GROUNDCOVER CARBON AND NITROGEN CYCLING AND LEGUME NITROGEN INPUTS IN A FREQUENTLY BURNED MIXED PINE FOREST

by

SARA J. DRAKE

(Under the Direction of Rebecca R. Sharitz)

ABSTRACT

Southeastern pine forests are often managed with prescribed burning to promote a pine overstory. Soil texture may influence fire's effect on vegetation and nutrient cycling. My objectives were 1) to examine the effects of fire frequency and soil texture on groundcover plant carbon (C) and nitrogen (N) cycling by measuring their biomass and C and N tissue concentrations, 2) to assess legume N_2-fixation rates, and 3) to predict the long-term effects of different fire frequencies on groundcover N cycling. Grasses had significantly greater aboveground biomass and C (g/m^2) and N (g/m^2) in clayey than in sandy sites, but had significantly greater tissue C concentration (%) in sandy sites. Legumes showed significant interaction effects between soil texture and fire frequency for aboveground tissue C (g/m^2) and N (g/m^2), biomass, and N_2-fixation activities. These findings suggest that soil texture can influence fire effects on ground layer biomass and nutrient cycling.

INDEX WORDS: Nitrogen, Ground layer biomass, N_2-fixation, Fire frequency, Soil texture, Stella model

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DEDICATION

This thesis is dedicated to my family – Mary, Eric, Jim, Ruth and Annie – for their encouragement and support. Special thanks to my mom for sharing her wisdom.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

Community or ecosystem characteristics, such as species diversity, plant productivity and nutrient cycling, can be greatly impacted by disturbances (Godron and Forman, 1983). Disturbances include some environmental fluctuations and destructive events, despite whether or not they are considered “normal” for a specific ecosystem (White and Pickett, 1985). The sum of all disturbance types through time, including intensity and frequency, is the disturbance regime (Godron and Forman, 1983). Fire, historically caused primarily by lightning, but also by indigenous populations, is a common disturbance in southeastern USA pine forests (Ware et al., 1993). Fire intensity, frequency and type, season of burn, and predictability, make up the fire regime (Christensen, 1985). Burn frequency, in particular, is an important aspect of the fire regime because of its influence on plant species composition (Glitzenstein, et al., 2003). Studies have shown that a short fire return interval (1 to 3 years) can sustain the high species richness that is typical of the ground layer in southeastern longleaf pine forests (Lewis and Harshbarger, 1976; Walker and Peet, 1983; Waldrop et al., 1992; Glitzenstein, et al., 2003). Although the pre-European burn frequency is unknown, it is thought that burning may have occurred as often as once every one to three years (Frost, 1998).

Longleaf pine forests evolved under a disturbance regime that included fire (Christensen, 1981; Ware et al., 1993). However, the arrival of Europeans into the region around 1700 (Martin and Boyce, 1993) eventually led to an alteration of the natural fire regime and the addition of anthropogenic disturbances, such as logging, commercial planting of loblolly pine, and agriculture (Hainds et al., 1999; Wilson et al., 1999; Provencher et al., 2001). Fire suppression in these forests began in the 1950's (Martin and Boyce, 1993) and has had numerous negative impacts, further contributing to a reduction in longleaf pine dominance from 37 million to less than 1.2 million ha (Brockway and Lewis, 1997). As a result, much of the longleaf pine forest has converted to hardwoods, shrubs, and more aggressive pines (Christensen, 1981; Ware et al., 1993; Brockway and Lewis, 1997). These shrubs and trees often replace herbaceous ground layer vegetation (Glitzenstein, et al., 2003), which serves as a reservoir for biological diversity (Outcalt, et al., 1999). Fire suppression has also led to an accumulation of surface litter, which can increase the risk of high intensity and potentially destructive wildfires as well as contribute to the immobilization of soil nitrogen and other nutrients necessary for plant growth (Brockway and Lewis, 1997).

Primary productivity is one of the major forces driving ecosystem function by supplying resources to consumers and by participating in the regulation of water and nutrient cycles (Roy and Saugier, 2001). As such, it is a fundamental characteristic of terrestrial ecosystems (Roy and Saugier, 2001) that may reflect ecosystem vitality (Mitchell et al., 1999; Day, et al., 2001). The importance of primary productivity in ecosystems makes it an appropriate measure for examining the effects of fire on ground layer plants. In southeastern longleaf pine forests, annual net primary productivity is roughly proportional to standing crop (ground layer) biomass. It is well documented that fire strongly impacts productivity (Raison, 1979; Dudley and Lajtha, 1993; Ojima et al., 1994; Wilson et al., 2002) as does soil nutrient availability (Dudley and Lajtha, 1993; Liu and Muller, 1993). Many studies have examined productivity in response to these variables, but relatively few have studied productivity patterns across landscapes (but see Kirkman et al., 2001 and Mitchell et al., 1999) and to my knowledge no previous study has examined the effects of fire frequency on productivity of ground layer vegetation in southeastern forests (but see Wilson et al., 2002).

Although fire frequency can affect the composition and productivity of herbaceous species, there is evidence suggesting that the availability of soil moisture and nutrients may have a stronger impact on species biomass and composition. One study showed that species composition was more closely associated with soil moisture than with fire frequency (Glitzenstein et al., 2003). In addition, ground layer biomass has been shown to be highest in wet-mesic sites compared with xeric sites in southeastern longleaf pine savannas (Mitchell et al., 1999; Kirkman et al., 2001) and in sites with higher soil net N mineralization rates (Reich et al., 2001).

Nitrogen is the nutrient that most limits terrestrial productivity in the temperate region (Vitousek, 1982; Pastor et al., 1984; Reich et al., 1997; Wilson et al., 2002) and is also one of the nutrients most impacted by fire (Neary et al., 1999). As a result, systems dominated by fire often have low levels of N (Turner et al., 1997; Wilson et al., 1999; Wilson et al., 2002). In the long-term, fire promotes N release and losses through volatilization, erosion and leaching (Van Lear and Johnson, 1983; Hainds et al., 1999; Neary et al., 1999). However, in the short-term, dead plants contribute a pulse of nutrients to the system, which are then available for use by new plants (Neary et al., 1999; Reich et al., 2001). These new plants quickly reestablish after a burn, resulting in productivity levels that are higher than before the fire (Raison, 1979; Dudley and Lajtha, 1993).

Fire-adapted, native herbaceous legumes may also contribute to increased productivity following fire (Cushwa et al., 1966; Van Lear and Johnson, 1983; Hiers et al., 2000). Through N_2-fixation, they may replenish or even exceed N lost due to burning (Hendricks and Boring, 1992, 1999; Caldwell et al., 2002). Few attempts have been made to quantify the relative abundance of legumes (but see Hainds et al., 1999) or the extent of N_2-fixation by legumes in southern forests (but see Hendricks and Boring, 1999), and to my knowledge no study has examined these measures under different fire frequencies.

The study of fire's effects on N inputs by legumes and C and N cycling of ground layer plants (herbaceous plants and woody stems < 1 cm basal diameter) may be more informative when soil texture is considered. Soil texture affects both soil moisture and nutrient availability, and there may be interactions between soil texture and fire frequency in mixed pine forests. Because sandy sites have lower levels of soil nutrients and moisture, plants in such sites may be more sensitive to frequent burning than those in clayey sites. Therefore, it may be important to consider soil texture when implementing a prescribed fire frequency if the goal is to increase productivity of ground layer plants.

Little is known about pre-European fire disturbance regimes, and the appropriate frequency with which prescription fire should be implemented can be debated. Knowledge of the effects of different fire frequencies in sites with different soil textures can aid land managers who use prescribed burning as a management tool. In addition, the use of models to predict the short- and long-term effects of fire frequency on N transformations and ground layer biomass may prove to be valuable for ecosystem management.

1.2 Purpose of Study

The purpose of this study was to examine the effects of fire frequency and underlying soil texture on peak aboveground ground layer biomass (~ productivity) and C and N cycling by ground layer plants and to predict the long-term effects of different fire frequencies on N transformations and ground layer biomass. These objectives were met by obtaining above- and belowground biomass and tissue C and N concentrations of ground layer plants and N_2-fixation rates of herbaceous legumes on sites with different fire frequencies and underlying soil textures. These data were then used to parameterize an ecosystem compartment model that examines the effects of different fire frequencies on N transformations over the long-term (25 years).

1.3 Literature Cited

Brockway, D.G. and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167-183.

Caldwell, T.G., Johnson, D.W. and W.W. Miller. 2002. Forest floor carbon and nitrogen losses due to prescription fire. *Soil Science Society of America Journal* 66: 262-267.

Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. In: Mooney, H.A., T.M. Bonnicksen, N.L. Christensen, J.E. Lotan and W.A. Reiners (Eds.). Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26, pp. 112-136.

Christensen, N.L. 1985. Shrubland fire regimes and their evolutionary consequences. In: Pickett, S.T.A. and P.S. White (Eds.). The ecology of natural disturbance and patch dynamics. Academic Press, Inc. New York, New York, USA, pp. 86-97.

Cushwa, C.T., E.V. Brender and R.W. Cooper. 1966. The response of herbaceous vegetation to prescribed burning. USDA Forest Service Research Note SE-53. 2 pp.

Day, F.P., E.R. Crawford and J.J. Dilustro. 2001. Aboveground plant biomass change along a coastal barrier island dune chronosequence over a six-year period. *Journal of the Torrey Botanical Society* 128: 197-207.

Dudley, J.L. and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *American Midland Naturalist* 130: 286-298.

Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: A first approximation. Tall Timbers Fire Ecology Conference Proceedings. 20: 70-81.

Glitzenstein, J.S., D.R. Streng and D.D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. *Natural Areas Journal* 23: 22-37.

Godron, M. and R.T.T. Forman. 1983. Landscape modification and changing ecological characteristics. In: Mooney, H.A., and M. Godron, (Eds.). Disturbance and Ecosystems. Springer-Verlag, New York, New York, USA, pp. 12-28.

Hainds, M.J., R.J. Mitchell, B.J. Palik, L.R. Boring and D.H. Gjerstad. 1999.

Distribution of native legumes (Leguminoseae) in frequently burned longleaf pine (Pinaceae)-wiregrass (Poaceae) ecosystems. *American Journal of Botany* 86: 1606-1614.

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.

Hendricks, J.J. and L.R. Boring. 1999. N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113: 167-177.

Hiers, J.K., Wyatt, R. and R.J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? *Oecologia* 125: 521-530.

Lewis, C.E. and T.J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina Coastal Plain. *Journal of Range Management* 29: 13-18.

Liu, Y. and R.N. Muller. 1993. Above-ground net primary productivity and nitrogen mineralization in a mixed mesophytic forest of eastern Kentucky. *Forest Ecology and Management* 59: 53-62.

Kirkman, L.K., R.J. Mitchell, R.C. Helton and M.B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88: 2119-2128.

Martin, W.H. and S.G. Boyce. 1993. Introduction: The southeastern setting. In: Martin, W.H., S.G. Boyce and A.C. Echternacht (Eds.). Biodiversity of the southeastern United States: Lowland terrestrial communities. John Wiley & Sons, Inc. New York, New York, USA, pp. 1-46.

Mitchell, R.J., L.K. Kirkman, S.D. Pecot, C.A. Wilson, B.J. Palik and L.R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. I. Aboveground net primary productivity. *Canadian Journal of Forest Research* 29: 743-751.

Neary, D.G., C.C. Klopatek, L.F. DeBano and P.F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51-57.

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. *Biogeochemistr*y 24: 67-84.

Outcalt, K.W., M.E. Williams and O. Onokpise. 1999. Restoring *Aristida stricta* to *Pinus palustris* ecosystems on the Atlantic Coastal Plain, U.S.A. *Restoration Ecology* 7: 262-270.

Pastor, J., J.D. Abor, C.A. McClaugherty and J.M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256-268.

Provencher, L., A.R. Litt, D.R. Gordon, H.L. Rodgers, B.J. Herring, K.E.M. Galley, J.P. McAdoo, S.J. McAdoo, N.M. Gobris and J.L. Hardesty. 2001. Restoration fire and hurricanes in longleaf pine sandhills. *Ecological Restoration* 19: 92-98.

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.

Reich, P.B., D.F. Grigal, J.D. Aber and S.T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78: 335-347.

Reich, P.B., D.W. Peterson, D.W. Wedin and K. Wrage. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82: 1703-1719.

Roy, J. and B. Saugier. 2001. Terrestrial primary productivity: Definitions and milestones. In: Roy, J., B. Saugier and H.A. Mooney, (Eds.). Terrestrial Global Productivity. Academic Press, San Diego, California, USA, pp. 1-6.

Turner, C.L., J.M. Blair, R.J. Schartz and J.C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. *Ecology* 78: 1832-1843.

Van Lear, D.H. and V.J. Johnson. 1983. Effects of prescribed burning in the southern Appalachian and upper Piedmont forests: a review. Clemson University Forestry Bulletin Number 36.

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

Waldrop, T.A., D.L. White and S.M. Jones. 1992. Fire regimes for pine-grassland communities in the southeastern United States. *Forest Ecology and Management* 47: 195-210.

Walker, J. and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55: 163-179.

Ware, S., C. Frost and P.D. Doerr. 1993. Southern Mixed Hardwood Forest: The former Longleaf Pine Forest. In: Martin, W.H., S.G. Boyce and A.C. Echternacht (Eds.). Biodiversity of the Southeastern United States: Lowland terrestrial communities, John Wiley & Sons, Inc., New York, New York, USA. 447-493.

White, P.S. and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction.

In: Pickett, S.T.A. and P.S. White (Eds.). The ecology of natural disturbance and patch dynamics. Academic Press, Inc. New York, New York, USA, pp. 3-9.

Wilson, C.A., R.J. Mitchell, J.J. Hendricks and L.R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. II. Nitrogen dynamics. *Canadian Journal of Forest Research* 29: 752-760.

Wilson, C.A., R.J. Mitchell, L.R. Boring and J.J. Hendricks. 2002. Soil nitrogen dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. *Soil Biology and Biochemistry* 34: 679-689.

CHAPTER 2

GROUNDCOVER CARBON AND NITROGEN CYCLING AND LEGUME NITROGEN INPUTS IN A FREQUENTLY BURNED MIXED PINE FOREST

2.1 Abstract

Many mixed pine forests in the southeastern United States undergo frequent (1-3 years) prescribed burning to promote a pine savanna with reduced hardwood understory. Underlying soil texture may influence the nature and/or extent of fire's effect on vegetation and nutrient cycling. My objectives were to examine the effects of fire frequency (2-year versus 4-year) and soil texture (clayey versus sandy) on ground layer carbon (C) and nitrogen (N) pools by measuring the biomass of ground layer plant species and their C and N tissue concentrations, as well as herbaceous legume N inputs via N_2-fixation. Mean belowground biomass was significantly greater on sandy than on clayey sites, but did not differ statistically between 2- and 4-year burn sites. Total aboveground mean biomass did not differ significantly between the two fire frequencies or between the soil textures, but grasses had significantly greater aboveground biomass in clayey than in sandy sites. Grasses also had significantly greater C (g/m^2) and N (g/m^2) in clayey than in sandy sites. In contrast, grasses had significantly greater C (%) in sandy sites. Legumes showed significant interaction effects between soil texture and fire frequency for aboveground tissue C (g/m^2) and N (g/m^2), above- and belowground biomass, and N_2-fixation activities. These results suggest that soil texture can influence fire's effects on ground layer vegetation composition and nutrient cycling, and should be considered when choosing prescribed fire frequency for managing southeastern mixed pine forests.

Key words: Nitrogen, ground layer biomass, herbaceous legumes, fire frequency, soil texture, mixed pine forests

2.2 Introduction

Prior to European settlement, longleaf pines (*Pinus palustris* Miller) dominated the vegetation of the southeastern United States Coastal Plain (Ware et al., 1993; Brockway and Lewis, 1997; Wilson et al., 1999; Heuberger and Putz, 2003). These forests evolved under a disturbance regime that included fires ignited primarily by lightning, but also by indigenous populations (Ware et al., 1993). With the arrival of Europeans in the 1700's came extensive harvesting, which, in addition to fire suppression beginning in the 1950's (Martin and Boyce, 1993), contributed to a 97 % reduction in area dominated by longleaf pine by the late 1980's (Brockway and Lewis, 1997; Glitzenstein et al., 2003). Today, much of the area along the southeastern Coastal Plain-Piedmont Fall Line is a mixed pine-oak-hickory forest (Skeen et al., 1993). Recently, land managers in the Southeast have focused their attention on promoting a longleaf pine dominated overstory, in part, because it is the preferred habitat of the federally endangered red-cockaded woodpecker (USAIC, 2001). Although little is known about the pre-European burn regime, fire frequency is believed to have ranged from once every one to three years (Frost, 1998). Since different fire frequencies can differentially effect the pine-hardwood vegetation (Whelan, 1995), an understanding of the effects of different fire frequencies may be necessary to restore a fire regime that promotes pine-dominated forests.

It is well documented that fire can have a short-term stimulatory effect on the standing crop biomass of herbaceous species, particularly in grasslands and pine savannas (Raison, 1979; Schoch and Binkley, 1986; Dudley and Lajtha, 1993; Brockway and Lewis, 1997; Wilson et al., 2002). Studies show that grasses and legumes, especially, are stimulated by fire; for example, annual or biennial burning has been shown to result in domination by grasses in ground layer communities of longleaf pine forests (Glitzenstein et al., 2003). Similarly, *Andropogon* spp. dominated the ground layer of longleaf pine forests in the western Gulf Coastal Plain when a biennial burn regime was imposed (Brockway and Lewis, 1997). Grasses, among other plant groups, may respond favorably to burning because, in addition to producing copious seeds, they are capable of storing nutrients in belowground structures and resprouting from meristems following fire (Brockway and Lewis, 1997). In addition to grasses, legume biomass (Dudley and Lajtha, 1993) and relative abundance (Cushwa et al., 1966; Van Lear and Johnson, 1983; Hendricks and Boring, 1999, 1992; Hiers et al., 2000; Caldwell et al., 2002) also may increase following fire. Such an increase may be due to the ability of legumes to fix N_2, and thus colonize disturbed and potentially nitrogen-deficient sites (Towne and Knapp, 1996). The removal of ground layer plants by burning is ideal for germination of many legume species (whose seeds often require scarification by fire) because competition for light, nutrients and water is reduced (Hendricks and Boring 1999). Many legumes are also perennials and resprout vigorously from underground structures following fire (Towne and Knapp, 1996). In contrast, frequent burning is thought to result in a decrease in biomass of woody ground layer species (Reich et al., 2001; Glitzenstein et al., 2003) that may compete with herbaceous plants.

Burning can also indirectly impact productivity of herbaceous species by altering nutrient cycles. Following fire, a short-term nutrient pulse may occur (Reich et al., 2001), which can be partially attributed to the release of nutrients immobilized in litter and soil organic matter (Brockway and Lewis, 1997). However, these nutrients may be in an organic form that is not readily available to plants (Christensen, 1977). Nitrogen availability to plants is controlled by rates of net N mineralization (Liu and Muller, 1993; Robertson et al., 1999); but in southeastern pine forests, soil moisture availability may be more important to plant productivity than N availability (Wilson et al., 1999). An inverse relationship has been observed between percent soil moisture and net N mineralization in a longleaf pine forest (Wilson et al., 1999). In addition, ground layer biomass has been shown to be greatest in wet-mesic longleaf pine sites (where N mineralization was lower; Mitchell et al., 1999), thus providing evidence that soil moisture is a more dominant factor than N availability in controlling patterns of productivity in these ecosystems.

Although a short-term pulse of nutrients may occur after fire (Reich et al., 2001), in the long-term, fire is thought to result in a loss of N from ecosystems (Raison, 1979; Ojima et al., 1994; Reich et al., 2001). Temperate ecosystems are generally N limited (Vitousek, 1982; Pastor et al., 1984; Reich et al., 1997) and this limitation is exacerbated in frequently burned sites, where the loss of N through combustion, volatilization and leaching is common (Van Lear and Johnson, 1983; Hainds et al., 1999; Neary et al., 1999). Volatilization alone may be responsible for the loss of as much as 10-40 kg N ha^{-1} y^{-1} in ecosystems that are frequently burned (Ojima et al., 1987; Reich et al., 2001). Through N_2-fixation, native herbaceous legumes may play an important role in the nitrogen cycle of burned forests by replenishing, or even exceeding the N that is lost due to burning (Hendricks and Boring, 1992, 1999; Caldwell et al., 2002; Hiers et al., 2003). However, the extent of N_2-fixation by legumes in southeastern forests has not been emphasized (but see Hendricks and Boring, 1999; Hiers et al. 2003) and to my knowledge, no study has examined this under different fire frequencies.

