Western Snowberry Biology

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Introduction

Western snowberry has biological mechanisms and processes that provide the shrub with capabilities to develop dense colonies that can invade grasslands, eliminate existing native grass community species, and convert the area into brush habitat, creating an environment conducive to encroachment by taller shrubs and trees. This conversion of grassland habitat into brush habitat is difficult, if not impossible, to correct through a single application of any treatment type. Reduction of western snowberry colony density to a tolerable level requires multiple treatment strategies followed by repeated maintenance treatments.

Understanding how western snowberry grows and when it has vulnerable periods in its life cycle is necessary for the development of successful treatment practices. This report summarizes the biological information needed for the development of strategies to manage western snowberry colonies in grasslands.

Plant Description

The scientific name of western snowberry is *Symphoricarpos occidentalis* Hook., and the plant belongs to the honeysuckle family, Caprifoliaceae. The common name "snowberry" comes from the whitish color of the fruits. In the Northern Plains, the plant's other common names are wolfberry, buckbrush, and badgerbrush.

Western snowberry is a native deciduous cool-season shrub that forms large colonies. Its rhizomes are long and sometimes branched (figure 1). Their diameter is usually 0.12 to 0.24 inches (3-6 mm). Clusters of stem bases or rhizome crowns develop at 1- to 3-foot (30-100 cm) intervals along interconnected rhizome systems. Roots with unequal growth develop as opposite pairs at rhizome nodes. Upright stems are 1 to more than 3 feet (0.3-1.0 m) tall. Stem diameter at 1 inch (3 cm) above the soil surface is 0.3 to 0.8 inches (0.8-2.0 cm). Lateral branches develop as opposite twig pairs at the nodes on the upper portions of stems after the first growing season. As the stem ages, the number of twigs and

the complexity of branching pattern increase, and the pith becomes hollow. Leaves are simple, thick, opposite, oval to elliptical, 1 to 2.4 inches (2-6 cm) long, and 0.3 to 1.5 inches (1-3.5 cm) wide. Upper leaf surfaces are smooth and dark green to gray green. Leaf undersides have short hairs and are light green. Leaf edges are usually not toothed, but occasionally young or shaded stems can have leaves with wavy, blunt teeth. Short leaf stalks are 0.25 to 0.33 inches (6-8 mm) long. The small, pinkish, bell-shaped flowers develop from buds formed in clusters of 5 to 20 on a short spike and grow from twig ends and axils of upper leaves. Two to four slightly fragrant flowers of a cluster open at night or early morning each day. The flowering period of a colony is long and occurs during June and July, lasting until mid August in some years. The fruit, a fleshy greenish-white drupe 0.25 to 0.35 inches (6-9 mm) in diameter, contains two slightly flattened oval or elliptical yellowish to brown nutlets 0.08 to 0.12 inches (2-3 mm) long and 0.06 to 0.08 inches (1.5-2 mm) wide. The fruits persist on the stem through winter and turn dark blue to black when they are dry (Great Plains Flora Association 1986, Johnson and Larson 1999, Pelton 1953).

Habitats

Western snowberry is widely distributed throughout most of the interior of North America. The plant's range extends from the southern portions of Northwest Territories to northern New Mexico and from central Washington to eastern Michigan and has expanded into the northern portions of New England (Pelton 1953).

Western snowberry grows in association with a great variety of plant communities and vegetation types on a wide variety of soils (Pelton 1953). It is commonly the ecotonal species on the transitional boundaries between two plant communities. It grows on the margins of openings or disturbed areas in woodlands and forests and on the borders of aspen bluffs and other types of groves with taller shrubs and trees; in grasslands, it can grow in large colonies as the only woody plant. Associated herbaceous plants tend to decrease as western snowberry stems increase. Shading of the understory

by stem canopy cover of western snowberry reduces and eliminates native grass and forb species. Kentucky bluegrass is the last grass to die out under invading colonies of western snowberry (Weaver and Fitzpatrick 1934). Kentucky bluegrass is the only ubiquitous species under the partially shaded portions of western snowberry colonies in Minnesota (Pelton 1953), as it is across most of the United States and Canada (figure 2).

In the more humid parts of its range, western snowberry occurs on the drier topographic sites, such as exposed south- and west-facing slopes, where there is less competition from tall, dense vegetation. In the drier and arid parts of its range, the plant occurs on slopes having aspects where evapotranspiration is lower, in depressions or at the base of slopes where water runin is received from the upper slopes, or on sites where snowdrifts accumulate (Pelton 1953, Mastel 1983, Ransom-Nelson 1985).

Other Snowberries

There are several species of snowberry in North America, most of which are difficult to distinguish from western snowberry. Common white snowberry (*S. albus* (L) Blake) has wide distribution across North America, and its range overlaps that of western snowberry in the northern United States and in Canada. Common white snowberry has small, thin leaves about 1 inch (2.5 cm) long; flowers growing 2 or 3, sometimes 5, in a cluster; and hollow pith in older stems. It commonly grows as scattered individual plants and occasionally produces long rhizomes. Coralberry (*S. orbiculatus* Moeuch) is primarily an eastern species whose distribution overlaps that of western snowberry in the eastern portions of the Central and Southern Plains. The fruits are coral-pink to purplish. The pith of older stems is solid and white. Palmer's snowberry (*S. palmeri* G.N. Jones) is distributed in the western portions of the Southern Plains. It has climbing or sprawling stems to 10 feet (3 m) long (Great Plains Flora Association 1986). Several other snowberry species grow in the western and southwestern portions of the United States: longflower snowberry (*S. longiflorus*), spreading or trailing snowberry (*S. mollis*), mountain snowberry (*S. oreophilus*), roundleaf snowberry (*S. rotundifolius*), and whortleleaf snowberry (*S. vaccinioides*).

Vegetative Growth and Development

Western snowberry colonies can range from a small number of stems covering a few square feet to extensive growths covering hundreds of acres. Pelton (1953) found the colonies in Minnesota to range in size from 1.1 to 2.2 yards (1-2 m) to 55 to 82 yards (50-75 m) in diameter. In southcentral North Dakota, Roel (1983) and Ransom-Nelson (1985) found typical colonies to range in size from 22 to 55 yards (20-50 m) in diameter.

Stem height of western snowberry tends to be greater towards the center of the colony (Pelton 1953). Growth in stem height has been correlated to soil moisture but not to any other environmental factor (Pelton 1953). Mastel (1983) found that low precipitation during April and May, the period of growth initiation and rapid twig elongation, was important in determining the quantity of total annual growth even if the remainder of the growing season received near-normal precipitation. The stem height measured in Minnesota averaged 29.5 inches (75 cm), with a range from 16 to 45 inches (40-115 cm) (Pelton 1953). The average mature stem height measured in southcentral North Dakota was 17.0 inches (43.2 cm) (Roel 1983).

Stem density of western snowberry colonies varies considerably. The densest colonies are commonly located on topographic sites that are relatively moist and exposed to full sun (Pelton 1953). An average colony Pelton (1953) examined in Minnesota had a density of 38.5 stems/sq. yard ($46/m^2$). In southcentral North Dakota, Roel (1983) found average colony densities of 40.7 stems/sq. yard ($48.7/m^2$), and Ransom-Nelson (1985) found average colony densities of 61.8 stems/sq. yard ($73.9/m^2$).

Stem densities within a colony also vary. The lowest density typically occurs at the periphery of a colony (Pelton 1953). Roel (1983) systematically measured stem density every 16.5 feet (5 m) from the center of each of 12 colonies outward along four transects toward the periphery and found the greatest density, 49.5 stems/sq. yard ($59.2/m^2$), near the center. The density progressively decreased outward, reaching 28.1 stems/sq. yard ($33.6/m^2$) near the edge (table 1).

Pelton (1953) observed that portions of about one half of the 20 western snowberry colonies in his Minnesota study had canopy cover dense enough to shade out Kentucky bluegrass completely. In southcentral North Dakota, Roel (1983) studied 15 colonies that had an average canopy cover of 24.0%, with a range from 12.3% to 47.3%, and Ransom-Nelson (1985) studied 15 colonies that had an average canopy cover of 44.9%, with a range from

17.6% to 93.1%. In western North Dakota, Mastel (1983) studied 8 colonies that had an average canopy cover of 32.6%, with a range from 14.7% to 46.8%.

