

Actinorhizal plants in rangelands of the western United States

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Abstract

Actinorhizal plants are a diverse group of trees and shrubs that have the ability to form a dinitrogen-fixing symbiosis with *Frankia* bacteria. Actinorhizal plants are found throughout the world and are a significant component of rangelands in the western United States. Many actinorhizal species play important ecological roles in the habitats where they occur. Actinorhizal shrubs such as bitterbrush (*Purshia tridentata* [Pursh DC.]), mountain mahogany (*Cercocarpus* spp), and *Ceanothus* spp. are among the most important wildlife browse species in the western U.S. Other actinorhizal taxa such as alders (*Alnus*) and dryads (*Dryas*) play important roles in soil development and community succession following disturbance. Despite their importance, the biology of these plants in rangeland ecosystems is poorly understood. Particularly lacking is understanding of the dinitrogen-fixing ability of these plants and how symbioses with *Frankia* bacteria affects the ecology of these plants in western U.S. rangelands. Difficulty in isolating and culturing *Frankia* bacteria and in measuring inputs of fixed N from actinorhizal plants has contributed to slow progress in this field. In spite of these shortcomings, the actinorhizal plants of western U.S. rangelands represent a valuable resource for expanded utilization. This review is a summary of current knowledge of actinorhizal range plants and their *Frankia* symbionts. It is intended to provide a scientific basis for the study and utilization of this symbiosis for those involved in rangeland research and management.

Key Words: *Frankia*, symbiosis, reclamation, dinitrogen fixation, browse.

Actinorhizal plants are a group of taxonomically diverse species capable of forming a symbiosis with N₂-fixing soil actinomycetes of the genus *Frankia*. The term "actinorhizal" is formed from the roots "actino" for the *Frankia* actinomycete and "rhiza" for the plant roots bearing the symbiosis (Baker and Schwintzer 1990). This symbiosis should not be confused with the more well-known symbioses between plants and non-N₂-fixing mycorrhizal fungi or between legumes and N₂-fixing *Rhizobia* bacteria. *Frankia* are filamentous, branching, and primarily saprophytic bacteria of the order Actinomycete. *Frankia* can live both symbiotically in root nodules and saprophytically in soil. Plants from 8 families and 25 genera are known to form a symbiosis with *Frankia* (Benson 1988, Dawson 1992). All acti-

Resúmen

Las plantas actinorizoides son un grupo diverso de arboles y arbustos que poseen la habilidad de formar una simbiosis fijadora de nitrógeno con bacterias del genero *Frankia*. Las plantas actinorizoides se encuentran por todo el mundo y comprenden un componente significativo de los pastizales del Oeste de los Estados Unidos. Muchas especies actinorizoides juegan un papel ecológico importante en los habitats en donde se encuentran. Los arbustos actinorizoides como *Purshia tridentata*, *Cercocarpus* spp. y *Ceanothus* spp., se encuentran entre las especies mas importantes para ramoneo por la fauna silvestre en el Oeste de los Estados Unidos. Otras especies actinorizoides, tales como *Alnus* y *Dryas*, juegan papeles importantes en el desarrollo del suelo y en la sucesión después de un disturbio. A pesar de su importancia, la biología de estas plantas en los ecosistemas de pastizales naturales es poco comprendida, desconociéndose la habilidad que tienen estas plantas de fijar nitrógeno y como las simbiosis con bacterias del genero *Frankia*, afectan la ecología de estas plantas en los pastizales del Oeste de los Estados Unidos. La dificultad en aislar y cultivar la bacteria *Frankia* y en medir los flujos del nitrógeno fijado por medio de las plantas actinorizoides, ha contribuido al lento progreso en este campo de estudio. A pesar de estas carencias, las plantas actinorizoides de los pastizales de los Estados Unidos representan un valioso recurso. Esta revisión es un resumen del actual conocimiento sobre las plantas actinorizoides de los pastizales y sus simbiotes. Esta revisión tiene como intención el proveer una base científica para el estudio y utilización de estas simbiosis y el manejo de pastizales con dichas especies.

norhizal plants are woody, with the exception of 2 subshrubs in the genus *Datisca* that have herbaceous shoots arising from woody perennial rootstocks. There are over 100 actinorhizal species native to the United States, and several introduced species are now widely naturalized and regarded as noxious weeds (e.g. Russian-olive [*Elaeagnus angustifolia* L.], autumn-olive [*Elaeagnus umbellata* Thunb.], Australian pine or she-oak [*Casuarina equisetifolia* Forst. & Forst.]). Most actinorhizal species are capable of growing in N-free culture and of fixing ecologically significant amounts of N in perennial woody root nodules (Fig. 1). This ability allows them to flourish in soils where low levels of available N may preclude the growth of other species.

Actinorhizal plants are found throughout the world from the tropics to the arctic. The vast majority of actinorhizal species, however, are native to temperate regions, where they fill the eco-

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Fig. 1. A root segment from an actinorhizal *Alnus rubra* Bong. tree showing numerous perennial, woody root nodules that contain N_2 -fixing *Frankia* bacteria. The coins in the photo are approximately 18 mm in diameter.

logical role occupied by woody legumes in tropical and subtropical regions. There are approximately 80 actinorhizal plant species native to western U.S. rangelands. These species represent approximately one third of the World's known actinorhizal plants, and 6 of the 8 known actinorhizal plant families (Table 1). The western U.S. is a center of diversity for actinorhizal plant genera in the family Rosaceae, and the genus *Ceanothus* (family Rhamnaceae) which is composed of over 40 species. Actinorhizal plants in the western U.S. are ecologically diverse, occurring in alpine, tundra, forest, shrubland, grassland, desert, and riparian habitats.

