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The Ecology and Management of
Bluebunch Wheatgrass
(*Agropyron spicatum*): A Review



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THE ECOLOGY AND MANAGEMENT OF BLUEBUNCH WHEATGRASS
(AGROPYRON SPICATUM): A REVIEW

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ABSTRACT

Agropyron spicatum, considered one of the most important native bunch-grasses in British Columbia, western Montana, the Columbia Basin and the area between the Cascades and Sierras and the Rockies, dominated millions of acres of pristine semiarid grass and sagebrush sites. It produced more herbage than all other associated species in these regions. A considerable amount of research has been done with this species since J. E. Weaver's work on roots in 1915. This review summarizes information from more than 300 articles relating to taxonomy, morphology, forage quality, ecology, physiology, and management of A. spicatum. It has been arranged so persons can easily locate articles relating A. spicatum to these various subject areas.

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Table of Contents

Summary-----	2
Introduction-----	4
Plant Description	
Taxon-----	5
Morphology-----	5
Phenology-----	6
Forage quality-----	7
Physiology-----	8
Distribution-----	9
Plant communities and associated species-----	9
Competition-----	10
Plant Response and Management	
Grazing-----	11
Drought-----	12
Fire-----	13
Fertilization-----	14
Herbicides-----	15
Seeding-----	15
Plant Pathology-----	16
Integrated Grazing Management-----	16
Literature Cited-----	18

SUMMARY

Agropyron spicatum (Pursh) Scribn. and Smith² (Bluebunch wheatgrass) considered one of the most important native bunchgrasses of the Palouse Prairie and Intermountain Sagebrush Province, has dominated millions of acres of pristine semiarid grass and sagebrush sites, and produced more herbage than all other associated species combined. It is a climax species of wide ecological amplitude and provides palatable forage for livestock and wildlife. The genetic variation of the taxon A. spicatum is as extensive as its ecological adaptation. Seed germination of A. spicatum normally begins in fall if adequate soil moisture is available. Temperatures for optimal germination range from 68 to 72 degrees F. Shoot development of mature plants occurs at the second and third nodes of the previous season's shoots. Tillers initiated in the fall overwinter and continue growth during spring. Shoots and roots reinitiate growth in early spring, as temperatures warm, with maximum growth frequently occurring in May. Shoot growth ends with summer dormancy but roots continue to grow late into August, even under drought stress. Stored carbohydrates begin to decline during early spring growth, reaching a minimum during the mid to late vegetative stage. Stored carbohydrates begin to increase in the roots and crown during the early flowering stage.

Agropyron spicatum grows throughout much of the western United States, south to the northern edge of the Sonoran Desert, extending north into Canada. After heavy disturbance, retrogression in A. spicatum communities is evidenced by the decline of perennial grasses, and increases in woody and annual species. Seedlings of annual grasses, Bromus tectorum (cheatgrass) and Taeniatherum asperum, (medusahead) developing from fall germinated seeds, produce root systems which elongate more rapidly than roots of A. spicatum seedlings and compete for moisture required for establishment. Artemisia tridentata (big sagebrush) competes with A. spicatum for nutrients and increases with disturbance and removal of periodic fire.

Under good grazing management, frequency of A. spicatum does not change when compared to adjacent sites protected from grazing. If defoliation is severe during the vegetative stage, stored carbohydrates are used for growth. However, if some green leaf tissue remains after grazing, few or no stored carbohydrates are used. Spring grazing is not likely to have serious effects on A. spicatum vigor as long as conditions are suitable for regrowth before entering summer dormancy. Close grazing during the boot stage, particularly if grazing also occurred during the vegetative stage, causes the greatest reduction in plant vigor. The boot stage generally occurs when carbohydrate levels are low, maximum photosynthetic area is displayed, and growing conditions are near optimal, but conditions for regrowth usually decline rapidly.

²Pseudoroegneria spicata (Pursh) A. Love has been proposed to replace the name Agropyron spicatum (Pursh) Scribn. and Smith (Dewey 1983 unpublished). This is an update from the proposed name change of Elytrigia spicata (Pursh) D.R. Dewey reported in Dewey, D.R. 1983. Historical and current taxonomic perspectives of Agropyron, Elymus and related genera. Crop Sci. 23:637-642.

Severe drought reportedly causes breaking up of A. spicatum bunches into smaller, individual plants during and immediately after drought. Despite adequate precipitation the year after drought, mortality of smaller plants reduces A. spicatum basal cover. Fall burning causes little or no mortality of A. spicatum, with plants usually returning to pre-burn production in 1 to 3 years. Burning, however, in hot conditions of summer can cause high mortality and a decline in production. If A. spicatum plants are being suppressed by an associated species, such as A. tridentata, release from competition by fire often outweighs any direct damage to the bunchgrass. Reducing nondesirable plants can result in both establishment of new plants and release of suppressed plants of A. spicatum. If burns are too frequent, annual species are favored. A minimum of 20 percent cover of A. spicatum or one plant per 10 square feet is recommended for successful release of this species from competition. If seeding is necessary, drilling in fairly thick stands with rows not wider than 12 inches is recommended. In favorable conditions, fertilization may increase production and vigor of A. spicatum plants, although the economic return may be questionable. Range fertilization also may reduce yields of A. spicatum if annual grasses are present.