The successful distribution, survival, and abundance of western snowberry across extreme physical and environmental conditions depend on the persistence of the rhizomes and clusters of stem bases and their ability to produce numerous growing points with meristematic tissue that can generate new cells. The shrub's underground organs are long lived. Pelton (1953) found 40-year-old rhizomes in Minnesota colonies. An important factor that contributes to their longevity is the protection provided by the soil. Most rhizomes grow between 2 to 6 inches (5-15 cm) below the soil surface, but rhizomes can be found at any depth from 0.75 to 14 inches (2-35 cm) below ground (Pelton 1953). Western snowberry rhizomes grow at greater soil depths under areas that have grass sod (Pelton 1953).

Rhizome nodes comprising opposite pairs of growing points with meristematic tissue develop on young growing rhizomes about every 0.5 to 1.0 inch (1.25-2.5 cm). The length of the rhizomes between stem base clusters tends to be about 1.0 to 3.0 feet (30.5-91 cm). In a Minnesota colony that was less than 10 years old, Pelton (1953) found the cumulative rhizome length to be 4.4 times longer than the cumulative live aerial stem length, and the average diameter of rhizomes to be 0.16 inches (4 mm). In western North Dakota, rhizome diameter is usually between 0.12 and 0.24 inches (3-6 mm), increasing to 0.39 inches (1 cm) at junctions with rhizome branches and to 0.79 inches (2 cm) at junctions with stem bases.

Roots originate as opposite pairs at most of the nodes along the rhizomes. The root pairs have unequal growth. One root in each pair is larger than the mate, and some root pair mates fail to develop. A few roots along a section of rhizome grow considerably larger than the others. Pelton (1953) found these larger roots could penetrate the soil to a depth of 61 inches (155 cm).

Western snowberry's lateral buds, produced as opposite pairs at each rhizome node, have the potential to develop into a long rhizome branch or a short rhizome branch that turns upward and develops into erect stems. Most of the buds along the midsection of a rhizome, however, never develop, but atrophy with age. When rhizome buds do develop, the young rhizomes and the rhizome branches grow horizontally away from their original growing point for a distance, usually about 3 feet (91 cm) or less,

turn upward, and develop into an erect aerial stem. Rhizome buds near a vertical stem base appear to have greater viability and can develop into long rhizomes, short rhizomes, and additional erect stems forming clusters of stem bases. These sections of vertical and horizontal rhizomes with several nodes actively producing rhizomes and aerial stems are rhizome crowns.

Aerial stems of western snowberry produced vegetatively from meristematic buds are suckers. Rhizome suckers develop from upturned rhizomes or rhizome branches, and crown suckers develop near stem base clusters. During the second year of growth, stems are young stems. During the third and subsequent years, stems are mature stems.

Sucker stems develop rapidly during the first growing season. The outer layer of young suckers is hairy or pubescent until bark develops during the latter portion of the first year or during the second year. Stem nodes comprising opposite pairs of growing points with meristematic tissue develop on sucker stems about every 1.0 to 2.0 inches (2.5-5.0 cm). Opposite pairs of leaves are produced at each node along the entire sucker stem. Lateral branches do not appear during the first year unless the lead apical meristem is damaged. The first lateral twigs usually appear from nodes along the upper portions of the young stem during the second year of growth. Most of the buds at the nodes along the lower portions of the stem never develop into twigs, but atrophy with age. Twigs originate as opposite pairs from meristematic buds located at the nodes that were the previous year's leaf axils. Twigs usually do not develop from every potential node. The uppermost undamaged pair of twig buds develops first. New leaves, produced as opposite pairs, develop at the nodes of only the current year's twigs, not on older twig material. Successive twigs growing from the previous year's leaf axils create a branch network that becomes more complex with each growing season. The age of intact stems can be determined from the pattern of twig branches.

Aerial stems do not survive as long as rhizomes and clusters of stem bases. Pelton (1953) determined the age of mature stems in Minnesota to average about 7.2 years, with the maximum age at 13 years. Portions of the twig branch system die as stems age. When more than 50% of the branch system no longer supports the growth of new twigs, the stem is considered to be decadent. This apparent twig senescence is not a symptom of reduced vigor of the stem (Pelton 1953) but is most likely the result of unfavorable environmental conditions, such as severe

winter cold or growing-season water stress. Under some unfavorable conditions, the stem can be killed to ground level.

The loss of a few stems does not hurt the colony: the lost stems are replaced by vegetative growth of rhizome buds. Vegetative reproduction of sucker stems is regulated by apical dominance of a lead stem through the production of inhibitory hormones that block or suppress the activity of growth hormones. When a lead stem is killed or damaged by some unfavorable condition, such as low temperatures, fire, browsing, mowing, or drought, the production of inhibitory hormones is reduced or stopped, and the growth hormones activate meristematic tissue in rhizome buds; the activation results in the development of several new rhizomes and sucker stems. The distance from which hormones produced by lead stems can regulate or influence growth activity of rhizome buds may be reflected in the long length of the rhizomes between adjacent stem base clusters.

Sexual Reproduction

Changes in day length (photoperiod) regulate the growth and development of most plants in the middle latitudes by activating or stopping physiological processes (Leopold and Kriedemann 1975). In a study of transplanted stems placed in light-proof boxes and subjected to light periods of four different durations, Pelton (1953) determined that western snowberry required day lengths of at least 14 hours to initiate flower bud development. Once the flower buds had reached visible size, their subsequent development did not depend on photoperiod or temperature (Pelton 1953). Pinkish flower buds form near the growing tip of young twigs towards the end of rapid spring growth. Additional flower buds form at the leaf axils of the current year's twigs. Flower bud development progresses in a hierarchical sequence from twig ends downward to the lower leaf axils.

Flowering (anthesis) does not have a photoperiod requirement in addition to the 14 hours of day length the plant needs to initiate flower bud development (Pelton 1953). The flowers, which open during the night or early morning, are insect pollinated. The sticky pollen grains are accessible by numerous types of bees, butterflies, and moths because the structure of the flower is not specialized. Open flowers are slightly fragrant, and the lower portion of the wide corolla tube is filled with nectar to attract the insects (Pelton 1953). Flowering progress follows the sequence of flower bud development,

from the flowers located at the twig ends downward to the flowers located at the lower leaf axils (figure 3). Western snowberry colonies can be in continuous bloom for much of the summer. Usually the flowering period occurs during June and July, but it can extend to mid August and sometimes later (Pelton 1953).

After a flower has been fertilized, the fruit develops for a period of several weeks as the ovary gradually enlarges. Fruit maturation does not depend on photoperiod or temperature requirements (Pelton 1953). Mature fruits are greenish white and contain two nutlets. Pelton (1953) measured fruit production of 500 stems collected from 6 colonies that included aerial stems of all age and size categories; he found the average number of fruits to be 32.5 per stem. Fruit production decreased from the center of a colony toward the periphery, where the stems were younger and competition from grass plants was more severe (Pelton 1953). Pelton (1953) also measured the fruit production of six healthy mature stems and found they developed an average of 160.3 flower buds that produced 119.6 mature fruits with 122.5 filled nutlets; about 48.8% of the nutlets were defective. Fruits composed 14.3% of the average total annual biomass production per mature stem in North Dakota (Roel 1983).

The stalk of the fruit does not have an abscission layer that would permit the fruit to drop shortly after it became ripe; as a result, the fruit remains attached to the stem over winter. The fruit stalks decay and the fruits drop during the following spring or summer (Pelton 1953).

Western snowberry nutlets have a complex double-dormancy mechanism that prevents the seed from germinating in the wrong place or at the wrong time of year. Germination of the seed cannot occur until after the seed coat has been broken down. The intact fruit and dried pulp are impervious to water and protect the seed coat while the fruit is attached to the stem. After the fruit drops and lands in warm, moist soil, the outer layers of the fruit decay in about one or two weeks. A physical restraint to embryo development, the seed coat is impervious to both water and gases and requires about one to two months to break down in response to fungal action in the soil. The afterripening process, the slow deterioration of the dormancy mechanism in the nutlet, can start after the seed coat has been broken down and usually requires one winter, sometimes two winters, to complete. Toward the final stages of the afterripening process, the embryo enlarges and expands to the full length of the nutlet (Pelton 1953).