Common actinorhizal species of western rangelands include bitterbrush (*Purshia tridentata* [Pursh] DC.), mountain mahogany (*Cercocarpus* spp.) (Fig. 2), cliffrose (*Cowania mexicana* [Torr.]), alders (*Alnus* spp.) (Fig. 2), buffaloberry (*Shepherdia* spp.) (Fig. 2), silverberry (*Elaeagnus commutata* Berbh.), Russian-olive (*Elaeagnus angustifolia*), and numerous species of *Ceanothus* (*Ceanothus* spp.) (Fig. 2). A single species in the genus *Rubus* (family Rosaceae) has been reported to be actinorhizal (Becking 1979), however, this observation has never been confirmed despite numerous surveys by several research teams (J.O. Dawson personal communication) *Rubus* is, thus, not currently accepted as an actinorhizal genera (Stowers 1985). The genus *Dryas* (family Rosaceae) is considered to be actinorhizal but it is interesting to note that alpine populations in the lower 48 states, and central and southern Europe, have never been reported to be nodulated. Most actinorhizal plants in the western U.S. are woody shrubs, therefore, they are most often found in mountain

and desert shrublands, chaparral, or open-canopy forests. Bitterbrush and mountain mahogany in the western U.S. form some of the most extensive stands of actinorhizal plants in the world, with bitterbrush alone occupying some 136 million ha in 11 states (Hormay 1943, Findley 1994).

There is little published research on actinorhizal rangeland shrub species despite the ecological importance of the actinorhizal symbiosis in the western U.S. (reviewed by Klemmedson 1979). The purpose of this review is to summarize the current state of knowledge regarding actinorhizal shrubs and their *Frankia* symbionts. It is intended to provide a scientific basis for the utilization and study of this symbiosis for those involved in rangeland research and management. For a more complete introduction to the biology of *Frankia* and actinorhizal plants, readers are referred to Schwintzer and Tjepkema (1990).

Ecological Importance of Actinorhizal Plants

Actinorhizal plants and their *Frankia* symbionts play an important role in the successional development of plant communities (Crocker and Major 1955, Lawrence et al. 1967, Conrad et al. 1985, Hibbs and Cromack 1990, Thilenius 1990). The ability to fix atmospheric N_2 allows actinorhizal plants to colonize sites where lack of available soil N may limit establishment and growth of other plants. Once established on a site, actinorhizal plants can fix N_2 and add N to the soil in the form of leaf litter and dead root tissue. Actinorhizal plants, therefore, build up soil organic matter and create a more favorable habitat for other plants (Crocker and Major 1955, Lawrence et al. 1967, Olf et al. 1993, Chapin et al. 1994) and soil organisms (Aplet 1990). Examples of important early successional actinorhizal plants in the western U.S. include sweetgale (*Myrica gale* L.) and sitka alder (*Alnus viridis sinuata* Regel.) in coastal wetlands of Alaska (Thilenius 1990), numerous species of *Ceanothus* in chaparral, forest, and mountain shrublands (Hickey and Leege 1970, Leege 1979, Conrad et al. 1985), the genus *Alnus* in the Pacific Northwest (Hibbs and Cromack 1990), and species of *Dryas* in arctic and alpine habitats in Alaska (Crocker and Major 1955, Lawrence et al. 1967). Alders and dryads were common colonizers of glacial till following the retreat of continental glaciation in the northern hemisphere (Ritchie 1987).

Other actinorhizal genera such as *Purshia*, *Shepherdia*, and *Ceanothus*, that are usually early successional shrubs, can occasionally persist as mid or later seral components of shrublands or open-canopied forests (Conrad et al. 1985, Dawson 1990). The ecological significance of the actinorhizal symbiosis in later seral communities is not as well-documented as in primary seres and is a topic deserving further study.

Most actinorhizal plants also possess a symbiotic relationship with mycorrhizae (Williams 1979, Rose and Youngberg 1981, Ba et al. 1987, Berliner and Torrey 1989). There is evidence that bitterbrush, mountain mahogany, and Australian she-oak (*Casuarina equisetifolia* L.), have the ability to simultaneously form a 3-way association with *Frankia*, vesicular-arbuscular mycorrhizae, and ectomycorrhizae (Williams 1979, Ba et al. 1987). The presence of mycorrhizae can lead to increased nodulation by *Frankia* (Fraga-Beddiar and Le Tacon 1990), and an increased phosphorus uptake from the mycorrhizal association may result in higher rates of N_2 -fixation relative to non-mycorrhizal plants (Rose and Youngberg 1981). The presence of mycorrhizal associations may also facilitate direct transfer of N from

Table 1. Actinorhizal plant taxa of rangelands in the western United States (number of subspecies).

