Disturbance, Functional Diversity, and Ecosystem Processes: Does Species Identity Matter?

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ABSTRACT

The role of disturbance is widely recognized as a fundamental driver of ecological organization from individual species to entire landscapes. Anthropogenic disturbances from military training provide a unique opportunity to examine effects of disturbance on vegetation dynamics, physicochemical soil properties, and ecosystem processes. Additionally, plant functional diversity has been suggested as the key to ecosystem processes such as productivity and nutrient dynamics. I investigated how disturbance and functional composition both singly and in combination affect vegetation dynamics, soil physicochemical properties, and ecosystem processes. I conducted my research at Fort Pickett, Virginia, USA to take advantage of the spatially and temporally predictable disturbance regime. In order to investigate the effect of plant functional composition on ecosystem properties, I used functional groups comprised of species with similar physiology and effects on ecosystem processes (C_4 grasses, C_3 grasses, legumes, forbs, woody plants). My study showed that two distinct disturbances associated with military training, vehicle maneuvers, and fire; affect functional group abundance, within functional group richness, and total species richness. I found strong effects of vehicle maneuvers on soil physical properties including an increase in bulk density and reduction in soil porosity. Fire also influenced soil physical properties but more indirectly through the reduction of above ground litter inputs. Though many of the measured physicochemical soil properties at Fort Pickett exhibited statistically significant effects of disturbance, the strength of these relationships

appears to be modulated by influences of previous land use. I found statistically significant ($P < 0.05$) effects of disturbance on chlorophyll fluorescence, and effect of functional composition on available soil N- NH_4^+. In addition, I detected a significant interactive effect of disturbance class and functional composition on soil CO_2 flux. The interactive effects of disturbance and functional composition on soil CO_2 flux demonstrated how the loss of functional diversity could lead to instability in ecosystem processes in disturbed ecosystems. In a dynamic ecosystem, I demonstrated that the abundance and diversity of plant functional groups was significantly influenced by disturbance. By experimentally altering the abundance and diversity of these functional groups in a disturbance-mediated ecosystem, I showed that functional groups and presumably species influence key ecosystem processes.

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CHAPTER 1: Introduction

BACKGROUND

How do the composition and diversity of plant communities, modulate the influence of disturbance on ecosystem processes? My overall research question addresses two topics in ecological research that Thompson (2001) identified as 'Frontiers of Ecology' that served as the basis of my research, 1) the role of perturbations (i.e. disturbance) in ecosystem organization and, 2) how species affect ecosystem function. I investigated how disturbance and functional diversity of plant communities both singly and in combination affect vegetation dynamics, soil physicochemical properties, and ecosystem processes. The purpose of this chapter is to review pertinent concepts and definitions related to disturbance and its effect on both vegetation and soils. In addition, I discuss the classification of plant functional groups and how functional diversity may affect ecosystem processes. Finally, I discuss the different and somewhat unique ecosystem used in my research, describe my study site, and present my research objectives.

CONCEPT REVIEW

Disturbance

The definition of disturbance in an ecological context has been widely debated and often resulted in contradictory views. Definitions range from being specific to a particular study, "A disturbance is defined here as a force that kills at least one canopy tree" (Runkle 1982) to very broad, "A disturbance opens a relatively large space, releasing resources" (Connell and Slayter

1977). Laska (2001) in a detailed review of disturbance definitions identified two broad and fundamentally different ways to define disturbance. The first is the simple destruction of plant biomass. The second defines disturbance as a deviation from the normal environmental circumstances caused by some discrete event that changes resource availability.

The first definition is based largely on the work of Grime (1974, 1979) who defined disturbance as … "the mechanisms which limit plant biomass by causing its partial or total destruction" and argues that disturbance thus causes organisms to adjust their strategy to fill available niches. Grime's (1979) competitive, stress tolerant, ruderal strategy is based upon this definition and to classifies plant species in terms of their ability to respond to stress or disturbance and the combination of traits each species uses. Grime's definition is similar to Sousa (1984) who adds "… that disturbance creates opportunities either directly or indirectly for individuals to establish."

The second broad definition of disturbance is based upon the work of Pickett and White (1985) who offered an expanded definition that incorporates the actual disturbance event as a key factor in understanding the ecological effects of a disturbance. Pickett and White (1985) defined disturbance as "…any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment."

The ecological role of disturbance is widely recognized as a fundamental factor affecting many levels of ecological organization from individual species to entire landscapes and is a primary abiotic process equal to soils and topography in influence on ecosystem properties (Svensson et al. 2010, Johnson and Miyanishi 2007). Disturbance operates across a wide range of spatial and temporal scales and plays a critical role in maintaining species diversity (Li et al. 2004), successional dynamics of many systems (Noble and Slayter 1980, Tunnell et al. 2004) and ecosystem processes (Amiro et al. 2010). Productivity, CO_2 fluxes, mineralization, and immobilization of nutrient elements are all ecosystem processes affected by different types and intensities of disturbance (Vitousek and Matson 1985, Svensson et al 2010). Disturbance can affect ecosystem processes through direct disruption of the abiotic environment (e.g. soil erosion, landslides). However, in terrestrial systems disturbance influences ecosystem processes most often through the destruction and alteration of plant community structure.

Disturbance influences the composition of many biological communities and plays a crucial role in the conservation and management of biodiversity (Hobbs and Hueneke 1992). In the early 20th century, Clements (1916) identified disturbance as the key event in plant community succession and by late-century the role of disturbance in shaping many plant communities was widely accepted (Pickett and White 1985). For example, the frequency and intensity of fire is critical to the maintenance of many plant communities ranging from southeastern US pine communities (Waldrop et al 1992), the prairie communities of the Great Plains of North America (Collins 2000), and the endemic-rich Fynbos plant communities of southern Africa (Cowling et al. 1992). In contrast, the physical disturbance from logging operations (Ampoorter et al. 2007) and trampling of biotic crusts (Belnap 2003) often adversely affect soils and the associated plant communities. However not all physical disturbance is necessarily detrimental. Fossorial rodent burrows in grassland communities (Reichman and Seabloom 2002) and bison wallows (Trager et al. 2004) are physical disturbances that create micro-habitats necessary to sustain community diversity.

The effect of disturbance on soil is variable and highly dependent upon the type, intensity, frequency, duration, and spatial distribution of the disturbance (Rogers and Harnett 2001). Disturbances that change soil physical structure have a relatively large influence on ecosystem processes, including soil nutrient resources (Collins and Gordon 1983, Guo et al. 2004) and soil hydrology (Guo et al. 2002).

Plant Functional Group Composition and Diversity

The classification of plants based upon phenology, growth forms, and developmental strategies has been the subject of research for over a century (Rusch et al. 2003). A goal of most of this work was to develop a functional description of how different plant species respond to the environment regardless of phylogeny (Rusch et al. 2003). Recent work in developing functional classifications involved the identification of plant functional types that show similar responses to one or several ecosystem functions (Lavorel and Garnier 2002). Lavorel et al. (1997) defined plant functional types …"as non-phylogenetic groupings of species, which perform similarly in an ecosystem based upon a set of common biological attributes."

The importance of diversity to ecosystem function has been an ongoing and somewhat controversial debate for many years (Diaz and Cabido 2001). Research in a variety of ecosystems has found relationships between biodiversity and ecosystem function, though the effects vary in magnitude and are largely species specific, making wider ecological comparisons difficult (Cardinale et al. 2006). Originally, species richness was used as the measure of diversity but because of problems of scale with richness measures, functional diversity has become the preferred alternative to assess a variety of ecosystem traits (Hooper and Vitousek 1998). Plant functional diversity has been suggested as the key to ecosystem processes such as productivity and been shown to positively correlate with soil respiration, soil available N and resistance to invasion (Walker et al. 1999, Symstad 2000, Diaz and Cabido 2001, Mason et al. 2003). Several authors have suggested that the use of plant functional types to assess ecosystem function in disturbed environments will allow for broader comparisons among different ecosystems (Lavorel et al. 1997, Lavorel and Garnier 2002, Mason et al. 2003, Rusch et al. 2003). A key concept related to functional group diversity is functional redundancy (Naeem 1998). Because functional groups are often defined, at least partially, by the role each group plays in an ecosystem, high diversity of functional groups would provide a buffer (i.e. insurance) against the localized extinction of a single species on ecosystem processes (Naeem 1998). In ecosystems subjected to long-term frequent disturbances, within functional group diversity would be an indirect measure of the potential resilience of that ecosystem (Yachi and Loreau 1999).

RESEARCH SYSTEM

I performed my research on a military installation in order to take advantage of two spatially and temporally predictable disturbance regimes: physical disturbance from large, heavy vehicles maneuvering across the landscape, and fire (Dale et al. 2002). Military training affects many structural aspects of ecosystems through physical destruction or alteration of above and below ground components. However, the relationship between military training and ecosystem function has only recently garnered scientific attention (Dale et. al 2002, Duda et. al 2003).

Anthropogenic disturbances from military training provide a unique opportunity to examine effects of historic and altered patterns of disturbance on vegetation dynamics and ecosystem processes. Since World War II, military training in the United States has focused on providing realistic training environments in order to prepare troops for combat. Training doctrine requires that United States Department of Defense (DoD) installations maintain large acreages of natural and semi-natural landscapes to simulate a variety of potential real-world combat scenarios (Anderson et al. 2005). As a result, many military installations are comprised of large land areas generally free from the effects of land use change caused by urbanization and agriculture (Fort Pickett INRMP 2006). Military disturbances cover large areas and effect ecological processes at several levels of biological organization ranging from individuals, to populations, communities, and ecosystem processes (Trame and Harper 1997, Dale et al 2002, Quist et al. 2003, Foster et al. 2006). Two types of disturbance related to training are common on military lands: physical disturbance from large, heavy vehicles maneuvering across the landscape, and fire (Dale et al. 2002).

Physical Disturbance

Military maneuvers involve an assortment of vehicles that range from 5-ton wheeled trucks to 60-ton track vehicles, and often produce intense localized disturbance through the rapidly executed movements during training exercises. Vehicle maneuvers directly damage plant biomass, can cause substantial soil displacement and compaction, and alter biogeochemical processes (Hirst et al. 2005, Althoff and Thien 2005). However, the effect of the disturbance, both spatially and temporally, is dependent upon vehicle type, the manner of travel (straight line vs. turn), soil type, soil moisture, and other environmental factors (Ayers 1994, Hirst 2003, Althoff and Thien 2005).

Vehicle maneuvers do not occur across the landscape as a series of stochastic events but in specific locations and frequencies dictated by the training scenario(s) and constrained by terrain features such as tree size and density, slope, presence of wetlands and other hydrological obstacles to movement (Demaris et al. 1999, Fort Pickett Integrated Natural Resource Management Plan 2006). Repeated disturbance from vehicle maneuvers training in suitable terrain substantially reduces vegetative cover, increases bare soil and bulk density, shifts community composition from perennial to annual, and increases the occurrence of non-native invasive plant species (Hirst et al 2005, Foster et al 2006). However, in some instances low to moderate levels of military vehicle disturbance do not significantly reduce vegetative cover or substantially alter species composition and may have a positive effect on species diversity (Quist et al. 2003, Warren et al. 2007).

Disturbance from maneuver training affects both physical and chemical soil properties and repeated training disrupts or eliminates the O and A horizons, increases soil compaction, bare soil, bulk density, and reduces soil porosity all of which lead to increased soil erosion (Garten et al. 2003, Althoff and Thien 2005, Perkins et al. 2007). The degree of physical damage to soils depends on many factors. Some of these include the number of passes of a vehicle, the weight of the vehicle, tire/track contact pressure, soil type, and soil moisture (Trame and Harper 1997, Hirst et al. 2003). Vehicles moving at higher speeds cause less compaction, but cause greater soil displacement (Braunack 1986). Soil compaction caused by military vehicle maneuvers has been shown to negatively affect soil micro-fauna (Althoff and Thien 2005), decrease C:N ratio and decrease organic matter, which are important constituents in maintaining soil productivity (Peacock et al 2001, Garten et al 2003). Soils with higher amounts of organic matter and litter are more resistant to compaction from military vehicles (Trumbull et al. 1994). Dale et al. (2003) found a significant increase in bulk density and significant decrease in N and C stocks as disturbance increased. Total soil C, soil organic C, and N tend to decrease as the intensity of military training increases (Garten et al 2003). In addition, soil disruption and erosion caused by military training reduces total P and extractable cations (Silveira et al. 2008).

Wildland Fire

The history of fire in North America is complex and varies regionally. In the southeastern United States, fire has been ecologically important from approximately 8000 years ago to the present, which corresponds roughly with the end of the retreat of the Wisconsin ice sheet. Since the end of the last ice age, climatic conditions have been relatively constant, with current vegetation patterns in the southeast stabilizing around 6000 years ago (Frost 1998). An investigation of palynological and charcoal evidence from a site in the southern Appalachians demonstrated a continuous presence of fire for 5000 years (Delcourt and Delcourt 1991). Since the current vegetation patterns have stabilized, it is generally accepted that the southeastern piedmont on average experienced fire every 4-10 years (Christensen 1977, Wright and Bailey 1982, Frost 1998). The only natural ignition source for wildland fire in the southeastern United States is lightning. Thunderstorms, and therefore lightning strikes, are more common in the southeast than any other region of North America (Kormarek 1968). However, because fuels are generally wetter in the southeastern U.S., the percentage of strikes resulting in wildland fire is much lower than in the Rocky Mountain region. Less than 0.0005 % of lightning strikes in the southeast actually result in fire (Kormarek 1968). Through time, the intensity, of wildfire appears polycyclic. Low-intensity fires have been common resulting in little disruption of plant communities and habitats. High intensity stand-replacement fires occurred much less frequently. Fire generally favors the establishment of all types of grasslands but growing season burns give C_4 grasses a competitive advantage over C_3 grasses (Hurlbert 1969, Towne and Owensby 1984, Gibson 1988, Whelan 1995). Biennial fire increases the diversity of herbaceous species in temperate grasslands (Turner and Knapp 1996). In addition, low to moderate intensity fires increase plant species diversity (Hobbs and Heuneke 1992).

Fire is common on military installations that have live-fire ranges. Live tracer rounds and other incendiary ordnance cause wildfires within impact areas and safety buffers. Fire frequencies have remained constant or increased on US military installations since World War II (Trame and Harper 1997). Outside of impact areas and buffers, many US military installations (especially in the southeastern USA) use prescribed fire for a variety of purposes that range from fuel reduction to endangered species habitat maintenance (Dilustro et al. 2007). As a result, large catastrophic wildfires are rare, but frequent, low-intensity fires have become relatively widespread on many US military installations. Because of the long history of fire on U.S. military installations, particularly in the southeastern USA, fire tolerant species have become dominant over large areas.

Research Site

My research site was in the predominantly rural Piedmont physiographic province of Virginia, USA (37-04-27.100N / 077-57-27.100W) approximately 100 kilometers southwest of Richmond and 5 kilometers east of the town of Blackstone at the 16,592-ha Army National Guard Maneuver Training Center-Fort Pickett (Fig. 1-1). The United States Government purchased this land in 1941 to create a military training site for World War II (Fort Pickett Integrated Natural Resource Management Plan 2006).

The Fort Pickett climate is temperate with hot, humid summers and mild winters with frequent short cold spells (National Climatic Data Center 1999). The mean annual temperature is 14.4°C, with a mean maximum of 20°C and mean minimum of 8.8°C. Precipitation is well distributed throughout the year with an annual mean of 115 cm. Fort Pickett is located on the boundary between the Piedmont and the Coastal Plain physiographic provinces. Soils at Fort Pickett generally consist of a quartz sandy loam surface layer ranging in depth from 15-46 cm over a micaceous clay loam, with a frost depth of 61 cm. Most upland soils at Fort Pickett are non-hydric, infrequently flooded Ultisols, and have a slow to moderate infiltration rate. Loams and sandy loams are the most common soil types with organic matter fraction ranging from 2 - 10%. The majority of these soils support forest vegetation under natural conditions (Nicholson 1998).

The current mission of Fort Pickett is to provide a training center capable of handling live-fire and maneuver training requirements for brigade-sized combat training. Military vehicles used for maneuver training at Fort Pickett range in size from the tracked 68-ton

M1A1Abrams main battle tank and tracked 25-ton M2A2 Bradley fighting vehicle to the wheeled HMMV and 5-ton truck. The distribution of the vehicle disturbance is constrained by

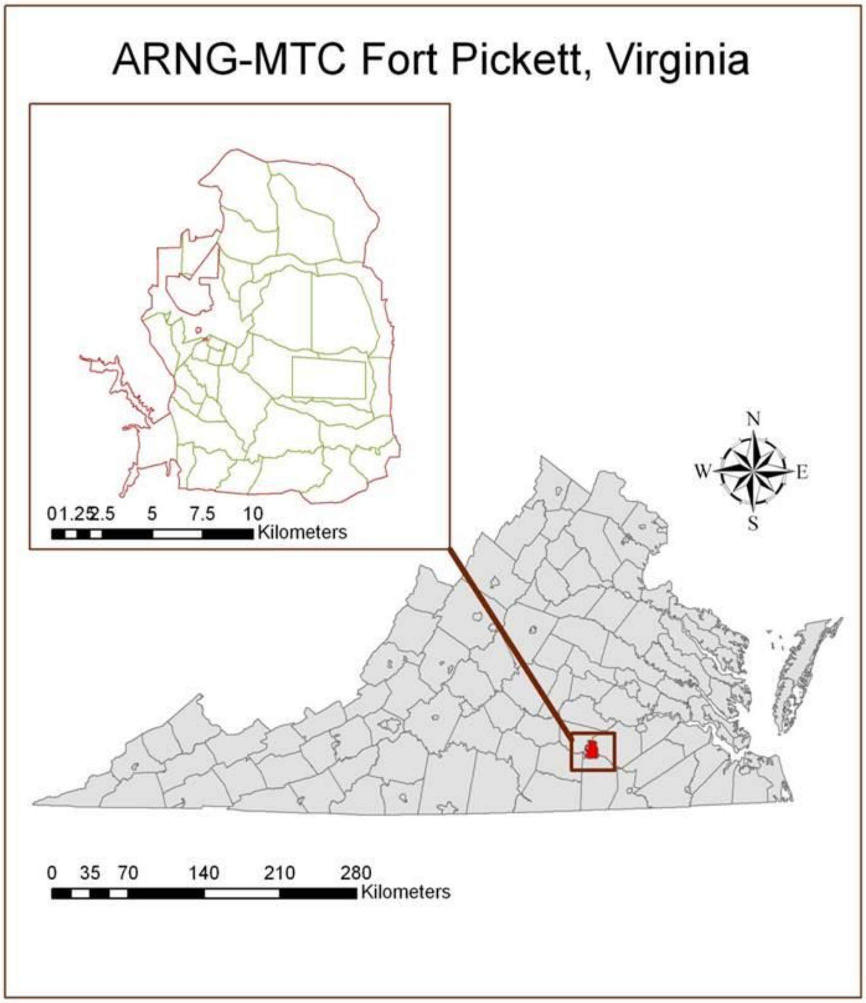

Fig 1-1. Location of the study site. The 16,592 ha Army National Guard Maneuver Training Center-Fort Pickett (Fort Pickett).

terrain features such as tree size and density, slope, presence of wetlands, and cultural features. Thus, the distribution of vehicle disturbance occurs across the landscape in an identifiable pattern, which has remained relatively constant over the life of the installation even as military vehicles have changed over the years.