The quantity of viable nutlets in the soil was investigated by Pelton (1953). He sampled 10 one-foot-square plots (30 cm^2) and found an average of 200 nutlets per sq. foot, but only about 1% were viable. The weight of 1000 viable nutlets collected from colonies in Minnesota was 6.53 grams (Pelton 1953); the weight of 1000 viable nutlets collected in North Dakota was 5.85 grams (Stevens 1932). Viable nutlets germinate soon after the soil thaws in spring. Germination occurs when the embryo root (radicle) breaks out of the nutlet. The optimum range of germination temperatures is between 41°F and 59°F (5°-15°C) (Pelton 1953). After germination, seedlings progress rapidly through several stages of juvenile growth. First-year seedlings do not produce flowers or rhizomes (Pelton 1953).

Mortality of seedlings is high because they have few defenses against insects, diseases, water stress, and competition from other plants. Over two growing seasons, Pelton (1953) carefully searched 20 colonies for seedlings. He found no seedlings during the first year; during the second year, he found no seedlings on 17 of the colonies and 50 seedlings on 3 colonies. Two seedlings were located on bare soil created from an animal disturbance. The other seedlings were located near the center of the colonies, where the canopy cover of the stems had completely shaded out the grasses and other herbaceous plants. No seedlings were found among the Kentucky bluegrass community growing in and around the colonies. Twenty of the seedlings survived through early July, and 7 seedlings survived to mid September: mortality rate of established seedlings was 86% (Pelton 1953). Western snowberry establishment by seed is rare (Pelton 1953). Seedlings probably do not become mature stems in and around existing colonies.

For seedlings to develop into adult plants, the nutlets must be transported to habitat sites that have sufficient soil water, few insects, low quantities of disease organisms, and little or no competition from dense grasses or canopy cover of shrubs. Western snowberry fruits are consumed by numerous types of birds and mammals. A few nutlets pass unharmed through the digestive tracts of some animals that inadvertently become important dispersal agents (Pelton 1953). Pelton (1953) force-fed nutlets to domesticated chickens and found that 10.7% passed intact. Pheasants, grouse, large herbivores, and livestock are known to have passed nutlets intact. However, rabbits and mice are known to pass only nutlet fragments. Despite the low viability of the nutlets and low seedling establishment, western snowberry is extremely successful and has wide distribution across North America.

Nonstructural Carbohydrates

Carbon is important to plants for energy transport and storage and as cellulose-based structural materials used in growth. Plants capture and fix carbon from atmospheric carbon dioxide during the process of photosynthesis. The assimilated carbon is combined in several ways to form various types of relatively simple sugars and starches that are collectively called carbohydrates (CHO). Some of the carbohydrates are used in growth as structural components, some are used in the formation of compounds of greater complexity, and some are used as energy in respiration; the remaining carbohydrates are stored as nonstructural carbohydrates for later use. The quantity of stored nonstructural carbohydrates is tied to plant growth and reproduction, and the amount of stored carbohydrates changes during the year, with periods of drawdown and replenishment (Coyne et al. 1995). Drawdown of stored nonstructural carbohydrates occurs when the rate of photosynthesis is insufficient to meet demands of the plant. During drawdown periods, material moves upward from the storage site in the rhizome crown to the active growing points. The plant replenishes stored nonstructural carbohydrates during periods when acquisition of carbon exceeds the flow to growth, reproduction, and maintenance of the plant so that an accumulation of carbohydrates results. During replenishment, material flows downward from the leaves to the rhizome crown (Coyne et al. 1995).

The nonstructural carbohydrate reserve cycle follows a typical pattern each growing season. The typical curve of the nonstructural carbohydrate cycle for western snowberry (figure 4) was adapted from data reported by Adams and Bailey (1983) and Krueger and Bedunah (1988). Nonstructural carbohydrates in rhizome crowns were collected from western snowberry (*S. occidentalis*) colonies every 10 days between 15 April and 16 October 1981, on rangeland near Ryley, Alberta, Canada (Adams and Bailey 1983), and from common white snowberry (*S. albus*) colonies every 14 days between 13 April and 20 October 1983, on rangeland clearcut from forested areas near Missoula, Montana, USA (Krueger and Bedunah 1988). In each study, the seasonal curve for stored nonstructural carbohydrates followed the same shape, starting in mid April with a sharp drawdown in carbohydrate reserves during the rapid growth of early spring. The low carbohydrate levels occurred for about 10 days between late May and early June (9
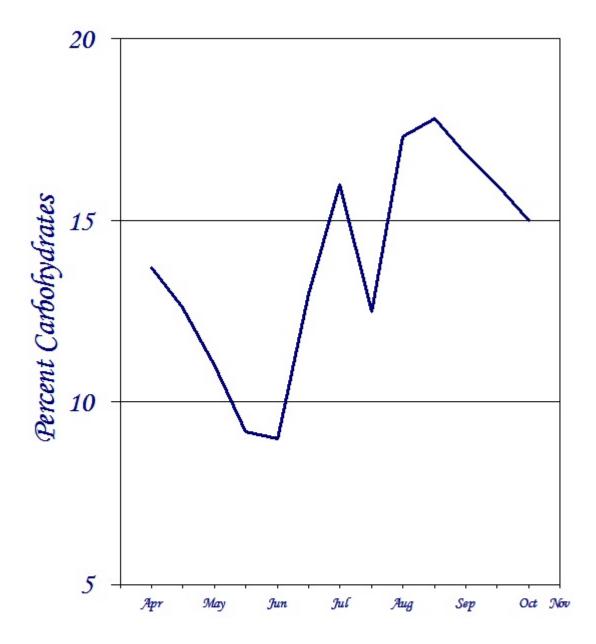
Fig. 4. Typical percent nonstructural carbohydrates
in western snowberry, adapted from
Adams and Bailey 1983
and Krueger and Bedunah 1988.

June), shortly after the full leaf growth stage and about the time the twigs had elongated to two-thirds of full length (Adams and Bailey 1983). Rapid replenishment occurred during a 40-day period from early June to mid July (10 June-20 July), which corresponded to the flowering stage. The carbohydrate levels of mid April were exceeded sometime around late June or early July. High levels of carbohydrates were reached in mid July, about two to three weeks after flowering commenced. A second drawdown occurred between mid July and early August. Both studies reported this carbohydrate decline to correspond to fruit fill. The Alberta data showed about a 3.5% carbohydrate decline, while the Montana data showed about a 1.5% decline. The greatest level of carbohydrate reserves was reached following the carbohydrate replenishment period that occurred between mid August and early September. A third drawdown occurred from early September to late October, a period of pre-winter root growth and bud development.

The three periods of carbohydrate drawdown--during rapid early spring growth, from mid April to early June; during fruit fill, from mid July to early August; and during fall growth, from early September to late October--indicate when western snowberry would have greater vulnerability to defoliation from natural events like hail or fire or from prescribed events like fire or mowing. Defoliation of western snowberry during early to mid June or early to mid August following drawdown periods would have greater negative effects on the colonies than defoliation during early to mid July following a replenishment period.

Phenology

Phenology is the relationship of plant growth stages and calendar date. Because the calendar is based on the solar year, phenological information shows relationships of plant growth to seasonal changes and changes in length of daylight. Perennial plants growing in temperate zones use daylight length, or photoperiod, to program their growth stages and biological activities appropriately with the seasonal conditions.

The seasons and length of daylight in temperate zones change during the earth's annual revolution around the sun because of the tilt of the earth's axis. The sun's apparent path crosses the equator two times each year, once at the start of spring, on the vernal equinox, 20 March, and again at the start of fall, on the autumnal equinox, 22 September. During each equinox, the lengths of day and night are nearly uniform at 12 hours. The sun's apparent path moves northward during spring, and the day length in the Northern Hemisphere increases. The increase in day length is greater with increases in north latitude. The longest day length occurs at the start of summer, on the summer solstice, 21 June, when the sun's apparent path is farthest north of the equator. As the sun's apparent path moves southward, the length of daylight decreases. The decrease in day length is greater with increases in north latitude. The shortest day length in the Northern Hemisphere occurs at the start of winter, on the winter solstice, 21 December, when the sun's apparent path is farthest south of the equator.