Family	Genus	native species	exotic species
Betulaceae	<i>Alnus</i>	<i>incana</i> (2) <i>maritima</i> , <i>oblongifolia</i> , <i>rhubifolia</i> , <i>rubra</i> , <i>serrulata</i> , <i>viridis</i> (2)	<i>cordata</i> , <i>glutinosa</i>
Casuarinaceae	<i>Casuarina</i>		<i>cunninghamiana</i> , <i>equisetifolia</i> , <i>stricta</i>
Datisceae	<i>Datisca</i>	<i>glomerata</i>	
Elaeagnaceae	<i>Elaeagnus</i>	<i>commutata</i>	<i>angustifolia</i> , <i>pungens</i> , <i>umbellata</i>
	<i>Shepherdia</i>	<i>argentea</i> , <i>canadensis</i> , <i>rotundifolia</i>	
Myricaceae	<i>Myrica</i>	<i>californica</i> , <i>cerifera</i> , <i>gale</i> , <i>hartwegii</i> , <i>heterophylla</i> , <i>pusilla</i>	
Rhamnaceae	<i>Aldolphia</i>	<i>californica</i>	
	<i>Ceanothus</i>	<i>americanus</i> , <i>arboreus</i> , <i>connivens</i> , <i>cordulatus</i> , <i>crassifolius</i> , <i>cuneatus</i> (4), <i>cyaneus</i> , <i>dentatus</i> , <i>diversifolius</i> , <i>fendleri</i> , <i>ferrisae</i> , <i>foliosus</i> (3), <i>fresnesis</i> , <i>gloriosus</i> (4), <i>greggii</i> (3), <i>griseus</i> , <i>hearstiorum</i> , <i>herbaceous</i> , <i>impressus</i> , <i>incanus</i> , <i>integerrimus</i> , <i>jepsonii</i> (2), <i>lemmonii</i> , <i>leucodermis</i> , <i>maritimus</i> , <i>martinii</i> , <i>masonii</i> , <i>megacarpus</i> (2), <i>oliganthus</i> (2), <i>ophiochilus</i> , <i>palmeri</i> , <i>papillosus</i> (2), <i>parryi</i> , <i>parvifolius</i> , <i>pinetorum</i> , <i>prostratus</i> (3), <i>purpureus</i> (2), <i>roderickii</i> , <i>sanguineus</i> , <i>serpyllifolius</i> , <i>spinous</i> , <i>thyrisiflorus</i> , <i>tomentosus</i> , <i>velutinus</i> (2), <i>verrucosus</i>	
Rosaceae	<i>Cercocarpus</i>	<i>intricatus</i> (2), <i>ledifolius</i> (3), <i>montanus</i> (7), <i>traskiae</i>	
	<i>Chamaebatia</i>	<i>australis</i> , <i>foliosa</i>	
	<i>Cowania</i>	<i>ericaefolia</i> , <i>mexicana</i> , <i>subintegra</i>	
	<i>Dryas</i>	<i>drummondii</i> , <i>integrifolia</i> (4), <i>octopetala</i> (5)	
	<i>Purshia</i>	<i>glandulosa</i> , <i>tridentata</i>	

Adapted from: Vines 1960, Hitchcock and Cronquist 1973, Stephens 1973, Barbour and Major 1988, Dawson 1992, and USDA 1995.

actinorhizal to associated plant species via shared fungal mycelia (Arnebrant et al. 1993).

The amount of fixed-N₂ added to ecosystems by actinorhizal plants varies considerably (Table 2). Rates of N accretion for slow-growing actinorhizal shrubs in the arid rangelands of the western U.S. do not approach those measured for alders (*Alnus* spp.) and snowbrush (*Ceanothus velutinus* Dougl.) in the more mesic forests of the Pacific Northwest (Table 2). However, this does not mean that the seemingly low rates of N accretion observed for plants such as bitterbrush and mountain mahogany are not ecologically significant. The actual percentage of the total ecosystem N pool resulting from N₂-fixation by actinorhizal plants may be similar in mesic and arid systems.

Nitrogen content in the litter of some actinorhizal plants is elevated due to a lack of N retranslocation from senescing leaves. Most deciduous plants will typically translocate one half or more of their foliar N prior to leaf abscission (Chapin and Kedrowski 1983, Côté and Dawson 1986). Several actinorhizal taxa, that

have been examined, translocate a much smaller fraction (11 to 24%) of their foliar N prior to abscission (Dawson and Funk 1981, Côté and Dawson 1986, Llinares et al. 1992, Killingbeck 1993).

There is relatively little direct information regarding the production and release of fixed N by actinorhizal shrubs in western U.S. rangelands. Tiedemann and Furniss (1985) found a 6-fold increase in soil total N beneath canopies of curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) relative to intershrub areas, compared to a 3-fold increase over intershrub areas for non-actinorhizal shrubs. Lepper and Fleschner (1977) found 4 times as much N under mixed stands of limber pine (*Pinus flexilis* James) and mountain mahogany than under adjacent limber pine stands lacking the actinorhizal shrub.

The lack of information regarding N inputs to western U.S. rangelands by actinorhizal plants can be attributed to the difficulty of making such measures. Typical methods for measuring N production and release from actinorhizal plants include acetylene

Table 2. Some estimates of nitrogen accretion by various actinorhizal plants.

Species	Location	Habitat	Methods	Reference	
			(kg N ha ⁻¹ yr ⁻¹)		
<i>Alnus rubra</i>	numerous	Pure stands	100-200	various	Binkley et al. 1994
<i>A. rubra</i>	numerous	Mixed forest stands	50-100	various	Binkley et al. 1994
<i>Shepherdia canadensis</i>	British Columbia	Clearcut	1	acetylene reduction	Hendrickson and Burgess 1989
<i>Ceanothus greggii</i>	California	Shrubland	0.1	acetylene reduction	Kummerow et al. 1978
<i>C. sanguineus</i>	British Columbia	Clearcut	24-50	N accretion	Binkley and Husted 1983
<i>C. velutinus</i>	Oregon	Burn /clearcut	70-108	N accretion	Youngberg and Wollum 1976
<i>C. velutinus</i>	Oregon	Clearcuts	101	acetylene reduction	McNabb and Cromack 1983
<i>C. velutinus</i>	Oregon	Clearcuts	95-100	N accretion	Binkley et al. 1982
<i>C. velutinus</i>	Oregon	Clearcuts	0-20	N accretion	Zavitkovski and Newton 1968
<i>Cercocarpus ledifolius</i>	California	Open forest	7	acetylene reduction	Lepper and Fleschner 1977
<i>Purshia tridentata</i>	Oregon	Open forest	<1	acetylene reduction	Dalton and Zobel 1977

