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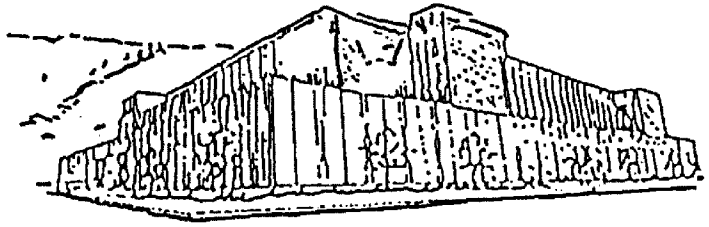
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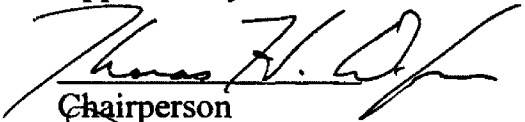


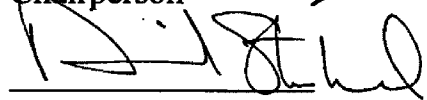
**ABUNDANCE AND OCCURRENCE OF NATIVE NITROGEN FIXING PLANTS IN FIRE EXPOSED  
AND FIRE EXCLUDED PONDEROSA PINE/DOUGLAS-FIR FORESTS IN WESTERN MONTANA**

by  
Jennifer Newland  
B.S. Stanford University, 1992

presented in partial fulfillment of the requirements  
for the degree of  
Masters of Science  
The University of Montana  
1998

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Abundance and occurrence of native nitrogen fixing plants in fire exposed and fire excluded ponderosa pine/Douglas-fir forests in western Montana

Advisor: Thomas H. DeLuca 

Nitrogen is a limiting nutrient in forests of the Inland Northwest, and recent studies indicate that fire and other disturbances may further reduce plant available N in these forests. Research in this region and other parts of the world suggest that N fixing plants play an important role in replacing the N lost from the soil of fire affected sites. The exclusion of fire from ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) forests of western Montana has caused widespread changes in forest structure, composition, and function. However, little is known about changes in understory communities resulting from fire exclusion. The first part of this study tested the germination response of seven native N fixing plants, common in dry western Montana forests, to exposure to heat, plant derived smoke, and nitric acid. Two species showed increased germination when exposed to smoke. No species showed positive differences in germination rates after exposure to heat, but two species showed a decrease in germination with heat exposure. Seeds of three species exposed to smoke also germinated more rapidly than seeds exposed to other treatments. In the second part of this study, the number of N fixing plant species, proportion of cover and frequency of occurrence of these plants, and soil N indices were compared at 11 paired sites in western Montana. Two types of sites were selected for sampling; sites that had been undisturbed since historic logging in the late 1800's and early 1900's, and sites where the second growth forests had been repeatedly opened by logging and/or fire over the last 80-100 years. Two types of stands were sampled in each site; a control stand was sampled along with a nearby area that had been affected by wildfire or an underburn in the last 3-10 years. Cover and frequency of N fixing plants were significantly higher in burned stands than in controls and also significantly higher in repeatedly opened sites than in undisturbed sites. Potentially mineralizable N (PMN), nitrate, and ratio of PMN to total soil N were all significantly lower in the same areas where N fixing plant cover and frequency were higher--in burned stands and repeatedly opened sites.

## **ACKNOWLEDGEMENTS**

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## PREFACE

Fire plays an integral role in determining plant community composition and structure in ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) forests in western Montana. Studies in this area place fire frequency intervals at 13-50 years which maintained open stands of uneven-aged ponderosa pine (Arno et al., 1995; Arno, 1976). The exclusion of these high frequency, low intensity fires along with selective cutting of larger ponderosa pine trees has led to the development of thick understory vegetation, mostly young Douglas-fir, and to large accumulations of forest floor litter (Arno et al., 1995). These changes are also blamed for increasing forest health problems, greater risk of high intensity stand replacing wildfires, and decreasing forest productivity (Arno, 1996; Harvey, 1994). How these changes are affecting understory shrubs and forbs has not yet been well documented (Fischer and Bradley, 1987). Many early succession plants require the open space created by disturbance to establish themselves or to thrive, and in these ponderosa pine/Douglas-fir forests, fire is the most common agent of change (Arno, 1996).

Nitrogen is limiting in most Western forest ecosystems because low moisture availability and cool temperatures limit N mineralization (Kimmins, 1996; Walley et al., 1996). Fire increases the recycling of N in forest litter and surface organic soil horizons resulting in a flush of mineral N that can last for up to two growing seasons after the fire (Covington and Sackett, 1992; DeLuca and Zouhar, 1998). However, recent studies in the Inland Northwest have shown that total N and potentially mineralizable N in soil can decrease after fire (DeLuca and Zouhar, 1998; Monleon et al., 1997) which may decrease both the short- and long-term N availability in these forest soils.

A wide variety of legumes and actinorhizal plants are common in western Montana forest ecosystems. These plants commonly form an association in their roots with nitrogen fixing bacteria, and are referred to generally as nitrogen fixing plants. Many scientists believe that these plants are an important part of the forest community, providing an important source of plant available N (Trowbridge and Holl, 1992; Hendricks and Boring, 1992; Klemmedson, 1979). In addition to their role in the N cycle in soils, some of these plants are also important species for wildlife browse and habitat (Noste and Bushey, 1987).

Leach and Givnish (1996) showed that N-fixing plant species of prairie environs have decreased in the absence of regular disturbance by fire because the conditions in which they are most able to compete are no longer exist. It is possible that changes in forest structure and composition in western Montana may be detrimental to N-fixing plants native to this area. In the development of a habitat typing system for the northern Rocky Mountains (Pfister et al., 1977) scientists noted that although native N-fixing species are scattered in older forests, it is likely that significant N accretion occurs in early successional stages (Jurgensen et al., 1991). These conclusions were based on intensive sampling of mature stands, but little work has examined understory vegetation in recently disturbed stands in these same forest types (Fischer and Bradley, 1987; Noste and Bushey, 1987; Jurgensen et al., 1991). Some N-fixing species have been studied in detail, and in some cases their autecology and N contributions have been demonstrated (see Conard et al., 1985). Species common to dry western Montana forests, like *Purshia tridentata* and *Ceanothus* spp., have been intensively studied, mostly because of their importance as wildlife browse and their perceived competition with tree regeneration

(Gratkowski, 1962), not because of their significance as N-fixers. The primary purpose of this study was to increase our basic understanding of how of native N-fixing plants are affected by recent wildfire, prescribed fire, and fire exclusion.

Studies of other ecosystems have shown that the seeds of some species are stimulated to germinate by fire related cues like heat, components of smoke, or destruction of allelopathic inhibitors (Cocks and Stock, 1997; Keeley and Fotheringham, 1997; Christensen and Muller, 1975). Past studies have shown that seeds of *Ceanothus* spp., including those common in western Montana, are stimulated to germinate by high temperatures (Gratkowski, 1962), and it is possible that such direct links to fire are affecting the occurrence of some other N-fixing species. The first chapter of this thesis summarizes a brief study comparing untreated seed germination rates to rates of seeds treated with different fire related cues; smoke, heat, and nitric acid. The second describes a field survey of eleven sites in western Montana, five that had been selectively harvested and underburned in the last three to ten years and six sites that have been exposed to wildfire in the last ten years. In addition to recording the presence and coverage of native N-fixing plants, soil samples were collected on burned and unburned plots and analyzed for ammonium, nitrate, potentially mineralizable N, total N and C, soil texture, and soil pH. Plant samples of N-fixing species and non N-fixing species were collected and used in  $^{15}\text{N}$  analysis. Chapter 3 summarizes the results and conclusions of this field study.

## Literature Cited

- Arno, S.F. 1996. The concept: restoring ecological structure and process in ponderosa pine forests. In: Hardy, C.C. and S.F. Arno, eds. The use of fire in forest restoration. Gen. Tech. Rep. INT-GTR-341.
- Arno, S.F. 1976. The historical role of fire on the Bitterroot National Forest. US For. Ser. Res. Note RM-413.
- Arno, S.F., J.H. Scott, and M.G. Hartwell. 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. Res. Rep. INT-RP-481.
- Christensen, N.L. and C.H. Muller. 1975. Relative importance of factors controlling germination and seedling survival in *Adenostoma* chaparral. *Am. Mid. Nat.* 93:71-78.
- Cocks, M.P. and W.D Stock. 1997. Heat stimulated germination in relation to seed characteristics in fynbos legumes of the Western Cape Province, South Africa. *S. Afr. J. Bot.* 63:129-132.
- ✧ Conard, S.G., A.E. Jaramillo, K. Cromack, Jr., and S. Rose. 1985. The role of the genus *Ceanothus* in western forest ecosystems. US For. Ser. Gen. Tech. Rep. PNW-182.
- Covington, W.W. and S.S. Sackett. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Mgmt.* 54:175-191.
- DeLuca, T.H. and K. Zouhar. 1998. Effects of selection harvest and prescribed burning on soil nitrogen dynamics in ponderosa pine forests. *For. Ecol. Mgmt.* In press.
- ✧ Fischer, W.C. and A.F. Bradley. 1987. Fire ecology of Western Montana forest habitat types. US For. Ser. Gen. Tech. Rep. INT-223.
- Gratkowski, H.J. 1962. Heat as a factor in germination of seeds of *Ceanothus velutinus* var. *laevigatus*. Ph. D. thesis, Oregon State University, Corvallis, OR.
- Harvey, A.E. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the inland western United States: past, present and future forest health. In: Assessing forest ecosystem health in the Inland Northwest, R.N. Sampson and D.L. Adams, eds. Forest Products Press, Bingham, NY.
- Hendricks, J.J., and L.R. Boring. 1992. Litter quality of native herbaceous legumes in a burned pine forest of the Georgia Piedmont. *Canadian Journal of Forest Research.* 22:2007-2010.

- Jurgensen, M.R., J.R. Tonn, R.T. Graham, A.E. Harvey, and K. Geier-Hayes. 1991. Nitrogen fixation in the forest soils of the Inland Northwest. pp. 101-109. In: Proceedings-Management and productivity of western-montane forest soils. Gen. Tech. Rep. INT-280.
- Keeley, J.E. and C.J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. *Science*. 276:1248-1250
- Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. *Soil Sci. Soc. Am. J.* 60:1643-1654.
- Klemmedson, J.O. 1979. Ecological importance of actinomycete-nodulated plants in the western United States. *Bot. Gaz.* 140(Suppl.):S91-S96.
- Leach, M.K. and T.J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science*. 273:1555-1558.
- Monleon, V.J., K. Cromack Jr., and J.D. Landsberg. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27:369-378.
- Noste, N.V. and C.L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. Gen. Tech. Rep. INT-239
- Pfister, R.D, B.L. Kovalchik, S.F. Arno, and R.C. Presby. 1977. Forest habitat types of Montana. US For. Ser. Gen. Tech. Rep. INT-34.
- Trowbridge, R. and F.B. Holl. 1992. Early growth of lodgepole pine after establishment of alsike clover-Rhizobium nitrogen-fixing symbiosis. *Can. J. For. Res.* 22:1089-1093.
- Walley, F.L., C. Van Kessel, and D.J. Pennock. 1996. Landscape-scale variability of N mineralization in forest soils. *Soil Biol. Biochem.* 28:383-391.

# CHAPTER 1. FIRE RELATED GERMINATION CUES OF NATIVE NITROGEN FIXING PLANTS COMMON IN PONDEROSA PINE/DOUGLAS-FIR FORESTS OF WESTERN MONTANA

## ABSTRACT

Previous studies have shown that many plant species common in fire sculpted ecosystems have higher germination rates with exposure to fire related cues. These studies have focused on plants from seasonally dry Mediterranean ecotypes, but have shown that a wide variety of plants including fire endemic herbs, succulents, grasses, legumes show increased germination when exposed to heat or smoke. Nitrogen fixing plants found in dry western Montana forest ecosystems require fire disturbance to maintain open stands and favorable growing conditions, but there is little understanding about the physiological responses of these plants that allow them to take advantage of post-fire environmental conditions. This study tested seven native nitrogen fixing plants common to ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) forests for germination response to heating, plant derived smoke, and nitric acid. Two species, one actinorhizal shrub and one legume, showed increased germination when exposed to smoke. No species showed positive differences in germination rates after exposure to heat, but two species showed a decrease in germination when exposed to heat. Nitric acid seemed to have little or no effect on all species. The overall germination rates of three species were generally high and similar between treatments. However, it appears that seeds of these species exposed, directly or indirectly, to smoke germinated more rapidly than seeds exposed to other treatments.

## INTRODUCTION

Nitrogen fixing plant species may be especially important in dry forest ecosystems of the northern Rocky Mountains because of the limited amount of N available for plant uptake in these systems. Native N fixing plants species have been recognized in this area and in other parts of North America as an important source of plant available N (Trowbridge and Holl, 1992; Hendricks and Boring, 1992; Hobbs and Schimel, 1984; Binkley et al., 1982). Nitrogen fixing plant species are dependent on disturbance to create conditions in which they can favorably compete with non-N fixing species (Leach and Givnish, 1996; Fischer and Bradley, 1987). In almost all cases these plants require openings or a sparse canopy cover caused by disturbance to thrive. Fire has been the most frequent disturbance agent in ponderosa pine/Douglas-fir forest

ecosystems in western Montana. Historic fire regimes, which have been recreated from tree scars, indicate that frequent low-intensity fires affected ponderosa pine/Douglas-fir forest types in western Montana on intervals from 13 to 50 years (Arno et al., 1995; Gruell et al., 1982; Arno, 1976). Frequent fires in these ecosystems maintained ponderosa pine in open park-like stands and prevented the development of a thick understory of young Douglas-fir and ponderosa pine (Wright and Bailey, 1982; Gruell et al., 1982).

Researchers have shown that plants from other fire dependent ecosystems are stimulated to germinate by cues related to fire--heat, destruction of allelopathic compounds, and unidentified compounds from smoke and charred wood (Keeley and Fotheringham, 1997; Baldwin et al., 1994; Christensen and Muller, 1975; Went et al., 1952). Most studies have focused on plants from Mediterranean type ecosystems where thick shrub vegetation prevents the development of herbaceous plants except after fires. Little is known about the direct effects of fire on germination of understory shrubs and forbs in fire dependent western Montana forests. *Ceanothus* species common in the northern Rocky Mountains are stimulated to germinate by high temperatures and are commonly abundant on fire affected sites (Conard et al., 1985) and the response of other shrub species to fire has been documented (Fischer and Bradley, 1987; Noste and Bushey, 1987). However, the focus on studying climax forests has lead to a dearth of information on early successional species and species common in fire climax forests, including native N fixing plants (Jurgensen et al., 1991).



## LITERATURE REVIEW

Nitrogen availability is limited in most forest ecosystems (Waring and Schlesinger, 1985) and forests in the northern Rocky Mountains are no exception (Kimmins, 1996; Edmonds et al., 1989; Binkley and Hart, 1989). The cool, dry climate limits N mineralization and unlike forests in other parts of the world (Magill et al., 1997) dry deposition and other anthropogenic inputs of N are very small. Because there is no mineral source of N in soils, the primary form of N input is biological N fixation in northwestern US forested ecosystems (Waring and Schlesinger, 1985). Fire and other types of disturbance favor N fixing plants and free living N fixing bacteria in these ecosystems, and native N fixing species in the region are very important components of the understory plant community. *Ceanothus velutinus*, *Cercocarpus ledifolius*, and *Purshia tridentata* are important for wildlife forage and habitat (Conard et al., 1985; Bunting, 1989; Noste and Bushey, 1987), and these species along with leguminous forbs are recognized as an important source of plant available N in fire dependent systems (Kimmins, 1996; Johnson, 1995; Trowbridge and Holl, 1992; Hendricks and Boring, 1992; Binkley et al., 1982).

Scientists and land managers have anecdotally recognized the dependence of these species on fire, but the actual interaction effects between fire and these plants are poorly understood (Arno and Wilson, 1986; Gruell et al., 1983). The symbiotic association of these plants with N-fixing bacteria requires large amounts of photosynthate produced in relatively high light intensities. Without open canopies, the native N fixing plants are out-competed by other understory plants. However, we know little about the actual traits of these plants which allow them to thrive in post-fire environments.

Changes in fire frequency over the last 100 years, attributed to fire suppression, grazing, and lack of ignitions by Native Americans (Bradley et al., 1992), have changed forest structure and composition (Busse et al., 1996; Arno et al., 1995), and prevent us from fully understanding the role of fire in developing community structure in western Montana forests. Nevertheless, fire has been and continues to be an important evolutionary and environmental control in dry forest ecosystems in the northern Rocky Mountains (Arno et al., 1995; Wright and Bailey, 1982). Researchers believe that frequent low intensity fires maintained lower and mid-elevation forests as open stands of all-aged ponderosa pine. Historical photographs and tree ring analysis provide the basis for descriptions of pre-1900 forest structure in western Montana (Gruell et al., 1982; Arno, 1976). Unfortunately, we know little about the composition of understory shrub and forb community in these forests. Gruell and associates (1982) were able to identify a few understory species in turn of the century forests using historical photographs of the Lick Creek drainage southwest of Hamilton, Montana. Native N fixing plants, lupine and bitterbrush, were abundant in multiple photographs from a 1909 timber sale in this area, and a dominant herbaceous understory was obvious in all of the earliest photographs. The work of Pfister and associates (1977) and other scientists (Jurgensen et al., 1979) showed that many species of N fixing plants are found in mature, most often fire excluded, ponderosa pine/Douglas-fir forests in western Montana, but these species usually occur in scattered areas and at low densities. Some of the same scientists point out that much of this work focused on undisturbed stands and we still know little about seral understory plant communities (Jurgensen et al., 1991). Observations of the

abundance of N fixing species in recently disturbed sites in western Montana, suggest that N fixing plants were common in turn of the century forests.

The fire ecology of Mediterranean type ecosystems has been extensively studied, perhaps because these areas are often heavily populated and support the production of important crops. Many herbaceous plants are found in these ecosystems only after fire removes thick overstory shrubs. Researchers propose many possible benefits of fire induced synchronized germination including increases in available nutrients after a fire, especially N and phosphorous, an allelochemical free soil environment, reduced herbivory and exposure to pathogens, and improved growing conditions due to canopy removal (Thanos and Rundel, 1995; Baldwin et al., 1994). Germination cues are one of the most striking ways that plants have adapted to take advantage of beneficial post-fire conditions. Many plants from systems like California chaparral, South African fynbos, Australian heath and eucalyptus forest, and Utah scrub demonstrate fire enhanced germination (Baldwin et al., 1994). Heat, destruction of allelopathic compounds, and unidentified compounds from smoke and charred wood have been identified as germination cues associated with fire (Keeley and Fotheringham, 1997; Baldwin et al., 1994; Christensen and Muller, 1975; Went et al., 1952).

In the past it has been difficult to uncouple actual germination cues from the positive nutrient and environmental changes. Chemicals produced by some plants, either in their litter or exudates in the rhizosphere, have long been suspected to be inhibitors preventing the germination and/or growth of other plants (Went et al., 1952). This type of ecological interaction is difficult to accurately study under field conditions or in laboratory settings meant to represent natural conditions. Some initial work on

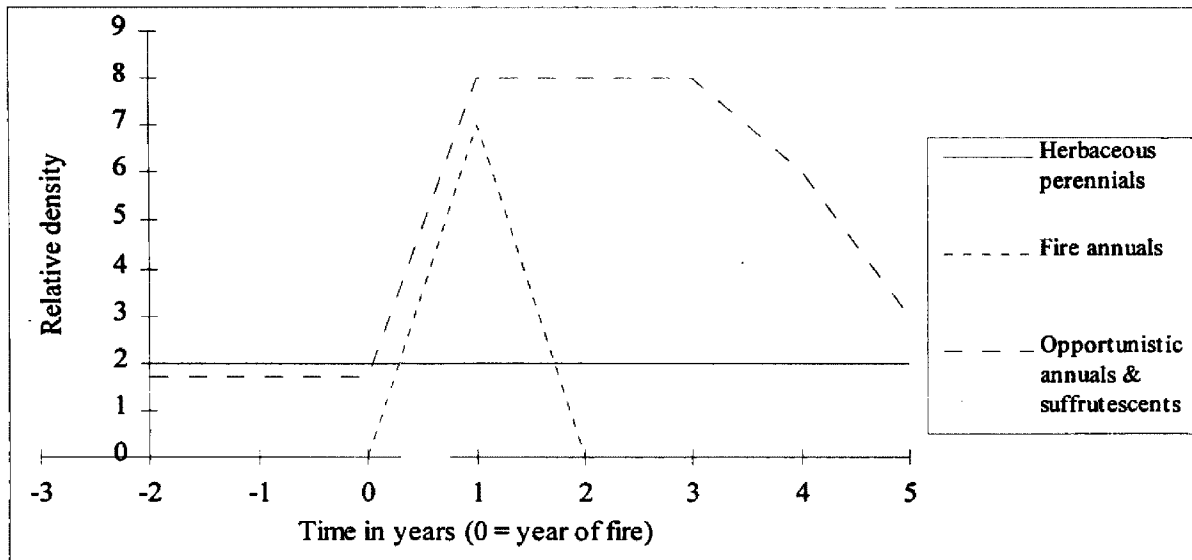
allelopathic controls of germination have been questioned (Keeley et al., 1985; Christensen and Muller, 1975). Smoke and heat, in comparison, can be recreated easily in laboratory settings, and researchers have shown seed bank stimulation by these two factors on many different species from a variety of families, ecosystems, and continents (see review by Brown and van Staden, 1997). Using these cues researchers have begun to isolate other effects of environmental changes and plant interactions on post-fire plant communities (Thanos and Rundel, 1995; Baldwin and Morse, 1994; Keeley et al., 1985).