The phenological development of western snowberry is triggered primarily by changes in the length of daylight, although other environmental factors produce secondary effects and cause variations in the pattern of phenological development. Changes in day length (photoperiod) function as the timer and trigger that activates or stops physiological processes initiating growth and flowering and activates the process of hardening for resistance to low temperatures that occur during the fall and winter. Vegetative growth is triggered by photoperiod and temperature (Dahl 1995), and reproductive development, which begins with the initiation of flower buds, is triggered primarily by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillan 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977, Dahl 1995).

Pelton (1953) did not find temperature requirements for bud formation and growth, but he did find that low temperatures, around 32°F (0°C), delayed shoot bud development. Photoperiod studies conducted by Pelton (1953) on western snowberry stems collected from Minnesota colonies found that day lengths shorter than 14 hours prevented normal vegetative growth and day lengths of at least 14 hours and longer strongly stimulated vegetative growth. The latitude at which a western snowberry colony grows determines the calendar date when day lengths greater than 14 hours occur. At the 46° 53' N latitude of Dickinson, in western North Dakota, long day lengths of 14 hours and longer occur between 20 April and 20 August (Manske 2005). Western snowberry has a wide latitudinal distribution, and Pelton (1953) expected colonies at locations north and south of Minnesota latitudes to show some genetic variations in photoperiod response.

During a phenological variation study that evaluated stems from plants growing in prairie habitat versus stems from the same plants growing in a uniform transplant garden separated by a distance of nine miles, McMillan and Pagel (1958) found genetic variation among 12 distinct colonies of western snowberry located within a single pasture in southeastern Nebraska. Because of genetic variation in the stems, leaf bud opening occurred over one week during favorable warm spring conditions. Genetic controls in the stems responded differently to adverse environmental conditions, and during cold spring conditions, leaf bud opening occurred over three weeks. McMillan and Pagel (1958) also found that habitat conditions and stem age affected the genetic material: the shorter young stems at the periphery of the colonies tended to open buds earlier than the older, taller stems towards the center. McMillan and Pagel (1958) concluded that phenological variation in western snowberry colonies resulted from variations in habitat conditions and year-to-year climatic differences and from genetic variations and differential responses of the genetic controls to environmental conditions.

Western snowberry has variation in its genetic material that responds differentially to environmental conditions, and it grows from about 35°N to almost 65°N latitude on a wide variety of habitats with a continental range in climates. In spite of all these variables, most of the reported phenological information from southern Nebraska to central Alberta is quite similiar (table 2).

Twig elongation usually starts around mid April and should be linked to calendar dates that have at least 14 hours of day length. In most of North and South Dakota, Minnesota, and Montana, 14 hours of daylight should occur within a few days of 20 April. Both twigs and leaves grow from the same buds located at the previous year's leaf axils. Rapid twig elongation and leaf opening occur at the same time and continue until late May or early June. Twig growth was measured in three North Dakota studies. Ransom-Nelson (1985) found that by early June (7 June) mature stems had completed 78% and young stems had completed 77% of their twig growth (table 4). Roel (1983) found that by mid June (14 June) mature stems had completed 90.2% and young stems had completed 90.4% of their twig growth and mature stems had completed 96.3% and young stems had completed 94.5% of their growth in height (table 3). Sucker stems develop at the same time as new twigs on mature stems but may not be obvious until a little later; sucker stems are reported to occur from late April to early June. Ransom-Nelson (1985) found

that by early June (7 June) crown suckers had completed 87% and rhizome suckers had completed 69% of their growth in height (table 4). Roel (1983) found that by mid June (14 June) crown suckers had completed 95.3% and rhizome suckers had completed 90.4% of their growth in height (table 3).

Full-leaf stage is difficult to clearly identify. This stage is correctly understood to be the stage when all the leaves are fully expanded; plants reach this stage near the end of rapid twig elongation, around mid May or late May. However, when this stage is understood to be identified merely by the presence of leaves on all of the twigs, it would occur at an earlier time.

Flower bud appearance is a specific stage at which the pinkish buds are visible at the ends of the twigs. The appearance of the flower buds, which occurs during late May to early June, ends the rapid twig elongation stage. Flower buds continue to appear in the leaf axils until about late June.

Initial flowering stage (anthesis) begins when the first flowers located on the twig ends are visible. First flowers occur on plants in the southern colonies a little earlier than the first flowers on plants in the northern colonies (table 2). The average first flower date is around mid June; however, genetic variables and environmental conditions can alter first flower dates by about plus or minus 15 days. Flowering continues through July and sometimes lasts into mid August or later. The flowering process progresses downward from flowers on the twig ends to the flower clusters at the leaf axils. Fruit maturation requires several weeks following fertilization, and the process progresses downward from the twig ends to the leaf axils. Fruits fill and ripen during mid July to late August, becoming white as they mature.

The twigs continue to elongate slowly until about mid August (table 3). In southcentral North Dakota, total twig length per stem during August (table 4) was 36.7 inches (93.2 cm) for mature stems, 24.0 inches (61.0 cm) for young stems, 11.2 inches (28.4 cm) for crown suckers, and 9.8 inches (24.9 cm) for rhizome suckers (Ransom-Nelson 1985). In western North Dakota, total twig length per stem during August (table 5) was 8.4 inches (21.3 cm) for decadent stems, 24.7 inches (62.7 cm) for mature stems, 16.0 inches (40.6 cm) for young stems, 11.3 inches (28.7 cm) for crown suckers, and 10.1 inches (25.7 cm) for rhizome suckers (Mastel 1983). In southcentral North Dakota, biomass of twigs, leaves, and fruits during August (table 4) was 62.3 lbs/ac

(69.8 kg/ha) for decadent stems, 804.2 lbs/ac (901.6 kg/ha) for mature stems, 127.7 lbs/ac (143.2 kg/ha) for young stems, 310.4 lbs/ac (348.0 kg/ha) for crown suckers, and 140.9 lbs/ac (158.0 kg/ha) for rhizome suckers; total biomass production was 1445.5 lbs/ac (1620.5 kg/ha) (Ransom-Nelson 1985). In western North Dakota, biomass of twigs, leaves, and fruits during August (table 5) was 30.8 lbs/ac (34.5 kg/ha) for decadent stems, 255.8 lbs/ac (286.8 kg/ha) for mature stems, 42.0 lbs/ac (47.1 kg/ha) for young stems, 81.0 lbs/ac (90.8 kg/ha) for crown suckers, and 245.5 lbs/ac (275.2 kg/ha) for rhizome suckers; total biomass production was 655.1 lbs/ac (734.4 kg/ha) (Mastel 1983). The biomass produced by western snowberry in North Dakota (table 6) was 74.0% leaf, 19.6% twig, and 6.4% fruit for decadent stems; 64.1% leaf, 21.6% twig, and 14.3% fruit for mature stems; 66.5% leaf, 24.6% twig, and 8.9% fruit for young stems; 58.4% leaf, 33.7% twig, and 7.9% fruit for crown suckers; and 39.2% leaf, 49.0% twig, and 11.8% fruit for rhizome suckers (Roel 1983).

The stalks of the fruits do not separate from the plant, and most mature fruits remain attached all winter if they are not consumed by an animal. The start of leaf senescence can occur nearly any time of the growing season if the plant is in water stress, but it usually occurs during late August to October. Many of the leaves remain attached to the stems over the winter.

Nutrient Content

Williamson (1979) conducted a study to describe the seasonal variation in nutrient quality of shrubs. Western snowberry twigs, leaves, and fruits were collected from colonies in both western and eastern North Dakota on a biweekly or monthly schedule from June 1977 through May 1978, and the samples were analyzed for nutrient content of dry matter by standard wet laboratory methods. The results are summarized in tables 7, 8, and 9.