The optimum grazing system or strategy an operator can implement depends on the animal operation and alternative sources of forage. If cattle are turned into an A. spicatum pasture during the boot stage, effect on plant health will be influenced by degree of defoliation occurring during this stage. The most common problem occurs when individual plants within a pasture are overgrazed year after year while many other plants go unused. Plant vigor decreases if plants actively regrow after a grazing event and are regrazed in the same growing season. Vigor also declines if plants are grazed annually during the boot stage.

Introduction

Agropyron spicatum, considered one of the most important native bunch-grasses of the Palouse Prairie and Intermountain Sagebrush Province (U.S. Forest Service 1937), dominated millions of acres of pristine semi-arid grass and sagebrush sites, and produced more herbage than all other associated species combined (Daubenmire 1940). It is a climax species of wide ecological amplitude and provides palatable forage for livestock and wildlife. Dense stands of A. spicatum are remarkably drought tolerant, recovering rapidly to predrought status (U.S. Forest Service 1937, Humphrey 1943, Harris 1967, Skovlin 1967, Sneva 1971, Ganskopp and Bedell 1979). This probably results from a combination of minimum competition from associated species, ample supply of A. spicatum seed, and rapid recovery of surviving plants. However, it is sensitive to defoliation at certain times of the season (McIlvanie 1942, Stoddart 1946a 1946b, Blaisdell and Pechanec 1949, Heady 1950, Mueggler 1950 1975, Branson 1956, Blaisdell 1958, Hyder and Sneva 1963a, Wilson et al. 1966b, Evans and Tisdale 1972, Harris and Goebel 1976, Caldwell et al. 1981), and its recovery after disturbance is seriously hindered by competition for soil moisture from associated species (Warg 1938, Daubenmire 1940, Harris 1967, Harris and Goebel 1976, Cline et al. 1977). Since the early 1900s, its abundance has significantly decreased because of frequent disturbance and widespread invasion of introduced annuals such as B. tectorum and T. asperum (Pickford 1932, Daubenmire 1940 1970, Hanson and Stoddart 1940, Young 1943, Tisdale 1947, Stewart and Hull 1949, Heady 1950, Harris 1967, Harris and Goebel 1976).

This paper summarizes information for land managers and scientists interested in the ecology and management of A. spicatum on western rangelands. Literature on its taxonomy, ecology, physiology, and management are summarized, with pertinent references in the topical discussion. Research on A. spicatum dates back to the early 1900s when Weaver (1915) studied plant roots in southeastern Washington. A bibliography of A. spicatum was published by Gould in 1965. Since then a great deal of information on the synecology and autecology of this species has been published.

Plant Description

Taxon

Genetic variation (Harris 1967 1968 1971, Chapman and Perry 1973) in the taxon A. spicatum is almost as extensive as its ecological adaptation. In accordance with Daubenmire (1960 1974), the name A. spicatum is now generally accepted to include ecotypes with divergent awns, all gradations to awnless³, as well as those with and without rhizomes. Caespitose ecotypes occur on more arid sites and intergrade into rhizomatous types in less arid conditions (Daubenmire 1939 1960, Stark et al. 1950, Passey and Hugie 1963a 1963b, Sturges 1977). Ecologic responses to environment are expressed by varying phenology (Pechanec et al. 1937, Heady 1950, Blaisdell 1958, Sauer and Uresk 1976, Daubenmire 1978) and morphology (Heady 1950, Passey and Hugie 1963a 1963b, Harris 1967, Harris and Goebel 1976). Two important cultivars, "Whitmar" (Hafenrichter et al. 1949) and "Secar" (USDA Soil Conservation Service 1980), have been released by the USDA Soil Conservation Service Plant Materials Center at Pullman, Washington⁴. Natural and synthetic hybrids of A. spicatum have also been investigated (Dewey 1964 1969 1971. 1976a 1976b, Pere-Trejo et al. 1979).

(See also: Asay and Dewey 1976, Asay et al. 1985, Cronquist et al. 1977, Gomm and Horton 1983, Hartung 1946, Hitchcock et al. 1969, Jefferies 1969, Robertson and Weaver 1942).

Morphology

Seedlings initially develop a diversely branched primary root system which sustains them in the early stage of development. If conditions are favorable, an extensive network of heavily suberized nodal roots (roots initiated from nodes) is initiated and penetrates deep into the soil profile. Roots of some ecotypes similar to "Whitmar" grow 8 to 20 inches parallel to the soil surface before turning downward (Harris 1967, Harris and Goebel 1976). Agropyron spicatum roots penetrating to 50- to 70-inch depths have been reported in eastern Washington (Weaver 1915) and Utah (Hanson and Stoddart 1940). Shallow lime zones occurring in dry grassland climates, however, may limit root development (Heady 1950).

A large portion of A. spicatum's biomass lies below ground (Hanson and Stoddart 1940, Branson 1956, Ganskopp and Bedell 1979). In southern Washington in an Artemisia tridentata/A. spicatum habitat type, approximately 20 and 41

³Formerly identified as beardless wheatgrass, A. inerme (Scribn. and Smith) Rydb.

⁴"Whitmar" is a widely distributed awnless, rhizomatous ecotype which has frequently been used in laboratory research. It also has been widely planted but seed is relatively expensive. "Secar," recently released, is a caespitose type with divergent awns, selected for its dryland establishment, root and crown production, and seed yield potentials.

percent of the belowground biomass were above the 4 and 8 inch soil depths, respectively (Rickard 1985b). Although leaf area indices are generally low in the cold desert, leaf area within the bunch is approximately 2.2 (foliar area/ground area) (Caldwell et al. 1983). (See also: Benson 1974, Branson 1953, Gardner 1942, Heady 1949, Owens and Fisser 1981, Richards and Caldwell 1982, Stocker 1976, Weaver and Albertson 1943, Weaver 1978).