N_2-fixation by legumes contributes to ecosystem N cycles, but in order to estimate the specific contributions of ground layer plants, including non-legumes, to C and N cycles, it is necessary to determine tissue concentrations of C and N. Perennial species in longleaf pine forests often allocate a greater proportion of their C and N stores (Wilson et al., 1999) and biomass (Hiers et al., 2003) to belowground parts, thus allowing them to resprout quickly and to protect nutrients from being lost during fire. As has been shown in a Minnesota Sand Plain, greater allocation of biomass to belowground structures could also be a response to a reduction in nutrient (Reich et al., 2001) or water availability. Although patterns of biomass and plant tissue C and N have been well studied in response to availability of soil nutrients and water, no previous study has examined the effects of fire frequency and soil texture on ground layer biomass in southeastern forests (but see Wilson et al., 2002). Fire's effects on ecosystems may be greater in sites with low soil fertility (Wilson et al., 2002). Therefore, examining these effects in sites with different underlying soil textures could reveal differences in patterns of C and N cycling, through changes in plant biomass, tissue C and N concentrations and legume N_2-fixation.

The purpose of this study was to examine the effects of fire frequency and underlying soil texture on biomass and C and N cycling by ground layer plants in southeastern mixed pine forests. This was achieved by measuring above- and belowground biomass and tissue C and N concentrations of ground layer plants and N_2-fixation rates of herbaceous legumes in sites with different fire frequencies and underlying soil textures. Since productivity in southeastern forests is roughly proportional to peak standing crop of ground layer biomass (Kirkman et al., 1999), overstory biomass was not considered in this study.

2.3 Materials and Methods

2.3.1 *Site description*

The study sites are mixed pine-hardwood forests located at Fort Benning, Georgia (32º33' N, 85º W), a 73,650-hectare military base situated on the Fall Line in the Upper Coastal Plain region of the southeastern United States. The climate is characterized as humid temperate with most summer days reaching temperatures greater than 90º F and mean winter temperature of 37º F. Mean annual precipitation is 129.5 cm (USAIC, 2001). Two geologic provinces characterize the region: Sand Hills and Southern Coastal Plain. Soils include Troup sandy loams, Nankin sandy loams, Lakeland sands and Siley loamy sands (Johnson, 1983).

Forests at Fort Benning are managed with prescribed burning to promote longleaf pine savannas, preferred habitat of the federally endangered red cockaded woodpecker (USAIC, 2001). The majority of forested areas are burned on a 3-year rotation, but for purposes of this study, sites were burned on either a 2- or 4-year burn cycle. Sites used in this study also had a range of soil textures (4.5% clay to 48.5% clay).

2.3.2 *Study design*

This study was part of a larger investigation focusing on the effects of disturbance (prescribed burning, military training use and forest thinning) on forest communities at Fort Benning (Dilustro et al., 2002). Forests at Fort Benning have typically been managed with prescribed burning on a 3-year rotation (for about 20 years). For this study, half of the sites were burned on a 2-year rotation and the other half were burned on a 4-year rotation (2-year sites burned in 2002; 4-year sites burned in 2004). I selected 16 sites (400 m × 400 m); four sites had sandy soils (< 13% clay) and a 2-year fire frequency; four had sandy soils and a 4-year fire frequency; four had clayey (> 19% clay) soils and a 2-year fire frequency; and four had clayey soils and a 4-year fire frequency. I sampled at one randomly chosen location in each of 12 subplots (100 m × 100 m) arranged in a grid within each site.

2.3.3 *Vegetation sampling*

Vegetation was sampled in July and early August 2002 and 2003 because peak biomass of herbaceous plants occurs during these months. Four-year burn sites were burned in 2000 and 2-year burn sites were burned in 2002; therefore, in 2002 (the first year of sampling) it had been two years since burning for the 4-year burn sites and 2-year burn sites had recently been burned. In 2003, it had been one year since burning for the 2-year burn sites and three years since burning for the 4-year burn sites. To obtain estimates of ground layer biomass, I placed a 0.64 m^2-circular vegetation plot (0.58 m^2 in 2003) in the center of each of the 12 subplots (12 subplots × 16 sites = 192 total vegetation plots sampled per year). Vegetation was clipped at ground level and sorted into categories (ferns, grasses, legumes, other forbs, woody plants <1 cm stem diameter at base and standing dead biomass). In 2003, the harvested legumes were separated into species (nomenclature follows that of Radford et al., 1968). All plant material was dried to constant mass at 60° C and weighed. In 2002, randomly chosen sub-samples of the forbs, grasses and legumes were ground in a Wiley and Spex mill and analyzed on a Carlo Erba NA 1500 elemental analyzer for C and N content. In 2003, C and N analysis was repeated, but only for the legumes.

Belowground biomass was measured by taking a 5 cm diameter soil core to a 10 cm depth within each circular vegetation plot. Roots and root nodules (on the legumes) were removed from the soil by hand and washed with water over a 2 mm sieve. Root and nodule mass were determined by drying them at 70º C for 24 hours and weighing them. Root samples were then ground and analyzed for C and N content as above.

2.3.4 *Acetylene reduction*

The acetylene reduction method is an indirect, yet sensitive technique that is commonly used for measuring N_2-fixation (Kenny and Cuany, 1990) and is based on the principle that acetylene (C_2H_2) is reduced to ethylene (C_2H_4) by the N_2-fixation enzyme, nitrogenase (Drevon, 1989). Gas chromatography is then employed to compare the amount of ethylene produced in a sample to an ethylene standard. This amount of acetylene reducing activity (ARA; nmol hr^{-1} g^{-1} nodule dry mass) is then divided by a theoretical ratio of moles of acetylene reduced per mole of N_2 fixed (3:1) to determine the amount of N_2 fixed (Myrold et al., 1999).

The accuracy of the acetylene reduction assay has been criticized as underestimating nitrogenase activity due to the disturbance of nodules and to an acetylene-induced decline in nitrogenase activity occurring within the first 30-60 minutes of root exposure to acetylene (Minchin, 1983; 1986). Although the assay may be less useful for measuring total nitrogenase activity, it can still be used to obtain a general estimate and it is considered a valuable measure of relative nitrogenase activity (Vessey, 1994).

I used the acetylene reduction method to measure N_2-fixation by herbaceous legumes from eight sites across Fort Benning that undergo different prescribed fire frequencies and have contrasting soil textures. The three most abundant legume species in each site at the time of assay were selected for N_2-fixation measurements. In total, these species were *Cassia nictitans* (L.), *Desmodium marilandicum* [(L.) DC], *Desmodium paniculatum* [(L.) DC], *Desmodium viridiflorum* [(L.) DC], *Lespedeza hirta* [(L.) Hornemann] and *Tephrosia virginiana* [(L.)

Persoon]. In addition to the acetylene reduction assay, aboveground, belowground and nodule biomass were obtained to estimate ecosystem-level N_2-fixation by these herbaceous legumes.

The acetylene reduction assays were performed from 14 July through 18 July 2003. Ten individuals of each species were chosen at random and excavated to a 30 cm radius and 15 cm depth (Hendricks and Boring, 1999). Small (~ 2.5 cm) fragments of nodulated roots were excised, placed into 10 ml glass test tubes, and capped with rubber serum stoppers. Acetylene generated from calcium carbide and stored in a gas sampling bag was injected into the test tubes (~ 10% of atmosphere) and the samples were allowed to incubate for 30 minutes. The reaction was terminated by transferring the samples to 10 ml Vacutainer tubes. Subsamples (1 ml) from the Vacutainers were analyzed on a Varian, Inc. gas chromatograph, equipped with a flame ionization detector. Operating parameters included a detector temperature of 160° C, an injector temperature of 135° C, 18 ml/min helium carrier gas flow rate, and a stainless steel column packed with Porapak N. An ethylene standard was obtained by injecting 1 ml of pure ethylene into a 1 liter Mason jar fitted with a rubber septum. The Vacutainers gave off a small amount of ethylene contamination, which was subtracted to obtain the final ARA.

Following this assay, the nodules were dried at 70° C to a constant mass, and weighed. Ten additional individuals of each legume species were randomly chosen from each site and excavated for estimation of biomass. These plants were separated into above- and belowground material and nodules, dried at 70º C, and weighed. This biomass (aboveground and nodule) was used to predict the nodule biomass of legumes of the same species from the 2003 ground layer biomass harvests (circular vegetation plots) according to the following:

$$\frac{\text{Aboveground biomass (g)}}{\text{Nodule biomass (g)}} = \frac{\text{Aboveground biomass (circular plots g/m}^2\text{)}}{\text{Predicted nodule biomass (circular plots g/m}^2\text{)}}$$

Using the theoretical ratio of acetylene reduced to N_2 fixed of 3:1, an ecosystem-level contribution of N by legumes (g $m^{2\ -1}$ yr^{-1}) was estimated by multiplying the predicted nodule biomass by ARA values. This overall value for N_2-fixation was determined by using the mean ARA value of the three *Desmodium* spp. examined to estimate N_2-fixation rates for other *Desmodium* spp. found in the vegetation plots; the ARA value for *L. hirta* was used to estimate N_2-fixation rates for other *Lespedeza* spp.; and the ARA for *T. virginiana* was used to estimate N_2-fixation rates for other *Tephrosia* spp. Finally, the mean ARA value for all six legume species examined was used to estimate stand-level N_2-fixation rates for the remaining eight legume genera found in the vegetation plots.

2.3.5 *Data analysis*

Differences in mean aboveground biomass between fire frequency treatments and soil texture were determined using a mixed model analysis of variance (ANOVA) procedure with year, site, fire and texture as fixed effects and subplot as a random effect (PROC MIXED; SAS, 2000). Statistically significant differences between plant groups were determined using the Bonferroni test of multiple pairwise comparisons. Differences in belowground biomass, plant C and N tissue concentrations, and legume N_2-fixation rates and above- and belowground biomass were determined using ANOVA. Statistically significant differences were accepted at $\alpha \leq 0.05$. ANOVA tables are in Appendix A.

2.4 Results

2.4.1 *Biomass and tissue C and N concentration*

Mean aboveground biomass did not differ between the two fire frequencies or between the soil textures in either year, although clayey sites tended to have greater biomass than sandy sites and 2-year burn sites had greater biomass than 4-year burn sites (Figs. 2.1a,b). However, when aboveground mean biomass of the plant groups was examined, grasses had significantly greater biomass in clayey than in sandy sites for both years ($P = 0.03$; Fig. 2.2). None of the other plant groups exhibited significant differences between fire treatments or soil textures. On average, for both years, woody species made up the greatest proportion of the total ground layer biomass (32%), followed by forbs (28%), grasses (21%), standing dead biomass (13%), legumes (4%) and ferns (2%). In contrast to the aboveground biomass measure, which included only ground layer vegetation, belowground biomass included ground layer roots as well as tree and shrub roots and was a measure at the stand level. Mean belowground biomass was significantly greater on sandy than on clayey sites in 2002 ($P = 0.007$) and in 2003 ($P = 0.03$) (Fig. 2.3a), but did not differ statistically between 2- and 4-year burn sites (Fig. 2.3b).

Carbon and N tissue concentrations (%) of forbs, grasses and legumes (Figs. 2.4a,b) were converted to stand-level biomass estimates of C and N pools (g/m^2) for these plant groups (Figs. 2.4c,d) by multiplying the percent concentration by the biomass (g/m^2). In 2002, grass aboveground tissues had significantly greater C (%) on sandy than on clayey sites ($P = 0.0006$) and significantly greater standing crop of N (g/m^2) and C (g/m^2) on clayey than on sandy sites ($P = 0.0112$ and $P = 0.01$, respectively). Legume aboveground tissue N (g/m^2) and C (g/m^2) showed significant interaction effects between soil texture and fire frequency ($P < 0.0001$ and $P = 0.0002$, respectively). Both legume N (g/m^2) and C (g/m^2) were greater on clayey sites with a 2-year fire frequency and on sandy sites with a 4-year fire frequency. Although legume tissue N concentration (%) did not differ between fire treatments or soil textures, it was higher than that of grasses and forbs. Carbon and N in woody leaves and stems did not differ statistically between soil textures or fire frequencies (data not shown). Finally, roots had significantly greater C (g/m^2) and N (g/m^2) in sandy than in clayey sites ($P = 0.006$ and $P = 0.01$, respectively; Table 2.1).

In 2003, legume aboveground tissue N concentration (%) showed a significant interaction effect between soil texture and fire frequency ($P = 0.007$) as did standing crop N (g/m^2) and C (g/m^2) pools ($P < 0.0001$ and $P < 0.0001$, respectively). These interaction patterns were the same as for legumes in 2002, with greater tissue nutrients on clayey sites with a 2-year fire frequency and on sandy sites with a 4-year fire frequency. Legumes were sorted by species in 2003 and tissue C and N concentrations and pools were determined. *Cassia nictitans* had significantly greater N concentrations (%) on 4-year than on 2-year burn sites (Fig. 2.5a; $P = 0.02$) and significantly greater C (g/m^2) and N (g/m^2) on sandy than on clayey sites (Fig. 2.5 c,d; $P = 0.01$ and $P = 0.02$, respectively). *Desmodium paniculatum* also had significantly greater N (%) on 4-year than on 2-year burn sites (Fig. 2.5a; $P = 0.01$) but was not observed in sandy sites with a 2-year fire frequency, so no interaction effect could be examined. *Desmodium marilandicum* showed a significant interaction effect between soil texture and fire frequency for tissue C (g/m^2) and N (g/m^2) (Fig. 2.5 c,d; $P = 0.02$ and $P = 0.01$, respectively), with greater C (g/m^2) and N (g/m^2) on both clayey and sandy sites with a 2-year than with a 4-year fire frequency; however, the magnitude of the difference was greater on sandy than on clayey sites. Finally, *D. viridiflorum* and *L. hirta* did not show any significant differences in tissue C and N concentrations between soil textures or fire frequencies. *Tephrosia virginiana* was not present in clayey sites with a 2-year fire frequency or in sandy sites with a 4-year fire frequency, so no differences between burn treatments or soil textures could be examined.

2.4.2 *N_2-fixation assay and biomass of legumes*

A significant interaction effect between soil texture and fire frequency was found for legume acetylene reduction activity (ARA) (nmol hr^{-1} mg nodule dry $mass^{-1}$) (total legume input) (Fig. 2.6a; $P < 0.0001$). In clayey sites, ARA was greater with a 2-year fire frequency; whereas, in sandy sites, ARA was greater with a 4-year fire frequency. *Cassia nictitans* also showed a significant interaction effect between fire frequency and soil texture and the pattern was the same as for legumes overall ($P = 0.0013$) (Fig. 2.6b). None of the other species differed significantly between burn treatments or soil textures in their ARA.

Overall, legume aboveground and belowground biomass exhibited significant interaction effects between soil texture and fire frequency (aboveground $P < 0.0001$, belowground $P = 0.0002$; Fig. 2.7a,b), with higher biomass on clayey sites with a 2-year fire frequency and on sandy sites with a 4-year fire frequency. *Cassia nictitans* also showed a significant interaction pattern with greater aboveground biomass on both clayey and sandy sites with a 2-year than a 4-year fire frequency; however, the magnitude of difference was greater on clayey than on sandy sites ($P = 0.0104$). *Cassia nictitans* also had a significantly greater belowground biomass in sandy than in clayey sites ($P = 0.0014$) (Fig. 2.8b). The sample size of *D. marilandicum* was not large enough in sandy sites with a 4-year fire frequency to examine interaction effects, but the main effects of soil texture and fire frequency both showed significant differences. Aboveground biomass for *D. marilandicum* was greater on 2-year burn sites ($P = 0.01$) and clayey sites ($P = 0.001$) (Fig. 2.8a; Table 2.2), but belowground biomass did not differ significantly (Fig. 2.8b). *Lespedeza hirta* showed the opposite pattern, with greater aboveground biomass on 4-year burn sites ($P = 0.0042$) (Fig. 2.8a; Table 2.2). Finally *T. virginiana* had greater belowground biomass on 2-year burn sites ($P = 0.0056$) (Fig. 2.8b; Table 2.2), but occurred in such small quantities in sandy sites that it was not harvested; as a result, no interaction could be evaluated. The other legume species did not show any significant differences between soil textures or fire treatments.

An ecosystem-level value for N_2-fixation rate was determined using the ARA (nmol hr^{-1} mg nodule dry $mass^{-1}$) for the legume species examined and aboveground biomass from the circular vegetation plots (Fig. 2.9). *Cassia nictitans* had the greatest N_2-fixation rate (g m^{2-1} y^{-1}) in clay sites with a 4-year fire frequency. Although *C. nictitans'* ARA was relatively similar across sites (Table 2.2), its nodule to aboveground biomass ratio was quite high in the 4-year/clay sites, resulting in a large predicted nodule biomass at the stand-level and thus, a high N_2-fixation rate. *Desmodium marilandicum* had the second highest N_2-fixation rate in 2-year/sand sites, followed by *L. hirta* in 4-year/sand sites. The overall value for N_2-fixation rate at the ecosystem-level was 0.054 (g m^{2-1} y^{-1}).

2.5 Discussion

Biomass of herbaceous species in southeastern pine forests is often greater on more frequently burned sites (Brockway and Lewis, 1997; Glitzenstein et al., 2003) and in wet-mesic compared with xeric sites (Kirkman et al. 2001). The relative increase in the biomass of herbaceous species observed under increasing fire frequency in a longleaf pine ecosystem (Glitzenstein et al., 2003) may be due to the ability of many herbaceous species to resprout or germinate from scarified seeds following fire (Brockway and Lewis, 1997; Hendricks and Boring, 1999). The greater herbaceous species biomass documented in wet-mesic compared with xeric sites is likely due to a water limitation (Kirkman et al., 2001). I did not find a significant difference in total aboveground biomass between fire frequency treatments or on sites with different soil textures. However, my results are consistent with the observation that some plants respond to nutrient or water stress by allocating a greater proportion of their biomass to belowground structures (Keyes and Grier, 1981). Indeed, I have found that belowground biomass was significantly greater on sandy than on clayey sites.

While patterns of species biomass were similar to those of Kirkman et al. (2001), total aboveground biomass of ground layer plants at Fort Benning was much smaller. Kirkman documented ground layer biomass ranging from 233 g/m^2 to 269 g/m^2 in wet-mesic sites and from 130 g/m^2 to 145 g/m^2 in xeric sites; whereas, at Fort Benning, total ground layer biomass ranged from 95 g/m^2 to 106 g/m^2 in clayey sites and was 85 g/m^2 in sandy sites. This difference in ground layer biomass is likely due to differences in site quality. Kirkman's longleaf pine-dominated site in southwestern Georgia has been maintained with prescribed burning on a 2-5 year rotation for more than 70 years (Kirkman et al., 2001). Fort Benning sites, on the other hand, have been managed with prescribed burning for only 20 years on a 3-year rotation and only 4 % of Fort Benning is dominated by longleaf pine. In contrast, Fort Benning biomass values were greater than those documented by Brockway and Lewis (60.2 g/m^2; 1997), whose research site is also a longleaf pine forest (also containing slash pine) in southern Georgia, that had experienced periods of fire suppression, although regular prescribed burning on a 1-3 year rotation has occurred since 1942.

Grasses have been shown to dominate the ground layer vegetation in a longleaf pine ecosystem when burning is on an annual or biennial schedule (Brockway and Lewis, 1997; Glitzenstein et al., 2003). At Fort Benning, grasses made up a greater proportion of the total ground layer biomass under a 2-year than a 4-year fire frequency in sandy mixed pine-hardwood sites, but this pattern was not observed in clayey sites, where the proportion of grass biomass was relatively similar between fire frequency treatments. However, in both clayey and sandy sites, grasses made up a smaller proportion (~12%) of the total ground layer biomass than both forbs (~32%) and woody species (~36%) for both fire frequencies. Although grasses did not dominate the ground layer vegetation at Fort Benning as they did in the sites of Brockway and Lewis (1997), total grass biomass values were similar. Brockway and Lewis reported grass (*Andropogon* spp.) biomass of 17.1 g/m^2, which is within the range of grass (*Andropogon* spp. and others) biomass at Fort Benning (10-20 g/m^2). They reported a lower ground layer biomass (all plant groups) than I found at Fort Benning; thus grass biomass at their site made up a much larger proportion (~28%) of the total ground layer vegetation. At Fort Benning, grasses also had significantly less biomass on sandy than on clayey sites, perhaps due to reduced availability of soil moisture in sandy sites. Soil moisture has been shown to be a limiting factor in total ground layer productivity (Mitchell et al., 1999) and may be more important than fire frequency in influencing vegetation patterns (Glitzenstein et al., 2003) in southeastern pine forests. In general, the other plant groups also had greater biomass in clayey sites, with the exception of woody species in 2002, and ferns and forbs in 2003.