The diets of mule deer, whitetail deer, and pronghorn antelope consist of a high percentage of browse from shrubs (table 10). Williamson (1979) reported that most of the wild ungulate rumens examined in the Northern Plains during fall and winter contained western snowberry browse, and in some mule deer and whitetail deer rumens, western snowberry composed about 27% of the rumen volume.

The nutrient requirements for maintenance, growth, lactation, and antler or horn development of wild ungulates have had considerable study, and most of the parameters equal or exceed the requirements of domestic livestock (Williamson 1979). Western snowberry twigs (table 7) meet wild ungulates' requirements for calcium and potassium every month of the year, for magnesium during May and December, for phosphorus during May, for crude protein during May, and for in vitro dry matter digestibility during May. Western snowberry leaves (table 8) meet wild ungulates' requirements for calcium, magnesium, and potassium during June through October, for phosphorus during June, for crude protein during June and July, and for in vitro dry matter digestibility during June, July, and August. Western snowberry fruits (table 9) meet wild ungulates' requirements for calcium and potassium during July and August, for magnesium at no time, for phosphorus during July, for crude protein at no time, and for in vitro dry matter digestibility during July. Fresh fruits of western snowberry are very astringent, making skin and mucous membrane tissue tighter, and mammals and birds appear to prefer the dried fruits that remain attached to the shrubs (Pelton 1953). Although western snowberry twigs, leaves, and fruits do not meet wild ungulates' requirements for in vitro dry matter digestibility, crude protein, and phosphorus at any time during the fall and winter, western snowberry has traditionally been considered an important browse plant for wild ungulates.

Williamson (1979) used the rumen of a domesticated cow to determine in vitro dry matter digestibility and found digestible dry matter of western snowberry averaged 25.5% during fall and winter (table 7). Dietz (1972) determined in vitro dry matter digestibility by using the rumen fluid from a whitetailed deer and found western snowberry to be 41.0% digestible dry matter during the dormant season in western South Dakota. Dietz (1972) suggested deer require a minimum of 50% digestible dry matter. Both methods, whether using the rumen of a cow or of a deer, showed that digestible dry matter content of western snowberry was below the requirements of wild ungulates during fall and winter.

The digestibility of western snowberry was influenced by the high acid detergent fiber content, and the percent digestible dry matter was low during most of the year. Williamson (1979) found a negative relationship that showed that as acid detergent fiber increased, in vitro dry matter digestibility decreased. Percent acid detergent fiber is a measurement of the structural carbon content of western snowberry twigs, leaves, and fruits (tables 7, 8, and 9). Structural carbon gives strength and shape to growing plant tissue and is primarily cellulose (a complex carbohydrate) and lignin (a high-carbon-

content complex alcohol), which are mostly nondigestible.

Evans and Dietz (1974) conducted a study that evaluated the nutritional value of winter food items consumed by sharp-tailed grouse. Western snowberry fruits collected during the fall and winter in western South Dakota were fed as a single-component diet to wild, trapped, captive male sharp-tailed grouse for a 4-day test period with 4 replications. The fruits and excreta were analyzed for gross energy and crude protein of dry matter; the differences in the respective values determined metabolizable energy and nitrogen balance.

Gross energy of western snowberry fruits was 4.92 kilocalories per gram of dry matter, and the metabolizable energy was 2.31 kilocalories per gram of dry matter. The grouse consumed an average of 39.9 grams of dry matter per day and metabolized an average of 92 kilocalories per day. During winter conditions, sharp-tailed grouse required an intake of at least 100 kilocalories of metabolizable energy per day to maintain a constant body weight (Evans and Dietz 1974). Western snowberry fruits consisted of 5.5 percent crude protein. The excreta of the grouse had an average of 0.84 grams of protein per day more than the 2.19 grams of protein per day in the ingested fruit. The nitrogen balance for the grouse in the feeding trial was -0.135 grams of nitrogen per day. A negative nitrogen balance indicates a loss of nitrogen from the body (Evans and Dietz 1974). The grouse fed air-dried western snowberry fruits lost weight. One male grouse lost 30.8 grams per day, about 3% of his body weight (Evans and Dietz 1974). Although the energy content and crude protein content of western snowberry fruits collected during fall and winter were inadequate for sharp-tailed grouse to maintain body weight, western snowberry has traditionally been considered an important food plant for birds.

Several neotropical birds, a few duck species, and sharp-tailed grouse use western snowberry colonies for escape cover and nesting habitat. Several small mammals use western snowberry during parts of the year for habitat and food. Wild ungulates use western snowberry for escape cover and as fall and winter food. Domesticated livestock browse leaves and twigs during late summer and fall, and calves find shelter from wind. Western snowberry is used by a wide variety of animals; however, none of the mammals and birds living in the Northern Plains depend exclusively on western snowberry during any portion of their life cycle.

Competition for Resources

The competitive ability of a plant to acquire aboveground and belowground resources determines that species' persistence and abundance in communities. Differences in competitive abilities between grasses and shrubs are related to growth form and biomass.

Grass vs. Shrubs

The degree of difference in competitive abilities between prairie grasses and western snowberry was investigated on an area of mixed grass prairie with colonies of western snowberry near Regina, Saskatchewan, Canada, in 1996 and 1997 (Kochy 1999, Kochy and Wilson 2000). The competitive abilities of grasses and western snowberry were compared by differences in biomass production and by differences in acquisition of sunlight, mineral (inorganic) nitrogen, and soil water. Data were collected from paired plots that consisted of a prairie habitat and a brush habitat, with four removal treatments on each habitat replicated at five sites. Selective herbicides were used to remove the shrubs, the grasses, or the shrubs and grasses from each habitat. Intact vegetation plots of each habitat with no removal treatments were used as reference controls. Aboveground biomass was harvested once each year during late August or early September. Shrub samples included previous years' woody stem accumulation. Grass samples included only current year's growth. Light was measured with a photon flux probe during August. Mineral nitrogen was measured by resin bags from May through August. Soil water was measured gravimetrically to a four-inch (10 cm) depth monthly (Kochy and Wilson 2000).

Shrub removal increased grass biomass production threefold on prairie habitat and sixfold on brush habitat. Grass removal increased shrub biomass production twofold on prairie habitat; however, grass removal had no effect on shrub production on brush habitat because the amount of grass growing on the brush habitat was small (Kochy 1999). Both growth forms were able to take up belowground resources not consumed by the removed growth form. The biomass production of grasses and shrubs decreased on both prairie habitat and brush habitat when the biomass production of the other growth form increased (Kochy 1999, Kochy and Wilson 2000).

Light was measured above the soil at a height of 1 inch (3 cm) and above the grass canopy at

a height of 12 inches (30 cm). Light penetration to the ground was greater on prairie habitat than on brush habitat. Removal of grasses or shrubs increased light penetration to the ground on both prairie habitat and brush habitat. Shrubs and grasses reduced light penetration to a similar degree even through shrub leaves are flat and wide and grass leaves are erect and linear (Kochy 1999). Light penetration to the grass canopy was lower on the brush habitat than on the prairie habitat. Light levels above the grass canopy on brush habitat were about 30% of the light levels above the grass canopy on prairie habitat. Removal of shrubs increased light penetration to the grass canopy on both prairie habitat and brush habitat (Kochy and Wilson 2000).

Unshaded grasses attenuated more light per gram of biomass than did shrubs. However, the taller shrubs preempted sunlight and shaded the grasses (Kochy 1999). The reduced quantity of light reaching the grass canopy was below the light saturation point of most open grassland species, and the shading reduced grass biomass production severely. Shading has a greater effect on warm-season (C_4) grasses because they have a higher light compensation point than cool-season (C_3) species (Kochy and Wilson 2000).

The quantity of mineral nitrogen was the same on prairie habitat and on brush habitat. Shrub removal increased available mineral nitrogen on both prairie habitat and brush habitat. Grass removal on both prairie habitat and brush habitat did not change the mineral nitrogen quantities. Grasses took up more mineral nitrogen per gram of biomass than did shrubs (Kochy and Wilson 2000). Insufficient nitrogen availability limits productivity more often than water in temperate grasslands (Tilman 1990).