Phenology

Seed germination normally begins in the fall when soil moisture increases and temperatures are cool. Temperatures for optimal *A. spicatum* germination range from 68 to 72 degrees F (Young et al. 1981). In early spring (March 9, in southeastern Washington), seedling roots were less than 7 inches deep (Harris 1967, Harris and Goebel 1976). Following winter dormancy, active root growth is initiated relatively late in the spring, coinciding with leaf development. If conditions are favorable, development of nodal roots is initiated. Nodal roots have been noted to develop at approximately the three-leaf stage with soil water in the upper 0.5 inch near field capacity (Evenden 1983).

Shoot development of mature plants occurs at the second and third nodes of the previous season's shoots (McIlvanie 1942). Shoots often begin growth in the fall with the initiation of precipitation. In the intermountain shrub region, growth ceases almost entirely in November with leaves and roots growing only slightly during the winter. Tillers initiated in the fall overwinter and continue growth in the spring (Nowak and Caldwell 1984b). Approximately 75 percent of the tillers survive winter with the first leaf initiated in the fall senescing during winter. Spring growth of roots and shoots generally begins in March or April when snow disappears (McIlvanie 1942, Hyder and Sneva 1963a, Evans and Tisdale 1972, Hall 1978). Rapid root growth does not begin until soil temperatures average 46 to 50 degrees F. Both rapid root and leaf elongation occur during May when vegetative development is at a peak and root reserves decrease to seasonal lows (McIlvanie 1942). The reproductive phase ends with summer dormancy in approximately mid-July (Harris and Goebel 1976) but roots have been reported to continue growth late into August at shoot xylem potentials below -2.5 MPa (-25 bars) (Caldwell et al. 1981). Flowering and seed production of *A. spicatum* are reportedly extremely erratic. Quinton et al. (1982) found seed production in British Columbia was poor especially at higher elevations. They reported extreme variability in seed production among plants and years with no apparent relationship to tiller density or basal area. Daubenmire (1978) reported similar findings in Washington. Aborted reproductive shoots (culms without a seedhead but elongated internodes) are common (Hyder and Sneva 1963a).

The date at which *A. spicatum* reaches a height of 2.5 inches has been used as a criterion for opening the grazing season for season-long use on the Upper Snake River Plains of Idaho. Blaisdell (1958) found this date could be predicted with reasonable accuracy (Standard Error = 5.66 days) from the mean temperature of March ($Y = 65.86 - 1.39 X$; where Y is the number of days after March 31 and X is the March mean temperature). Finding a close correlation

between herbage weight and precipitation of the preceding July-to-March period, Blaisdell also offered a method for predicting herbage yield ($Y = 133.40 + 38.23 X$; where Y is air-dry herbage yield in pounds per acre and X is precipitation in inches of the preceding July-to-March period. Standard Error = 55.2 pounds). This provides an opportunity for adjusting animal numbers before opening of the grazing season.

(See also: DeWitt 1969, Owens and Fisser 1981, Quenet 1974, Rosenquist and Gates 1961, Smith 1944, Sneva and Hyder 1962, Wilson et al. 1974).

Forage Quality

Agropyron spicatum is grazed by all classes of livestock throughout the year (Skovlin 1967) and may provide good deer forage if plants have been grazed by livestock to maximize availability of new growth (Willms and Mclean 1978, Leckenby et al. 1982, Willms et al. 1980c 1980d. Protein and phosphorous are sufficient for lactating animals during early spring but decline markedly after flowering (Stoddart 1946, Cook et al. 1956, Hickman 1966, Skovlin 1967, Wight and White 1974). Cook et al. (1956), in Utah, reported digestible protein levels in A. spicatum of 9.9 percent during the four-leaf stage (June 1, 1954) compared with 5.2 percent during the boot stage (June 23, 1954). Metabolizable energy averaged 1,142 calories per pound and 877 calories per pound for the four-leaf and boot stages, respectively. In eastern Oregon, in vitro cellulose digestibility of A. spicatum forage declined from 72.6 percent on April 30, 1959, to 62.4 percent on June 2, 1959, and continued to decline more rapidly during summer (Wallace et al. 1961). A wide calcium/phosphorous ratio develops especially after maturity (Skovlin 1967). Cattle and sheep in grazing trials have shown a preference for introduced grasses such as Agropyron cristatum in early spring, but A. spicatum was more palatable late in the season (Cook et al. 1956). Fall green-up, which may occur after late summer precipitation events, makes A. spicatum valuable for fall grazing.

Some ranchers claim excellent animal gains from spring grazing of A. spicatum in drought years. Generally, nutrient content in early spring is superior in drought years because of larger nutrient concentrations in the smaller volume of biomass. A higher ratio of vegetative shoots (which are usually more nutritious) to reproductive shoots is also common for A. spicatum during drought. Skovlin (1967), however, noted protein levels from June through September were significantly reduced by severe drought. This may be explained by the advancement of maturity and curing of A. spicatum, caused by drought conditions, and reduced protein intake caused by decreased forage availability restricting selectivity.