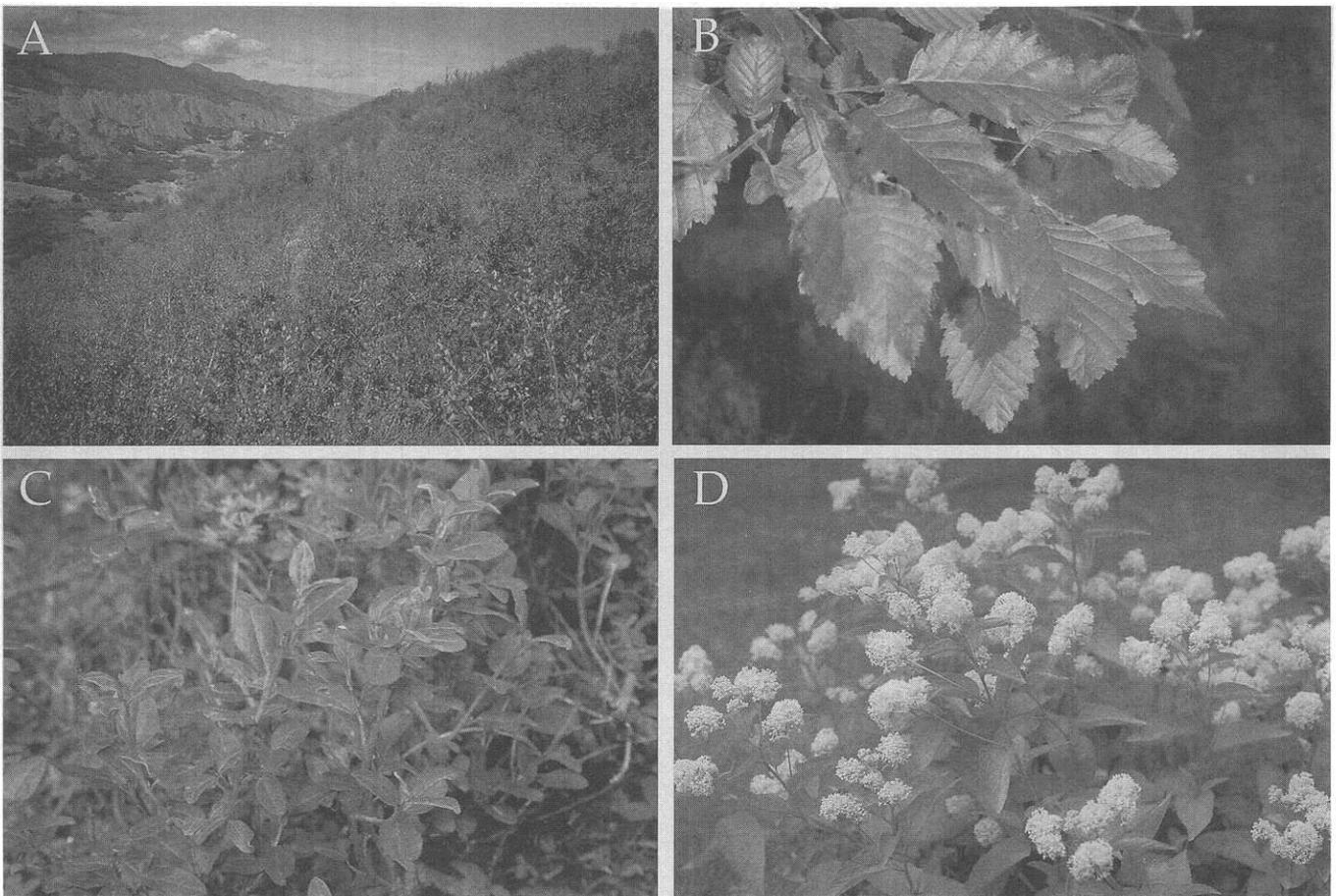


Fig. 2. Some actinorhizal plants characteristic of western U.S. rangelands: **A)** A stand of mountain mahogany (*Cercocarpus montanus* Raf.) shrubs in the Front Range of Colorado, **B)** Thinleaf alder (*Alnus incana tenuifolia* Nutt.) along a mountain stream in New Mexico, **C)** Russet buffaloberry (*Shepherdia canadensis* Nutt.) growing beneath an open pine forest in Wyoming, **D)** New Jersey tea (*Ceanothus americanus* L.) from a prairie in Kansas.

reduction, natural isotope (^{15}N) techniques, and N accretion studies (Table 2). For a detailed description of these and other methods see Silvester (1983) or Winship and Tjepkema (1990). There is a great deal of uncertainty in estimating community or ecosystem level inputs of fixed-N using these methods. These uncertainties are especially difficult to address in arid and semiarid systems where the relatively low rates of N_2 -fixation require greater sensitivity of measurement.

The role of facilitation often attributed to actinorhizal plants during primary succession (Lawrence et al. 1967, Blundon et al. 1993, Chapin et al. 1994) may have as much to do with the addition of organic matter to soils as the direct effects of N inputs. Crocker and Major (1955) demonstrated that within 50 years of glacial retreat at Glacier Bay, Alaska, thickets of actinorhizal alders had built an organic surface horizon 6–7 cm deep amounting to 5–6 kg m^{-2} of organic matter. Actinorhizal species of *Ceanothus* and *Purshia*, which commonly colonize burned areas in western U.S. rangelands (Martin 1983, Conrad et al. 1985), may also provide inputs of soil organic matter. The ecological importance of N_2 -fixation in these situations may simply be that it enables actinorhizal plants to colonize the site, allowing for their subsequent role in soil organic matter development.

Many actinorhizal plants provide nutritious forage for herbivores because of low foliar C:N ratios, high protein content, and

high N content of dormant tissue (Table 3). Many actinorhizal species have evolved under high levels of herbivory, and for some, growth may be stimulated by browsing (Urness and Jensen 1983, Bilbrough and Richards 1989). Rapid growth of actinorhizal plants following herbivory may be due to the relative availability of fixed- N_2 from their *Frankia* symbionts. This type of response is common in plants provided with high nutrient levels (Maschinski and Whitham 1989).