There was a significant interaction effect between soil texture and fire frequency on the combined biomass of the six abundant harvested legumes, which had greater biomass in clayey sites burned under a 2-year fire frequency and greater biomass in sandy sites with a 4-year fire frequency. This is not surprising, since legumes are known to be affected by both fire frequency and nutrient availability and have been shown to increase in biomass following fire when it occurs on 2-4 year intervals (Cushwa et al., 1966; Hendricks and Boring, 1999). Since legumes can utilize atmospheric N_2, they may have an advantage in disturbed, nitrogen-poor areas, such as those immediately following fire (Towne and Knapp, 1996). However, legume populations are usually limited by availability of water (Lauenroth and Dodd, 1979), which may explain why legume biomass was reduced on sandy sites and increased on clayey sites soon after burning.

Legumes made up a small proportion (4%) of the total ground layer biomass compared with that of other forbs and grasses; however, they had the greatest tissue C (%) and N (%) concentrations. Thus, legumes provide a high-quality, nitrogen-rich litter input to the ecosystem, but because they made up such a small proportion of the biomass, their N contribution in g/m^2 may be small. Among the legume species examined, *T. virginiana* had the greatest tissue N (%) concentrations in 4-year/clay sites and also contributed the greatest N (g/m^2) to the ecosystem as it had the greatest biomass per plant and per m^2 in sites in which it was found. *Cassia nictitans* had the second highest tissue N (%) concentrations in 4-year clay and sand sites.

Cassia nictitans had the highest N_2-fixation rate (g m$^{2-1}$ y^{-1}) of all the legume species examined; this occurred in clayey sites with a 4-year fire frequency. This may be due to a greater availability of soil moisture in those sites. Water stress has been shown to negatively impact N_2-fixation rates; both directly, as a result of a decline in leaf water potentials, and indirectly as a result of reduced leaf areas (Hendricks and Boring, 1999). In addition, sites unburned for longer periods of time have a larger accumulation of litter, which may result in greater availability of soil moisture and more favorable growth conditions. Also, *C. nictitans* was the only annual species examined and it is possible that it relies on N_2-fixation more than the perennials because it does not have stores of N from which it can draw. *Desmodium marilandicum* had the second highest N_2-fixation rate, which occurred in sandy sites with a 2-year fire frequency, and was due to the large amount of biomass it produced in these sites. *Lespedeza hirta* had the third highest N_2-fixation rate, in sandy sites with a 4-year fire frequency.

It also had the greatest nodule biomass of any species in these sites and a large aboveground biomass. All three of these species had large nodule to aboveground biomass ratios, which were used to calculate a predicted nodule biomass for the estimated stand-level legume biomass. As a result of their prevalence and the large predicted nodule biomass, they had high rates of N_2-fixation. Although *T. virginiana* had a high ARA (nmol acetylene reduced hr^{-1} g^{-1} nodule biomass) in clayey sites, it did not have a high ecosystem-level N_2-fixation rate (g N $m^{2\ -1}$ y^{-1}) because it was not very prevalent across all sites.

In general, stand-level values for N_2-fixation rates of the six legume species examined ranged from 0.02 to 0.05 g N $m^{2\ -1}$ y^{-1} at Fort Benning, with an overall N_2-fixation value of 0.054 g N $m^{2\ -1}$ y^{-1} at the ecosystem-level. Hendricks and Boring (1999) estimated an ecosystem-level N_2-fixation rate of 0.7 to 0.9 g N $m^{2\ -1}$ y^{-1} for their Piedmont National Wildlife Refuge (longleaf pine dominated) site and less than 0.03 g N $m^{2\ -1}$ y^{-1} for their Oconee National Forest (loblolly pine-hardwood dominated) site. Estimated N_2-fixation rates for the Piedmont National Wildlife Refuge were much greater than mine, whereas, the rate for the Oconee National Forest was similar. The Piedmont sites have been managed with prescribed burning on 4-5 year rotations since 1962 and, as a result, likely have a large biomass and density of legumes. In contrast, the Oconee sites had only burned once at the time of sampling (2-3 years following the burn) and had a much lower frequency and density of legumes than the Piedmont site (Hendricks and Boring, 1999). While sites at Fort Benning have been managed with prescribed burning for longer (~20 years) than those at the Oconee National Forest, their management histories are more similar to each other than to those of the Piedmont National Wildlife Refuge, and both sites are dominated by hardwoods and by pines other than longleaf. Therefore, it was expected that N_2-fixation rates at Fort Benning and the Oconee National Forest would be similar.

Hendricks and Boring examined acetylene reduction activities of three legume species (*D. viridiflorum*, *L. hirta* and *Lespedeza procumbens* Michaux) in their longleaf pine dominated Piedmont National Wildlife Refuge site. They found that *D. viridiflorum* had the highest acetylene reduction activity, followed by *L. procumbens* (75.4 and 39 nmol hr^{-1} mg nodule dry $mass^{-1}$, respectively). No acetylene reduction activity was detected for *L. hirta*. At Fort Benning, *D. viridiflorum* had a much smaller acetylene reduction rate (12.8 nmol hr^{-1} mg nodule dry $mass^{-1}$) and acetylene reduction activity was detected for *L. hirta* (8.2 nmol hr^{-1} mg nodule dry $mass^{-1}$). This discrepancy in acetylene reduction activities is likely due to differences in nodule biomass. Hendricks and Boring report nodule biomass values of 56.3 mg dry mass/plant for *D. viridiflorum* and 0.9 mg dry mass/plant for *L. hirta*, whereas at Fort Benning, *D. viridiflorum* had a nodule biomass of 5.81 mg dry mass/plant and *L. hirta* had a nodule biomass of 26.78 mg dry mass/plant.

The ecosystem-level N_2-fixation rates estimated by Hendricks and Boring are based on several assumptions and should not be considered precise. They measured N_2-fixation rates on a per plant basis, using nodule biomass, for only three legume species, followed by a gross estimation of N_2-fixation rates at the ecosystem-level. While my value should still be considered a rough estimate, it is based not only on measured N_2-fixation rates per plant for six legume species, but is extrapolated to the stand-level using measured nodule and aboveground biomass estimates. This method allows for a more accurate estimation of N_2-fixation rates at the ecosystem-level.

The significant interaction between soil texture and fire frequency in influencing legume N_2-fixation rate demonstrates the complexity of the effects of disturbance on plant ecological processes (Towne and Knapp, 1996). Fire may lead to greater N_2-fixation rates as a result of increased legume biomass (Cushwa et al., 1966; Van Lear and Johnson, 1983; Hendricks and Boring, 1999, 1992; Hiers et al., 2000; Caldwell et al., 2002) and through the scarification of seeds, which stimulates germination and increases abundance (Martin and Cushwa, 1966). My findings suggest that N_2-fixation rates will be higher in clayey sites when a 2-year fire frequency is used; whereas in sandy sites, a 4-year fire frequency may result in higher rates of N_2-fixation. The response of legume biomass is likely the reason for the N_2-fixation pattern.

Southeastern pine forests evolved under a disturbance regime that included frequent and low-intensity fires (Ware et al., 1993). The goal of land managers is often the implementation of a prescribed burning regime that mimics the natural fire regime. However, the effects of prescribed burning are mixed and can vary by current site condition and site history (Carter and Foster, 2004). In addition, concerns have arisen recently regarding the usefulness of prescribed burning as a management tool in forests that experience additional disturbances such as thinning (Carter and Foster, 2004), and in the case of Fort Benning, military use as well. Such additional sources of disturbance may stress the ecosystem to the point that nutrients are lost and productivity declines, a scenario that might not occur if burning were the only disturbance (Carter and Foster, 2004). While it was not within the scope of this study to examine the effects of fire as they relate to the effects of other disturbances, this work contributes to a growing body of knowledge on the effects of prescribed burning and soil texture on ground layer vegetation biomass and nutrient cycling. A key finding is the existence of interaction effects between fire frequency and soil texture on legume above- and belowground biomass, tissue C and N pools in legumes, and on legume acetylene reduction activities. At least one other study has observed a significant interaction pattern between soil moisture (texture) and fire frequency (Glitzenstein et al., 2003), which may be a common pattern in southeastern forests. These results may have implications for land managers who use prescribed burning as a management tool and suggest that consideration of the underlying soil texture may be important when choosing a prescribed burn frequency.

In conclusion, I found that mean belowground biomass was significantly greater on sandy than on clayey sites, but did not differ statistically between 2- and 4-year burn sites. Total aboveground mean biomass did not differ significantly between the two fire frequencies or between the soil textures, but grasses had significantly greater aboveground biomass in clayey than in sandy sites. Grasses also had significantly greater C (g/m^2) and N (g/m^2) in clayey than in sandy sites. In contrast, grasses had significantly greater C (%) in sandy sites. Legumes showed significant interaction effects between soil texture and fire frequency for aboveground tissue C (g/m^2) and N (g/m^2), above- and belowground biomass, and N_2-fixation activities. The prevalence of significant interaction effects between fire frequency and soil texture suggest that soil texture can influence fire's effects on ground layer vegetation composition and nutrient cycling, and should be considered when choosing prescribed fire frequency for managing southeastern mixed pine forests.

2.6 Literature Cited

Brockway, D.G. and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167-183.

Caldwell, T.G., D.W. Johnson and W.W. Miller. 2002. Forest floor carbon and nitrogen losses due to prescription fire. *Soil Science Society of America Journal* 66: 262-267.

Carter, M.C. and C.D. Foster. 2004. Prescribed burning and productivity in southern pine forests: a review. *Forest Ecology and Management* 191: 93-109.

Chapin III, F.S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Sytematics*. 11: 233-260.

Christensen, N.L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the Coastal Plain of North Carolina. *Oecologia* 31: 27-44.

Cushwa, C.T., E.V. Brender and R.W. Cooper. 1966. The response of herbaceous vegetation to prescribed burning. USDA Forest Service Research Note SE-53. 2 pp.

Dilustro, J.J., B.S. Collins, L.K. Duncan and R.R. Sharitz. 2002. Soil texture, land-use intensity, and vegetation of Fort Benning upland forest sites. *Journal of the Torrey Botanical Society* 129: 289-297.

Drevon, J.J. 1989. Evaluation of the nitrogenase activity of legume nodules using the measure of the acetylene reducing activity. In: Technical Handbook on Symbiotic Nitrogen Fixation. Food and Agriculture Organization of the United Nations, 5 pp.

Dudley, J.L. and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *American Midland Naturalist* 130: 286-298.

Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: A first approximation. Tall Timbers Fire Ecology Conference Proceedings 20: 70-81.

Glitzenstein, J.S., D.R. Streng and D.D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. *Natural Areas Journal* 23: 22-37.

Hainds, M.J., R.J. Mitchell, B.J. Palik, L.R. Boring and D.H. Gjerstad. 1999. Distribution of native legumes (Leguminoseae) in frequently burned longleaf pine (Pinaceae)-wiregrass (Poaceae) ecosystems. *American Journal of Botany* 86: 1606-1614.

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.

Hendricks, J.J. and L.R. Boring. 1999. N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113: 167-177.

Heuberger K.A. and F.E. Putz. 2003. Fire in the suburbs: Ecological impacts of prescribed fire in small remnants of longleaf pine (*Pinus palustris*) sandhill. *Restoration Ecology* 11: 72-81.

Hiers, J.K., R. Wyatt and R.J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? *Oecologia* 125: 521-530.

Hiers, J.K., R.J. Mitchell, L.R. Boring, J.J. Hendricks and R. Wyatt. 2003. Legumes native to longleaf pine savannas exhibit capacity for high N_2-fixation rates and negligible impacts due to timing of fire. *New Phytologist* 157: 327-338.

Johnson, J.A. 1983. Soil survey of Muscogee County, Georgia. U.S. Department of Agriculture, Soil Conservation Service.

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

Keyes, M.R. and C.C. Grier. 1981. Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research* 11: 599-605.

Kirkman, L.K., R.J. Mitchell, R.C. Helton and M.B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *American Journal of Botany* 88: 2119-2128.

Lauenroth, W.K. and J.L. Dodd. 1979. Response of native grassland legumes to water and nitrogen treatments. *Journal of Range Management* 32: 292-294.

Liu, Y. and R.N. Muller. 1993. Above-ground net primary productivity and nitrogen mineralization in a mixed mesophytic forest of eastern Kentucky. *Forest Ecology and Management* 59: 53-62.

Martin, R.E. and C.T. Cushwa. 1966. Effects of heat and moisture on leguminous seed. *Tall Timbers Fire Ecology Conference Proceedings* 5: 159-175.

Minchin, F.R., J.F. Witty, J.E. Sheehy and M. Müller. 1983. A major error in the acetylene reduction assay: Decreases in nodular nitrogenase activity under assay conditions. *Journal of Experimental Botany* 34: 641-649.

Minchin, F.R., J.E. Sheehy and J.F. Witty. 1986. Further errors in the acetylene reduction assay: Effects of plant disturbance. *Journal of Experimental Botany* 37: 1581-1591.

Mitchell, R.J., L.K. Kirkman, S.D. Pecot, C.A. Wilson, B.J. Palik and L.R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. I. Aboveground net primary productivity. *Canadian Journal of Forest Research* 29: 743-751.

Myrold, D.D., R.W. Ruess and M.J. Klug. 1999. Dinitrogen fixation. In: Robertson, G.P., et al.

(Eds.). Standard Soil Methods for Long-Term Ecological Research, pp. 241-257.

Neary, D.G., C.C. Klopatek, L.F. DeBano and P.F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51-57.

Ojima, D.S. 1987. The short-term and long-term effects of burning on tallgrass ecosystem properties and dynamics. PhD Dissertation. Colorado State University. Fort Collins, Colorado.

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. *Biogeochemistry* 24: 67-84.

Pastor, J., J.D. Abor, C.A. McClaugherty and J.M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256-268.

Radford, A.E., H.E. Ahles and C.R. Bell. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill, North Carolina, USA.

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.

Reich, P.B., D.F. Grigal, J.D. Aber and S.T. Gower. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78: 335-347.

Reich, P.B., D.W. Peterson, D.W. Wedin and K. Wrage. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82: 1703-1719.

Robertson, G.P., D.W. Wedin, P.M. Groffman, J.M. Blair, E.A. Holland, K.J. Nadelhoffer and D.H. Harris. 1999. Soil carbon and nitrogen availability. In: Robertson, G.P., D.C. Coleman, C.S. Bledsoe and P.S. Sollins. (Eds.). Standard soil methods for long-term ecological research. New York, Oxford University Press, Inc., New York, New York, USA, pp. 258-271.

SAS. 2000. SAS v. 8.1. SAS Institute, Cary, North Carolina, USA.

Schoch, P. and D. Binkley. 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. *Forest Ecology and Management* 14: 13-22.

Skeen, J.N., P.D. Doerr and D.H. Van Lear. 1993. Oak-Hickory-Pine Forests. In: Martin, W.H., S.G. Boyce and A.C. Echternacht (Eds.). Biodiversity of the Southeastern United States Upland Terrestrial Communities. John Wiley & Sons, Inc., New York, New York, USA, pp. 1-34.

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

USAIC. United States Army Infantry Center. 2001. Integrated natural resources management plan, Fort Benning Army Installation, Preliminary Draft 2. Unpublished draft.

Van Lear, D.H. and V.J. Johnson. 1983. Effects of prescribed burning in the southern Appalachian and upper Piedmont forests: a review. Clemson University Forestry Bulletin Number 36.

Vessey, J.K. 1994. Measurement of nitrogenase activity in legume root nodules: In defense of the acetylene reduction assay. *Plant and Soil* 158: 151-162.

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

Ware, S., C. Frost and P.D. Doerr. 1993. Southern Mixed Hardwood Forest: The former Longleaf Pine Forest. In: Martin, W.H., S.G. Boyce and A.C. Echternacht (Eds.). Biodiversity of the Southeastern United States: Lowland terrestrial communities, John Wiley & Sons, Inc., New York, New York, USA. 447-493.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press, New York, New York, USA, 346 pp.

Wilson, C.A., R.J. Mitchell, J.J. Hendricks and L.R. Boring. 1999. Patterns and controls of ecosystem function in longleaf pine-wiregrass savannas. II. Nitrogen dynamics. *Canadian Journal of Forest Research* 29: 752-760.

Wilson, C.A., R.J. Mitchell, L.R. Boring and J.J. Hendricks. 2002. Soil nitrogen dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. *Soil Biology and Biochemistry* 34: 679-689.

Table 2.1 – C and N concentrations in belowground biomass in 2002.

	Mean N (g/m^2)	% N	Mean C (g/m^2)	%C	C/N
2-year	0.29	0.49	22.19	35.04	80.76
4-year	0.26	0.48	22.96	36.74	87.10
Clay	0.23	0.52	17.29	36.87	80.94
Sand	0.32*	0.46	27.45*	34.96	86.56

* Concentrations significantly greater on sandy than on clayey sites.

Table 2.2 – Mean aboveground biomass, nodule biomass, acetylene reduction and N_2-fixation rate per plant for all the legume species sampled. Dashes indicate the absence of a species in a particular site. N_2-fixation rates for *D. paniculatum* in 2/sand sites and *T. virginiana* in 2/clay sites were unable to be determined because they were not present in the vegetation plots in those sites.

Species		*Cassia nictitans*	*Desmodium marilandicum*	*Desmodium paniculatum*	*Desmodium viridiflorum*	*Lespedeza hirta*	*Tephrosia virginiana*
Mean aboveground biomass (g/m^2)	2/clay	0.22	8.77	3.00	1.74	7.18	-----
	2/sand	0.55	22.45	-----	2.34	3.45	17.00
	4/clay	0.38	2.11	0.86	1.79	2.21	18.27
	4/sand	0.33	-----	1.51	3.22	8.00	-----
Mean aboveground biomass per plant	2/clay	0.11	5.62	-----	5.62	5.97	14.65
	2/sand	0.15	2.49	2.05	-----	-----	-----
	4/clay	0.01	3.86	0.95	-----	-----	8.69
	4/sand	0.14	-----	-----	24.83	9.52	-----
Mean nodule biomass per plant	2/clay	2.46	1.40	-----	4.81	5.98	7.63
	2/sand	1.41	2.81	2.10	-----	-----	-----
	4/clay	2.01	3.58	1.37	-----	-----	2.9
	4/sand	0.66	-----	-----	5.81	26.78	-----
Acetylene reduction activity (nmol hr^{-1} mg^{-1} nodule dry mass	2/clay	8.65	7.44	-----	5.98	7.65	6.32
	2/sand	6.77	9.06	3.66	-----	-----	-----
	4/clay	4.08	8.39	1.90	-----	-----	4.75
	4/sand	11.76	-----	-----	12.76	8.2	-----
N_2-fixation rate (g m$^{2-1}$ y^{-1})	2/clay	0.0035	0.0013	-----	0.0007	0.0045	-----
	2/sand	0.0029	0.0187	-----	-----	-----	-----
	4/clay	0.0253	0.0013	0.0002	-----	-----	0.0024
	4/sand	0.0014	-----	-----	0.0006	0.0151	-----

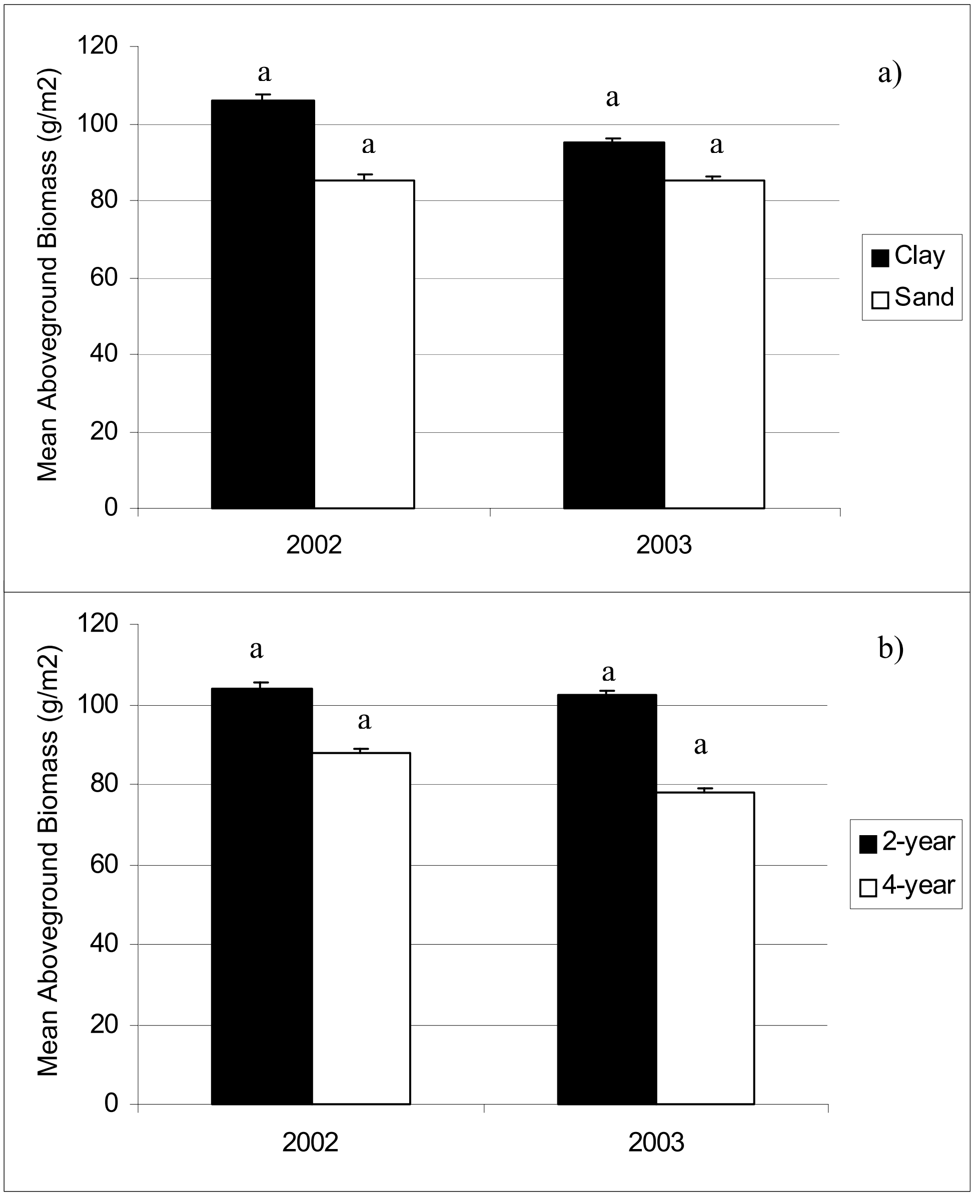

Figure 2.1 – Total aboveground mean biomass of ground layer plants (does not include standing dead biomass) on sites with different (a) soil textures and (b) fire frequencies. Error bars are 1 standard error. Similar letters (a) above bars within each year indicate no significant differences at $\alpha = 0.05$.

