 cohort were different (p=0.081) but that those of the November 1988 cohort were not[1].

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[1] The Mantel-Haenszel test is sensitive to consistent differences in survival patterns. It also gives more weight to mortality occurring in early time intervals than in later ones.

Table 4.9. Results of the Mantel-Haenszel test for consistent differences in ramet mortality in western wheatgrass due to competition (p-values).

Cohort	Grazed irrigated	Grazed dry	Not grazed irrigated	Not grazed dry
11/05/88	0.020 *	ns	0.003 *	0.005 *
03/29/89	ns	ns	ns	ns
05/14/89	0.095	ns	0.004 *	ns
06/23/89	ns	-	-	-
07/27/89	-	-	-	-
08/29/89	-	-	-	-
09/27/89	-	-	-	-
10/26/89	0.087 *	-	-	-
04/10/90	ns	ns	ns	ns
05/13/90	ns	-	ns	-
06/14/90	ns	-	-	-
07/18/90	-	-	-	-

* positive effect of competition on ramet survival

removed. Under dry conditions, competition from intermediate wheatgrass did not influence the survival of western wheatgrass in any of the cohorts when plants were grazed. When plants were protected from grazing, only the cohort of 11/05/1988 showed increased tiller survival of western wheatgrass in response to the presence of intermediate wheatgrass. Reduced tiller survival with the removal of intermediate wheatgrass was probably not due to the application of glyphosate. The differences between the survivorship distributions did not become apparent before the June or July 1989 censuses.

Tiller density

During the course of this study, tiller density of intermediate wheatgrass increased markedly under irrigation but not under normal growing conditions ($F_{1,12}$=35.04, p<0.001). Grazing, on the other hand, did not significantly affect the magnitude of the change in tiller density between June 1988 and 1990 ($F_{1,12}$=1.41, p=0.258) but competition with western wheatgrass decreased tiller density ($F_{1,16}$=16.72, p<0.001). No significant interactions between these three factors were detected. The only significant declines in tiller density of intermediate wheatgrass during these two years were found in the unirrigated plots where it competed with western wheatgrass (t_4=3.16, p=0.034 and t_4=3.49, p=0.025 for protected and grazed, respectively). In these two cases, tiller density declined 77 and 51 percent, respectively (Fig. 4.6).

In western wheatgrass, grazing, irrigation, and the removal of intermediate wheatgrass all stimulated tiller production ($F_{1,12}$=15.01, p=0.002, $F_{1,12}$=41.31, p<0.001, and $F_{1,16}$=4.11, p=0.059, respectively). The positive effect of grazing was more conspicuous in plots from which intermediate wheatgrass was removed (interaction $F_{1,16}$=6.45, p=0.022). Similarly, the increase in tiller density as a result of grazing was more pronounced under irrigation than under natural precipitation (interaction

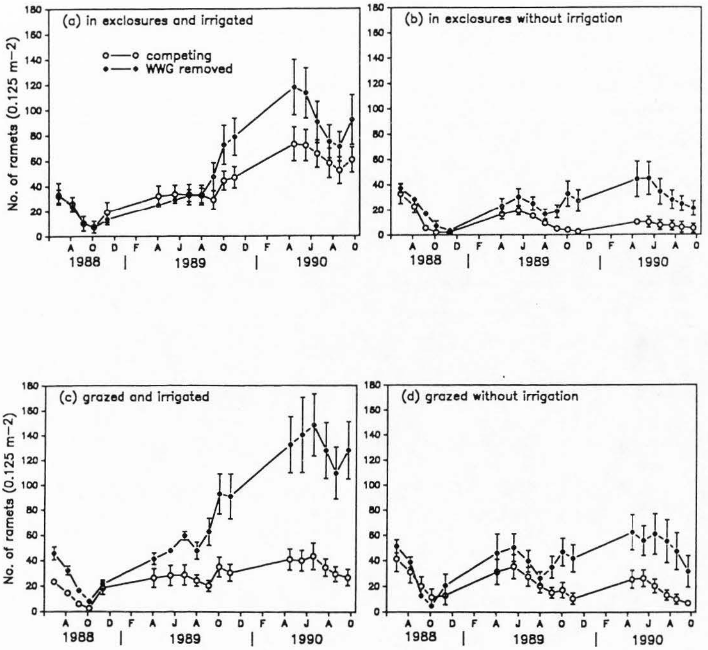

Fig. 4.6. Mean number of live intermediate wheatgrass ramets (± 1 SE) per 0.125 m^2 from June 1988 to September 1990 as affected by interference from western wheatgrass (n=5).

$F_{1,12}$=7.47, p=0.018). Tiller density of western wheatgrass that did not receive supplemental water remained approximately constant in these two years; only when plots were grazed and intermediate wheatgrass was removed did tiller density tend to increase (t_4=2.62, p=0.058) (Fig. 4.7).

In the plots where western wheatgrass and intermediate wheatgrass competed, the ratio of intermediate wheatgrass ramets to western wheatgrass ramets narrowed in the first year under all four treatments: from 0.67 to 0.52 in exclosures and irrigated, from 0.64 to 0.28 in exclosures without irrrigation, from 0.60 to 0.51 when grazed and irrigated, and from 1.03 to 0.61 when grazed without irrigation. This trend continued during the second year in the plots that did not receive supplemental water, but was reversed in the irrigated plots. Two years after the start of this experiment this ratio was 0.13 in the exclosures without irrigation and 0.49 in the grazed plots that did not receive additional water; this ratio widened to 0.88 and 0.63 in the irrigated plots that were protected and grazed, respectively (Fig. 4.8).

Reproductive efforts

Sexual reproduction played only a very minor role in the propagation of intermediate wheatgrass and essentially no role in that of western wheatgrass during the three years of this study (Table 4.10). Although the low

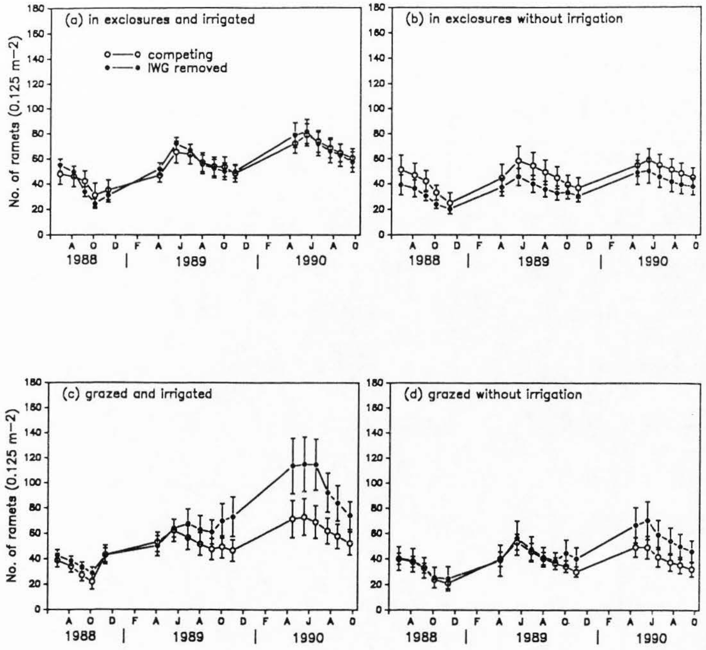

Fig. 4.7. Mean number of live western wheatgrass ramets (± 1 SE) per 0.125 m^2 from June 1988 to September 1990 as affected by interference from intermediate wheatgrass (n=5).

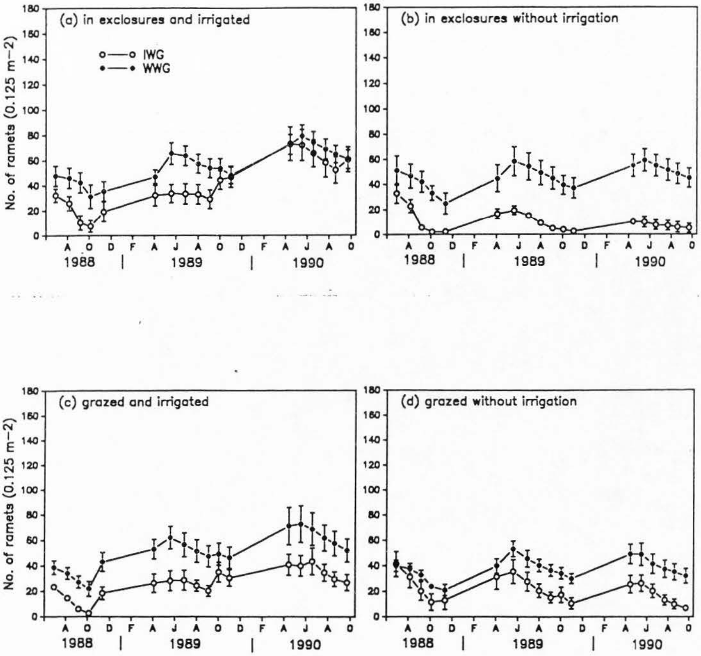

Fig. 4.8. Mean number of live ramets (± 1 SE) per 0.125 m^2 at the interface of intermediate wheatgrass and western wheatgrass from June 1988 to September 1990 (n=5).

Table 4.10. The effects of supplemental water, grazing, and competition on the number of reproductive tillers in (a) intermediate wheatgrass and (b) western wheatgrass expressed as percentages of the live tillers present in early May 1989 and 1990.

(a)		Irrigation		No Irrigation	
		Grazed	Protected	Grazed	Protected
Competitor present	1989	-	0.6	-	-
	1990	0.5	4.2	-	-
Competitor removed	1989	-	-	-	-
	1990	2.6	11.1	-	3.6

(b)		Irrigation		No Irrigation	
		Grazed	Protected	Grazed	Protected
Competitor present	1989	0.3	1.5	-	-
	1990	-	1.5	-	-
Competitor removed	1989	3.2	0.3	-	-
	1990	0.2	-	0.3	1.2

percentages of fertile tillers and the spatial variability in response make an interpretation somewhat tentative, increased moisture availability and removal of western wheatgrass apparently do have a positive effect on the sexual reproduction of intermediate wheatgrass. Grazing reduced the number of reproductive tillers. This probably was a direct consequence of defoliation of rudimentary inflorescences but may also reflect a general reduction in plant vigor. The beneficial effect of irrigation on sexual reproduction took almost two years to express itself.

The potential of a tiller to become reproductive apparently increases with age. Of the 106 reproductive tillers of intermediate wheatgrass observed in this study, 76 (71.7 percent) were members of cohorts originating between July and November of the previous year; all others were members of the first spring cohort. Viable seeds were only produced in the irrigated and protected plots in 1990.

In western wheatgrass grazing, irrigation or competition had essentially no effect on reproductive performance. As in intermediate wheatgrass, tiller age was an important determinant of it becoming reproductive or not. Of the 28 reproductive tillers recorded in this study only one belonged to the first spring cohort of the same year. All other tillers, except one, emerged in the fall of the previous year; the one exception was a member of the May cohort of the previous year. No seeds were observed.

Discussion

Competition

Our data show that competitive interactions between intermediate wheatgrass and western wheatgrass did occur during the two years of this study. They also showed that intermediate wheatgrass was clearly the subordinate species, thereby confirming the results obtained in Chapter III.

Removal of western wheatgrass from the interface led to an improvement in the performance of intermediate wheatgrass over a wide range of environmental conditions. This was expressed in terms of improved phytomass production -- a consequence of increased tiller densities and, in the case of natural precipitation, higher tiller weights -- but particularly in improved ramet recruitment. Competitive interactions were shown to strongly affect tillering in grasses. Liddle et al. (1982) demonstrated that the number of tillers produced by Festuca rubra plants was positively correlated with the distance to neighboring plants. Robberecht et al. (1983) and Nobel and Franco (1986) found large increases in the tiller production of Hilaria rigida in response to the removal of adjacent vegetation.

In contrast, ramet survival was a fairly poor and inconsistent indicator of competitive stress in intermediate wheatgrass. In most of the cohorts, regardless of irrigation or grazing regime, the presence of western wheatgrass had little effect on the longevity of intermediate wheatgrass tillers. Slightly negative effects were found particularly in the May-June-July cohorts. This may be because phenologically western wheatgrass develops later than intermediate wheatgrass (Frank et al. 1985). This has a proportionally greater effect on the survival of intermediate wheatgrass tillers that are produced later in the season and which have diminished physiological support from older interconnected ramets.