Soil water was lower on prairie habitat than on brush habitat. Greater soil water on brush habitat suggests that western snowberry colonies increase soil water by snow trapping, hydraulic lift from lower levels, or reduced evapotranspiration. Grasses took up more soil water per gram of biomass than did shrubs (Kochy and Wilson 2000).

Grasses and western snowberry compete for sunlight, mineral nitrogen, and soil water. The per gram of biomass effects on resources are smaller for shrub growth forms than for grass growth forms. Grasses have a 1.4 times greater per gram of biomass effect than shrubs. Western snowberry requires six times greater aboveground biomass than the grasses before grass production is decreased as a result of

competition from the shrubs (Kochy 1999). Shrubs must use a portion of the photosynthates produced in the leaves to build and maintain their unproductive woody stems; the result is a great reduction in resource uptake efficiency. Grass aboveground biomass is primarily productive photosynthetic leaves; the result is a high resource uptake efficiency. Because grasses have high root : shoot ratios and no woody stems to maintain; grasses are good competitors for belowground resources and superior competitors for mineral nitrogen. Shrubs' taller growth makes the plants superior competitors for aboveground resources (Kochy and Wilson 2000).

During early stages of western snowberry expansion into prairie habitat on the periphery of the colonies, competition is primarily for belowground resources of nutrients and soil water; under these conditions, grasses have the advantage and the shrubs are suppressed. The taller shrubs shade some of the shorter grasses. Reductions in sunlight decrease grass biomass production; these decreases result in reductions in competitive effect of grasses for belowground resources. Shrubs take up the belowground resources not consumed by the smaller, less vigorous grasses. As shrub stem density increases, the competition is primarily for the aboveground resource of light; under these conditions, shrubs have the advantage and the grasses are strongly suppressed. Competition on brush habitat is strongest for sunlight. Competition on prairie habitat is strongest for mineral nitrogen (Kochy and Wilson 2000).

The study that Kochy (1999) conducted to evaluate the competitive abilities of prairie grasses and western snowberry was continued by Peltzer and Kochy (2001), with the same treatments on the same plots at the same location near Regina, Saskatchewan, Canada. Peltzer and Kochy (2001) also evaluated the competitive effects from prairie grasses and western snowberry on grass and shrub seedlings.

Selective herbicides were used to remove the shrubs, the grasses, or the shrubs and grasses on prairie habitat and brush habitat paired plots for a third year (1998). Intact vegetation plots of each habitat with no removal treatments were used as reference controls. Aboveground biomass was harvested once each year during late July. Light was measured with a photon flux probe during July. Mineral nitrogen was measured by resin bags from May through mid September. Soil water was measured gravimetrically to an eight-inch (20 cm) depth in late July. Ten seedlings each of blue grama and silverberry were transplanted into each

competition plot during early June. Shoots of seedlings were harvested and weighed in mid September (Peltzer and Kochy 2001).

Three years of shrub removal increased grass biomass production to equal the total biomass production of the intact vegetation treatments on both prairie habitat and brush habitat. Three years of grass removal increased shrub biomass production to equal the total biomass production of the intact vegetation treatment on prairie habitat. Shrub biomass production on the grass removal treatment was equal to the total biomass production of the intact vegetation treatment on brush habitat (Peltzer and Kochy 2001). Grass removal on brush habitat had no effect on shrub production because the amount of grass growing there was small (Kochy 1999). Belowground biomass on the treatments with three years of shrub removal or of grass removal was equal to the belowground biomass on the intact vegetation treatments on both prairie habitat and brush habitat (Peltzer and Kochy 2001). After three years of selective herbicide treatments for shrub removal and grass removal, the remaining respective growth forms produced the same total quantities of aboveground and belowground biomass as the intact vegetation treatments produced.

Light penetration to the ground on the treatments with three years of shrub removal or of grass removal was equal to the light penetration on the intact vegetation treatments on prairie habitat. Light penetration to the ground on the treatments with three years of shrub removal on brush habitat was equal to light penetration on the treatments on prairie habitat. Light penetration to the ground on the treatments with three years of grass removal was equal to the light penetration on the intact vegetation treatments on brush habitat. Light levels penetrating the shrub canopy on brush habitat were low, at about 20% of the light levels above the plant canopy (Peltzer and Kochy 2001).

Available mineral nitrogen on the treatments with three years of shrub removal was greater than that on the intact vegetation treatments on both prairie habitat and brush habitat. Available mineral nitrogen on the treatments with three years of grass removal was not changed and was equal to that on the intact vegetation treatment on both prairie habitat and brush habitat (Peltzer and Kochy 2001).

Soil water in July was the same on the treatments with three years of shrub removal and of grass removal as on the intact vegetation treatments on both prairie habitat and brush habitat. Both

grasses and shrubs decreased soil water to about the same extent (Peltzer and Kochy 2001).

Seedlings of blue grama and silverberry that were growing in established plant communities were unable to compete effectively for resources. Competition for resources from prairie grasses or western snowberry strongly reduced the growth of blue grama and silverberry seedlings on both prairie habitat and brush habitat. Growth of blue grama and silverberry seedlings was greater on treatments with no competition (Peltzer and Kochy 2001).

Competition for sunlight, nutrients, and soil water from prairie grass or from western snowberry can suppress growth of the other growth form. Selective removal of grass or shrub growth forms from plant communities reduces competition for resources. The aboveground and belowground resources become available for use by the growth form that remains in the community. After three successive years of selective herbicide application, both remaining prairie grasses and western snowberry were able to use these additional available resources to produce biomass equal to the total amount of biomass produced on the intact vegetation treatments.

Grass vs. Rhizome Suckers

Shrub establishment in grasslands frequently occurs in clumps. A study was conducted to determine whether young shrub vegetative rhizome suckers' growing at high density increases the shrubs' ability to compete against grasses. Sections of western snowberry rhizomes were transplanted into small plots in an old field of smooth bromegrass near Regina, Saskatchewan, Canada, in 1994 and 1995 (Li and Wilson 1998). Small plots with 27.4 sq. inches (176.7 cm^2) of soil surface were defined by placing individual solid galvanized steel tubes, 6 inches (15 cm) in diameter and 6 inches (15 cm) deep, into the soil along transects at 39.4 inch (1 m) intervals. Western snowberry rhizomes were transplanted at low and high densities of one or five per plot, respectively. Twenty replicated plots of each rhizome density had the grass removed with a herbicide treatment. Forty replicated plots of each rhizome density had the grass remain intact. Fifteen replicated plots without transplanted rhizomes were used to evaluate performance of grass alone (Li and Wilson 1998).

Aboveground and belowground biomass of transplanted suckers and grass plants of each plot was harvested during early September after two growing seasons. Mineral nitrogen was measured in soil

samples collected four times using an ion selective electrode. Soil water was measured gravimetrically to a four-inch (10 cm) depth four times (Li and Wilson 1998).

Soil mineral nitrogen was lower in the experimental old field of smooth bromegrass than in a nearby mixed grass prairie. The soil of the previously cultivated old field had relatively little organic matter remaining to be mineralized. Removal of grass on the old field increased available mineral nitrogen (Li and Wilson 1998).

Soil water was higher in the experimental old field of smooth bromegrass than in a nearby mixed grass prairie. The soil of the mixed grass prairie was sandy and unsuitable for annual crop agriculture. Soil water was consistently lower on the high transplant density plots than on the low density plots (Li and Wilson 1998).

Competition from grass decreased growth of western snowberry rhizome suckers at both high and low transplant densities. Shoot growth was suppressed more than root growth on plots with grass present; the result was greater root : shoot ratios than on plots with grass removed. Survival rates of rhizome suckers were lower on plots with grass present than on plots with grass removed. Growth rates of transplanted rhizome suckers were higher on plots with grass removed. High transplant densities reduced growth rates of rhizome suckers on plots with grass removed. Growth rates of rhizome suckers were greater at low transplant densities on plots with grass removed. Rhizome sucker survival rates were lower at high transplant densities. Growth rates of rhizome suckers were greater at high transplant densities than at low transplant densities on plots with grass present. High transplant density enhanced the ability of western snowberry rhizome suckers to compete against grasses. Grass biomass and grass root : shoot ratios were not affected by the presence of transplanted western snowberry rhizome suckers (Li and Wilson 1998).