In western U.S. rangelands, most actinorhizal shrubs are important browse species for big game. Austin and Urness (1983) found the summer diet of mule deer (*Odocoileus hemionus*) in Utah consisted of 8% bitterbrush in May and increased steadily to 92% by September. Woodis (1989) found that over a 2-year period Nevada mule deer's diets consisted of 51% bitterbrush. Rominger et al. (1988) found 74 to 92% of the summer diet of bighorn sheep (*Ovis canadensis*) in the Front Range of Colorado consisted of actinorhizal mountain mahogany leaves. In Idaho, 25 to 85% of the annual production of actinorhizal redstem ceanothus (*Ceanothus sanguineus* Pursh.) and 68 to 80% of snowbrush were utilized by elk (*Cervus elaphus*) (McCulloch 1955).

Many actinorhizal shrubs are also browsed by livestock (Van Dersal 1938, Hormay 1943, Young and Payne 1948, Furbush 1962, Thilenius and Hungerford 1967, Hickey and Legee 1970, Phillips 1970, Leckenby et al. 1982, Shaw and Monsen 1986).

Table 3. Nutritional value of some actinorhizal browse species.

Shrub	Location	plant part	CP ^a	NDF ^b	ADF ^c	ADL ^d	IVDDM ^e	Reference
			%	%	%	%	%	
<i>Ceanothus cordulatus</i>	California	Leaves	13.6	27.2	15.2	7.9	33.6	Kie 1986
<i>C. greggii</i>	Arizona	Stems +& leaves	10.0		30.0		55.0	Urness et al. 1977
<i>C. integerrimus</i>	California	Leaves	17.5	31.5	17.2	8.1	58.8	Kie 1986
<i>Cercocarpus ledifolius</i>	Utah	Stems + leaves					53.5	Urness et al. 1977
<i>C. ledifolius</i>	Nevada	Stems + leaves	12.0				65.3	Woodis 1989
<i>C. montanus</i>	Colorado	Stems (dormant)	6.4				29.7	Kufeld et al. 1985
<i>C. montanus</i>	New Mexico	Leaves	12.8	42.6	28.4	15.7		Nunez-Hernandez et al. 1991
<i>C. montanus</i>	Utah	Stems					28.5	Urness et al. 1977
<i>C. montanus</i>	Colorado	Stems + leaves	6.6 - 16.3					Dietz et al. 1962
<i>C. montanus</i>	Colorado	Stems + leaves (dormant)	7.9		47.9	23.2	36.6	Gibbs 1978
<i>C. spp.</i>	Colorado	Stems + leaves	18.1					Cook et al. 1977
<i>Cowania mexicana</i>	Utah	Stems (dormant)	8.8				37.6	Welch et al. 1983
<i>Purshia glandulosa</i>	California	Stems (dormant)	9.3				37.0	Welch et al. 1983
<i>P. tridentata</i>	Nevada	Stems + leaves	15.2				63.6	Woodis 1989
<i>P. tridentata</i>	Colorado	Stems + leaves	19.4					Cook et al. 1977
<i>P. tridentata</i>	Colorado	Stems + leaves	7.4 - 13.9					Dietz et al. 1962
<i>P. tridentata</i>	Colorado	Stems + leaves (dormant)	7.4		50.7	27.4	37.3	Gibbs 1978
<i>P. tridentata</i>	Colorado	Stems (dormant)	5.9				24.1	Welch et al. 1983
<i>P. tridentata</i>	Idaho	Stems (dormant)	6.9				28.3	Welch et al. 1983
<i>P. tridentata</i>	California	Stems (dormant)	7.9				30.6	Welch et al. 1983
<i>P. tridentata</i>	Utah	Stems + leaves					30.0	Urness et al. 1977

^aCP = Crude protein, ^bNDF = Neutral detergent fiber, ^cADF = Acid detergent fiber, ^dADL = Acid detergent lignin, ^eIVDDM = In vitro digestible dry matter

Carefully managed livestock grazing may be a valuable tool for stimulating browse production of some actinorhizal shrubs (Garrison 1953, Tueller and Tower 1979, Leckenby et al. 1982, Urness and Jensen 1983, Bilbrough and Richards 1989, Woodis 1989). Hormay (1943) suggests that bitterbrush becomes unpalatable to livestock if it is not grazed moderately each year. Heavy grazing by livestock followed by a rest period may be a useful tool for encouraging regeneration of bitterbrush stands (Phillips 1970). Although grazing can be beneficial for increasing browse production of actinorhizal shrubs, the long-term survival of individual shrubs can be reduced by heavy browsing (McConnell and Smith 1977), especially during the summer (Young and Payne 1948). Frequent light grazing may be detrimental to actinorhizal shrubs in areas where they are a small component of the plant community, as livestock may preferentially browse them (Hormay 1943).

Many small mammals and birds use actinorhizal plants for food and shelter (McAtee 1936, Van Dersal 1938, Evans et al. 1983, Knopf and Olson 1984, Vander Wall 1994). Inputs of N and organic matter to soils by actinorhizal plants may stimulate soil biological activity (Aplet 1990), which in turn may benefit higher trophic groups. Dawson (1990) suggests that riparian alder trees might be an important source of N to planktonic organisms at the beginning of food chains in cold infertile streams and montane lakes supporting important trout fisheries. Many actinorhizal species have rich nectaries that attract insects (Hayes 1976, Ferris and Brown 1981) and many ornamental species of *Ceanothus* can be cultivated in order to attract nectar-feeding butterflies.

Biology of Frankia

Frankia is a slow-growing filamentous actinomycete that produces 3 cell types: hyphae, vesicles, and spores. Hyphae are vegetative cells that are usually branched and less than 1 µm in diameter. The hyphae differentiate to form vesicles and sporangia. Vesicles are terminal swellings on hyphae and are the sites of N₂-fixation. *Frankia* hyphae often produce sporangia which are structures containing numerous spores. The spores are resting structures and probably play an important role in the dormancy and survival of *Frankia* under adverse conditions (Sussman and Halvorson 1966, Burleigh and Torrey 1990, Burleigh and Dawson 1995). Sporangia can be produced in actinorhizal nodules and in vitro in most *Frankia* strains, depending on cultural conditions. Sporulation of *Frankia* in vitro appears to be controlled by temperature, carbon (C) source, and osmotic stress (Tisa et al. 1983, Burleigh and Dawson 1991). Sporulation coincides with the seasonal senescence of vesicles in infected cells of actinorhizal nodules (Becking et al. 1964, Becking 1970, VandenBosch and Torrey 1985). In arid regions sporulation may be triggered by soil drying (Burleigh and Dawson 1991).