In another study we found that the probability of survival of intermediate wheatgrass was negatively affected by competition from western wheatgrass when plants were grazed but not when they were protected from grazing (Chapter III). In that study, however, the benchmark was ramet survival in monospecific stands whereas in this study it was compared to ramet survival in plots from which western wheatgrass was removed. In these latter plots, intermediate wheatgrass responded with a change in the spatial structure of the sward in that it assumed a more tufted growth form with locally high concentrations of tillers. These aggregations of tillers may have experienced a reduction in overall probability of survival due to strong intraclonal competition.

Failure to reproduce is a common response to competitive stress (Weiner 1988). In our study the percentage of reproductive tillers in intermediate wheatgrass was increased markedly in 1990, when interference from western wheatgrass was eliminated.

This improved performance of intermediate wheatgrass as a result of the removal of western wheatgrass was most likely due to a more favorable soil water regime (cf. Fonteyn and Mahall 1981, Robberecht et al. 1983) because the dominance of western wheatgrass in our study was magnified by lower levels of precipitation. Under natural growth conditions without grazing, the interaction between the two species was one of absolute asymmetry with no measurable effect of intermediate wheatgrass on the performance of western wheatgrass. With supplemental irrigation, the effect of intermediate wheatgrass on western wheatgrass' performance was also negligible. However, the two cases differ in that interference from western wheatgrass under irrigation did not nearly affect the performance of intermediate wheatgrass to the same degree as when only natural precipitation was available. Our data (see Fig. 4.1) suggest that under these specific conditions intermediate wheatgrass and western wheatgrass might be able to coexist because the intraspecific competition appears to be approximately equal to the interspecific competition (Goldberg and Werner 1983). A greater degree of reciprocity sensu Silander and Antonovics (1982) was found when short-duration grazing was implemented, but in this situation also western wheatgrass emerged as the dominant competitor.

Our results do not permit a generalization on the relationship between intensity of competition and resource availability. The intensity of competition experienced by the two species, which is measured as the difference between the performance in the control plots and in the plots from which the competitor had been removed (Welden and Slauson 1986), varied greatly. In the grazed plots the interference experienced by both species was somewhat more intense when supplemental water was provided, but the differences between the two water regimes were relatively small. Wilson and Keddy (in Keddy 1989) and Friedman and Orshan (1974) found similar, though far more pronounced, inverse relationships between abiotic stress and intensity of competition. On the other hand, when intermediate wheatgrass was protected from grazing it experienced much more intense competition from western wheatgrass under conditions of lower moisture availability.

Western wheatgrass experienced more intense competition from intermediate wheatgrass under short-duration grazing than in exclosures, regardless of irrigation regime. The root system of western wheatgrass is sensitive to defoliation (e.g., Polley and Detling 1988, 1989) with the root mass distribution shifting upward under herbivory. Defoliation in our study may thus have led to greater overlap in depth of the root systems of the two species, resulting in an intensification of the competition for water, particularly in the upper portions of the soil profile. Nevertheless, the depressing effect of western wheatgrass on the performance of intermediate wheatgrass when plants were grazed and received supplemental water was contrary to our expectations. It may be explained by the substantial difference in percentage utilization between the two species in 1989 (Table 4.1) and by the grazing history of this site, where greater grazing pressure was placed on intermediate wheatgrass during the preceding five years. The initial advantage of western wheatgrass over intermediate wheatgrass in the capture of resources may have resulted in positive feedbacks which culminated in the observed outcome to their competitive interactions (Keddy 1989).

The performance of intermediate wheatgrass in plots where western wheatgrass was removed was generally better than its performance in monoculture under improved soil water conditions but not under natural precipitation. Although the validity of this observation is diminished by the fact that the randomization of the competition treatments did not include the monospecific stands, it may indicate that intraspecific competition in intermediate wheatgrass is of low intensity when growing conditions are less favorable. In this species, density-dependent factors probably became less important when the ramet population was substantially reduced in size in the fall of 1988 (cf.

Fowler 1986b). In western wheatgrass, on the other hand, intraspecific competition was apparently greater under dry conditions. Ramet density of this species was far less affected by the drought in 1988 (see also Chapter II).

The response of intermediate wheatgrass to interspecific as well as intraspecific competition under water deficit is almost identical under grazing and protection from grazing. This could be indicative of a high degree of grazing tolerance. It may also be an artifact of the grazing history of this pasture. It is plausible that due to several years of severe defoliation (B.E. Norton, personal observations), plants that grew in the exclosures were unable to show a measurable response to the absence of herbivory within the two years of this study.

Surprisingly, the performance of intermediate wheatgrass under short-duration grazing was reduced due to competition from western wheatgrass, but western wheatgrass did not respond with a phytomass production that was higher than that found in monospecifc stands. Under protection from grazing, however, such an increase in phytomass was evident, as expected, particularly under dry conditions. We speculate, therefore, that either western wheatgrass' improved access to resources was not expressed in higher phytomass production but, possibly, in belowground growth, or that under a grazing regime certain costs were associated with the dominance of western wheatgrass over intermediate wheatgrass. These costs, such as a reduction in the pool of reserve carbohydrates, may have prevented western wheatgrass from expressing its competitive advantage within the time-frame of this study.

It is important to consider that the outcome of competition as reported in this study represents little more than a snapshot of a process that continues to evolve through time. Compared to the phytomass data of 1989, the proportion of intermediate wheatgrass to total aboveground biomass increased in 1990 when plants were growing in exclosures but decreased when grazing took place, irrespective of irrigation regime. A similar recovery of intermediate wheatgrass when protected from grazing was observed in Chapter III. While our data do not show a complete reversal of the competitive hierarchy, under protection from grazing the competitive ability of intermediate wheatgrass versus western wheatgrass was enhanced by supplemental moisture.

The root systems of the two species in undisturbed sites are characterized by significantly different distributions with western wheatgrass having higher root densities below 80 cm depth and intermediate wheatgrass having significantly higher root densities in the top 20 cm of the soil profile (Appendix A). When rainfall during the growing season is sparse, as was the case in the three years of this study, these grass species become increasingly dependent upon soil-stored winter precipitation. As the growing season progresses, the upper soil layers dry out and water is extracted mainly from those layers in which western wheatgrass roots more profusely. Regular application of water, as in the irrigation treatment, would boost the competitive ability of intermediate wheatgrass because recharges take place in those soil layers where much of its root system is concentrated.

These differences in root distribution, which most likely were accentuated by the grazing history of this site, would also explain why under protection from grazing and natural precipitation western wheatgrass performed better at the interface than in monospecific stands. It would also explain why the removal of intermediate wheatgrass in mixed stands did not elicit a marked response in western wheatgrass. Observations similar to these were made by Manning and Barbour (1988) studying the competition between two shrubs, the shallow-rooted _Haplopappus cooperi_ and the deeper-rooted _Chrysothamnus teretifolius_.

Grazing

Grazing markedly affected the pattern of ramet recruitment in intermediate wheatgrass. This was particularly evident during 1990 when grazing resulted in high tiller appearance rates during early June; recruitment in the protected plots at that time was almost zero. Thus, while protected plants had only one period of intense tillering in late summer or fall, grazed plants had two such periods, early June and late summer/early fall. Robson (1968) found two such peaks in the tiller appearance rate of non-defoliated _Festuca_ _arundinacea_, while Langer et al. (1964) and Garwood (1969) found a similar tiller recruitment pattern in defoliated _Phleum pratense_. In the study of Langer et al. (1964) these peaks in tiller appearance rate were more pronounced when clipping occurred more frequently.

Our data suggest a high level of control over the development of axillary buds in intact elongating stems of intermediate wheatgrass. Stem elongation in this species starts in late April/early May. At the time of grazing, 19-21 May 1989 and 23-25 May 1990, many apices were elevated to heights that placed them within reach of the grazing animal. Removal of or damage to meristems must have allowed a large number of basal axillary buds to initiate new growth. This response in tiller recruitment to defoliation apparently is related to available water. It was expressed clearly when plants received supplemental water and was found under natural precipitation only in plots from which western wheatgrass was eliminated. Such a peak in tiller appearance rate following defoliation was not noticed in another experiment in which intermediate wheatgrass grew without relaxation of competitive stress (see Chapter II).

A release from apical dominance may not be the only requirement to initiate tillering; the availability of resources plays a role as well (Langer 1963). The second peak in recruitment in August/September was most likely the result of tiller formation from second order buds while a loss of apical dominance due to the senescence of apices and floral primordia which had escaped damage during grazing also may have played a role. This second flush in tiller production coincided with maximum tiller appearance rates in plants that had been protected from grazing. Cable (1982) found that a second phase of sprouting on Trichachne californica culms that had their apices removed was almost entirely from buds on first order shoots.

Grazing not only altered the pattern of tiller production in intermediate wheatgrass, it also increased the number of tillers produced, regardless of moisture regime, but only when the competitor was removed. This was most likely due to the fact that this species was grazed during stem elongation. In the plots that were irrigated and where western wheatgrass had been removed, improved light conditions following defoliation may have been an additional factor. In these plots intermediate wheatgrass often exhibited a tufted growth form with extremely high concentrations of tillers. Tillering in many grass species is hindered by low light intensities (Mitchell 1953, Jewiss 1972) and unfavorable spectral composition (Deregibus et al. 1985). Tiller formation within these tufts may have been restricted due to self-shading of the foliage.

Grazing had a markedly negative impact on the survival of intermediate wheatgrass ramets. In most instances this negative effect became apparent at the census immediately following the grazing period, suggesting significant mortality due to the mechanical impact of the animals. Although determination of the cause of death for each tiller individually was not part of our study, trampling apparently was a major factor contributing to these higher rates of ramet mortality. The higher stocking densities of the short-duration grazing system probably encouraged this cause of tiller death. In the last year of our study, however, cohorts of tillers in the grazed plots had already experienced higher mortality rates in early spring prior to the grazing period. This was true especially for plots receiving only natural precipitation. Fetcher and Shaver (1983) also found that the probability of tiller survival in the sedge Eriophorum vaginatum was greatly enhanced when mechanical disturbances were prevented. Survival of tillers of Schizachyrium scoparium was affected negatively by grazing but only at the highest stocking density in an experiment by Butler and Briske (1988).

The effects of grazing on tiller dynamics were less striking in western wheatgrass. Tillering in this species was stimulated by defoliation in plots where intermediate wheatgrass was eliminated but, except for the fact that the season of tiller recruitment was extended somewhat into early summer, the overall pattern of ramet recruitment was not affected. Butler and Briske (1988) also found that herbivory on the bunchgrass *Schizachyrium scoparium* resulted in an extended period of ramet recruitment. In contrast to our results, however, higher recruitment during the summer months in grazed *Schizachyrium scoparium* plants was neutralized by reduced recruitment during the months that followed. As a result, total level of recruitment was not affected by grazing.

In the two wheatgrasses, intermediate wheatgrass in particular, the activation of axillary buds in June as a result of defoliation did not diminish the number of buds that were activated later, at least not in the plots receiving supplemental water moisture and where competitors were eliminated. Similar results were obtained by Langer et al. (1964) in a developing sward of *Phleum pratense*. This would suggest that improved tillering as a result of defoliation may only be expected in conditions of improved resource availability. With competition and natural precipitation prevailing, the effects of grazing on total tiller recruitment in our experiment were similar to those reported by Butler and Briske (1988).

Irrigation

Irrigation clearly had a positive effect on overall tiller density and productivity of both species. These results are similar to those for several temperate grass species (Hebblethwaite 1977, Jones et al. 1980, Norris and Thomas 1982a). Irrigation changed the pattern of recruitment of tillers in intermediate wheatgrass and in western wheatgrass with a somewhat extended recruitment towards the end of spring and earlier recruitment in summer and fall. Garwood (1969) found that in temperate species such as Lolium perenne and Phleum pratense dry soil conditions could delay the recruitment of new ramets between June and August. He showed, however, that such a delay in recruitment during the summer months does not have to affect the total number of new tillers recruited; the recruitment of new tillers in fall was always higher in the unirrigated plots.