Studies have examined germination cues of plant species from different ecosystems with different life forms, different reproductive strategies, symbiotic associations, and varying dependence on fire. Based on these studies it is likely that native N fixing plants found in ponderosa/Douglas-fir forests of western Montana also respond to some fire dependent germination cues.

Herbaceous annuals have been the group most widely shown to have smoke stimulated germination, but some suffrutescents, succulents, and a fire-climax grass species are also stimulated by smoke (Baldwin et al., 1994; Keeley et al., 1985; Pierce et al., 1995; Baxter et al., 1994; Brown, 1993). The positive germination response to smoke seems to be independent of seed size, plant life form (annual, perennial, or herbaceous), or whether the plants commonly reseed or resprout after fire (Brown and van Staden, 1997). Other scientists in South Africa demonstrate that plants from fire-free ecosystems seem to be just as likely or more likely to have a positive germination response to smoke as species of the same family from fire-prone areas (Pierce et al., 1995). The active agent in smoke has so far eluded identification, although researchers note that it is stable for

months, soluble in water, and produced between 160-200°C (Brown and van Staden, 1997; Baldwin et al., 1994).

**Figure 1.1.** Generalized population densities of chaparral plants with different life histories, from Keeley et al., 1985



Keeley and associates (1985) divided plants that are common in chaparral after fires into life history groups, herbaceous perennials, suffrutescents, opportunistic annuals, and fire annuals. These researchers showed that fire annuals and some suffrutescents were cued to germinate by charred wood and/or heat, while the seeds of herbaceous perennials germinated readily without treatment. Opportunistic annuals were shown to have polymorphic seeds, some which germinated readily without treatment and others that germinated after heat or charred wood treatment. This result in observable population patterns (generalized in Figure 1.1) and gives us a basis for predicting whether or not selected species rely on fire cues based on the plants life history.

Legume species have also been the focus of studies on fire associated germination cues. Many species from the Fabaceae family have very hard seed coats and long life spans and heating has been shown to be an important agent in breaking the dormancy of

many of these species. Tests of species from the southeastern US, jarrah forests of Australia, and South African fynbos showed most tested species had highest germination rates with exposure to temperatures between 80-100°C (Martin et al., 1975; Auld and O'Connell 1991; Cocks and Stock, 1997). Actinorhizal shrubs from the Inland Northwest have also shown a positive germination response to heating. Scientists recognized the longevity and heat dependence of *Ceanothus* spp. long before this plant's association with N fixing bacteria was recognized (Gratkowski, 1962). Early research on *Ceanothus velutinus* indicated that seeds of this species stay dormant in the soil for very long periods and are stimulated to germinate by high soil temperatures, supporting observations of increased occurrence and coverage of *C. velutinus* after fires (Conard et al., 1985).

In another interesting study (Baxter et al., 1994) researchers tested a fire-climax grass species from South Africa. This important graze species, *Themeda triandra*, is maintained by frequent fires and without this disturbance it is replaced by other less palatable species. Baxter and associates (1994) hypothesized that smoke from burning *T. triandra* might be a necessary germination cue that precludes the germination of this grass in the absence of fire. Their results showed increased germination of *T. triandra* seeds exposed to smoke.

Other studies have focused on separating out the effects of increased mineral N in soils after fires. Thanos and Rundel (1995) showed that levels of nitrate and ammonium that can be found in soils after fire promote increased seed germination of some chaparral fire annuals. They used some of the same species studied by Keeley and associates

(1985) and found that the response with elevated mineral N levels was very similar to the germination response when extracts from charred wood were applied to the seeds. These results did not point to nitrogenous compounds as the active agent in smoke or charred wood extracts because the concentration of mineral N in these compounds did not match the levels used in the experiment carried out by Thanos and Rundel (1995). Other researchers (Baldwin and Morse, 1994) working in a different ecosystem, scrub lands in Utah, found that nitrate and smoke together stimulate increased germination in some burned and unburned soils, although burned soils showed higher germination rates even without additional treatments. These researchers suggest that germination cues are a combination of exposure to smoke and elevated mineral N levels and that burned soils are not generally saturated with these cues after a fire, increasing their levels continues to increase germination response. To complicate matters, they also found that seeds would not germinate in unburned soil collected under some plants even with addition of smoke extracts and nitrate. Baldwin and Morse (1994) conclude that these plants alter the soil around them in some way that inhibits germination of other plants and that this condition is reversed by fire.

Obviously there is still much that we do not understand about the complex post-fire response of plant communities. This is certainly true of N fixing species from dry northern Rocky Mountains forests. The study of fire related germination cues is still in its infancy and the scope of the research is still expanding. Smoke treatments are already being used to stimulate germination of seeds on mining disturbed sites in Australia and for production of important commercial species (Brown and van Staden, 1997).

Understanding germination cues will help scientist untangle ecological interactions

associated with fire responses and help managers predict where plants can be found in the landscape (Baldwin et al., 1994). Scientists may be able to use fire related cues like smoke to find out if plants are limited by N availability in pre-fire soils (Thanos and Rundel, 1995). By applying smoke and combinations of mineral N compounds, Baldwin and Morse (1994) were able to isolate the effect on germination of possible allelopathic interactions and increased nitrate concentrations in the soil after fire. There are many opportunities to manage N fixing plants to increase total soil N levels (Binkley et al., 1982; Jurgensen et al., 1991), prevent long-term soil organic matter loss (Boring and Hendricks, 1992), increase soil nutrient levels (Johnson, 1995), and even increase mineral N in the soil (Kenny and Cuany, 1990). We must understand more about the ecology of these plants before we can integrate their use into ecosystem management plans. Identifying any fire related germination responses is good first step learning more about how N fixing plants are affected by fire and fire exclusion.



## PURPOSE AND OBJECTIVES

The purpose of the work reported was to examine seed germination of seven native plant species identified as N fixing species and common to ponderosa pine/Douglas-fir forest types. Specific objectives for this study were to determine if germination rates and speed of germination of untreated controls differed from seeds exposed to:

- 1) heat shock at 80°C for two hours
- 2) heat shock at 110°C for five minutes
- 3) smoke for one minute
- 4) smoked exposed filter paper
- 5) 500µM nitric acid.

## METHODS AND MATERIALS

Common N fixing understory species found in dry forest habitats in western Montana used in this study were: *Ceanothus velutinus* (deerbrush, snowbrush), *Cercocarpus ledifolius* (curleaf mountain-mahogany), *Hedysarum boreale* (northern sweetvetch), *Lupinus argenteus* (silvery lupine), *Lupinus sericeus* (silky lupine), *Thermopsis montana* (golden banner), and *Vicia americana* (American vetch) (Lackschewitz, 1991; Pfister et al., 1977). The seeds used in the study were collected in 1997 by Wind River Seed of Manderson, Wyoming and cold stored until treatments began in March 1998.

Seeds of each plant species were exposed to six treatments based on recent work: no treatment control, direct seed exposure to smoke for one minute, indirect seed exposure by exposing filter paper to smoke for one minute, incubation of seeds with nitric acid ( $500\mu\text{M HNO}_3$ ), seed exposure to heat shock ( $110^\circ\text{C}$ ) for five minutes, and seed exposure to heat shock ( $80^\circ\text{C}$ ) for two hours. Past trials have shown that scarification of lupine seeds promotes germination, so for the two lupine species a seventh treatment, nicking of the seed coat with a razor was added. Seeds were germinated in 9 cm glass petri-dishes. With six treatments, seven species, and six replications, there were initially 252 dishes. The six replications of the extra treatment to the two lupine species brought the total number of dishes to 264.

The no treatment control petri-dishes were set up first. Thirty seeds were placed on #2 Whatman filters in the petri-dishes that had been previously washed and rinsed in a 50% Clorox solution. The dishes were then wetted with 4 ml of deionized water and sealed with parafilm to prevent desiccation. This was repeated six times for each species. Nitric acid treatments were done in the same manner, the only difference was the use of 4 ml of a  $500\mu\text{M HNO}_3$  solution rather than deionized water (Keeley and Fotheringham, 1997). I made this solution by adding .0123 g of 70%  $\text{HNO}_3$  liquid to 250 ml of deionized water.

The remaining treatments were performed on dry seeds. For  $110^\circ\text{C}$  heat treatments, 180 seeds of each species were placed in glass petri-dishes and placed in a convection drying oven at  $108^\circ\text{C}$  for five minutes. Seeds were prepared for incubation using the same procedures as above by placing 30 seeds in each petri-dish lined with a

filter, adding 4 ml of deionized water, and sealing with parafilm. This was repeated for 180 seeds of each species placed in the convection oven at 81°C for two hours.

Scarification treatment for the two lupine species was accomplished by nicking the coat of each seed by hand with a razor. These seeds were prepared for incubation in the same way as the previous treatments.

To safely expose seeds and filter papers to smoke, a seven liter desiccation chamber was fitted with a two-way stop cock. One valve was connected by a rubber hose to a vacuum port, while the other was connected to a hose with a glass funnel at the end (Fotheringham, personal communication; Keeley et al., 1985). Seeds, 180 of each species, were placed in glass petri-dishes and put into the desiccation chamber. Smoke was generated by burning one gram of dry duff collected from ponderosa pine forests in a metal container. The vacuum valve was opened to evacuate the chamber, and then switched to release smoke from the funnel side. The funnel was placed over the metal container containing the burning duff and the smoke was pulled into the desiccation chamber by vacuum. After one minute the valves were switched back to vacuum the smoke out of the chamber. The exposed seeds were divided into six petri-dishes per species with unexposed filters and prepared for incubation. Dry Whatman #2 filter papers were spread out on racks in the desiccation chamber and exposed to smoke using the same procedure. Then filter papers were placed in petri-dishes and the dishes prepared as above, with thirty unexposed seeds each, 4 ml of distilled water, and sealed with parafilm. These treatments were done last to prevent smoke exposure to seeds of any other treatments.

Since it was unknown which species might require cold stratification (Thanos and Rundel, 1995), all dishes were incubated in the dark at 5°C for 21 days. This was followed by incubation in a Conviron growth chamber, with a 12 hour photoperiod, at 25°C with a 12 hour dark period at 18°C for 16 days. Germination was recorded every seven days in the cold treatment and every four days in the heat treatment (Keeley et al., 1985). All germinating seeds were removed at the time they were counted, and counting was conducted in normal light.

Levene's test for homogeneity of variance was performed on data of each species. Those data not found to be homogeneous were transformed with an arcsine transformation for percentage values. Data were then analyzed using ANOVA to detect mean separation between treatments within each (SPSS version 8.0, 1997). Tukey's W was used to compare control germination rates to each other treatment separately for those species with significant ANOVA results. Two equations were used to transform germination data in order to evaluate differences in the speed of germination between control and smoke exposure treatments (Chiapusio et al., 1997). The transformed data was then analyzed using the non-parametric Mann-Whitney U test to determine significance of mean separation between treatments.

## RESULTS

Data from ceanothus, silvery lupine and silky lupine showed heterogeneity of variance and analyses were carried out on transformed data. Two of the species tested showed increased germination rates with exposure to smoke, and three species showed faster germination rates with exposure to smoke. No increases in germination rates were seen with exposure to heat or nitric acid.

Ceanothus and golden banner had very low germination rates across all treatments, while American vetch had high germination rates across all treatments. These species showed no significant differences across all treatments, while the other four species had significantly different germination rates among the treatments (Table 1.1).

**Table 1.1.** Mean total percent germination for all species

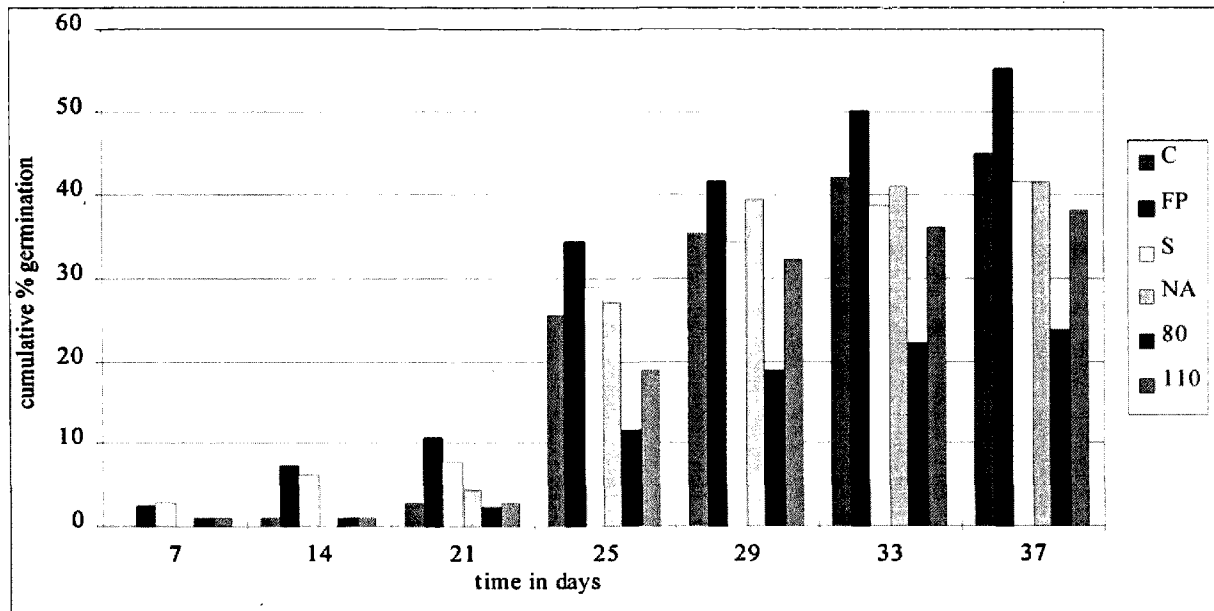
Treatment	CeLe	CeVe	HeBo	LuAr	LuSe	ThMo	ViAm
Control	31.1	1.7	44.4	12.8	20.6	8.9	83.3
Filter paper	54.4*	2.2	55.0	32.2*	18.3	12.2	86.1
Smoke	65.6*	0.0	41.7	31.1	18.9	10.6	89.4
Nitric acid	28.3*	0.0	41.7	23.3	20.6	8.9	87.8
80C	22.8*	1.7	23.9*	13.9	16.1	6.7	76.1
110C	15.0*	1.1	38.3	24.4	15.0	13.3	78.3
Scarification	----	----	----	28.3	64.4*	----	----

\* significantly different from control at  $\alpha = 0.05$

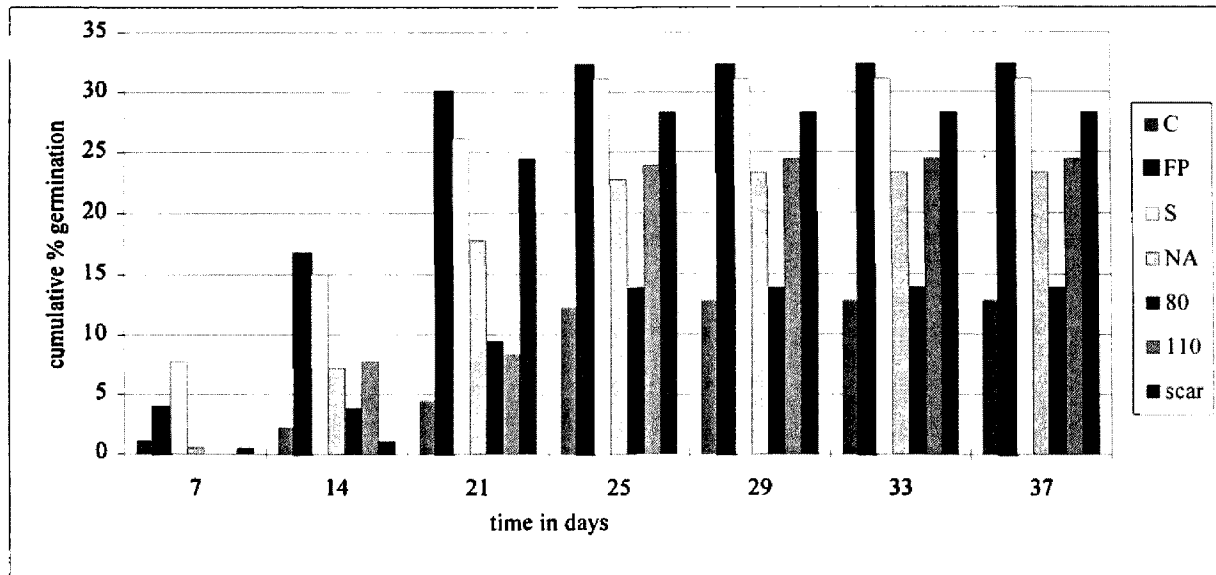
Mountain-mahogany seeds exposed directly to smoke or incubated on filter papers exposed to smoke showed significantly ( $\alpha = 0.05$ ) higher germination rates than control treatment. Seeds of this same species exposed to heat or germinated with dilute nitric acid showed significantly lower germination rates than the control. The lupine species seemed to have different responses to the treatments. Silvery lupine seeds incubated on smoke exposed filter paper had significantly higher germination rates than the control,

while silky lupine seeds that had been scarified showed significantly higher germination rates than any other treatments including the control. Northern sweetvetch seeds exposed to the 80°C heat shock had significantly lower germination rates than the control or seeds grown on smoke exposed filter paper.

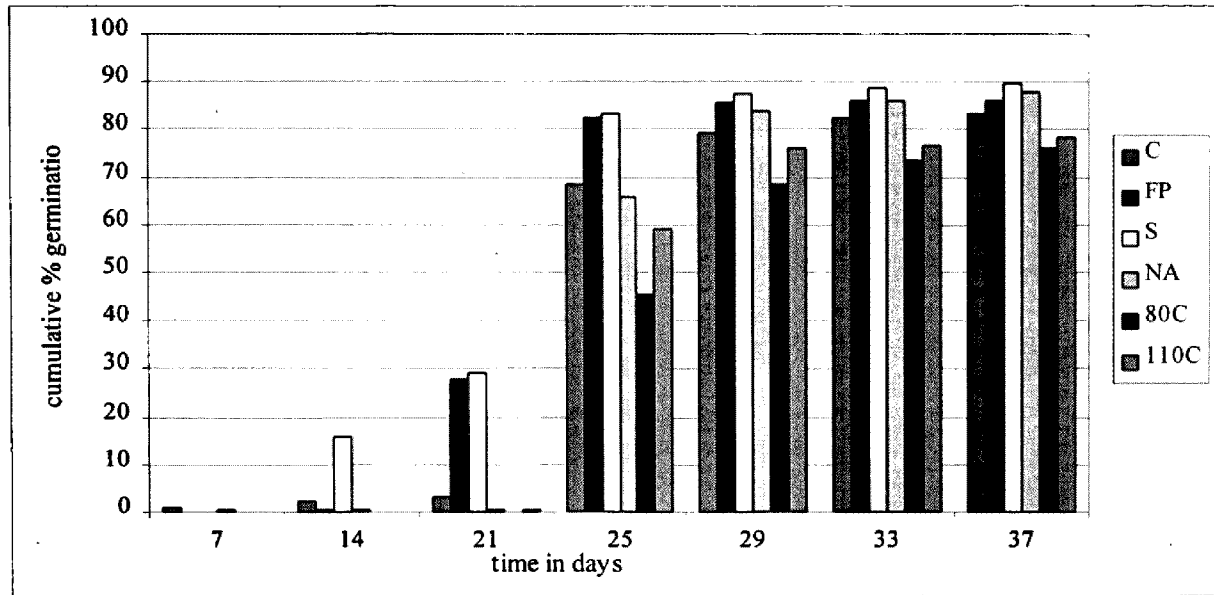
**Figure 1.2.** Cumulative germination over the study period of a) northern sweetvetch b) silvery lupine, and c) American vetch



a) northern sweetvetch



b) silvery lupine



c) American vetch

An unexpected pattern was seen in the timing of germination of seeds exposed to different treatments. Figure 1.2 shows the cumulative germination for each treatment at each examination date for three species, northern sweetvetch, silvery lupine, and American vetch. It appears that seeds of these species exposed to smoke germinated more rapidly than seeds exposed to other treatments. This response was especially noticeable with seeds of American vetch, northern sweetvetch and silvery lupine, and Chiapusio and associates (1997) suggest that comparisons of total germination may not adequately describe the effects of treatments over the time of observation. These researchers review a variety of equations used to evaluate differences in germination over the time of observation. An equation describing the speed of accumulated germination seemed most appropriate for this study. Once the data was recalculated using the following equation:

$$AS = [N_1/1 + N_2/2 + N_3/3 + \dots + N_n/n] \text{ where } N_1, N_2, \dots, N_n = \text{cumulative \# of seeds germinated at each time, } 1, 2, \dots, n \text{ (} n = 7 \text{ in this experiment).}$$

The results of the non-parametric tests used to determine differences between the accumulated speed of the control versus smoke exposed seeds are reported in Table 1.2. Seeds exposed directly to smoke and incubated on smoke exposed filter paper showed significant faster germination in American vetch and silvery lupine. Northern sweetvetch showed significantly faster accumulated germination only for seeds incubated on filter paper exposed to smoke.

**Table 1.2.** P-values for tests of accumulated speed of germination

	<b>American vetch</b>	<b>Silvery lupine</b>	<b>Northern sweetvetch</b>
Control vs. filter paper	0.026	0.002	0.015
Control vs. smoke	0.002	0.002	0.24

## **DISCUSSION**

Heating seeds at either 80°C or 110°C did not cause positive changes in seed germination for any of the species tested, and in fact had a negative effect on mountain mahogany and northern sweetvetch. These results did not support existing literature showing positive germination responses of hard coated legumes and ceanothus species to heat (Cocks and Stock, 1997; Conard et al., 1985; Gratkowski, 1962). Ceanothus had very low germination rates across all treatments, 0.1% or less. It is possible that the stratification period may not have been long enough or that the temperatures in the growth chamber were too high to stimulate germination. The legume species used in this study have not been studied in this way before, and it is not unreasonable to assume that the results do not follow those seen for the legumes from the southeastern US or South Africa (Cocks and Stock, 1997; Martin et al., 1975). These researchers used a much



wider variety of temperature and time combinations in their studies, and to truly rule out heat as a germination cue for western Montana species, a more in depth study patterned after their work must be done.