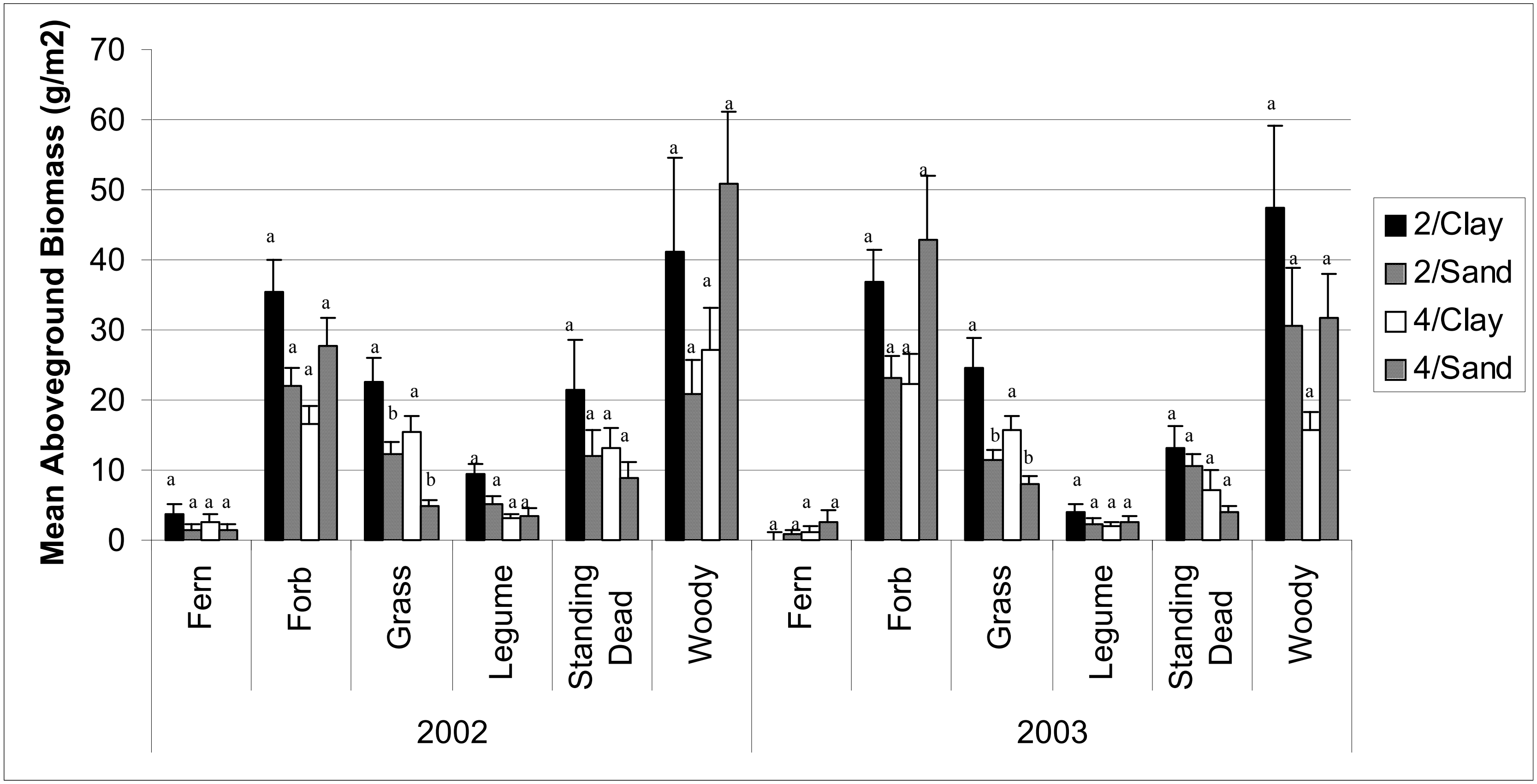

Figure 2.2 – Mean aboveground biomass for ground layer plant groups. Means within a plant group that have different letters were significantly different at α = 0.05.

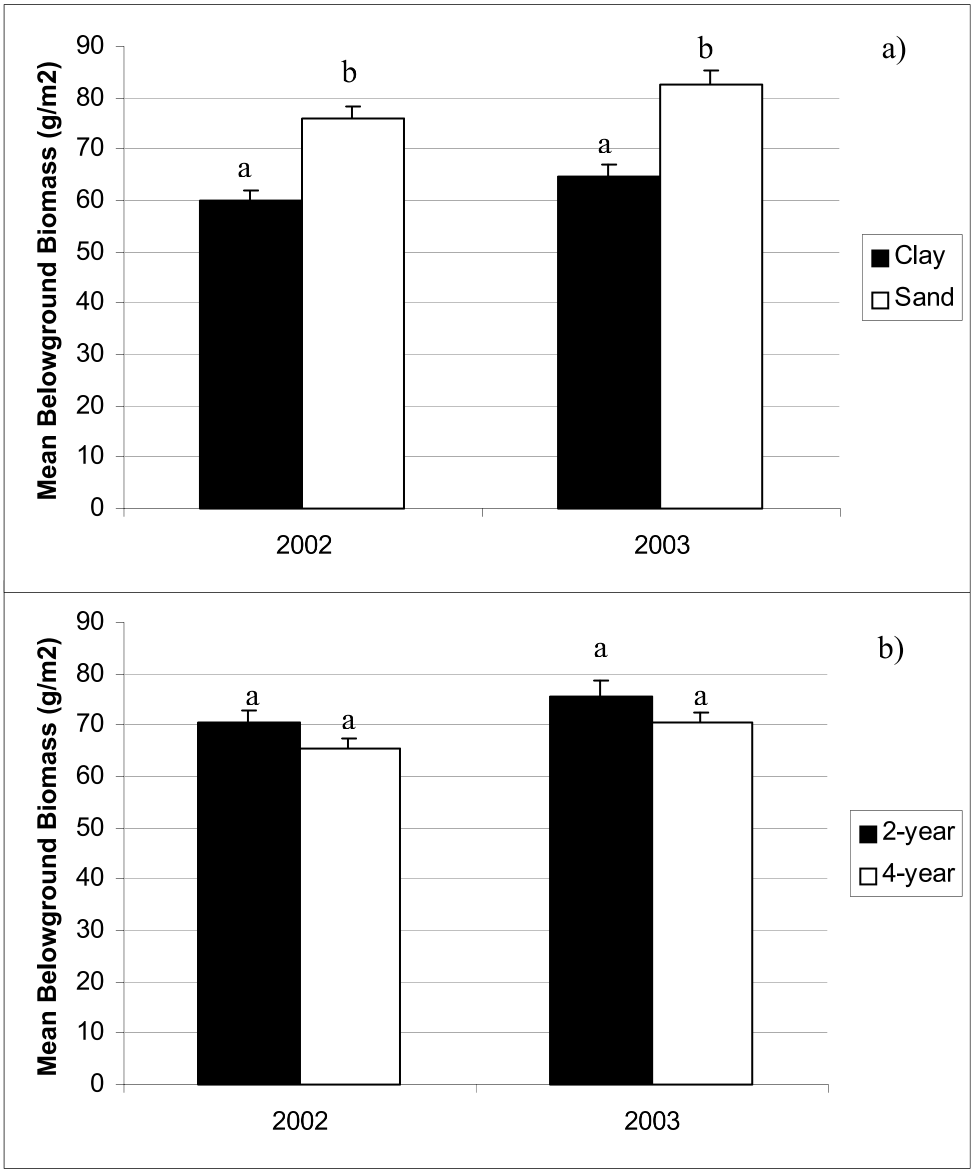

Figure 2.3 – Mean belowground biomass on sites with different (a) soil textures and (b) fire frequencies. Means for the same year with different letters were significantly different at α = 0.05.

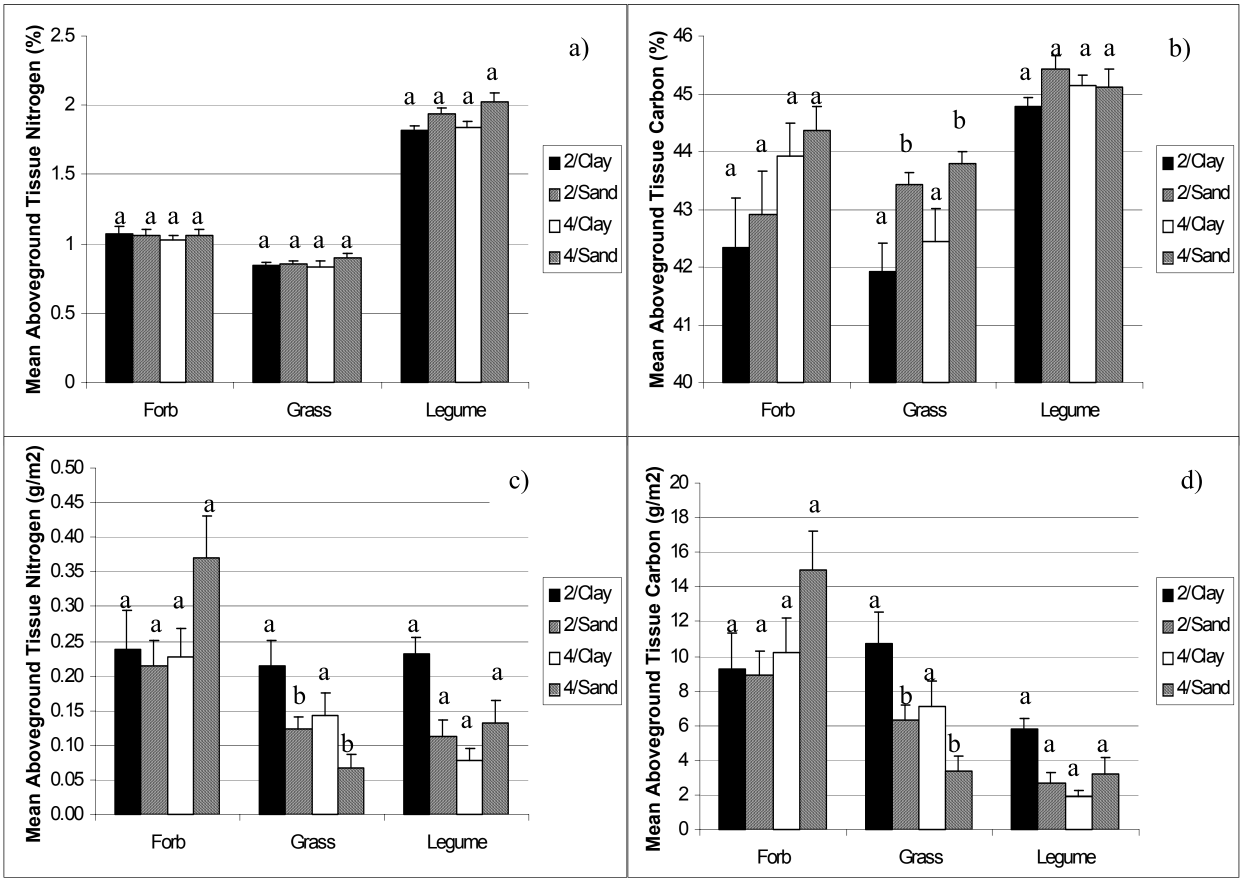

Figure 2.4 – Mean aboveground tissue (a) N (%), (b) C (%), (c) N (g/m^2) and (d) C (g/m^2) in forbs, grasses and legumes in 2002. Means for the same plant groups corresponding with letters were significantly different at α = 0.05.

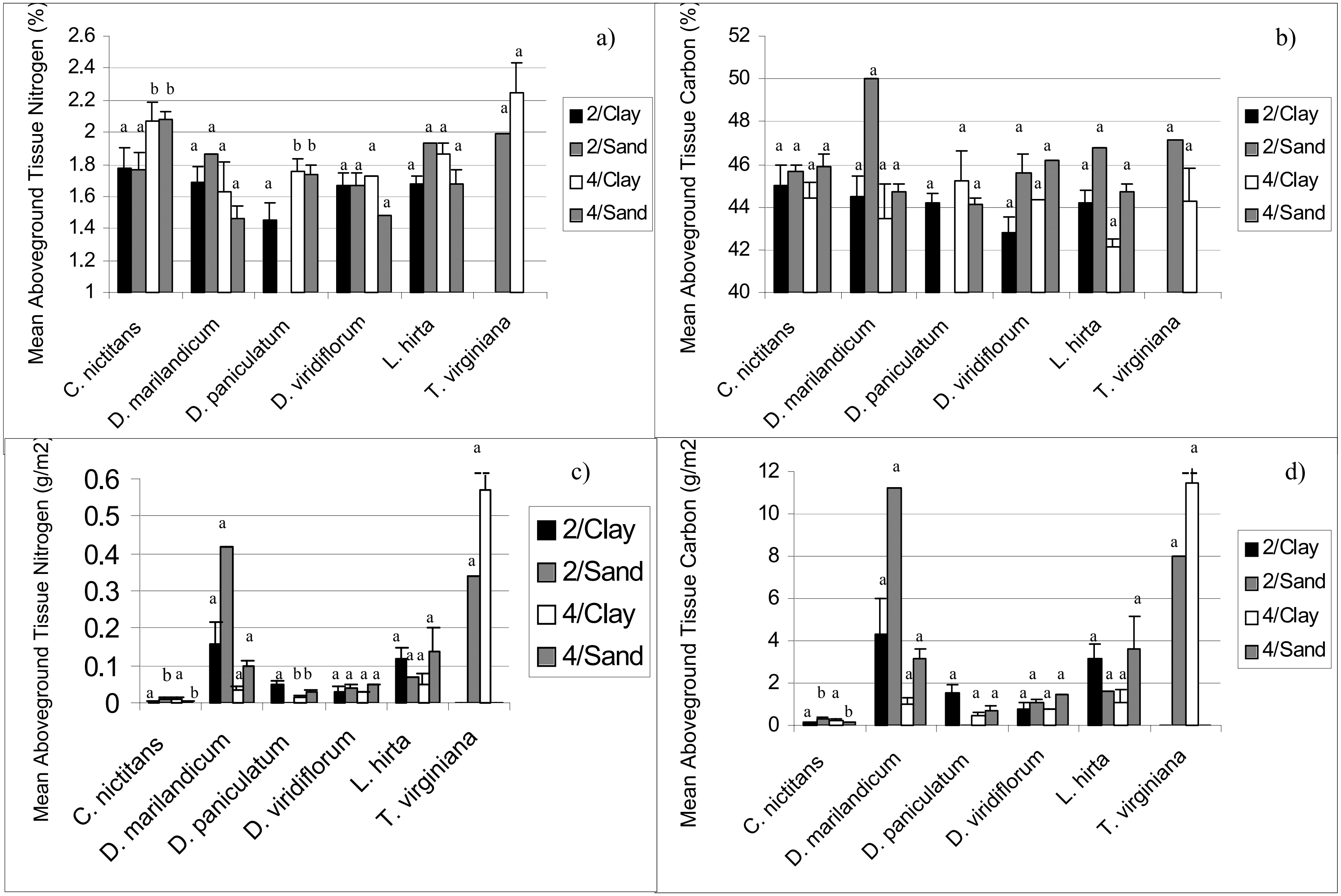

Figure 2.5 – Mean aboveground tissue (a) N (%), (b) C (%), (c) N (g/m^2) and (d) C (g/m^2) in legumes in 2003. Means for the same species with different letters were significantly different at α = 0.05. Missing error bars indicate a sample size of one individual.

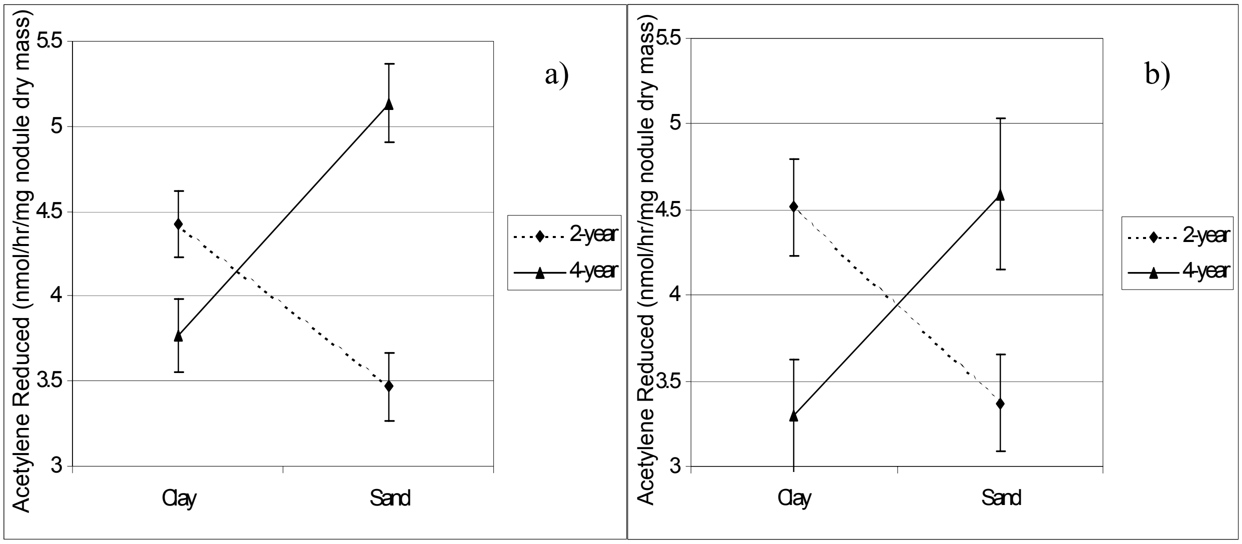

Figure 2.6 – Acetylene reduction activity (nmol hr^{-1} mg nodule dry $mass^{-1}$) by (a) six of the most common herbaceous legume species at Fort Benning combined and (b) *Cassia nictitans*. A significant interaction effect between soil texture and fire frequency was observed for legume acetylene reduction overall ($P < 0.0001$). A significant interaction effect was also observed between soil texture and fire frequency for *C. nictitans* ($P = 0.0013$).

