NODULATING LEGUMES FROM THE TAHOE BASIN, CALIFORNIA

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ABSTRACT

A survey was conducted to determine the nodulating ability of 44 legume species from the Tahoe Basin. All were found to nodulate under natural soil conditions. Nodulation is reported for the first time in nine species in five genera of Papilionoideae. These species are distributed in tribes Galegeae, Genisteae, Thermopsideae, Trifolieae and Vicieae. Nodule color, shape and frequency are also described. The results support using the morphology of nodular structures to classify legumes. The soils of the Tahoe Basin are generally nutrient poor. However, legumes survive and grow well there. Healthy plants with lush green foliage growing in nutrient-limited environments, suggest that they were nurtured by nitrogen-fixing nodules. Exploitation of legume-*Rhizobium* symbiosis may help to improve nutrient poor soils and may provide refuge and quality browse for wildlife in the Tahoe Basin.

RESUMEN

Los condicionantes geológicos y bioclimáticos han permitido la existencia en el área de Tahoe de un entorno único. Nuestra investigación se centró en la determinación de la capacidad de nodulación de algunas especies de leguminosas en el área del lago Tahoe donde predominan los suelos pobres en nutrientes. Todas las especies estudiadas resultaron nodulantes en condiciones edáficas naturales. En nueve de ellas, pertenecientes a cinco géneros de Papilionoideae e incluidas en las tribus Galegeae, Genisteae, Thermopsideae, Trifolieae y Vicieae, se describe por primera vez el proceso de nodulación indicándose la coloración, forma y frecuencia de las formaciones nodulares. Los resultados apoyan la estrecha relación existente entre los diferentes grupos taxonómicos y la morfología estructural de los nódulos. El desarrollo de poblaciones sanas con follaje exuberante colonizando estaciones con suelos pobres en nutrientes puede ser utilizado como bioindicador del proceso nodular de fijación del nitrógeno. La utilización de la simbiosis leguminosa-*Rhizobium* quizás ayude a mejorar la pobreza en nutrientes de los suelos del área de Tahoe así como, en general, a proveer de mejores hábitats para el incremento y la supervivencia de la vida silvestre en la cuenca del lago Tahoe.

INTRODUCTION

The California flora is rich in Fabaceae members or legumes; there are 69 genera and 491 species found in California (Hickman 1993). Most legumes are indigenous while others are naturalized, often widely so (Witham 1994). Bacteria associated with legumes fix atmospheric nitrogen and are helpful in improving and maintaining soil fertility both in agriculture and natural ecosystems. This novel legume-*Rhizobium* association provides an ideal system for the study of plant-microbe interactions. Athar (1996a) studied nodu-

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lation in 66 Papilionoid species from Sacramento Valley, California and found that the majority of the species were abundantly nodulated under natural soil conditions. However, a majority of the legumes found in California have not been examined for their nodulating ability under natural conditions. A survey was conducted to determine the nodulating ability of some legume species from the Tahoe Basin of California's Sierra Nevada Range (39° N, 120° W). Plants were collected from accessible areas within the Basin, ranging from Desolation Wilderness in the west to the Carson Ridge in the east, Alpine Meadows in the north, and Hope Valley and Carson and Luther passes in the south.

Geologic and climatic forces have combined to form Tahoe's unique and varied environment (Blackwell 1997; Graf 1999). Tahoe's floral diversity can be attributed in part to its central location between plant communities of the Sierra Nevada western foothills, the western Great Basin desert, and the northern and southern Sierra Nevada. The variety of plant species can further be explained by the area's rapidly changing and varied habitats, which have contributed to the large number of Tahoe plants with limited geographic ranges (Graf 1999; Strong 1999). Although vegetation in the basin is mixed due to variations in temperature, precipitation and soil, coniferous forests dominate (Blackwell 1997; Strong 1999).

MATERIALS AND METHODS

Legume species growing under natural conditions were surveyed for their nodulating ability. Periodic field trips were made from late spring to early fall in various parts of Tahoe Basin. Observations were made as described previously (Athar 1996a). Legumes examined included indigenous and introduced herbs, shrubs and vines. At least five plants of each species were examined to minimize error. Legumes were identified by specimens of mature plants. Nodules were distinguished from other kinds of morphological modifications or pathogenic root malformation, and nodulation data were recorded. In some cases, nodule smears and nodule slices were prepared and examined under the microscope (Somasegaran & Hoben1994).