Norris and Thomas (1982a,b) found similar compensatory recruitment mechanisms. They showed that in some species regrowth was stimulated by previous exposure to drought. This compensation in tiller recruitment resulted in tiller densities in droughted Lolium perenne that were the same as in the well-watered control. Lolium multiflorum, on the other hand, did not possess this ability to recover from a drought. In our study no such compensatory tillering was detected, presumably because of the duration and intensity of the drought experienced by the two wheatgrasses. Busso et al. (1989) showed that prolonged drought may reduce the number of metabolically active buds per tiller in Agropyron desertorum and Agropyron spicatum (syn. Pseudoroegneria spicata), particularly when plants are subjected to defoliation.

Ramet survival of intermediate wheatgrass responded favorably to supplemental water, but the survival of western wheatgrass ramets was generally negatively affected by additional moisture. Only the small cohorts originating in May and June tended to benefit somewhat from irrigation, indicating that only during these late spring/early summer months the successful establishment of western wheatgrass ramets may depend upon moisture availability.

The reduced longevity of western wheatgrass ramets with supplemental water is attributed to a greater proportion of the tillers growing under these more favorable conditions elevating their apices. Subsequently, these apices are killed by frosts, causing a high level of ramet mortality in this species during winter and the recruitment of new ramets in spring. Between 3 and 8 percent of the spring-produced tillers survived the following winter when western wheatgrass received supplemental water. Under natural rainfall these values ranged from 17 to 29 percent.

Irrigation apparently improved the competitive ability of intermediate wheatgrass versus western wheatgrass under grazing as indicated by a gradual increase in tiller density at the interface of the two species (Fig. 4.8). However, one should be wary of interpreting this to mean that intermediate wheatgrass may outcompete western wheatgrass under short-duration grazing in wet years. The irrigated plots were conspicuously lush in the otherwise dry paddock. As a result, western wheatgrass in these plots was defoliated to a greater degree than if the whole paddock had received the same amount of enhanced precipitation. Competition between intermediate wheatgrass and western wheatgrass in years with improved forage production will be far more asymmetric than in this experiment, unless the grazing period is lengthened sufficiently to force animals to consume greater amounts of western wheatgrass.

CHAPTER V

RESPONSES OF YOUNG *THINOPYRUM INTERMEDIUM* AND *PASCOPYRUM SMITHII* SHOOTS TO DEFOLIATION AND INTRASPECIFIC COMPETITION

Abstract. Physiological interdependence of ramets may be an important aspect of a species' grazing resistance. The objective of this study in central Utah was to examine how individual shoots of the rhizomatous species intermediate wheatgrass (*Thinopyrum intermedium*) and western wheatgrass (*Pascopyrum smithii*) react to simulated grazing in monospecific stands in terms of regrowth, mortality, and the recruitment of axillary tillers. Fourteen defoliation regimes were used to vary the time and frequency of defoliation of target shoots and to alter the level of intraclonal support or intraspecific competition experienced by these shoots. Virtually all intermediate wheatgrass and western wheatgrass shoots whose rhizome connections were severed about 45 days after their emergence died within a few days, indicating their continued dependence on the import of resources. Young interconnected shoots of intermediate wheatgrass showed signs of overcompensation in response to defoliation, particularly when surrounding ramets were defoliated at the same time. The phytomass production of young western wheatgrass shoots, however, declined with defoliation. Shoot mass in both species increased following defoliation

of neighboring ramets. Defoliation of intermediate wheatgrass shoots after internode elongation increased their mortality rate but only when surrounding ramets remained intact. Intraspecific and/or intraclonal competition also had a negative impact on the formation of new tillers in intermediate wheatgrass. Likewise, the survival of western wheatgrass shoots increased when surrounding ramets were defoliated, but this treatment did not affect the formation of new tillers. In this species recruitment decreased when the shoots were defoliated twice during the growing season. Under the conditions of this experiment, the foremost effect of defoliation on the growth and development of young shoots apparently was a reduction of competitive stress, possibly accompanied by the rapid mobilization of stored carbon, rather than a decline in the transport of photoassimialtes from undefoliated to defoliated ramets belonging to the same Integrated Physiological Unit. Unusually low levels of winter and spring precipitation probably were responsible for this effect. The results of this study suggest that intermediate wheatgrass is more grazing tolerant than western wheatgrass. A higher degree of physiological integration of ramets in intermediate wheatgrass than in western wheatgrass may contribute to this greater tolerance.

Introduction

Clonal plants may be viewed as populations of interconnected ramets that may, depending on the persistence of their connections, be more or less functionally interdependent (White 1979). In rhizomatous graminoids young emerging shoots are supported by older ramets through acropetal transport of assimilates (Forde 1966b, Nyahoza et al. 1973, Noble and Marshall 1983). When established tillers are defoliated, they too receive carbohydrates from non-defoliated tillers along the rhizome axis, as was shown by Nyahoza et al. (1973, 1974) for Poa pratensis and Rogan and Smith (1974) for Agropyron repens. However, reserve carbohydrates may act as a buffer. For example, Forde (1966a,b) imposed repeated defoliations on Elymus repens and Cynodon dactylon before similar distribution patterns of photoassimilates were detected in these two grasses.

The physiological integration of clonal plants does not only involve their carbon economy but extends to the sharing of water and mineral nutrients among constituent ramets and to hormonal control of growth and development. A young developing ramet receives its water and nutrients from older parts of the clone, but once its own roots are formed such a ramet may become quite independent. However, as Marshall (1990) points out, absolute independence occurs only when ramets are physically separated from the clonal system. Thus, the response of individual ramets to environmental changes regarding demographic behavior and biomass production depends largely on the degree of physiological integration between them. Some ecologically important consequences of physiological integration are maternal support for young ramets which increases the probability of their survival to maturity; support for ramets stressed by localized resource deficiencies, competition, and herbivory; and coordinated clonal growth and expansion in such a way that competition among ramets is minimized (Cook 1985, Pitelka and Ashmun 1985, Hutchings and Bradbury 1986).

Grazing seldom results in uniform defoliation; some ramets are defoliated severely while others may remain virtually untouched. Within a clone, defoliated ramets may be supported by those that are left intact or less severely defoliated. Matches (1966) showed that leaving as little as 10 percent intact tillers on otherwise clipped plants of Festuca arundinacea greatly enhanced growth rates, tillering and survival of these plants compared to complete defoliation. Alternatively, defoliated ramets may also have to compete with their non-defoliated counterparts for scarce resources. Archer and Detling (1984) observed the response of single tillers of the grass Andropogon gerardi and the sedge Carex filifolia to the defoliation of tillers surrounding them. They found that the negative effects of competition outweighed any positive effect of resource sharing among interconnected ramets following defoliation.

To understand the effects of defoliation on the growth and the population dynamics of intermediate wheatgrass and western wheatgrass ramets and, ultimately, on the competitive interactions between these two species, it is necessary to evaluate the degree of physiological integration among clonal ramets of each species. Schmid and Bazzaz (1987) have predicted that ramet integration would be higher in clones with closely aggregated ramets ("phalanx" type) than in clones with loosely aggregated ramets ("guerilla" type). Based on the differences in clonal architecture between the two species, intermediate wheatgrass has a "phalanx" and western wheatgrass a "guerilla" type of growth form, we expected to find a higher degree of ramet interdependence in intermediate wheatgrass than in western wheatgrass. Also, the beneficial effects of integration for recently established shoots were expected to be more conspicuous during the early part of the growing season than later on because in early spring competition for moisture among interconnected ramets may not yet be very important.

Materials and methods

A description of the study site and its climatic characteristics can be found in Chapter II. Paddock number

10 of the short-duration grazing cell was used for the present study. Soil type was the same as in the experiments described in Chapters II, III, and IV: a coarse-loamy, mixed (calcareous), mesic, Torrifluventic Haploxeroll (Jensen 1983). During the course of this experiment the paddock was not grazed.

The study started on 5 April 1989, with the marking of 272 newly emerged shoots of western wheatgrass (1-2 leaf stage) in homogeneous monospecific stands. This was followed on 12 April 1989 by the marking of 200 similar shoots of intermediate wheatgrass. The marked western wheatgrass shoots were allocated to 16 different blocks, each block containing 14 shoots. [The distance between individual target shoots within a block was at least 2.5 m.] The shoots were then randomly assigned to one of the following 14 clipping treatments:

1 defoliated to 5 cm stubble height before stem elongation[1]; the same for surrounding ramets within a 1 m radius.

2 defoliated to 5 cm stubble height after stem elongation; the same for surrounding ramets within a 1 m radius.

3 defoliated to 5 cm stubble height before stem elongation, target ramet only.

4 defoliated to 5 cm stubble height after stem elongation, target ramet only.

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[1] Not all western wheatgrass shoots showed internode elongation.

5 defoliated to 5 cm stubble height twice, before and after stem elongation; the same for surrounding ramets within a 1 m radius.

6 defoliated to 5 cm stubble height twice, before and after stem elongation, target ramet only.

7 defoliated to 5 cm stubble height once before stem elongation; surrounding ramets within a 1 m radius twice.

8 defoliated to 5 cm stubble height once after stem elongation; surrounding ramets within radius twice.

9 defoliated to 5 cm stubble height twice; surrounding ramets within a 1 m radius once before stem elongation.

10 defoliated to 5 cm stubble height twice; surrounding ramets within a 1 m radius once after stem elongation.

11 no defoliation of target tiller, but ramets within a 1 m radius defoliated to 5 cm stubble height once before stem elongation.

12 no defoliation of target tiller, but ramets within a 1 m radius defoliated to 5 cm stubble height once after stem elongation.

13 no defoliation of target tiller, but ramets within a 1 m radius defoliated to 5 cm stubble height twice.

14 no defoliation at all (control).

The 200 intermediate wheatgrass shoots were assigned to 20 different blocks. Each block comprised 10 shoots, seven of which were randomly assigned clipping treatment 1, 2, 3, 4, 5, 6, or 14, and three of which had their clonal rhizome connections severed. Again, the minimum distance between target shoots within a block was 2.5 m. The shoot was severed from other modules by cutting rhizome connections at a distance of approximately 4 cm from the target shoot with a long (20 cm) knife. These severed shoots then received treatments 5, 6, or 14. An identical severing treatment, with 16 replicates, was applied to western wheatgrass. Because of the young age of the shoots, imposition of the severing treatments was delayed until 16 May 1989, approximately 45 days after shoot emergence.

The first defoliation of intermediate wheatgrass took place on 27 April 1989, and the second on 2 June 1989. Western wheatgrass was clipped on 2 May and 11 June 1989. Surviving ramets of western wheatgrass were defoliated again the following year, on 8 May and 6 June 1990; dead leaves on shoots were not included in the determination of phytomass in 1990. The dry weight of the clipped foliage of the target shoots was determined directly while the phytomass of ramets which were not defoliated was established by clipping and weighing nearby tillers of identical size and with the same number of leaves.

The growth and fate of each target tiller was monitored at regular intervals for one year in the case of intermediate wheatgrass and for nearly 19 months in the case of western wheatgrass. Numbers of leaves produced were counted; this was facilitated by the fact that dead leaves or parts thereof remained attached to the ramet as long as it was alive. However, following winter, the number of leaves produced by western wheatgrass shoots could no longer be determined accurately. Tiller height was measured as the distance from ground level to the tip of the latest fully expanded leaf. A ramet was considered dead when it had lost all green color. New axillary tillers were marked with color-coded rings denoting the census date on which they were first observed.

The experimental design for both species was a randomized complete block design with 20 replicates for intermediate wheatgrass and 16 replicates for western wheatgrass. Analysis of covariance was used to test for the significance of treatment effects on phytomass production by target ramets of intermediate wheatgrass with initial ramet weight on 27 April 1989, as the covariate. Analysis of variance was used for assessing the effects of the various clipping regimes on the phytomass produced by western wheatgrass ramets and on the tiller height and number of leaves of both species. Where necessary, data transformations were carried out to meet the assumptions of homoscedasticity and normality. A chi-square goodness-of-fit test was used to test for significant differences in tiller recruitment. Testing of certain pre-planned comparisons was done by constructing the appropriate linear contrasts which were not necessarily mutually orthogonal. A *post hoc* test, Fischer's protected LSD (FPLSD), was used to test for significant differences in shoot height. The influence of the different clipping regimes on the survival of the target shoots was evaluated by employing Peto and Peto's log-rank test (Pyke and Thompson 1986).