Military live-fire training (i.e. artillery, flares, and tracer rounds) began at Fort Pickett in 1942 and has occurred in most years, periodically igniting vegetation within buffer (i.e. safety) zones surrounding the live fire ranges. The combined buffer zones or Controlled Access Area (CAA) comprises an area of approximately 4521-ha, in which wildfires are allowed to burn unhindered if there is no threat to range buildings or property (Fort Pickett Integrated Natural Resource Management Plan 2006). This policy has generally been in effect since the creation of Fort Pickett and has resulted in an assortment of fire influenced plant communities. Training-caused wildfires can occur at any time of the year, but are more common from early fall through early spring and vary in frequency and severity depending upon fuel accumulation and local weather conditions.

Humans occupied the region in which Fort Pickett is located for at least 12,000 years B.P.[1] (College of William and Mary 1995). Europeans began to construct permanent settlements in and around the present day Fort Pickett in the late seventeenth century. By the late eighteenth century large plantations cultivating tobacco, wheat, corn, and livestock had developed on what is now Fort Pickett property (College of William and Mary 1995). The establishment and growth of these large plantations corresponded with large slave populations, which outnumbered the free in Nottoway, Lunenburg, Brunswick, and Dinwiddie Counties at end of the eighteenth century. By the mid nineteenth- century, African-American slaves outnumbered whites by a three-to-one ratio in Nottoway County. After the Civil War and emancipation southside Virginia and the Fort Pickett region specifically, became an important area for tobacco production on small to medium sized farms. Small farming dominated the region's economy and land use until the onset of World War II.

Indirect evidence suggests that the land, which became Fort Pickett, had substantially lower forest cover at the time of acquisition than at present. The United States Government purchased land totaling approximately 18,210 hectares of southeastern Virginia in 1941 from nearly 500 private landowners, corporations, and churches to create what was then known as

[1] A putative pre-Clovis site (Cactus Hill) has been identified approximately 25 miles east of Fort Pickett which if confirmed extends the date of human occupation in the region to approximately 16,000 years B.P. (Wagner and McAvoy 2004)

Camp Pickett. Approximately, 1100 people were displaced (Installation Design Guide 1992). At the time of the acquisition the land was a mosaic of relatively small (mean parcel size was 35 hectares) subsistence farms with crops of tobacco, wheat, corn, and pastures located within a matrix of mixed pine and hardwood forests.

Fort Pickett is within the oak-hickory-pine region described by Braun (1950). However, due to a long history of agriculture and military training, uplands at Fort Pickett are currently a mosaic of forests, woodlands, shrublands, and grasslands. There are 1128 ha of native grasslands dominated by *Schizachyrium scoparius*, *Sorghastrum nutans*, and *Panicum* spp. interspersed with 669 ha of native shrublands and over 400 ha of mixed deciduous and coniferous woodlands with an open understory dominated by native grasses and forbs (Dorr et al. 2007). Many of these plant communities are uncommon or absent altogether in the surrounding Piedmont and several are considered state and/or globally rare (Fleming and Patterson 2012).

RESEARCH OBJECTIVES

To investigate the relationship between disturbance, functional composition and diversity, soil physicochemical properties, and ecosystem processes I developed three general research objectives to guide my research:

1. Identify the relationships between disturbance and plant community composition, richness, and diversity.
2. Examine the effects of disturbance on soil chemical and physical properties.
3. Experimentally examine the effect of disturbance and plant community composition on ecosystem processes.

In order to address the research objectives I divided my research into three distinct phases. In the first phase, I examined the effect of disturbance on plant functional group cover/diversity with different measures of disturbance. I selected functional groups comprised of species with similar physiology and known effects on ecosystem processes. These functional groups were C_4 grasses, C_3 grasses, forbs, legumes, and woody plants. I predicted that the two types of disturbance found on military lands would act synergistically to modify plant community structure by shifting functional group abundance and altering within-functional group diversity. Because functional groups tend to differ in their profile of physiological traits (Lavorel et al. 1997, Rusch et al. 2003), I expected that the two disturbance types would have interacting rather than additive effects on total community structure.

In the second phase, I investigated the decades-long effects of military disturbances on soil chemical and physical properties. Repeated events, such as long-term military training, are additive and can effect soil properties long after the visible effects of disturbance have disappeared (Sharrat 1998). I expected that the effect of military disturbance would be apparent in many of the soil physical and chemical properties that directly influence ecosystem processes.

Finally, in the third phase I experimentally examined the effect of disturbance combined with the manipulation of plant functional group composition on ecosystem processes. I used functional groups comprised of species with similar physiology and effects on ecosystem processes and three response variables that reflect many underlying ecosystem processes: soil CO_2 flux, available N-NH_4, and chlorophyll fluorescence.

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CHAPTER 2: The Abundance and Diversity of Plant Functional Groups in Response to Disturbance Gradients

ABSTRACT:

Disturbance influences the composition of many biological communities and plays a crucial role in the conservation and management of biodiversity. Anthropogenic disturbances from military training provide a unique opportunity to examine effects of disturbance on vegetation dynamics. I measured plant functional group (C_4 grasses, C_3 grasses, legumes, forbs, woody plants) cover and diversity on plots subject to different types and intensities of military disturbance (vehicle maneuvers and fire). I used a combination of multivariate analyses to assess the effects of disturbance on plant functional group cover, within plant functional group richness and total species richness. Legume and C_3 grass cover were positively correlated with fire and vehicle maneuvers, respectively, whereas forbs and C_4 grass were positively correlated with both fire and vehicle maneuvers. Woody plants cover was negatively correlated with both types of disturbance. Within functional group richness showed very similar patterns of response to disturbances; i.e., where cover increased or decreased, diversity usually did as well. Total species richness was negatively correlated with the intensity of vehicle maneuvers. My study showed that two distinct disturbances associated with military training, i.e. vehicle maneuvers and fire; do affect functional group abundance, within functional group richness, and total species richness. Non- woody functional groups increased in abundance and diversity as disturbance increased, and woody plants responded in the opposite direction. However, because some individual functional types were more strongly influenced by vehicle maneuvers than fire or vice

versa, I conclude that the two disturbance types have an interacting, and not just a cumulative, influence on total community structure. Within functional group richness, a measure of functional redundancy, generally increased in response to fire and decreased in response military vehicle disturbance.

INTRODUCTION

Disturbance influences the composition of many biological communities and plays a crucial role in the conservation and management of biodiversity (Hobbs and Hueneke 1992). The role of disturbance in governing the structure and composition of plant communities has been recognized since Native Americans used fire to alter the local landscape to improve opportunities for resource acquisition and agriculture (Barden 1997). In the early 20th century, Clements (1916) identified disturbance as the key event in plant community succession and by late-century the role of disturbance in shaping many plant communities was widely accepted (Pickett and White 1985). Disturbance is now considered a primary abiotic process equal to soils and topography in determining the distribution and structure of plant communities (Johnson and Miyanishi 2007).

The frequency and intensity of fire is critical to the maintenance of many plant communities ranging from southeastern US pine communities (Waldrop et al 1992), the prairie communities of the Great Plains of North America (Collins 2000), and the endemic rich Fynbos plant communities of southern Africa (Cowling et al. 1992). In contrast, the physical disturbance from logging operations (Ampoorter et al. 2007) and trampling of biotic crusts (Belnap 2003) often adversely affect soils and the associated plant communities. However not all physical disturbance is necessarily detrimental. Fossorial rodent burrows in grassland communities (Reichman and Seabloom 2002) and bison wallows (Trager et al 2004) are physical disturbances that play a crucial role in plant community dynamics.

Anthropogenic disturbances from military training provide a unique opportunity to examine effects of historic and altered patterns of disturbance on vegetation dynamics and ecosystem processes. Since World War II, military training in the United States has focused on providing realistic training environments in order to prepare troops for combat. Training doctrine requires that United States Department of Defense (DoD) installations maintain large acreages of natural and semi-natural landscapes to simulate a variety of potential real world combat scenarios (Anderson et al 2005). Because of the large acreages involved, military disturbance affects landscapes at several levels of biological organization ranging from individual species to ecosystem processes (Trame and Harper 1997, Dale et al 2002, Quist 2003, Foster et al 2006). As a result, many military installations are comprised of large land areas that have relatively intact ecosystems and are generally free from the direct influences of land use change caused by urbanization and agriculture (Fort Pickett INRMP 2006).

Two types of training related disturbance are common on military lands: physical disturbance from large, heavy vehicles maneuvering across the landscape, and fire (Dale et al 2002). Military maneuvers involve an assortment of vehicles that range from 5 ton wheeled trucks to 60-ton track vehicles, and often produce intense localized disturbance through the rapidly executed movements during training exercises. Vehicle maneuvers directly damage plant biomass, can cause substantial soil displacement and compaction, and alter biogeochemical processes (Hirst et al 2005, Althoff and Thien 2005). However, the effect of the disturbance, both spatially and temporally, is dependent upon vehicle type, the manner of travel (straight line vs. turn), soil type, soil moisture, and other environmental factors (Ayers 1994, Hirst 2003, Althoff and Thien 2005). Vehicle maneuvers do not occur across the landscape as a series of stochastic events but in specific locations and frequencies dictated by the training scenario(s) and constrained by terrain features such as tree size and density, slope, presence of wetlands and other hydrological obstacles to movement (Demaris et al 1999, Fort Pickett Integrated Natural Resource Management Plan 2006). Repeated disturbance from maneuver training in suitable training terrain substantially reduces vegetative cover, with herbaceous species suffering the greatest decline, increases bare soil and bulk density, shifts community composition from perennial to annual, and increases the occurrence of non-native invasive plant species (Hirst et al 2005, Foster et al 2006). However, in some instances low to moderate levels of military vehicle disturbance do not significantly reduce vegetative cover or substantially alter species composition and may have a positive effect on species diversity (Quist et al 2003, Warren et al 2007).

Fire is common on military installations that have live-fire ranges. Live tracer rounds and other incendiary ordnance cause wildfires within impact areas and safety buffers. Fire frequencies have remained constant or increased on US military installations since World War II (Trame and Harper 1997). Outside of impact areas and buffers, many US military installations (especially in the southeastern USA) use prescribed fire for a variety of purposes that range from fuel reduction to endangered species habitat maintenance (Dilustro et al 2007). Because of the long history of fire on US military installations, particularly in the southeastern USA, many plant communities have developed over time that are adapted to frequent fire. As a result, large catastrophic wildfires are relatively rare, but frequent, low intensity fires have become relatively widespread on many US military installations.

The individual influences of fire (Collins 1992, Rogers and Harnett 2001a, Fynn et al. 2004, Li et al. 2004), herbivory (Coffin et al. 1998, Wilby and Brown 2001), drought (Wardle et al. 2000, Fukami 2001), physical soil disturbance (Ikeada 2003, Fulbright 2004), and forest gap creation (Runkle 1982) on vegetation and ecosystem dynamics have been widely examined but usually as single or at most two discrete disturbance events. Military installations provide a unique setting to investigate the long term, cumulative ecological effects of disturbance that occurs episodically in a definable spatial and temporal pattern.

In this study, I sought to identify the effect of disturbance on plant functional group cover and diversity. Developing an understanding of these relationships may help explain the effects of long-term cumulative disturbance on ecosystem processes. Furthermore, the use of plant functional group abundance and diversity to assess ecosystem processes in a disturbed environment will allow for broader comparisons among different ecosystems (Lavorel and Garnier 2002, Mason et al. 2003). A key concept related to functional group diversity is functional redundancy (Naeem 1998). Because functional groups are often defined, at least partially, by the role each group plays in ecosystem function, high diversity of functional groups would provide a buffer (i.e. insurance) against localized extinction of a single species adversely affecting ecosystem function (Naeem 1998). In ecosystems subjected to long term frequent disturbances, within functional group diversity would be an indirect measure of the potential resilience of that ecosystem (Yachi and Loreau 1999). Unlike previous studies that defined functional group richness in terms of the number of functional groups present (e.g. Diaz and Cabido 2001, Tilman 2001), I examined the relationship between **within** functional group richness and disturbance. I believed that within functional group richness is a better measure of functional redundancy and ecosystem resilience in response to disturbance than total species richness (Naeem 1998). For this study, I selected functional groups comprised of species with similar physiology and effects on ecosystem processes. These functional groups were C_4 grasses, C_3 grasses, forbs, legumes, and woody plants.

I predicted that the two types of disturbance will act synergistically to modify plant community structure by shifting functional group abundance and altering within-functional group diversity. Because functional groups tend to differ in their tolerance of environmental conditions and therefore in their profile of physiological traits (Lavorel et al. 1997, Rusch et al. 2003), I expected that the two disturbance types would have interacting rather than additive effects on total community structure.

To investigate these predictions I asked the following questions:

1. How do different levels of disturbance from military vehicle maneuvers affect individual plant functional group abundance and within group diversity?
2. How does fire frequency affect individual plant functional group abundance and diversity?
3. Do fire and vehicle maneuvers interact to alter plant functional group abundance and diversity?

METHODS

Study Site

The study was conducted in the predominantly rural Piedmont physiographic province of Virginia, USA (37-04-27.100N / 077-57-27.100W) approximately 100 kilometers southwest of Richmond and 5 kilometers east of the town of Blackstone at the 16,592 ha Army National Guard Maneuver Training Center-Fort Pickett (Fig. 2-1). The United States Government purchased this land in 1941 to create a military training site for World War II (Fort Pickett Integrated Natural Resource Management Plan 2006). The current mission of Fort Pickett is to provide a training center capable of handling live-fire and maneuver training requirements for brigade-sized combat.

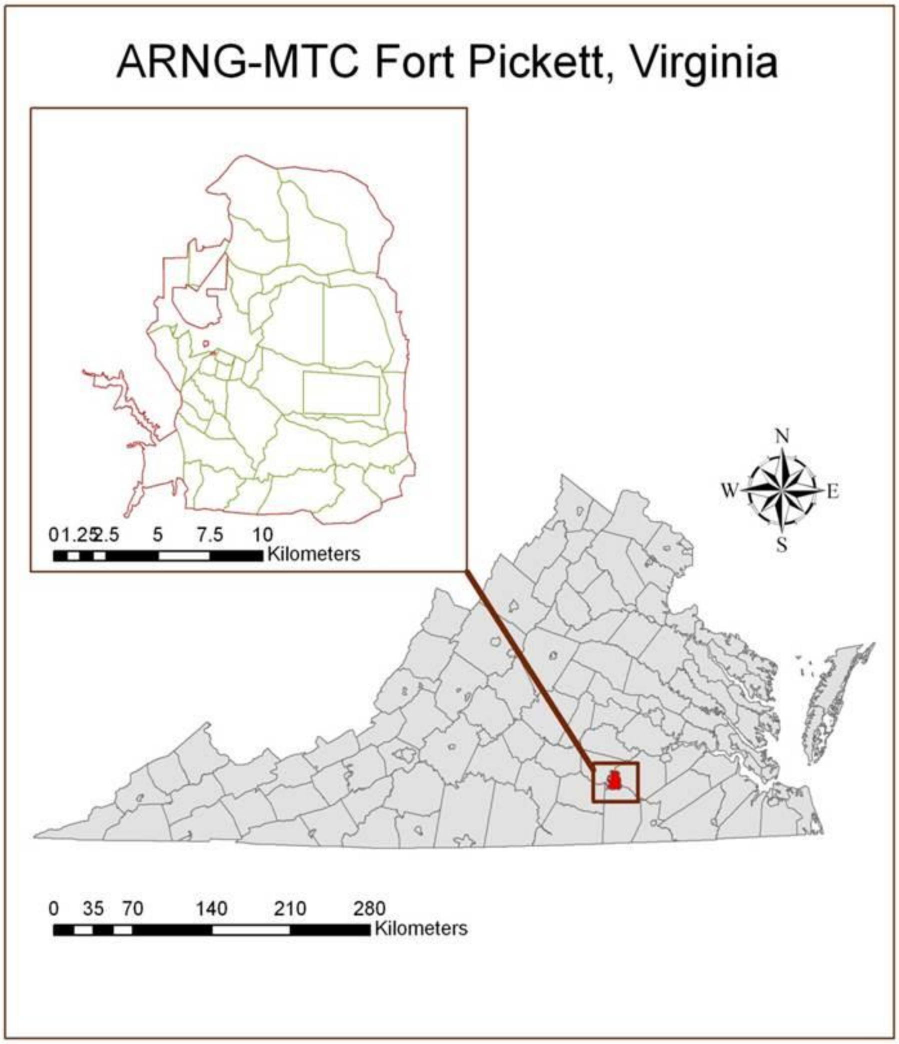

Fig 2-1. Location of the study site. The 16,592 ha Army National Guard Maneuver Training Center-Fort Pickett (Fort Pickett).