Wallace et al. (1966) investigated chemical curing of A. spicatum and other forages with June applications of 1 pound paraquat per acre. With this method of chemical versus natural curing, forages retained higher nitrogen and cellulose digestibility for late summer and fall grazing. However, paraquat has not been approved by the Environmental Protection Agency for this use. (See also: Blaisdell et al. 1952, Costello 1944, Currie et al. 1981, Demarchi 1968 1973, Dillon and Wallenmeyer 1966, Hansen et al. 1977, Harner and Harper 1973, Holecheck et al. 1982a 1982b, Hurd and Pearse 1944, Irwin 1979, McCall 1937, McLean and Willms 1977, Raleigh 1970, Stoddart 1945, Uresk and Cline

1976, Uresk and Rickard 1976a 1976b, Uresk et al. 1976b, Willms et al. 1980e, Willms et al. 1981a).

Physiology

McIlvanie (1942) classified the phenological and physiological development of A. spicatum into five stages based on studies in Montana:

1. Formative stage (shoot initiation): The greatest percentage of seasonal carbohydrates is stored in the lower two to three internodes, followed by roots. The balance of total carbohydrates is retained in old herbage. Total nitrogen is also near the seasonal maximum with approximately equal amounts stored in herbage and roots.
2. Vegetative development (approximately 2 months): Sucrose and reserve polysaccharides (important in carbohydrate storage) decline sharply during this period. Minimum total carbohydrates, root nitrogen, and carbon/nitrogen ratios are reached at the 7-inch height stage (early May).
3. Flower stalks first evident to seedheads fully out of the leaf sheath: Total carbohydrate content is at a maximum in herbage, but roots contain only 60 percent of the final total maximum. Nitrogen in herbage begins to decline and nitrogen in roots begins increasing.
4. Seed maturation to early yellowing: Carbohydrates decline rapidly in herbage as root carbohydrates reach their seasonal maximum. Nitrogen continues to decline in herbage and to increase in roots. This trend reverses during transition to secondary growth.
5. Fall curing to secondary growth: A slight increase in total carbohydrates occurs in both herbage and roots by the end of this period.

Hyder and Sneva (1963a) and Caldwell et al. (1981) reported similar trends of total soluble carbon pools in A. spicatum. The major investment of carbon during vegetative development occurred in shoots and sheaths (Caldwell et al. 1981).

Optimum temperatures for maximum photosynthesis rates range between 68 and 77 degrees F (DePuit and Caldwell 1975). Net assimilation rates of carbon are highest during the spring and early summer when both temperatures and soil water are near optimum. Dark respiration rates increase with temperatures. Stomatal conductance was also found to be sensitive to hot, dry conditions. Under these conditions, stomates decrease aperture size which decreases water loss through transpiration and allows maintenance of more leaves. (Also see: Anderson and McNaughton 1973, Dauber and Willard 1981, DePuit 1975, Dewey 1960, Johnson and Brown 1977, McCarty and Price 1942, O'Toole et al. 1981, Richards and Caldwell 1985, Trlica and Singh 1980).

Distribution

Agropyron spicatum flourishes on deep well-drained loamy soils but is adapted to coarser textured soils with shallow (15 to 24 inches) calcareous hardpans (Heady 1950). Summer droughts are common throughout its range. It is found from northern Michigan to Alaska, south to western South Dakota, New Mexico, and California, and throughout the Great Basin (Hitchcock 1950).

Plant Communities and Associated Species

Agropyron spicatum occurs as a co-dominant with several Artemisia sub-species (Winward and Tisdale 1977, Winward 1980) on arid sites (8- to 17-inch precipitation zone) ranging from 500 to 9,000 feet elevation. Of these, the Artemisia tridentata ssp. wyomingensis (Wyoming big sagebrush)/A. spicatum habitat type is probably the most common big sagebrush/bluebunch wheatgrass habitat type. In the Palouse Prairie and other more mesic environments, A. spicatum is associated with Festuca idahoensis (Idaho fescue) on deeper soils and with Sandbergs bluegrass Poa secunda (Sandbergs bluegrass) on the more shallow soils. It is also found growing with Juniperus occidentalis (western juniper), Cercocarpus ledifolius (curlleaf mountain mahogany), Pseudotsuga menziesii (Douglas-fir) and Pinus ponderosa (ponderosa pine).

With prudent grazing, frequencies of dominant grasses in an Artemisia tridentata/A. spicatum habitat type were similar between exclosures protected from cattle grazing for 50 years and outside adjacent areas, grazed annually by cattle for 50 years (Sneva et al. 1984). After heavy disturbance, however, retrogression in A. spicatum communities was evidenced by the decline of perennial grass density and increases in woody species and annuals. Severe grazing and prevention of natural fire have increased dominance of Artemisia species on sagebrush/bunchgrass ranges. Combinations of overgrazing, cultivation, and frequent burning have allowed widespread invasion of B. tectorum on several million acres of abandoned cropland and overgrazed ranges (Pickford 1932, Young 1943, Stewart and Hull 1949, Piemeisel 1951, Moomaw 1957, Harris 1967, Franklin and Dyrness 1973, Harniss and Murray 1973, Daubenmire 1975). Further retrogression to other low value, low-producing species such as T. asperum and Chrysothamnus (rabbitbrush) species also occurs (Daubenmire 1940 1970, Harris and Goebel 1976, Hilken and Miller 1980). Aristida longiseta (red three-awn), a perennial grass of low palatability, invaded 500,000 acres in north-central Idaho, where A. spicatum was reduced with overgrazing (Evans and Tisdale 1972).