Seeds of mountain-mahogany and silvery lupine exposed to smoke had significantly higher germination rates than controls. Smoke treated seeds had higher germination rates than any other treatments for both species. Mountain-mahogany has been studied in some detail because of its importance for wildlife forage and habitat and its perceived decline with decreasing fire frequency. Past research has shown that fire is essential in maintaining mountain-mahogany in ponderosa pine/Douglas-fir forests (Arno and Wilson, 1986; Gruell et al., 1985). Gruell and associates (1985) reported immediate reseeded on fire exposed sites in Montana and also noted vigorous seedling establishment in areas where slash piles had been burned. A study by Arno and Wilson (1986) showed fire intervals of 13 to 22 years in mature mountain-mahogany stands in central Idaho indicating a close relationship between this species and low intensity, frequent fires. Thus increased germination with exposure to smoke appears to be a plausible and useful finding for managing this important browse species.

Although only the indirect exposure of silvery lupine seeds resulted in significantly higher germination rates than the control (32.2 versus 12.8), direct exposure to smoke gave the second highest average germination rate (31.1) supporting the trend that smoke exposure increases germination of this species. It is not clear why this species of lupine showed a positive response to smoke while silky lupine did not, when both species similar in appearance and often occur together (Lackschewitz, 1991). This type

of subtle response to smoke may be great enough on a large scale to result in delicate differences that may help explain the arrangement of plants in the landscape.

The earlier germination of some seeds exposed to smoke is another trend that raised unexpected questions. American vetch and northern sweetvetch had similar germination rates across treatments and relatively high rates overall (83.5% and 41.8%). These species would be classified as opportunistic suffrutescents using Keeley and associates' (1985) life history categories, but their response to smoke might give them an advantage over other opportunistic plants. It may be rate of germination and not increased total germination that allow American vetch and northern sweetvetch to quickly monopolize unoccupied growing space in post-fire environments (Brown and van Staden, 1997; Baldwin et al., 1994). Faster germination would seem to favor American vetch, northern sweetvetch, and silvery lupine in western Montana forest exposed to frequent fire. These plants could more rapidly re-occupy open growing space before other opportunistic plants. Further investigations to determine the prevalence of this response among other plants are needed in order to determine if more rapid germination rates are actually an advantage for the species tested in this study.

An additional problem with the study surrounds the use of a incubation regime based on work done on chaparral species in California. Temperatures in the growth chamber were too warm for northern Rocky Mountain species. Temperatures in the spring when Rocky Mountain species would likely germinate are cooler than 25°C. The lupine species seem to have been infected by a bacteria that caused the seeds to decompose from the inside out, and perhaps this process was sped up by the relatively

high temperatures in the growth chamber. The seeds were placed in the growth chamber on April 10, and after April 14 very few seeds of either species of lupine germinated (see data for silvery lupine in Figure 1.2).

The infestation of some dishes by fungi was another problem that may have led to different standard variations between treatments. For future studies the application of a mild fungicide and sterilizing tweezers used to remove germinated seeds after each use might reduce some of the unexplained variation seen between treatments. Plates that had few germinated seeds, like ceanothus, seemed to have a lower incidence of fungal infestation, so the removal of germinated seeds could well have been an agent of spread. Some seeds that had fungi on the surface still germinated, particularly mountain-mahogany seeds, and it is not clear whether mold is harmful to any or all of the species. Regardless, such confounding factors should be eliminated to identify differences among treatments more accurately.

## CONCLUSIONS

This study gives ample reason to continue research into fire related germination cues of understory plants in the northern Rocky Mountains. The elucidation of these cues can be used to examine such important ecological factors as soil N status and allelopathic interactions. Keys to predicting post-fire understory community composition are important tools in ecosystem management, especially for management of beneficial native N fixing plants. Fire ecology of ponderosa pine/Douglas-fir forests of the northern Rockies remains an enigma, the identification of possible germination cues is only one piece of the puzzle. Knowledge about the abundance and occurrence of these species in

seral forests and how they have been affected by decreasing fire frequencies will shed more light on the actual contributions of N fixing plants to the N budgets of western Montana forests. Estimates of N accretion due to these plants will also be needed by forest managers in the continued push to implement ecosystem management. The more we know about the fire ecology of these forests, including understory plant communities, the better equipped we will be to promote sustainable management of our forest lands.

## LITERATURE CITED

- Arno, S.F. 1976. The historical role of fire on the Bitterroot National Forest. US For. Ser. Res. Note RM-413.
- Arno, S.F., J.H. Scott, and M.G. Hartwell. 1995. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relationship to fire history. Res. Rep. INT-RP-481.
- Arno, S.F. and A.E. Wilson. 1986. Dating past fires in curleaf mountain-mahogany communities. J. Range Mgt. 39:241-243.
- Auld, T.D. and M.A. O'Connell. 1991. Predicting patterns of post fire germination in 35 eastern Australian Fabaceae. Aust. J. Ecol. 16:53-69.
- Baldwin, I.T. and L. Morse. 1994. Up in smoke: II. germination of *Nicotiana attenuata* in response to smoke-derived cues and nutrients in burned and unburned soils. J. Chem. Ecol. 20:2373-2391.
- Baldwin, I.T., L. Staszak-Kozinski, and R. Davidson. 1994. Up in smoke: I. smoke-derived germination cues for postfire annual, *Nicotiana attenuata* Torr. Ex. Watson. J. Chem. Ecol. 20:2345-2371.
- Baxter, B.J.M., J. Van Staden, J.E. Granger, and N.A.C. Brown. 1994. Plant-derived smoke and smoke extracts stimulate seed germination of the fire-climax grass *Themeda triandra*. Env. Exp. Bot. 34:217-223.
- Binkley, D. and S.C. Hart. 1989. The components of nitrogen availability assessments in forest soils. Adv. Soil Sci. 10:57-112.
- Binkley, D., K. Cromack, Jr., and R.L. Fredriksen. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. For. Sci. 28:720-724.
- Bradley, A.F, W.C. Fischer, N.V. Noste. 1992. Fire ecology of the forest habitat types of eastern Idaho and western Wyoming. Gen. Tech. Rep. INT-290.
- Brown, N.A.C. 1993. Promotion of germination of fynbos seeds by plant-derived smoke. New Phytol. 123:575-583.
- Brown, N.A.C and J. van Staden. 1997. Smoke as a germination cue: a review. Plant Growth Regulation. 22:115-124.
- Bunting, S.C. 1989. Effects of prescribed fire on rangeland shrubs in the intermountain region. In: Prescribed fire in the intermountain region, D.M. Baumgartner, D.W. Breuer,

B.A. Zamora, L.F. Neuenschwander, and R.H. Wakimoto, eds. Washington State University, Pullman, WA.

A Busse, M.D., P.H. Cochran, and J.W. Barrett. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. *Soil. Sci. Soc. Am. J.* 60:1614-1621.

Chiapusio, G. A.M. Sanchez, M.J. Reigosa, L. Gonzalez, and F. Pellissier. 1997. Do germination indices adequately reflect allelochemical effects on the germination process? *J. Chem. Ecol.* 23:2445-2453.

Christensen, N.L. and C.H. Muller. 1975. Relative importance of factors controlling germination and seedling survival in *Adenostoma chaparral*. *Am. Mid. Nat.* 93:71-78.

Cocks, M.P. and W.D Stock. 1997. Heat stimulated germination in relation to seed characteristics in fynbos legumes of the Western Cape Province, South Africa. *S. Afr. J. Bot.* 63:129-132.

Conard, S.G., A.E. Jaramillo, K. Cromack, Jr., and S. Rose. 1985. The role of the genus *Ceanothus* in western forest ecosystems. US For. Ser. Gen. Tech. Rep. PNW-182.

Edmonds, R.L., D. Binkley, M.C. Feller, P. Sollins, A. Abee, and D.D. Myrold. 1989. Nutrient cycling: effects on productivity of Northwest forests. In: *Maintaining the long-term productivity of Pacific Northwest forest ecosystems*, D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R.F. Powers (eds). Portland, Oregon. Timber Press.

Fischer, W.C. and A.F. Bradley. 1987. Fire ecology of Western Montana forest habitat types. US For. Ser. Gen. Tech. Rep. INT-223.

Gratkowski, H.J. 1962. Heat as a factor in germination of seeds of *Ceanothus velutinus* var. *laevigatus*. Ph. D. thesis, Oregon State University, Corvallis, OR.

Gruell, G.E., W.C. Schmidt, S.F. Arno, and W.J. Reich. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana-implications for resource management. US For. Ser. Gen. Tech. Rep. INT-158.

Gruell, G.E., S. Bunting, and L. Neuenschwander. 1985. Influence of fire on curlleaf mountain-mahogany in the intermountain west. In: *Fire's effects on wildlife habitat--symposium proceedings*, J.E. Lotan and J.K. Brown, comp. US For. Ser. Gen. Tech. Rep. INT-186.

Hendricks, J.J., and L.R. Boring. 1992. Litter quality of native herbaceous legumes in a burned pine forest of the Georgia Piedmont. *Canadian Journal of Forest Research.* 22:2007-2010.

Hobbs, N.T., and D.S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. *Journal of Range Management*. 37(5):402-405.

Johnson, D.W. 1995. Soil properties beneath ceanothus and pine stands in the Eastern Sierra Nevada. *Soil Sci. Soc. Am. J.* 59:918-924.

Jurgensen, M.F, S.F. Arno, A.E. Harvey, M.J. Larsen, and R.D. Pfister. 1979. Symbiotic and nonsymbiotic nitrogen fixation in northern Rocky Mountain ecosystems. pp. 294-308. In: *Symbiotic nitrogen fixation in the management of temperate forests*, Gordon, J.C., C.T. Wheeler, and D.A. Perry (eds). Oregon State University.

Jurgensen, M.R., J.R. Tonn, R.T. Graham, A.E. Harvey, and K. Geier-Hayes. 1991. Nitrogen fixation in the forest soils of the Inland Northwest. pp. 101-109. In: *Proceedings-Management and productivity of western-montane forest soils*. US For. Ser. Gen. Tech. Rep. INT-280.

Keeley, J.E., B.A. Morton, A. Pedrosa, and P. Trotter. 1985. Role of allelopathy, heat and charred wood in the germination of chaparral herbs and suffrutescents. *Journal of Ecology*. 73:445-458.

Keeley, J.E. and C.J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. *Science*. 276:1248-1250.

Kenny, S.T. and R.L. Cuany. 1990. Nitrogen accumulation and acetylene reduction activity of native lupines on disturbed mountain sites in Colorado. *J. Range Management*. 43:49-51.

Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. *Soil Sci. Soc. Am. J.* 60:1643-1654.

Lackschewitz, C. 1991. *Vascular plants of west-central Montana: identification guide book*. US For. Ser. Gen. Tech. Rep. INT-277.

Leach, M.K. and T.J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science*. 273:1555-1558.

Magill, A.H., J.D. Aber, J.J. Hendricks, R.D. Bowen, J.M. Melillo, and P.A. Steudler. 1997. Biogeochemical response of forest ecosystems to stimulated chronic nitrogen deposition. *Ecol. App.* 7:402-415.

Martin, R.E., R.L. Miller, and T.C. Cushwa. 1975. Germination response of legume seeds subjected to moist and dry heat. *Ecology*. 56:1441-1445.

Noste, N.V. and C.L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. US For. Ser. Gen. Tech. Rep. INT-239.

Pfister, R.D, B.L. Kovalchik, S.F. Arno, and R.C. Presby. 1977. Forest habitat types of Montana. US For. Ser. Gen. Tech. Rep. INT-34.

Pierce, S.M., K. Esler, and R.M. Cowling. 1995. Smoke-induced germination of succulents (Mesembryanthemaceae) from fire-prone and fire-free habitats in South Africa. *Oecologia*. 102:520-522.

Thanos, C.A. and P.W. Rundel. 1995. Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *J. of Ecol.* 83:207-216.

Trowbridge, R. and F.B. Holl. 1992. Early growth of lodgepole pine after establishment of alsike clover-Rhizobium nitrogen-fixing symbiosis. *Can. J. For. Res.* 22:1089-1093.

Waring, R.H. and W.H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, New York and Toronto.

Went, F.W., G. Juhren, and M.C. Juhren. 1952. Fire and biotic factors affecting germination. *Ecology*. 33:351-364.

Wright, H.A. and A.W. Bailey. 1982. Fire ecology. John Wiley & Sons, New York.



## **CHAPTER 2. OCCURRENCE AND ABUNDANCE OF NATIVE NITROGEN FIXING PLANTS IN FIRE EXPOSED PONDEROSA PINE/DOUGLAS-FIR FORESTS IN WESTERN MONTANA**

### **ABSTRACT**

Nitrogen (N) is a limiting nutrient in forests of the Inland Northwest, and recent studies indicate that fire and other disturbances may reduce plant available N in these forests. Past studies in this region and other parts of the world suggest that N fixing plants play an important role in replacing the N lost from the soil on fire affected sites. While the exclusion of fire has been shown to reduce the diversity and abundance of N fixing plants in prairie ecosystems, the response of N fixing plants to fire exclusion in dry forest ecosystems has been rarely studied. The exclusion of fire from ponderosa pine/Douglas-fir forests of western Montana has caused widespread changes in forest structure, composition, and function, but little is known about changes in understory communities due to fire exclusion and other management activities. The purpose of the work reported was to investigate the occurrence and abundance of native N fixing plant species in second growth ponderosa pine (*Pinus ponderosa*)/Douglas-fir (*Pseudotsuga menziesii*) forests. The number of N fixing species, their cover and frequency of occurrence, evidence of active N fixation, and soil N availability were compared at 11 paired sites in western Montana. Two types of sites were selected for sampling: sites that had been undisturbed since historic logging in the late 1800's and early 1900's, and sites where the second growth forests had been repeatedly opened by logging and/or fire over the last 80-100 years. In the undisturbed sites, a control treatment was sampled along with a similar, nearby area that had been affected by wildfire in the last 3-10 years. Areas that had been commercially thinned or selection harvested and treated with an underburn in the last 3-10 years were sampled in repeatedly opened sites, along with a control that had not been affected by the most recent management activities. Cover and frequency of N fixing plants were significantly greater in burned stands than in controls and also significantly higher in repeatedly opened sites than in undisturbed sites. Potentially mineralizable N (PMN), nitrate, and ratio of PMN to total soil N were all significantly lower in the same areas where N fixing plant cover and frequency were greater, burned stands and repeatedly opened sites. However, no direct correlation between PMN levels and cover and frequency of N fixing plants was detected, likely because of the low density of N fixing plants in all plots. Increased density of N fixing plants in repeatedly opened sites indicated that N fixing plants may have been more widespread in pre-settlement forests. It is also possible that N fixing plants have played an important role in maintaining long-term productivity in frequently burned ponderosa pine/Douglas-fir forests.

### **INTRODUCTION**

Nitrogen (N) is limiting in most Western forest ecosystems, because low moisture availability and cool temperatures limit N mineralization (Kimmins, 1996; Walley et al.,

1996; Edmonds et al., 1989). Unlike other nutrients, there is no mineral resource of N in soil to replenish N losses. Available N comes from only four sources; N in precipitation and dry deposition, symbiotic N fixation, N fixation by free living organisms, and synthetic fertilizers. In natural forested ecosystems of the Inland Northwest the primary form of N input is biological N fixation (Jurgensen et al., 1991; Gosz, 1981).

A recent study of prairie remnants suggests that 100 years of fire suppression has reduced the diversity and abundance of N fixing species, and may have seriously affected the ability of these plants to recolonize burned sites (Leach and Givnish, 1996). Many studies have illustrated the changes in forest stand structure, composition, and health in dry ponderosa pine (*Pinus ponderosa*)/ Douglas-fir (*Pseudotsuga menziesii*) forests in the Inland Northwest due to fire suppression (Keane et al., 1990; Arno et al., 1995), but there has been little emphasis on changes in understory vegetation dynamics (Fischer and Bradley, 1987). It is likely that changes in overstory structure and composition and nutrient deficiencies also directly affect the structure and composition of understory communities. Fire and other types of disturbance favor N fixing plants and free living N fixing bacteria in these ecosystems (Leach and Givnish, 1996; Boring et al., 1990). The exclusion of fire from forest ecosystems may have direct impacts on the diversity and abundance of native N fixing organisms in low elevation forests in the northern Rocky Mountains.

Both wildfire and prescribed fire recycle some of the slowly mineralized N and result in a flush of mineral N that may last for two growing seasons after the fire (DeLuca and Zouhar, 1998; Covington and Sackett, 1992). However, fire can cause a reduction in total soil N and potentially mineralizable N as a result of volatilization (Zouhar unpub.

thesis, 1997; Kimmins, 1996; Covington and Sackett, 1992; Hungerford et al., 1991; Hobbs and Schimel, 1984). Studies in other parts of the United States and Canada suggest that N fixing plants play an important role in replacing N lost from the soil on fire affected sites (Trowbridge and Holl, 1992; Hendricks and Boring, 1992; Schoenberger et al., 1989; Hobbs and Schimel, 1984).

Nearly 40 million acres of overstocked, disease and insect infested, and wildfire susceptible second growth ponderosa pine/Douglas-fir forests exist across the western US (Arno, 1996; Harvey, 1994). These forest are a product of management activities of the last 100 years--selective harvesting of large ponderosa pines and fire exclusion. Our improved understanding of the role of disturbance in ecosystem function (Rogers, 1996) and the realization that past management policies are creating forest productivity and health problems (Harvey, 1994) has inspired interest in restoration of pre-1900 forest structure and reintroduction of fire in western Montana (Arno, 1996). It is becoming even more important for researchers and managers to understand the role of native N fixing plants in these ecosystems as management goals are redesigned to focus on re-establishing or maintaining ecosystem processes (Jurgensen et al., 1998; Tilman, 1996). To date there have few studies of N fixing plant success in forest of the Inland Northwest that have been affected by recent wildfire, prescribed fire, and/or fire exclusion. The purpose of the research reported was to examine the abundance and occurrence of native N fixing plants in stands that have been differently affected by management. Sites were selected in second growth forests that had been undisturbed since historic logging in the early 1900's. In these areas, unburned control stands were compared to similar, adjacent areas that had been burned by wildfire between 10 and 3 years before present. These sites

were also compared to other second growth sites that had been opened either by fire or harvest multiple times in the last 100 years. Areas treated with harvest and prescribed underburning in the last 3-10 years were examined in these repeatedly opened sites, along with similar areas that had not been affected by the most recent harvest and burn treatments.

## LITERATURE REVIEW

Fire ecology, nitrogen limitations, the ecology of native legumes and actinorhizal plants, and current trends in management are subjects integral to the development of this project. This review of past research will examine these areas and summarize how past work led to my study questions and design.

### *Fire Ecology*

Fire is the most common disturbance affecting ponderosa pine/Douglas-fir forests in the northern Rockies. Fire-free intervals of 13-50 years for these forests have been estimated from tree fire scar dating studies (Arno, 1976; Brown et al., 1994) These studies and others (Gruell et al., 1982; Barrett, 1988) using both fire scars and historical accounts and photographs describe pre-1900 ponderosa pine/Douglas-fir forests as open park-like stands consisting largely of all-aged ponderosa pine. Photographs taken in 1909 in the Bitterroot Valley of western Montana show open forests with a dominantly herbaceous understory that included N fixing forbs and low shrubs, lupines, ceanothus, and bitterbrush (Gruell et al., 1982; Wright and Bailey, 1982).

The influence of fire on forest composition and structure in the northern Rocky Mountains has been recognized by scientists and land stewards for almost 100 years

(Agee, 1993). Low intensity fires in these systems pruned lower branches of ponderosa pine trees and eliminated young trees, favoring herbaceous understory plants (Agee, 1993; Gruell et al., 1982; Arno, 1976). These fires did not always occur on regular intervals, and these researchers note that longer than average fire-free periods led to more intense underburning and occasionally to mortality of a few overstory trees. In this manner, seral forests composed mostly of ponderosa pine with scattered Douglas-fir and/or western larch (*Larix occidentalis*) were maintained for centuries as open stands of multi-aged trees (Arno et al., 1995; Gruell et al., 1982; Wright and Bailey, 1982).

Changes in human use and management around the turn of the century led to a variety of changes in seral ponderosa pine forests of western Montana. Large ponderosa pines from these open stands were highly valuable and accessible on low mountain slopes and thus were heavily logged for over 100 years. Today less than one percent of seral ponderosa pine forests have no logging history (Arno et al., 1995). Fire exclusion policies, largely established after intense fires burned extensive areas in the early 1900's, have also altered these forest ecosystems (Agee, 1993). Series of photographs taken in the same locations over an 80 year period in the Lick Creek drainage in the Bitterroot Nation Forest in western Montana (Gruell et al., 1982), showed a rapid build up of young pine and Douglas-fir seedlings. A dominant herbaceous understory is seen only in photographs of repeatedly disturbed areas. The removal of large trees, mainly ponderosa pine, has caused a shift in tree species composition to forests that are often equally divided between small ponderosa pine and Douglas-fir (Arno, 1996). The structure of these forests has also changed dramatically from open all-aged stands to dense stands of nearly even aged trees (Arno et al., 1995; Fiedler et al., 1992). Fire exclusion policies

exacerbate these changes, and the build up of forest fire fuels makes these forests susceptible to high intensity fires, in effect changing the fire ecology of the systems (Brown et al., 1994). Decreased nutrient availability as a result of nutrients storage in thick layers of forest floor litter, combined with increased competition for nutrients in dense stands, have created additional forest health problems (Harvey, 1994; Monnig and Byler, 1992; Hungerford et al., 1991). Researchers have noted that the interaction of diseases, insects, and fire is integral in the cycling of carbon (C), N, and other nutrients in Inland Northwest forests, and that traditional forestry practices have disrupted these relationships (Harvey, 1994; Monnig and Byler, 1992).