RESULTS AND DISCUSSION

Nodulation status was examined in 44 Papilionoid species growing under natural conditions in the Tahoe Basin. All the species observed were nodulated to various extents (Table 1). These results were compared with the available reports on nodulation (Aguilar et al. 1994; Allen & Allen 1981; Athar 1996a,b, 1997a,b; Athar & Mahmood 1990; Corby 1988; de Faria et al. 1994; Nasim et al. 1998; Roggy & Prevost 1999). Nodulation is reported for the first time in nine species within five genera of Papilionoideae. These species are distributed in tribes Galegeae, Genisteae, Thermopsideae, Trifolieae and Vicieae. Joe Kirkbride, USDA, Beltsville, Maryland has been scanning the literature to create a database that records the presence or absence of root nodules. The database currently contains about 3,000 taxa reported with nodules and about 400 taxa reported without nodules. The results of the present investigation were also sent to him for comparison. Kirkbride

TABLE 1. Nodulation characteristics of some legume species from the Tahoe Basin, California.

Nodulating Species[1]	Previous Report[2]	Frequency[3]	Color	Shape
Galegeae				
Astragalus bolanderi A. Gray	B	++	Brown	Elongated
Astragalus gambelianus E. Sheld.	A	++	Brown	Elongated
Astragalus tener A. Gray	A	+	Reddish brown	Elongated
Astragalus whitneyii A. Gray	B	++	Brown	Elongated
Genisteae				
**Lupinus affinis* J. Agardh	A	++	Pink	Globose
**Lupinus albifrons* Benth.	A	+	Brown	Globose
**Lupinus albus* L.	A	+	Brown	Globose
**Lupinus angustiflorus* Eastw.	B	++	Pink	Globose
Lupinus arbustus Douglas ex Lindl.	B	++	Pink	Globose
Lupinus argenteus Pursh	A	+	Brown	Globose
**Lupinus arizonicus* (S. Watson) S. Watson	A	+	Reddish brown	Globose
Lupinus brewri A. Gray	B	+++	Pink	Globose
Lupinus fulcratus Greene	B	+++	Pink	Globose
Lupinus grayi (S. Watson) S. Watson	A	++	Pink	Globose
Lupinus lepidus Douglas ex Lindl.	A	++	Pink	Globose
**Lupinus microcarpus* Sims	A	+	Reddish brown	Globose
Lupinus polyphyllus Lindl.	A	+	Brown	Globose
**Lupinus succulentus* Douglas ex K. Koch	A	+	Brown	Globose
Loteae				
**Lotus corniculatus* L.	A	+++	Pink	Elongated
Lotus nevadensis (S. Watson) Greene	A	+	Pink	Elongated
**Lotus unifoliatus* Benth.	A	++	Pink	Elongated
Millettieae				
**Wisteria chinensis* DC.	A	+	Brown	Globose
Thermopsideae				
**Thermopsis montana* Nutt.	B	++	Brown	Semi-globose
Trifolieae				
**Medicago lupulina* L.	A	+++	Pink	Elongated
**Medicago polymorpha* L.	A	++	Pink	Elongated
**Medicago sativa* L.	A	+++	Pink	Elongated
**Melilotus alba* Medik.	A	+++	Pink	Elongated
**Melilotus indicus* (L.) All.	A	+++	Pink	Elongated
Trifolium barbigerum Torr.	A	+++	Pink	Elongated
**Trifolium campestre* Schreb.	A	++	Pink	Elongated
**Trifolium dubium* Sibth.	A	+	Pink	Elongated
**Trifolium hirtum* All.	A	++	Pink	Elongated
Trifolium kingii S. Watson	A	+++	Pink	Elongated
Trifolium longipes Nutt.	B	++	Pink	Elongated
**Trifolium repens* L.	A	+++	Pink	Elongated
**Trifolium pratense* L.	A	+++	Pink	Elongated