Results

Effects of severing clonal connections

All shoots of intermediate wheatgrass and virtually all western wheatgrass shoots that had been severed from their respective clones died within two weeks. Closer examination of the shoots revealed that the three surviving western wheatgrass shoots (out of a total of 48) had been able to form some adventitious roots. We had planned to mark the shoots for this study in the fall of 1988 but due to a lack of precipitation very few shoots emerged at that time. Evidently the young shoots emerging in early April 1989 had insufficient time to become physiologically independent by the middle of May with respect to their water and nutrient requirements.

Effects of defoliation on Intermediate wheatgrass

Shoot growth

Early growth of intermediate wheatgrass was determined at the same time the second defoliation was imposed, June 2nd. Therefore, with respect to the effects of defoliation on early shoot growth, several of the original seven clipping treatments were identical. There were basically only three treatments: (1) no defoliation at all (treatments 2,4 and 14), (2) defoliation of the target shoot only (treatments 3 and 6), and (3) defoliation of shoot and surrounding ramets (treatments 1 and 5). Table 5.1 shows the aboveground biomass produced by the target shoots under these seven different clipping regimes.

Intermediate wheatgrass shoots displayed overcompensation (sensu Belsky 1986) in response to defoliation. Clipping to a 5 cm stubble height resulted in improved early growth of the target shoots (t_{109}=1.73, p=0.086) compared to the control shoots. This response to defoliation was even more pronounced when surrounding ramets were defoliated at the same time (t_{109}=2.21, p=0.029).

Shoot survival

The defoliation treatments differed in their effect on the survival of the target shoots. Defoliation of shoots twice (treatment 6) or once after internode elongation (treatment 4) but not of the surrounding ramets led to earlier mortality (Fig. 5.1). No significant difference was detected between the survival distributions of the ramets subjected to these two clipping treatments. The survival distributions of shoots receiving any of the four other defoliation treatments did not differ from that of the control shoots (Table 5.2).

Table 5.1. Phytomass produced by intermediate wheatgrass shoots (g DM) subjected to seven different clipping regimes. Data are the adjusted means of the analysis of covariance (Root MSE = 0.031). For a description of the treatments, see text.

Treatment	Phytomass	n
	g	
No defoliation		
2	0.100	19
4	0.104	20
14	0.094	20
Target shoot defoliated		
3	0.108	19
6	0.112	19
Uniform defoliation		
1	0.115	20
5	0.112	19

Tiller proliferation

Defoliation of the shoot itself had relatively little impact on the formation of new tillers (Table 5.3). Also time of defoliation had no significant effect on the recruitment of new tillers. However, when defoliation was uniform, i.e., when the target shoot and the ramets surrounding it were defoliated, there was some indication that more frequent defoliation (treatment 5 vs. treatments 1 and 2) may have a negative effect on the recruitment of tillers (X^2_1=2.11, p=0.146).

The effect of clipping as a modifier of competitive stress on the recruitment of tillers was more pronounced.

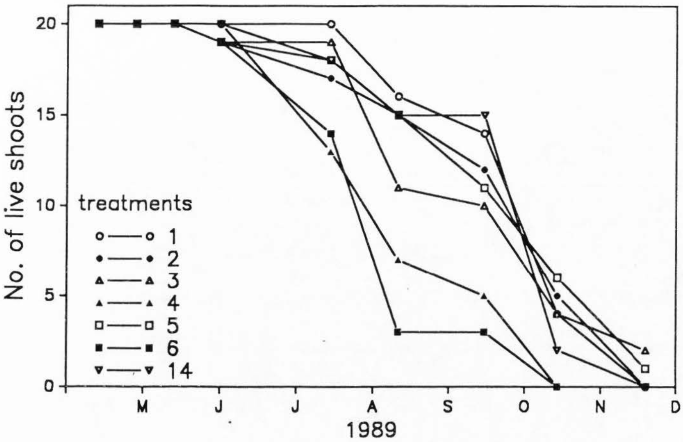

Fig. 5.1. The survivorship of intermediate wheatgrass shoots subjected to various defoliation treatments. For a description of the different treatments, see text.

Table 5.2. Pairwise comparisons of survival distributions of intermediate wheatgrass shoots subjected to various defoliation regimes (Peto and Peto's log-rank test: p-values). For a description of the treatments, see text.

Treatment	1	2	3	4	5	6	14
1		ns	ns	<0.001	ns	<0.001	ns
2			ns	0.007	ns	0.002	ns
3				0.020	ns	0.005	ns
4					0.006	ns	0.002
5						0.002	ns
6							<0.001

ns: not significant (p>0.100)

Clipping of the surrounding ramets (treatments 3,4,6 vs. 1,2,5) increased the number of recruits produced by the target shoots (X^2_1=3.15, p=0.076).

Winter mortality of the axillary tillers produced in this study was very low. Of the 213 axillary tillers produced in the fall of 1989, only three died during the winter: one (3.2 percent of the total number) on a shoot subjected to treatment 5, and two (7.4 percent) on shoots subjected to treatment 6. It appears that in intermediate wheatgrass a shoot is not just replaced by a new tiller; rather, the emergence of a new shoot marks the beginning of the formation of a new cluster of tillers. Under all defoliation regimes, a shoot produced, on average, two axillary tillers or more.

Table 5.3. Number of intermediate wheatgrass axillary tillers produced per original shoot within one year of the implementation of the defoliation treatments. For a description of the treatments, see text.

Treatment	Recruits
1	2.80
2	2.90
3	2.00
4	2.35
5	2.20
6	2.05
14 (control)	2.35

Leaf number

The defoliation treatments did not affect the number of leaves produced per live shoot. At none of the eight census dates did clipping significantly affect the number of leaves produced. Following the defoliation on June 2, 1989, most new leaves were produced by shoots assigned to clipping treatments 1, 3, and the control, indicating that clipping at 5 cm on that date removed most of the apical meristems (Fig. 5.2).

Shoot height

Significant differences in tiller height occurred as a result of the clipping treatments (Fig. 5.3). On 12 May 1989, 15 days after the first defoliation, shoots that had been defoliated at that time were shorter than the control shoots ($p<0.050$). However, the shoots which were not clipped for a second time on the 2nd of June, viz.,

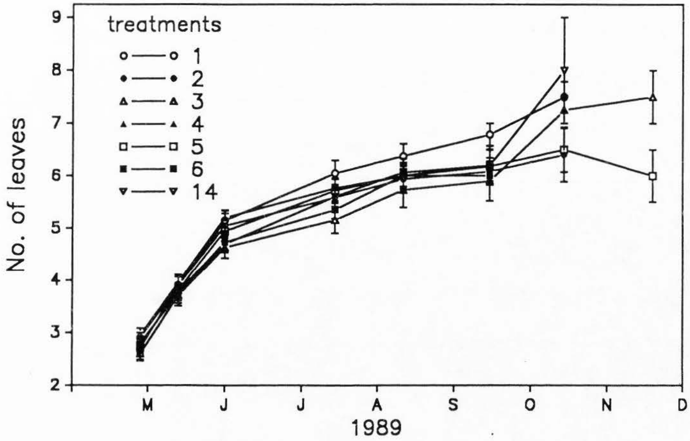

Fig. 5.2. The number of leaves (± 1 SE) produced by intermediate wheatgrass shoots subjected to various defoliation treatments. For a description of the different treatments, see text. (n varies for each date and treatment, see Fig. 5.1).

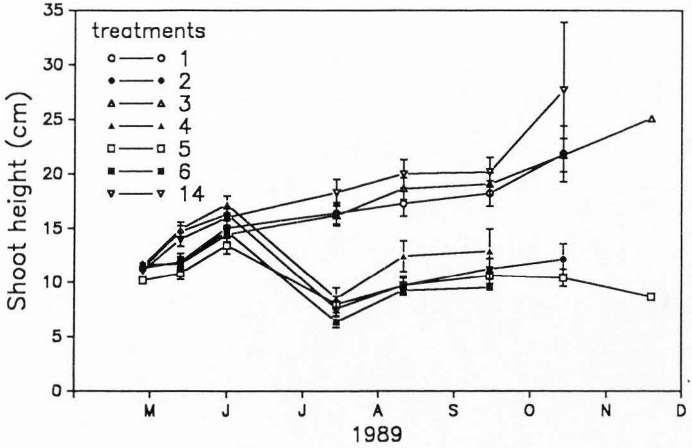

Fig. 5.3. Height (± 1 SE) of intermediate wheatgrass shoots subjected to various defoliation treatments. For a description of the different treatments, see text. (n varies for each date and treatment, see Fig. 5.1).

treatments 1 and 3, ceased to be significantly shorter than those of the control after that date. Shoots of these three treatments stayed significantly taller for the remainder of this experiment than those that were clipped on the 2nd of June ($p<0.050$).

Effects of defoliation on Western wheatgrass

Shoot growth

With regard to shoot phytomass production up to the 2nd of June in the first year, there were four different treatments: (1) no defoliation at all (treatments 2,4,12,14), (2) defoliation of the target shoot only (treatments 3,6,10), (3) defoliation of the shoot as well as that of ramets in a 1 m radius (treatments 1,5,7,9), and (4) defoliation of a 1 m radius but not of the target shoot (treatments 8,11,13). Defoliation of shoots on 2 May 1989, had a negative effect on their phytomass production ($t_{190}=3.00$, $p=0.003$) whereas defoliation of the surrounding ramets had a highly significant positive effect on the growth of the target shoots ($t_{190}=4.50$, $p<0.001$). These effects of defoliation were additive (Fig. 5.4).

The negative effects of clipping of the target shoots carried into the following year (Fig. 5.5). On 8 May 1990, the size of the surviving shoots that had not been defoliated was significantly larger than that of shoots

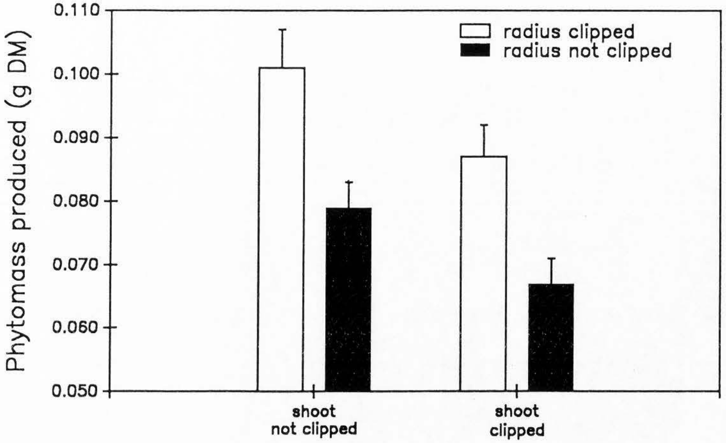

Fig. 5.4. The phytomass produced (+ 1 SE) by clipped and intact western wheatgrass shoots as affected by the defoliation of surrounding ramets (n=47 for radius clipped/shoot intact; n=52 for radius not clipped/shoot intact; n=53 for radius clipped/shoot clipped; n=47 for radius not clipped/shoot clipped).

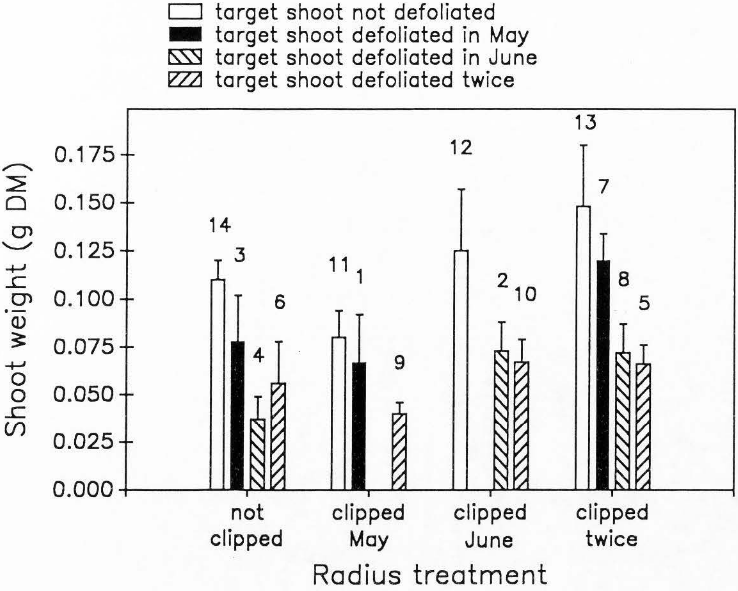

Fig. 5.5. The phytomass (+ 1 SE) of surviving western wheatgrass shoots on 8 May 1990. For a description of the different treatments, see text. (n varies for each treatment, see Fig. 5.6).

that had been clipped twice during the previous growing season (t_{64}=3.32, p=0.001). They were also heavier than those clipped in June 1989 (t_{64}=3.15, p=0.002). The difference in size between undefoliated shoots and shoots clipped in May of the previous year was not statistically significant (t_{64}=1.54, p=0.128).