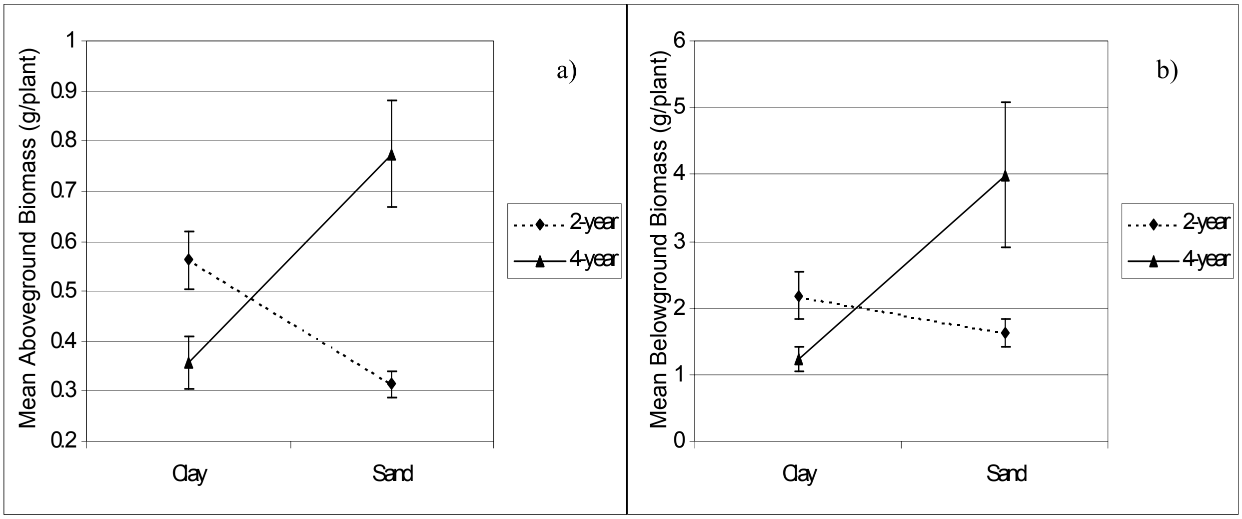

Figure 2.7 – Mean (a) aboveground biomass and (b) belowground biomass for six of the most common legume species in the sample plots. Interaction effect between fire frequency and soil texture was observed for aboveground biomass ($P < 0.0001$) and belowground biomass ($P = 0.0002$).

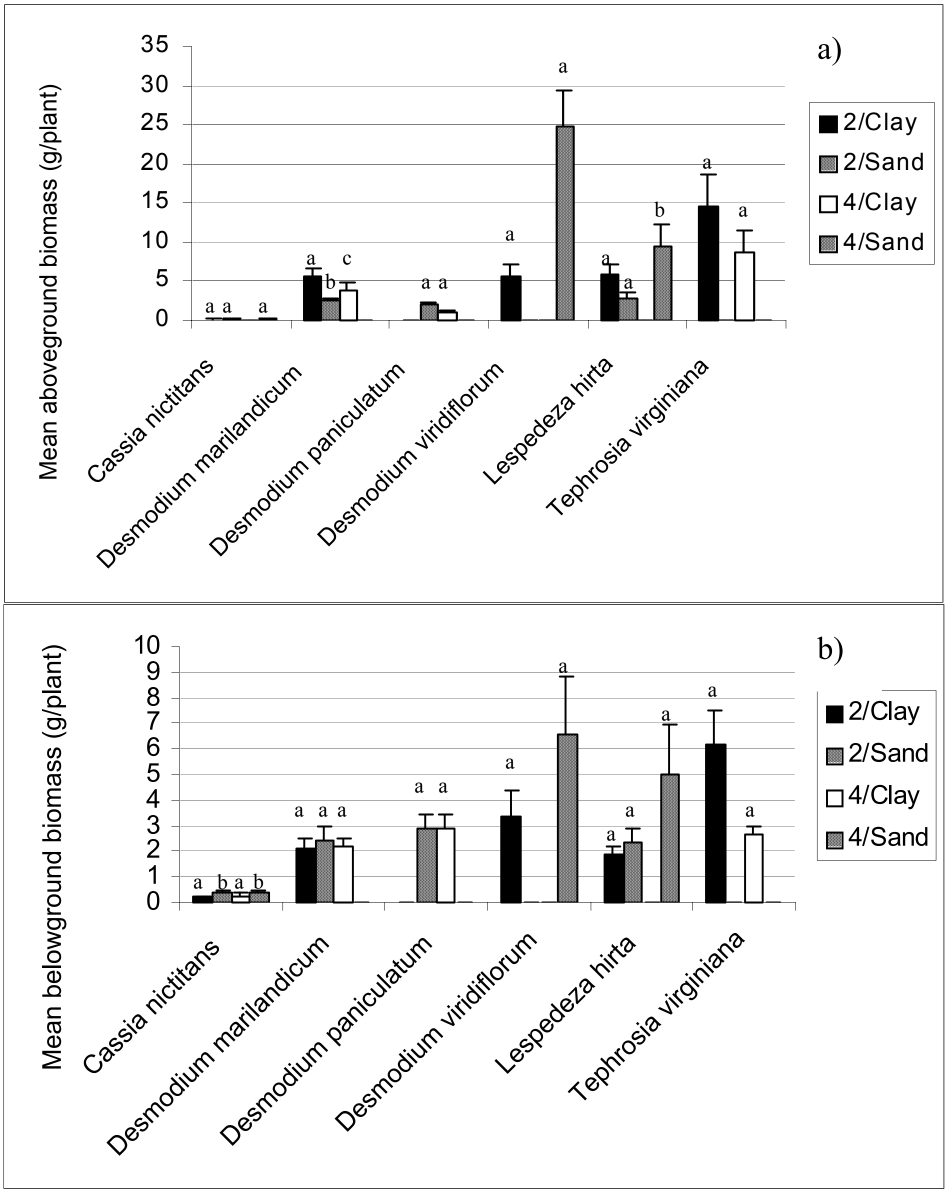

Figure 2.8 – Mean legume (a) aboveground biomass and (b) belowground biomass per plant of plants harvested for the acetylene reduction assay. Means for the same species corresponding to different letters were significantly different at α = 0.05.

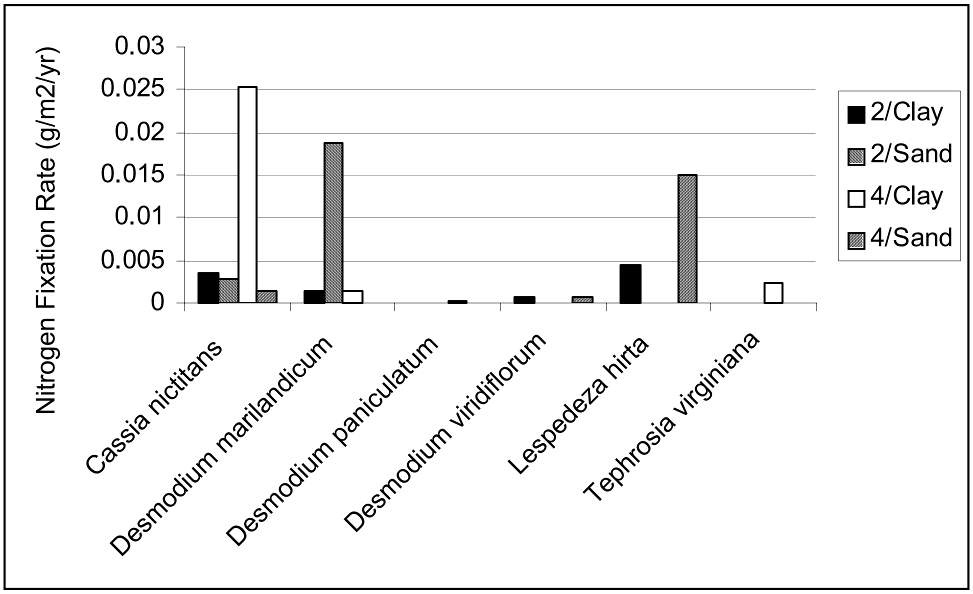

Figure 2.9 – Estimated ecosystem-level N_2-fixation rates for six of the most common legume species at Fort Benning.

CHAPTER 3

A MODEL FOR PREDICTING NITROGEN TRANSFORMATIONS AND GROUND COVER NITROGEN CYCLING UNDER DIFFERENT FIRE FREQUENCIES IN A SOUTHEASTERN MIXED PINE-HARDWOOD FOREST

3.1 Abstract

Fire can regulate nutrient cycling and pine dominance in southeastern forests and the ability to predict effects of different fire frequencies can help land managers select an optimal burn regime. Frequent low-intensity burning has been shown to result in increased above- and belowground plant biomass in the short-term; but in the long-term, frequent burning may result in lower quality litter inputs, leading to reduced soil organic nitrogen (N) and N availability. However, in southeastern pine forests, legumes may play an important role in offsetting these reductions through their ability to fix N_2. Several nutrient cycling models have been developed for southeastern forests; however, to our knowledge, no model has considered the effects of fire frequency on nutrient cycling and nitrogen concentration of ground layer plants. My objective was to develop a model using data from field studies at Fort Benning, GA, to predict N transformations and ground layer N cycling under different fire frequencies. Model runs reveal a trend for higher levels of soil organic N, aboveground ground layer N, root N, and soil NO_3^- and NH_4^+ with a 2-year versus a 4-year burn interval.

Key words: N_2-fixation, nitrogen cycling, Stella model, prescribed burning, ground layer biomass

3.2 Introduction

Fire is an important component of southeastern forests because of its influence on productivity and nutrient cycling dynamics (Wilson et al., 2002). Frequent burning can inhibit the regeneration of hardwoods and large woody shrubs, while promoting increased biomass of ground layer plants, such as ferns, grasses, legumes and other forbs (Glitzenstein, et al., 2003). Increased biomass of ground layer plants may result from a release of inorganic (plant available) N due to the combustion of live plant biomass and litter, both of which would otherwise immobilize inorganic N (Brockway and Lewis, 1997), or due to an increase in soil temperature after burning, which is thought to enhance N mineralization rates (Woodmansee and Wallach, 1981; Ojima et al., 1994; Grogan et al., 2000). In addition, increased nitrogen-use efficiency (NUE) by plants, or the amount of dry biomass per gram N utilized (Chapin III, 1980), as a result of frequent burning, may also contribute to enhanced plant production (Ojima et al. 1994). A short-term pulse of nutrients following fire has been documented in other fire-prone regions (Reich et al., 2001); however, it has been suggested that although some inorganic N may be released, a large proportion of this N may not be in a form that is available to plants (Christensen, 1977). Herbaceous legumes may be an important source of N because of their ability to convert N_2 into inorganic N.

Legume populations are often enhanced following fire (Cushwa et al., 1966; Hendricks and Boring, 1992, 1999; Hiers et al., 2000; Caldwell et al., 2002). This may be due to increased germination from seeds scarified by fire as well as a reduction in competition for light, nutrients and water (Hendricks and Boring, 1999). Enhanced legume populations allow for greater N_2-fixation rates, which may contribute to increased productivity of other plant groups. Legumes also contribute N to the soil through the decay of nitrogen-rich leaf litter and through nodule turnover (Hendricks and Boring, 1992). Through mineralization, this N is converted to inorganic forms useable by other plants. Therefore, legumes play an important role in the N cycle of frequently burned forests, such as those in the southeastern United States.

Although the effects of burning in the short-term are well studied (Schoch and Binkley, 1986; Ojima et al., 1994; Hendricks and Boring, 1999; Grogan et al., 2000; Reich et al., 2001; Hiers et al., 2003), little is known about how frequent burning will effect nutrient cycles and productivity in the long-term (but see Ojima et al., 1994 and Bonito, 2001). Frequent burning over a long time period enhances both N release and losses through volatilization, erosion and leaching (Van Lear and Johnson, 1983; Hainds et al., 1999; Neary et al., 1999). Decreased immobilization from the removal of plant biomass and litter, resulting in decreased soil organic matter, may be another result of long-term frequent burning (Ojima, 1987). Plant litter is the most important pathway providing N to the soil (Staaf and Berg, 1981); therefore, the continual combustion, or immobilization of the nutrients in plant litter could be expected to dampen nutrient cycles and result in decreased plant productivity. Nevertheless, productivity often remains stable through time due to increased NUE in response to burning (Ojima, 1994).

In general, the short-term effects of fire include a loss of N via volatilization and reduced inputs from decaying biomass, but burning also may result in increased N availability through the release of nutrients immobilized in litter and soil organic matter and through increased N_2-fixation rates. In the long-term, frequent burning is thought to result in a loss of N if not offset by added inputs (such as N_2-fixation); however, plant productivity could remain stable if NUE increases due to burning. The use of nutrient models may prove to be useful for predicting nutrient pool sizes in the future. Therefore, the objective of this model was to examine major N pools in the long-term (after 25 years of frequent burning). In addition, the effect of different fire frequencies on these pools was investigated by comparing a 2-year with a 4-year fire frequency.

3.3 Materials and Methods

3.3.1 *Site description*

The study site is a mixed pine-hardwood forest located at Fort Benning, Georgia (32º33' N, 85º W), a 73,650-hectare military base situated on the Fall Line in the Upper Coastal Plain region of the southeastern United States. The climate is characterized as humid temperate with most summer days reaching temperatures of greater than 90º F and a mean winter temperature of 37º F. Mean annual precipitation is 129.5 cm (USAIC, 2001). Two geologic provinces characterize the region: Sand Hills and Southern Coastal Plain. Included in these are Troup sandy loams, Nankin sandy loams, Lakeland sands, and Siley loamy sands (Johnson, 1983).

Forests at Fort Benning are managed with prescribed burning to promote longleaf pine savanna, preferred habitat of the federally endangered red-cockaded woodpecker (USAIC, 2001). This model contributes to a larger investigation focusing on the effects of disturbance (prescribed burning, military training use and forest thinning) on forest communities at Fort Benning (Dilustro et al., 2002). For the project as a whole, burn regimes were assigned such that half the sites were burned on a 2-year rotation and half on a 4-year rotation.

3.3.2 *Stella model structure*

Stella 6.0 was used to model long-term forest N cycling dynamics under different fire frequencies (Figure 3.1). The model was run separately for 25 years under the Runge-Kutta 4 integration method (average of derivatives taken at beginning and end of time increment, and at two points in the center) with an annual time step. First order kinetics characterize all flow rates. State variables include N pools from litterfall, organic soil, mineral soil NH_4^+ and NO_3^-, roots, and aboveground tissues of ground layer plants. Nitrogen transformations (flows) include litterfall from overstory and understory plants, litter layer decomposition, soil N mineralization, ground layer plant aboveground production, root uptake, root death, N_2-fixation and volatilization. All flows are multiplied by a constant (units/year), with the exception of N_2-fixation and overstory litterfall, which are rates in g $m^{2\ -1}$ y^{-1}, obtained either from the literature or estimated based on data taken at Fort Benning (Table 3.1). Initial N pool size values are in Table 3.2.

Model parameters obtained from Fort Benning data included overstory litterfall rate, litter layer N, root N, ground layer plant aboveground N, and soil N mineralization constant (Tables 3.1 and 3.2). Overstory litterfall rate and the litter layer N pool were obtained by Dilustro et al. (unpublished) as part of a study examining biogeochemical cycling at Fort Benning. Root N and aboveground ground layer N concentration were obtained by Drake et al. (unpublished) in a study to examine the effects of different fire frequencies and soil textures on ground layer C and N cycling. The soil N mineralization constant was taken from a Fort Benning study by Garten (unpublished) who examined soil N and C. The understory litterfall constant, litter decomposition constant, ground layer plant production constant, and the initial value for the soil organic N pool were estimates based on preliminary data taken at Fort Benning. The remaining parameters were borrowed from the literature (Tables 3.1 and 3.2). Values and parameters used in this model are in Appendix B.

Fire frequency is a variable that impacts flow rates by increasing or decreasing rate constants depending on its value. Data from Fort Benning and from the literature were used to parameterize the fire frequency function. The model did not include forest overstory production due to difficulties associated with calculations based on the long harvest rotation length required for longleaf pine (desired future condition for Fort Benning sites). Since the model was run for 25 years, which is less than the rotation length of longleaf pine forests, consideration of overstory production was less important.

The role of N_2-fixation by legumes in the N cycle was of particular interest, especially its impact on ground layer plant tissue N. Native herbaceous legumes at Fort Benning contribute approximately 0.054 g N $m^{2\,-1}$ y^{-1} (Drake et al., unpublished). This value is quite low when compared to the 0.8 g N $m^{2\,-1}$ y^{-1} estimated by Hendricks and Boring (1999) for sites at the Piedmont National Wildlife refuge, which are similar to those at Fort Benning, but with greater amounts of longleaf pine. Because of the considerable difference in these values, the model was run using both to determine what effect N_2-fixation rate would have in the model.

Sensitivity analyses were performed for plant production, soil N mineralization and litter layer N because these transformations most directly influenced the N pools of greater interest. All parameters affecting each transformation were increased and decreased by 10, 20 and 30 % to examine how these incremental changes affected the final values of the N pools.

3.4 Results

3.4.1 *Simulations of N Flows*

Although some researchers have shown that burning results in a loss of N from the system (Raison et al., 1979; Ojima et al., 1994; Reich et al., 2001), my model predicts an increase in N in most pools (starting and ending balances are in Table 3.2). Over a 25-year period, soil organic N increased from 15 g/m^2 to about 18.09 g/m^2 with a 2-year fire frequency

(2-year burn results are in Figure 3.2) and to 16.54 g/m^2 with a 4-year fire frequency (4-year burn results are in Figure 3.3). Aboveground ground layer N increased from 0.175 g/m^2 to 0.19 g/m^2 with a 2-year fire frequency, and to 0.18 g/m^2 with a 4-year fire frequency and root N increased from 0.33 g/m^2 to 1.68 g/m^2 with a 2-year fire frequency and to 1.70 g/m^2 with a 4-year fire frequency. In contrast, plant available N (soil NO_3^- and NH_4^+) decreased from 2.61 g/m^2 to 0.75 g/m^2 with a 2-year fire frequency and decreased to 0.69 g/m^2 with a 4-year fire frequency. Finally, litter layer N changed only slightly from 7 g/m^2 to 6.69 g/m^2 with a 2-year fire frequency and to 7.29 g/m^2 with a 4-year fire frequency, but was much more variable under the 4-year burning.

The differences between the 2-year and 4-year fire frequencies were minimal, although the 2-year burn resulted in slightly greater N pools at the end of the model run (25 years) for all pools except root N and litter layer N (Table 3.2). Data taken at Fort Benning (in the short-term) support the model's long-term prediction that aboveground ground layer N will be increased with a 2-year burn (0.206 g/m^2) relative to a 4-year burn (0.141 g/m^2). However, data do not support the model's predicted increase in root N with a 4-year burn (0.263 g/m^2) relative to a 2-year burn (0.293 g/m^2) (Drake et al., unpublished).

3.4.2 *The Effect of N_2-fixation Rate*

N_2-fixation rate had a dramatic impact on N pool sizes at the end of the simulation. In addition to running the model with the Fort Benning N_2-fixation value (0.054 g N m$^{2\ -1}$ y^{-1}), a value of 0.8 g N m$^{2\ -1}$ y^{-1} (Hendricks and Boring, 1999) was also used (beginning and ending balances are in Table 3.3). With a N_2-fixation value of 0.8 g N m$^{2\ -1}$ y^{-1}, aboveground ground layer N more than doubled after 25 years (for both fire frequencies) (Figures 3.4 and 3.5), compared with those estimated from Fort Benning, which resulted in ground layer N increasing by less than ten percent (for both fire frequencies) (Figures 3.2 and 3.3). Root N showed the same pattern; a N_2-fixation value of 0.8 g N $m^{2\ -1}$ y^{-1} resulted in a final pool size of 4.35 g/m^2 with a 2-year burn (Figure 3.4) and 3.53 g/m^2 with a 4-year burn (Figure 3.5) compared with 1.68 g/m^2 with a 2-year burn (Figure 3.2) and 1.7 g/m^2 with a 4-year burn (Figure 3.3) using the Fort Benning N_2-fixation value. Plant available N (soil NO_3^- and NH_4^+), soil organic N, and litter layer N also were greater with a N_2-fixation of 0.8 g N $m^{2\ -1}$ y^{-1} compared with 0.054 g N $m^{2\ -1}$ y^{-1} (Tables 3.2 and 3.3).