Environmental Setting

The climate is temperate with hot, humid summers and mild winters with frequent short cold spells (National Climatic Data Center 1999). The mean annual temperature is 14.4°C, with a mean maximum of 20°C and mean minimum of 8.8°C. Precipitation is well distributed throughout the year with an annual mean of 115 cm. Most upland soils at Fort Pickett are non-hydric, infrequently flooded Ultisols, and have a slow to moderate infiltration rate. Loams and sandy loams are the most common soil types with organic matter fraction ranging from 2 - 10%. The majority of these soils support forest vegetation under undisturbed conditions (Nicholson 1998).

Humans occupied the region in which Fort Pickett is located for at least 12,000 years B.P.[2] (The College of William and Mary 1995). Europeans began to construct permanent settlements in and around the present day Fort Pickett in the late seventeenth century. By the late eighteenth century large plantations cultivating tobacco, wheat, corn, and livestock had developed in the regions of present day Fort Pickett (The College of William and Mary 1995). The establishment and growth of these large plantations is exemplified by the fact that the slave population outnumbered the free in Nottoway, Lunenburg, Brunswick, and Dinwiddie Counties at end of the eighteenth century and by the mid nineteenth- century, African-American slaves outnumbered whites by a three-to-one ratio in Nottoway County. After the Civil War and emancipation southside Virginia and the Fort Pickett region specifically, became an important area for tobacco production on small to medium sized farms. Small farming dominated the region's economy and land use until the onset of World War II.

[2] A putative pre-Clovis site (Cactus Hill) has been identified approximately 25 miles east of Fort Pickett which if confirmed extends the date of human occupation in the region to approximately 16,000 years B.P. (Wagner and McAvoy 2004)

Indirect evidence suggests that the land which became Fort Pickett had substantially lower forest cover at the time of acquisition than it does today. The United States Government purchased land totaling approximately 45,000 acres of southside Virginia land in 1941 from nearly 500 private landowners, corporations, and churches to create what was then known as Camp Pickett displacing approximately 1100 individuals (Installation Design Guide 1992). At the time of the acquisition the land was a mosaic of relatively small (mean parcel size was 87 acres) subsistence farms with crops of tobacco, wheat, corn, and pastures located within a matrix of mixed pine and hardwood forests (Coleburn 1998).

Current vegetation of the region surrounding Fort Pickett is part of the oak-hickory-pine region described by Braun (1950). However, because of the unique disturbances associated with the long history of military training at Fort Pickett the uplands are a unique mosaic of open forests, woodlands, shrublands, and grassland plant communities (Emrick and Jones 2008). There are 1128-ha of grasslands dominated by native grasses such as *Schizachyrium scoparius, Sorghastrum nutans* and *Panicum spp*. (Barden 1997) interspersed with 669-ha of shrublands comprised of native woody and herbaceous species (Dorr et. al 2007). Frequent fires from military training have resulted in over 400-ha of mixed deciduous and coniferous woodlands with an open understory dominated by native grasses and forbs (Dorr et al. 2007). Many of these plant communities are uncommon or absent altogether in the surrounding Piedmont and several are considered state and/or globally rare (Fleming and Patterson 2012).

Military Disturbance-Fort Pickett

Military vehicles used for maneuver training at Fort Pickett range in size from the tracked 68-ton M1A1Abrams main battle tank and tracked 25- ton M2A2 Bradley fighting vehicle to the wheeled HMMV and 5-ton truck. The distribution of the vehicle disturbance is constrained by terrain features such as tree size and density, slope, presence of wetlands and cultural features. Thus, the distribution of vehicle disturbance occurs across the landscape in an identifiable pattern, which has remained relatively constant over the life of the installation, even as military vehicles have changed over the years.

Military live fire training (i.e. artillery, flares, and tracer rounds) began at Fort Pickett in 1942 and has occurred in most years, periodically igniting vegetation within buffer (i.e. safety) zones surrounding the live fire ranges. The combined buffer zones or Controlled Access Area (CAA) comprises an area of approximately 4521-ha in which wildfires are allowed to burn unhindered if there is no threat to range buildings or property (Fort Pickett Integrated Natural Resource Management Plan 2006). This policy has generally been in effect since the creation of Fort Pickett and has resulted in an assortment of fire influenced plant communities. Training-caused wildfires can occur at any time of the year, but are more common from early fall through early spring and vary in frequency and intensity depending upon fuel accumulation and weather. Military training caused wildfires outside of the CAA are rare and are immediately contained. However, prescribed fire is used extensively outside of the CAA to manage fuel loads, improve wildlife habitat, and manage training land. Because prescribed fire, outside of the CAA, has been used haphazardly over the life of the installation, its influence on plant communities is not as pronounced (Fort Pickett Integrated Natural Resource Management Plan 2006).

Data Collection

Fort Pickett maintains a series of 130 ecological monitoring sites across the landscape to monitor the effect of military training on vegetation composition and land condition. These sites were originally allocated in a stratified random manner using the potential for disturbance from fire (wildfire or prescribed) and/or military maneuvers as the strata (Fort Pickett Range and Training Land Assessment 2007) and thus encompassing the full range of potential disturbance that occurs at Fort Pickett. I assessed the applicability of the original 130 sites to my research questions and eliminated 21 due to ongoing construction and land rehabilitation activities. I used the remaining 109 sites for my study.

To determine plant functional group composition and diversity I used fixed area vegetation plots at each of the 109 sites. Using species area curves to ensure efficient sampling for species diversity, I chose plot sizes of 100 m^2 in grasslands and shrublands and 400 m^2 in forests and woodlands. For each species in the plots, I estimated vegetative cover using a modified Braun-Blanquet cover abundance scale (+ = 0-1%, 1 = 1-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-95%, 6 = 95-100%) (Bonham 1989). To maximize my ability to identify all species, all plots were surveyed during the height of the growing season in the summer of 2005.

I used a modified point intercept method to quantitatively assess the military maneuver disturbance at each plot location. Two 25 m transects crossing at plot center and running in cardinal directions were constructed to measure directly (wheeled, tracked, unidentified vehicular pass) and indirectly (bare soil and leaf litter) the military vehicle disturbance within and immediately adjacent to the plot. Every meter a small diameter steel rod was lowered and the disturbance type (direct) and ground cover (indirect) at that point was recorded. I used the Fort Pickett Integrated Natural Resources Management Plan (2006), GIS records, and personal observations since early 1994 to calculate a fire frequency for each plot location.

Data Analysis

Using raw plot data, I placed all plant species identified into one of five functional groups (C_4 grasses, C_3 grasses, forbs, legumes, and woody plants). Plant functional group cover was calculated by summing the class midpoints for the observed cover abundance value for each member species in each plot. I calculated species richness within each functional group and for all groups combined on a per plot basis by summing the total number of species in each group.

I summarized raw disturbance data by calculating the frequency of "hits" along each transect for both the direct measures and indirect measures. The direct measures of vehicle maneuver disturbance were combined into a single "vehicle pass" category due to the difficulty of discerning tracked and wheeled vehicle passes in the field. Fire frequency data were expressed as the number of fires calculated to have occurred at that location during a 10 year period from 1994 to 2004 (Peterson et al. 2007).

I used Canonical Correspondence Analysis (CCA) to explore the relationships between functional group cover, richness, and the measures of disturbance (vehicle pass, bare soil, leaf litter, and fire frequency) using the program CANOCO (ter Braak 1998). A Monte Carlo test was used to test whether the canonical axes were significant ($P < 0.05$).

I used regression analyses to explore the relationship between disturbance and functional group cover and diversity. Prior to univariate statistical analyses, I used a Shapiro-Wilks Test to test for normality of all data. All vegetation and disturbance data exhibited non-normal distributions. Each variable was square root transformed prior to analysis following the recommendations of Gotelli and Ellison (2004). All but two direct measures of disturbance - fire frequency (FF) and vehicle pass frequency (VPF) - varied collinearly. I used these uncorrelated

(FF and VPF) variables in a stepwise multiple linear regression (forward selection) to examine the relationship of linear combinations of the direct disturbance variables and plant functional group cover and diversity.

RESULTS

In the first CCA (relating species cover by functional group with disturbance measures), the first and second canonical axes explained 94.9 percent of the functional group cover and environmental (disturbance) relationship. The Monte Carlo test demonstrated a significant relationship between functional group cover and environmental variables on the first canonical axis *(F-ratio = 29.381, P-value = 0.0020)* and with all canonical axes (*F-ratio = 8.675, P-value = 0.0020*). An examination of the biplot of the first CCA showed that functional groups were distributed along two primary axes related to disturbance. The vertical (Y) axes corresponded to the type of disturbance (vehicle maneuvers, fire frequency) whereas the horizontal (X) axes represented a gradient of the intensity level of disturbance (Fig. 2-2). The cover of legumes and C_3 grasses were positively related to high levels of disturbances, with legumes positively influenced by fire and C_3 grasses favored by vehicle maneuvers. Forbs and C_4 grass abundance were positively related to both fire and vehicle maneuvers. In only one functional group, woody plants, was cover negatively related to intensity of both kinds of disturbance[3].

[3] See Appendix A for complete list of plant species identified and their functional classification.

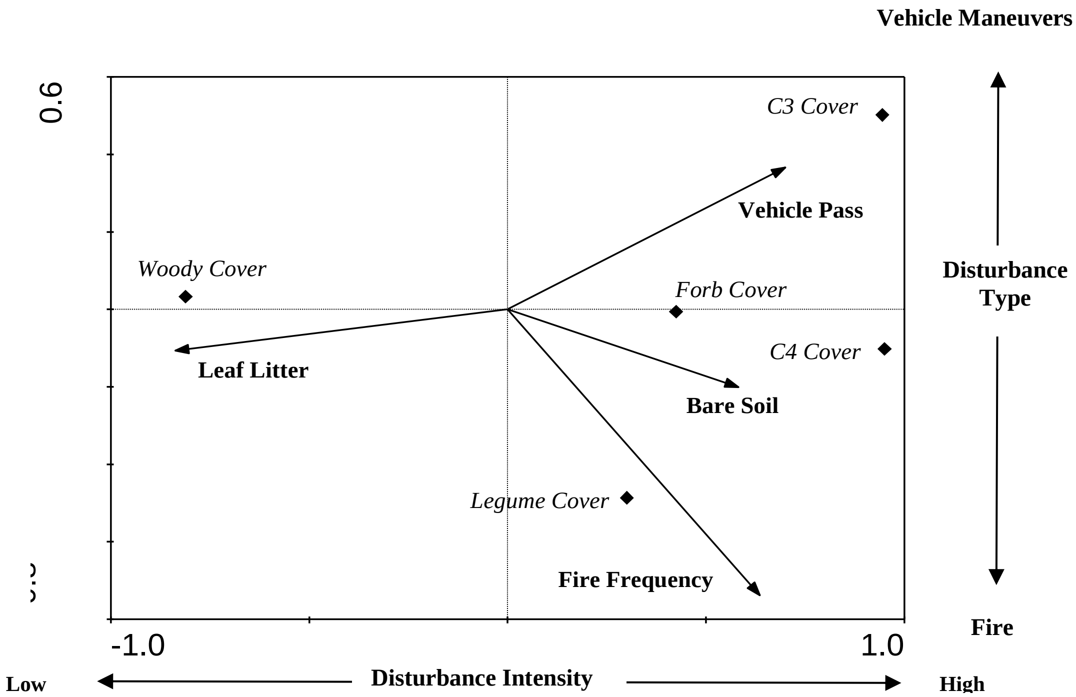

Fig 2-2. Biplot of functional group cover, by functional group, and disturbance (i.e. environmental) variables. The first and second canonical axes explained 94.9 percent of the species environment relationship. Monte Carlo test shows a significant relationship between species and environmental variables on the first canonical axis *(F-ratio = 29.381, P-value = 0.0020)*. All canonical axes are significant (*F-ratio = 8.675, P-value = 0.0020*).

In the second CCA (relating species richness by functional group with disturbance measures) the first canonical axis explained 83.4 percent of the species richness environmental (i.e., disturbance) relationship. The Monte Carlo test showed a significant relationship between species richness and environmental variables on the first canonical axis *(F-ratio = 16.650, P-value = 0.0020)* and with all canonical axes (*F-ratio = 5.443, P-value = 0.0020*). The biplot of the second CCA analysis showed that functional groups were distributed along two primary axes related to disturbance. As in figure 2-2, the vertical (Y) axes corresponded to the type of disturbance (vehicle maneuvers, fire frequency) whereas the horizontal (X) axes represented a gradient of the intensity level of disturbance (Fig. 2-3). The biplot of functional group richness was similar to the biplot of functional group cover.

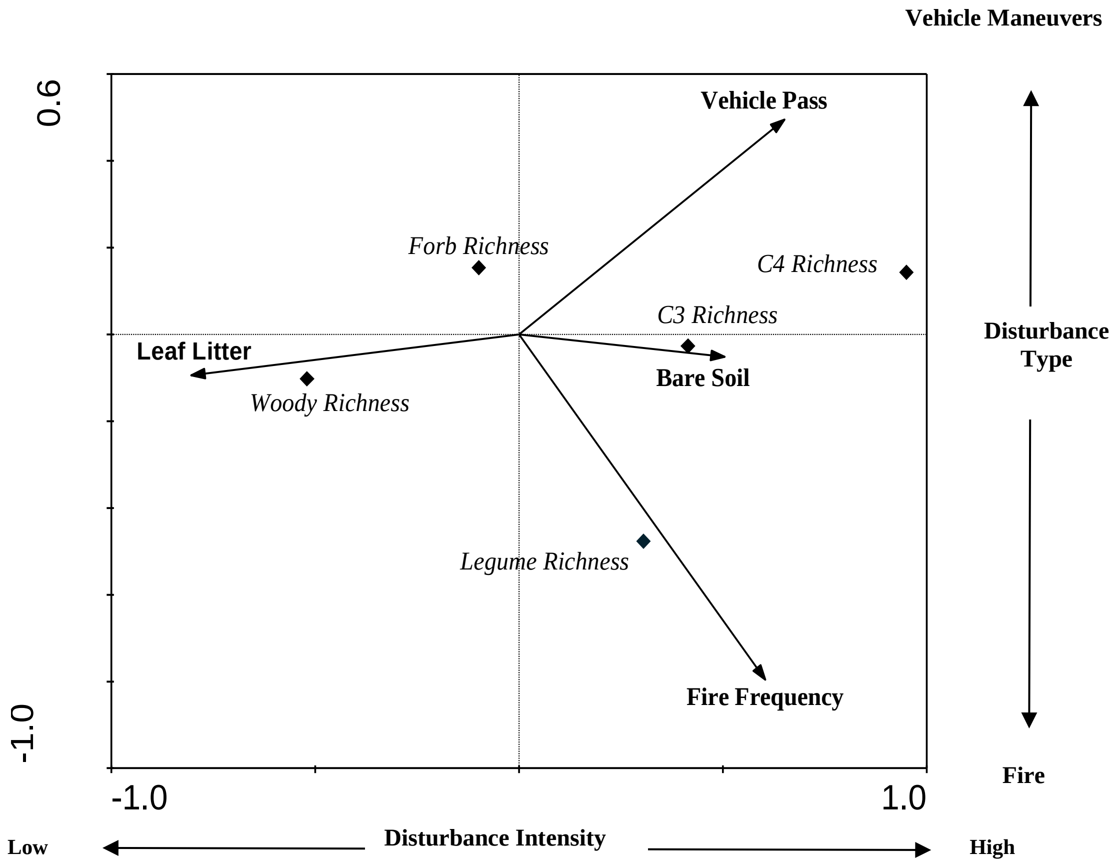

Fig 2-3. Biplot of functional group richness, by functional group, and disturbance (i.e. environmental) variables. The first canonical axis explained 83.4 percent of the species environment relationship. Monte Carlo test shows a significant relationship between species and environmental variables on the first canonical axis *(F-ratio = 16.650 , P-value = 0.0020)*. All canonical axes are also significant (*F-ratio = 5.443, P-value = 0.0020*).

The results of CCA guided my selection of the two direct measures of disturbance, vehicle pass and fire frequencies (VPF and FF) as explanatory variables in the multiple regression analysis.

Only C_4 grass species richness ($P < 0.05$, F – *ratio* 11.53, $r^2 = 0.27$) was positively related to a linear combination of both FF and VPF. Legume species richness ($P < 0.05$, F –

ratio 14.26, r^2 = 0.21) and C_3 grass species richness (*$P < 0.05$, F – ratio 5.40, r^2 = 0.09)* were positively related to just FF. Conversely, forb species richness (*$P < 0.05$, F – ratio 3.91, r^2 = 0.07)* and woody species richness (*$P < 0.05$, F – ratio 6.56, r^2 = 0.11)* were negatively related to VPF and showed no significant relationship to FF (Table 2-1). Total species richness *($P < 0.05$, F – ratio 9.53, r^2 = 0.10)* was negatively related to just VPF.

Table 2-1. Effects of the interaction of fire frequency and vehicle pass frequency on species richness of plant functional groups at Fort Pickett, Va.

Plant Functional Group Richness	**Disturbance Type**				**Total Model**
	Vehicle Pass Frequency		Fire Frequency		
	p - value	β_1	p - value	β_1	r^2
C4 Grasses	0.00	2.76	0.00	6.18	0.27
C3 Grasses	0.20	--	0.00	3.39	0.09
Forbs	0.01	-1.72	0.59	--	0.07
Legumes	0.21	--	0.00	5.63	0.21
Woody	0.00	-3.63	0.36	--	0.11
Total	0.00	-2.51	0.08	--	0.10

Multiple regression analysis showed that there was a significant ($P < 0.05$) positive relationship between C_4 grass cover (*F – ratio 18.84, r^2 = 0.26)* and a linear combination of FF and VPF (Table 1). Forb cover (*F – ratio 5.28, r^2 = 0.05)* and legume cover *(F – ratio 9.24, r^2 = 0.08*) were positively related to FF and C_3 grass cover (*$P < 0.05$, F – ratio 12.12, r^2 = 0.10)* was positively related to VPF (Table 2). Woody cover showed a significant ($P < 0.05$) negative relationship (*F – ratio 22.05, r^2 = 0.30)* with the linear combination of FF and VPF (Table 2-2).