Research on *Frankia* has been hampered due to the difficulty of isolating and culturing *Frankia* from root nodules. Despite numerous efforts, it was not until 1978 that *Frankia* was successfully isolated and cultured by Callaham et al. (1978). As a result of these difficulties, a reliable set of criteria for classifying *Frankia* taxa has not yet been established in the scientific community. Pure cultures of *Frankia* isolates are often classified based on their host affinities as first defined by Baker (1987), and they are usually given identifying codes based on the plant

species from which they were isolated (Lechevalier 1983). Lalonde et al. (1988) proposed the assignment of some *Frankia* strains to 2 species, *Frankia alni* and *Frankia elaeagni*, based on genotypic and phenotypic differences (Lalonde et al., 1988). This classification, however, was not widely accepted by *Frankia* researchers. Recent studies based on DNA relatedness have identified 8 (Nazaret et al. 1991), 9 (Fernandez et al. 1989, Akimov and Dobritsa 1992), and 4 (Normand et al. 1996) genomic groups of *Frankia*.

About half of the genera, but only a small fraction of actinorhizal species, have had pure cultures of *Frankia* isolated from their root nodules. Most cultures are from the genera *Alnus*, *Casuarina*, *Myrica*, and *Elaeagnus* (Lechevalier 1986), and many of these cultures have been isolated from actinorhizal plants growing outside their native range. There is a possibility, therefore, that *Frankia* cultures may have been identified with host plants that are not of the actinorhizal taxa with which these strains evolved naturally. There are numerous genera of actinorhizal plants from which isolates of symbiotic *Frankia* have not been obtained, and many *Frankia* cultures that have been obtained are not capable of re-infecting the host plants from which they were isolated (Lechevalier 1986). Notably missing from culture collections are isolates from Rosaceae and Rhamnaceae actinorhizal shrubs of the western U.S. Until culture collections become more representative of the true diversity of actinorhizal species, it is unlikely that an acceptable taxonomic classification of *Frankia* will be possible. Current efforts by Philippe Normand in Lyon, France to combine PCR techniques in conjunction with 16S ribosomal RNA sequences derived from *Frankia* in intact nodules have enabled some taxonomic relationships to be established among isolated and nonisolated *Frankia* (Normand et al. 1996).

Frankia bacteria are usually found in soils beneath nodulated host plants (Van Dijk 1979, Oremus 1980, Dawson and Klemp 1987, Smolander and Sundman 1987, Arveby and Huss-Danell 1988, Smolander 1990), probably due to the release of *Frankia* from decaying root nodules (Van Dijk 1984). There are numerous reports of *Frankia* in soils lacking actinorhizal host plants (Rodriguez-Barrueco 1968, Bermudez de Castro et al. 1976, Van Dijk 1984, Huss-Danell and Frej 1986, Dawson and Klemp 1987, Zitzer et al. 1991, Paschke and Dawson 1992a, 1992b, Paschke et al. 1994), which indicates that *Frankia* is not an obligate symbiont. *Frankia* can apparently be spread in the environment via the activity of some bird species (Paschke and Dawson 1993, Burleigh and Dawson 1995) and other biological vectors (Paschke 1993).

Most actinorhizal plants are usually found to be nodulated in their native habitats. Root nodules can account for a notable portion of belowground biomass in some systems. For instance, McNabb and Kromack (1983) reported 750 kg ha⁻¹ of nodule biomass for snowbrush growing in western Oregon. There are actinorhizal plant genera, however, that seem to be sparsely nodulated. The most notable of these are bitterbrush and cliffrose that are native to the arid western U.S. (Dalton and Zobel 1977, Nelson 1983, Righetti et al. 1983) and certain species of she-oak (*Casuarina* spp. and *Allocasuarina* spp.) which are native to the arid interior of Australia (Lawrie 1982). Low levels of nodulation in these plants may be due to the low density of infective *Frankia* in the arid surface soils where these plants grow (Lawrie 1982, Righetti and Munns 1982). Lack of moisture (Righetti et al. 1986,

Dawson et al. 1989), or other factors may limit the growth of free-living saprophytic *Frankia* in arid regions.

The presence of nodules on host plants is a good indication that *Frankia* is present in the soil. There is no simple test for determining presence or absence of *Frankia* in soil that is devoid of host plants. One method to test for *Frankia* is to grow actinorhizal plants in the test soil and check for nodulation. Quantitative estimates of *Frankia*-propagule abundance can be made by inoculating host plants with a series of soil dilutions and measuring the relationship between soil quantity and the number of nodules formed (Van Dijk 1984, Paschke 1993). Such tests need to be conducted under aseptic and N-limiting conditions. Another approach is the use of molecular probes to detect *Frankia* DNA and RNA in situ. Molecular methods have been used to study *Frankia* ecology in soils (e.g. Hahn et al. 1990b, Myrold and Huss-Danell 1994), but the cost and difficulty of interpreting results may limit widespread use by researchers.

Methodology for Working with Actinorhizal Plants

Methods for propagating actinorhizal species of western rangelands have been developed for most major taxa (Table 4) while many minor species still await cultivation. Ease of propagation varies considerably within this diverse group of species.

Nursery stock of actinorhizal species often lack root nodules (Danielson and Visser 1990). Seedlings of actinorhizal plants have been experimentally inoculated with *Frankia* and mycorrhizal fungi prior to planting in order to increase nodulation and mycorrhizal infection (Benoit and Berry 1990, Torrey 1992). This can greatly increase the survivability of planted seedlings. It may also be beneficial, in some cases, to inoculate existing stands of actinorhizal plants with *Frankia*, although, this has never been attempted on a large scale. As techniques for mass-culturing of *Frankia* are refined and cultures become more readily available, this might become a possible management tool for stimulating the vigor of actinorhizal shrub stands.