Sensitivity analyses showed that plant production rate is influenced most by the plant production constant (Figure 3.6) and was not at all affected by the size of the plant available N (soil NO_3^- and NH_4^+) pool. Litter decomposition rate also followed this pattern. The litter decomposition constant strongly influenced the rate; whereas, the size of the litter layer N pool did not have an effect (Figure 3.7). In contrast, both the soil N mineralization constant and the soil organic N pool influenced soil N mineralization rate, with the soil N mineralization constant exerting slightly greater influence (Figure 3.8).

3.5 Discussion

Over a 25-year period, soil organic N unexpectedly increased 1.2 times with a 2-year fire. Other models have predicted a decline in soil organic N with frequent burning due to inputs of lower quality plant residues and to an increase in soil N mineralization rates from increased soil temperatures (Ojima et al., 1994), root turnover and combustion of aboveground litter (Woodmansee and Wallach, 1981). While increased soil N mineralization rates are not sustained for an extended period of time following fire, they do increase throughout the time span of this model as a result of repeated burning. An increased soil mineralization rate, in turn, would be expected to result in a larger pool of plant available N (soil NO_3^- and NH_4^+), but model results showed a decline in soil NO_3^- and NH_4^+ through time (true for both N_2-fixation rates). The soil NO_3^- and NH_4^+ pool is fed by soil N mineralization and N_2-fixation, and is depleted by roots and aboveground ground layer plant tissues. Although the soil NO_3^- and NH_4^+ pool decreased, both root N and aboveground ground layer N increased after 25 years. This is due to the fact that the plant production rate was not affected by the size of the soil NO_3^- and NH_4^+ pool as shown in the sensitivity analysis of this parameter. The mechanism for the increase in aboveground ground layer N, despite the decrease in soil NO_3^- and NH_4^+, is unclear. The soil NO_3^- and NH_4^+ obviously remained large enough through N_2-fixation and soil mineralization inputs to support the growth of these N pools. It has been suggested that frequent burning may result in the maintenance of productivity or even an increase due to greater plant NUE (Ojima et al., 1994). Plant productivity may also be related more to availability of soil moisture than to soil nutrients (Wilson et al., 1999).

Model results support the claim that increases in N_2-fixation rates following fire are large enough to exceed the amount of N lost during a burn event (Hainds et al., 1999; Hendricks and Boring, 1999). However, of the two N inputs to the system (N_2-fixation and overstory litterfall), N from overstory litterfall is primarily responsible for offsetting the N lost through volatilization because it is much larger (1.1 g N $m^{2\ -1}$ y^{-1}) than the N_2-fixation rate (0.054 g N $m^{2\ -1}$ y^{-1}). The model does not include other potential losses such as leaching, though the combined inputs of overstory litterfall and legume N_2-fixation would likely be large enough to offset these losses as well.

Model results show that the soil organic N pool increases steadily through time. This is not consistent with the results of others, who have found that unhumified organic matter decreases immediately following fire (Fernandez et al., 1996) and that when subjected to frequent burning, N in soil organic matter decreases in the long-term due to lower quality plant inputs (plant aboveground N concentration is reduced due to burning) (Ojima et al., 1994). However, results from the model and from data collected by Drake et al. (unpublished) indicate that at Fort Benning, legumes represent a relatively high-quality input that contributes to higher soil organic N. In reality, soil organic N could be even greater given that standing dead biomass, which contains large amounts of N (Staaf and Berg, 1981), was not included in the model.

The differences between the 2-year and 4-year fire frequencies after 25 years were relatively small; however, the 2-year burn resulted in slightly greater N pools for all pools except root N and litter layer N. Data taken at Fort Benning sites do not support the model results for root N (Drake et al., unpublished). Root N concentration was slightly higher with a 2-year burn at Fort Benning. In contrast, the 4-year fire frequency resulted in a slightly higher value for the litter layer N pool in the model, which seems reasonable given that it takes time to accumulate litter biomass. The data showed no difference between fire frequency treatments for aboveground ground layer N concentrations (Drake et al., unpublished).

The different results generated by the use of two different N_2-fixation rates (0.054 g $m^{2\ -1}$ y^{-1} and 0.8 g $m^{2\ -1}$ y^{-1}) demonstrate not only the importance of N_2-fixation in the N cycle in these systems, but also the necessity for generating model parameters that are specifically tailored to the site being studied. If the N_2-fixation rate for legumes at Fort Benning had not been measured and a rate from a similar system nearby had been used (0.8 g $m^{2\ -1}$ y^{-1} - that of Hendricks and Boring, 1999), results of the model would have been inaccurate. Thus, the model could be improved by replacing other parameters that were taken from the literature with actual parameters derived from field measurements at Fort Benning. Likewise, those parameters that are estimates for Fort Benning could be refined.

Fire is an important force in southeastern forests that has impacted community species composition (Ware et al., 1993; Glitzenstein, et al., 2003), productivity (Raison, 1979; Dudley and Lajtha, 1993; Wilson et al., 2002), and nutrient cycles (Van Lear and Johnson, 1983; Schoch and Binkley, 1986; Neary et al., 1999; Reich et al., 2001). Little is known about the pre-European fire regime, although it has been documented that different fire frequencies (a component of regime) can differentially effect vegetation (Whelan, 1995) and nutrient cycling. Therefore, an understanding of the effects of fire frequency is necessary to restore a fire regime effectively. This model has the potential to aid land managers who use prescribed burning as a management tool in determining the long-term effects of different fire frequencies on future N pools. Model results suggest that N inputs from legume N_2-fixation can offset losses due to burning. Additional model applications should include an investigation of N inputs by different legume species. Such information could lead to a management program that includes seeding with native legume species that fix greater amounts of N_2. In addition, this model could help to determine which fire frequency reduces nutrient losses and increases productivity for sites at Fort Benning.

3.6 Literature Cited

Bonito, G.M. 2001. Factors regulating nitrogen mineralization rates of an oak pine and hardwood forest along an elevation gradient. M.S. Thesis. The University of Georgia. Athens, Georgia.

Brockway, D.G. and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167-183.

Caldwell, T.G., D.W. Johnson and W.W. Miller. 2002. Forest floor carbon and nitrogen losses due to prescription fire. *Soil Science Society of America Journal* 66: 262-267.

Chapin III, F.S. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Sytematics*. 11: 233-260.

Christensen, N.L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass savanna on the Coastal Plain of North Carolina. *Oecologia* 31: 27-44.

Cushwa, C.T., E.V. Brender and R.W. Cooper. 1966. The response of herbaceous vegetation to prescribed burning. USDA Forest Service Research Note SE-53. 2 pp.

Drake, S.J., J.J. Dilustro, B.S. Collins and R.R. Sharitz. Unpublished. Ground layer carbon and nitrogen cycling and legume nitrogen inputs in a frequently burned mixed pine forest.

Dudley, J.L. and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *American Midland Naturalist* 130: 286-298.

Fernandez, I., A. Cabaneiro and T. Carballas. Organic matter changes immediately after a wildfire in an Atlantic forest soil and comparison with laboratory soil heating. *Soil Biology and Biochemistry* 29: 1-11.

Glitzenstein, J.S., D.R. Streng and D.D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. *Natural Areas Journal* 23: 22-37.

Grogan, P., T.D. Bruns and F.S. Chapin III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* 122: 537-544.

Hainds, M.J., R.J. Mitchell, B.J. Palik, L.R. Boring and D.H. Gjerstad. 1999. Distribution of native legumes (Leguminoseae) in frequently burned longleaf pine (Pinaceae)-wiregrass (Poaceae) ecosystems. *American Journal of Botany* 86: 1606-1614.

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.

Hendricks, J.J. and L.R. Boring. 1999. N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113: 167-177.

Hiers, J.K., R., Wyatt and R.J. Mitchell. 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? *Oecologia* 125: 521-530.

Hiers, J.K., R.J. Mitchell, L.R. Boring, J.J. Hendricks and R. Wyatt. 2003. Legumes native to longleaf pine savannas exhibit capacity for high N_2-fixation rates and negligible impacts due to timing of fire. *New Phytologist* 157: 327-338.

Johnson, J.A. 1983. Soil survey of Muscogee County, Georgia. U.S. Department of Agriculture, Soil Conservation Service.

Neary, D.G., C.C. Klopatek, L.F. Debano and P.F. Ffolliott. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51-57.

Ojima, D.S. 1987. The short-term and long-term effects of burning on tallgrass ecosystem properties and dynamics. PhD Dissertation. Colorado State University. Fort Collins, Colorado.

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. *Biogeochemistry* 24: 67-84.

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.

Reich, P.B., D.W. Peterson, D.W. Wedin and K. Wrage. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82: 1703-1719.

Schoch, P. and D. Binkley. 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. *Forest Ecology and Management* 14: 13-22.

Staaf, H. and B. Berg. 1981. Plant litter input to soil. In: Clark, F.E. and T. Rosswall (Eds.) Terrestrial nitrogen cycles. Ecological Bulletin (Stockholm) 33: 147-162.

USAIC. United States Army Infantry Center. 2001. Integrated natural resources management plan, Fort Benning Army Installation, Preliminary Draft 2. Unpublished draft.

Van Lear, D.H. and V.J. Johnson. 1983. Effects of prescribed burning in the southern Appalachian and upper Piedmont forests: a review. Clemson University Forestry Bulletin Number 36.

Ware, S., C. Frost and P.D. Doerr. 1993. Southern Mixed Hardwood Forest: The former Longleaf Pine Forest. In: Martin, W.H., S.G. Boyce and A.C. Echternacht (Eds.). Biodiversity of the Southeastern United States: Lowland terrestrial communities, John Wiley & Sons, Inc., New York, New York, USA. 447-493.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press. New York, New York, USA. 346 pp.

Wilson, C.A., R.J. Mitchell, L.R. Boring and J.J. Hendricks. 2002. Soil nitrogen dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. *Soil Biology and Biochemistry* 34: 679-689.

Woodmansee, R.G. and L.S. Wallach. 1981. Effects of fire regimes on biogeochemical cycles. In: Mooney, H.A., T.M. Bonnicksen, N.L. Christensen, J.E. Lotan and W.A. Reiners (Eds.). Fire regimes and ecosystem properties. U.S. Department of Agriculture, Forest Service, General Technical Report WO-26. June 1981, pp. 379-400.

Table 3.1 – Model rates and constants. Estimates are based on preliminary data taken at Fort Benning.

	Rate or Constant	Reference
Overstory Litterfall Rate	1.1 g $m^{2\ -1}$ y^{-1}	Fort Benning (Dilustro, unpublished)
Understory Litterfall Constant	0.9 per year	Fort Benning (estimate)
Litter Decomposition Constant	0.15 per year	Fort Benning (estimate)
Soil N Mineralization Constant	0.025 per year	Fort Benning (Garten, unpublished)
Root Uptake Constant	0.39 per year	Bonito (2001)
Root Death Constant	0.34 per year	Bonito (2001)
Ground layer Plant Aboveground Production Constant	0.20 per year	Fort Benning (estimate)
Litter Volatilization Constant	0.20 per year	Fort Benning (estimate)
N_2-fixation Rate	0.054 g $m^{2\ -1}$ y^{-1}	Fort Benning (Drake, unpublished)
N_2-fixation Rate	0.8 g $m^{2\ -1}$ y^{-1}	Hendricks and Boring (1999)

Table 3.2 – Nitrogen pool values for 2-year and 4-year fire frequencies using a N_2-fixation rate of 0.054 g $m^{2\,-1}$ y^{-1} (Drake et al., unpublished). Initial values are those used at time = 0 and final values are after 25 years. Estimates are based on preliminary data taken at Fort Benning.

	2-year Fire Frequency		4-year Fire Frequency		Reference (Initial Value)
	Initial	Final	Initial	Final	
Litter Layer N	7 g/m^2	6.69 g/m^2	7 g/m^2	7.29 g/m^2	Fort Benning (Dilustro, unpublished)
Soil Organic N	15 g/m^2	18.09 g/m^2	15 g/m^2	16.54 g/m^2	Fort Benning (estimate)
Soil NO_3^- and NH_4^+	2.61 g/m^2	0.75 g/m^2	2.61 g/m^2	0.69 g/m^2	Bonito (2001)
Root N	0.33 g/m^2	1.68 g/m^2	0.33 g/m^2	1.70 g/m^2	Fort Benning (Drake, unpublished)
Aboveground Ground layer N	0.175 g/m^2	0.19 g/m^2	0.175 g/m^2	0.18 g/m^2	Fort Benning (Drake, unpublished)

Table 3.3 – Nitrogen pool values for 2-year and 4-year fire frequencies using a N_2-fixation rate of 0.8 g $m^{2\ -1}$ y^{-1} (Hendricks and Boring, 1999). Initial values are those used at time = 0 and final values are after 25 years. Estimates are based on preliminary data taken at Fort Benning.

	2-year Fire Frequency		4-year Fire Frequency		Reference (Initial Value)
	Initial	Final	Initial	Final	
Litter Layer N	7 g/m^2	8.02 g/m^2	7 g/m^2	6.26 g/m^2	Fort Benning (Dilustro, unpublished)
Soil Organic N	15 g/m^2	36.93 g/m^2	15 g/m^2	27.09 g/m^2	Fort Benning (estimate)
Soil NO_3^- and NH_4^+	2.61 g/m^2	1.91 g/m^2	2.61 g/m^2	1.48 g/m^2	Bonito (2001)
Root N	0.33 g/m^2	4.35 g/m^2	0.33 g/m^2	3.53 g/m^2	Fort Benning (Drake, unpublished)
Aboveground Ground layer N	0.175 g/m^2	0.51 g/m^2	0.175 g/m^2	0.39 g/m^2	Fort Benning (Drake, unpublished)

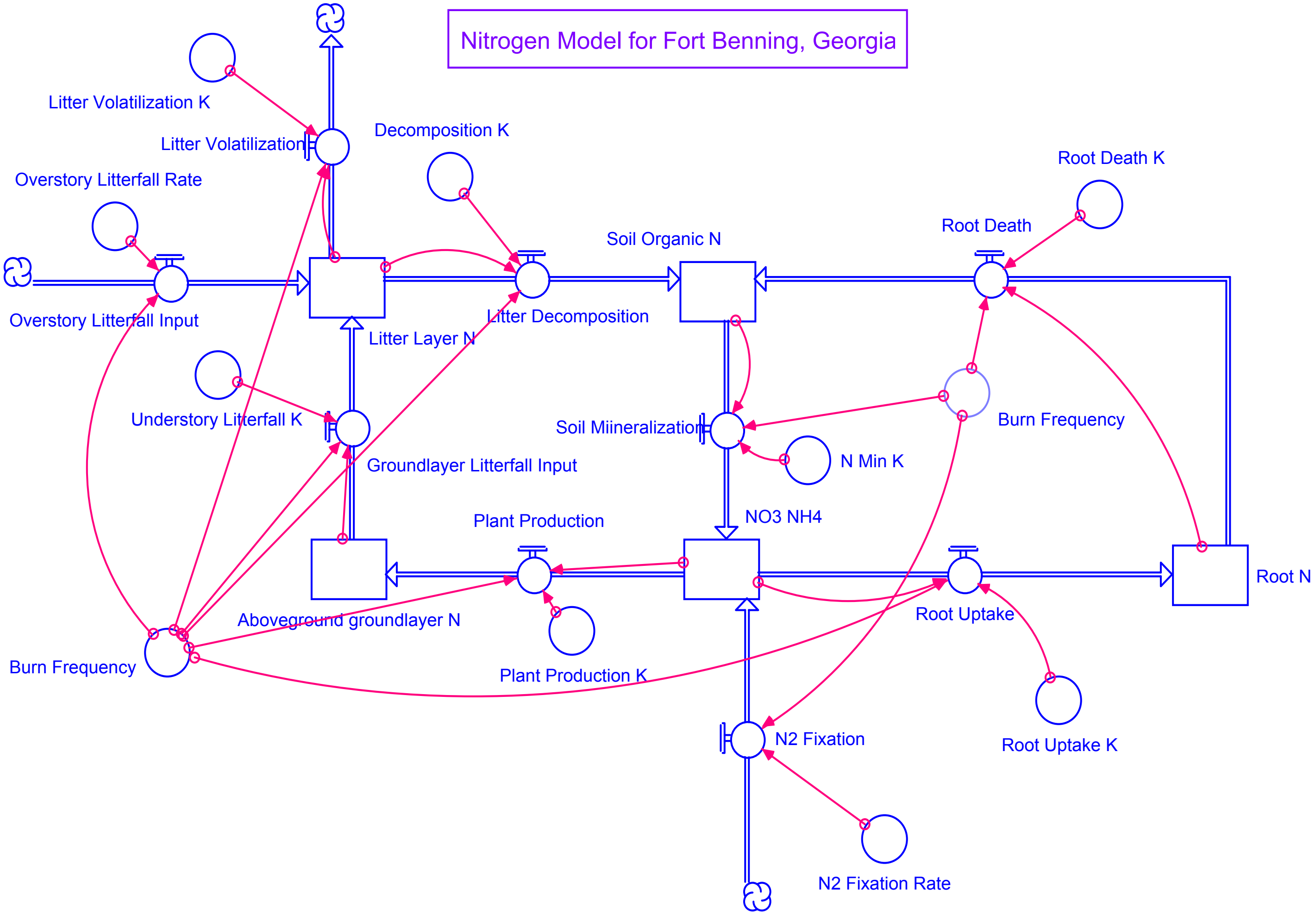

Figure 3.1 – Stella model for Fort Benning, Georgia including major N pools and transformations. Boxes represent N pools and contain a value for the initial pool size at time = 0. Arrows represent N flows and circles represent rates or constants that modify flows.

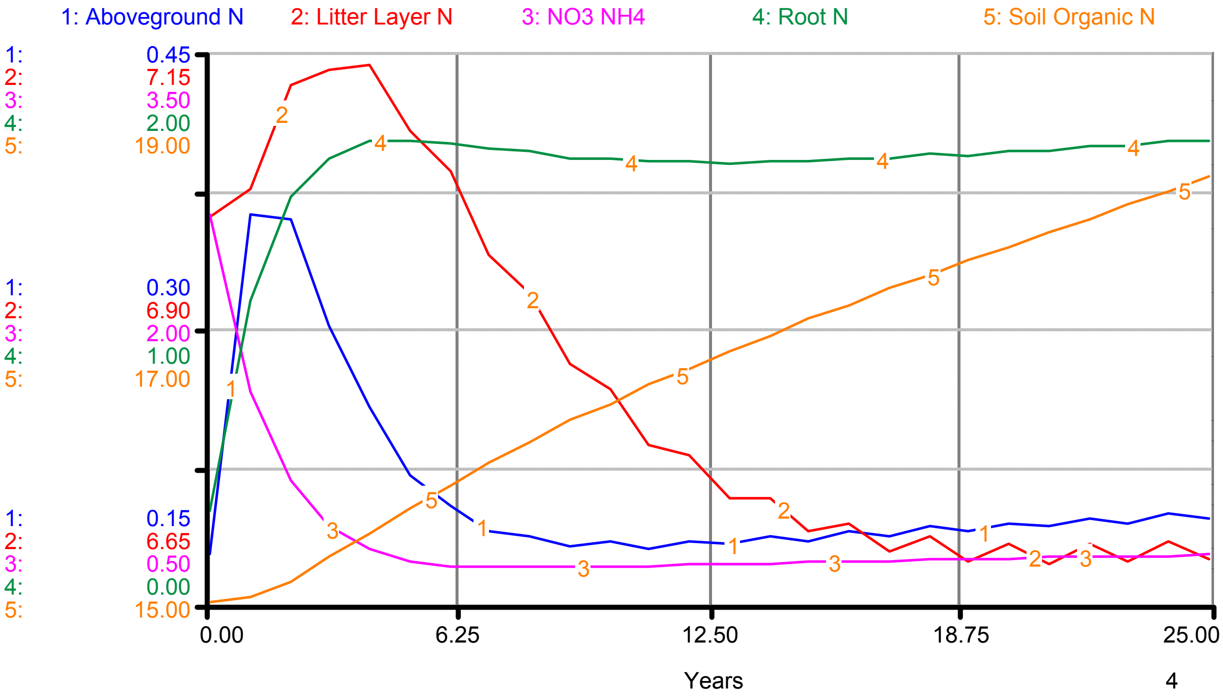

Figure 3.2 - Simulation of major N pools (g N m^{2-1} y^{-1}) with a 2-year fire frequency. Note: Scales are different for different N pools.