Table 2-2. Effects of the interaction of fire frequency (FF) and vehicle pass frequency (VPF) on cover of plant functional group at Fort Pickett, Va.

Plant Functional Group Cover	Disturbance Type				Total Model
	Vehicle Pass Frequency		Fire Frequency		
	p - value	β_1	p - value	β_1	r_2
C4 Grasses	0.00	2.61	0.00	5.49	0.26
C3 Grasses	0.00	2.06	0.31	--	0.10
Forbs	0.329	--	0.024	1.59	0.02
Legumes	0.99	--	0.00	2.75	0.08
Woody	0.00	-3.76	0.00	-4.18	0.30

DISCUSSION

Plant Functional Groups and Disturbance

As predicted, I found that military disturbance influenced the abundance and diversity of plant functional groups, which is consistent with previous work (Dale et. al 2002, Hirst et al. 2003, Althoff and Thien. 2005, Hirst et al. 2005). Furthermore, I found evidence that plant functional groups responded differently to the interactions of military disturbance based upon the traits of each group. The results of the CCA (Fig. 2-2) revealed that two direct measures of disturbance, vehicle pass frequency (VPF) and fire frequency (FF) exerted a significant influence on functional group cover and further differentiated based upon the intensity of disturbance.

Because legumes fix nitrogen and therefore have large effects on ecosystem function, I was particularly interested in their responses to disturbance. Nitrogen in living plants and soil organic matter is volatilized by fire at relatively low temperatures, thus the ability of legumes to fix atmospheric N_2 confers a competitive advantage in areas where moderate intensity fires are common (Reich et al. 2001). In addition, many species of legume require fire to scarify the seeds and reduce competition for other resources (Hendricks and Boring 1999). Legume cover showed a positive but relatively weak statistical relationship with FF (Table 2-2). However, legume cover was not related, negatively or positively, with VPF at Fort Pickett though some of the effects of vehicle maneuvers (e.g. destruction of biomass, increase in bare ground) are similar to those caused by fire. Frequent fire, particularly in the southeastern United States, generally has a positive effect on legume abundance and though the correlation I found at Fort Pickett was weak it was is consistent with previous findings (Christensen 1981, Hendricks and Boring 1999, Lajeunesse et al. 2006).

The positive response of C_3 grass and forb cover to relatively high intensity military vehicle disturbance in the CCA analysis (Fig. 2-2) was consistent with multiple linear regression results, though the correlations were weak (Table 2-2). No significant relationships were found between C_3 grass or forb cover and FF. Many C_3 grass and forb species are weedy and/or invasive and tend to respond to soil disturbance such as that caused by military maneuvers (Quist et al. 2003). Disturbance caused by military vehicle maneuvers damages vegetation and exposes mineral soil and the spatial and temporal extent of bare soil is directly related to the intensity of vehicle maneuvers (Hirst 2003). Both fire and military maneuvers expose soil, though the manner in which each disturbance acts is distinctly different. Moderate to intense fires expose soil by combusting the above ground vegetation and exposing mineral soil. However, military vehicles (particularly tracked vehicles) “churn” the top 10-30 cm of the soil profile including vegetation, exposing not only soil but buried seeds, rhizomes, and other reproductive organs. Thus, the exposed and churned soils resulting from vehicle maneuvers provide an ideal environment for forbs and C_3 grasses to colonize either through seed or vegetative reproduction (Hirst et al. 2003, Renne and Tracy 2007).

As expected, woody plant cover was negatively affected by disturbance (Fig. 2-2, Table 2-2). At low frequencies of disturbance, woody species dominated the herbaceous (0-1 m) and shrub (1-3 m) strata. However, across my study area, disturbance was nonetheless sufficient to keep a closed canopy forest from developing. This low level of disturbance allowed a dense coppice growth of woody species to occur that resembles, in composition and physiognomy, a 2 - 4 year old regenerating southeastern piedmont forest following a canopy replacing disturbance such as logging or blow-down. However, unlike a regenerating forest, which will eventually form a closed canopy forest, low level military disturbance perpetuates this “shrubland” community of coppice growth of canopy species and is unique to military installations. However, at moderate levels of disturbance the differential effects of disturbance type (fire vs. vehicle) on woody plant cover was most apparent. In areas of Fort Pickett where there was a moderate fire frequency (i.e. ~ 3-year return interval), overall woody plant cover decreased primarily in the herbaceous and shrub strata with a lower effect on mature trees resulting in open savannas. Conversely moderate levels of vehicle disturbance decreased woody plant cover in all strata. At high VPF and FF woody cover was substantially reduced or eliminated as would be expected.

The positive response of C_4 grass cover to fire (Table 2-2) is consistent with other studies. Fire generally favors the establishment of all types of grasslands at the expense of woody species, while growing season burns give C_4 grasses a competitive advantage over C_3 grasses and forbs (Towne and Owensby 1984, Collins 1992). At Fort Pickett, areas with the highest FF were dominated by C_4 grasses and resembled historic eastern native prairies (Barden 1997). As VPF increases, even in areas of high FF, forbs and C_3 grasses increase in abundance though C_4 grass cover remains high.

The positive relationship between C4 grass cover and VPF was unexpected. The resilience of perennial C4 grasses likely results from their extensive perennial root systems, which were left intact when the soil disturbance caused by vehicle maneuvers crushed or buried above ground vegetation. The intact root systems allowed C_4 grasses to regrow relatively quickly, even though mounded soil caused by vehicle maneuvers (Rogers and Hartnett 2001b). Furthermore, the majority of vehicle maneuvers at Fort Pickett occur during the spring and summer often during periods of high temperature and increased water stress, which would favor growth of C_4 grasses over C_3 grasses or forbs (Fort Pickett Range and Training Land Assessment 2007). Thus, vehicle maneuvers coupled with occasional fires would favor the development and maintenance of C_4 grass dominated plant communities in areas of relatively high VPF and FF suggesting that the traits of C_4 grasses, such as water use efficiency, make them well suited for environments where multiple disturbances occur. Only in those areas of Fort Pickett where VPF is most intense do annual Forbs and C_3 grasses supplant C_4 grasses as the dominant functional group.

Diversity and Disturbance

One of the key roles of biodiversity is to provide insurance against the loss of key ecosystem processes by providing functional redundancy (Walker 1995, Yachi and Loreau 1999). At Fort Pickett, I found that within functional group richness was related to direct measures of disturbance (Fig. 2-3), but each functional group responded differently to each type of disturbance, presumably depending upon the traits of that functional group. There was a relatively weak positive relationship between C_3 grass richness and FF while woody plant richness and forb richness were negatively related to VPF (Table 2-1). However, the richness of two functional groups, C_4 grasses and legumes, showed relatively strong positive relationships with disturbance (Table 2-1).

Each of these functional groups are important to basic ecosystem processes. The fixation of atmospheric N_2 by legumes in the relatively poor soils at Fort Pickett serves a critical biogeochemical function by maintaining soil fertility. Additionally, C_4 grasses are able to survive stressful growing conditions to provide native perennial vegetative cover that reduces erosion and maintains soil organic matter. However, only C_4 grass richness was positively related to both VPF and FF (Table 2-1). These results suggest that disturbance from military vehicle maneuvers and fire may have opposing effects on ecosystem processes and thus long- term ecosystem function. Military vehicle maneuvers may adversely affect long-term ecosystem resilience at Fort Pickett by suppressing legume richness and by extension, the functional redundancy within this important plant functional group. Conversely, fire may have the opposite effect on ecosystem resilience due to its positive influence on the richness of all herbaceous functional groups.

Single disturbances, such as fire, generally have a positive influence on species diversity through increasing environmental heterogeneity and reducing the competitive ability of dominant species (Peterson and Reich 2008). Frequent, low-to--moderate intensity fires increase species richness in both woodlands and temperate grasslands (Hobbs and Heuneke 1992, Whelan 1995, Turner and Knapp 1996). However, the effect vehicle maneuvers on diversity is unclear. Quist et al. (2003) and Dale et al (2002) both reported a significant decrease in species richness in response to increased disturbance from military vehicle training. Conversely, Shaeffer et al. (1990) reported that plant species diversity was positively correlated with military vehicle disturbance at Fort Riley. Wilson (1988) suggested that the timing of vehicle disturbance is important and may have negative effects on plant diversity when conducted during the early growing season (May and June), which coincides with heaviest training at Fort Pickett (Range and Training Land Assessment 2007). I found that total species richness was negatively correlated with VPF, although the relationship was not very strong (Table 2-1). Conversely, I found no significant relationship between FF and total species richness (Table 2-1). At Fort Pickett, the negative effect of vehicle disturbance on species richness appears to counteract the positive effects of fire within plant communities. However, at Fort Pickett, as with many other military installations, the total area of severe vehicle disturbance (i.e. high VPF) is relatively small compared to the overall size of the installation (Demaris et al 1999, Quist 2003). Thus, at the landscape scale the effect of military vehicle maneuvers coupled with fire increased landscape heterogeneity, which may have an overall positive effect on diversity (Warren et al 2007).

Conclusions

At Fort Pickett, as with other military installations, disturbance caused by landscape level military training (i.e. vehicle maneuvers and fire) interacts spatially and temporally to create a gradient of disturbance intensity across the landscape. Military training of this nature has been occurring on many installations for a number of years thus allowing the biological communities time to adjust their distribution and occurrence in response to the unique gradient of disturbance. In this study, I used the unique land use that occurs on military installations to investigate the long-term effect of multiple disturbances on plant functional group abundance and diversity. Because of the unique disturbance regime present on military installations and Fort Pickett specifically (> 60 years of consistent disturbance patterns), I investigated not only the effects of long-term disturbance but the effect of their interaction on functional group abundance and diversity. I chose functional groups (C_4 grasses, C_3 grasses, forbs, legumes, and woody plants) that consisted of species with similar physiology and effects on ecosystem processes. At Fort Pickett the disturbances associated with military training, fire and vehicle maneuvers, have occurred consistently for over 60 years, allowing time for the system to reach a new equilibrium with respect to species distributions and ecosystem processes. My study showed that two distinct disturbances associated with military training, vehicle maneuvers, and fire; do affect functional group abundance, within functional group richness, and total species richness. In general, non-woody functional groups increased in abundance as both types of disturbance increased and within functional group richness, a measure of functional redundancy, generally increased in response to fire and decreased in response to military vehicle disturbance.

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APPENDIX A: Species and Functional Group Classification

Table A.1. List of all species identified during the field survey and their functional group classification.

Species	Functional Group	Species	Functional Group
Agrostis gigantea	C_3 grasses	*Parthenocissus quinquefolia*	Forb
Agrostis hyemalis	C_3 grasses	*Passiflora incarnata*	Forb
Aira caryaphylla	C_3 grasses	*Passiflora lutea*	Forb
Aira elegans	C_3 grasses	*Penthorum sedoides*	Forb
Aira spp.	C_3 grasses	*Phryma leptostachya*	Forb
Anthoxanthum odoratum	C_3 grasses	*Physalis virginia*	Forb
Bromus ciliatus	C_3 grasses	*Phytolacca americana*	Forb
Bromus commutatus	C_3 grasses	*Phytolacca americana*	Forb
Bromus japonicus	C_3 grasses	*Pilea pumila*	Forb
Carex amphibola	C_3 grasses	*Plantago aristata*	Forb
Carex annectans	C_3 grasses	*Plantago lanceolata*	Forb
Carex caroliniana	C_3 grasses	*Plantago major*	Forb
Carex cephalophora	C_3 grasses	*Podophyllum peltatum*	Forb
Carex crinita	C_3 grasses	*Polemonium reptans*	Forb
Carex debilis	C_3 grasses	*Polemonium van-bruntiae*	Forb
Carex hirsutella	C_3 grasses	*Polygala nuttallii*	Forb
Carex lupulina	C_3 grasses	*Polygonatum biflorum*	Forb
Carex scoparia	C_3 grasses	*Polygonatum canaliculatum*	Forb
Carex spicata	C_3 grasses	*Polygonum sagittatum*	Forb
Carex styloflexa	C_3 grasses	*Polystichum acrostichoides*	Forb
Carex swanii	C_3 grasses	*Potentilla canadensis*	Forb
Chasmanthium latifolium	C_3 grasses	*Potentilla simplex*	Forb
Cyperus ovularis	C_3 grasses	*Prunella vulgaris*	Forb
Cyperus strigosus	C_3 grasses	*Pteridium aquilinum*	Forb
Dactylis glomerata	C_3 grasses	*Pycanthemum incanum*	Forb
Danthonia sericea	C_3 grasses	*Pycanthemum tenuifolium*	Forb
Danthonia spicata	C_3 grasses	*Ratibida pinnata*	Forb
Elymus canadensis	C_3 grasses	*Rhexia mariana*	Forb
Elymus virginicus	C_3 grasses	*Rhexia virginica*	Forb
Festuca eliator	C_3 grasses	*Rosa carolina*	Forb
Festuca obtusa	C_3 grasses	*Rosa multiflora*	Forb
Festuca paradoxa	C_3 grasses	*Rosa palustris*	Forb
Glyceria spp.	C_3 grasses	*Rosa virginiana*	Forb

Holcus lanatus	C_3 grasses	*Rubus flagellaris*	Forb
Hordeum vulgare	C_3 grasses	*Rubus spp.*	Forb
Hystrix patula	C_3 grasses	*Rudbeckia hirta*	Forb
Juncus coriaceus	C_3 grasses	*Rudbeckia laciniata*	Forb
Juncus effusus	C_3 grasses	*Rudbeckia serotina*	Forb
Juncus platyphyllus	C_3 grasses	*Ruellia caroliniensis*	Forb
Juncus tenuis	C_3 grasses	*Rumex acetosella*	Forb
Leersia oryzoides	C_3 grasses	*Rumex crispus*	Forb
Panicum acuminatum	C_3 grasses	*Salvia lyrata*	Forb
Panicum boscii	C_3 grasses	*Sanicula canadensis*	Forb
Panicum clandestinum	C_3 grasses	*Saxifraga virginiensis*	Forb
Panicum commutatum	C_3 grasses	*Scutellaria epilobiifolia*	Forb
Panicum depauperatum	C_3 grasses	*Scutellaria integrifolia*	Forb
Panicum dichotomum	C_3 grasses	*Scutellaria ovata*	Forb
Panicum lanuginosum	C_3 grasses	*Sedum spp.*	Forb
Panicum laxiflorum	C_3 grasses	*Senecio anonymus*	Forb
Panicum scoparium	C_3 grasses	*Senecio aureus*	Forb
Panicum sphaerocarpon	C_3 grasses	*Seriocarpus asteroides*	Forb
Poa pratensis	C_3 grasses	*Sida spinosa*	Forb
Poa spp.	C_3 grasses	*Silphium compositae*	Forb
Scirpus atrovirens	C_3 grasses	*Silphium trifoliatum*	Forb
Scirpus georgianus	C_3 grasses	*Sisyrinchium angustifolium*	Forb
Scirpus spp.	C_3 grasses	*Smilacina racemosa*	Forb
Scleria pauciflora	C_3 grasses	*Smilax bona-nox*	Forb
Sphenopholis intermedia	C_3 grasses	*Smilax rotundifolia*	Forb
Sphenopholis obtusata	C_3 grasses	*Smilax walterii*	Forb
Triticum aestivum	C_3 grasses	*Solanum carolinense*	Forb
Typha spp.	C_3 grasses	*Solidago altissima*	Forb
Vulpia octoflora	C_3 grasses	*Solidago graminifolia*	Forb
Andropogon gerardi	C_4 grasses	*Solidago hispida*	Forb
Andropogon virginicus	C_4 grasses	*Solidago odora*	Forb
Cynodon dactylon	C_4 grasses	*Solidago pinetorum*	Forb
Digitaria spp.	C_4 grasses	*Solidago rugosa*	Forb
Eragrostis curvula	C_4 grasses	*Solidago speciosa*	Forb
Eragrostis pilosa	C_4 grasses	*Solidago tenuifolia*	Forb
Eragrostis spectabilis	C_4 grasses	*Sonchus arvensis*	Forb
Erianthus alopecuroides	C_4 grasses	*Specularia perfoliata*	Forb
Gymnopogon ambiguus	C_4 grasses	*Spiraea tomentosa*	Forb
Leptoloma cognatum	C_4 grasses	*Spiranthes gracilis*	Forb
Microstegium verminium	C_4 grasses	*Streptopus amplexifolius*	Forb
Panicum anceps	C_4 grasses	*Strophostyles umbellata*	Forb
Panicum clandestinum	C_4 grasses	*Tephrosia spicata*	Forb