Recent studies have focused on changes in the tree component of ponderosa pine/Douglas-fir forest, and less is known about how logging and fire exclusion have affected understory plant communities (Jurgensen et al., 1998). Unlike long-lived slowly decomposing trees, most shrubs, forbs, and grasses leave little evidence of their past distributions and abundance. The response of common understory shrubs, forbs, and grasses to fire has been identified and classified (Fischer and Bradley, 1987; Noste and Bushey, 1987), however we have little information on the pre-1900 distributions of these plants. From these studies we can only speculate about which species might have been more common in open more frequently burned forests.

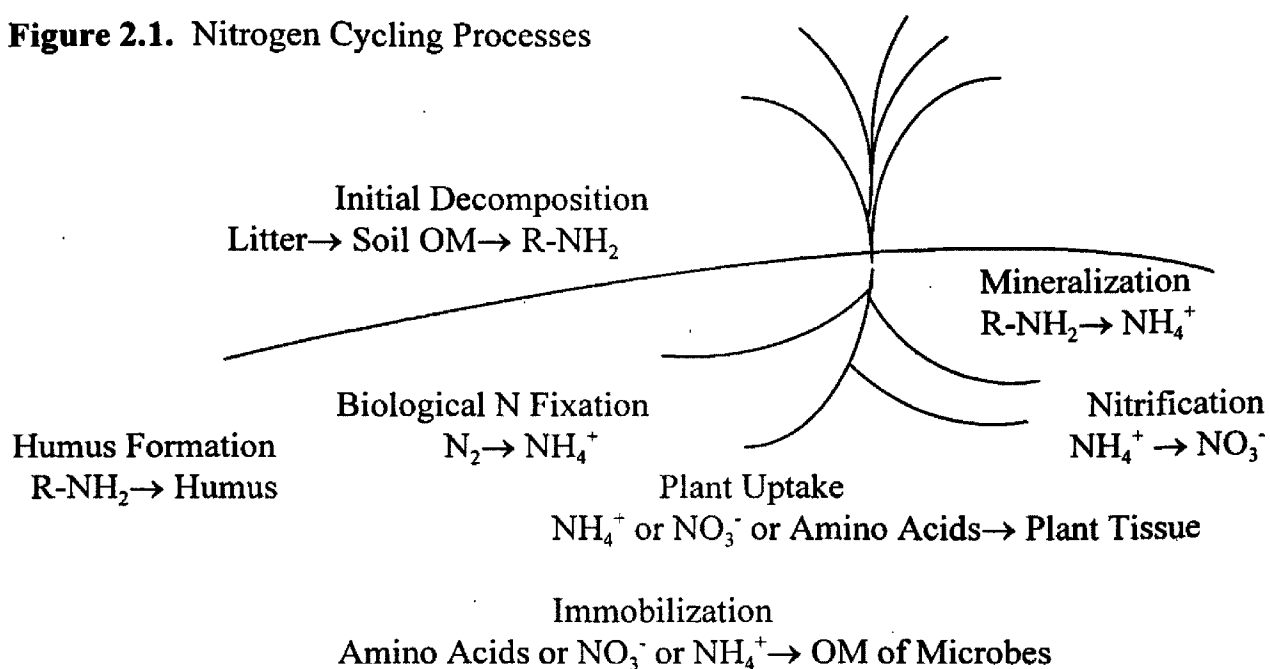
Initial theories of vegetation ecology focused on single species or the interaction of a few species, and viewed disturbance as an outside influence that generally destroyed vegetative communities (Rogers, 1996). The role fire and other disturbances is now seen as an integral part of ecosystem function and the focus of ecology has shifted to analyzing interactions among species and ecosystem processes (Tilman, 1996). This change in

perspective, along with mounting evidence of the harm and danger of fire exclusion, has prompted much interest in using fire as a tool in ecosystem management (Arno, 1996). This approach is designed to protect the function rather than the current state of forest ecosystems (Rogers, 1996). There is, however, still much to be learned about the effects of fire in these systems, especially on the understory plants.

### *Nitrogen Status in Forest Soils*

Nitrogen limitation has been recognized in many forest ecosystems of North America (Waring and Schlesinger, 1985), boreal forest of central Canada, mixed deciduous/conifer forests of the northeastern US, and cool, dry forests of the Pacific Northwest (Edmonds et al., 1989; Jurgensen et al., 1991). Effective forest management requires an understanding of the origins of N in terrestrial ecosystems, N cycling through these systems, and how fire affects N availability. Internal N cycling in soil is the result of complex interactions between abiotic environmental conditions and biological processes. Figure 2.1 is a simplified representation of the transformation mechanisms that form the controls of N availability.

Dinitrogen gas makes up nearly 80 percent of our atmosphere, but is unavailable to plants and all but a few highly specialized bacteria. Most plants take up nitrate and ammonium and convert these mineral forms of N to different organic compounds that make up plant tissue. These compounds eventually end up in the soil as litter and are not readily accessible to other plants. Fungi, bacteria, and macro- and microscopic animals release some ammonia from organic compounds which then is ionized rapidly in the soil solution to ammonium. This process of mineralization provides ammonium available for plant uptake (Waring and Schlesinger, 1985).

**Figure 2.1.** Nitrogen Cycling Processes

Only a small portion of the N in plant tissue is rapidly released through mineralization, and the majority of N from plant tissue added to the soil becomes part of other soil N pools (Stevens, 1986). Large amounts of N are incorporated into humic materials in the soil. Amino acids, for example, are integral to humification of OM in the soil, and once incorporated into humus, the N in these amino acids is unavailable to plants and is released very slowly (Kogel-Knabner, 1993). Immobilization, the term used to describe the uptake of ammonium by microbes in the soil for use in their own growth and reproduction, is another way that N from plant derived OM is tied up in soil. This process is dependent on the availability of reduced C (the energy source) and the concentration of ammonium in soil. Nitrification, the conversion of ammonium to nitrate, has been shown to correlate directly with the rate at which plants in the surrounding soil take up nitrate (White, 1986), so if plants are rapidly taking nitrate out of the soil solution, the microbes will respond by producing more nitrate. When anaerobic



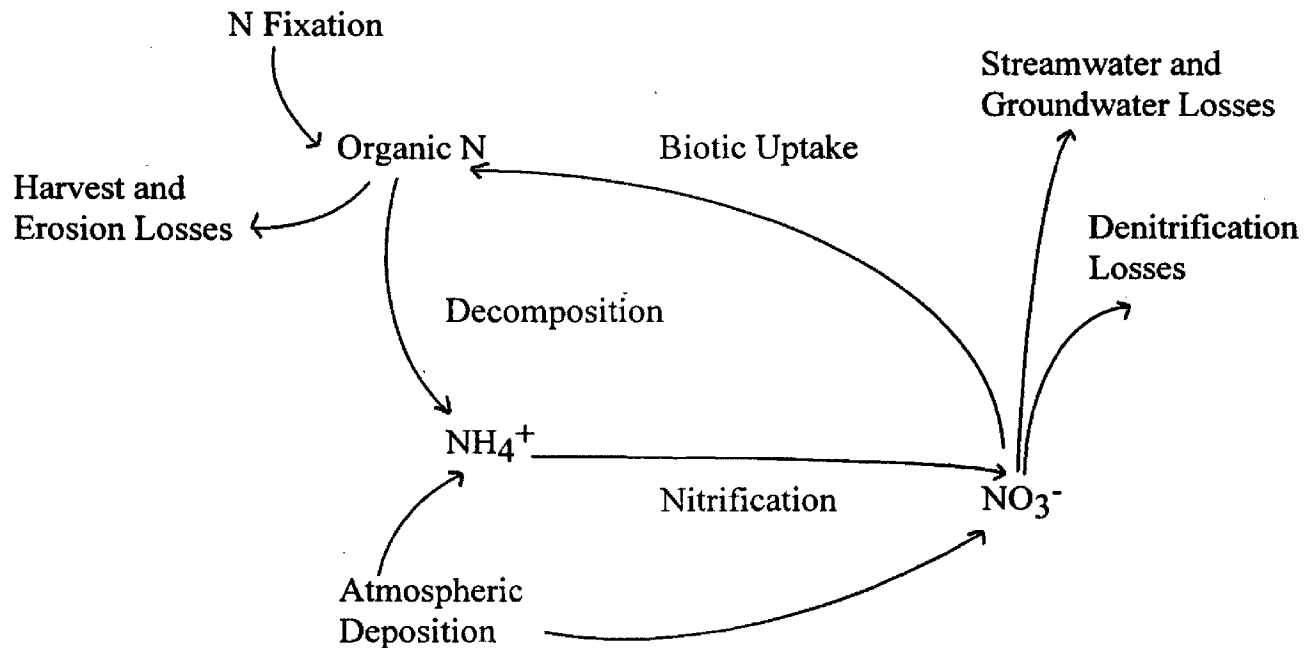
conditions exist, other bacteria in the soil convert nitrate to dinitrogen gas in a process called denitrification.

There is evidence that some organisms have adapted strategies to take up reduced (organic) N forms. By doing this the organisms eliminated the need to expend energy assimilating inorganic forms of N into organic compounds (Kielland, 1994; Abuzinadah and Read, 1986). Of course there is a cost associated with this manipulation of the system. The mechanisms by which these organisms absorb organic N compounds is poorly understood, but it undoubtedly involves a facilitated transport system that requires an investment in infrastructure and photosynthate. It also puts these organisms into competition with saprophytic organisms that use the breakdown of these simple organic compounds as a source of energy (Dighton et al., 1987). Still, this becomes a very attractive strategy in systems where decomposition is slow and OM accumulates in the soil, for example in the arctic tundra (Kielland, 1994) or in alpine coniferous forests (Keller, 1996). It is possible that some organisms in forests of the northern Rocky Mountains have also developed the ability to take up reduced N, but at this time little research has been done in this area.

By necessity most forest ecosystems are conservative of N because inputs of N to forest systems are small (Vitousek, 1982). Precipitation contributes differing amounts of anthropogenic N (Hedin et al., 1995) and smaller amounts of N from fires and volcanic eruptions. Near industrial areas eolian particles also contain N and atmospheric deposition can be a net source of N in some ecosystems. Nitrogen can also be added to the soil cycle by bacteria that can reduce dinitrogen from the air to ammonium (Waring and Schlesinger, 1985). These bacteria can be free living or can grow symbiotically in

the roots of certain plants. Nitrogen fixing bacteria are the major producers of biologically available N in areas with low rates of atmospheric deposition (Boring et al., 1990). Inputs and outputs of N to soil are represented in Figure 2.2.

**Figure 2.2.** Nitrogen inputs and outputs to soil systems (from Waring and Schlesinger, 1985)



Nitrogen can be lost from the soil cycle in numerous ways. Erosion of soil obviously carries all nutrients away along with the matrix needed to store them. The loss of litter or duff in forest systems to erosion is of special concern because these layers are the source of most readily available N in the soil (Jurgensen et al., 1998; Hungerford et al., 1991). The forms of N most important to biological activity, especially ammonium and nitrate, are highly soluble and are easily leached from the soil profile ending up in streamwater or aquifers. Harvesting or removal of forest biomass also removes N from the soil cycle. Nitrogen stored in leaves and woody tissue is not in a form accessible to plants, but it comprises the largest N reserve in forest systems.

In the Inland Northwest low availability of moisture during warm months results in slow mineralization of accumulated organic matter and low available N (Kimmins, 1996). Low rates of atmospheric deposition of N in the Intermountain West, 0.5-2 kg N ha<sup>-1</sup>yr<sup>-1</sup>, suggest N additions due to biological N fixation are probably essential (Jurgensen et al., 1998).

### *Fire Effects on Nitrogen Availability*

The effects of fire on forest soils can be divided into two general categories; physical and biological. Physical effects refer to changes in soil properties and concentrations of compounds in the soil caused directly by heating or mechanical loss. These effects are sometimes referred to as primary effects of fire (Raison, 1979). Changes in the species composition of soil microbes or changes in rates at which residual microbes function are considered biological or secondary effects of fire. The divisions that have been created are constructions to aid in understanding the interactions between fire and soil, and it is important to keep in mind that they are interconnected and interdependent.

The complex nature of the interactions between soil microbes and plants makes it difficult to isolate individual fire effects and often leads to unsatisfying research results (Raison, 1979). It is also important to note that scientists studying effects of fire on soil often use the word intensity to describe the amount of fuel consumed which may or may not correspond to the intensity in BTU/second/feet measured by fire management researchers (Byram, 1959). Fire severity in this paper refers to the effect of fire on an ecosystem and is related directly to the amount of OM lost due to burning (Ryan and Noste, 1985). Fire intensity is used to refer to the heat pulse affecting above and below

ground biomass during a fire in this paper, again following usage defined by Ryan and Noste (1985). A low intensity, slow moving fire, for example, can result in high consumption of forest floor litter (Hungerford et al., 1991). One of the reasons for the varied results seen in research on effects of fire on soil is the inconsistent way in which study fires are described, making it difficult to compare between studies (Raison, 1979). However, some general conclusion can be draw from past research in the northern Rocky Mountains and throughout the western US.

The physical effects of heating soil are controlled by the depth of organic matter present and the moisture content of this OM and also the mineral soil (Hungerford et al., 1991). The heat impulse to the soil is short but intense and OM in the soil acts as insulation, absorbing the energy impulse and burning up itself while protecting the mineral soil below. Conductivity increases with soil moisture, heating dry soil causes greater rise in temperature, but results in a shallower depth of penetration. Moist soils can not rise above 100°C until all the water has been evaporated, however plant roots and soil organisms can be damaged or killed at temperatures below 100°C. The heat impulse can also affect soil physical properties; structure, water holding capacity, and permeability, which will in turn affect plant and soil microbial growth and susceptibility to erosion. Heating also causes volatilization of organic compounds and leads to some loss of total C and N from the system, especially with temperatures over 200°C (Covington and Sackett, 1992). Nitrogen loss during intense fires in Douglas-fir forests of the western US have been estimated as high as 1000 kg ha<sup>-1</sup> (Boring et al., 1990). Recent studies have shown large post-burn increases in ammonium concentrations that

are directly correlated with the amount of OM consumed even though the total N in the soil may decrease with OM consumption (White, 1986; Covington and Sackett, 1992). This portion of N lost to the fire from forest floor litter and soil OM may be the most detrimental to long-term site productivity (Monleon et al., 1997; Hungerford et al., 1991; Jurgensen et al., 1998). Estimates of OM lost from soils in the Inland Northwest range from 60 to 12 percent in clearcuts burned for site preparation to and up to 84 percent on sites exposed to intense fire (Hungerford et al., 1991). These losses and those due to harvest have been tied to decreased potentially mineralizable N in burned soils (DeLuca and Zouhar, 1998). In Australia and the southeastern US concerns about chronic N loss from removal of OM have prompted researchers to look at the use of N fixing understory plants to replace organic N stores in the soil (Grove and Malajczuk, 1992; Hendricks and Boring, 1992).

The heat associated with fire kills soil fungi, protozoa, and bacteria, in effect sterilizing the soil to some depth dependent on fire intensity, soil moisture, soil bulk density, and percent coarse fragments (Choromanska and DeLuca, 1998; Diaz-Riviña et al., 1996; Hungerford et al., 1991). In some cases this removes disease and competitors, however it may be only a short-term advantage because beneficial organisms are also lost. An initial decline in the total microorganism population is followed by a rapid increase in total microbial biomass as microorganisms begin to re-colonize the favorable post-fire environment (Diaz-Riviña et al., 1996; Pietikainen and Fritze, 1993; Hungerford et al., 1991). Some researchers also suggest that changes in the C:N of post-fire microbial biomass are the result of changes in species composition of the microbial population (Choromanska and DeLuca, 1998; Pietikainen and Fritze, 1993). This has led

others to suggest that microbial driven processes in the soil may also be affected by changes in population composition. White (1986) has shown that decomposition rates are lower after prescribed burns, but that this reduction is a result of reduced OM in the soil. When normalized by OM content, White (1986) found similar rates of decomposition in burned and unburned sites. Other researchers investigated whether fire reduces the C:N ratio in the soil by volatilizing labile C in the OM (Bell and Binkley, 1989). They hypothesized that a reduction in the available C pool would lead to less immobilization and a greater availability of nitrate in the soil. Their results did not support their hypothesis because large amounts of N were lost along with the C, actually causing an increase in the C:N ratio. In spite of this, it is still possible that frequent, low intensity burns adjust the C:N ratio to favor nitrification and plant nitrate uptake.

Soils experience greater temperature extremes and more frequent temperature fluctuations after fire, because black charred material absorbs more heat from the sun and protective plant cover has been removed (Raison, 1979). These changes in the temperature regime of the soil affect both new plant growth and microbial communities. Higher temperatures can increase microbial activity in the soil leading to increased mineralization (Ojima et al., 1994). Changes in moisture content and temperature fluctuations can also cause changes in the number and species composition of soil microbes (Pietikainen and Fritze, 1993).

Nitrogen and other nutrients can be directly lost through convective transportation of ash or post-fire erosion by water or wind. Ash is high in soluble cations that rapidly dissolve when wetted, and post-fire weather can have a major effect on the ultimate fate of these nutrients. They are extremely susceptible to leaching in sandy soils, but in the

absence of excess precipitation they may accumulate (Raison, 1979).

The nutrients available from ash and the ammonium produced pyromorphically often result in a flush of new growth immediately after fires (Harris and Covington, 1983).

These available nutrients can also affect the species composition of soil microbes. Some researchers believe that fast growing colonizers take advantage of the higher nutrient concentration and in the process increase immobilization of N and other nutrients (Walley et al, 1996; Pietikainen and Fritze, 1993).

Plants with a higher N use efficiency (NUE), meaning they need less N per unit of biomass increase, are favored by low N availability (Ojima et al., 1994). These plants produce detritus with a higher C:N ratio, again increasing immobilization and creating an environment that favors their growth over plants with a lower NUE. These researchers suggest this as a reason why post-fire environments continue to be productive even with repeated fires leading to decreased N availability in the soil. There has been little work done on how the changes in plant species composition after fires affects the soil N cycle. It would seem logical that plants adapted to fire would be adept at utilizing available resources, and thus effectively re-colonize fire affected sites. Nitrogen fixing plants take advantage of the immediate flush of nutrients to establish themselves, and then when the post-fire effects begin to lessen their ready source of N allows them to out compete neighboring plants (Leach and Givnish, 1996).

#### *Importance of N Fixing Plants*

The importance of native N fixing species for wildlife browse and habitat has been long recognized (Gratkowski, 1962; Klemmedson, 1979; Noste and Bushey, 1987). However, we know little about the role that these plants play in the total N budget of

forests in the northern Rockies (Jurgensen et al., 1991). The positive effects of N fixing plant species have been documented in many other parts of the world (Quinos et al., 1998; Boring et al., 1990; Sprent and Silvester, 1973), but concerns over competition for light and water has tempered enthusiasm for use of N fixing plants in the management of Inland Northwest forests (Jurgensen et al., 1998).

Accumulations of N in ecosystems as a direct result of N fixation has been a general measure of improvements in N status, however, the ability of N fixing plants to increase mineral N, total N, base saturation and cation exchange capacity has also been documented by some researchers (Johnson, 1995; Kenny and Cuany, 1990). Rates of accretion have been based on acetylene reduction analysis, nodule weight, and area covered by a plant (Grove and Malajczuk, 1992; Permar and Fischer, 1983; Sprent and Silvester, 1973). Acetylene reduction is used to estimate N fixation by measuring the amount of ethylene produced by nodules incubated in an acetylene rich atmosphere. The reduction of acetylene to ethylene is a side reaction of biological N fixation, and generally occurs at a fixed rate that has been correlated to actual fixation rates using  $^{15}\text{N}$  (Sprent and Silvester, 1973). Healthy functioning nodules are weighed after incubation and the initial results are reported on a  $\text{nmol C}_2\text{H}_4 \text{ g}^{-1} \text{ minute}^{-1}$  basis. Absolute rates of fixation have been estimated by incubating nodules in  $^{15}\text{N}$  enriched atmosphere and then analyzing for nodule enrichment of  $^{15}\text{N}$  (Sprent and Silvester, 1973), and rates of incorporation of  $^{15}\text{N}$  are related to ethylene production rate and a ratio of ethylene production to reduction of dinitrogen gas is created. Nodule biomass per plant and cover area per species are then used to estimate N fixation rates over large areas, and are usually reported on a  $\text{kg N ha}^{-1} \text{ week}^{-1}$  or  $\text{year}^{-1}$  basis. These conversions may underestimate



fixation rates as all nodules are difficult to recover from the soil (Grove and Malajczuk, 1992). The acetylene reduction method is relatively straight forward and easily adapted to field conditions (McNabb and Geist, 1979), however it measures fixation rates over a short period of time in disturbed root sections and may not adequately measure actual fixation rates. Incubation temperature, atmosphere composition, and inclusion of asymbiotic N fixing bacteria may also result in less accurate estimates (Nohrstedt, 1983).