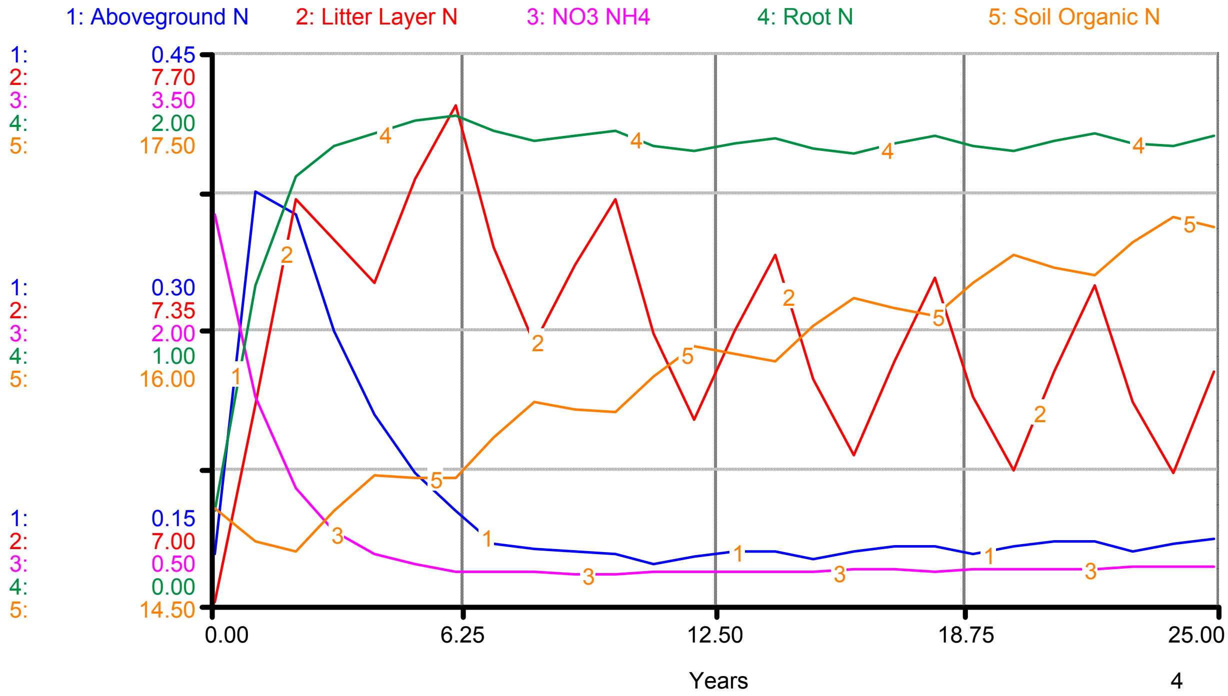

Figure 3.3 - Simulation of major N pools (g N m^{2-1} y^{-1}) with a 4-year fire frequency. Note: Scales are different for different N pools.

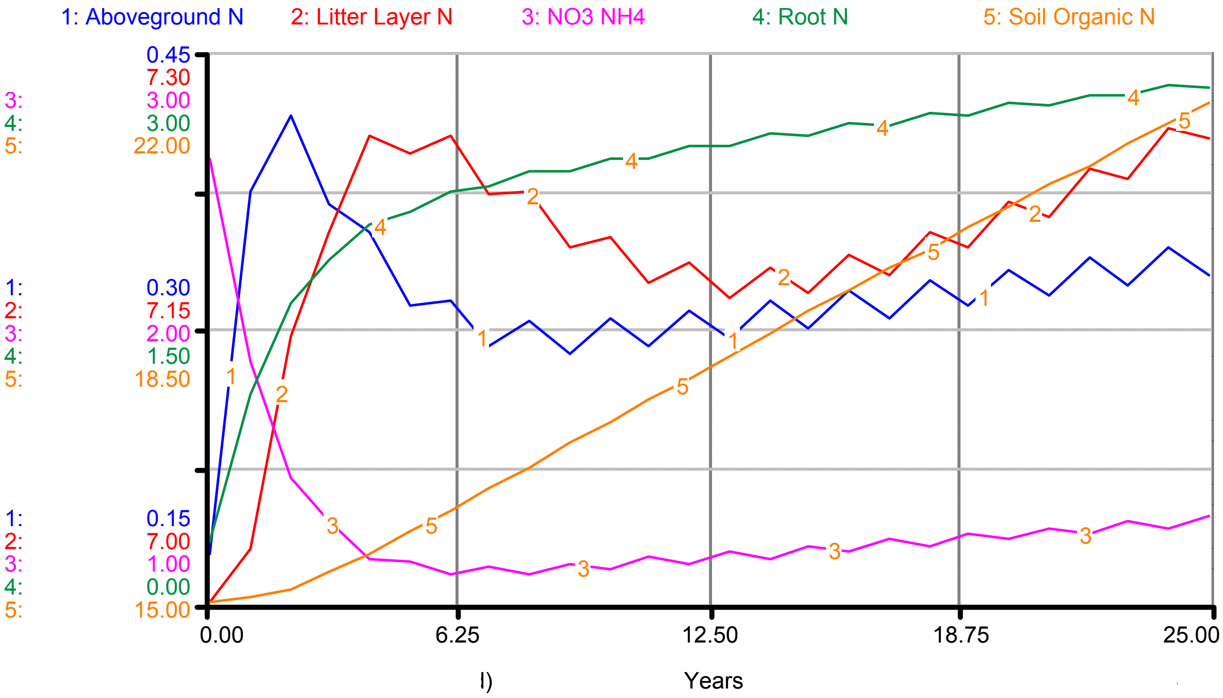

Figure 3.4 - Simulation of major N pools (g N m^{2-1} y^{-1}) with a 2-year fire frequency using a N_2-fixation rate of 0.8 g m^{2-1} y^{-1} (Hendricks and Boring, 1999).

Note: Scales are different for different N pools.

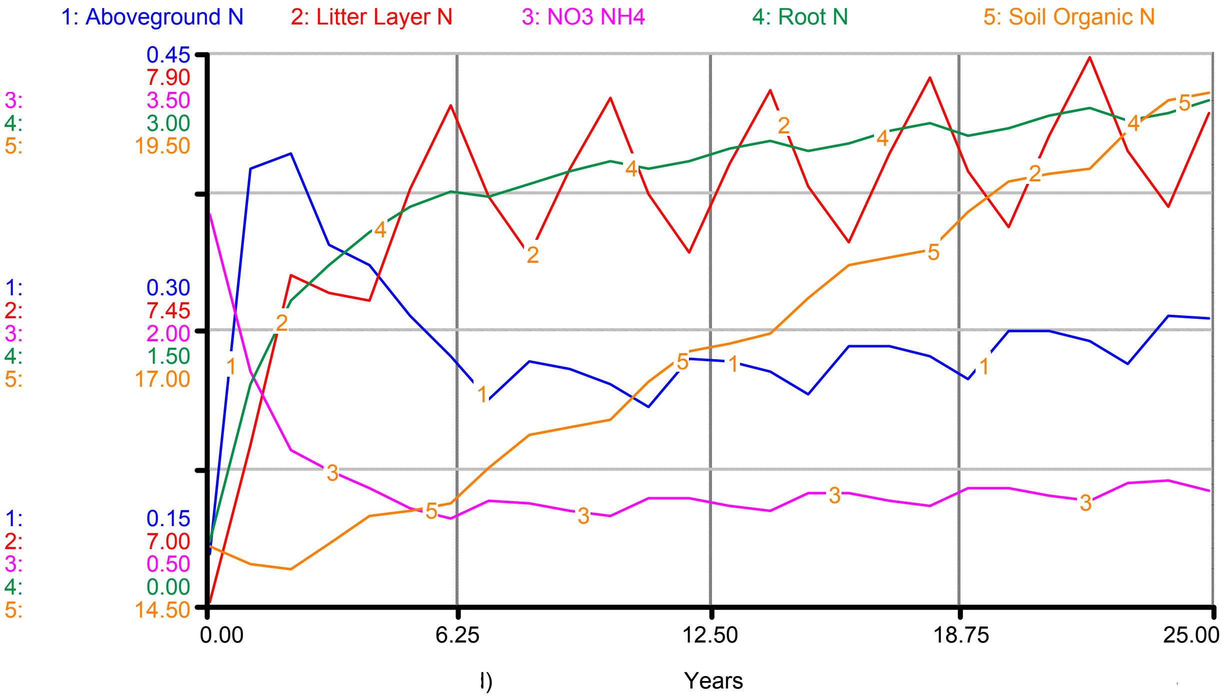

Figure 3.5 - Simulation of major N pools (g N m^{2-1} y^{-1}) with a 4-year fire frequency using a N_2-fixation rate of 0.8 g m^{2-1} y^{-1} (Hendricks and Boring, 1999).

Note: Scales are different for different N pools.

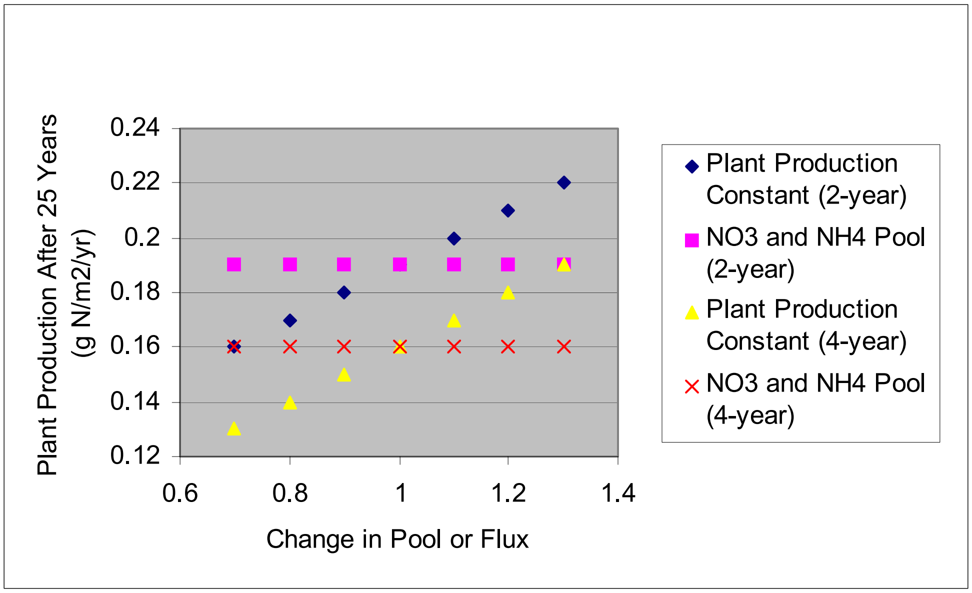

Figure 3.6 - Sensitivity analysis for ground layer plant aboveground N production.

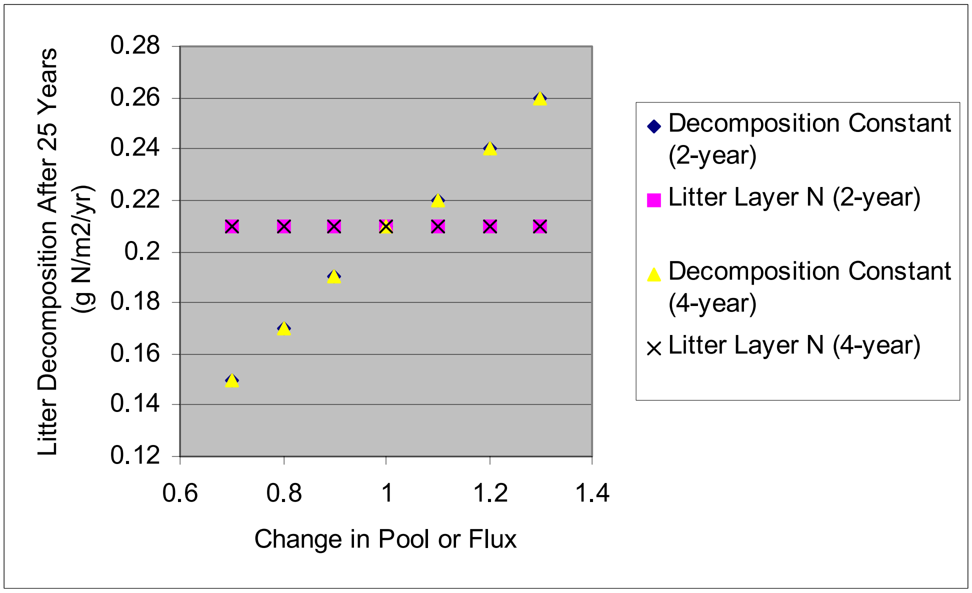

Figure 3.7 – Sensitivity analysis for litter decomposition.

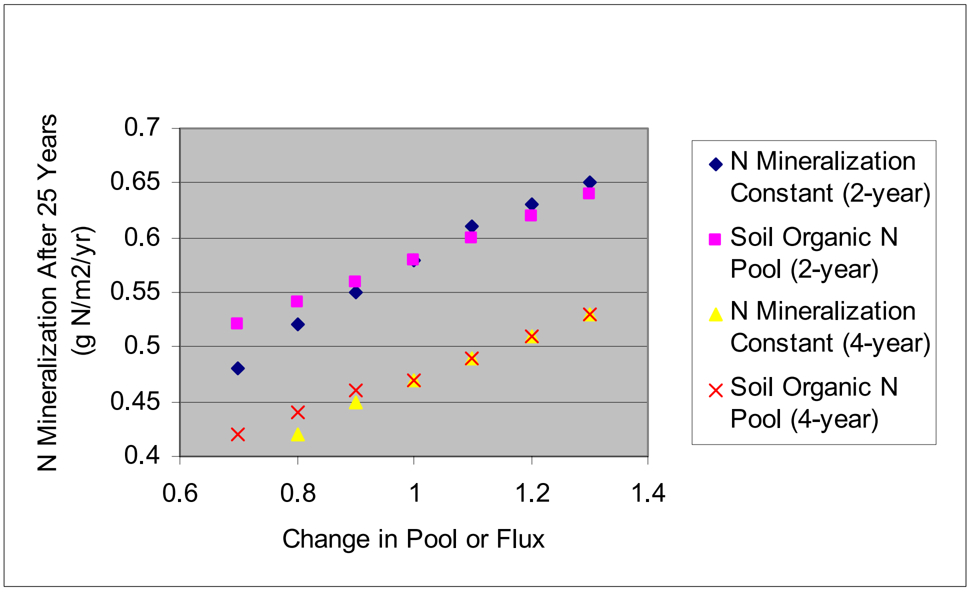

Figure 3.8 – Sensitivity analysis for soil N mineralization.

CHAPTER 4

CONCLUSIONS

4.1 Conclusions

The purpose of these studies was to examine the effects of fire frequency and underlying soil texture in southeastern mixed pine forests on ground layer vegetation biomass and C and N cycling in the short-term and to predict the effects of fire frequency on N pools in the long-term. Fire can regulate nutrient cycling and pine dominance in southeastern forests and underlying soil texture influences the nature and/or extent of fire's effect on vegetation and nutrient cycling. Studies have shown that, in the short-term, biomass of herbaceous species is stimulated by fire (Raison, 1979; Dudley and Lajtha, 1993; Ojima et al., 1994; Brockway and Lewis, 1997; Wilson et al., 2002) and that grasses (Glitzenstein, et al., 2003) and legumes (Dudley and Lajtha, 1993), in particular, respond to fire with increasing biomass. Because of their prevalence in burned ecosystems, grasses and legumes play an important role in C and N cycling dynamics and legumes are uniquely important because of their ability to fix atmospheric N_2. However, the role of underlying soil texture on biomass and C and N cycling is not well understood, and the long-term effect of burning on N pools also is poorly understood (but see Ojima et al., 1994).

The first study compared biomass and tissue C and N concentrations of ground layer plants in sites with different fire frequencies (2-year versus 4-year) and contrasting soil textures (clayey versus sandy). In addition, N_2-fixation rates of six of the most prevalent legume species at Fort Benning were compared. Results showed that, on average, legumes made up a small proportion (4%) of the total ground layer biomass compared with that of grasses (21%) and other forbs (28%); however, they had a much higher tissue N (%) concentration. Therefore, legumes represent a high-quality, nitrogen-rich litter input to the system, but because they make up such a small proportion of the biomass, their N contribution in g/m^2 is small. Grasses had greater biomass in clayey than in sandy sites, perhaps reflecting their dependence on sufficient soil moisture. However, the most interesting results from this study were the significant interaction effects observed between soil texture and fire frequency for legume above- and belowground biomass, aboveground tissue C and N concentrations and N_2-fixation rates. These interaction effects suggest that consideration of soil texture may be important when choosing a prescribed fire frequency for a particular site.

The second study employed a Stella model to predict the effects of a 2-year and a 4-year fire frequency on N pools in the long-term (25 years). Little is known about the long-term effects of frequent burning (but see Ojima et al., 1994) and an understanding of such effects may be useful to managers who use prescribed burning as a management tool. It is generally understood that frequent burning results in a loss of N from the system (Raison, 1979; Ojima et al., 1994; Reich et al., 2001), but that inputs from legume N_2-fixation are important in offsetting these losses (Hendricks and Boring, 1992, 1999; Caldwell et al., 2002; Hiers et al., 2003).

In this model, data from field studies at Fort Benning including legume N_2-fixation rate, above- and belowground ground layer tissue N concentrations, litter layer N, over- and understory litterfall rate, and soil N mineralization rate were used to parameterize the model. Other parameters from sites similar to Fort Benning were taken from the literature. Model runs revealed a trend for higher levels of soil organic N, aboveground ground layer N, and soil NO_3^- and NH_4^+ with a 2-year compared to a 4-year burn interval. In addition, the model was run with the N_2-fixation rate estimated from legumes at Fort Benning as well as the higher value estimated by Hendricks and Boring (1999). Both rates were sufficiently high to offset the N losses from volatilization. Despite the small proportion of total ground layer biomass comprised of legumes, the N_2-fixation rate from Fort Benning was high enough to compensate for N losses under long-term frequent burning.

Many ecosystems in the southeast evolved within a disturbance regime that included fire Ware et al., 1993). Fire can regulate nutrient cycling, and the ability to predict the effects of different fire frequencies can help land managers select an optimal fire regime. Because fire-prone systems are N stressed, it is necessary to understand the effects of burning on N cycling dynamics. Legume N_2-fixation plays an important role in the N cycle of burned systems and the amount of N_2 fixed is related to the amount of legume biomass, which, in turn, is impacted by fire frequency and underlying soil texture. Determination of these values is important for the study of ground layer C and N cycling in the short-term, but also for the prediction of future conditions in the long-term. However, the effects of prescribed burning are mixed and can vary by site and site history (Carter and Foster, 2004). In addition, concerns have recently arisen regarding the usefulness of prescribed burning as a management tool in forests that experience additional disturbances such as thinning (Carter and Foster, 2004), and in the case of Fort Benning, military use as well. Such additional sources of disturbance may stress the ecosystem to the point that nutrients are lost and productivity declines, a scenario that might not occur if burning were the only disturbance (Carter and Foster, 2004). While it was not within the scope of this study to examine the effects of fire as they relate to the effects of other disturbances, this work contributes to a growing body of knowledge on the effects of prescribed burning and soil texture on ground layer productivity and nutrient cycling. These results may have implications for land managers who use prescribed burning as a management tool and suggest that consideration of the underlying soil texture may be important when choosing a prescribed fire frequency.

4.2 Literature Cited

Brockway, D.G. and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96: 167-183.

Caldwell, T.G., D.W. Johnson and W.W. Miller. 2002. Forest floor carbon and nitrogen losses due to prescription fire. *Soil Science Society of America Journal* 66: 262-267.

Carter, M.C. and C.D. Foster. 2004. Prescribed burning and productivity in southern forests: a review. *Forest Ecology and Management* 191: 93-109.

Dudley, J.L. and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. *American Midland Naturalist* 130: 286-298.

Glitzenstein, J.S., D.R. Streng and D.D. Wade. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and Northeast Florida, USA. *Natural Areas Journal* 23: 22-37.

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.

Hendricks, J.J. and L.R. Boring. 1999. N_2-fixation by native herbaceous legumes in burned pine ecosystems of the southeastern United States. *Forest Ecology and Management* 113: 167-177.