Whereas defoliation of surrounding ramets on 2 May 1989 had an immediate positive impact on the growth of the target shoots (Fig 5.4), there was little carryover effect into the following year (Fig. 5.5). On 8 May 1990, the size of shoots whose radii had been clipped in May 1989 did not differ from those whose radii remained intact. When the radii, however, were clipped twice in 1989, a significant increase in shoot size was observed the following year (t_{64}=2.31, p=0.024). The phytomass of the shoots whose radii were clipped in June 1989 was intermediate between those whose radii were either clipped early May 1989 or not clipped at all, and those whose radii were clipped twice. These effects of defoliation were reflected in the total phytomass produced by the surviving shoots during the 1990 growing season (Table 5.4). In this case, though, the contrast between no defoliation of the target shoots (treatments 12,13 and 14) and defoliation of these shoots in June (treatments 2,8 and 4) was the only one that was statistically significant (t_{46}=2.44, p=0.018).

Table 5.4. Phytomass (g DM) produced by western wheatgrass shoots (± 1 SE) in two seasons as affected by 14 clipping regimes. For a description of the treatments, see text.

Treatment	1989	n	1990	n
	g		g	
1	0.089 (± 0.009)	15	0.153 (± 0.075)	3
2	0.084 (± 0.010)	16	0.090 (± 0.022)	7
3	0.070 (± 0.008)	16	0.119 (± 0.040)	7
4	0.076 (± 0.008)	16	0.040 (± 0.010)	3
5	0.081 (± 0.009)	14	0.108 (± 0.021)	6
6	0.066 (± 0.007)	16	0.115 (± 0.039)	4
7	0.089 (± 0.007)	14	0.207 (± 0.038)	3
8	0.099 (± 0.012)	16	0.084 (± 0.020)	9
9	0.091 (± 0.015)	10	0.080 (± 0.015)	3
10	0.066 (± 0.007)	15	0.088 (± 0.021)	5
11	0.089 (± 0.010)	15	0.090 (± 0.025)	8
12	0.073 (± 0.009)	15	0.206 (± 0.084)	5
13	0.115 (± 0.010)	16	0.164 (± 0.034)	7
14	0.083 (± 0.007)	15	0.102 (± 0.008)	4

Shoot survival

Results were somewhat inconclusive concerning the effects of defoliation on the survival of western wheatgrass shoots (Table 5.5, Fig 5.6). Defoliation of the target shoot twice appeared to increase the risk of mortality of young western wheatgrass shoots (treatments 5,6,9,10 vs. 13,14,11,12), but this effect was not significant (p=0.164) using Peto and Peto's log-rank test. However, clipping of the surrounding ramets twice (treatments 5,7,8,13 vs. 6,3,4,14) decreased the risk of shoot mortality as compared to leaving the radius intact (p=0.070). Time of clipping of either the shoot itself or its radius had little effect on the survival of western

Table 5.5. Pairwise comparisons of survival distributions of western wheatgrass shoots subjected to various defoliation regimes (p-values) (see Fig. 5.6). Only the differences that were significant ($p<0.100$) according to Peto and Peto's log-rank test are reported. For a description of the treatments, see text.

Treatment	3	4	5	6	8	9	11	12	13
1	0.077								
2	0.087								
3		0.012		0.050		0.052			
4			0.048		0.017		0.051	0.077	0.021
5									
6					0.076				0.098
7									
8						0.067			
9									0.082
10									
11									
12									
13									
14									

wheatgrass shoots.

Cumulative phytomass production

The combined effects of defoliation regime on shoot productivity and longevity are reflected in the phytomass produced per original shoot (Table 5.6). Clipping the shoots twice during the growing season significantly reduced their overall performance compared to both nondefoliated shoots ($t_{195}=3.06$, $p=0.003$) and shoots defoliated early in the growing season ($t_{195}=2.11$, $p=0.036$). Clipping all the ramets in the immediate vicinity of target shoots increased the cumulative

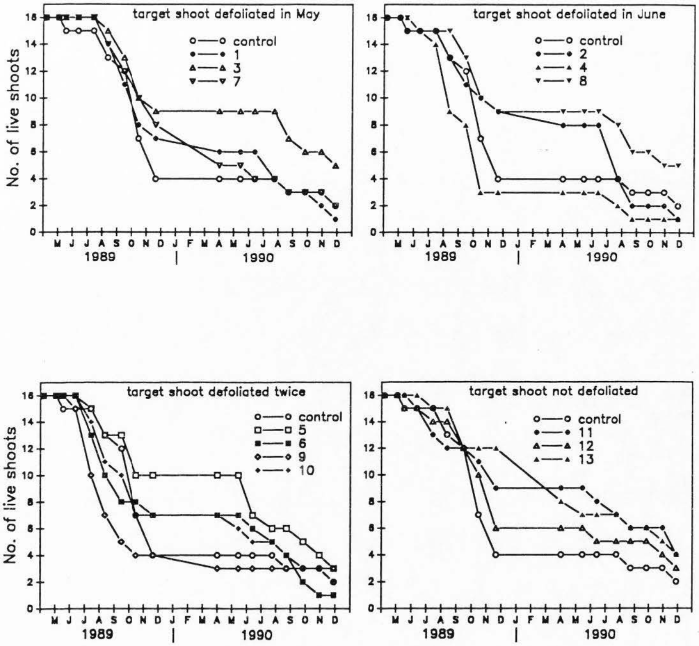

Fig. 5.6. The survivorship of western wheatgrass shoots subjected to various defoliation treatments. For a description of the different treatments, see text. The survivorship of the control shoots is depicted in all four panels to facilitate comparison between the various treatments.

Table 5.6. Total phytomass produced by western wheatgrass shoots in 1989 and 1990 under various clipping regimes (g DM). For each individual shoot the highest recorded phytomass production was used. Data are geometric means.

Shoot	Not clipped	Clipped May	Clipped June	Clipped twice
Radius				
Not clipped	0.093^{abc}	0.106^{bcd}	0.076^{ab}	0.078^{ab}
Clipped May	0.109^{bcd}	0.100^{bc}	-	0.063^{a}
Clipped June	0.096^{abc}	-	0.104^{bc}	0.085^{abc}
Clipped twice	0.162^{d}	0.102^{bc}	0.128^{cd}	0.099^{bc}

Data followed by the same letter are not significantly different according to $FPLSD_{0.05}$.

phytomass produced by these target shoots but this effect was statistically significant only when the surrounding ramets were clipped twice during the growing season (t_{195}=2.93, p=0.004). Clipping the surrounding ramets twice also resulted in significantly higher phytomass production by the target shoots than either clipping early (t_{195}=2.27, p=0.024) or late (t_{195}=2.33, p=0.021) in the growing season.

Tiller proliferation

Defoliation of the radii had no significant effect on the recruitment of new ramets, but clipping of the shoots themselves resulted in the production of fewer new tillers

(Table 5.7). The difference in tiller recruitment between shoots that were clipped twice per year (treatments 5,6,9 and 10) and those that were not defoliated (treatments 13,14,11 and 12) was significant (X^2_1=6.04, p=0.014). Apparently in western wheatgrass, shoots are merely replaced by axillary tillers, and defoliation, especially when it takes place late in the growing season, is capable of reducing the degree of this replacement markedly.

Leaf number

The different defoliation treatments had relatively little impact on the leaf production of western wheatgrass shoots. None of these treatments resulted in shoots exserting significantly more or fewer leaves than the control shoots. However, there was a tendency for shoots with defoliated radii to resume leaf production somewhat earlier after summer dormancy than those that had their radii still intact, viz. treatments 3,4,6 and 14 (Fig. 5.7). The apparent exception was shoots subjected to treatment 3, but this may be somewhat of an artifact. In the fall of 1989, the number of leaves produced under this clipping treatment could be determined on only three of the ten shoots that were still alive at the time. During the previous months, shoots subjected to clipping treatment 3 behaved much like other shoots that had their radii still intact.

Table 5.7. Number of western wheatgrass axillary tillers produced per original shoot between April 1989 and November 1990 as affected by 14 different clipping treatments. For a description of the treatments, see text.

Treatment	Recruits
1	1.12
2	0.81
3	0.88
4	0.81
5	0.69
6	0.88
7	1.00
8	0.75
9	0.50
10	0.62
11	1.00
12	1.25
13	1.06
14 (control)	1.00

Shoot height

Defoliation of surrounding ramets had no significant effect on the height of the target shoot (Fig. 5.8). However, defoliation of the shoot itself in 1989 influenced the height of the surviving shoots in the spring of 1990. The heights of shoots clipped in June 1989 were significantly lower than those of unclipped shoots (May 1990: t_{18}=2.09, p=0.051 and June 1990: t_{17}=1.76, p=0.096), although the heights of these shoots did not differ in March 1990, immediately following the winter (treatments 2,4,8 vs. 12,14,13).

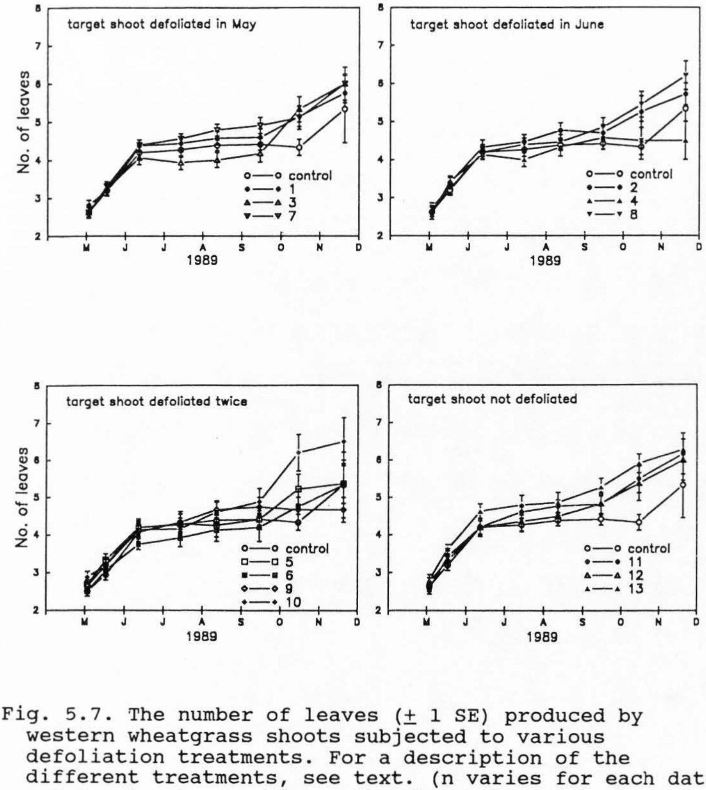

Fig. 5.7. The number of leaves (± 1 SE) produced by western wheatgrass shoots subjected to various defoliation treatments. For a description of the different treatments, see text. (n varies for each date and treatment, see Fig. 5.6). The number of leaves of the control shoots is depicted in all four panels to facilitate comparison between the various treatments.