(Also see: Burkhardt and Tisdale 1976, Christensen 1963, Daubenmire 1942 1952 1977, Daubenmire and Daubenmire 1968, Driscoll 1964, Eckert 1957, Erhard 1979, Franklin and Dyrness 1969, Gibbens 1972, Hall 1973, Hironaka et al. 1983, Hironaka and Tisdale 1963, Hoffman and Alexander 1976, Hoover 1939, Humphrey and Miller 1945, Jones 1972, Laycock 1980, McLean 1970, McLean and Marchand 1968, Mitchell and Cormak 1960, Morris et al. 1950, Mueggler and Handle 1974, Pfister et al. 1977, Pickford 1940, Poulton 1955, Rasmussen 1954, Sampson and Chase 1927, Sampson et al. 1951, Schlatterer 1972, Sharp and Sanders 1978, Spilsbury and Tisdale 1944, Stoddart 1941, Tidestrom 1925, Tisdale 1961 1979

1982, Volland 1976, Weaver 1917, Weaver and Clements 1939, Wright and Wright 1948).

Competition

Bromus tectorum and T. asperum are winter annuals which often limit reestablishment of A. spicatum after severe disturbance. Hull and Stewart (1948), in Idaho, reported successful establishment of seeded perennials in B. tectorum stands thinned to 50 to 100 annual plants per square foot, as compared to poor success in densities of 1,000 annual plants per square foot. Roots of T. asperum and B. tectorum seedlings elongate more rapidly during winter than roots of A. spicatum seedlings (Harris and Goebel 1976). Soil temperatures average about 3.5 degrees F warmer at B. tectorum root tips and 5.5 degrees F warmer at T. asperum root tips compared with temperatures at the more shallow depths occupied by A. spicatum roots (Harris 1967, Harris and Goebel 1976). Morphology and phenology of annuals also make them less susceptible to grazing injury. The competitive advantage of annuals appears to result from their ability to deplete soil moisture at deeper levels in advance of developing roots of A. spicatum seedlings. During years of above average precipitation, however, annuals are relatively poor competitors (Harris 1967, Stewart and Hull 1949). Stewart and Hull (1949) reported perennials have a good chance of regaining dominance over B. tectorum in areas where annual precipitation exceeds 9 inches. Newly seeded perennials may establish in young stands of A. tridentata although their yields will be severely reduced. Earlier growth and development of grasses, successfully established in the year Artemisia is controlled, will usually suppress Artemisia reestablishment for several years (Blaisdell 1949).

Aristida longiseta, in contrast to A. spicatum, increases with heavy grazing pressure. Aristida longiseta lacks early spring and fall growth, maintains apical meristems in a sheltered position and is low in palatability (Evans and Tisdale 1972). Saturated soils inhibit the growth of A. longiseta, but seed germination at high temperatures and a rapidly elongating root system allow the species to compete strongly on droughty coarse-textured soils.

Artemisia species, subjected to little or no grazing pressure, compete strongly for soil moisture and nitrogen (Hyder and Sneva 1956). Artemisia is capable of absorbing greater levels of soil nutrients (at least phosphorus) than A. spicatum (Caldwell et al. 1985). They reported A. tridentata absorbed 86% of the available P added to the soil in the interspace between the shrub and A. spicatum. Within plant communities dominated by A. tridentata, significant patterns of horizontal and vertical distributions of soil nutrients have been shown (Doescher et al. 1984). Higher concentrations of N, P, K, and Ca occurred under Artemisia than either A. spicatum, F. idahoensis, or in the interspaces. Concentrations of nutrients under A. tridentata did not increase as range conditions declined (Doescher et al. 1984). However, as the prevalence of shrubs increased, the size of the nutrient pool within this component of the community increased, probably at the expense of increased interspace and decreased bunchgrass cover.

(See also; Cook and Lewis 1963, Day 1975, Harris 1977, Harris and Wilson 1970, Hulbert 1955, Hull 1949, Hull and Pechanec 1947, Leopold 1941, Ndawula-Senyimba

et al. 1971, Parish 1956, Piemeisel and Chamberlain 1936, Rickard et al. 1977b, Risser 1969, Young et al. 1969).

Plant Response and Management

Grazing

Agropyron spicatum is considered sensitive to heavy grazing during the growing season because of its upright stature, slender shoots, early elevation of apical meristems to grazing height, and high ratio of reproductive to vegetative shoots (Branson 1956, Harris 1967, Evans and Tisdale 1972). Conflicting results are found in the literature regarding the phenological stage at which A. spicatum is most sensitive to defoliation. This is primarily because of different levels of defoliation and growing conditions after defoliation. McIlvanie (1942) found A. spicatum is most vulnerable to defoliation during the stage of minimum root reserves. Clipping at this time delayed normal seasonal replenishment of carbohydrate reserves. Donart and Cook (1970) found more root reserves were utilized for regrowth after early spring defoliation than defoliation during the boot stage, however, clipping intensities were severe (90 percent defoliation). Caldwell et al. (1981) reported the major source of carbon used for regrowth was assimilated after the defoliation event and not before. This emphasizes the importance of green leaf tissue remaining on the grazed plant.