Expansion of western snowberry into grassland habitat at the periphery of the colonies is slowed or suppressed by competition for belowground resources of mineral nitrogen and soil water from grass plants. Competition from grasses reduces growth rates of western snowberry rhizome suckers and causes a relatively high mortality rate of young suckers. When grass competition is present, mortality rates of rhizome suckers are higher when stems are clustered and densities are high; however, the surviving rhizome suckers have greater growth

rates at high stem densities than at low stem densities. When grass competition for belowground resources is reduced or removed, rhizome suckers have increased growth rates. Single rhizome suckers have higher survival rates and greater growth rates than clusters of rhizome suckers when grass competition is removed.

Rhizosphere Fungi

Grassland soils sampled at any single point in time reveal low levels of mineral nitrogen, but grassland soils are not low in nitrogen. Grassland soils contain abundant quantities of nitrogen, although most of it is in the organic form and unavailable for direct use by plants. Rhizosphere soil organisms can convert organic nitrogen to mineral nitrogen.

The soil rhizosphere around perennial roots is the zone where a symbiotic relationship occurs between the roots of plants and microorganisms living in the soil. Grassland rhizosphere organisms interact in a complex trophic web and play a major role in the biogeochemical nutrient cycles that are necessary for an ecosystem to function properly (Manske 1999).

One of the major organisms of the rhizosphere is fungi. Rhizosphere fungi are primarily vesicular arbuscular mycorrhizae that form endomycorrhiza in which the vesicles, arbuscules, and hyphae of the fungus enter the cells and tissue of the host plant (Harley and Smith 1983). The symbiotic function of endomycorrhiza fungi in grassland plant rhizospheres is the nitrification of ammonia (Ingham et al. 1985, Clarholm 1985, Biondini et al. 1988, Frederick and Klein 1994, Frank and Groffman 1998) and the enhancement of the absorption of phosphorus, other mineral nutrients, and water (Moorman and Reeves 1979, Harley and Smith 1983, Allen and Allen 1990, Koide 1993, Marschner and Dell 1994, Smith and Read 1997). Rhizosphere organism activity results in increased conversion of organic nitrogen into mineral nitrogen and in greater availability of water, minerals, and nutrients for the grassland plants.

Pelton (1953) excavated the root system of a western snowberry stem and rhizome following methods used by John E. Weaver. Pelton (1953) observed that the roots were mycorrhizal in appearance, with the concentration increasing towards the tips, and that the roots had a fine covering of closely adherent soil particles.

Williams and Aldon (1976) collected snowberry (*Symphoricarpos spp.*) roots in northern New Mexico between August and October 1972 and examined them for infection by fungi. Glomus type vesicular arbuscular endomycorrhizal fungi were found in association with young snowberry roots. The glomus endomycorrhizal fungi produced round to ovoid vesicles 12 to 80 microns in diameter, arbuscules, coiling hyphae, and chlamydospores 40 to 135 microns in diameter within the tissue of the roots (Williams and Aldon 1976).

Manske (1992) evaluated mycorrhizal fungi infection of grass and shrub roots of plants growing in western snowberry colonies that had not been burned in over 80 years at a mixed grass prairie location in northwestern North Dakota. Roots of three plants of each species were collected from each of 6 replicated sites and analyzed individually. Roots of western snowberry, smooth bromegrass, western wheatgrass, and blue grama were cleared and stained, then assessed for fungi infection by presence or absence on a grid-intersect method (Manske 1992).

Western snowberry had encroached and expanded into idle prairie and developed dense colonies that covered over 50% of the upland landscape. The brush habitat consisted mainly of western snowberry and Kentucky bluegrass. Smooth bromegrass, an introduced species, had become established and increased on the decadent portions at colony centers. The native grasses, western wheatgrass and blue grama, had been greatly reduced in abundance and were only small components of the mature brush community (table 11).

Nearly all of the western snowberry (93.8%) roots were infected with fungi. Most of the roots of western wheatgrass (66.0%) and blue grama (78.8%) were infected. The roots of smooth bromegrass (32.3%) were only partially infected with fungi (table 11).

The symbiotic relationship between roots of perennial plants and soil organisms in the rhizosphere enhances the plants' abilities to compete for belowground resources. Native grassland shrubs and grasses have well developed rhizospheres and are effective at acquiring needed resources.

Summary

Western snowberry is a native shrub that forms large dense colonies. This biologically successful shrub is widely distributed throughout most of the interior of North America and it grows in association with a great variety of plant communities and vegetation types on a wide variety of soils. The shrub has a long interconnected branching rhizome system with clusters of stem bases at the crowns. The aerial stems are one to three feet tall and are readily replaced by vegetative growth from meristematic buds on the rhizomes and crowns when unfavorable environmental conditions or management practices destroy any aerial stems. Vegetative growth is regulated by apical dominance with hormones. Sexual reproduction in western snowberry has a low success rate and establishment by seed is rare because the nutlets have low viability and seedlings have high mortality.

Western snowberry starts growing in mid to late April when there is at least 14 hours of daylight. Rapid twig elongation and leaf growth and expansion occur at the same time and continue until late May or early June when the pinkish flower buds appear at the twig tips. By early June, the twigs are about 75% of full growth and the leaves are near full expansion. Twigs continue growing at a slower rate and by mid June they have completed about 95% of their annual growth. Flower buds continue to appear in the leaf axils until about late June. The first flowers begin to open around mid June, with new flowers opening at lower leaf axils through July and sometimes extending into mid August. After fertilization, the fruits fill and ripen during mid July to late August. Most of the fruits remain attached to the stems all winter. Leaf senescence usually occurs during late August to October.

The quantity of stored nonstructural carbohydrates is related to plant growth and reproduction, with the cycles of drawdown and replenishment following a typical pattern each growing season. A sharp drawdown in carbohydrate reserves occurs during the rapid growth of early spring, from mid April to early June. Rapid replenishment occurs during the flowering stage, from early June to mid July. A second drawdown period occurs during fruit fill, between mid July and early August. A second replenishment period occurs between mid August and early September. A gradual third drawdown occurs during pre-winter root growth and bud development, from early September to late October.

Western snowberry competes with grasses for sunlight, mineral nitrogen, and soil water. Healthy grasses are superior competitors for the belowground resources of mineral nitrogen and soil water; their presence retards and reverses the shrub's encroachment. Less than healthy grasses have

diminished competitive abilities and relinquish proportional quantities of belowground resources to the shrubs. The additional resources available for western snowberry growth facilitate the enlargement and spreading of the colonies and the increase in stem density. Increases in aerial stem canopy cover increase the competitiveness of the shrubs for the aboveground resources of sunlight. Reductions in sunlight reaching the understory vegetation cause severe reductions in grass biomass production. Effects from shading by dense aerial stems can completely eliminate the understory vegetation.

Development of treatment practices to effectively manage western snowberry using biological, burning, mechanical, and chemical methods requires an understanding of how the plant grows, its strong characteristics, and its weaknesses and periods of vulnerability.

Table 1. Western snowberry stem density at systematic distances from the center of 12 colonies in southcentral North Dakota, 1981.

	Distance from center of colony				
	16.5 feet	33.0 feet	49.5 feet	66.0 feet	82.5 feet
Density Stems per sq. yard	49.5	47.8	43.1	40.1	28.1

Data from Roel 1983

Table 2. Reported phenological information for western snowberry.