Hiers, J.K., R.J. Mitchell, L.R. Boring, J.J. Hendricks and R. Wyatt. 2003. Legumes native to longleaf pine savannas exhibit capacity for high N_2-fixation rates and negligible impacts due to timing of fire. *New Phytologist* 157: 327-338.

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. *Biogeochemistry* 24: 67-84.

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.

Reich, P.B., D.W. Peterson, D.W. Wedin and K. Wrage. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82: 1703-1719.

Ware, S., C. Frost and P.D. Doerr. 1993. Southern Mixed Hardwood Forest: The former

Longleaf Pine Forest. In: Martin, W.H., S.G. Boyce and A.C. Echternacht (Eds.). Biodiversity of the Southeastern United States: Lowland terrestrial communities, John Wiley & Sons, Inc., New York, New York, USA. 447-493.

Wilson, C.A., R.J. Mitchell, L.R. Boring and J.J. Hendricks. 2002. Soil nitrogen dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. *Soil Biology and Biochemistry* 34: 679-689.

Appendix A – ANOVA tables for above- and belowground biomass, tissue C and N concentrations and legume acetylene reduction. Tables are not included for legume tissue C and N, acetylene reduction, and above- and belowground biomass for species where no significant differences between fire treatments or soil textures was observed.

Appendix A.1 - ANOVA table for aboveground biomass in 2002 via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Fire	1	501	0.12	0.7316
Texture	1	501	3.34	0.0683
Fire*texture	1	501	0.06	0.8001

Appendix A.2 - ANOVA table for aboveground biomass in 2003 via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Fire	1	490	0.27	0.6052
Texture	1	490	0.00	0.9827
Fire*texture	1	490	1.72	0.1902

Appendix A.3 - ANOVA table for fern aboveground biomass via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Year	1	174	0.27	0.5540
Fire	1	174	0.00	0.9977
Texture	1	174	0.26	0.6079
Year*Fire	1	174	0.02	0.8953
Year*Texture	1	174	0.70	0.4048
Fire*texture	1	174	0.22	0.6404

Appendix A.4 - ANOVA table for forb aboveground biomass via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Year	1	174	1.70	0.1941
Fire	1	174	0.36	0.5475
Texture	1	174	0.01	0.9344
Year*Fire	1	174	1.54	0.2163
Year*Texture	1	174	1.23	0.2694
Fire*texture	1	174	1.18	0.2784

Appendix A.5 - ANOVA table for grass aboveground biomass via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Year	1	174	2.04	0.1547
Fire	1	174	2.38	0.1247
Texture	1	174	4.77	0.0303
Year*Fire	1	174	0.05	0.8211
Year*Texture	1	174	0.44	0.5086
Fire*texture	1	174	0.10	0.7467

Appendix A.6 - ANOVA table for legume aboveground biomass via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Year	1	174	1.33	0.2506
Fire	1	174	2.49	0.1163
Texture	1	174	1.52	0.2196
Year*Fire	1	174	2.49	0.1166
Year*Texture	1	174	0.76	0.3843
Fire*texture	1	174	0.88	0.3505

Appendix A.7 - ANOVA table for standing dead aboveground biomass via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Year	1	174	2.90	0.0904
Fire	1	174	1.29	0.2569
Texture	1	174	0.27	0.6032
Year*Fire	1	174	23.23	<0.0001
Year*Texture	1	174	0.01	0.9244
Fire*texture	1	174	0.06	0.8012

Appendix A.8 - ANOVA table for woody aboveground biomass via PROC MIXED with fixed site and random subplot.

Source	Num DF	Den DF	F value	P value
Year	1	174	0.53	0.4667
Fire	1	174	0.97	0.3260
Texture	1	174	0.00	0.9945
Year*Fire	1	174	1.72	0.1914
Year*Texture	1	174	0.00	0.9759
Fire*texture	1	174	2.64	0.1058

Appendix A.9 - ANOVA table for belowground biomass in 2002 via PROC GLM with fixed site and random subplot.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.00048532	0.00048532	0.00	0.9732
Texture	1	3.26179662	3.26179662	7.59	0.0065
Fire*texture	1	0.55886590	0.55886590	1.30	0.2556

Appendix A.10 - ANOVA table for belowground biomass in 2003 via PROC GLM with fixed site and random subplot.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.14740549	0.14740549	0.28	0.5987
Texture	1	2.60987437	2.60987437	4.92	0.0278
Fire*texture	1	0.62378929	0.62378929	1.18	0.2796

Appendix A.11 - ANOVA table for C and N concentrations in forb aboveground tissue (2002) via PROC GLM with fixed site and random subplot.

	Source	DF	Type III SS	MS	F value	P value
N (g/m^2)	Fire	1	2.99755	2.99755	1.82	0.1814
	Texture	1	3.40710	3.40710	2.06	0.1545
	Fire*texture	1	1.98231	1.98231	1.20	0.2763
N (%)	Fire	1	0.00703	0.00703	0.21	0.6492
	Texture	1	0.00755	0.00755	0.22	0.6374
	Fire*texture	1	0.00731	0.00731	0.22	0.6428
C (g/m^2)	Fire	1	3.68970	3.68970	2.23	0.1391
	Texture	1	3.36821	3.36821	2.04	0.1574
	Fire*texture	1	1.56858	1.56858	0.95	0.3331
C (%)	Fire	1	0.01911	0.01911	3.74	0.0564
	Texture	1	0.01083	0.01083	2.12	0.1491
	Fire*texture	1	0.00254	0.00254	0.50	0.4826

Appendix A.12 - ANOVA table for C and N concentrations in grass aboveground tissue (2002) via PROC GLM with fixed site and random subplot.

	Source	DF	Type III SS	MS	F value	P value
N (g/m^2)	Fire	1	9.67547	9.67547	3.56	0.0622
	Texture	1	18.15135	18.15135	6.67	0.0112
	Fire*texture	1	2.20767	2.20767	0.81	0.3699
N (%)	Fire	1	0.00665	0.00665	0.14	0.7101
	Texture	1	0.07011	0.07011	2.70	0.1033
	Fire*texture	1	0.03916	0.03916	1.51	0.2222
C (g/m^2)	Fire	1	9.36331	9.36331	3.38	0.0690
	Texture	1	18.42777	18.42777	6.65	0.0113
	Fire*texture	1	2.69416	2.69416	0.97	0.3266
C (%)	Fire	1	0.00307	0.00307	1.32	0.2533
	Texture	1	0.02907	0.02907	12.48	0.0006
	Fire*texture	1	0.00011	0.00011	0.05	0.8293

Appendix A.13 - ANOVA table for C and N concentrations in legume aboveground tissue (2002) via PROC GLM with fixed site and random subplot.

	Source	DF	Type III SS	MS	F value	P value
N (g/m^2)	Fire	1	18.40223	18.40223	13.73	0.0003
	Texture	1	1.64647	1.64647	1.23	0.2699
	Fire*texture	1	23.33704	23.33704	17.41	<0.0001
N (%)	Fire	1	0.06208	0.06208	1.66	0.1998
	Texture	1	0.08262	0.08262	2.21	0.1395
	Fire*texture	1	0.03839	0.03839	1.03	0.3128
C (g/m^2)	Fire	1	20.47172	20.47172	15.20	0.0002
	Texture	1	2.36954	2.36954	1.76	0.1871
	Fire*texture	1	20.33917	20.33917	15.10	0.0002
C (%)	Fire	1	0.05682	0.05682	0.65	0.4233
	Texture	1	0.03886	0.03886	0.44	0.5077
	Fire*texture	1	0.03738	0.03738	0.42	0.5159

Appendix A.14 - ANOVA table for C and N concentration of woody aboveground tissues (leaves and stems) via PROC GLM with fixed site and random subplot.

		Source	DF	Type III SS	MS	F value	P value
Woody leaves	N (%)	Fire	1	0.31586	0.31586	3.52	0.0633
		Texture	1	0.04963	0.04963	0.55	0.4585
		Fire*texture	1	0.12633	0.12633	1.41	0.2379
	C (%)	Fire	1	0.00300	0.00300	1.07	0.3026
		Texture	1	0.00199	0.00199	0.71	0.4005
		Fire*texture	1	0.00011	0.00011	0.04	0.8457
Woody stems	N (%)	Fire	1	0.55223	0.55223	2.58	0.1115
		Texture	1	0.11342	0.11342	0.53	0.4683
		Fire*texture	1	0.00037	0.00037	0.00	0.9671
	C (%)	Fire	1	0.00023	0.00023	0.22	0.6373
		Texture	1	0.00256	0.00256	2.52	0.1159
		Fire*texture	1	0.00000	0.00000	0.00	0.9535

Appendix A.15 - ANOVA table for C and N concentrations in roots (2002) via PROC GLM with fixed site and random subplot.

	Source	DF	Type III SS	MS	F value	P value
N (g/m^2)	Fire	1	0.27371	0.27371	0.69	0.4094
	Texture	1	2.60909	2.60909	6.54	0.0121
	Fire*texture	1	0.13826	0.13826	0.35	0.5573
N (%)	Fire	1	0.03805	0.03805	0.31	0.5761
	Texture	1	0.23754	0.23754	1.96	0.1643
	Fire*texture	1	0.43488	0.43488	3.60	0.0609
C (g/m^2)	Fire	1	0.00468	0.00468	0.01	0.9183
	Texture	1	3.46351	3.46351	7.83	0.0062
	Fire*texture	1	1.08591	1.08591	2.46	0.1204
C (%)	Fire	1	0.06746	0.06746	2.10	0.1504
	Texture	1	0.05837	0.05837	1.82	0.1807
	Fire*texture	1	0.00012	0.00012	0.00	0.9521

Appendix A.16 - ANOVA table for C and N concentrations in legume aboveground tissues (2003) via PROC GLM.

	Source	DF	Anova SS	MS	F value	P value
N (g/m^2)	Fire	1	23.12735	23.12735	10.47	0.0013
	Texture	1	4.38881	4.38881	1.99	0.1597
	Fire*texture	1	41.73125	41.73125	18.89	<0.0001
N (%)	Fire	1	0.12418	0.12418	3.53	0.0611
	Texture	1	0.07117	0.07117	2.02	0.1557
	Fire*texture	1	0.25629	0.25629	7.29	0.0073
C (g/m^2)	Fire	1	26.83748	26.83748	11.83	0.0007
	Texture	1	3.60407	3.60407	1.59	0.2085
	Fire*texture	1	48.80176	48.80176	21.51	<0.0001
C (%)	Fire	1	0.00036	0.00036	0.07	0.7885
	Texture	1	0.00494	0.00494	0.98	0.3218
	Fire*texture	1	0.00048	0.00048	0.10	0.7575

Appendix A.17 - ANOVA table for C and N concentrations in *Cassia nictitans* aboveground tissues (2003) via PROC GLM.

	Source	DF	Anova SS	MS	F value	P value
N (g/m^2)	Fire	1	0.62429	0.62429	0.43	0.5195
	Texture	1	8.32458	8.32458	5.67	0.0240
	Fire*texture	1	0.14405	0.14405	0.10	0.7563
N (%)	Fire	1	0.23421	0.23421	5.60	0.0248
	Texture	1	0.00148	0.00148	0.04	0.8522
	Fire*texture	1	0.00019	0.00019	0.00	0.9465
C (g/m^2)	Fire	1	1.69582	1.69582	1.31	0.2620
	Texture	1	8.96386	8.96386	6.92	0.0135
	Fire*texture	1	0.00000	0.00000	0.00	1.0000
C (%)	Fire	1	0.00079	0.00079	0.34	0.5668
	Texture	1	0.00494	0.00494	2.09	0.1588
	Fire*texture	1	0.00004	0.00004	0.02	0.8944

Appendix A.18 - ANOVA table for C and N concentrations in *Desmodium marilandicum* aboveground tissues (2003) via PROC GLM.

	Source	DF	Anova SS	MS	F value	P value
N (g/m^2)	Fire	1	2.85367	2.85367	6.86	0.0202
	Texture	1	1.00312	1.00312	2.41	0.1427
	Fire*texture	1	3.34630	3.34630	8.04	0.0132
N (%)	Fire	1	0.06501	0.06501	2.36	0.1469
	Texture	1	0.04014	0.04014	1.46	0.2476
	Fire*texture	1	0.00000	0.00000	0.00	1.0000
C (g/m^2)	Fire	1	2.18376	2.18376	4.43	0.0539
	Texture	1	1.60379	1.60379	3.25	0.0929
	Fire*texture	1	3.53122	3.53122	7.16	0.0181
C (%)	Fire	1	0.00189	0.00189	0.81	0.3822
	Texture	1	0.00416	0.00416	1.79	0.2017
	Fire*texture	1	0.01044	0.01044	4.50	0.0522

Appendix A.19 - ANOVA table for C and N concentrations in *Desmodium paniculatum* aboveground tissues (2003) via PROC GLM. An interaction effect between fire frequency and soil texture could not be examined because *D. paniculatum* was not observed in sandy sites with a 2-year fire frequency during the ground layer vegetation harvests.

	Source	DF	Anova SS	MS	F value	P value
N (g/m^2)	Fire	1	8.72123	8.72123	3.68	0.0744
	Texture	1	0.92878	0.92878	0.39	0.5408
	Fire*texture	1	0.00000	--	--	--
N (%)	Fire	1	0.12740	0.12740	7.95	0.0129
	Texture	1	0.16818	0.16818	1.05	0.3218
	Fire*texture	1	0.00000	--	--	--
C (g/m^2)	Fire	1	10.81230	10.81230	4.28	0.0564
	Texture	1	0.64909	0.64909	0.26	0.6198
	Fire*texture	1	0.00000	--	--	--
C (%)	Fire	1	0.00048	0.00048	0.14	0.7112
	Texture	1	0.00081	0.00081	0.24	0.6318
	Fire*texture	1	0.00000	--	--	--

Appendix A.20 - ANOVA table for legume acetylene reduction activity (species combined) via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	11.63919	11.63919	5.15	0.0243
Texture	1	1.87943	1.87943	0.83	0.3635
Fire*texture	1	61.25148	61.25148	27.11	<0.0001

Appendix A.21 - ANOVA table for *Cassia nictitans* acetylene reduction activity via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.09905	0.09905	0.04	0.8331
Texture	1	0.00003	0.00003	0.00	0.9972
Fire*texture	1	0.66870	0.66870	11.13	0.0013

Appendix A.22 - ANOVA table for legume aboveground biomass (species combined) via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.82011	0.82011	5.30	0.0222
Texture	1	0.35654	0.35654	2.31	0.1303
Fire*texture	1	5.55729	5.55729	35.94	<0.0001

Appendix A.23 - ANOVA table for *Cassia nictitans* aboveground biomass via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.00732	0.00732	7.92	0.0062
Texture	1	0.01954	0.01954	21.14	<0.0001
Fire*texture	1	0.00639	0.00639	6.91	0.0104

Appendix A.24 - ANOVA table for *Desmodium marilandicum* aboveground biomass via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.48918	0.48918	7.11	0.0100
Texture	1	0.83782	0.83782	12.18	0.0010
Fire*texture	1	0.00000	--	--	--

Appendix A.25 - ANOVA table for *Lespedeza hirta* aboveground biomass via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.73722	0.73722	10.88	0.0042
Texture	1	0.00000	--	--	--
Fire*texture	1	0.00000	--	--	--

Appendix A.26 - ANOVA table for legume belowground biomass (species combined) via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.29512	0.29512	0.71	0.4015
Texture	1	2.43416	2.43416	5.83	0.0166
Fire*texture	1	6.05547	6.05547	14.49	0.0002

Appendix A.27 - ANOVA table for *Cassia nictitans* belowground biomass via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	0.00027	0.00027	0.01	0.9388
Texture	1	0.49972	0.49972	11.07	0.0014
Fire*texture	1	0.01807	0.01807	0.40	0.5289

Appendix A.28 - ANOVA table for *Tephrosia virginiana* belowground biomass via PROC GLM.

Source	DF	Type III SS	MS	F value	P value
Fire	1	1.45351	1.45351	10.45	0.0056
Texture	1	0.00000	--	--	--
Fire*texture	1	0.00000	--	--	--

Appendix B – Stella values and equations.

Aboveground N(t) = Aboveground N(t - dt) + (Plant Aboveground Production – Ground layer Litterfall Input) * dt

INITIAL Aboveground N = 0.175 g/m^2

INFLOWS:

Plant Aboveground Production = If (Burn Frequency = 1) then (Soil NO_3^- and NH_4^+) * (Plant Aboveground Production K) Else (Soil NO_3^- and NH_4^+) * (Plant Aboveground Production K) * 1.1

OUTFLOWS:

Ground layer Litterfall Input = If (Burn Frequency = 1) then (Aboveground N) * (Understory Litterfall K) Else (Aboveground N) * (Understory Litterfall K) * 0.9

Litter Layer N(t) = Litter Layer N(t - dt) + (Overstory Litterfall Input + Ground layer Litterfall Input – Litter Decomposition – Litter Volatilization) * dt

INITIAL Litter Layer N = 7 g/m^2

INFLOWS:

Overstory Litterfall Input = If (Burn Frequency = 1) then (Overstory Litterfall Rate) Else (Overstory Litterfall Rate)

Ground layer Litterfall Input = If (Burn Frequency = 1) then (Aboveground N) * (Understory Litterfall K) Else (Aboveground N) * (Understory Litterfall K) * 0.9

OUTFLOWS:

Litter Decomposition = If (Burn Frequency = 1) then (Litter Layer N) * (Litter Decomposition K) Else (Litter Layer N) * (Litter Decomposition K) * 0.1

Litter Volatilization = If (Burn Frequency = 1) then (Litter Layer N) * (Litter Volatilization K) Else (Litter Layer N) * (Litter Volatilization K) * 0.70

Soil NO_3^- and NH_4^+(t) = Soil NO_3^- and NH_4^+(t - dt) + (Soil Mineralization + N_2-Fixation – Plant Aboveground Production – Root Uptake) * dt

INITIAL Soil NO_3^- and NH_4^+ = 2.61 g/m^2

INFLOWS:

Soil Mineralization = If (Burn Frequency = 1) then (Soil Organic N) * (Soil N Mineralization K) Else (Soil Organic N) * (Soil N Mineralization K) * 1.1

N_2-Fixation = If (Burn Frequency = 1) then (N_2-Fixation Rate)
Else (N_2-Fixation Rate) * 0.25

OUTFLOWS:

Plant Aboveground Production = If (Burn Frequency = 1) then (Soil NO_3^- and NH_4^+) * (Plant Aboveground Production K) Else (Soil NO_3^- and NH_4^+) * (Plant Production K) * 1.1

Root Uptake = If (Burn Frequency = 1) then (Soil NO_3^- and NH_4^+) * (Root Uptake K) Else (Soil NO_3^- and NH_4^+) * (Root Uptake K) * 1.2

Root N(t) = Root N(t - dt) + (Root Uptake – Root Death) * dt

INITIAL Root N = 0.3262 g/m^2

INFLOWS:

Root Uptake = If (Burn Frequency = 1) then (Soil NO_3^- and NH_4^+) * (Root Uptake K) Else (Soil NO_3^- and NH_4^+) * (Root Uptake K) * 1.2

OUTFLOWS:

Root Death = If (Burn Frequency = 1) then (Root N) * (Root Death K)
Else (Root N) * (Root Death K) * 0.5

Soil Organic N(t) = Soil Organic N(t - dt) + (Litter Decomposition + Root Death – Soil Mineralization) * dt

INITIAL Soil Organic N = 15 g/m^2

INFLOWS:

Litter Decomposition = If (Burn Frequency = 1) then (Litter Layer N) * (Litter Decomposition K) Else (Litter Layer N) * (Litter Decomposition K) * 0.1

Root Death = If (Burn Frequency = 1) then (Root N) * (Root Death K)
Else (Root N) * (Root Death K) * 0.5

OUTFLOWS:
Soil Mineralization = If (Burn Frequency = 1) then (Soil Organic N) * (Soil N Mineralization K) Else (Soil Organic N) * (Soil N Mineralization K) * 1.1

Burn Frequency (2-year burn) = If Mod (Time, 2) + 1=2 then 1 else 0

Burn Frequency (4-year burn) = If Mod (Time, 4) + 1=4 then 1 else 0

Litter Decomposition K = 0.15

Litter Volatilization K = 0.2

N_2-Fixation Rate = 0.054

Soil N Mineralization K = 0.025

Overstory Litterfall Rate = 1.1

Plant Aboveground Production K = 0.2

Root Death K = 0.34

Root Uptake K = 0.39

Understory Litterfall K = 0.9