Most researchers have found A. spicatum is most sensitive to clipping just before and during the boot stage, which usually occurs in early June (Daubenmire 1940, Stoddart 1946, Blaisdell and Pechanec 1949, Wilson et al. 1966a, Harris 1967, Trlica and Cook 1971, Harris and Goebel 1976). Limited regrowth, after leaf removal at the boot stage, apparently is caused by high temperatures and limited soil moisture during most years (Stoddart 1946, Wilson et al. 1966). Defoliation also appears to suppress rather than stimulate new tiller development (Branson 1956, Caldwell et al. 1981). This may be caused by the late development of axillary buds (Hyder and Sneva 1963a) and allocation of photosynthate to the roots rather than for development of new leaf tissue (Caldwell et al. 1981). Clipping A. spicatum in mid-November and early March did not affect the rate of tiller elongation in spring (Willms et al. 1980a 1980b). The level of carbohydrates stored at fall quiescence affects the ability of a plant to regrow after defoliation and to complete its annual growth cycle before summer dormancy (Trlica and Cook 1971).

Defoliation has been shown to increase photosynthetic rates, on a per unit leaf area basis, by 27 percent compared to undefoliated plants (Nowak and Caldwell 1984a). Defoliation also delayed senescence in older leaves by approximately 2 weeks (Nowak and Caldwell 1984a) and increased light saturation of the lower leaves (Caldwell et al. 1983). Overall photosynthesis, however, declined on a per plant basis because of a 60 percent reduction in leaf biomass. Water use efficiency also declined (photosynthesis/transpiration) on defoliated plants, probably because of an increase in proportion of old foliage. Delaying growth later into the summer may also decrease water use efficiency because of increasing seasonal evaporative potentials.

Reducing competition has been reported to offset adverse effects of heavy defoliation on A. spicatum (Mueggler 1972). When competition was eliminated, a six-fold increase in A. spicatum herbage production and a ten-fold increase in flower stalk density resulted, compared to defoliated plants competing with undefoliated neighbors. Where B. tectorum is a problem, properly timed "flash" grazing (short grazing period) is a helpful control technique. Bromus tectorum reaches grazing height approximately 2 to 3 weeks before other associated species. It is highly palatable, matures quickly, and generally dies by late May (Harris 1967). Agropyron spicatum tolerates intense grazing for short time before the boot stage. This coincides with B. tectorum shoot and flower development. Roots of well established A. spicatum plants may not be free of competition from B. tectorum roots until roots reach a depth of 20 to 30 inches (Harris 1967, Cline et al. 1977). Hanson and Stoddart (1940) reported an average root depth of 26 inches on ungrazed plots and 18 inches on grazed areas.

Agropyron spicatum, compared to A. desertorum, has several traits that make it more sensitive to grazing. Carbohydrate reserves accumulate later and are maintained at lower levels in A. spicatum (Hyder and Sneva 1963a 1963b, Caldwell et al. 1981). Agropyron spicatum has a greater carbon and nitrogen investment per unit of photosynthetic area in the shoot and per unit root surface absorption area (Caldwell et al. 1981). Although plants of equal size produce approximately the same biomass, A. spicatum has thicker leaves and larger diameter roots (which decreases the ratio between leaf or root surface area/weight) than A. desertorum. Agropyron desertorum roots are significantly more dense throughout the soil profile. After defoliation, A. desertorum quickly reallocated both reserves and assimilated food material for new leaf growth. Agropyron spicatum, after defoliation continued to allocate carbon to roots, which continued to grow, at the expense of leaf growth. Continued root growth in A. spicatum apparently does not benefit the plant since root mortality increased in the winter and growing season after defoliation (Richards 1984). Replacement of new photosynthetic area by A. spicatum is far inferior to A. desertorum, because of lower reserve levels of carbohydrates, greater carbon and nitrogen investments per unit leaf area produced, and unabated root growth after defoliation.

(See also: Bleak and Keller 1973, Branson 1953, Cooper 1953, Costello and Price 1939, Crider 1955, Currier 1956, Donart and Cook 1970, Evanko and Peterson 1955, Garrison 1966, Gooding 1957, Harris 1954, Hewitt et al. 1976, Hormay and Talbot 1961, Hudson 1976, Hyder and Sawyer 1951, Ikeler 1943, Kamm et al. 1978, Liethead 1960, McLean and Tisdale 1972, McShane 1981, Miller and Krueger 1976, Mueggler 1967 1975, Nielson 1940, Packer 1953, Payne 1960, Pickford and Reid 1948, Richards and Caldwell 1981 1982, Rickard et al. 1975 1977, Roath and Krueger 1982, Sauer 1978, Skovlin et al. 1976, Slaughter 1951, Sneva 1980, Sprague 1934, Wash. Agric. Exp. Sta. 1932, Willms et al. 1979 1981b, Wyoming Agric. Exp. Sta. 1960).

Drought

Rates of net carbon assimilation for A. spicatum are usually highest during spring and early summer, when water supply is least limiting, and

temperatures are close to optimal for photosynthesis (68 to 77 degrees F) (DePuit and Caldwell 1975). The effects of severe drought on A. spicatum carbohydrate accumulation and mobilization have not been researched (Ganskopp and Bedell 1979). With normal mid-summer temperatures, A. spicatum becomes photosynthetically dormant but root growth continues (Caldwell et al. 1981). In drought years, termination of shoot and leaf growth may be advanced by as much as 1 month (Pechanec 1937). Production of flower stalks is curtailed during drought with most plants remaining vegetative throughout the grazing season (Heady 1950, Blaisdell 1958, Harris 1967, Harris and Goebel 1976). In southern Idaho, breaking up of A. spicatum bunches into smaller, individual plants occurred during and after the drought of 1934 (Pechanec et al. 1937, Craddock and Forsling 1938). Despite adequate precipitation the next year, mortality of smaller plants caused a subsequent reduction in A. spicatum cover.