Another method used to determine N accretion due to nitrogen fixation is the natural abundance method which uses the natural difference in the  $^{15}\text{N}:^{14}\text{N}$  between soil and atmosphere. Soil N is enriched in  $^{15}\text{N}$  relative to atmospheric  $^{15}\text{N}$  because  $^{14}\text{N}$  is preferentially lost to the atmosphere during N cycle transformations (Weaver and Danso, 1994; Shearer and Kohl, 1986). The atmospheric percent of  $^{15}\text{N}$  atoms is defined as zero and  $\delta^{15}\text{N}$  units represent the atom percent of  $^{15}\text{N}$  in excess of the atmospheric value (0.3663%  $^{15}\text{N}$ ) (Bremer and van Kessel, 1990). The  $\delta^{15}\text{N}$  units are expressed as the difference in the proportion of  $^{15}\text{N}$  atoms multiplied by 1000 because natural differences in the  $^{15}\text{N}:^{14}\text{N}$  are very small (Weaver and Danso, 1994; Binkley et al., 1985). Plants fixing N get a portion of their N from the atmosphere resulting in lower  $\delta^{15}\text{N}$  values for these plants relative to non-N fixing plants. This difference can be used to estimate the percent of N in legumes and actinorhizal plants derived from fixation (Bremer and van Kessel, 1990). Adoption of this method has been limited the need for precision in measuring small differences, especially in soils that are inherently low in  $^{15}\text{N}$  (Weaver and Danso, 1994). Variability in  $\delta^{15}\text{N}$  values in the soil also make differences difficult to distinguish, and it is important to choose reference plants growing near the N fixing plant

to minimize variation (Bremer and van Kessel, 1990). Researchers have shown that with careful analytical procedure the natural abundance methods gives similar estimates of percent of N derived from fixation as those found with the more complicated and invasive isotope dilution method. Other scientists note that the natural abundance method quick, non-destructive, and provides estimates based on longer periods of plant function than other methods like acetylene reduction or isotope dilution (Stock et al., 1995). However,  $^{15}\text{N}$  analyses are often expensive and can limit the number of samples analyzed. Weaver and Danso (1994) point out that lower  $\delta^{15}\text{N}$  values in above ground biomass of N fixing plants compared to non-fixing plants indicate N fixation activity and suggest that this method is appropriate for identifying the capacity of plants to fix N, but large scale estimations of N accretion based on natural abundance differences may be less reliable.

It is difficult predict with confidence how much N fixed by legumes and actinorhizal plants becomes plant available N, even if estimates of N fixation rates are available. The complexity of the N cycle makes estimating increased plant available N from fixation rates difficult. Fixed N may be stored in plants, consumed by grazing animals or soil biota, lost to leaching, or stored indefinitely in soil OM. Some researchers have tried to trace the  $\delta^{15}\text{N}$  signature of N fixing plant material through the N cycle in soil with mixed results (van Kessel et al., 1994; Binkley et al., 1985). Binkley and associates (1985) found differences in  $\delta^{15}\text{N}$  values of total soil N, ammonium, nitrate, and in mixed stands of conifers and red alder. These differences were not consistent across sites, however, preventing them from following the N fixed by alder through the soil to plant available mineral N. In contrast, a decline in  $\delta^{15}\text{N}$  values of *Leucaena leucocephala*, a

leguminous tropical plantation tree, were found in the first four years after establishment in Hawaii (van Kessel et al., 1994). These researchers argue that declining  $\delta^{15}\text{N}$  values of both the tree and understory tissue indicate the incorporation of N fixed by *L.*

*leucocephala* from soil OM, however, they did not try to trace the N fixed by the tree through soil N pools.

Complimentary studies have shown that N fixing plants have a much lower resorption efficiency than non-N fixing plants (Killingbeck, 1996), and that detritus from N fixing plants has a moderate ratio of total N to lignin (Hendricks and Boring, 1992; White et al., 1988). This results in litter that decomposes at an intermediate rate, providing plant available N without excess mineralization that can cause leaching and loss of N. Researchers agree that N fixation in plant roots results in increased N content in biomass (living and dead) regardless of N losses from the system. Increased N content of biomass under N fixing plants and evidence that plants are actively fixing has become acceptable evidence that the activity of these plants is resulting in N accretion to a system (Miller et al., 1993; Hendricks and Boring, 1992; White et al., 1988).

The ability of legumes and actinorhizal plants to add N to otherwise N limited systems has been used in a variety of management situations. Native and non-native N fixing plants has been commonly seeded in reclamation and restoration of degraded lands (Quinos et al., 1998; Brown and Lugo, 1994). Early work in the US and Canada was reviewed by Fessenden (1979) and who reported that 35 species of actinorhizal plants were then being used in mine reclamation and restoration efforts and over 45 species were being investigated for expanded or future use. Accelerated revegetation, less use of

fertilizers, soil stabilization by taproots, and high quality forage were some of the benefits of N fixing plant establishment identified by researchers working on coal mine reclamation efforts in the Ohio River Valley area of the US (Feagley et al., 1994). Other studies cite increased storage of N on site and increased biological activity associated with N fixing plants that speed up the re-establishment of ecosystem productivity in abandoned mines (Zeleznik and Skousen, 1996; Gonzalez-Sangregorio et al., 1991; Wade and Halverson, 1988).

Many other studies have been devoted to demonstrating the benefits of biological N fixation in N limited forest ecosystems. In some cases N fixing plants have been shown to improve growth of neighboring trees. Nitrogen fixing tree species like red alder (*Alnus rubra*) and autumn-olive (*Elaeagnus umbellata*) have been shown to increase the growth of more valuable timber tree species grown in association with them (Funk et al., 1979; DeBell and Rodwan, 1979). Douglas-fir trees grown in mixed plantations with red alder in the Pacific Northwest have shown substantial increases in growth over pure Douglas-fir stands (Miller et al., 1993). In this case average bole volume of Douglas-fir trees interplanted with red alder on poor sites was more than twice the average of Douglas-fir trees grown more than fifteen meters from the mixed stands. Increased soil N and OM under N fixing plants in California has also been proposed as indirect evidence of increased growth of associated trees, because other studies have shown improvement in soil OM status leads to significant increases in growth of commercially important tree species (Johnson, 1995). Extensive studies in radiata pine (*Pinus radiata*) stands in New Zealand and Australia have also shown increased growth rates of trees grown in association with N fixing plants (Sprent and Silvester, 1973). Vast forest plantations of

fast growing radiata pine in New Zealand have been established on N deficient coastal sands where rapid declines in site productivity after initial harvest have been noted. The establishment and promotion of legume species can forestall this decline in productivity. The seeding of *Lupinus arboeus* is a standard practice in these plantations and management activities like timing of thinnings and seeding of more shade tolerant cultivars are used to increase lupine cover (Sprent and Silvester, 1973). In the Pacific Northwest, Trowbridge and Holl (1992) found increased needle mass and foliar N content in lodgepole pine (*Pinus contorta*) trees in British Columbia established with clover after extensive site preparation that included fire.

The role of N fixing plants in replacement of N loss in fire disturbed systems is another beneficial interaction that has been studied. In the southeastern US, short rotation periods and intensive site preparation results in loss of OM and N from these systems (Hendricks and Boring, 1992). Nitrogen accretion rates of  $9 \text{ kg N ha}^{-1}\text{yr}^{-1}$  and N rich detritus from native legumes have been found to play an important role in maintaining N levels in these frequently burned forests. Binkley and associates (1982) studied another system where fire is a common site preparation tool. In the eastern Cascade mountains of Oregon, *Ceanothus velutinus* is a common component of young forests, and that N accretion by this species is critical in replenishing N lost to logging and site preparation burning.

Nitrogen fixing plants depend on disturbance to thrive because the symbiotic N fixation association is only an ecological advantage on open, N poor sites (Leach and Givnish, 1996). Researchers in New Zealand have found lupine growth, nodule biomass, and N fixation rates closely correlate to light transmission radiata pine plantations (Sprent

and Silvester, 1973). These researchers note that the lupines are virtually excluded from the understory after canopy closure. Nitrogen fixing plants in the Inland Northwest show similar light sensitivities, especially important actinorhizal shrub species (Noste and Bushey, 1987; Binkley et al., 1982). Boring and associates (1990) suggest that open conditions, reduced competition, and reduced soil N content all combine to make more photosynthate available for N fixation in fire disturbed sites.

Removing fire or other disturbance agents has been shown to decrease abundance of N fixing plants (Leach and Givnish, 1996) and decrease N fixation rates and nodule biomass of remaining plants (Sprent and Silvester, 1973). Fire exclusion from ponderosa pine/Douglas-fir forests of western Montana has resulted in many changes in tree species composition and forest structure, but little is known about how the removal of this disturbance agent has affected native N fixing plant species.

#### *Problems with Use of Nitrogen Fixing Plants in Forest Systems*

The role of N fixing plants in fire dependent forests of the northern Rockies is still poorly understood (Jurgensen et al., 1991). Less intensive management of Inland Northwest forests and a dearth of information on N fixation and accretion rates of native legumes and actinorhizal plants in this area are likely reasons why studies like those done in the southeastern US (Hendricks and Boring, 1992) and in New Zealand (Sprent and Silvester, 1973) have not been undertaken in this region. Jurgensen and associates (1991) suggest that the true role of native N fixing plants may be masked by changes in forest structure and function as a result of fire exclusion. Additionally, early research on N fixing plants in the region was also discouraged by work on habitat typing systems that

emphasized mature, undisturbed stands (Pfister et al., 1977) and likely underestimated the abundance of seral N fixing plants (Jurgensen et al., 1979).

In spite of the plethora of studies showing the benefits of biological N fixation, forest management plans considering N fixing plants have not been widely adopted. Scientists have identified competition from N fixing plants leading to slower tree regeneration or slower growth rates as a problem in the Inland Northwest (Jurgensen et al., 1998; Binkley et al., 1982). Others, however, have demonstrated the positive effects of understory N fixing plants on tree growth, regeneration, and soil fertility in this same region (Busse et al., 1996; Trowbridge and Holl, 1992). Some insist that biological N fixation is not economically feasible when compared to the application of commercial fertilizers (Tarrant, 1983; Turvey and Smethurst, 1983). Researchers have quantified the effects of applying commercial fertilizers to forest soils in the interior northwest with mixed results (Moore et al., 1991), and other scientists warn of problems associated with chemically dependent forest management plans (Oikarinen, 1996; Harvey et al., 1989). Harvey and co-workers (1989) caution that nutrient applications alone will not maintain soil physical conditions nor site productivity. Oikarinen (1996) contends that applying inorganic fertilizers at long intervals exposes plants in forest ecosystems to a short-term overdose of nutrients followed by a lengthy period of nutrient deficiency. He contends that biological soil amelioration provides the necessary nutrients at a rate which allows for maximum plant growth and prevents the creation of an open, leaky nutrient cycle. Beuter (1979) argues that not all costs of using synthetic fertilizers on forest ecosystems have been included in economic analyses, nor have all the benefits of using N fixing plants been included.

Forest managers are also leery of implementing new and regionally untested technologies, like using N fixing plants to increased N availability in soil, because of the lack of research on specific systems (Turvey and Smethurst, 1983; Jurgensen et al., 1991). Little information is available on the response of N fixing plants species to fire disturbance or the effects of fire on their abundance in the dry, cool northern Rocky Mountains. It is possible, in fact likely, that these plants are responsible for replenishing N stores lost to fire, providing a biological source of available N in otherwise N limited forest ecosystems of this region. However, the current scattered distribution and low density of these plants in fire excluded sites has discouraged researchers (Jurgensen et al., 1991). In order to understand more completely the role of legume and actinorhizal plants native to western Montana ponderosa pine/Douglas-fir forests, more information is needed about their distributions after fire and whether these distributions have been affected by past and current forest management practices.

Forest land management in the Inland Northwest is now beginning to emphasize the importance of activities that are consistent with ecological processes (Arno, 1996; O'Hara et al., 1994; Harvey, 1994). However there are many more aspects of ecosystem function that must be investigated in order to design ecologically sound forest management plans. The recent emphasis on reintroduction of fire to Western ecosystems (Arno, 1996) and on restoration of pre-1900 forest structure makes it even more important for researchers and managers to understand the role of native N fixing plants in these widespread dry forest habitats. Evidence that legumes and actinorhizal plants are important in replenishing organic stores of N in other fire dependent ecosystems, and the important role of fire in developing plant community structure in the Inland Northwest



suggests that N fixing plants are important components of western Montana forest ecosystems. The effects of fire exclusion policies on the structure and composition of these forests (Arno, 1996) and declining numbers of N fixing plants in other fire excluded ecosystems led to the development of this study.

## **PURPOSE AND OBJECTIVES**

The purpose of this research was to examine the abundance and occurrence of native N fixing plants in stands that have been differently affected by management and to provide some basic information on the distribution of native N fixing plants species in fire disturbed forests of western Montana.

Specific objectives of this study were to assess the abundance, coverage, and evidence of active N fixation of native N fixing plants in second-growth Douglas-fir/ponderosa pine forests that arose after the historic logging of the late 1800's and early 1900's. The following stand types were sampled and compared:

- 1a) stands undisturbed since historic logging
- 1b) stands undisturbed since historic logging and exposed to wildfire in the last 10 years  
and
- 2a) stands opened by harvest and/or fire at least twice during the last century
- 2b) stands opened by harvest and/or fire at least twice during the last century, and  
commercially thinned and underburned in the last 3-10 years.

## **MATERIALS AND METHODS**

### *Site Description*

Possible wildfire study sites were identified using a US Forest Service database listing all stands affected by wildfire in the last 3-10 years. Sites on south to west facing slopes with a ponderosa pine or mixed ponderosa pine/Douglas-fir coevertype and a Douglas-fir/ninebark habitat type (Pfister et al., 1977) that had not been disturbed in at least fifty years were selected for inspection. Six sites which had burned and unburned areas with similar elevation, aspect, slope, and soil type were selected from an initial list of over 30. Finding appropriate sites was difficult mainly because unburned areas were rare on the same aspect and slope, and within a short distance of a relatively homogeneously burned area. Similar unburned control plots were only found where a road across a slope acted as a fire break or the fire was actively fought and a fire line separated burned from unburned areas. Four of the six sites are located in the Lolo National Forest (LNF) and two on the Bitterroot National Forest (BNF). Underburned sites were identified with the assistance of researchers from the US Forest Service Intermountain Fire Sciences Laboratory and Forest Service district personnel, two sites on the Ninemile District of the LNF and three sites at the Lick Creek Resource Demonstration Area on the Darby District of the BNF. Prescribed fires had been carried out in these sites in an orderly fashion with well defined boundaries and nearby unburned controls. The Lick Creek site is part of a larger research project investigating the use of prescribed fire in restoring pre-settlement conditions to seral ponderosa pine forests. Three units of the larger project were sampled for this study, two areas that had been

selection harvested in 1992 and burned in the spring of 1993 and one that had been treated with a commercial thinning cut and a prescribed burn in the fall of 1993.

The 11 study sites were selected to have similar habitat type and cover type, but other characteristics were allowed to vary between sites. Site characteristics are summarized in Table 2.1. Fire intensity and severity also differed across sites. Some wildfires left no live trees while in other sites not all trees were killed. Prescribed underburns were also not equal as some were carried out in the cooler and wetter spring months and others in the drier fall months. Physical characteristics across the sites also differed--slope, aspect, and elevation all vary across the sites.

**Table 2.1.** Selected site characteristic from all 11 study sites

Site	Forest	Elev. (ft)	Aspect (deg)	Slope (%)	Habitat Type	Soil Type	Soil Texture	Fire Type	Fire Year
Frenchtown	LNF	3600	170-180	10	PsMe/SyAl	Mollic Eutoboralf	silt loam	underburn	1995
Cinderella Mtn.	LNF	3750	210-220	50-55	PsMe/AgSp	Typic Xerochrept	loam	wildfire	1988
Squaw Peak	LNF	4320	190-220	30-35	PsMe/PhMa	Dystic Eutrochrept	silt loam	wildfire	1994
Alberton	LNF	4800	180-190	40-45	PsMe/CaGe	Typic Xerochrept	loam	wildfire	1988
Henry Peak	LNF	4650	240-250	55-60	PsMe/PhMa	Typic Ustochrept	loam	wildfire	1994
Echo Canyon	LNF	3750	270-280	15-20	PsMe/SyAl	Typic Haploxeroll	loam	underburn	1989
Ward Mtn.	BNF	5300	90-100	25-30	PsMe/PhMa	Dystic Cryochrept	loam	wildfire	1994
Rock Creek	BNF	4720	150	25-30	PsMe/SyAl	Typic Ustochrept	sandy loam	wildfire	1988
Lick Creek 1	BNF	4650	180-190	20	PsMe/SyAl	Typic Ustochrept	sandy loam	underburn	1993
Lick Creek 2.	BNF	4550	170-180	10	PsMe/CaRu	Typic Ustochrept	sandy loam	underburn	1993
Lick Creek 3	BNF	4600	160-180	20-25	PsMe/CaRu	Typic Ustochrept	sandy loam	underburn	1993

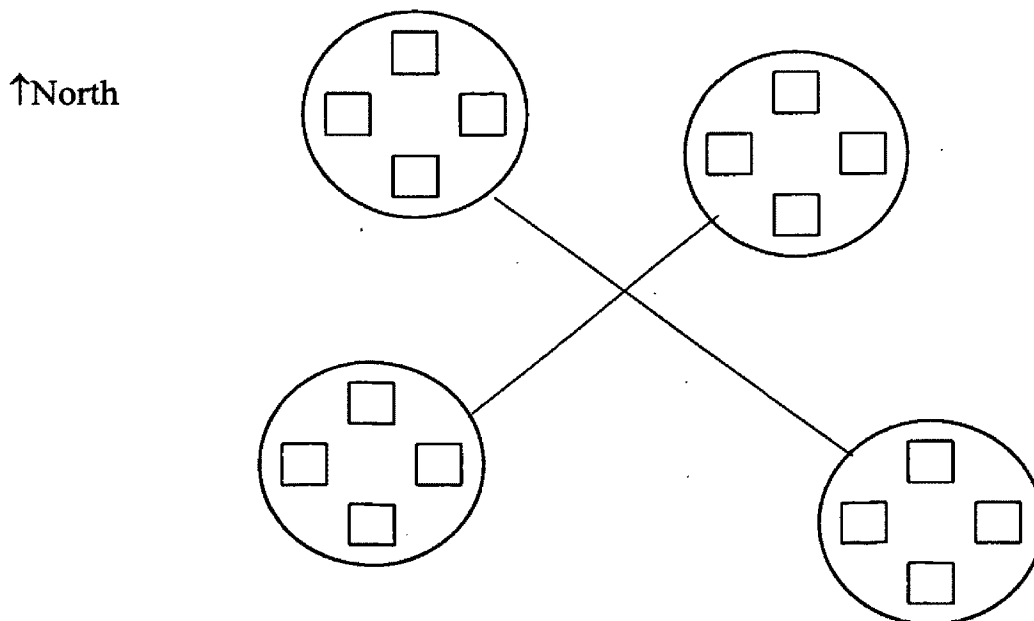
### *Sampling Design*

Habitat types (Pfister et al., 1977) were determined, soil surface horizons were described and other features--percent slope, aspect, and tree basal area, were measured in burned and unburned areas. Color, texture, O horizon depth, and surface horizon depth were recorded from shallow soil pits dug in random locations in the different areas for soil type descriptions. Basal area was estimated using a prism and variable radius plots,

and in sites where salvage logging or thinning has occurred, pre-fire stand density was estimated from snags, downed trees, and/or stumps. Plot centers were located in burned and unburned areas that were the similar based on this collected information. Some possible sites were ruled out because of variable soil characteristics and abrupt changes in slope, or because stand conditions did not other site selection criteria.

Once plot centers had been located in similar burned and unburned areas, fixed points were located at random distances between 0-15 meters from the plot centers at compass setting of 45, 135, 225, and 315 degrees. Native N fixing shrubs were identified (see Appendix 1), and the percent ground cover estimated for each shrub species present was estimated within 16 m<sup>2</sup> circles centered at each of these fixed subplot centers (Mueller-Dombois and Ellenberg, 1974). Percent ground coverage for identified N-fixing forbs was estimated in four 1 m<sup>2</sup> squares located at the cardinal directions from the subplot center (see Figure 2.3). Three sets of these plots were surveyed in each control and burned stand.

**Figure 2.3.** Plot Design



Within sub-plots containing native N fixing plant species, the above ground biomass of each N fixing species identified was harvested. These plants were collected from inside the study subplot if possible, or from adjacent areas if there was only a small amount of biomass. Known non-N fixing plants, one shrub and one forb for each site if both N fixing shrubs and forbs were found, were also harvested. Non-N fixing plants were selected with the same life form at the same development stage and growing near N fixing plants (Weaver and Danso, 1994; Bremer and van Kessel, 1990; Shearer and Kohl, 1986).

Soil samples were also collected from each of the 1 m<sup>2</sup> forb sampling areas in one of the plot sets in each control and burned stand to create four composited soil samples from each burned and unburned plot. Soil cores were collected at two sites to a depth of 10 cm after any O horizon material was removed. A small garden trowel was used to carefully remove samples to a depth of 10 cm in the other sites because the extremely rocky nature of the soils made collecting cores with a standard soil probe difficult. All samples were returned immediately to the laboratory or placed in a cooler for transport if travel times were greater than one hour.

Percent cover of N fixing species is reported as a proportion of the plot, for example a 1 m<sup>2</sup> square having five percent *Lupinus sericeus* is reported as having 0.05 *L. sericeus*. The numbers reported for each treatment at each site represent the average of 48 of the 1 m<sup>2</sup> squares, 16 squares in three sets of plots sampled in each treatment. The frequency of occurrence of N fixing plants was determined by dividing the number of 1 m<sup>2</sup> squares at each subplots that contained N fixing plants by the number of 1 m<sup>2</sup> squares surveyed at each subplot.