Phenological Stages	Nebraska McMillan and Pagel 1958	Nebraska McCarthy 1967	Minnesota Pelton 1953	North Dakota Stevens 1972	North Dakota Manske 1980	North Dakota Roel 1983	Montana Krueger and Bedunah 1988	Wyoming Ferrell 1986, 1992	Alberta Adams and Bailey 1983	Compiled Summary
Bud Swell							Apr			Apr
Twig Elongation	mid Apr	early May	same as most shrubs				late Apr to early Jun			mid Apr to early Jun
Leaf Opening	13-21 Apr	early May 4-6 leaf				14 May	late Apr to early Jun		mid Apr	mid Apr to early Jun
Sucker Development		before early May							late Apr to early Jun	late Apr to early Jun
Full Leaf		late May	mid May to late May					before 7 Jun	late May	mid May to late May
Flower Buds Appear	30 May		20 May							late May to late Jun
Initial Flowering (Anthesis)	16-18 Jun		12 Jun	26 Jun 9 yr Mean	21 Jun 3 yr Mean	22 Jun			late Jun	mid Jun to late Jun
Flower Development	mid Jun to Jul		mid Jun to 15 Aug			6 Jul	mid Jun to mid Aug	before 4 Jul		mid Jun to mid Aug
Fruit Development	22 Jul to 28 Aug		several weeks each						late Jun to mid Aug	late Jul to mid Aug
Fruit Mature							Aug to Sep			Aug to Sep
Leaf Senescence						10 Aug	Sep to Oct			late Aug to Oct

Table 3. Western snowberry current year's growth in stem height and twig length of stem types on 15 colonies in southcentral North Dakota, 1981.

Stem Types	Sample Periods			
	14 Jun	5 Jul	26 Jul	16 Aug
Decadent Stems				
Height (inches)	-	-	-	-
% of peak				
Twig Length (inches)	-	-	-	-
% of peak				
Mature Stems				
Height (inches)	16.4	16.7	16.9	17.0
% of peak	96.3	98.3	99.7	100.0
Twig Length (inches)	3.4	3.6	3.7	3.8
% of peak	90.2	95.8	98.9	100.0
Young Stems				
Height (inches)	11.4	11.8	12.0	12.1
% of peak	94.5	97.4	99.3	100.0
Twig Length (inches)	3.8	4.0	4.1	4.2
% of peak	90.4	94.7	98.8	100.0
Crown Suckers				
Height (inches)	12.6	13.0	13.2	13.3
% of peak	95.3	98.2	99.3	100.0
Twig Length (inches)	3.4	3.6	3.7	3.8
% of peak	90.7	95.7	99.2	100.0
Rhizome Suckers				
Height (inches)	11.6	12.3	12.7	12.8
% of peak	90.4	96.1	99.6	100.0.
Twig Length (inches)	11.6	12.3	12.7	12.8
% of peak	90.4	96.1	99.6	100.0

Data from Roel 1983

Table 4. Western snowberry current year's growth of stem types on 15 colonies in southcentral North Dakota, 1982.

Stem Types	Density stems per square yard	Percent Twig Growth Completed 7 Jun (%)	Total Twig Length per Stem 7 Aug (inches)	Biomass of Twigs, Leaves, and Fruits (lbs/ac)
Decadent Stems	8.4	-	-	62.3
Mature Stems	15.6	78	36.7	804.2
Young Stems	11.0	77	24.0	127.7
Crown Suckers	15.9	87	11.2	310.4
Rhizome Suckers	10.8	69	9.8	140.9
	61.8 stems/sq. yd			1445.5 lbs/ac

Data from Ransom-Nelson 1985

Table 5. Western snowberry current year's growth of stem types on 8 colonies in western North Dakota, August 1981.

Stem Types	Number Twigs per Stem	Total Twig Length per Stem (inches)	Mean Twig Length (inches)	Biomass of Twigs, Leaves, and Fruits (lbs/ac)
Decadent Stems	4.1	8.4	2.1	30.8
Mature Stems	11.2	24.7	2.2	255.8
Young Stems	4.5	16.0	3.5	42.0
Crown Suckers	1.4	11.3	8.1	81.0
Rhizome Suckers	1.2	10.1	8.3	245.5
				655.1 lbs/ac

Data from Mastel 1983

Table 6. Western snowberry current year's biomass of leaves, twigs, and fruits per stem on 15 colonies in southcentral North Dakota, mid August 1981.

Stem Types	Plant Parts			
	Leaf	Twig	Fruit	Total
Decadent Stems				
Weight (gm)	1.5	0.4	0.1	2.0
% of total	74.0	19.6	6.4	
Mature Stems				
Weight (gm)	3.1	1.1	0.7	4.9
% of total	64.1	21.6	14.3	
Young Stems				
Weight (gm)	1.6	0.6	0.2	2.4
% of total	66.5	24.6	8.9	
Crown Suckers				
Weight (gm)	2.4	1.4	0.3	4.2
% of total	58.4	33.7	7.9	
Rhizome Suckers				
Weight (gm)	1.2	1.5	0.4	3.1
% of total	39.2	49.0	11.8	

Data from Roel 1983

Table 7. Mean percent nutrient content of western snowberry twigs in North Dakota.

	Calcium Ca	Magnesium Mg	Phosphorus P	Potassium K	Acid Detergent Fiber ADF	Crude Protein CP	In Vitro Dry Matter Digestibility IVDMD
Apr	0.69	0.13	0.08	0.90	57.3	4.8	22.5
May	0.39	0.20	0.43	2.16	19.7	21.6	73.4
Jun	0.51	0.12	0.12	1.15	45.6	5.1	39.2
Jul	0.56	0.16	0.09	1.09	51.2	3.8	27.8
Aug	0.48	0.11	0.09	1.02	52.1	3.9	27.6
Sep							
Oct	0.54	0.11	0.07	0.90	54.2	4.0	28.9
Nov	0.60	0.15	0.09	0.96	53.8	4.4	26.7
Dec	0.76	0.14	0.08	0.91	53.2	5.1	27.4
Jan	0.69	0.14	0.08	0.88	54.7	4.9	23.7
Feb	0.59	0.14	0.07	0.70	53.9	4.4	23.0
Mar	0.65	0.13	0.05	0.81	56.4	4.4	23.5

Data from Williamson 1979

Table 8. Mean percent nutrient content of western snowberry leaves in North Dakota.

	Calcium Ca	Magnesium Mg	Phosphorus P	Potassium K	Acid Detergent Fiber ADF	Crude Protein CP	In Vitro Dry Matter Digestibility IVDMD
Apr							
May							
Jun	0.65	0.26	0.20	1.97	31.5	12.6	56.7
Jul	0.76	0.30	0.14	1.31	20.8	10.5	64.5
Aug	0.90	0.30	0.14	1.33	21.6	9.2	62.9
Sep							
Oct	1.31	0.26	0.14	1.11	28.8	6.8	51.7
Nov							
Dec							
Jan							
Feb							
Mar							

Data from Williamson 1979

Table 9. Mean percent nutrient content of western snowberry fruits in North Dakota.

	Calcium Ca	Magnesium Mg	Phosphorus P	Potassium K	Acid Detergent Fiber ADF	Crude Protein CP	In Vitro Dry Matter Digestibility IVDMD
Apr							
May							
Jun							
Jul	0.37	0.16	0.21	1.71	18.9	8.3	63.0
Aug	0.28	0.11	0.16	1.44	19.9	6.5	53.7
Sep							
Oct							
Nov							
Dec							
Jan							
Feb							
Mar							

Data from Williamson 1979

Table 10. Percent diet comprised of browse from shrubs for wild ungulates in the Northern Plains.

Wild Ungulates	Spring Apr, May, Jun	Summer Jul, Aug, Sep	Fall Oct, Nov, Dec	Winter Jan, Feb, Mar	Mean for Year
Mule Deer	59	43	81	60	61
Whitetail Deer	43	45	81	65	59
Pronghorn Antelope	18	25	50	43	34

Data from Holechek, Pieper, and Herbel 1995

Table 11. Percent shoot frequency of plants growing in western snowberry colonies and percent fungi infection of roots.

		Western Snowberry	Kentucky Bluegrass	Smooth Bromegrass	Western Wheatgrass	Blue Grama
Shoot frequency in brush habitat	%	58.3a	59.5a	17.5b	15.5b	8.0b
Root infection by mycorrhizal fungi	%	93.8a		32.3c	66.0b	78.8ab

Data from Manske 1992

Means in the same row and followed by the same letter are not significantly different (P<0.05).

Fig. 1. Excavated western snowberry rhizomes and rhizome crowns with clusters of aerial stems.

Fig. 2. Kentucky bluegrass associated with western snowberry colonies.

Fig. 3. Flowering western snowberry.

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