Vigorous plants of A. spicatum are adapted to normally dry summers. However, the magnitude of the effects of severe drought, particularly combined with overgrazing, can extend beyond the year(s) in which severe drought occurs. Although the effects of drought vary with ecological condition, substantial increases in density and cover of forbs and deep-rooted shrubs, after drought, may superficially mask declining conditions of grasses (Pechanec et al. 1937). Failure to attain favorable forage responses during years of above average annual precipitation may be the result of lowered vigor after drought, intensive grazing, or a combination of both. (See also: Bleak and Keller 1973, Collins and Weaver 1978, Eddleman and Nimlos 1972, Jardine and Forsling 1922, Julander 1945, Kleinman 1977, Schlatterer and Hironaka 1972, Sneva and Rittenhouse 1970).

Fire

The effect of fire on A. spicatum depends on frequency and season of burning. Estimates of frequencies of natural fires in sagebrush/grass ecosystems range from 25 to 70 years (Wright et al. 1979). When burned in the fall, little or no mortality has been reported for A. spicatum, with plants usually returning to pre-burn production in 1 to 3 years (Blaisdell 1953, Moomaw 1957, Conrad and Poulton 1966, Harniss and Murray 1973, Uresk et al. 1976, Britton et al. 1978). Willms et al. (1980a 1980b) reported burning A. spicatum in the fall (mid-November) and late winter (early March) reduced the rate of tiller elongation in the spring. Reductions in spring growth caused by burning during the dormant season may be caused by: (a) destroying fall regrowth and thereby reducing photosynthetic surface; (b) exposing meristematic tissue to extreme temperatures; (c) increasing soil temperatures which caused a moisture deficit; and/or (d) causing greater evaporative cooling from burned soil.

Removing standing litter by burning affects the morphological development of A. spicatum (Uresk et al. 1976a, Willms 1980a 1980b). During the first 3 years after a lightning fire in mid-August, Uresk et al. (1976a) reported average leaf length decreased, reproductive shoot height and seedhead lengths increased, and production increased 31 percent to 131 percent. Increased tiller densities, the second year after fall burning, have also been reported (Willms et al. 1980a). How quickly A. spicatum responds positively to burning

depends on: (1) the vigor of the plants before burning, (2) fire conditions, and (3) growing conditions (i.e., soil moisture) following the fire.

Where natural fire has been suppressed, dense canopies of Artemisia predominate at the expense of A. spicatum. Burning within the proper conditions can effectively reduce competition and release A. spicatum. Artemisia tridentata is easily killed by fire, although the rate of reoccupation depends on the subspecies, seed reserves, percent kill, and moisture availability on the site (Sturges 1977, Winward and Tisdale 1977, Britton and Ralphs 1979). Little or no mortality of A. spicatum has been reported from fall burns (Blaisdell 1953, Moomaw 1957, Conrad and Poulton 1966, Harniss and Murray 1973, Uresk et al. 1976). Spring and summer burns decrease basal area of A. spicatum and can result in high mortality (Wright et al. 1979). However, if A. spicatum is suppressed by an associated species such as A. tridentata release from competition by fire usually outweighs any direct damage to the bunchgrass in the overall stand.

Early summer burns (at a time when native perennials are easily killed) may offer a temporary setback to B. tectorum, but burning generally increases its dominance (Wright and Klemmedson 1965). As annual grasses and forbs increase, the time period between burns shortens. Repeated burning depletes perennial grasses and causes sharp increases in annual grasses, especially B. tectorum (Pickford 1932, Wright and Klemmedson 1965). A combination of burning and herbicide application has been shown to be very effective in controlling annual grasses on several A. spicatum habitat types (Parish 1956, Goebel et al. 1970, Eckert et al. 1972, Harris and Goebel 1976, Hilken and Miller 1980).

Fire has also been shown to increase the palatability of A. spicatum. Both cattle and deer readily preferred plants that had either been burned or grazed during the previous growing season while they least preferred plants that had neither been burned nor grazed (Willms et al. 1980c 1980d). Deer preferred burned plants over grazed plants.

Guidelines for prescribed burning in sagebrush ecosystems are summarized by Wright et al. (1979) and Britton and Ralphs (1979). Grazing should not be resumed until at least 1 year after treatment to allow for a full, uninterrupted growth cycle. Harniss and Murray (1973) found beneficial effects from burning lasted 12 to 30 years in Idaho. (See also: Burkhardt and Tisdale 1976, Keay and Peek 1980, McShane 1981, Pechanec et al. 1944, Peek et al. 1979, Robocker et al. 1965).

Fertilization

Moderate fertilization may increase the vigor, yield, and seed production of A. spicatum in stands where B. tectorum is absent. Mason and Miltimore (1959) reported yield of A. spicatum more than doubled from nitrogen fertilization on a site in British Columbia receiving 11 inches of precipitation. Crude protein levels of high-desert grasses are temporarily increased with fertilization. However, the advantage of increased protein diminishes as soil water is depleted and plants mature earlier in the season (Sneva 1963, Sneva and Hyder

1965). Increases in production from fertilization may be negligible in dry years. Harris and Goebel (1976) reported vigor of A. spicatum declined with repeated applications of nitrogen at 100 pounds per acre.

Range fertilization has direct, as well as indirect, effects on production of A. spicatum growing with competing species, as responses to soil nitrate levels differ between plant species. Agropyron spicatum and F. idahoensis yields are reduced on fertilized plots where B. tectorum is present. Nitrogen stimulates B. tectorum growth and increases moisture utilization by this species (Sneva 1963, Wilson et al. 1966a). Perennial seedlings are restricted more by moisture competition than benefited by increased fertilization (Harris and Goebel 1976). Taeniatherum asperum appears to have a competitive advantage over both A. spicatum and B. tectorum on sites where nitrogen is deficient (Harris and Goebel 1976, Brannon 1972).