### *Laboratory Analyses*

Nitrogen fixing and non-N fixing plant samples were returned to the lab and placed in a convection oven at 60°C to dry. Once dry, the samples of each species were ground. These samples were sent to Woods Hole National Laboratory and analyzed for atom percent  $^{15}\text{N}$ . As much visible root matter as possible was removed by hand from the composite soil samples. Gravimetric moisture content was determined with approximately 10 g of soil (Gardner, 1986). Subsamples of each composite were extracted with 50 ml 2M KCl, shaken for 30 minutes, filtered through #42 Whatman filter papers, and analyzed for nitrate (Cataldo et al., 1975) and ammonium (Willis et al., 1993). Incubations were set up for potentially mineralizable N (PMN) following Keeney (1982). Five g of soil were placed in a centrifuge tube, covered with 12.5 ml water and  $\text{N}_2$  gas was used to create an anaerobic headspace. Tubes were quickly sealed and then incubated for 14 days at 30°C. These samples were then extracted with 12.5 ml 4M KCl and analyzed for ammonium using the procedure cited above. Remaining portions of each composite sample were spread to air dry. Air dry soil was sieved through a 2 mm sieve. Ten grams of this soil were wetted with 20 ml 0.01M  $\text{CaCl}_2$  and pH was measured with an Orion 701A pH meter. Particle size analysis was completed using the hydrometer method (Gee and Bauder, 1986). Total C and N was analyzed by dry combustion (Fission EA 1100, Milano, Italy).

### *Statistical Analyses*

Student's t-tests were used to determine significant differences in PMN values between control and burn plots at each site. Potentially mineralizable N values, grouped

by site type--undisturbed or repeatedly opened, were also analyzed with student's t-tests. Past work has shown that vegetation survey data is often non-normally distributed (Towne and Knapp, 1996; Mueller-Dombois and Ellenberg, 1974), so cover and frequency proportions were tested for normality using Kolmogorov-Smirnov test. This test showed significant non-normality in the data so the non-parametric Mann-Whitney U test was used in comparisons of vegetation data. Cover and frequency of N fixing plants in burned and unburned plots were compared at each site in which N fixing plants were found. Occurrence and abundance of N fixing plants in wildfire and underburned sites were compared in the same manner.

## CHAPTER 3

### RESULTS

#### *Soil Properties and Selected Site Characteristics*

Study pairs were chosen to preserve as much similarity as possible between treatments (Tables 2.1 and 3.2). These factors and others, like fire intensity and severity, elevation, and aspect, did vary between sites and to analyze the effects of these differences a much larger number of sites would have to be sampled. Comparisons between control and burned stands and between undisturbed and repeatedly opened sites were the focus of this study.

Pre-fire tree basal area is an example of a factor that did not differ significantly between control and burned stands when all sites were analyzed together Table 3.1. Mean basal area varied somewhat across all sites, but the majority of sampled stands fell between 90-120 ft<sup>2</sup>ac<sup>-1</sup>.

**Table 3.1.** Basal area (ft<sup>2</sup>ac<sup>-1</sup>) in sample plots control (1) and burned (2) for all 11 sites

Plot	French-town	Cinderella Mtn.	Squaw Peak	Alberton	Henry Peak	Echo Canyon	Ward Mtn.	Rock Creek	Lick Creek 1	Lick Creek 2	Lick Creek 3
1a	105	75	120	90	90	105	75	90	105	120	120
1b	105	75	135	105	75	60	90	120	120	120	135
1c	75	60	60	105	60	105	105	120	90	120	105
<b>Means</b>	<b>95</b>	<b>70</b>	<b>105</b>	<b>100</b>	<b>75</b>	<b>90</b>	<b>90</b>	<b>110</b>	<b>105</b>	<b>120</b>	<b>120</b>
2a	120	90	120	105	90	120	75	105	120	120	90
2b	105	75	90	105	75	120	75	105	90	135	135
2c	75	75	90	75	60	60	105	105	75	105	105
<b>Means</b>	<b>100</b>	<b>80</b>	<b>100</b>	<b>95</b>	<b>75</b>	<b>100</b>	<b>85</b>	<b>105</b>	<b>95</b>	<b>120</b>	<b>110</b>

Table 3.1 summarizes data collected on soil physical and chemical properties for all sites. Soil textures were generally coarser in the Bitterroot National Forest sites where soils formed predominantly from granitic parent material. Soils from Lolo National



Forest sites formed from heterogeneous Belt Supergroup rocks, and had finer textures but higher percentages of coarse fragments. Surface soil horizons in the Echo Canyon site were unusually deep, high in OM, and strongly acidic--characteristics more typical of grassland soils than forest. A possible explanation for these unusual characteristics is the calcareous parent material at this site. Limestone parent materials from the Belt Supergroup have been shown to promote the development of organic rich surface horizons elsewhere in western Montana (Goldin and Nimlos, 1977).

**Table 3.2.** Selected physical and chemical properties of sample plots

Site	Treatment	%sand/silt/clay	pH	% WHC	Total C g/kg	Total N g/kg	C:N
Frenchtown	control	23/53/24	5.7	0.3141	12.8	0.85	15.06
	burn	22/53/25	4.6**	0.3197	15.7	0.95	16.53
Cinderalla Mtn.	control	46/33/21	5.8	0.1800	27.8	1.3	21.38
	burn	46/35/19	5.4†	0.2262	23.2	1.29	17.98
Squaw Peak	control	33/57/11	5.5	0.2524	15.9	0.92	17.28
	burn	24/53/23	5.6	0.3081	17.5	1.07	16.36
Alberton	control	34/51/15	5.6	0.3781	20.9	1.09	19.17
	burn	35/47/17	5.9	0.3072	24.4	1.5	16.27
Henry Peak	control	39/45/16	5.9	0.4148	25.5	1.29	19.77
	burn	37/48/15	5.8	0.3379	15	1.02	14.71
Echo Canyon	control	46/36/19	4.6	0.4752	82.6	4.2	19.67
	burn	51/33/16	4.8	0.4744	56.7	3.39	16.73
Ward Mtn.	control	51/36/14	5.4	0.3695	40.2	1.75	22.97
	burn	48/38/14	6.1*	0.2561	21.9	1.35	16.22
Rock Creek	control	64/27/9	5.3	0.1703	21.7	0.97	22.37
	burn	60/30/10	5.1	0.1354	20.2	0.96	21.04
Lick Creek 1	control	59/29/12	5	0.2005	20.9	1.03	20.29
	burn	65/27/8	5.3	0.1588	23.8	1.01	23.56
Lick Creek 2	control	53/37/10	4.9	0.2799	22.6	1	22.60
	burn	55/34/11	4.7	0.2740	31.7	1.38	22.97
Lick Creek 3	control	63/29/9	5	0.1798	17.4	0.85	20.47
	burn	62/31/8	5.3	0.1672	17.4	0.8	21.75

\*\* significantly different from control at  $\alpha = 0.001$

\*  $\alpha = 0.05$

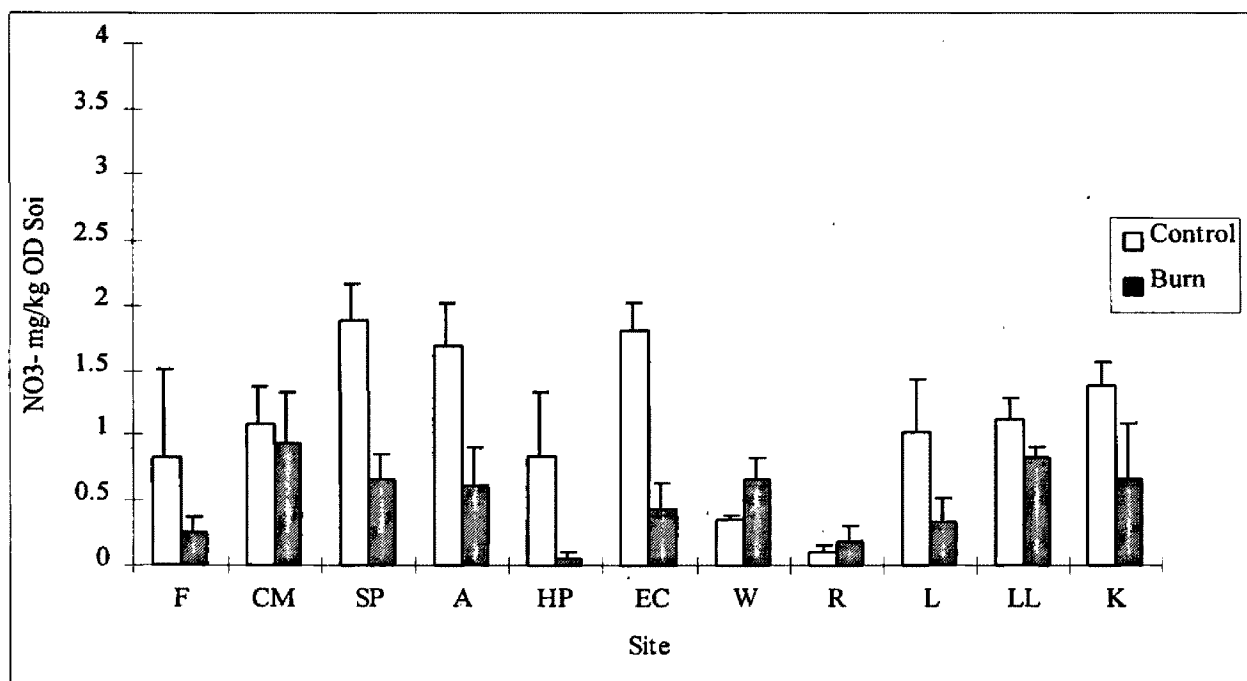
†  $\alpha = 0.1$

Soil textures and water holding capacity (WHC) did not differ significantly between treatments at each site. Soil pH, however, varied somewhat between control and burned stands at three sites. Total C and N data along with C:N are also presented in Table 3.2, and overall there were no significant differences in these values between control and burned stands. There did not appear to be any patterns in area covered or frequency of occurrence of N fixing plants with respect to soil physical and chemical properties in the 11 sites sampled for this study.

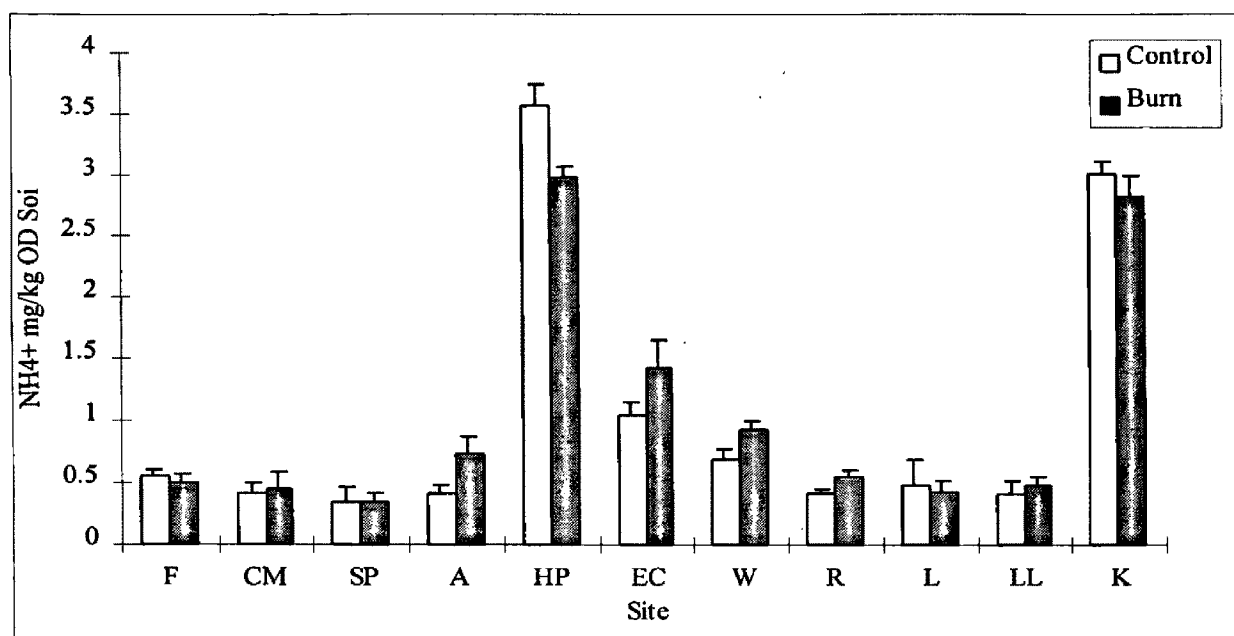
### *Soil Nitrogen Indices*

Levels of nitrate in control stands were generally higher than in burned stands, and significantly higher when averaged across sites ( $\alpha = 0.001$ ). Levels of extractable ammonium were not different between control and burned stands.

**Figure 3.1.** Nitrate (a) and ammonium (b) level for all sites [F = Frenchtown, CM = Cinderella Mountain, SP = Squaw Peak, A = Alberton, HP = Henry Peak, EC = Echo Canyon, W = Ward Mountain, R = Rock Creek, LC = Lick Creek 1, LL = Lick Creek 2, K = Lick Creek 3]



a)



b)

Potentially mineralizable N values tended to be greater in control stands than in burned and were significantly higher than PMN values for burned stands at  $\alpha = 0.05$  when all sites were analyzed together. Mean PMN values and significant differences for each site are summarized for all sites in Table 3.3.

**Table 3.3.** Mean PMN values and fraction of PMN to total N for all sampled sites

Site	PMN mg/kg OD Soil		PMN/total N	
	Control	Burn	Control	Burned
Frenchtown	10.981	10.540	0.01292	0.01109
Cinderella Mtn.	11.685	4.726**	0.00899	0.00366**
Squaw Peak	14.727	12.652	0.01601	0.01182
Alborton	18.660	25.597	0.01712	0.01706
Henry Peak	30.539	11.394	0.02367	0.01150
Echo Canyon	35.073	19.290†	0.00861	0.00569
Ward Mtn.	27.920	8.881*	0.01595	0.00658*
Rock Creek	5.372	5.302	0.00554	0.00552
Lick Creek 1	12.889	7.204	0.01251	0.00713
Lick Creek 2	14.745	14.747	0.01474	0.01069
Lick Creek 3	8.562	5.341	0.01007	0.00690
<b>Means</b>	<b>11.471</b>	<b>17.477*</b>	<b>0.01329</b>	<b>0.00888*</b>

\*\* different from control,  $\alpha = 0.001$

\*  $\alpha = 0.05$

†  $\alpha = 0.1$

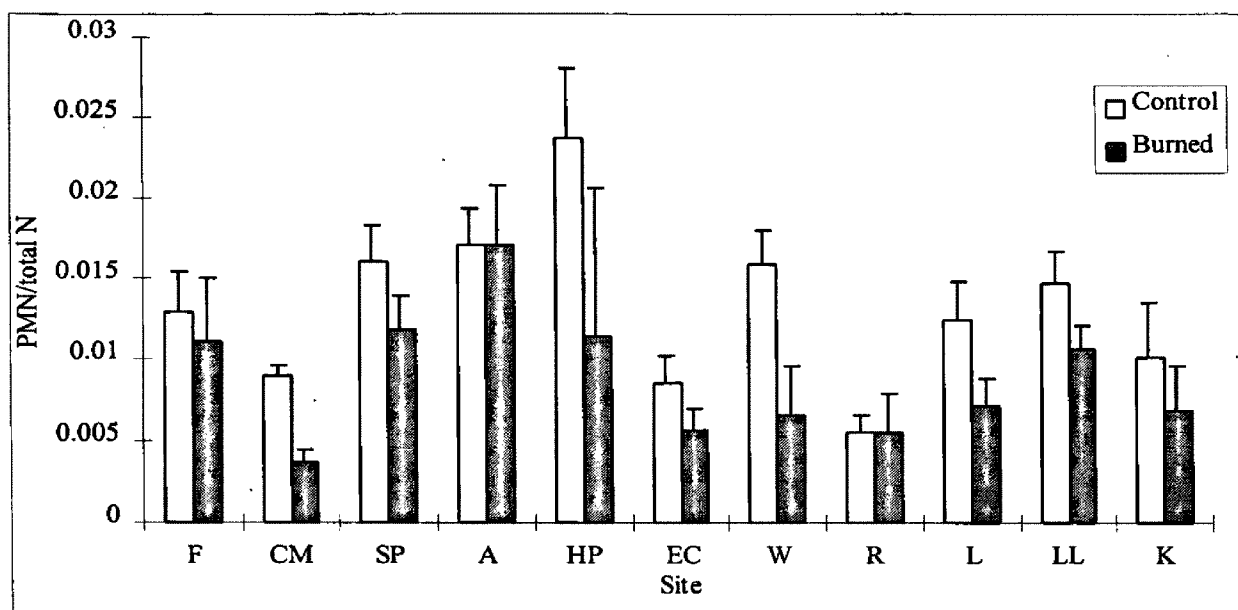
Repeatedly opened sites and undisturbed sites were analyzed separately, and both groups showed significantly higher PMN values in control stands versus burned stands (Table 3.4). Control stands in repeatedly opened sites were significantly greater than burned at  $\alpha = 0.1$  and PMN values in control stands of undisturbed sites were significantly greater than in burned stands at  $\alpha = 0.05$ . When the two types of sites were compared, undisturbed sites had significantly higher PMN values than those sites that were repeatedly opened with data from both control and burned stands included ( $\alpha = 0.05$ ). Control and burned stands of undisturbed sites were significantly higher in PMN than their counterparts in repeatedly opened sites (control stands at  $\alpha = 0.05$  and burned at  $\alpha = 0.1$ ) (Table 3.4).

**Table 3.4.** Comparisons of PMN, cover, and frequency between site types

Comparison	PMN mg/kg		Cover proportion		Frequency proportion	
	Means	p-value	Means	p-value	Means	p-value
Repeatedly opened vs. Undisturbed	11.51	0.004	0.026	0.001	0.285	0.001
	18.03		0.007		0.107	
Control rep. opened vs. Control undist.	13.85	0.016	0.018	0.200	0.188	0.143
	21.83		0.006		0.078	
Burn rep. opened vs. Burn undist.	9.17	0.089	0.035	0.001	0.383	0.001
	14.23		0.008		0.135	
Control rep. opened vs. Burn rep. opened	13.85	0.085	0.018	0.010	0.188	0.006
	9.17		0.035		0.383	
Control undist. vs. Burn undist	21.83	0.033	0.006	0.613	0.078	0.492
	14.23		0.008		0.135	

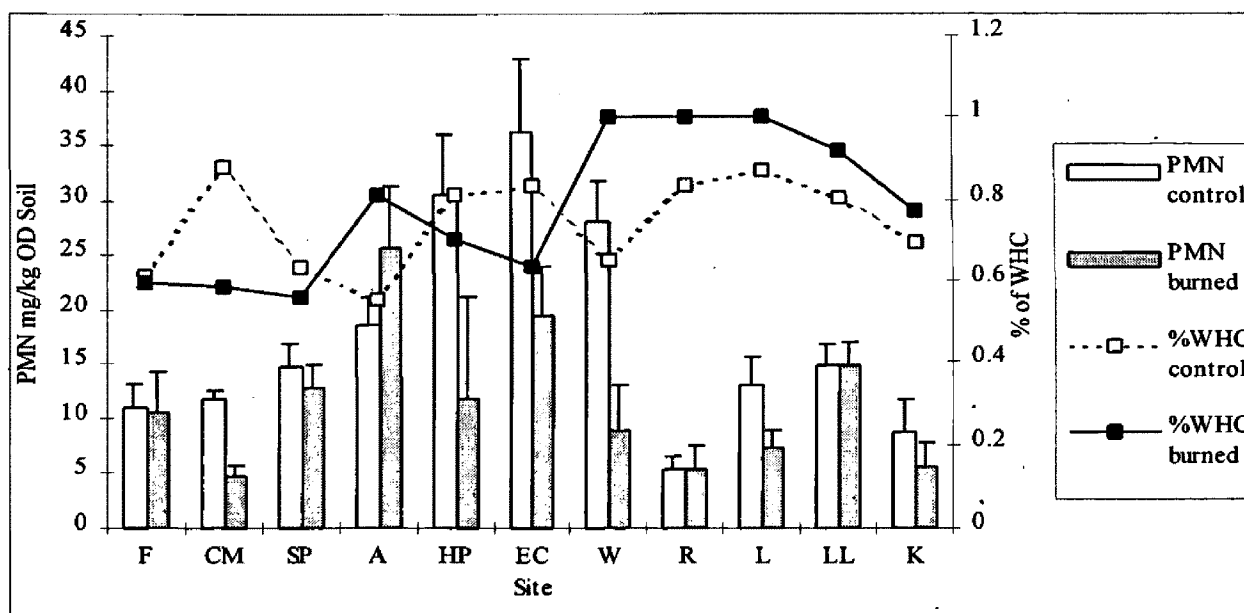
Potentially mineralizable N expressed as a fraction of total N (see Figure 3.2) was also significantly greater ( $\alpha = 0.05$ ) in control stands over burned stands when averaged across all sites. Two sites also significantly different fractions of PMN to total N when sites were examine individually (Table 3.3).

**Figure 3.2.** PMN as a fraction of total soil N in control and burned stands from all sites



Moisture availability, presented as a percentage of field capacity, and PMN values are graphed together in Figure 3.3. Moisture content of samples are expressed a percentage of moisture content at field capacity. The high ratios were the result of wet spring and early summer weather.

**Figure 3.3.** PMN and moisture content as % of WHC



There does not appear to be a pattern relating PMN level and moisture content across all sites, however, PMN levels do seem to vary with moisture content in the first six sites from the Lolo National Forest. There are not significant differences in moisture content between control and burned stands when averaged across all sites.