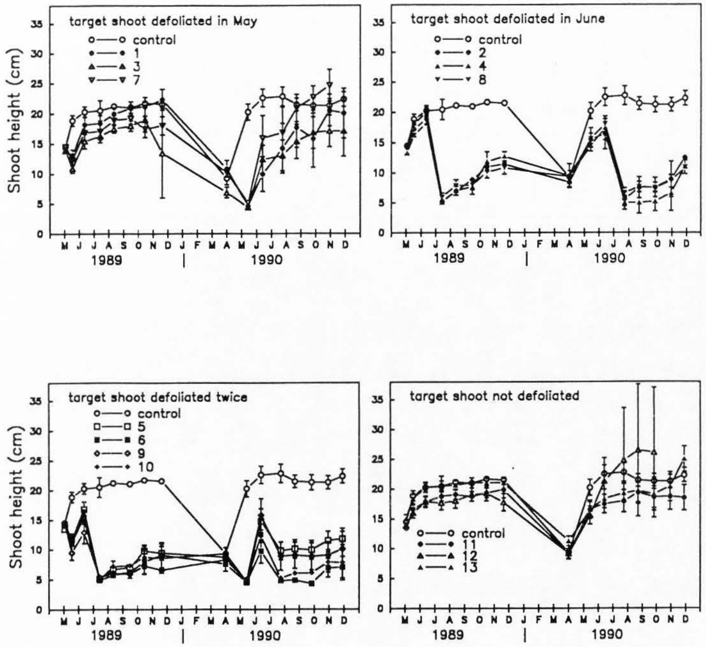

Fig. 5.8. Height (± 1 SE) of western wheatgrass shoots subjected to various defoliation treatments. For a description of the different treatments, see text. (n varies for each date and treatment, see Fig. 5.6). The shoot length of the control shoots is depicted in all four panels to facilitate comparison between the various treatments.

Discussion

The growth of young shoots in many rhizomatous and stoloniferous graminoids is supported by the acropetal transport of photoassimilates produced by established ramets (Forde 1966a,b, Fiveland et al. 1972, Nyahoza et al. 1973, Rogan and Smith 1974, Allessio and Tieszen 1975, Tietema 1980, Noble and Marshall 1983, Callaghan 1984). Young ramets are also dependent on water and mineral nutrients provided by older parts of the clone, at least until they have developed adventitious roots (Marshall 1990). A ramet usually attains photosynthetic self-sufficiency at a time when it still depends on water and nutrients imported from other parts of the clone (Marshall 1990). In the young shoots of both intermediate wheatgrass and western wheatgrass, the initiation of adventitious roots was preceded by considerable aboveground development. Approximately 45-day old shoots that were severed from the rest of their clones virtually all died within a few days, indicating that they were still dependent on the import of water and mineral nutrients two to three weeks after the imposition of the clipping treatments. Hartnett and Bazzaz (1983) and Slade and Hutchings (1987) demonstrated that early severing of ramets greatly increased their risk of mortality. Jonsdottir and Callaghan (1988) found the same to be true for <u>Carex</u> <u>bigelowii</u>, but in their study the survival of severed shoots was substantially higher when they already had developed roots. In our study, the three western wheatgrass shoots that did not die immediately after their isolation by physical severance of rhizomes had all developed some adventitious roots.

For the purpose of this experiment, we use the following definition of competition (Begon et al. 1986:203): " ...an interaction between individuals, brought about by a shared requirement for a resource in limited supply, and leading to a reduction in the survivorship, growth and/or reproduction of the competing individuals concerned." Within the radii of our experiment, competitive interactions may have occurred at three levels. Competition may have been intra-clonal[2]: target shoots may have competed for scarce resources with other ramets belonging to the same Integrated Physiological Unit (IPU)[3] (Watson and Caspar 1984). This IPU may have competed with other IPU's belonging to the same genet (intra-genotypic competition) and/or with other IPU's belonging to other genets (intra-specific or inter-genotypic competition (cf. Harper 1977). The interpretation of the data with respect to these

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[2] A more appropriate name would be intra-organismal competition (cf. Keddy 1989) because a clone may consist of many physiologically independent clonal fractions.

[3] Some would be hesitant to speak of "competition" in this case and would prefer usage of terms such as "resource allocation" and "coordinated growth and development."

competitive interactions is inevitably somewhat tentative because neither clonal identity nor the performance of the ramets in the radii is known.

The death of their severed counterparts indicates that the target shoots of the two grasses in this study were not physiologically independent when they were clipped late April/early May 1989. At that time, they were almost certainly receiving water and mineral nutrients from parent or sibling ramets and possibly photoassimilates as well. Thus, the early performance and the demographic behavior of these shoots was determined by the support each shoot received from ramets to which it was still interconnected. The magnitude of this support depended on the physiological status and the requirements of these interconnected ramets. Competitive interference from other ramets to which no such connection existed because they belonged to different clonal fragments or clones may also have affected the performance of the target shoot. This could have occurred indirectly through interference with the IPU of which the target shoot was a module, or directly after the target shoot had developed adventitious roots.

Clipping of surrounding ramets, which presumably reduces their competitive ability but also diminishes the level of support that young shoots may receive from interconnected ramets in the form of photosynthates, did not negatively impact the growth of target shoots. In fact, early growth of target shoots was stimulated by the defoliation of surrounding ramets, significantly so in western wheatgrass. This suggests that in this species under the conditions of our experiment, support for the young target shoots in the form of assimilates produced by interconnected and intact ramets was a less important factor influencing the growth of these shoots than the capture of nutrients and water by the clonal fraction of which the target shoot was a module.

In intermediate wheatgrass, support for defoliated shoots by interconnected and undefoliated ramets, either directly in the form of translocated photosynthates or indirectly through mobilization of stored carbohydrates, apparently was strong. A reduction in the translocation of photoassimilates through defoliation of interconnected ramets and a concurrent relaxation of competitive interference from unconnected ramets did not significantly affect the growth of the defoliated target shoots during May 1989. It is not known whether an increase in photosynthetic rates following defoliation contributed to the response of the target tiller.

The finding that a defoliated ramet performed as well or even better when surrounding ramets are clipped concurrently contrasts with a large body of experimental evidence which shows that when certain parts of a clone are stressed, for instance as a result of defoliation, the stressed ramets are supported by their intact counterparts (Nyahoza et al. 1973, Rogan and Smith 1974, Pitelka and Ashmun 1985, Schmid et al. 1988, Jonsdottir and Callaghan 1989). Noble and Marshall (1983), on the other hand, found no evidence that defoliated ramets of Carex arenaria in the field imported ^{14}C-labelled assimilates from intact shoots, although such transport was observed in a greenhouse experiment. They attributed this difference to the presence of a readily available pool of reserve carbohydrates in the belowground organs of the field-grown plants. We assume that at the time of defoliation the target shoots in our study were already largely self-sufficient in terms of their carbon economy (cf. Alpert and Mooney 1986) and that a sufficiently large pool of stored carbohydrates was available in the below ground organs of these rhizomatous species to buffer any temporary shortfall in photosynthates.

The finding that the performance of the target shoots generally improved as a result of the defoliation of surrounding ramets agrees to some extent with those of Mattheis et al. (1976). They found in a severance experiment that young shoots of Dupontia fischeri were supported by older ramets. However, when they compared the leaf production on a single defoliated tiller with that of a defoliated tiller whose parent and sibling ramets were clipped as well, they noticed that leaf production of the single defoliated tiller was lower. Based on this they tentatively concluded that the tillers of this arctic grass do not support one another, but they thought that a "canopy effect" might have obscured the actual response. Archer and Detling (1984), who found that defoliated tillers of Andropogon gerardi and Carex filifolia produced more biomass and lived longer when neighboring ramets were defoliated as well, also suggested that the clipped tillers might have been shaded by undefoliated ramets, thereby reducing their chances for recovery.

We too believe that the improved performance of the target shoots with clipping of the radii in our study was due to an alleviation of the competitive stress experienced by these shoots (and by the ramets functionally connected to them) from unconnected ramet groups. This decrease in intensity of competition between IPU's was more important for the growth and development of the target shoots than any reduction in intraclonal support that might have occurred concurrently as a result of defoliation of interconnected ramets. However, the structure of the intermediate wheatgrass and western wheatgrass swards at the study site makes it highly unlikely that shading was a factor in the regrowth of clipped shoots. Young shoots of intermediate wheatgrass were all placed at some distance away from tiller tufts while in western wheatgrass the foliage was generally sparse with a uniform distribution of tillers. Defoliation has been shown to relieve water stress in plants and to promote soil water conservation (Svejcar and Christiansen 1987, Wraith et al. 1987). These effects may have been responsible for the better vegetative growth and improved survival of ramets (cf. McNaughton 1983, McNaughton et al. 1983). Olson and Richards (1988), working at the same site where our study was conducted, likewise attributed an increase in the number and height of replacement tillers in Agropyron desertorum tussocks to a reduction in soil moisture extraction under more frequent defoliation.

Young unrooted ramets are supplied with water and nutrients by their older and established counterparts (Alpert and Mooney 1986, Jonsdottir and Callaghan 1990), but the direction of water and nutrients transport between integrated ramets may be altered as a result of differential water potentials within a clone. Tietema and van der Aa (1981) found that due to their larger leaf area, older shoots on rhizome axes of Carex arenaria had lower water potentials than younger shoots. Consequently, the water flow in the rhizomes was basipetal. This agrees with findings of Alpert and Mooney (1986) who under favorable conditions measured a water potential gradient along the stolon axis of the herbaceous perennial Fragaria _chiloensis_. This gradient allowed unrooted rosettes to draw water from older established rosettes; however, when the whole plant became droughted, these unrooted ramets wilted first. Together with interference from unconnected ramets, such a difference in transpirational demand among integrated ramets may explain why the worst performing target shoots in the present study were those that were defoliated but whose surroundings remained intact.

It was somewhat surprising that the positive response to the defoliation of surrounding ramets was evident relatively early in the growing season. However, precipitation during the period November 1988 to May 1989 amounted to less than 59 percent of the long term average, which represented a deficit of 103 mm. The positive consequences of the defoliation of surrounding ramets for shoot survival were not unanticipated. Competition for water is an important determinant of the growth and development of these grasses during the later part of the growing season.

Early clipping had no detrimental impact on the growth of intermediate wheatgrass shoots, regardless of whether surrounding ramets were defoliated simultaneously or not. Early defoliation of the young intermediate wheatgrass shoots even had a small beneficial effect on their growth. This suggests, but does not prove, that these shoots following defoliation to 5 cm were strongly supported by undefoliated parent and sibling ramets.

Increased translocation of carbon from intact to defoliated modules was demonstrated in several graminoid species (Forde 1966b, Nyahoza et al. 1973, Jonsdottir and Callaghan 1989) but no such increase in carbon translocation was found when all modules of a clone were defoliated (Rogan and Smith 1974, Jonsdottir and Callaghan 1989). In addition to improved soil moisture availability, the strong regrowth of defoliated intermediate wheatgrass shoots whose parent and sibling tillers were defoliated at the same time may also have resulted from a rapid mobilization of stored carbohydrate reserves. Shoots of Panicum virgatum showed significant overcompensation in growth following uniform defoliation of all ramets, but the fraction of biomass allocated to rhizomes was markedly reduced (Hartnett 1989).

The strong regrowth of early-defoliated shoots of intermediate wheatgrass with their surrounding ramets still intact differs sharply from that of similarly treated shoots in western wheatgrass. This suggests that the support for young shoots by undefoliated ramets was greater in intermediate wheatgrass than in western wheatgrass or, conversely, that competition from surrounding intact ramets was greater in western wheatgrass. This observation seems to support the thesis that species with a phalanx type clonal architecture, such as intermediate wheatgrass, have a higher degree of physiological integration than those with a guerilla type of architecture (Schmid and Bazzaz 1987, Hutchings and Mogie 1990), such as western wheatgrass. However, in our study, neither the clonal identity of the ramets in the radii, nor the functionality of their connections was known exactly. In this context, it may be significant that, on average, a shoot of intermediate wheatgrass produced two axillary tillers. It could indicate that a shoot of intermediate wheatgrass enjoys a special position among the ramets of an IPU (see also Chapter VI).

Time of defoliation apparently was not an important factor affecting the demography of intermediate wheatgrass shoots, as long as defoliation was uniform. Though defoliation on 2 June 1989 must have removed the apical meristem in most shoots, the survival of these shoots, as indicated by the continued presence of green tissue, was only negatively impacted by this late defoliation when surrounding ramets remained intact. When surrounding ramets were also defoliated on that date, survival of the defoliated target shoots did not differ from those of the control shoots. The same was true in western wheatgrass.