Panicum virgatum	C_4 grasses	*Thalictrum spp.*	Forb
Paspalum setaceum	C_4 grasses	*Thelypteris spp.*	Forb
Paspalum spp.	C_4 grasses	*Toxicodendron radicans*	Forb
Schizachyrium scoparium	C_4 grasses	*Tragopogon pratensis*	Forb
Setaria viridis	C_4 grasses	*Trillium pusillum*	Forb
Sorghastrum nutans	C_4 grasses	*Urtica dioica*	Forb
Tridens flavus	C_4 grasses	*Uvularia perfoliata*	Forb
Achillea millefolium	Forb	*Uvularia sessilifolia*	Forb
Agalinis tenuifolia	Forb	*Verbascum thapsus*	Forb
Agrimonia gryposepala	Forb	*Verbena urticifolia*	Forb
Agrimonia parviflora	Forb	*Vinca minor*	Forb
Agrimonia rostellata	Forb	*Viola triloba*	Forb
Allium vineale	Forb	*Woodwardia areolata*	Forb
Ambrosia artemisiifolia	Forb	*Woodwardia virginica*	Forb
Angelica venenosa	Forb	*Yucca filamentosa*	Forb
Antennaria neglecta	Forb	*Amphicarpa bracteata*	Legume
Antennaria parlinii	Forb	*Baptisia tinctoria*	Legume
Antennaria plantaginifolia	Forb	*Cassia fasciculata*	Legume
Apocynum cannabinum	Forb	*Cercis canadensis*	Legume
Arisaema atrorubens	Forb	*Clitoria mariana*	Legume
Asclepias amplexicaulis	Forb	*Desmodium canescens*	Legume
Asclepias syriaca	Forb	*Desmodium ciliare*	Legume
Asclepias tuberosa	Forb	*Desmodium dillenii*	Legume
Asplenium platyneuron	Forb	*Desmodium glabellum*	Legume
Aster dumosus	Forb	*Desmodium nudiflorum*	Legume
Aster paternus	Forb	*Desmodium paniculatum*	Legume
Aster pilosus	Forb	*Desmodium rotundifolium*	Legume
Aster vimineus	Forb	*Desmodium sessilifolium*	Legume
Athyrium filix-femina var. asplenioides	Forb	*Lathyrus hirsutus*	Legume
Bidens coronata	Forb	*Lespedeza bicolor*	Legume
Bigonia capreolata	Forb	*Lespedeza cuneata*	Legume
Boehmeria cylindrica	Forb	*Lespedeza hirta*	Legume
Botrychium virginianum	Forb	*Lespedeza intermedia*	Legume
Campsis radicans	Forb	*Lespedeza procumbens*	Legume
Centaurea maculosa	Forb	*Lespedeza repens*	Legume
Ceonothus americanus	Forb	*Lespedeza violacea*	Legume
Chimaphila maculata	Forb	*Lespedeza virginica*	Legume
Chrysanthemum leucanthemum	Forb	*Medicago lupulina*	Legume

Circaea lutetiana	Forb	*Pueraria lobata*	Legume
Cirsium discolor	Forb	*Robinia pseudo-acacia*	Legume
Cirsium pumilum	Forb	*Stylosanthes biflora*	legume
Cirsium vulgare	Forb	*Trifolium agrarium*	Legume
Commelina virginica	Forb	*Trifolium arvense*	Legume
Conopholis americana	Forb	*Trifolium pratense*	Legume
Convolvulus arvensis	Forb	*Trifolium repens*	Legume
Coreopsis verticillata	Forb	*Vicia cracca*	Legume
Cryptotaenia canadensis	Forb	*Acer barbatum*	Woody
Cunila origanoides	Forb	*Acer negundo*	Woody
Cuscuta gronovii	Forb	*Acer rubrum*	Woody
Daucus carota	Forb	*Ailanthus altissima*	Woody
Desmodium canadense	Forb	*Albizia julibrissin*	Woody
Dianthus armeria	Forb	*Alnus serrulata*	Woody
Diodia teres	Forb	*Amelanchier arborea*	Woody
Dioscorea villosa	Forb	*Aralia spinosa*	Woody
Elephantopus tomentosus	Forb	*Aronia arbutifolia*	Woody
Erigeron annuus	Forb	*Asimina triloba*	Woody
Erigeron canadensis	Forb	*Betula nigra*	Woody
Erigeron strigosus	Forb	*Carpinus caroliniana*	Woody
Eupatorium album	Forb	*Carya cordiformis*	Woody
Eupatorium cappilifolium	Forb	*Carya glabra*	Woody
Eupatorium godfreyanum	Forb	*Carya ovata*	Woody
Eupatorium hyssopifolium	Forb	*Carya tomentosa*	Woody
Eupatorium leucolepis	Forb	*Castanea pumila*	Woody
Eupatorium perfoliatum	Forb	*Celtis laevigata*	Woody
Eupatorium pubescens	Forb	*Celtis occidentalis*	Woody
Eupatorium rotundifolia	Forb	*Cornus amomum*	Woody
Eupatorium sessilifolium	Forb	*Cornus florida*	Woody
Euphorbia corollata	Forb	*Crataegus spp.*	Woody
Euphorbia maculata	Forb	*Diospyros virginiana*	Woody
Foeniculum vulgare	Forb	*Elaeagnus umbellata*	Woody
Fragaria virginiana	Forb	*Fagus grandifolia*	Woody
Galium aparine	Forb	*Fraxinus americana*	Woody
Galium asprellum	Forb	*Fraxinus pennsylvanica*	Woody
Galium boreale	Forb	*Ilex decidua*	Woody
Galium circaezans	Forb	*Ilex glabra*	Woody
Galium palustre	Forb	*Ilex opaca*	Woody
Galium pilosum	Forb	*Juglans nigra*	Woody
Gamochaeta purpurea	Forb	*Juniperus virginiana*	Woody
Gaultheria procumbens	Forb	*Ligustrum sinense*	Woody
Gaylussacia spp.	Forb	*Liquidambar styraciflua*	Woody
Geranium carolinianum	Forb	*Liriodendron tulipifera*	Woody

Geum canadense	Forb	*Menziesia pilosa*	Woody
Goodyera pubescens	Forb	*Morus rubra*	Woody
Helenium spp.	Forb	*Nyssa sylvatica*	Woody
Helianthus spp.	Forb	*Ostrya virginiana*	Woody
Hemerocallis fulva	Forb	*Oxydendron arboreum*	Woody
Heterotheca aspera	Forb	*Pinus echinata*	Woody
Hexastylis spp.	Forb	*Pinus taeda*	Woody
Hieracium gronovii	Forb	*Pinus virginiana*	Woody
Hieracium venosum	Forb	*Plantanus occidentalis*	Woody
Houstonia purpurea	Forb	*Polonia tomentosa*	Woody
Houstonia tenuifolia	Forb	*Populus heterophylla*	Woody
Hypericum gentianoides	Forb	*Prunus angustifolia*	Woody
Hypericum hypericoides	Forb	*Prunus serotina*	Woody
Hypericum perforatum	Forb	*Prunus serotina*	Woody
Hypericum punctatum	Forb	*Pyrus spp.*	Woody
Hypericum pyramidatum	Forb	*Quercus alba*	Woody
Hypericum spathulatum	Forb	*Quercus coccinea*	Woody
Impatiens pallida	Forb	*Quercus falcata*	Woody
Ipomoea hederacea	Forb	*Quercus imbricaria*	Woody
Ipomoea lacunosa	Forb	*Quercus marilandica*	Woody
Ipomoea pandurata	Forb	*Quercus michauxii*	Woody
Ipomoea purpurea	Forb	*Quercus muehlenbergii*	Woody
Isotria verticillata	Forb	*Quercus phellos*	Woody
Krigia virginica	Forb	*Quercus prinus*	Woody
Lactuca canadensis	Forb	*Quercus rubra*	Woody
Lactuca scariola	Forb	*Quercus stellata*	Woody
Lechea tenuifolia	Forb	*Quercus velutina*	Woody
Lepidium campestre	Forb	*Rhus copallina*	Woody
Liatris squarrosa	Forb	*Rhus glabra*	Woody
Lilium michauxii	Forb	*Rhus michauxii*	Woody
Linaria canadense	Forb	*Salix spp.*	Woody
Linum medium	Forb	*Sassafrass albidum*	Woody
Linum virginianum	Forb	*Staphylea trifolia*	Woody
Lobelia inflata	Forb	*Tilia americana*	Woody
Lonicera japonica	Forb	*Ulmus alata*	Woody
Lycopodium digitatum	Forb	*Ulmus americana*	Woody
Lysimachia ciliata	Forb	*Ulmus rubra*	Woody
Lysimachia quadrifolia	Forb	*Ulmus rubra*	Woody
Malaxis brachypoda	Forb	*Ulmus rubra*	Woody
Malaxis unifolia	Forb	*Ulmus rubra*	Woody
Mitchella repens	Forb	*Vaccinium spp.*	Woody
Mollugo verticillata	Forb	*Viburnum dentatum*	Woody
Monarda fistulosa	Forb	*Viburnum lentago*	Woody
Monotropa uniflora	Forb	*Viburnum nudum*	Woody
Oenothera laciniata	Forb	*Viburnum prunifolium*	Woody

Onoclea sensibilis	Forb	*Viburnum prunifolium*	Woody
Orchis spp.	Forb	*Vitis rotundifolia*	Woody
Osmunda regalis	Forb	*Hedera helix*	Woody
Oxalis europea	Forb	*Vitis aestivalis*	Woody
Oxalis spp.	Forb	*Vitis vulpina*	Woody

CHAPTER 3: Relationships between Soil Physicochemical Properties and Six Decades of Fire and Vehicle Disturbances in the Piedmont of Virginia

ABSTRACT:

I examined soils across a gradient of disturbance types and intensities to determine how two fundamentally different types of disturbance associated with military training – vehicle traffic and fire – independently and jointly influence physical and chemical properties of soil. I found strong effects of vehicle maneuvers on soil physical properties including an increase in bulk density and reduction in soil porosity. Fire also influenced soil physical properties but more indirectly through the reduction of above-ground litter inputs. Impacts on soil chemical properties were more subtle. Extractable Mg, Ca, and K and soil properties associated with these base cations, including base saturation, and pH were each positively related to the intensity of disturbance. Vehicle maneuvers may accelerate biogeochemical cycling by increasing mineralization rates through the physical actions upon vegetation and litter. Fire produces more pronounced effects due to the partial consumption of above-ground vegetation and subsequent rapid mineralization of organic matter and ash. Though many of the measured physicochemical soil properties at Fort Pickett showed statistically significant relationships to disturbance, the strength of these relationships appears to be modulated by influences of previous land use.

INTRODUCTION

Land use practices have profound influences on ecosystem functioning through the modification of the chemical, biological, and physical components of soils (Vitousek et al. 1997). For example, military training and testing activities that alter soil may cause directional changes in desirable ecosystem function, such as production and organic matter stabilization, thereby jeopardizing the sustainability of military installations. There are a wide array of other disturbances that may have similar effects on soils, including trampling by domesticated or wild herding animals (Cumming and Cumming 2003), excavation of burrows by fossorial animals (Gabet et al. 2003), and vehicle passes over soil during agricultural and forestry operations (Block et al. 2002). In each of these examples, physical disturbances cause soil compaction, increase bulk density, reduce porosity, and decrease water holding capacity (Dexter 2003), which negatively affect ecosystem sustainability through increased runoff, erosion, poor soil aeration, lower available volume for rooting, and reduced plant growth (Lipiec and Hatano 2003).

Soil disturbance usually implies a physical alteration or displacement of part of the mineral soil profile. However, other disturbances that don't physically churn or move mineral soil particles, such as fire, can also have profound effects on litter inputs, soil chemistry, and structure. The immediate effect of fire is a function of fire severity, (i.e. duration and intensity), is dependent upon the amount of above-ground vegetation and surface organic matter consumed, and heat transfer to the soil (Certini 2005). Long- term effects are related to not simply fire severity but also fire frequency.

Military training can have multiple and potentially interacting effects on soils that may result in complex patterns in ecosystem response. In the absence of active management and rehabilitation, military exercises can reduce vegetative cover, increase soil erosion, and result in degradation of desirable ecosystem functions (Silveira et al. 2009). Two types of training related disturbances are common on military lands: physical disturbance from large, heavy vehicles maneuvering across the landscape and fire (Trame and Harper 1997, Dale et al 2002). Military maneuvers involve an assortment of vehicles that range from 5-ton (4-mt) wheeled trucks to 65-ton (61-mt) track vehicles and often produce intense localized disturbance through the rapidly executed movements during training exercises. Vehicle maneuvers directly damage plant biomass, can cause substantial soil displacement and compaction, and alter biogeochemical processes (Hirst et al 2005, Althoff and Thien 2005). However, the immediate effect of disturbance, both spatially and temporally, on soil properties is dependent upon vehicle type, the manner of travel (straight line vs. turn), soil type, soil moisture, and other environmental factors (Ayers 1994, Hirst 2003, Althoff and Thien 2005). Vehicle maneuvers do not occur across the landscape as a series of stochastic events but in specific locations and frequencies dictated by the training scenario(s) and are constrained by terrain features such as tree size and density, slope, presence of wetlands, and other hydrological obstacles to movement (Demaris et al 1999).

Disturbance from maneuver training affects both physical and chemical soil properties. Repeated military maneuver training activities disrupts or eliminates the O and A horizons, increases soil compaction, bare soil, bulk density, and reduces soil porosity all of which lead to increased soil erosion (Garten et al 2003, Althoff and Thien 2005, Perkins et al 2007). Total soil C, soil organic C and N tend to decrease as the intensity of military training increases (Garten et al 2003). Soil disruption and erosion caused by military training also reduces total P and extractable cations (Silveira et al. 2008).

Wildfire is common on military installations that have live fire ranges. Live tracer rounds and other incendiary ordnance cause wildfires within impact areas and safety buffers. Fire frequencies have remained constant or increased on US military installations since World War II (Trame and Harper 1997, Garten 2006). Outside of impact areas and buffers, many US military installations (especially in the southeastern USA) use prescribed fire for a variety of purposes that range from fuel reduction to endangered species habitat maintenance (Dilustro et al 2007).

The effect that fire has on soil properties can range from beneficial to damaging (as defined by plant productivity, nutrient retention, and other desirable ecosystem processes) and is dependent upon the severity and frequency of fire events. Moderate to low severity fires increase available soil nutrients through partial combustion of vegetation and encourage vegetative growth that promotes soil fertility and water infiltration (Neary et al. 1999). Conversely, severe fires can substantially reduce soil fertility through chemical volatilization and increase erosion through almost complete combustion of vegetation and litter, resulting in the loss of the O horizon and the creation of water repellent soil aggregates in the upper 6-8 cm of the profile (Certini 2005).

Long-term effects of soil disturbances are difficult to measure. Many of the effects are immediate and can be directly attributed to a specific event or series of events. However, unlike vegetation, which can recover (at least superficially) to a pre-disturbance state relatively quickly, the effect of disturbance on soil properties can last for decades (Brevik 2002). Furthermore, repeated events, such as long-term military training, are additive and can effect soil properties long after the visible effects of disturbance have disappeared (Sharrat 1998).

Military training sites in the USA offer an opportunity to examine long-term influences of repeated disturbances. At Maneuver Training Center-Fort Pickett, Virginia (Fort Pickett) the intensity and geographic distribution of specific types of training, such as vehicle maneuvers and live fire training, have been consistent since World War II (Personal communication LTC David Weisnicht, Director Fort Pickett Plans, Training and Security). The overall objective of this study was to investigate the decades-long effects of these disturbances on soil chemical and physical properties. Specifically I asked:

1. Do soil physical and chemical properties show a discernible pattern in response to disturbance from military vehicle maneuvers?

2. What is the relationship between fire frequency and soil physical and chemical properties?

3. Are the influences of these two disturbance types additive, or non-additive (i.e., do they interact)?

METHODS

Study Site

The study was conducted in the Piedmont physiographic province of Virginia, USA (37-04-27.100N / 077-57-27.100W) approximately 100 kilometers southwest of Richmond and 5 kilometers east of the town of Blackstone at the 16,592 ha Army National Guard Maneuver Training Center-Fort Pickett (Fig. 3-1). The United States Government purchased this land in 1941 to create a military training site for World War II (Fort Pickett Integrated Natural Resource Management Plan 2006).

The climate is temperate with hot, humid summers and mild winters with frequent short cold spells (National Climatic Data Center 1999). The mean annual temperature is 14.4°C, with a mean maximum of 20°C and mean minimum of 8.8°C. Precipitation is well-distributed throughout the year with an annual mean of 115 cm. Fort Pickett is located on the boundary between the Piedmont and the Coastal Plain physiographic provinces. Soils generally consist of a quartz sandy loam surface layer ranging in depth from 15-46 cm over a micaceous clay loam, with a frost depth of 61 cm. Most upland soils at Fort Pickett are non-hydric, infrequently flooded Ultisols, and have a slow to moderate infiltration rate. Loams and sandy loams are the most common soil types with organic matter fraction ranging from 2 - 10%. The majority of these soils support forest vegetation under natural conditions (Nicholson 1998).

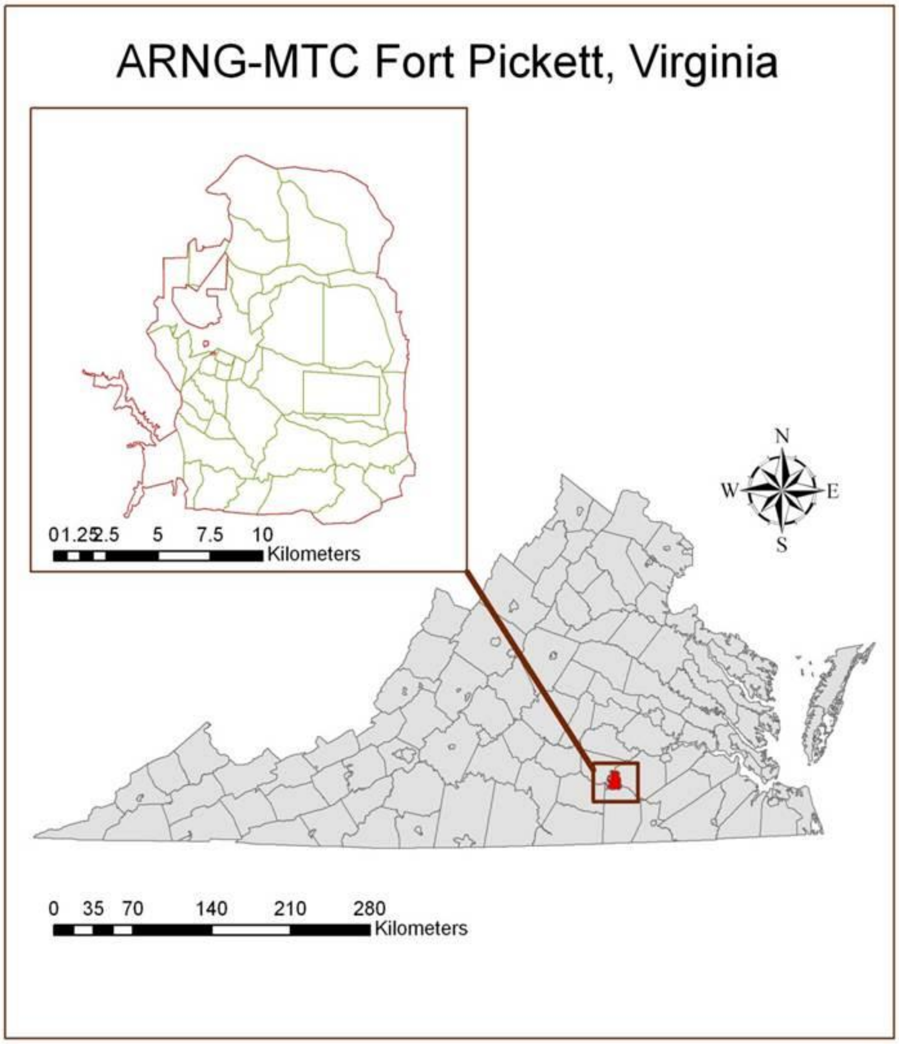

Fig 3-1. Location of the study site. The 16,592 ha Army National Guard Maneuver Training Center-Fort Pickett (Fort Pickett).