Actinorhizal plants within the families Betulaceae, Myricaceae, and Elaeagnaceae can be readily nodulated by *Frankia* cultures or nodules from species within the same family (Torrey 1990). A lack of pure cultures of *Frankia* from other actinorhizal taxa native to western U.S. rangelands, and a lack of knowledge of host-specificity, precludes specific recommendations for optimum plant-*Frankia* combinations. Most *Frankia* cultures that are currently available do not effectively nodulate actinorhizal plants in the Rosaceae (Kohls et al. 1994) and Rhamnaceae (Torrey 1990) families. Crushed nodules of these plants offer a viable alternative to pure cultures. Kohls et al. (1994) were able to nodulate several Rosaceous shrubs using crushed nodules of yellow dryad (*Dryas drummondii* Richards) collected in Alaska.

Common to *Frankia*-host plant associations is the development of nodules that do not fix N₂ (VandenBosch and Torrey 1983, Hahn et al. 1988, Hahn et al. 1990a). These nodules and the *Frankia* strains that inhabit them are referred to as "ineffective". Ineffective nodules that use carbohydrates from the host plant might actually be pathogenic and demonstrate the fine line between a pathogen and a symbiont. The occurrence of ineffective strains of *Frankia* and the potential for competitive interactions between ineffective and effective *Frankia* beneath stands of European black alder (*Alnus glutinosa* (L.) Gaertn.) has been

Table 4. A brief guide to the cultivation of common actinorhizal plant species of western U.S. rangelands.

Taxa	Scarification	Stratification ^a	Germination temperature	Notes	In vitro Reference ^b	References ^b
<i>Alnus incana tenuifolia</i>		0 to 90 days	20 to 30 °C	Will root from cuttings treated with hormone	5	7, 13
<i>A. rubra</i>		0	15 to 25	12 hr in aerated H ₂ O improves germination	5, 7	1, 7, 14
<i>A. viridis crispata</i>		60 to 90	20 to 25		5	1, 7, 14
<i>A. viridis sinuata</i>					5	14
<i>Elaeagnus angustifolia</i>		0 to 90	20 to 25	12 hr in aerated H ₂ O improves germination	6	1, 7, 14
<i>E. commutata</i>		0 to 90	20 to 25	H ₂ O soluble inhibitor in seed coat	4	1, 7
<i>Shepherdia argentea</i>		60 to 90	20 to 25			1, 7, 14
<i>S. canadensis</i>	30 min conc. H ₂ SO ₄	0 to 90	20 to 25	Cuttings root with some difficulty		1, 7, 9, 14, 15
<i>Myrica cerifera</i>		30 to 90		Will root from cuttings treated with hormone		7, 14
<i>M. gale</i>		30 to 90	20 to 25	Root cuttings will produce shoots, light required for germination		1, 7, 11, 14
<i>Ceanothus americanus</i>	30 min H ₂ O at 57°C or 5 min at 100°C	0 to 90		Preventative fungicide needed, cuttings root well		1, 7, 14
<i>C. cordulatus</i>	H ₂ O at 70°C until cool	0		Preventative fungicide needed		1, 14
<i>C. cuneatus</i>	H ₂ O at 70°C until cool	90		Preventative fungicide needed		1, 14
<i>C. diversifolius</i>	H ₂ O at 70°C until cool	60 to 90		Preventative fungicide needed		1, 14
<i>C. fendleri</i>	H ₂ O at 85°C until cool			Preventative fungicide needed	8	1, 9
<i>C. integerrimus</i>	H ₂ O at 85°C until cool	60 to 90		Preventative fungicide needed		1, 14
<i>C. prostratus</i>	30 sec H ₂ O at 100°C	90 to 115		Preventative fungicide needed		1, 14
<i>C. sanguineus</i>	H ₂ O at 88°C until cool	0 to 115		Preventative fungicide needed		1, 14
<i>C. velutinus</i>	H ₂ O at 85°C until cool	30 to 90		Preventative fungicide needed		1, 9, 14
<i>Cercocarpus ledifolius</i>		0 to 90	3 to 20	Pretreat seeds 15 min in 30% H ₂ O ₂		1, 2, 14
<i>C. montanus</i>	5 min conc. H ₂ SO ₄	0 to 90	3 to 20			1, 14
<i>Cowania mexicana</i>		15 to 30	25 day / 10 night			1, 3, 14
<i>Dryas drummondii</i>		0 to 120	5 to 15	Pretreat seeds 15 min in 30% H ₂ O ₂		12
<i>Purshia tridentata</i>		0 to 90	3 to 20	Pretreat seeds 15 min in 30% H ₂ O ₂		1, 3, 10, 14

^aCold stratification is usually done in moist sand at 3°C.

^bReferences: ¹USDA For. Serv. 1974, ²Young et al. 1978, ³Young and Evans 1981, ⁴Fung 1984, ⁵Tremblay and Lalonde 1984, ⁶Bertrand and Lalonde 1985, ⁷Dirr and Heuser 1987, ⁸Borland 1989, ⁹Krishnan 1989, ¹⁰Meyer and Monsen 1989, ¹¹Schwintzer and Ostrofsky 1989, ¹²Benoit and Berry 1990, ¹³Java and Everett 1992, ¹⁴Young and Young 1992.

reported by Van Dijk and Sluimer-Stolk (1990). These observations illustrate the danger of introducing *Frankia* that is not well characterized into western U.S. rangelands without prior considerations of effectivity and competition with native *Frankia* strains.