In a review, Schmisser and Miller (1978) reported effects of fertilization on yields from seeded high desert range are more substantial than from native high desert range. Substantial increases in production of native grasses appeared to be more consistent, and perhaps more economically feasible, in areas of milder climates (e.g., British Columbia, or southeastern Washington).

(See also: Bayoumi and Smith 1976, Heady 1952, Hyder and Sneva 1961, Macqueen and Bierne 1975, Main 1974, Miltimore et al. 1962).

Herbicides

Reducing undesirable plants can result in both the release of suppressed established A. spicatum plants and establishment of new plants (Hyder and Sneva 1956, Hedrick et al. 1966, Sneva 1972, Schumaker and Hanson 1977, Sturges 1977, Miller et al. 1980). A minimum of one A. spicatum per 10 square feet (Plummer et al. 1965) is recommended for successful release. The primary source of A. spicatum production for several years after treatment comes from plants occupying the site before treatment (Blaisdell and Mueggler 1956, Miller et al. 1980).

(See also: Findley 1974, Robocker et al. 1965, Schmisser and Miller 1980, Sturges 1977, West et al. 1978, Young et al. 1969).

Seeding

The A. inerme variant, Whitmar, becomes established rather slowly, exhibiting maximum productivity in the third harvest year (Hyder and Sneva 1963a). Secar is being evaluated for its grazing resistance and ability to establish.

Hyder and Sneva (1963a) recommended drilling in fairly thick stands with rows not wider than 12 inches, for better productivity, weed control, and palatability. Selection of seed which has been produced in optimum (versus harsh) environments for seed production should provide more viable seed (Miltimore et al. 1962, Young et al. 1981). Agropyron spicatum seed is highly germinable at a wide range of temperatures (Young et al. 1981), but limited

moisture and excessive competition appear to be the most limiting factors hindering successful establishment of seedlings. (See also: Asay et al. 1985, Berg et al. 1979, Bleak and Walker 1974, Cook and Lewis 1963, Coop. Ext. Ser. 1975, Eddleman 1979, Goebel 1978, Gomm and Horton 1983, Heady 1952, Harris and Dobrowolski 1986, Ikeler 1943, Lavin and Springfield 1955, Lewis et al. 1978, Marquiss et al. 1974, Plummer 1943, Plummer et al. 1955, Robocker et al. 1965, Short 1943, Stark 1946, Stark et al. 1946, U.S. Dept. Agric. 1936, Vogel 1963, Young et al. 1969).

Plant Pathology

(See: Fischer 1936 1939, Fischer and Claassen 1944, Sprague 1934, Young 1937)

Integrated Grazing Management

The optimum grazing system or strategy an operator can implement on A. spicatum depends on their animal operation and alternative forage sources such as A. desertorum or A. cristatum. Maximum sustained forage yields and live-stock production in A. spicatum pastures are not known because of highly variable growing conditions across sites and years as well as limited research. Integrating basic principles with management experience and careful observation are necessary. Grazing strategies can be successfully developed by using the following basic principles:

Past research and experience regarding grazing A. spicatum can be summarized into the following:

1. Continuous grazing of individual plants throughout the grazing season seriously restrict plant growth and storage of carbohydrates for maintenance of plant vigor.
2. Grazing during plant dormancy has the least detrimental effect on the plant. However, to attain maximum livestock gains plants must be grazed during the growing season.
3. Plants can withstand utilization early in the growing season if conditions allow adequate growth after grazing. This will usually occur if animals are removed before the boot stage and there is adequate soil moisture.
4. Retaining only small levels of leaf area during the boot stage has the greatest negative effect on carbohydrate storage and plant vigor.

In the above four principles, the manager or livestock operator must contend with words like adequate, small, etc., that do not provide exact guidelines. Experience and close observation must fill the gap. The harder the resource is pushed to maximize production, the greater will be the demand placed on the manager to make decisions throughout the year.

The amount of green plant material present during various stages of phenological development greatly affects the future health and ability of the plant to compete. If cattle are turned into an A. spicatum pasture during the boot stage, the effect on plant health is influenced by the degree of defoliation occurring during this stage. If only light use occurs from boot to seed maturity, little effect on plant health results. If more than light use during the boot stage is permitted, adjustments in grazing will be needed in the following growing season(s) to maintain plant vigor. The amount of deferment required depends on plant health and environmental conditions. Experience and observation must be employed to decide what adjustments are needed. A problem can potentially arise under continuous use. Even if a pasture is moderately stocked (and more than likely understocked) individual plants within the pasture are frequently overgrazed while much of the pasture is only lightly grazed or not used at all. The greatest potential damage comes from repeated overuse of individual plants within the pasture year after year. Fencing pastures and implementing some type of rotational grazing management plan can decrease potential overuse of certain portions of the pasture, improve distribution of use, and increase flexibility of overall management of the operation. Control of grazing duration and season of use within a pasture are of utmost importance in a grazing management plan.

If A. desertorum is available, it should be used during spring with native pastures providing the main forage source during summer dormancy. Residual forage remaining on native pastures from the previous growing season can provide an excellent feed for cattle in late winter and early spring before adequate forage growth in A. desertorum pastures.

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