The current mission of Fort Pickett is to provide a training center capable of handling live-fire and maneuver training requirements for brigade-sized combat training. Military vehicles used for maneuver training at Fort Pickett range in size from the tracked 68 ton M1A1Abrams main battle tank and tracked 25 ton M2A2 Bradley fighting vehicle to the wheeled HMMV and 5-ton truck. The distribution of the vehicle disturbance is constrained by terrain features such as tree size and density, slope, presence of wetlands, and cultural features. Thus, the distribution of vehicle disturbance occurs across the landscape in an identifiable pattern, which has remained relatively constant over the life of the installation, even as military vehicles have changed over the years.

Military live fire training (i.e. artillery, flares, and tracer rounds) began at Fort Pickett in 1942 and has occurred in most years, periodically igniting vegetation within buffer (i.e. safety) zones surrounding the live fire ranges. The combined buffer zones or Controlled Access Area (CAA) comprises an area of approximately 4521 ha, in which wildfires are allowed to burn unhindered if there is no threat to range buildings or property (Fort Pickett Integrated Natural Resource Management Plan 2006). This policy has generally been in effect since the creation of Fort Pickett and has resulted in an assortment of fire influenced plant communities. Training-caused wildfires can occur at any time of the year, but are more common from early fall through early spring and vary in frequency and severity depending upon fuel accumulation and local weather conditions.

Humans occupied the region in which Fort Pickett is located for at least 12,000 years B.P.[4] (The College of William and Mary 1995). Europeans began to construct permanent settlements in and around the present day Fort Pickett in the late seventeenth century. By the late eighteenth century large plantations cultivating tobacco, wheat, corn, and livestock had developed in the region of present day Fort Pickett (The College of William and Mary 1995). The establishment and growth of these large plantations is exemplified by the fact that the slave population outnumbered the free in Nottoway, Lunenburg, Brunswick, and Dinwiddie Counties at end of the eighteenth century and by the mid nineteenth- century, African-American slaves outnumbered whites by a three-to-one ratio in Nottoway County. After the Civil War and emancipation southside Virginia and the Fort Pickett region specifically, became an important

[4] A putative pre-Clovis site (Cactus Hill) has been identified approximately 25 miles east of Fort Pickett which if confirmed extends the date of human occupation in the region to approximately 16,000 years B.P. (Wagner and McAvoy 2004)

area for tobacco production on small to medium sized farms. Small farming dominated the region's economy and land use until the onset of World War II.

Indirect evidence suggests that the land which became Fort Pickett had substantially lower forest cover at the time of acquisition than it does today. The United States Government purchased land totaling approximately 18,210 hectares of southside Virginia land in 1941 from nearly 500 private landowners, corporations, and churches to create what was then known as Camp Pickett displacing approximately 1100 individuals (Installation Design Guide 1992). At the time of the acquisition the land was a mosaic of relatively small (mean parcel size was 35 hectares) subsistence farms with crops of tobacco, wheat, corn, and pastures located within a matrix of mixed pine and hardwood forests.

Fort Pickett is located within the oak-hickory-pine region described by Braun (1950). However, due to a long history of agriculture and military training, uplands at Fort Pickett are currently a mosaic of forests, woodlands, shrublands, and grasslands. There are 1128 ha of native grasslands dominated by *Schizachyrium scoparius*, *Sorghastrum nutans* and *Panicum spp*. interspersed with 669 ha of native shrublands and over 400 ha of mixed deciduous and coniferous woodlands with an open understory dominated by native grasses and forbs (Dorr et al. 2007). Many of these plant communities are uncommon or absent altogether in the surrounding Piedmont and several are considered state and/or globally rare (Fleming and Patterson 2012).

Data Collection

Fort Pickett maintains a series of 130 ecological monitoring sites across the landscape to monitor the effect of military training on vegetation composition and land condition. These sites were originally allocated in a stratified random manner using the potential for disturbance from fire (wildfire or prescribed) and/or military maneuvers as the strata (Fort Pickett Range and Training Land Assessment 2007) and thus encompassing the full range of potential disturbance that occurs at Fort Pickett. I assessed the applicability of the original 130 sites to my research questions and eliminated 21 due to ongoing construction and land rehabilitation activities. I used the remaining 109 sites for my study.

In 2005, vegetation and disturbance data were collected in the remaining 109 plots to investigate the relationship between military disturbance and vegetation (Chapter 2). In the previous study, I used a modified point intercept method to assess the military maneuver disturbance at each plot location. Two 25 m transects crossing at plot center and running in cardinal directions were constructed to collect direct measures (Wheeled, Tracked, Unidentified Vehicular Pass) and indirect measures (Bare Soil and Leaf Litter) of the military vehicle disturbance within and immediately adjacent to the plot. Every meter a small diameter steel rod was lowered and the disturbance type (direct) and ground cover (indirect) at that point was recorded. We used the Fort Pickett Integrated Natural Resources Management Plan (2006), GIS records, and personal observations since early 1994 to calculate a fire frequency for each plot location.

In the summer of 2006, each plot was revisited to characterize the horizonation of the soil profile and to collect soil samples for laboratory analysis of soil chemical and physical properties. Because of potential dangers from unexploded ordnance, soils were measured on only

104 plot locations. To determine soil chemical properties, 12 shovel samples were systematically collected on a 5 m x 5 m grid surrounding the plot center. At each location, the surface litter was removed and an augur sample of the top 30 cm of mineral soil collected. All 12 samples were homogenized in a bucket onsite to obtain a single 50 g sample. Samples were air dried and sieved with a 2 mm soil sieve. Total Soil C and N were determined using dry combustion method in a Vario Max CNS analyzer (Elementar Instrument, Mt Laurel, NJ.). The remaining major soil cations (Ca, P, K, and Mg), pH, and base saturation were measured at the Virginia Tech Soil Testing Laboratory using an ICAP- 61E spectrometer. Effective CEC was estimated by the summation of the extractable bases and the exchangeable acidity.

To measure soil physical properties 3 hammer core samples were randomly collected from the top 20 cm of the soil profile within 5 m of the plot center. In the lab, I measured soil macro and micro porosity using a standard tension table procedure. Field capacity by weight and volume was determined using a pressure plate apparatus and bulk density calculated from the oven dry weight of each cylinder.

Data Analysis[5]

I summarized raw disturbance data by calculating the frequency of “hits” along each transect for both the direct measures and indirect measures of disturbance. The direct measures of vehicle maneuver disturbance were combined into a single “vehicle pass” category due to the difficulty of discerning tracked and wheeled vehicle passes in the field. Fire frequency data were

[5] Appendix A provides soil property data summarized by the predominant disturbance class (i.e. low, moderate, high physical disturbance, and fire). These data were not statistically analyzed due to the unbalanced nature of the data resulting from the ex-post classification. Data are presented in this format in order to provide tangible values for the measured soil properties.

expressed as the number of fires calculated to have occurred at that location during a 10 year period from 1994 to 2004 (Peterson et al. 2007).

Multivariate analysis

I used Canonical Correspondence Analysis (CCA) to explore the relationships between soil chemical properties in the top 30cm of the soil profile, physical soil properties in the top 20cm of the soil profile and both direct and indirect measures of disturbance (Vehicle Pass, Bare Soil, Leaf Litter, and Fire Frequency) using the program CANOCO (ter Braak 1998). A Monte Carlo test was used to test whether the canonical axes were significant ($P < 0.05$).

Multiple Linear Regression Analysis

Prior to univariate statistical analyses, I used a Shapiro-Wilks Test to test for normality of the response data. All vegetation and disturbance data were non-normal. Each variable was square root transformed prior to analysis following the recommendations of Gotelli and Ellison (2004). All but two direct measures of disturbance - fire frequency (FF) and vehicle pass frequency (VPF) - varied collinearly. I used these uncorrelated (FF and VPF) variables in a stepwise multiple linear regression (forward selection) to examine the relationship between linear combinations of the direct disturbance variables and soil physical and chemical properties. All multiple regressions were performed using SYSTAT 13.0 (SYSTAT 2009).

RESULTS

In the CCA relating soil physical properties to disturbance measures, the first and second canonical axes explained 95.6% of the relationship between the two sets of variables (Fig. 3-2). The Monte Carlo test demonstrated a significant relationship between soil physical properties and environmental variables on the first canonical axis *(F-ratio =8.16, p = 0.01*) and with all canonical axes (*F-ratio =2.58, p = 0.01*). An examination of the CCA biplot showed that soil physical properties were distributed along two primary axes related to disturbance. The vertical (Y) axes corresponded to the type of disturbance (vehicle maneuvers, fire frequency) whereas the horizontal (X) axes represented a gradient of the intensity level of disturbance (Fig. 2). The width of the A horizon was positively associated with both direct measures of disturbance, though the relationship was not strong. Conversely, the width of the O horizon was strongly associated with leaf litter, an indirect measure of disturbance, and showed a strong inverse relationship to both direct measures of disturbance; particularly FF. Macro-porosity exhibited a slightly negative relationship to FF. All other soil properties measured showed little or no relationship to either the direct measures or indirect measures of disturbance.

In the CCA relating soil chemical properties to disturbance measures, the first and second canonical axes explained 98.7 percent of the relationship, and the Monte Carlo test demonstrated a significant relationship on the first canonical axis (*F-ratio =6.69, p = 0.03*) and with all canonical axes (*F-ratio =2.01, p = 0.03*) (Fig 3-3.). An examination of the biplot showed that soil chemical properties were distributed along two primary axes related to disturbance. The vertical (Y) axes corresponded to the type of disturbance (vehicle maneuvers, fire frequency) whereas the horizontal (X) axes represented a gradient of the intensity level of disturbance (Fig.

3). Base cations, particularly Ca, Mg, and P, exhibited a strongly positive relationship with both direct measures of disturbance. Soil C had a positive relationship with leaf litter, indicating a negative relationship with disturbance. Soil N did not vary across locations subject to the different types disturbance though it was clearly negatively related to FF.

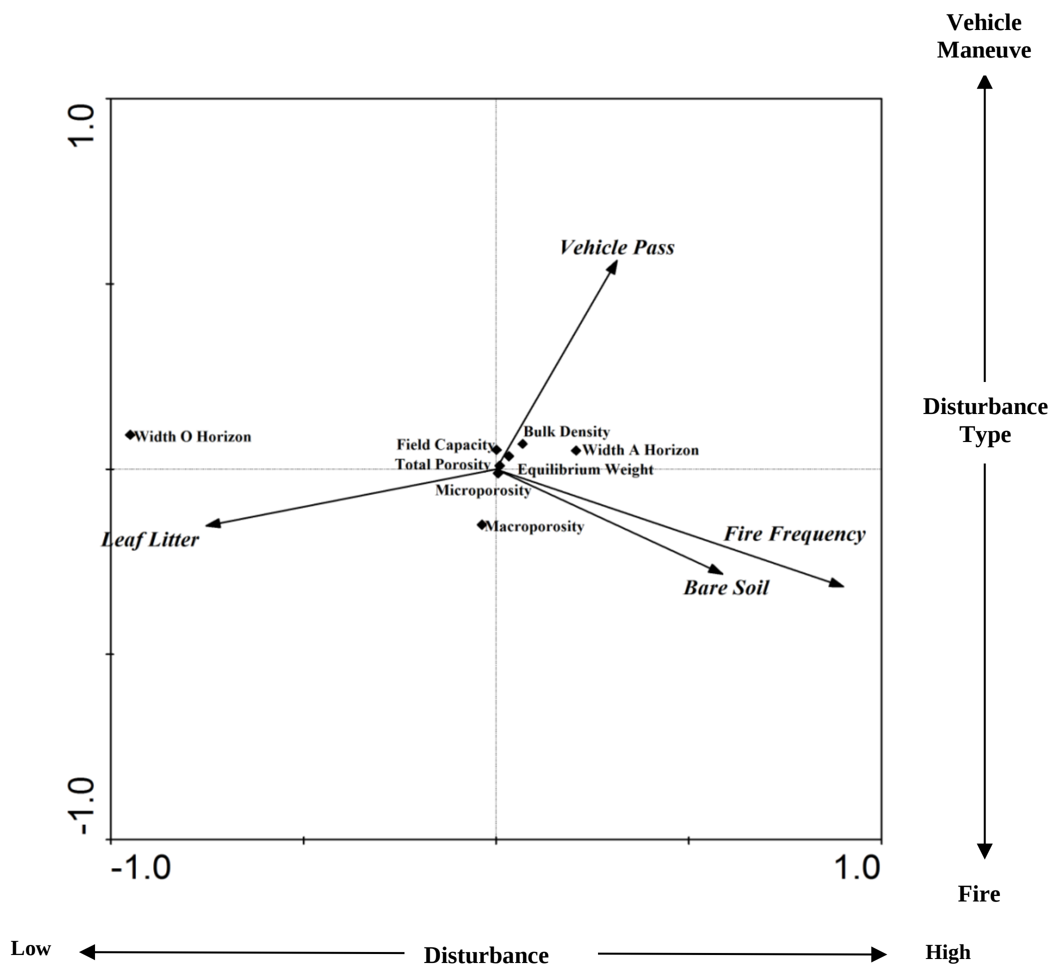

Fig 3-2. Biplot of soil physical properties (top 20 cm of soil profile) and disturbance (i.e. environmental) variables. The first and second canonical axes explain 95.6 percent of the soil physical properties-disturbance relationship. Monte Carlo test shows a significant relationship between soil physical properties and disturbance variables on the first canonical axis (*F-ratio =8.16, p = 0.01*). All canonical axes are significant (*F-ratio =2.58, p = 0.01*).

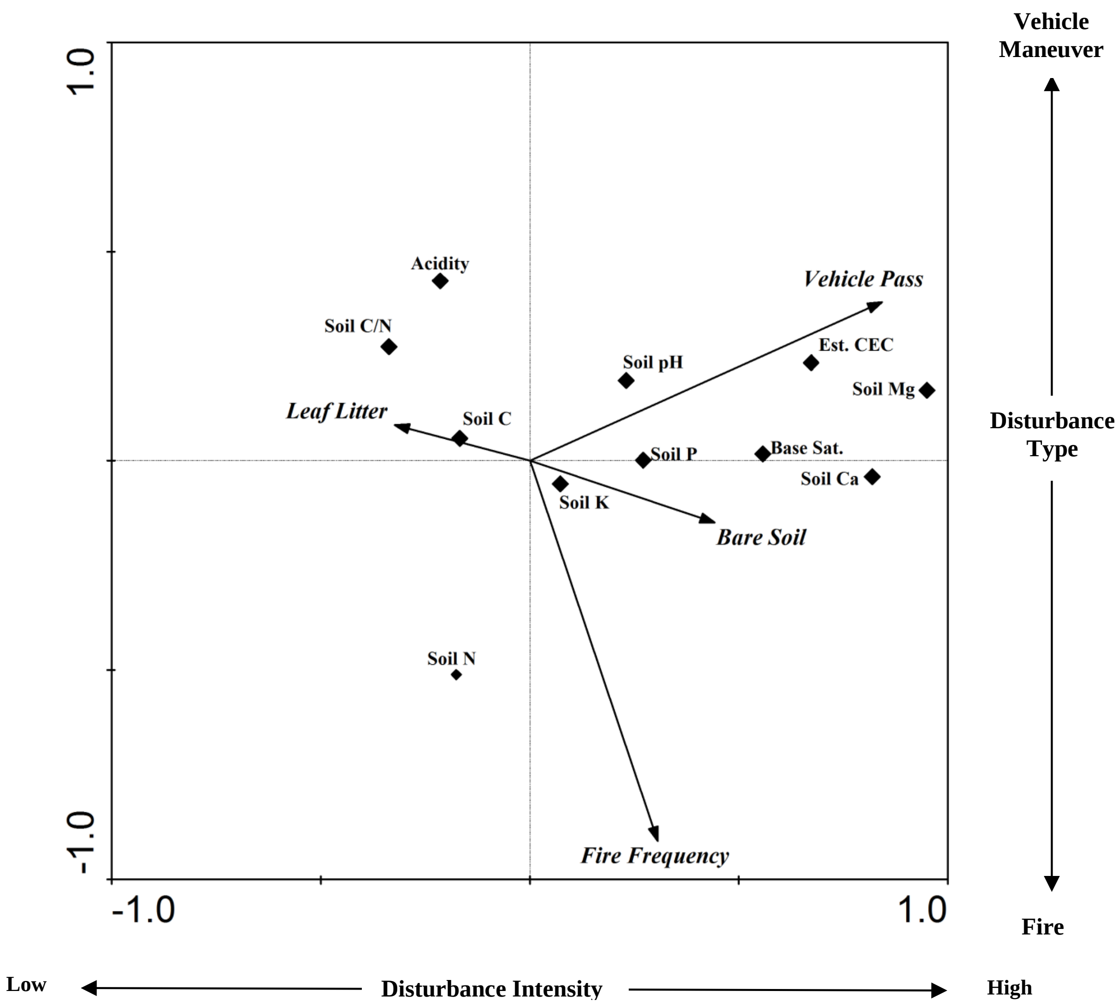

Fig. 3-3. Biplot of soil chemical properties (top 30 cm of soil profile) and disturbance (i.e. environmental) variables. The first and second canonical axes explains 98.7 percent of the soil chemical properties-disturbance relationship. Monte Carlo test shows a significant relationship between soil chemical properties and disturbance variables on the first canonical axis (*F-ratio =6.69, p = 0.03*). All canonical axes are significant (*F-ratio =2.01, p = 0.03*).