TABLE 1. continued

Nodulating Species[1]	Previous Report[2]	Frequency[3]	Color	Shape
**Trifolium subterraneum* L.	A	+++	Pink	Elongated
Trifolium variegatum Nutt.	A	++	Pink	Elongated
Vicieae				
Lathyrus nevadensis S.Watson	B	++	Pink	Elongated
**Lathyrus odoratus* L.	A	+++	Pink	Elongated
**Vicia faba* L.	A	++	Pink	Elongated
Vicia hirsuta (L.) Gray	A	+++	Pink	Elongated
**Vicia sativa* L.	A	++	Pink	Elongated
**Vicia villosa* Roth	A	++	Pink	Elongated

[1]Species are arranged alphabetically within genera. The nomenclature and tribal classification are as described by Polhill and Raven (1981). Author citations are quoted following instructions of Brummitt and Powell (1992). Introduced species are marked with an asterisk (*).
[2]Nodulating status
A = Nodulation previously observed
B = Nodulation reported for the first time
[3]Nodule frequency
+ = Indicates sparse nodulation (1 to 5 nodules per plant)
++ = Indicates moderate nodulation (6 to 10 nodules per plant)
+++ = Indicates abundant nodulation (more than 10 nodules per plant)

compared the results with his global listing and has confirmed the new reports. The nodules observed in other species corroborate earlier studies (Allen & Allen 1981; Athar 1996a, b; Athar & Shabbir 1997; Corby 1988).

Nodules in most of these species were generally distributed on the main, as well as lateral roots, and were found in the 10 cm layer of the soil. Nodules of some legumes, particularly *Lupinus* spp., sometimes grew on the surface of the soil and were covered by a layer of damp litter. Similar observations were made by Athar (1996a) for some legumes from the Sacramento Valley. The size, number and color of the nodules varied for various species, as well as with the growth stage of the plants. Nodules varied from semi-globose to globose with streaked or smooth surfaces, to elongated and branched forms (Table 1). They occurred singly or as lobed structures. Nodule morphology strongly coincided with the descriptions of earlier workers (Allen & Allen 1981; Athar 1996a; Corby 1988; Pueppke & Broughton 1999; Roggy & Prevost 1999; Somasegaran & Hoben 1994). Nodules were mostly pink or brown with reddish interiors. Nodule morphologies in legume species described by Corby (1988), showed that they were uniform at the tribal level and linked to their position in the evolution of the family. It is becoming clear that nodulation is a robust taxonomic character, both at the presence/absence level and at the structural/physiological level (Sprent 1999). The pioneer work of Corby (1988), linking the morphology of nodular structures to the taxonomy of the legumes, is still relevant, provided that it is coupled to anatomical analyses taking into account the modes of establishment of the symbiosis between the two partners (Pueppke & Broughton 1999; Roggy & Prevost 1999; Sprent 1999).

Attempts to isolate rhizobia or to test nitrogenase activity were not made for these nodulated legumes. However, healthy plants with lush green foliage growing in a nutrient-limited environment imply that they were nurtured by nitrogen-fixing nodules (Hartwig 1998; Somasegaran & Hoben 1994). This is supported by the generally accepted view that nodulated legumes have an internal regulatory system to allow them to adjust nitrogen fixation to environmental conditions (Hartwig 1998; Sprent 1999).

Lupinus (Lupines) were the most prevalent nodulated legumes in Tahoe Basin with 14 species followed by *Trifolium* (clovers), *Vicia* (vetch) and *Astragalus* (locoweeds) with 10, 4 and 4 species each respectively (Table 1). The soils of the Tahoe Basin generally are nutrient poor, especially near the surface where drainage greatly exceeds the rate of chemical erosion from individual soil particles. All the legumes grew well in the nutrient poor environment of the Tahoe Basin. Physiological processes that plants undergo to survive in the Basin help in understanding Tahoe's vegetation ecology. Nutrient limitation plays an important role in plant distribution. Plants cope with nutrient deficiency through mutualisms with mycorrhizal fungi or through associations with bacteria capable of nitrogen fixation. Nitrogen fixation is a crucial component of many plant communities in the Sierra Nevada Range, where nitrogen is ways in short supply. Exploitation of the legume-*Rhizobium* symbiosis in nutrient poor environment of the Tahoe Basin may help improve natural ecosystem, and provide refuge and quality browse for wildlife.

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