When the target shoots were clipped early (May 2) but the surrounding ramets were left intact, no such increase in mortality risk was found. The longer presence of an active apical meristem and a larger leaf area may have made these early-clipped shoots better competitors for water later in the growing season than those defoliated 40 days later (June 11). If translocation of assimilates from intact to defoliated shoots played a role in this experiment, this support was probably more prominent early in the experiment. Environmental conditions play a role in the translocation of assimilates; when plants are drought stressed, the movement of assimilates in plants is often reduced (Moser 1977). Early in the growing season, conditions were more favorable and the defoliated shoots still had apical meristems acting as strong sinks for photoassimilates produced in other parts of the clone.

Generally, intermediate wheatgrass shoots reacted better to defoliation than western wheatgrass shoots. In addition to the possibility of a higher degree of physiological integration in intermediate wheatgrass, this difference may also be due to a larger photosynthetic area remaining on the shoots of intermediate wheatgrass following clipping than on shoots of western wheatgrass. Recruitment of new tillers was reduced more by defoliation in western wheatgrass than in intermediate wheatgrass. In intermediate wheatgrass tiller recruitment was not significantly affected by time or frequency of defoliation as long as defoliation was uniform. In western wheatgrass, on the other hand, shoots that were clipped twice during the growing season formed significantly fewer axillary tillers than their undefoliated counterparts.

Because of the contrary effects of defoliation on shoot growth on the one hand and on the intensity of competition among western wheatgrass ramets on the other, uniform clipping had little effect on the performance of the target shoots. None of the uniform clipping treatments, viz., 1, 2 and 5, significantly affected shoot performance compared to the control. Although no short-term effect of uniform defoliation could be detected in western wheatgrass, a long-term negative effect of uniform defoliation may be present in the form of reduced levels of reserve carbohydrates. Often the more obvious negative responses to defoliation occur in the levels of stored carbohydrates rather than in aboveground biomass production (e.g., Mattheis et al. 1976, Archer and Detling 1984, Stout and Brooke 1985, Hartnett 1989).

CHAPTER VI

SYNTHESIS

Plants can respond to defoliation in a number of ways. The type of response and its intensity depend on a variety of factors such as the time, severity, frequency, and uniformity of defoliation, and are mediated by the plant's phenological stage and its physiological status as determined by resource availability, competitive background, and defoliation history. Inherent factors determining a plant's grazing resistance play a major role as well (Briske 1990).

The use of a grazing system is a way in which the grazier can control to some extent the factors of time, severity, frequency, and uniformity of defoliation of individual plants. The degree of defoliation may affect a plant's competitive ability with other plants of the same or different species and, through time discrepancies in competitive abilities, can result in community changes.

The principal objective of this study was to examine whether short-duration grazing played a role in the competitive interactions between intermediate wheatgrass (*Thinopyrum intermedium*) and western wheatgrass (*Pascopyrum smithii*). Particular emphasis was placed on the confirmation or refutation of earlier observations concerning the competitive superiority of intermediate wheatgrass under this type of grazing system. An affirmation of these observations would be a strong endorsement of this grazing system because intermediate wheatgrass is preferred by the grazing animal.

Intermediate wheatgrass and western wheatgrass have distinctly different growth forms. Intermediate wheatgrass produces rhizomes that have been called "determinate" (Berg 1972); they terminate in a single shoot or a cluster of tillers. Rhizomes in western wheatgrass, on the other hand, are "indeterminate" with aerial shoots produced progressively along rhizome axes. These different growth forms have been classified as, respectively, "phalanx" and "guerilla" by L. Clegg (in Harper 1978).

Rhizomes are stout in intermediate wheatgrass whereas they are slender with relatively long internodes in western wheatgrass. However, significant variation exists in internode length. Horizontal spread is greater in western wheatgrass than in intermediate wheatgrass. In intermediate wheatgrass buds on young established ramets develop into aerial shoots, whereas buds on western wheatgrass ramets mostly tend to form plagiotropic rhizomes or to remain dormant. Sometimes, however, they produce orthotropic tillers as well.

This difference in bud development partly explains the higher tiller recruitment on shoots of intermediate wheatgrass observed in Chapter V. Occasionally, though, intermediate wheatgrass ramets will produce a runner, particularly after significant accumulation of tillers in tufts (G.B. Bartels, personal observations). Because of these differences in bud development and rhizome morphology, western wheatgrass not only has a greater allocation of biomass in belowground structures than intermediate wheatgrass (G.B. Bartels and B.E. Norton, unpublished data) but its modules and buds are also more dispersed and more evenly distributed than those of intermediate wheatgrass, which has localized aggregations of tillers. The stands of these two species, therefore, possess very different spatial structures. In this dry ecosystem ramets of western wheatgrass are loosely arranged. This probably contributes to the low acceptance of this grass by grazing animals.

Related to these differences in clonal architecture are growth strategies that differ with respect to resource acquisition (Harper 1985, de Kroon and Schieving 1990). Although a certain degree of plasticity seems to be present in western wheatgrass with respect to internode length and rhizome branching, morphologically this species is ideally suited to rapidly colonize open space. Intermediate wheatgrass clones, on the other hand, are unable to expand rapidly; this species relies on consolidation of the occupancy of sites by dense tiller growth and concentration of roots, which precludes the invasion and establishment of other species. Clonal expansion can only be very gradual.

The primary focus of this study was on the competitive interactions between intermediate wheatgrass and western wheatgrass. The possibility of allelopathy playing a role in these interactions was considered but it was found to be unimportant (Appendix D). The phenomenological approach of Chapter III showed that during the four years covered by the study, western wheatgrass was the dominant competitor. The contrasting clonal morphologies and growth strategies referred to earlier may have contributed to the outcome of the competitive interactions observed in our studies.

Schmid and Harper (1985) studied the competition between the phalanx type _Bellis perennis_ and the guerilla type _Prunella vulgaris_ and found that competition between these two species was density-dependent, which they attributed to differences in growth form. They noted a density-dependent reversal in competitive hierarchy with the phalanx type being aggressive at high ramet densities but subordinate when densities were low. At low densities the guerilla type was able to exploit space more quickly than the phalanx type, whereas at high densities the phalanx type was able to persist, occupy sites, and gradually expand into space previously held by the guerilla type.

In our experiment with different water regimes we did not see such a complete reversal in the outcome of competition between intermediate wheatgrass and western wheatgrass. However, data showed the competitive ability of intermediate wheatgrass improved when more water was available. Schmid and Harper's (1985) results and models (Sutherland and Stillman 1990) showed that the competitively inferior guerilla growth form could dominate communities when disturbances occur. This suggests that the outcome of the competitive interactions in our studies (Chapters III and IV) was likely as much a consequence of distinct differences in clonal growth form as of physiological, phenological, demographic, and other morphological characteristics that differentiate these two species.

The fact that western wheatgrass emerged as the dominant competitor in our studies should not be accepted uncritically, though, since doing so would overlook aspects of asymmetry in the competitive interactions between these two species that do not pertain to the species *per se* nor to the treatments imposed. Rather, the results should be viewed within the context of the grazing history of the site. During a number of years prior to the start of our experiments, intermediate wheatgrass was grazed heavily while western wheatgrass was virtually neglected (B.E. Norton, personal observations). This discrepancy in the intensity of defoliation was also in evidence during the first two years of our study. It most likely diminished the competitive ability of intermediate wheatgrass versus western wheatgrass from the first year of data collection. Because of the greater sensitivity of western wheatgrass to defoliation (Chapter V), the possibility that the outcome could have been different if such historically determined asymmetry had been absent can not be completely ruled out. The results of Chapters II and III indicated that growth of intermediate wheatgrass suffered the most from the presence of western wheatgrass when the degree of defoliation between them was greatly different. This alludes to the inadequacy of the "high productivity grazing" concept (Booysen and Tainton 1978) in this particular case. Unfortunately, our data (Chapter IV, in particular) can merely hint at the possibility that uniform grazing of both species simultaneously may shift the competitive balance between them. The short time-span of this study does not allow demonstration of this conclusively.

More proof of a possible reversal in the competitive hierarchy of these two species was found in response to supplemental water, both under short-duration grazing and, especially, protection from grazing. The improved ability of intermediate wheatgrass to compete with western wheatgrass in wetter conditions under short-duration grazing as indicated by our experiment, however, has limited practical significance. The irrigated areas comprised only a small portion of the paddock and the animals were attracted to these areas. This resulted in artificially high levels of western wheatgrass utilization.

Methodological emphasis in our studies was on the observation of tiller dynamics. This was done on the basis of cohorts rather than individual ramets. This choice of level of organization resulted in larger samples and, therefore, allowed a more realistic representation of the vegetational dynamics occurring in the paddocks. However, this approach had drawbacks in that certain details requiring finer scales of measurement and destructive sampling, such as the elevation of apical meristems, could not be ascertained, complicating the interpretation of the results. The selection of a methodology with greater resolution would have yielded more accurate information on the growth, phenology, and the actual agents of death of individual ramets. Ideally, when temporal constraints allow, measurements should be made at both scales simultaneously.

Our approach revealed that intermediate wheatgrass and western wheatgrass differed appreciably in their strategies to cope with environmental variation. The strategy of intermediate wheatgrass resulted in large yearly fluctuations in ramet density, whereas these fluctuations were dampened in western wheatgrass. The patterns of tiller recruitment and death in both species, but particularly in intermediate wheatgrass, apparently were dominated by the flowering process.

The different ramet life histories of these two grasses are best symbolized by their different survivorship curves. Ramets of intermediate wheatgrass belonging to the same cohort died more or less simultaneously after a certain life span whereas those of western wheatgrass appeared to exhibit an age-independent mortality rate, though some seasonal fluctuations in mortality rate were observed. This difference in pattern of ramet mortality between these two species is believed to be due to fundamental differences in the environmental requirements for sexual reproduction and, by association or independently, internode elongation. These requirements are more stringent in intermediate wheatgrass than in western wheatgrass. Consequently, intermediate wheatgrass has to replace its tillers each year because virtually every cohort starts to senesce at the same time regardless of its time of origin.

Intermediate wheatgrass, then, tracks yearly climatic variation by adjusting tiller birth rates to resource availability. Recruitment of new ramets appeared to be density-dependent, a feature which would be characteristic of perennial species with a phalanx growth form (Dickerman and Wetzel 1985, Schmid and Harper 1985, de Kroon and Schieving 1990). The average life span of intermediate wheatgrass ramets was not greatly altered by defoliation or supplemental moisture. Western wheatgrass, on the other hand, reacted to worsening growing conditions with a reduction in ramet turnover, a conservative strategy that has adaptive value in nutrient-poor situations (cf. Noble et al. 1979, Fetcher and Shaver 1983, Carlsson et al. 1990) and probably also in dry environments.

Because genet survival depends on the replacement of ramets, the opportunistic strategy of intermediate wheatgrass means that there is a critical period each year in the life of its clones which does not exist, at least not to the same degree, for western wheatgrass. Any circumstance which delays or restricts the recruitment of new intermediate wheatgrass ramets during late summer or fall will reduce ramet density of this species and, consequently, its competitive ability. Our data and theoretical considerations suggest that time of grazing may have some effect, with grazing after internode elongation being somewhat better, especially in dry years.

The results of Chapter II, however, clearly indicate that rainfall events of sufficient size during the months of August and September are crucial for stand maintenance of this species. These rainfall events do not have to be particularly big. We observed that precipitation equalling two to three times the daily evaporative demand will initiate recruitment of a new generation of ramets in intermediate wheatgrass. Winter mortality of fall-produced tillers was apparently not an important factor for this rhizomatous grass in this ecosystem. Thus, these early ramets contribute the most to the growth and development of the clone because they are more vigorous, attain greater size, and have longer life spans than later-produced ramets.

The importance of these rains for the performance of intermediate wheatgrass is illustrated too by the rainfall distribution at Maikop in the Caucasus, Russia. This area, from which the likely (C.W. Cook and K.H. Asay, personal communications) progenitor of the commercial seed used at our sites, P.I. 98568, was introduced (Hanson 1972), is characterized by an average annual precipitation of 640 mm with the highest monthly rainfall during the summer (Walter and Lieth 1960). Based on similarities in rainfall distribution, plant material originating from eastern Turkey or Iran (Mariam and Ross 1972, Dewey 1978) would be expected to be better adapted to the growing conditions found at Tintic. It would be of interest to find out whether ecotypic differences are also reflected in the basic tiller dynamics.