Multiple linear regression revealed that only one physical soil property, bulk density, was positively related (*P < 0.05, F – ratio 11.32,* r^2 *= 0.20*) with a linear combination of both VPF and FF. Total porosity (*P < 0.05, F – ratio 11.56,* r^2 *= 0.20)* and macro-porosity *P < 0.05, F – ratio 2.99,* r^2 *= 0.06)* were negatively related with VPF while equilibrium weight was positively related (*P < 0.05, F – ratio 7.31,* r^2 *= 0.14)* with VPF. The width of the O horizon was negatively related (*P < 0.05, F – ratio 8.37,* r^2 *= 0.17)* with FF (Table 3-1).

Table 3-1: Effects of the interaction of fire frequency (FF) and vehicle pass frequency (VPF) on soil physical properties at Fort Pickett, Va.

Soil Physical Properties	Disturbance Type				Total Model
	Vehicle Pass Frequency		Fire Frequency		
	p - value	*β 1*	*p - value*	*β 1*	r^2
Bulk Density ($g\ cm^3$)	0.00	0.08	0.04	0.06	0.20
Total porosity %	0.00	-0.45	0.06	--	0.20
Micro-porosity %	0.09	--	0.51	--	--
Macro-porosity %	0.03	-0.47	0.64	--	0.06
Width of O Horizon	0.10	--	0.00	-0.396	0.17
Width of A Horizon	0.56	--	0.44	--	--
Equilibrium Weight(g)	0.00	0.61	0.14	--	0.14
Field capacity (% by weight)	0.13	--	0.46	--	--

Soil Mg *(P < 0.05, F – ratio 6.37,* r^2 *= 0.13),* base saturation *(P < 0.05, F – ratio 12.27,* r^2 *= 0.14)* and pH *(P < 0.05, F – ratio 12.82,* r^2 *= 0.22)* were all positively related with a linear combination of both VPF and FF. Soil C:N was related (*P < 0.05, F – ratio 3.80,* r^2 *= 0.10)* with FF and was the only chemical property negatively related to either direct measure of disturbance. Soil Ca (*P < 0.05, F – ratio 4.58,* r^2 *= 0.10),* K (*P < 0.05, F – ratio 2.88,* r^2 *= 0.06)* and acidity (*P < 0.05, F – ratio 7.18,* r^2 *= 0.14)* were all positively related to FF).

Table 3-2: Effects of the interaction of fire frequency (FF) and vehicle pass frequency (VPF) on soil chemical properties at Fort Pickett, Va.

Soil Chemical Properties	Disturbance Type				Total Model
	Vehicle Pass Frequency		Fire Frequency		
	p - value	β_1	*p - value*	β_1	r^2
N kg ha $^{-1}$	0.53	--	0.15	--	--
C kg ha $^{-1}$	0.29	--	0.26	--	--
Soil C:N ratio	0.34	--	0.02	-0.97	0.10
Ca kg ha $^{-1}$	0.33	--	0.01	21.51	0.10
Mg kg ha $^{-1}$	0.02	4.79	0.02	7.48	0.13
P kg ha $^{-1}$	0.61	--	0.15	--	--
K kg ha $^{-1}$	0.16	--	0.04	4.243	0.06
Estimated CEC	0.86	--	0.13	--	--
Base Saturation	0.01	1.04	0.00	2.427	0.21
pH	0.01	0.34	0.00	0.72	0.22
Acidity	0.08		0.00	-1.90	0.14

DISCUSSION

Vehicle Maneuvers

Among the effects that military training activities can have on soils, disturbances from vehicle maneuvers have the greatest potential to influence soil properties primarily by physical compaction and dislocation of the soil profile (Perkins et al. 2007, Leis et al. 2005). Vehicle maneuver disturbance, measured as the frequency of vehicle passes, had the strongest relationship with bulk density and porosity (Table 3-A.1, Appendix 3-A). At Fort Pickett, bulk density increased and soil porosity decreased in response to vehicle maneuvers, which is consistent with other military disturbance studies (e.g. Althoff and Thien 2005, Perkins et al 2007, Maloney et al 2008). These responses to military vehicle maneuvers have the potential to negatively affect over all soil quality and ecosystem processes (Garten et al. 2003). In addition to the direct effect of vehicles on the soil, the displacement of the litter layer and consequent reduction of the width of the O horizon through erosion, may have indirectly contributed to increases in bulk density. Soil disturbance caused by vehicle maneuvers not only reduces bulk density but can also alter soil pore distribution thus reducing macro-porosity and total porosity (Perkins et. al. 2007). At Fort Pickett, both total porosity and macro-porosity decreased in relation to vehicle maneuvers (Table 3-1). Soil porosity and more critically macro-porosity (> 0.06 mm pore size) performs a crucial role in maintaining soil quality (Dexter 2003). Macro-pores allow for easy root penetration and permit ready movement of air and drainage of water.

At Fort Pickett, there was a clear relationship between disturbance resulting from vehicle maneuvers and base cations and associated soil properties (Fig. 3-3). Specifically Mg, base saturation, and pH were all positively related with vehicle maneuvers (Fig. 3-3). In addition, soil stocks of almost all cations were higher in the moderate and high physical disturbance classes (Table 3-A.1, Appendix 3-A). The damage to vegetation and mixing of the litter layer and O horizon with upper layers of the soil profile by vehicle maneuvers may increase mineralization of organic matter, as has been shown in other studies (Silveira et al. 2010, DeBusk et al. 2005, Garten et al. 2003). Therefore, disturbance from vehicle maneuvers at Fort Pickett may in some cases accelerate biogeochemical cycling and availability of nutrients by increasing mineralization rates through the physical actions of crushing and churning vegetation. A similar effect or pulse of base cations has been observed after the physical disturbance associated with forestry operations (Thiffault et al. 2007). However, Silveira et al. (2009) found that concentrations of base cations decreased as the intensity of military training increased at Fort Benning, Ga. The contrast between the Fort Benning and Fort Pickett results is likely related to the greater intensities of disturbance at the former and to study design differences. Silveria et al. (2009) selected low, moderate, and severely disturbed sites based upon an *a priori* classification, thus maximizing the differences between sample units. Whereas, the present study used a continuous (gradient) approach to sampling and thus a lower percentage of sample locations occurred in severely affected sites. In addition, Fort Benning is an “active duty” army installation, which means it experiences higher use levels than does Fort Pickett. Silveria et al. (2009) reported that sites with high levels of disturbance at Fort Benning had almost a complete removal of the litter and ground vegetation resulting in high levels of soil erosion. At Fort Pickett, sites with a near absence of vegetation and/or litter were uncommon.

Fire

Many of the effects of fire on soil properties detected at Fort Pickett were directly attributable to the consumption of above ground vegetation and the subsequent effect on litter inputs to the soil profile (Debano 1990). Fire influenced the physical properties of soils indirectly, presumably through the reduction of above ground litter inputs as evidenced by the negative correlation between fire frequency and the width of the O horizon (Table 3-1). Fire frequency was also positively related with higher bulk density at Fort Pickett (Table 3-1). The reduction or elimination of the O horizon by frequent fire reduces organic matter inputs to the upper soil layers which can increase bulk density over time (Hubbert et al. 2005). Recurrent fire, caused primarily by weapons training at Fort Pickett, may have also acted to increase bulk density through the breakdown of organic mineral aggregates and ash that clog soil pores (Certini 2005). In addition, recurrent, moderate fires, such as those common at Fort Pickett, can create hydrophobic substances in the upper mineral soil layers that reduce permeability, porosity, and water infiltration (Neary et al. 1999).

Fire increases nutrient availability through the partial consumption and combustion of above ground vegetation and subsequent rapid mineralization of organic matter and partially consumed biomass (Certini 2005). At Fort Pickett, concentrations of Mg, K, Ca, base saturation and pH were all positively related to fire frequency (Table 3-2). Because of the relatively high volatilization temperatures of base cations (Christensen 1977, DeBano 1990), these results suggest that fire severity at Fort Pickett has been historically low to moderate. Fire severity (i.e. duration and intensity) dictates the amount of litter and above-ground vegetation consumed, the types of chemicals volatilized from the vegetation, and depth of heat penetration in the soil. The low to moderate fire severity is likely a function of the relatively frequent fires that reduce fuel loads and have occurred over a large portion of the installation for several decades. Repeated wildfires at Fort Pickett have the potential to reduce above ground litter inputs and negatively alter both the physical and chemical properties of soils (Neary et al. 1999). Nevertheless, the overall influence of repeated fires, in terms of species diversity (see chapter 2), outweigh the minor negative effects on soil properties.

Additive Effects

As expected, disturbance from vehicle maneuvers showed a stronger effect on physical soil properties than fire did at Fort Pickett (Table 3-A.2, Appendix 3-A). However, where the two disturbances co-occur, fire exacerbated the effect of vehicle maneuver disturbance on physical soil properties through the reduction of organic matter inputs to the soil profile (Table 3-1). Thus, the reduction in organic matter inputs from fire coupled with vehicles involved in military maneuvers may have created an additive, adverse effect on soil physical properties.

Both disturbance types at Fort Pickett increase biogeochemical cycling rates for base cations and related soil properties, presumably by increasing the mineralization rate of organic matter (Table 3- 2). Total soil C and C:N showed a clear negative relationship to disturbance in general and fire in particular in CCA (Fig. 3-3). The consumption of above ground vegetation by fire coupled with the increased mineralization and erosion caused by vehicle maneuvers may have resulted in lower soil C concentrations at Fort Pickett (Garten et al. 2003, Silveira et al. 2010). Total soil N was also negatively associated with FF and is likely affected by many of the same processes governing soil C. However, there were no significant relations between soil N and either measure of disturbance in the regression analysis (Table 3- 2). Because C and N are tightly coupled to many biogeochemical soil processes, measurements of total stocks do not necessarily reflect actual responses to disturbance.

Although many of the measured soil properties at Fort Pickett showed statistically significant relationships to disturbance related to military training, there was a legacy of intense land use at Fort Pickett prior to establishment that may have confounded my attempts to assess the relationship of military disturbance on soil properties. The southeastern piedmont has experienced severe erosion due to previous farming practices, and Trimble (1974) estimated that the Virginia piedmont has lost on average 14 cm of topsoil since 1700. Prior to the establishment of Fort Pickett, much of the land area was in small farms that grew a variety row crops (Fort Pickett INRMP 2006). It is well established that previous land use, such as farming, can affect soil properties decades after the land use ceases (Maloney et al. 2008). As a result many areas of Fort Pickett that had little obvious ‘above ground’ signs of military disturbance may still be recovering from the effects of previous land use; thus confounding the ability to detect strong correlations between military related disturbance and soil physicochemical properties.

Conclusions

Soils are the medium in which many biogeochemical processes occur that affect ecosystem structure and function, and thus soil disturbance can have profound effect on overall ecosystem processes. At Fort Pickett, as with other military installations, disturbance caused by landscape-level military training (i.e. vehicle maneuvers and fire) interacts spatially and temporally to create a gradient of disturbance intensity across the landscape. The most apparent effect of disturbance from military training to ecosystem structure is the destruction of vegetation (Leis et al. 2005, Dilustro 2006). In chapter 2, I provided clear evidence that military disturbance occurring at Fort Pickett affects the composition and diversity of plant communities. Conversely, effects caused by military maneuvers to the physicochemical properties of soil are less apparent but may still have important effects on ecosystem processes, including a reduction in above and below-ground productivity (Debusk et al. 2005).

In this study, I used the unique land-use practices that occur on military installations to investigate the long-term effect of multiple disturbances on physicochemical soil properties. At Fort Pickett, physical disturbance from military maneuvers adversely effected physical soil structure by increasing bulk density and decreasing overall porosity and more importantly macroporosity (Table B.2, Appendix B). Wildfire from military training also affected physical soil properties through the consumption of above-ground vegetation and resultant reduction in litter inputs to the soil profile. This effect was more pronounced when both types of disturbance co-occur. Both types of disturbance were related to higher stocks of soil cations, presumably through increased mineralization rates of organic matter (Table B.1, Appendix B). However, the strength of these relationships was moderate at best, which may reflect the influence of previous land use. The signatures from years of varied and at times intense land use associated with typical small farms of the Virginia piedmont (e.g. a mosaic of pasture, row crops, and woodlots) are still evident in many of the soils found at Fort Pickett. This historic land use is an underlying source of variation that complicates attempts to isolate the precise response of soil physicochemical properties to military training.

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APPENDIX B: Chemical and Physical Soil Properties within Disturbance Classes

Table B.1. Chemical soil properties among the four categorical disturbance classes (low, Moderate, high and fire) at Fort Pickett, Va.

Soil Chemical Properties		Disturbance Category			
		Low (n=47)	Moderate (n=13)	High (n=25)	Fire (n=19)
N stock kg ha $^{-1}$	x̄	1133.1	2210.2	1058.8	2001.3
	SEM	176.9	724.2	106.0	586.4
C stock kg ha $^{-1}$	x̄	12817.2	12856.0	11753.4	15137.1
	SEM	707.1	492.2	1098.6	1680.4
C/N	x̄	14.0	9.3	11.1	12.4
	SEM	0.7	1.6	0.8	1.4
Ca stock kg ha $^{-1}$	x̄	1595.3	2505.8	2248.6	2209.1
	SEM	188.5	375.8	603.5	549.9
Mg stock kg ha $^{-1}$	x̄	315.1	543.6	512.7	320.6
	SEM	35.4	101.0	115.0	41.1
P stock kg ha $^{-1}$	x̄	14.3	16.4	16.5	19.3
	SEM	0.8	3.9	2.3	1.9
K stock kg ha $^{-1}$	x̄	306.9	417.5	287.1	360.0
	SEM	20.0	66.4	25.9	26.8
Estimated CEC	x̄	4.3	4.7	6.7	4.3
	SEM	0.2	0.4	2.2	0.5
Base Saturation %	x̄	*40.3*	*59.0*	*52.3*	*48.7*
	SEM	2.9	4.8	4.0	4.1
pH	x̄	5.1	5.5	5.4	5.3
	SEM	0.1	0.1	0.1	0.1

Table B.2. Physical soil properties among the four categorical disturbance classes (Low, moderate, high and Fire) at Fort Pickett, Va.

Soil Physical Properties		Disturbance Category			
		Low (n=47)	Moderate (n=13)	High (n=25)	Fire (n=19)
Depth A (cm)	$\bar{x}$	7.7	7.8	7.2	7.7
	SEM	1.1	1.9	1.3	0.8
Depth O (cm)	$\bar{x}$	2.41	0.86	0.69	0.44
	SEM	0.58	0.45	0.23	0.20
Bulk Density (g/cm^3)	$\bar{x}$	1.21	1.29	1.32	1.13
	SEM	0.02	0.02	0.03	0.03
Equilibrium weight (g)	$\bar{x}$	138.5	147.4	147.2	129.0
	SEM	2.3	2.2	3.2	2.8
Total porosity (%)	$\bar{x}$	54.4	60.0	49.9	57.0
	SEM	0.9	0.9	1.1	0.9
Micro-porosity (%)	$\bar{x}$	20.3	20.6	17.6	17.7
	SEM	0.9	1.4	1.4	0.9
Macro-porosity (%)	$\bar{x}$	34.0	30.4	31.9	39.3
	SEM	1.1	1.4	1.7	1.5
Field Capacity (% by volume)	$\bar{x}$	17.5	17.4	17.1	14.7
	SEM	0.5	0.9	0.7	0.9

CHAPTER 4: The Influence of Fire, Military Vehicle Disturbance and Plant Functional Group Composition on Ecosystem Processes

ABSTRACT:

I used a field experiment to examine the interactions effects of disturbance and plant functional group composition on ecosystem processes. The experiment was conducted at Fort Pickett, Virginia, to take advantage of two predictable (spatially and temporally) disturbance regimes: physical disturbance from large, heavy vehicles maneuvering across the landscape, and fire. I used functional groups comprised of species with similar physiology and effects on ecosystem processes and three response variables that reflect many underlying ecosystem processes: soil CO_2 flux, available N-NH_4, and chlorophyll fluorescence. I found statistically significant ($P < 0.05$) effects of disturbance on chlorophyll fluorescence, and functional composition on available soil N- NH_4^+. In addition, I detected a significant interactive effect of disturbance class and functional composition on soil CO_2 flux. Fire had the greatest influence on chlorophyll fluorescence, possibly because of fire's effect on soil nutrient availability. Two competing processes, mineralization and immobilization, altered soil N-NH_4^+ availability, initially increasing then immobilizing N-NH_4^+ as functional diversity decreased. The interactive effects of disturbance and functional composition on soil CO_2 flux demonstrated how the loss of functional diversity can lead to instability in ecosystem processes in disturbed ecosystems.