### *Vegetation Surveys*

Occurrence of native N fixing plants was highly inconsistent in most sites and percent coverage of these plants was generally low. *Lupinus* was the most common genus encountered, and it was represented by three different species. Nitrogen fixing shrub species were much more scattered, often seen in small numbers near plot centers but only falling within shrub subplots at the Henry Peak site. There were no sites with multiple species of N fixing plants found in sampled areas, but other species were sometimes seen in small numbers around the sampled subplots. Table 3.5 lists species found within subplots at each site and species found between plot centers and subplots but outside of sampled areas.

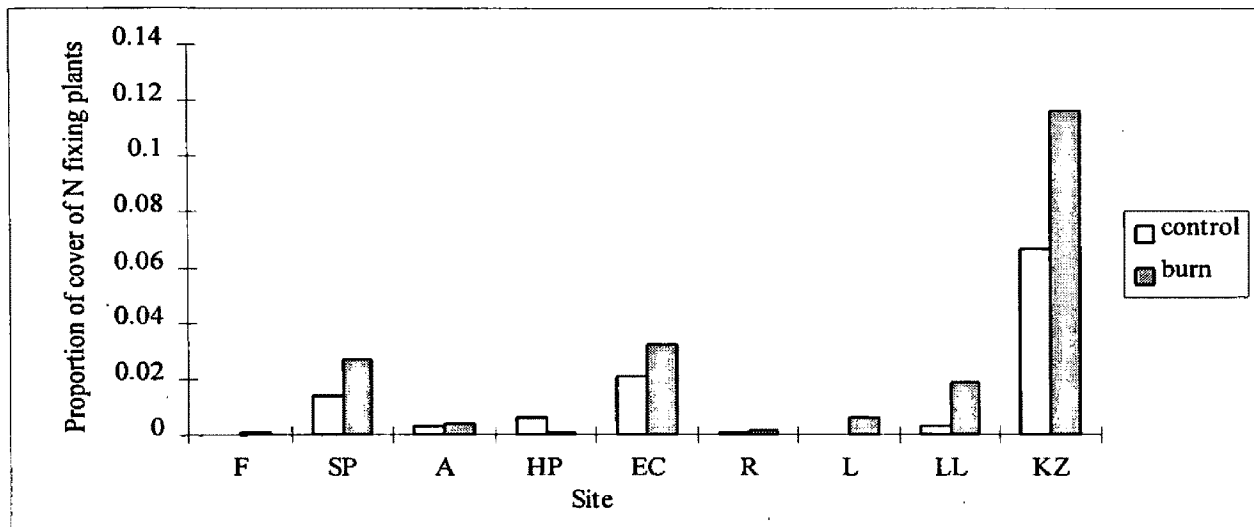
**Table 3.5.** Nitrogen fixing species found in study sites

Species	In sample subplots	Near plot centers
<i>Ceanothus velutinus</i>	HP	R
<i>Lupinus argenteus</i>		A
<i>L. laxiflorus</i>	EC	
<i>L. leucophyllus</i>	R, LC, LL, K	
<i>L. sericeus</i>	F, SP, A	
<i>Purshia tridentata</i>		HP, LL
<i>Shepherdia canadensis</i>		HP, R, LC

Nitrogen fixing plants were found in sampled areas in 9 out of 11 sites, but only seven of the species typically found in western Montana (Jurgensen et al., 1979;

Lackschewitz, 1991) were seen. The numbers reported for each site are averages of all subplots from the three sets of plots on which vegetation surveys were conducted. Figure 3.4 reports the average proportion of area covered by N fixing plants. Averages of frequency values showed a similar pattern, but values were generally higher (Table 3.6).

**Figure 3.4.** Proportion of area covered by N fixing species in sample plots



Large numbers of plots without N fixing plants resulted in skewed, non-normal distributions. Efforts to normalize the data using various transformations were not successful, so non-parametric tests were used for statistical analysis. Proportion of cover occupied by N fixing plants was significantly higher in burned treatments over controls ( $\alpha = 0.05$ ) when all sites were analyzed together, however, when sites were analyzed separately only one site in the Lick Creek Demonstration Area showed a significantly higher proportion of cover ( $\alpha = 0.1$ ). Comparisons of grouped data were also done in the same way as for PMN analysis (Table 3.3). The proportion of cover of N fixing species was significantly higher in the burned stands when repeatedly opened sites were analyzed separately ( $\alpha = 0.05$ ), while undisturbed sites showed no significant differences between control and burned stands. When management histories were compared, repeatedly

opened sites showed higher cover proportions of N fixing plants than undisturbed sites with data from both control and burned stands included ( $\alpha = .001$ ). Similarly, burned stands from repeatedly open sites showed significantly higher cover proportions than the burned stands in undisturbed sites ( $\alpha = 0.001$ ), but control stands were not significantly different between repeatedly opened and undisturbed sites.

**Table 3.6.** Mean cover and frequency values for all sampled plots

Site	Cover Proportion		Frequency	
	control	burn	control	burn
Frenchtown	0.0000	0.0010	0.0000	0.0625
Squaw Peak	0.0140	0.0267	0.2083	0.3750
Alberton	0.0027	0.0042	0.0625	0.1042
Henry Peak	0.0058	0.0010	0.0069	0.0069
Echo Canyon	0.0204	0.0325	0.3125	0.5208
Rock Creek	0.0004	0.0019	0.0208	0.0417
Lick Creek 1	0.0000	0.0060	0.0000	0.1875
Lick Creek 2	0.0033	0.0183	0.0833	0.2708
Lick Creek 3	0.0663	0.11625†	0.5417	0.875*
<b>Means</b>	<b>0.0125</b>	<b>0.0231*</b>	<b>0.1402</b>	<b>0.2731*</b>

\* significantly different from control at  $\alpha = 0.05$

†  $\alpha = 0.1$

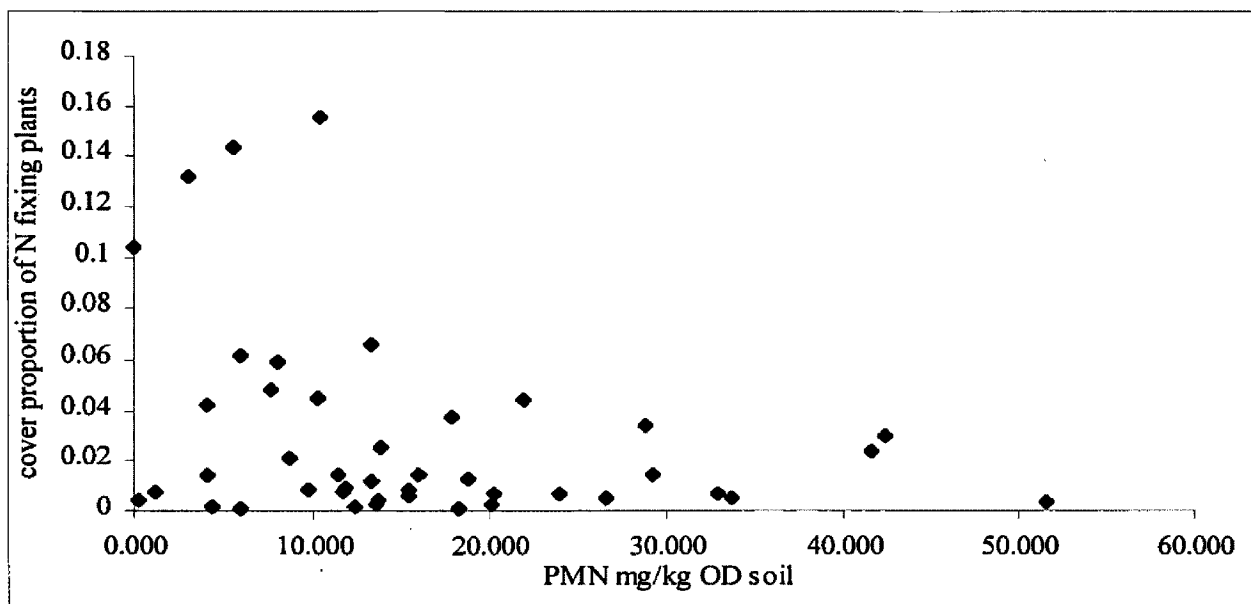
Data on frequency of occurrence of N fixing plants showed similar trends-- overall, burned stands showed higher frequencies than controls ( $\alpha = 0.001$ ). Again, repeatedly opened sites had significantly higher frequency of occurrence ( $\alpha = 0.05$ ), while undisturbed sites did not show a significant difference between control and burned stands. Repeatedly opened sites showed higher frequency of occurrence of N fixers than undisturbed sites when control and burned stands were included in the analysis ( $\alpha = 0.001$ ). When analyzed separately control stands were not significantly different between repeatedly opened sites and undisturbed sites, but burned stands in opened sites had



higher frequencies of occurrence ( $\alpha = 0.001$ ). Averages of cover and frequency data for all sites in which N fixing plants were found are presented in Table 3.6.

There does not seem to be any correlation between PMN levels and proportion of cover or frequency of N fixing plants even though parallel trends were seen in these data. Potentially mineralizable N values were significantly higher on control treatments and in undisturbed sites, while cover and frequency of N fixing plants were lower in control treatment and undisturbed sites (Table 3.3). Neither PMN values nor the ratio of PMN to total N, show any significant correlation to cover or frequency of N fixing plants. Figure 3.5 does show the possibility of a non-linear relationship between PMN levels and proportion of cover of N fixing plants, but the large quantity of zero values in the vegetation data may be preventing a clear demonstration of underlying patterns.

**Figure 3.5.** Scatter plot of cover of N fixing plants versus PMN in all sampled plots with N fixing plants



### *<sup>15</sup>N Analysis*

Results from <sup>15</sup>N analysis of collected plant samples are summarized in Table 3.7. Nitrogen fixing plants had lower δ<sup>15</sup>N values than non-fixing plants for all of the samples except in the case of the non-N fixing weed *Centaurea maculosa* (spotted knapweed). Two of the N fixing species were collected at the same site and the same non-fixing reference plant was used for both. These data are presented as descriptive information only. Budget constraints prevented the collection of replicates and thus no statistical analysis was done on this data.

**Table 3.7.** δ<sup>15</sup>N values for N fixing and non-fixing plants

Echo Canyon	N fixer	Lula	-0.5
	non-N fixer	Arco	2.8
Henry Peak	N fixer	Putr	-1.1
	non-N fixer	Phma	1.5
Henry Peak	N fixer	Ceve	-0.6
	non-N fixer	Phma	1.5
Lick Creek 1	N fixer	Shca	-0.2
	non-N fixer	Sasc	0.4
Lick Creek 2	N fixer	Lule	-0.4
	non-N fixer	Cema	-1

**means**                      **N fixers**                                      **-0.55**  
    **non-N fixers**                                      **1.04**

Lula = *Lupinus laxiflorus*

Arco = *Arnica cordifolia*

Putr = *Purshia tridentata*

Phma = *Physocarpus malvaceus*

Ceve = *Ceanothus velutinus*

Sase = *Salix scoulerana*

Shca = *Shepherdia canadensis*

CeMa = *Centaurea maculosa*

Lule = *Lupinus leucophyllus*

## DISCUSSION

### *Soil Nitrogen Levels*

Results showing decreased PMN levels in soil samples from burned stands compared to control stands in this study are consistent with other work in ponderosa pine forests (DeLuca and Zouhar, 1998; Monleon et al., 1997). Lower levels of PMN in repeatedly opened sites compared to the less disturbed sites, regardless of stand type, suggest that other types of disturbance and repeated disturbance also reduce PMN levels. Most researchers attribute lower levels of PMN in fire affected areas to reduced amounts of surface OM, and warn that loss of surface OM may result in long-term declines in the quality of soil OM (DeLuca and Zouhar, 1998; Kimmins, 1996; Covington and Sackett, 1992; Hungerford et al., 1991; Boring et al., 1990; White, 1986).

Total C and N in soils sampled in this study were not significantly different between control and burned stands. Other studies of similar systems have shown mixed results with respect to changes in total C and N after exposure to fire. Monleon and associates (1997) found that total C and N increased immediately after fire, decreased over five years, and were unchanged from unburned levels after 12 years in ponderosa pine forests of central Oregon. DeLuca and Zouhar (1998) also found little difference in total C and N contents in control and burn treatments two years or more after treatment. Sparling (1992) suggested that changes in the ratio of labile C to total organic C is a more sensitive measure of soil OM status than monitoring amounts of total C. The variability of total organic C in soils across even small areas and the relatively large amounts of total organic C may overshadow changes in much smaller labile C pools. These problems may also affect monitoring of N availability in soils, and it is possible that declines in soil OM

quality are represented by lower ratios of PMN to total N. This ratio was significantly lower in burned stands and in the repeatedly opened sites than in their less disturbed counterparts.

The significantly higher levels of nitrate ( $p < 0.001$ ) in control versus burned stands also point to reduced plant available N in fire disturbed sites. This pattern was not seen in ammonium levels, nor have consistent reductions in nitrate levels been documented by other researchers in this region (DeLuca and Zouhar, 1998; Monleon et al., 1997). It is possible that, in extracting soil samples, fulvic acids were liberated from OM accidentally contaminating mineral soil samples. These organic acids are yellowish brown in color and may have interfered with colorimetric nitrate analysis (Cataldo et al., 1975).

Unusually high levels of ammonium in two sites while other sites had low values compared to past work are more difficult to explain. One site with relatively high ammonium levels (3-3.7 mg/kg), Henry Peak, also had high PMN levels (30-11 mg/kg), but the other site with high ammonium levels, Lick Creek 3 (K), had relatively low levels of PMN (5.3-8.5 mg/kg). Studies in ponderosa pine forests of California and central Oregon have shown increases in OM and mineral N content under N fixing plants (Busse et al., 1996; Johnson, 1995), and it is possible that the high percent cover (7-12%) of N fixing plants in the Lick Creek 3 site may be contributing to increased mineral N levels. Intensive studies examining N availability under N fixing plants in sites with high densities of N fixing plants compared to areas without them are needed in western Montana before any weight can be given to this hypothesis. The high densities of *Lupinus leucophyllus* at the Lick Creek 3 site provide incentive for continued examination of the possible role of these plants in western Montana forests.

### *Vegetation Response*

Sites that had been opened repeatedly had greater cover ( $p=0.001$ ) and frequency ( $P=0.001$ ) of N fixing plants, and recently burned stands from both types of sites also showed higher cover ( $p=0.017$ ) and frequency ( $p=0.008$ ). This is in agreement with previous findings that have shown increased density of N fixing plants after fire. A similar study in southeastern US pine/hardwood forests also showed significantly higher densities of legumes in sites burned on a four year cycle (Boring et al., 1990). Legumes and actinorhizal plants have adapted to flourish in highly disturbed areas that are inhospitable to non-N fixing plants. Mine tailings and other abandoned mine lands are areas where low available N and low OM content of the soil limit re-colonization by non-N fixing plants (Feagley, et al., 1994; Fessenden, 1979). Conditions after wildfire or thinning and underburning in western Montana forests are often more hospitable than mine reclamation sites, however, results of the current study show that cover and frequency of N fixing plants significantly increased even with less severe disturbance due to fire.

Repeatedly opened sites and burned stands examined in this study showed lower PMN values along with higher cover and frequency of N fixing plants. Nitrogen fixing plants in prairie ecosystems have also shown greater abundance in more N limited lowlands than uplands and also greater abundance in fire exposed sites than undisturbed sites (Towne and Knapp, 1996). Ojima and associates (1994) noted that plants with higher nitrogen use efficiency (NUE) are favored in sites with low N availability and that these plants may be responsible for maintaining high productivity levels even with repeated N loss. Nitrogen fixing plants may function in this manner in repeatedly burned

systems. Legumes and actinorhizal plants may have a low NUE overall (Vitousek, 1982), but actively fixing plants have a high NUE with respect to available soil N (Sanginga et al., 1992) and are favored by low soil N availability (Leach and Givnish, 1996). Unlike the C4 plants examined by Ojima and associates (1994), N fixing plants also provide relatively easily decomposed, high N content litter to the soil systems (Killingbeck, 1996; Hendricks and Boring, 1992; White et al., 1988). Legumes and actinorhizal plants may colonize N limited sites, and while protecting the short-term productivity of the site, they also begin to increase N levels in the soil to protect long-term productivity.

Such a system may support claims that western Montana ponderosa pine/Douglas-fir forest affected by frequent fires were more productive than fire excluded second growth forests. The documented decrease in growth of trees in old growth areas where fire has been excluded and the suppressed growth of second growth forests (Arno, 1996) indicate that frequently burned, repeated opened sites historically showed higher tree productivity. Lower PMN levels and reduced labile N pools and higher productivity seem difficult to reconcile, but composition and function of understory plants may have played an important role in maintaining long-term productivity of sites with low levels of PMN and mineral N. Sites with well developed understory communities in ponderosa pine forests in central Oregon showed increased long-term growth of trees, total OM, and microbial biomass compared to sites in which understory vegetation had been excluded for 35 years (Busse et al., 1996). Two actinorhizal shrubs, *Ceanothus velutinus* and *Purshia tridentata*, were dominant plants in the understory community at this site and  $^{15}\text{N}$  analysis was used to estimate that 45-70% of N in these plants was derived from fixation. Results from the study reported here suggest that the N fixing plants sampled for  $^{15}\text{N}$

analysis were actively fixing N, and it is likely that fixation contributed a significant amount of N to the biomass of these plants. More data, however, is needed on the  $^{15}\text{N}$  content on plants grown hydroponically and completely depended on fixation to estimate the percent of biomass N of these plants that comes from fixation.

It is difficult to accurately assess the overall productivity of pre-settlement old growth stands, as few exist and a very small portion of those that do exist have been repeatedly exposed to fire in this century. Some researchers have shown decreased productivity in repeated burned ponderosa pine forests and contend that repeated removal of forest biomass led to reductions in soil nutrient status and decreased productivity (Monleon et al., 1997; Grier, 1989). It is possible that pre-settlement forests did not have greater productivity than the forests we see today, but such measures of ecosystem function are difficult to estimate from ponderosa pine/Douglas-fir forests as they exist today. The lack of forest stands that adequately represent pre-settlement forest structure will continue to hinder studies of pre-settlement ecosystem function.

Low densities of N fixing plants may reduce their importance in maintaining long-term productivity, however the results of this study suggest that ponderosa pine/Douglas-fir forests with high frequency fires may have had higher densities of N fixing plants. Repeatedly opened sites in ponderosa pine/Douglas-fir forests are likely the best representation of pre-settlement forest structure in western Montana because of the paucity of remaining old growth stands (Arno, 1996), and it was in sites that greater cover and frequency of N fixing plants were seen. Although overall cover and frequency of N fixing plants was low, means across all sites of 0.018 and 0.21 respectively, some repeatedly opened sites had significant amounts of N fixing plants in

the understory (up to 0.33). Increased cover of N fixing plants in recently burned repeatedly opened sites over recently burned undisturbed sites in this study may have specific management implications. It is possible that efforts to restore pre-settlement forest conditions in these forests may allow managers to increase the density of N fixing plants while meeting other management objectives. It is important to learn more about the contribution of the plants seen in this study to the N cycle of western Montana forests. If N fixing plants become more common with increasing disturbance and available soil N becomes lower, input of N from N fixing plants may become very important in maintaining forest productivity.

Only a few species of N fixing plants were identified in sampled areas of the study sites and in no sites were multiple N fixing species found in sampled areas. It is impossible to tell if fire exclusion has affected the total number of N fixing species seen in western Montana forests in the same way as fire exclusion in prairie remnants (Leach and Givnish, 1996). Large areas of forested lands have been exposed to disturbance, from clearcutting to intensive grazing, that promote the growth of N fixing species. Conclusions cannot be drawn, however, without implementing a study to examine the number of N fixing species and their density in sites that have been frequently burned compared to areas where fire has been completely excluded.

It is interesting to note that N fixing plants were found in both control and burned stands in seven of the nine sites. Low light intensities and competition from young trees seem to be plausible reasons for loss of N fixing plants from second growth forests. It is possible that once N fixing plants have been excluded from these systems for long periods some factor, like decreased seed bank or loss of source of colonizing symbiotic



bacteria, prevent the re-establishment of these plants with the reintroduction of disturbance. This line of thinking may be supported by the findings of Leach and Givnish (1996) in unburned prairie remnants, and by agricultural research that has shown loss of inoculants in cultivated systems after as little as three or four years (Delorit et al., 1984). Another possible reason for the loss of N fixing species from fire excluded sites might be the build up available N in undisturbed systems. Leach and Givnish (1996) propose this a possible mechanism, and the higher PMN levels in undisturbed stands in this study also support this hypothesis. This study was not able to accurately gage such changes because of the difficulty in finding seral old growth ponderosa pine stands that have been affected by fire repeatedly in this century with which to compare undisturbed second growth.

## CONCLUSIONS

Exclusion of fire from Inland Northwest forests has caused changes in forest structure, composition, and function. The results of this study indicate that abundance of important understory plants may have also been affected by past fire suppression policies. Significant increases in cover and frequency of native N fixing plants were seen in burned stands versus controls and also in repeatedly opened sites compared to undisturbed sites. Lower levels of PMN and ratios of PMN to total N were seen in the same types of sites that had higher N fixing plant occurrence and abundance. The increased abundance of N fixing plants in more disturbed areas with lower available N followed predicted distribution patterns based on past work and the ecology of N fixing plants. Legumes and actinorhizal plants were found in low densities in most sites, limiting the likelihood that

they are significantly increasing current N availability. Increased cover and frequency of N fixing plants in repeatedly opened sites, however, suggest that pre-settlement forests may have had higher densities of N fixing plants.