Research into the relative importance of small rainfall events during the months of August and September for the following year's sward condition and productivity of this and other grasses with similar tiller dynamics, such as crested wheatgrass, Agropyron desertorum (cf. Olson 1986), seems warranted. If such a correlation can be established, the amount of summer rainfall may have potential predictive value in allowing operators to adjust stocking rates well in advance of the actual grazing season.

Considering that Tintic is probably on the south-western fringe of intermediate wheatgrass' distribution in the USA (Stubbendieck et al. 1986), it is quite remarkable that this species was able to perform as well in monospecific stands as it did during the four dry years of this study. Two factors seem important, namely a high degree of resilience for ramet density, due to the density-dependent nature of tiller recruitment, and the extremely low mortality of fall-produced ramets during winter. This contrasts with relatively high winter mortality rates reported for fall-produced tillers of the bunchgrass crested wheatgrass growing at the same site (Olson and Richards 1988). This difference in ramet survival between these two species may be one explanation for the observation that intermediate wheatgrass produced nearly the same amount of forage as crested wheatgrass despite the dry growing conditions in the years of this study (G.B. Bartels and B.E. Norton, unpublished data).

In conclusion, we found no evidence to support the hypothesis that the observed ability of intermediate wheatgrass to compete with western wheatgrass during the years 1983-1986 prior to our study was a direct consequence of the implementation of a short-duration grazing system. A far more likely explanation for these observations would be the above-average levels of precipitation during those years and the concomitant absence of conspicuous competitive asymmetry. This conclusion does not mean that short-duration grazing is unable to influence competitive interactions. It merely underlines the criticism (e.g., Gammon 1978) that the adherence to fixed grazing periods in this grazing system, irrespective of forage availability, as was done at Tintic, strongly reduces its capability to affect the composition of plant communities. Rotational grazing needs to be flexible and grazing periods must be adjusted to forage availability before a reduction in the animals' opportunity to graze selectively can start to impact competitive interactions between species that differ greatly in palatability and defoliation resistance.

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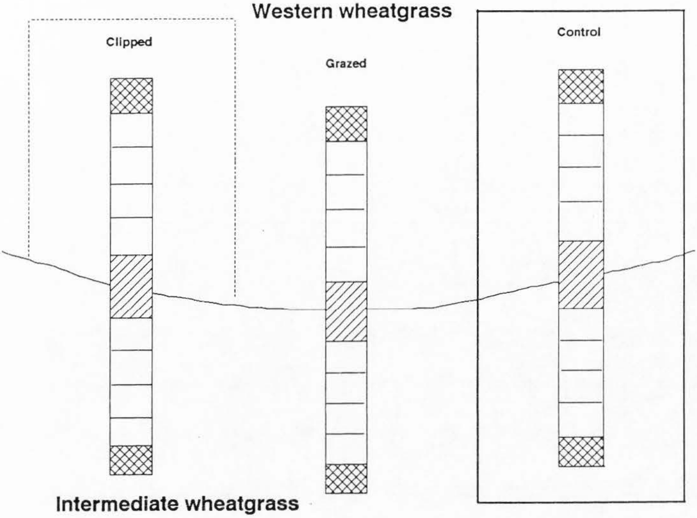
APPENDICES

APPENDIX A. Diagrammatic representation of the layout of the experiment described in Chapters II and III.



APPENDIX B. Root distributions of intermediate wheatgrass and western wheatgrass.

In August 1989 root densities of intermediate wheatgrass and western wheatgrass were assessed using the profile wall method as described by Boehm (1979). Two trenches were dug across the interface of the two species in areas that had not been grazed for at least two years. Depth of the trenches was approximately 180 cm. In both species smooth profile walls were prepared that were located at least 1.50 m from the interface, and roots were exposed using small-toothed scrapers and brushes. For each species the profile was 120 cm wide and 160 cm deep and counting of the exposed roots was done in 10 x 10 cm grids.

Figure B.1 shows the root distribution of the two species in both trenches. Three-dimensional contingency table analysis (Zar 1984) indicated that trench was not independent of species and depth (X^2_{15}=124.4, p<0.001) and that pooling of the data from the two trenches, therefore, was not permissible. Analysis of both trenches separately indicated that species and rooting depth were not independent (p<0.001) (X^2-values 208.6 and 197.1 for trench 1 and 2, respectively, with 7 df each). Intermediate wheatgrass had a higher proportion of its roots in the top 20 cm of the profile whereas western wheatgrass had a higher proportion of its roots in the

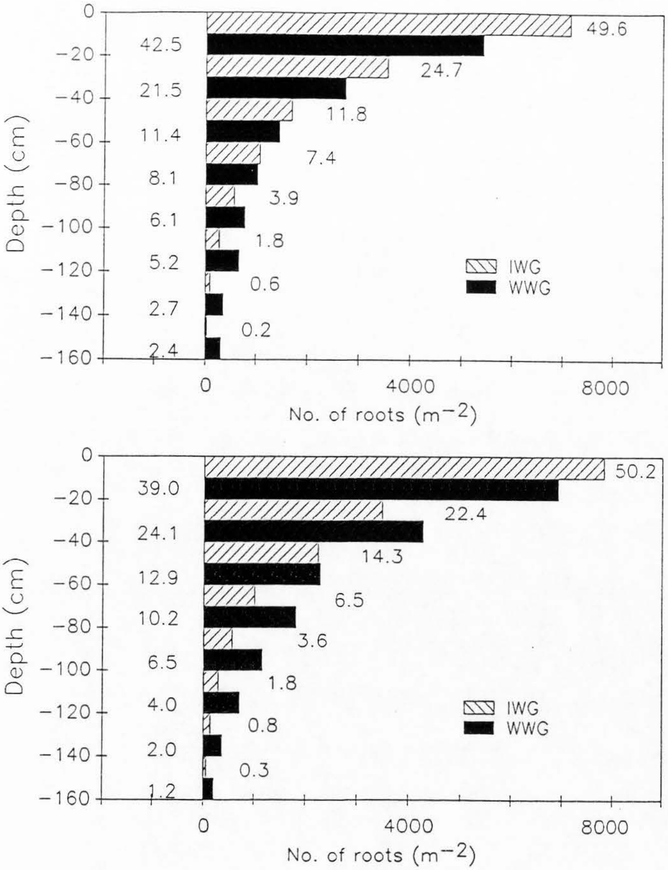
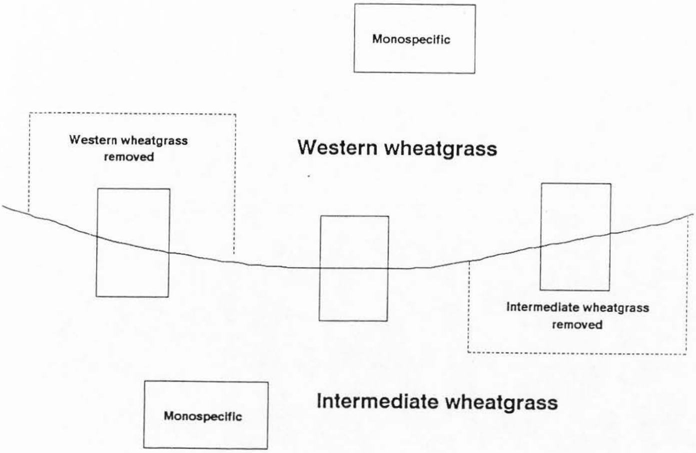


Fig. B.1. The number of exposed roots in the soil profiles of two trenches dug across the interface of two different western wheatgrass patches in an intermediate wheatgrass pasture. The proportion (%) of the total number of roots exposed in a particular layer is printed to the right (IWG) or left (WWG) of the horizontal bars. IWG = intermediate wheatgrass, WWG = western wheatgrass soil layers below 100 cm.

Analysis of variance on the square root-transformed data using a split-plot design indicated a significant interaction between species and depth ($F_{7,14}=4.09$, $p=0.012$). Employing Fisher's protected LSD, root density in the top 20 cm of the profile was significantly higher for intermediate wheatgrass than for western wheatgrass ($p<0.100$). Western wheatgrass, on the other hand, had significantly higher root densities in the 80-100 cm ($p<0.100$), the 100-120 cm ($p<0.050$), the 120-140 cm ($p<0.100$), and the 140-160 cm ($p<0.050$) layers.

APPENDIX C. Diagrammatic representation of the layout of the experiment described in Chapter IV.



APPENDIX D. Allelopathic aglycons in western wheatgrass.

Bokhari (1978) showed that western wheatgrass has phytotoxic properties that could be ecologically significant. Allelopathy has also been demonstrated in the closely related quack grass (Agropyron repens (L.) Beauv.). In a study on the effects of root extracts on the germination and seedling growth of various grasses, Lawrence and Kilcher (1962) demonstrated that seedling growth of intermediate wheatgrass was more seriously affected by root extracts of couch grass than any other grass species, with the exception of Elymus angustus Trin. (Altai wild ryegrass). In a recent paper, Hagin (1989) identified 5-hydroxyindole-3-acetic acid (5-HIAA) and 5-hydroxytryptophan (5-HTP) as the compounds in quackgrass responsible for the inhibition of growth in other plants. We were interested to see if these compounds were also present in western wheatgrass.

Plant material was collected at the Tintic Range Experiment Area on September 20, 1990, and separated into tillers, rhizomes, and roots. Material was taken from sites that had been irrigated for two years (see Chapter IV) and from sites that had received only natural precipitation. After rinsing with distilled water, half of each sample was oven-dried at 65 °C, the other half stored in a freezer (hereafter referred to as fresh material).

The extraction of the phenolic glycosides was done as described by Hagin (1989), except for the fact that samples were blended in a Waring Blendor for 15 minutes. The high-pressure liquid chromatography (HPLC) analysis method as described by Hagin (1989) was modified because of extremely high pressures in the system even at low flow rates. This resulted in very long retention times for the compounds of interest, making accurate quantification difficult. A modification, developed by R. Hess (Plant Science Department, Utah State University) was used instead (G.J. Mileski, personal communications).

The results of these analyses indicated that very little 5-HTP and 5-HIAA was present in western wheatgrass (Table D.1). Compared to the values presented by Hagin (1989), the contents of these two compounds in western wheatgrass were three to four orders of magnitude lower than in quackgrass. Confirmation of these results using more plant material and spiking material with IAA is suggested (G.J. Mileski, personal communications).

Table D.1. 5-HTP and 5-HIAA contents (ng/g dry weight) of western wheatgrass tillers, roots, and rhizomes.

Plant material	5-HTP	5-HIAA
	ng/g	ng/g
Tillers (dried)	119	30[1]
Tillers (fresh)	494	1664
Irrigated tillers (dried)	ND	273
Roots (dried)	1154	438
Roots (fresh)	567	444
Rhizomes (dried)	ND	206

ND = none detected

[1] The detection limit for the analyses was 50 ng, thus any value below 50 ng cannot be considered quantitative

VITA

Gerrit B. Bartels

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Interactions between populations of intermediate wheatgrass and western wheatgrass as influenced by short-duration grazing and moisture availability

Major Field: Range Science

Biographical Information:

Personal Data: Born in Hellendoorn, the Netherlands, December 2, 1950, son of Hendrik Jan and Cathrien Bartels; married Margret Mayer July 25, 1983; children -- Marie-Catherine and Hendrik Jan.

Education: Graduated from Christelijk Lyceum in Almelo, the Netherlands in 1969; received "Landbouwkundig Ingenieur" degree (Tropical Agriculture) from the Agricultural University Wageningen, the Netherlands in 1978; completed the requirements for the Doctor of Philosophy degree with a major in Range Science at Utah State University in 1992.

Professional Experience: Farm management assistant, Kenya Seed Company, Kitale, Kenya 1974; Forage crop researcher in Suweon, Republic of Korea, German Agency for Technical Cooperation (GTZ) 1978-1979; Adviser for agricultural research and farm management in Dacca, Bangladesh, GTZ 1979; Adviser for extension in Suweon, Republic of Korea, GTZ 1980-1983; Station manager and adviser for agricultural extension in Al Boun, Arab Republic of Yemen, GTZ 1983-1986; Adviser for agricultural extension in Kharga, Egypt, Beller Consult Ltd. 1986; Research assistant, Department of Range Science, Utah State University 1987-1991.