At this time, there is no commercially available *Frankia* inoculum for actinorhizal plants. Several university and government laboratories maintain collections of *Frankia* cultures for research. For now, nurseries and land managers must rely on field-collected soil or nodules for establishing actinorhizal symbioses. A reliable source of soil or nodules for inoculum is from beneath nodulated actinorhizal plants near the planting site. Methods for inoculating actinorhizal plants with *Frankia* can be found in Périnet et al. (1985), Benoit and Berry (1990) and Molina et al. (1994).

Future Recommendations

The study of the actinorhizal symbiosis is in its infancy. Despite the abundance of actinorhizal plants in western U.S. rangelands, this region and its actinorhizal flora are greatly underrepresented in the actinorhizal literature. Many questions need to be addressed. These include: 1) to what extent do actinorhizal shrubs contribute to the N economy of rangelands? 2) with what types of *Frankia* do actinorhizal shrubs in the Rosaceae and Rhamnaceae families form a symbiosis? 3) what factors limit nodulation and N₂-fixation in actinorhizal rangeland vegetation? 4) can browse productivity be enhanced by large-

scale inoculation of rangelands with *Frankia*? Other areas that need to be addressed are the isolation and culture of *Frankia* strains from the Rosaceae and Rhamnaceae families, methods for the large-scale production of actinorhizal seedlings and their appropriate *Frankia* and mycorrhizal symbionts, and the possible transfer of the actinorhizal symbiosis to non-actinorhizal taxa.

Because of their importance in natural ecosystems, actinorhizal plants are slowly gaining recognition as valuable trees and shrubs for diverse uses by humans. Throughout the world, actinorhizal plants are used for reclamation of disturbed soils, windbreaks and soil stabilization, interplanting with food and wood crops, commercial products, and to provide food and cover for wildlife and livestock (Dawson 1986, Bulloch 1987, Baker and Schwintzer 1990, Diem and Dommergues 1990, Wheeler and Miller 1990, Dawson 1992). The actinorhizal species of rangelands in the western U.S. have the potential for similar utility (Table 5). Many of the actinorhizal shrubs in the Rhamnaceae and Rosaceae families are adapted to survive on harsh sites, which makes them ideally suited for reclamation. Species of *Elaeagnus*, *Shepherdia*, and *Alnus* have the potential to add large amounts of fixed N and C to soils and they should be given more consideration as soil-improvement tools. The development of sterile cultivars of the weedy exotics Russian- and autumn-olive would allow for their expanded use and would be a major achievement for the reclamation industry.

The Rosaceous actinorhizal plants of the western U.S. perhaps hold great promise for progress in actinorhizal research. It is within this family that numerous non-actinorhizal genera coexist.

Table 5. Actinorhizal plant species characteristic of western U.S. rangelands and their possible uses.

Taxa	Range	Habitat	Uses
<i>Alnus rubra</i>	Pacific N.W., N. Idaho	Streambanks, moist slopes and floodplains	Lumber, soil stabilization, soil improvement
<i>A. viridis sinuata</i>	Coastal Alaska to Cascades	Moist rocky streambanks and slopes, open woodlands	Soil stabilization, reclamation
<i>Elaeagnus commutata</i>	N. Rockies to Minnesota	Dry rocky slopes, rocky stream beds	Wildlife, reclamation, ornamental
<i>Shepherdia canadensis</i>	W. Cascades to Rockies	Open forests, dry rocky slopes	Reclamation, wildlife
<i>S. argentea</i>	California to Upper Midwest	Streambanks, alkaline soils, low meadows	Ornamental, wildlife
<i>Myrica spp.</i>	Coastal regions	Streambanks, lakeshores, moist slopes and floodplains, coastal bogs	Soil stabilization, wildlife, reclamation
<i>Ceanothus cordulatus</i>	S. Oregon to Baja California	Open forests, disturbed sites	Browse
<i>C. cuneatus</i>	California to Oregon	Chaparral, open dry forests	Browse
<i>C. diversifolius</i>	California	Forest understory	Soil stabilization
<i>C. gloriosus</i>	Coastal California	Coastal bluffs	Ornamental, soil stabilization
<i>C. griseus</i>	California	Open slopes, bluffs	Ornamental
<i>C. integerrimus</i>	Oregon to S. Rockies	Chaparral, open forests, riparian forests	Browse
<i>C. prostratus</i>	Sierra Nevada to S. Cascades	Dry disturbed sites, open forests	Soil stabilization, ornamental
<i>C. sanguineus</i>	Cascades to N. Rockies	Mountain shrublands, forest clearings	Browse, reclamation
<i>C. velutinus</i>	Cascades, Sierra Nevada, Rockies	Forest understories and clearings, disturbed sites	Reclamation, browse, ornamental
<i>Cercocarpus spp.</i>	Western U.S.	Dry slopes and ridges, canyon bottoms, chaparral foothills	Browse, reclamation, soil stabilization, ornamental
<i>Cowania spp.</i>	Great Basin to W. Texas	Dry shallow soils	Browse, ornamental
<i>Dryas drummondii</i> ^a	Alaska to S. Rockies	Tundra, alpine and polar rocky terraces	Reclamation
<i>Purshia tridentata</i>	W. Cascades to Rockies	Chaparral, dry slopes, open dry forests	Browse, reclamation, soil stabilization

^a Nodulation status uncertain in alpine habitats of lower 48 states.

Many of these non-actinorhizal genera are closely related to actinorhizal species, which suggests the possibility of future genetic manipulation. Non-nodulating Apache plume (*Fallugia paradoxa* [D. Don] Endl.), for example, can be grafted onto the nodulated root stock of cliffrose (Kyle et al. 1986). The genetic transfer of nodulating ability has been attempted in non-actinorhizal birch (*Betula* spp.) trees (a close relative of alders) (Séguin and Lalonde 1990). If successful, genetic transfer of nodulating ability to species of the Rosaceae (e.g. strawberry, cherry, apple, and raspberry), could represent a significant use of gene transfer technology. Before these goals are pursued however, the more immediate task of understanding the basic biology of this symbiosis in rangeland systems is at hand.

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