Lower PMN levels and decreased ratios of PMN to total N intimate changes in quality of soil OM in burned stands and repeatedly opened sites. This does not correspond with evidence of higher productivity in frequently burned pre-settlement forests, and further research in this area is warranted. Past research has shown improved soil OM status and N availability under N fixing plants. This combined with the ability of N fixing plants to thrive in N limited sites, suggests that N fixing plants may have played an important role in maintaining site productivity in frequently disturbed western Montana forests.

**Appendix 1. Common Nitrogen Fixing Plants Occurring in Western Montana Dry Forest Habitat Types (From Jurgensen et al., 1979 and Lackschewitz, 1995)**

**Shrubs**

<i>Shepherdia canadensis</i>	buffalo berry
<i>Ceanothus sanguineus</i>	red stem ceanothus
<i>C. velutinus</i>	shiny ceanothus/snowbrush
<i>Cercocarpus ledifolius</i>	curl leaf cercocarpus/mountain mahogany
<i>Purshia tridentata</i>	antelope bitterbrush

**Forbs**

<i>Astragalus adsurgens</i>	standing milkvetch
<i>A. canadensis</i>	canada milkvetch
<i>A. miser</i>	weedy milkvetch
<i>Hedysarum boreale</i>	northern sweetvetch
<i>Lupinus argenteus</i>	silvery lupine
<i>L. caudatus</i>	tailcup lupine
<i>L. laxiflorus</i>	spurred lupine
<i>L. lepidus</i>	pacific lupine
<i>L. leucophyllus</i>	velvet lupine
<i>L. polyphyllus</i>	washington lupine
<i>L. sericeus</i>	silky lupine, blue bonnet
<i>Oxytropis deflexa</i>	pendant pod crazyweed
<i>Thermopsis montana</i>	golden banner
<i>Vicia americana</i>	american vetch

## LITERATURE CITED

Abuzinadah, R.A. and D.J. Read. 1986. Utilization of peptides and proteins by ectomycorrhizal fungi. *New Phytol.* 103:481-493.

BK → Agee, J.K. 1993. *Fire ecology of Pacific Northwest forests.* Island Press, Washington, DC.

→ Arno, S.F. 1976. The historical role of fire on the Bitterroot National Forest. *US For. Ser. Res. Note RM-413.*

Arno, S.F. 1996. The concept: restoring ecological structure and process in ponderosa pine forests. In: Hardy, C.C. and S.F. Arno, eds. *The use of fire in forest restoration.* Gen. Tech. Rep. INT-GTR-341.

Arno, S.F., J.H. Scott, and M.G. Hartwell. 1995. Age-class structure of old growth ponderosa pine/douglas-fir stands and its relationship to fire history. *Res. Rep. INT-RP-481.*

Barrett, S.W. 1988. Fire suppression's effects on forest succession within a central Idaho wilderness. *W. J. Appl. For.* 3:76-80.

Bell, R.L. and D. Binkley. 1989. Soil nitrogen mineralization and immobilization in response to periodic prescribed fire in a loblolly pine plantation. *Can. J. For. Res.* 19:816-820.

Beuter, J. 1979. Forest fertilization and the economics of perpetual motion machines. pp. 4-13. In: *Symbiotic nitrogen fixation in the management of temperate forests,* Gordon, J.C., C.T. Wheeler, and D.A. Perry (eds). Oregon State University.

Binkley, D, K. Cromack, Jr., and R.L. Fredriksen. 1982. Nitrogen accretion and availability in some snowbrush ecosystems. *For. Sci.* 28:720-724.

✓ Binkley, D, P. Sollins, and W.B. McGill. 1985. Natural abundance of nitrogen-15 as a tool for tracing alder-fixed nitrogen. *Soil Sci. Soc. Am. J.* 49:44-447.

Boring, L.R., J.J. Hendricks, and M.B. Edwards. 1990. Loss, retention, and replacement of nitrogen associated with site preparation burning in southern pine-hardwood forests. pp. 145-153. In: *Fire and the environment: ecological and cultural perspectives: proceedings of an international symposium.* Gen. Tech. Rep. GTR SE-69.

✓ Bremer, E. and C. van Kessel. 1990. Appraisal of the nitrogen-15 natural-abundance method for quantifying dinitrogen fixation. *Soil Sci. Soc. Am. J.* 54:404-411.

- x Brown, J.K., S.F. Arno, S.W. Barrett, and J.P. Menakis. 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway-Bitterroot Wilderness. *Int. J. Wildland Fire*. 4:157-168.
- Brown, S. and A.E. Lugo. 1994. Rehabilitation of tropical lands: a key to sustaining development. *Rest. Ecol.* 2:97-111.
- Busse, M.D., P.H. Cochran, and J.W. Barrett. 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. *Soil. Sci. Soc. Am. J.* 60:1614-1621.
- Byram, G.M. 1959. Combustion of forest fuels. In: *Forest fire control and use*, K.P. Davis, ed. McGraw-Hill, New York.
- Cataldo, D.A., M. Haroon, L.E. Schrader, V.L. Youngs. 1975. Rapid colorimetric determination of nitrate in plant tissue by nitration of salicylic acid. *Commun. Soil Sci. Plant Anal.* 6:71-80.
- Choromanska, U. 1998. Influence of fire exclusion and carbon removal on soil nutrient cycling in ponderosa pine forest. In prep.
- Choromanska, U. and T.H. DeLuca. 1998. Immediate effects of soil heating under different moisture regimes on carbon and nitrogen dynamics in forest soils. In prep.
- Covington, W.W. and S.S. Sackett. 1992. Soil mineral nitrogen changes following prescribed burning in ponderosa pine. *For. Ecol. Mgmt.* 54:175-191.
- DeBell, D.S. and M.A. Rodwan. 1979. Growth and nitrogen relations of coppiced black cottonwood and red alder in pure and mixed plantings. *Bot. Gaz.* 140(Supplement):S97-S101.
- Delorit, R.J., L.J. Greub, and H.L. Ahlgren. 1984. *Crop production*. Prentice-Hall, Englewood Cliffs, New Jersey.
- DeLuca, T.H. and K. Zouhar. 1998. Effects of selection harvest and prescribed burning on soil nitrogen dynamics in ponderosa pine forests. *For. Ecol. Mgmt.* In review.
- Diaz-Ravina, M., A. Prieto, and E. Baath. 1996. Bacterial activity in a forest soil after soil heating and organic amendments measured by the thymidine and leucine incorporation techniques. *Soil Biol. Biochem.* 28:419-426.
- Dighton, J. E.D. Thomas, and P.M. Latter. 1987. Interactions between tree roots, mycorrhizas, a saprotrophic fungus and the decomposition of organic substrates in a microcosm. *Boil. Fert. Soil.* 4:145-150.

Edmonds, R.L., D. Binkley, M.C. Feller, P. Sollins, A. Abee, and D.D. Myrold. 1989. Nutrient cycling: effects on productivity of Northwest forests. pp 17-35. In: *Maintaining the long-term productivity of Pacific Northwest forest ecosystems*, D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R.F. Powers (eds). Portland, Oregon. Timber Press.

Feagley, S.E., M.S. Valdez, and W.H. Hudnall. 1994. Papermill sludge, phosphorus, potassium, and lime effect on clover grown on a mine soil. *J. Environ. Qual.* 23:759-765.

Fessenden, R.J. 1979. Use of actinorhizal plants for land reclamation and amenity planting in the USA and Canada. pp. 403-419. In: *Symbiotic nitrogen fixation in the management of temperate forests*, Gordon, J.C., C.T. Wheeler, and D.A. Perry (eds). Oregon State University.

Fiedler, C.E., S.F. Arno, C.E. Carlson, and M.G. Harrington. 1992. Management prescriptions for restoring biodiversity in inland northwest ponderosa pine-fir forests. *Northwest Envir. J.* 8:211-213.

Fischer, W.C. and A.F. Bradley. 1987. Fire ecology of Western Montana forest habitat types. US For. Ser. Gen. Tech. Rep. INT-223.

Funk, D.T., R.C. Schlesinger, and F. Ponder. 1979. Autumn-olive as a nurse plant for black walnut. *Bot. Gaz.* 140(Supplement):S110-S114.

Gardner, W.H. 1986. Water content. In: *Methods of soil analysis: Part 1--Physical and mineralogical methods*. A. Klute, (ed.). Soil Sci. Soc. Am., Madison, WI.

Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. In: *Methods of soil analysis: Part 1--Physical and mineralogical methods*. A. Klute, (ed.). Soil Sci. Soc. Am., Madison, WI.

Goldin, A. and T. Nimlos. 1977. Vegetation patterns on limestone and acid parent materials in the Garnet Mountains of Western Montana. *Northwest Sci.* 51:149-160.

Gonzalez-Sangregorio, M.V., M.C. Trasar-Cepeda, M.C. Leiros, F. Gil-Sotres, and F. Guitian-Ojea. 1991. Early stages of lignite mine soil genesis: changes in biochemical properties. *Soil Biol. Biochem.* 23:589-595.

Gosz, J.R. 1981. Nitrogen cycling in coniferous ecosystems. In: *Terrestrial nitrogen cycles*. F.E. Clark and T. Rosswall, eds. *Ecol. Bull.* 33:405-426.

Gratkowski, H.J. 1962. Heat as a factor in germination of seeds of *Ceanothus velutinus* var. *laevigatus*. Ph. D. thesis, Oregon State University, Corvallis, OR.

- Grier, C.C. 1989. Effects of prescribed springtime underburning on production and nutrient status of a young ponderosa pine stand. In: Multiresource management of ponderosa pine forests, proceedings, A. Teale, W.W. Covington, and R.H. Hamre, (eds.). US For. Ser. Gen. Tech. Rep. RM-185.
- Grove, T.S. and N. Malajczuk. 1992. Nodule production and nitrogen fixation (acetylene reduction) by an understory legume (*Bossiaea laidlawiana*) in *Ecucalyptus* forest. J. Ecol. 80:303-314.
- Gruell, G.E., W.C. Schmidt, S.F. Arno, and W.J. Reich. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana-implications for resource management. US For. Ser. Gen. Tech. Rep. INT-130.
- Harvey, A.E. 1994. Integrated roles for insects, diseases and decomposers in fire dominated forests of the inland western United States: past, present and future forest health. In: Assessing forest ecosystem health in the Inland Northwest, R.N. Sampson and D.L. Adams, eds. Forest Products Press, Bingham, NY.
- Harvey, A.E., R.T. Meurisse, J.M. Geist, M.F. Jurgensen, G.I. McDonald, R.T. Graham, and N. Stark. 1989. Managing productivity processes in the Inland Northwest--mixed conifers and pines. pp. 164-184. In: Maintaining the long-term productivity of Pacific Northwest forest ecosystems, D.A. Perry, R. Meurisse, B. Thomas, R. Miller, J. Boyle, J. Means, C.R. Perry, and R.F. Powers (eds). Portland, Oregon. Timber Press.
- Harris, G.R. and W.W. Covington. 1983. The effect of a prescribed fire on nutrient concentration and standing crop of understory vegetation in ponderosa pine. Can. J. For. Res. 13:501-507.
- Hedin, L.O., J.J. Armesto, and A.H. Johnson. 1995. Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. Ecol. 76:493-509.
- Hendricks, J.J., and L.R. Boring. 1992. Litter quality of native herbaceous legumes in a burned pine forest of the Georgia Piedmont. Canadian Journal of Forest Research. 22:2007-2010.
- Hobbs, N.T., and D.S. Schimel. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. Journal of Range Management. 37(5):402-405.
- Hungerford, R.D., M.G. Harrington, W.H. Frandsen, K.C. Ryan, and G.J. Niehoff. 1991. Influence of fire on factors that affect site productivity. US For. Ser. Gen. Tech. Rep. INT-280.

- Jonhnsn, D.W. 1995. Soil properties beneath ceanothus and pine stands in the Eastern Sierra Nevada. *Soil Sci. Soc. Am. J.* 59:918-924.
- Jurgensen, M.F., S.F. Arno, A.E. Harvey, M.J. Larsen, and R.D. Pfister. 1979. Symbiotic and nonsymbiotic nitrogen fixation in northern Rocky Mountain ecosystems. pp. 294-308. In: *Symbiotic nitrogen fixation in the management of temperate forests*, Gordon, J.C., C.T. Wheeler, and D.A. Perry (eds). Oregon State University.
- Jurgensen, M.F., A.E. Harvey, R.T. Graham, D.S. Page-Dumroese, J.R. Tonn, M.J. Larsen, and J.B. Jain. 1998. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. *For. Sci.* 43:234-251.
- Jurgensen, M.R., J.R. Tonn, R.T. Graham, A.E. Harvey, and K. Geier-Hayes. 1991. Nitrogen fixation in the forest soils of the Inland Northwest. pp. 101-109. In: *Proceedings-Management and productivity of western-montane forest soils*. Gen. Tech. Rep. INT-280.
- Keane, R.E, S.F. Arno, and J.K. Brown. 1990. Simulating cumulative fire effects in ponderosa pine/douglas-fir forests. *Ecology.* 71:189-203.
- Keeney, D.R. 1982. Nitrogen-availability indices. In: *Methods of soil analysis, Part 2, chemical and biological methods*. A.L. Page, R.H. Miller, and D.R. Keeney, eds. Soil Science Society of America book series, no. 9, Madison, WI.
- Keller, G. 1996. Utilization of inorganic and organic nitrogen sources by high-subalpine ectomycorrhizal fungi of *Pinus cembra* in pure culture. *Mycol. Res.* 100:989-998.
- \* Kenny, S.T. and R.L. Cuany. 1990. Nitrogen accumulation and acetylene reduction activity of native lupines on disturbed mountain sites in Colorado. *J. Range Management.* 43:49-51.
- Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrient and nitrogen cycling. *Ecology.* 75:2373-2383.
- Killingbeck, K.T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology.* 77:1716-1727.
- Kimmins, J.P. 1996. Importance of soil and role of ecosystem disturbance for sustained productivity of cool temperate and boreal forests. *Soil Sci. Soc. Am. J.* 60:1643-1654.
- Klemmedson, J.O. 1979. Ecological importance of actinomycete-nodulated plants in the western United States. *Bot. Gaz.* 140(Suppl.):S91-S96.
- Kogel-Knabner, I. 1993. Biodegradation and humification processes in forest soils. *Soil Biochem.* 8:101-136.



- Lackschewitz, C. 1991. Vascular plants of west-central Montana: identification guide book. US For. Ser. Gen. Tech. Rep. INT-277.
- Leach, M.K. and T.J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science*. 273:1555-1558.
- McNabb, D.H. and J.M. Geist. 1979. Acetylene reduction assay of symbiotic N<sub>2</sub> fixation under field conditions. *Ecol.* 60:1070-1072.
- \* Miller, R.E., D.L. Reukema, and T.A. Max. 1993. Size of Douglas-fir trees in relation to distance from a mixed red alder-Douglas-fir stand. *Can. J. For. Res.* 23:2413-2418.
- Monleon, V.J., K. Cromack Jr., and J.D. Landsberg. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Can. J. For. Res.* 27:369-378.
- Monnig, E. and J. Byler. 1992. Forest Health and ecological integrity in the Northern Rockies. US For. Ser. FPM Rep. 92-7.
- Moore, J.A., P.G. Mika, and J.L. Vander Ploeg. 1991. Nitrogen fertilizer response of Rocky Mountain douglas-fir by geographic area across the Inland Northwest. *West. J. Appl. For.* 6:94-98.
- Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York. 547pp.
- ✧ Nohrstedt, H. 1983. Natural formation of ethylene in forest soils and methods to correct results given by the acetylene reduction assay. *Soil Boil. Biochem.* 15:281-286.
- Noste, N.V. and C.L. Bushey. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. Gen. Tech. Rep. INT-239.
- O'Hara, K.L., R.S. Seymour, S.D. Tesch, and J.M. Guldin. 1994. Silviculture and our changing profession: leadership for shifting paradigms. *J. For.* 92:8-13.
- Oikarinen, M. 1996. Biological soil amelioration as the basis of sustainable agriculture and forestry. *Biol. Fertil. Soils.* 22:342-344.
- Ojima, D.S., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochem.* 24:67-84.
- \* Permar, T.A. and R.F. Fisher. 1983. Nitrogen fixation and accretion by wax myrtle (*Myrica cerifera*) in slash pine (*Pinus elliottii*) plantations. *Forest Ecol. and Mgt.* 5:39-46.

Pfister, R.D, B.L. Kovalchik, S.F. Arno, and R.C. Presby. 1977. Forest habitat types of Montana. US For. Ser. Gen. Tech. Rep. INT-34.

Pietikainen, J. and H. Fritze. 1993. Microbial biomass and activity in the humus layer following burning: short-term effects of two different fires. Can. J. For. Res. 23:1275-1285.

Quinos, P.M., P. Insausti, and A. Soriano. 1998. Facilitative effect of *Lotus tenuis* on *Paspalum dilatatum* in a lowland grassland of Argentina. Oecologia. 114:427-431.

Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant and Soil. 51:73-108.

Rogers, P. 1996. Disturbance ecology and forest management: a review of the literature. US For. Ser. Gen. Tech. Rep. INT-GTR-336.

Ryan, K.C. and N.V. Noste. 1985. Evaluating prescribed fires. In: Proceedings--symposium and workshop on wilderness fire. US For. Ser. Gen. Tech. Rep. INT-182.

Sanginga, N., S.K.A. Danso, and G.D. Bowen. 1992. Variation in growth, sources of nitrogen and N-use efficiency by provenances of *Gliricidia sepium*. Soil Biol. Biochem. 24:1021-1026.

\* Schoenberger, M.M., R.J. Volk, and C.B. Davey. 1989. Factors influencing early performance of leguminous plants in forest soils. Soil Sci. Soc. Am. J. 53:1429-1434.

\* Shearer, G. and D.H. Kohl. 1986. N<sub>2</sub>-fixation in field settings: estimations based on natural <sup>15</sup>N abundance. Aust. J. Plant Physiol. 13:699-756.

Sparling, G.P. 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. Aust. J. Soil Res. 30:195-207.

\* Sprent, J.I. and W.B. Silvester. 1973. Nitrogen fixation by *Lupinus arboeus* grown in the open and under different aged of *Pinus Radiata*. New Phytol. 72:99-1003.

Stevens, F.J. 1986. Cycles of soil. John Wiley & Sons, New York.

Stock, W.D., K.T. Wienand, and A.C. Baker. 1995. Impacts of invading N<sub>2</sub>-fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and <sup>15</sup>N natural abundance values. Oecologia. 101:375-382.

Tarrant, R.F. 1983. Nitrogen fixation in North American forestry: research and application. pp. 261-278. In: Biological nitrogen fixation in forest ecosystems:

foundations and applications. Gordon, J.C. and C.T. Wheeler, (eds). Martinus Nijhoff/Dr. W. Junk. Budapest.

Tilman, D. 1996. The benefits of natural disasters. *Science*. 273:1528.

Towne, E.G. and A.K. Knapp. 1996. Biomass and density responses in tallgrass prairie legumes to annual fire and topographic position. *Am. J. Bot.* 83:175-179.

Trowbridge, R. and F.B. Holl. 1992. Early growth of lodgepole pine after establishment of alsike clover-Rhizobium nitrogen-fixing symbiosis. *Can. J. For. Res.* 22:1089-1093.

Turvey, N.D. and P.J. Smethurst. 1983. Nitrogen fixing plants in forest plantation management. pp. 233-260. In: *Biological nitrogen fixation in forest ecosystems: foundations and applications*. Gordon, J.C. and C.T. Wheeler, (eds). Martinus Nijhoff/Dr. W. Junk. Budapest.

van Kessel, C., R.E. Farrell, J.P. Roskoski and K.M. Keane. 1994. Recycling of the naturally-occurring  $^{15}\text{N}$  in an established stand of *Leucaena leucocephala*. *Soil Biol. Biochem.* 26:757-762

Vitousek, P.M. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist*. 119:553-572.

Wade, G.L. and H.G. Halverson. 1988. Soil development under 22-year-old mixed hardwood, pine, and black locust plantation on a surface mine. In: *Mine drainage and surface mine reclamation*. Bureau of Mines Information Circular. IC-9184.

Walley, F.L., C. Van Kessel, and D.J. Pennock. 1996. Landscape-scale variability of N mineralization in forest soils. *Soil Biol. Biochem.* 28:383-391.

Waring, R.H. and W.H. Schlesinger. 1985. *Forest ecosystems: concepts and management*. Academic Press, New York and Toronto.

Weaver, R.W. and S.K.A. Danso. 1994. Dinitrogen fixation. pp. 1019-1046. In: *Methods of soil analysis: Part 2--microbiological and biochemical properties*. Weaver, R.W., J.S. Angle, and P.S. Bottomley, (eds). Soil Sci. Soc. Am., Madison, WI.

White, C.S. 1986. Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem. *Soil. Fert. Soils.* 2:87-95.

White, D.L., B.L. Haines, and L.R. Boring. 1988. Litter decomposition in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics. *Can. J. For. Res.* 18:54-63.

Willis, R.B., G.J. Schwab, and C.E. Gentry. 1993. Elimination of interferences in the colorimetric analysis of ammonium in water and soil extracts. *Commun. Soil Sci. Plant Anal.* 24:1009-1019.

Wright, H.A. and A.W. Bailey. 1982. *Fire ecology*. John Wiley & Sons, New York.

Youngberg, C.T. and A.G. Wollum. 1976. Nitrogen accretion in developing *Ceanothus velutinus* stands. *Soil Sci. Soc. Am. J.* 40:109-112.

Zeleznik, J.D. and J.G. Skousen. 1996. Survival of three tree species on old reclaimed surface mines in Ohio. *J. Environ. Qual.* 25:1429-1435.

Zouhar, K.A. 1997. Effects of selection harvest and prescribed burning on nitrogen availability in the mineral soil under ponderosa pine. Unpub. MS Thesis, University of Montana.