INTRODUCTION

The role of disturbance is widely recognized as a fundamental factor affecting many levels of ecological organization from individual species to entire landscapes (Svensson et al. 2010). In terrestrial ecosystems, the most obvious effect of disturbance is to vegetation, both individual species and communities. Disturbance is considered a primary abiotic process equal to soils and topography in determining the distribution and structure of plant communities (Johnson and Miyanishi 2007). Disturbance operates across a wide range of spatial and temporal scales and plays a critical role in maintaining species diversity (Li et al. 2004), successional dynamics of many systems (Noble and Slayter 1980, Tunnell et al. 2004) and ecosystem processes (Amiro et al. 2010). Productivity, CO_2 fluxes, mineralization, and immobilization of nutrient elements are all ecosystem processes affected by different types and intensities of disturbance (Vitousek and Matson 1985, Svensson et al 2010). Disturbance can affect ecosystem processes through direct disruption of the abiotic environment (e.g. soil erosion, landslides). However, in terrestrial systems disturbance influences ecosystem processes most often through the destruction and alteration of vegetation and vegetation communities.

A number of research projects have found significant relationships between vegetation and ecosystem function. Tilman et al. (1996, 2001) reported a positive relationship between biodiversity and ecosystem productivity in Minnesota grasslands where plant species composition and diversity were experimentally manipulated. These results were supported by a series of studies using experimentally assembled grasslands in Europe, which combined results from eight sites that found a loss in productivity was related to decreased species richness (Hector et al. 1999). However, an alternative explanation for the relationship between species diversity and productivity suggested that the functional traits of species were responsible for the reported diversity-productivity relationship (Huston 1997, Wardle et al. 1999). Recent studies demonstrated a positive relationship between plant species diversity and productivity, C sequestration, and N availability (Reich et al. 2004, van Ruijven and Berendese 2004). Conversely, other research found no demonstrable link between species richness and ecosystem processes (Schwarz et al. 2000, Thompson et al. 2005). Overall, research in a variety of systems has found relationships between biodiversity and ecosystem function, though the effects vary in magnitude and are largely species specific making wider ecological comparisons difficult (Cardinale et al. 2006).

Grime (1998) suggested that the influence of plants and plant communities on ecosystem function is related to the traits of the dominant species, not the species richness specifically. Plant functional groups, defined by Lavorel et al. (1997) as…" non-phylogenetic groupings of species which perform similarly in an ecosystem based upon a set of common biological attributes", incorporate the ecological traits of species into larger groups that reflect the functional role of each species in an ecosystem. Functional group composition has been positively correlated with biomass (McLaren and Turkington 2010), soil extractable N (Hooper and Vitousek 1997, Davies et al. 2007) and resistance to invasion (Symstad 2000, Diaz and Cabido 2001). The use of plant functional group composition to assess ecosystem processes in a disturbed environment will allow for broader comparisons among different ecosystems (Lavorel and Garnier 2002, Mason et al. 2003).

The primary objective of my study was to perform an in situ experiment designed to examine the effect of disturbance combined with the manipulation of plant functional group composition on ecosystem processes. The experiment was performed on a military installation, Fort Pickett, Virginia, in order to take advantage of two predictable (spatially and temporally) disturbance regimes; physical disturbance from large, heavy vehicles maneuvering across the landscape, and fire (Dale et al. 2002). I selected the following functional groups comprised of species with similar physiology and effects on ecosystem processes, and very responsive to the disturbance treatments (Chapter 1): C_4 grasses, legumes, and woody plants; and three response variables that reflect many underlying ecosystem processes: soil CO_2 flux, available N-NH_4, and chlorophyll fluorescence. Measures of CO_2 efflux from soils integrate soil heterotrophic root respiration and are associated with both primary and secondary productivity (Knapp et al 1998). Ammonium is the inorganic species of N initially mobilized by heterotrophic processing of organic matter and is an essential substrate for bacteria and that oxidize ammonium to nitrite, the rate-limiting step in nitrification. Thus, available N-NH_4^+ is important to both autotrophic and heterotrophic productivity and can be a sensitive measurement of ecosystem response to disturbance and resulting losses of the mobile nitrate anion (Anderson et al. 2006). Measurements of chlorophyll fluorescence have been used to detect the effects of disturbance and environmental stress on plants (Duda et al. 2003). The light energy absorbed by the chlorophyll molecule has one of three fates. It is used in photosynthesis by photosystem II (PSII), dissipated as heat, or re-emitted as light (chlorophyll fluorescence) (Maxwell and Johnson 2000). These processes are competitive, which means a decrease in efficiency of one, photosynthesis for instance, results in an increase in the yield of the others. Thus, chlorophyll fluorescence is an indirect measure of the efficiency of photosystem II and overall photosynthetic function.

In general, I predicted that type and intensity of disturbance would be a fundamental abiotic force affecting ecosystem processes (e.g. soil respiration, soil N availability, photosynthesis). In addition, I predicted that the modification of plant functional group composition would alter ecosystem processes. Finally, I predicted that the combination of disturbance and plant functional group composition would modify ecosystem processes differently than the singular effects of disturbance or functional group composition.

To investigate these predictions I asked the following questions:

1. What are the direct effects of different intensity levels and types of disturbance on soil CO_2 flux, available soil N and photosynthetic function?
2. Does functional group composition alter soil CO_2 flux and available soil N?
3. Do disturbance and functional group composition interact to affect soil CO_2 flux and available soil N?

METHODS

Study Site

The study was conducted in the predominantly rural Piedmont physiographic province of Virginia, USA (37-04-27.100N / 077-57-27.100W) approximately 100 kilometers southwest of Richmond and 5 kilometers east of the town of Blackstone at the 16,592 ha Army National Guard Maneuver Training Center-Fort Pickett (Fig. 4-1). The United States Government purchased this land in 1941 to create a military training site for World War II (Fort Pickett Integrated Natural Resource Management Plan 2006). The climate is temperate with hot, humid summers and mild winters with frequent short cold spells (National Climatic Data Center 1999).

The mean annual temperature is 14.4°C, with a mean maximum of 20°C and mean minimum of 8.8°C. Precipitation is distributed throughout the year with an annual mean of 115 cm.

Fort Pickett is located on the boundary between the Piedmont and the Coastal Plain physiographic provinces. Soils at Fort Pickett generally consist of a quartz sandy loam surface layer ranging in depth from 15-46 cm over a micaceous clay loam, with a frost depth of 61 cm. Most upland soils at Fort Pickett are non-hydric, infrequently flooded Ultisols, and have a slow to moderate infiltration rate. Loams and sandy loams are the most common soil types with organic matter fraction ranging from 2 - 10%. The majority of these soils support forest vegetation under natural conditions (Nicholson 1998).

The current mission of Fort Pickett is to provide a training center capable of handling live-fire and maneuver training requirements for brigade-sized combat training. Military vehicles used for maneuver training at Fort Pickett range in size from the tracked 68 ton M1A1Abrams main battle tank and tracked 25 ton M2A2 Bradley fighting vehicle to the wheeled HMMV and 5-ton truck. The distribution of the vehicle disturbance is constrained by terrain features such as tree size and density, slope, presence of wetlands and cultural features. Thus, the distribution of vehicle disturbance occurs across the landscape in an identifiable pattern, which has remained relatively constant over the life of the installation, even as military vehicles have changed over the years.

Military live fire training (i.e. artillery, flares, and tracer rounds) began at Fort Pickett in 1942 and has occurred in most years, periodically igniting vegetation within buffer (i.e. safety) zones surrounding the live fire ranges. The combined buffer zones or Controlled Access Area

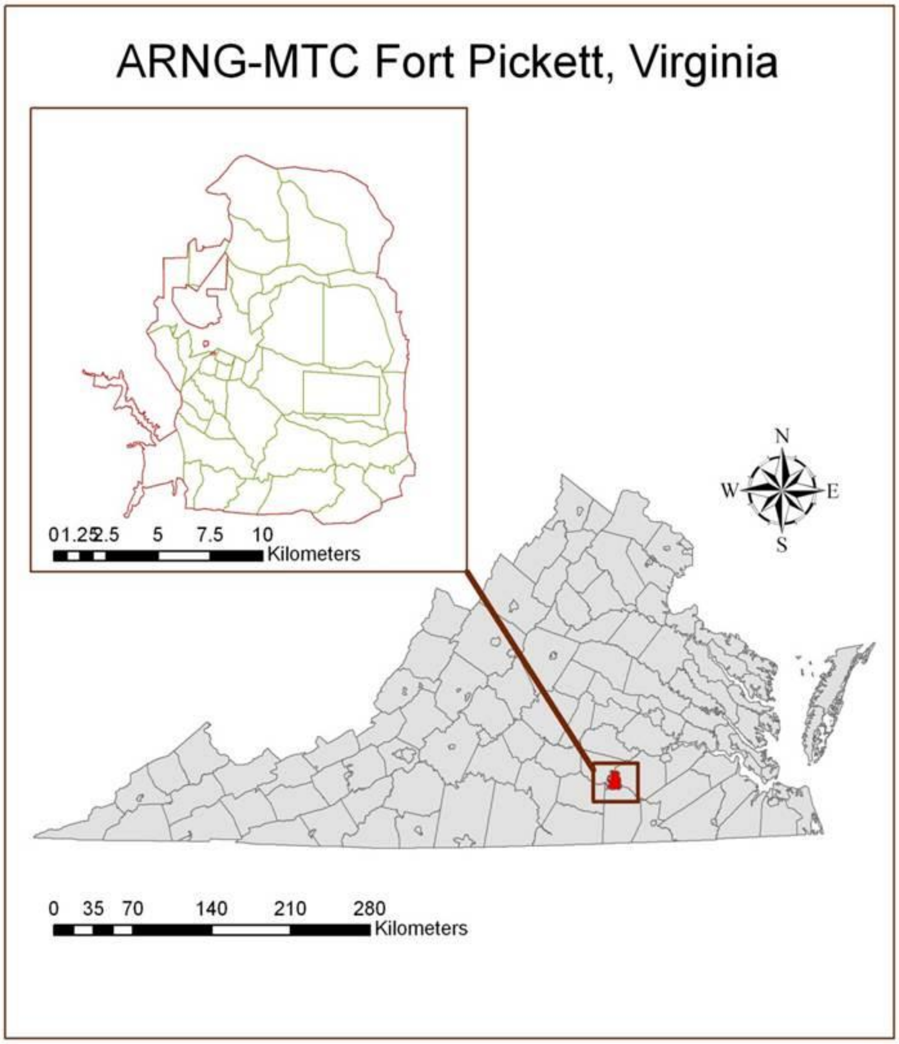

Fig 4-1. Location of the study site. The 16,592-ha Army National Guard Maneuver Training Center-Fort Pickett (Fort Pickett).

(CAA) comprises an area of approximately 4521-ha in which wildfires are allowed to burn unhindered if there is no threat to range buildings or property (Fort Pickett Integrated Natural Resource Management Plan 2006). This policy has generally been in effect since the creation of Fort Pickett and has resulted in an assortment of fire influenced plant communities. Training-caused wildfires can occur at any time of the year but are more common from early fall through early spring and vary in frequency and severity depending upon fuel accumulation and local weather conditions.

Humans occupied the region in which Fort Pickett is located for at least 12,000 years B.P.[6] (The College of William and Mary 1995). Europeans began to construct permanent settlements in and around the present day Fort Pickett in the late seventeenth century. By the late eighteenth century, large plantations cultivating tobacco, wheat, corn, and livestock had developed in the regions of present day Fort Pickett (The College of William and Mary 1995). The establishment and growth of these large plantations is exemplified by the fact that the slave population outnumbered the free in Nottoway, Lunenburg, Brunswick, and Dinwiddie Counties at end of the eighteenth century and by the mid nineteenth- century, African-American slaves outnumbered whites by a three-to-one ratio in Nottoway County. After the Civil War and emancipation, southside Virginia and the Fort Pickett region specifically, became an important area for tobacco production on small to medium sized farms. Small farming dominated the region's economy and land use until the onset of World War II.

Indirect evidence suggests that the land that became Fort Pickett had substantially lower forest cover at the time of acquisition. The United States Government purchased land totaling approximately 18,210 hectares of southside Virginia land in 1941 from nearly 500 private landowners, corporations, and churches to create what was then known as Camp Pickett displacing approximately 1100 individuals (Installation Design Guide 1992). At the time of the acquisition the land was a mosaic of relatively small (mean parcel size was 35 hectares)

[6] A putative pre-Clovis site (Cactus Hill) has been identified approximately 25 miles east of Fort Pickett which if confirmed extends the date of human occupation in the region to approximately 16,000 years B.P. (Wagner and McAvoy 2004)

subsistence farms with crops of tobacco, wheat, corn, and pastures located within a matrix of mixed pine and hardwood forests.

Fort Pickett is located within the oak-hickory-pine region described by Braun (1950). However, due to a long history of agriculture and military training, uplands at Fort Pickett are currently a mosaic of forests, woodlands, shrublands, and grasslands. There are 1128 ha of native grasslands dominated by *Schizachyrium scoparius*, *Sorghastrum nutans, and Panicum spp*. interspersed with 669 ha of native shrublands and over 400 ha of mixed deciduous and coniferous woodlands with an open understory dominated by native grasses and forbs (Dorr et al. 2007). Many of these plant communities are uncommon or absent altogether in the surrounding Piedmont and several are considered state and/or globally rare (Fleming and Patterson 2012).

Experimental Design

The experiment was designed to test the effects of two different types of disturbance, plant functional group composition, and their interaction on ecosystem processes. A split plot design was used to conduct the experiment. A split plot design has single treatment applied to the entire macro-plot (whole plot treatment) and a series of different treatments assigned to subplots (within plot treatment) nested within the macro-plot. For my research, the 'whole plot treatment' was the disturbance classes identified and reported in chapter 3 (low, moderate, high physical disturbance and fire). Plant functional group composition was the within plot treatment. The desired composition was accomplished by a full factorial removal of three plant functional groups (C_4 grasses, legumes, and woody species) that are abundant and showed the strongest response to the disturbances at Fort Pickett (Table 4-1).

There are two methods in which plant functional group composition can be manipulated to reach the desired composition; a planted, synthetically assembled community and removal of plants from naturally assemble communities. In my study, there were several advantages to using a removal experiment. The experiment was conducted in plant communities that had acclimated and were subject to decades-long disturbance regimes caused by military training at Fort Pickett. Synthetically assembled communities via transplanting of greenhouse-grown plants would cause substantial physical disturbance to the soil. Using removals of plant functional groups in naturally assembled communities maintains many of the effects of the underlying ecological factors, such as climate, local species pool, and biotic interactions that resulted in the current composition (Diaz et al. 2003).

Table 4-1. Split-plot experimental design used at Fort Pickett replicated at 5 locations within each disturbance class.

Whole plot Treatments (Disturbance Class)	**Within Plot treatments (Functional Group Removal)**							
Low, Moderate, High Physical, or Fire disturbance	No removals	Woody removal	Legume removal	C_4 removal	Woody and Legume removal	C_4 and Woody removal	C_4 and Legume removal	Woody, C_4 and Legume removal

Macro-plots were randomly selected from pool of 76 of the original 109 plots that I established (chapter 2) to quantify the relationship between plant functional type and disturbance. The 76 macro-plots were either grasslands or shrublands and had all 5 functional (C_4 grasses, C_3 grasses, forbs, legumes, and woody plants) identified in chapter 2. Furthermore, each macro-plot had at least 10% cover of the three targeted plant functional types (C_4 grasses, legumes, and woody species). An additional 4 macro-plots were eliminated because key soil physicochemical variables (e.g. total C, N, and bulk density) were not within the 90% confidence interval of the overall mean for these variables (Chapter 3). The remaining 72 macro-plots were stratified according to their disturbance class (low, moderate, high physical disturbance and fire) and 5 macro-plots were randomly selected from each class for the experiment.

At the macro-plot location, nine circular 2-m^2 subplots were established within the immediate vicinity (< 20-m radius) of the macro-plot center. All subplots were as similar as possible in plant functional group composition. Once established, composition data were collected for each subplot by naming all plant species rooted within the circular subplot and estimating vegetative cover using a modified Braun-Blanquet cover abundance scale (+ = 0-1%, 1 = 1-5%, 2 = 5-25%, 3 = 25-50%, 4 = 50-75%, 5 = 75-95%, 6 = 95-100%). Each individual species was assigned to one of 5 plant functional groups (C_4 grasses, C_3 grasses, forbs, legumes, and woody plants). Once the subplots were established and functional composition determined each subplot was randomly assigned one of the functional removal treatments (Table 1).

Functional groups were removed using a combination of hand clipping and/or non-residual herbicide. Woody species were removed by hand cutting the stem(s) as close to ground level as possible, removing all material and carefully applying Triclopyr (3,5,6 Trichloro-2-Pyridinyl) to the remaining "stump' using a brush and taking great care not to contaminate surrounding non-target species. Legumes and C_4 grasses were removed by clipping to ground level, removing all clipped materiel and carefully treating the remaining basal cover with Glyphosate (N-phoshonomethyl) using a brush or small sprayer taking great care not to contaminate surrounding non-target species. After the removals were complete, all vegetation for 0.5m surrounding each subplot was eliminated, using a combination of hand clipping and herbicide, to isolate each subplot from roots of neighboring plants.[7] The initial functional group

[7] Trenching is often used to isolate experimental plots. However since my experiment was occurring on an active military installation trenching was not feasible because of safety concerns.

removals were performed during the first two weeks of May 2007. Each plot was visited once/month thereafter during the growing season (April –September) and additional removals performed as needed to maintain the desired functional composition within each subplot. By the summer of 2008, functional group composition had stabilized though minor monthly maintenance continued through June of 2009. From July 2009 through September 2009, no further herbicide applications were performed due to the initiation of ecosystem response measurements. At the conclusion of the experiment final functional composition data were collected for each subplot.

Field Data Collection[8]

Response data for soil CO_2 flux and available soil $N\text{-}NH_4^+$ were collected during two sample periods, July 7, 2009 and September 5, 2009. Chlorophyll fluorescence data were also collected during two sample periods, August 19-21, 2009 and September 5-7, 2009. Final plot composition data were collected from August 19-21, 2009.

Soil CO_2 Flux Measurement Using Soda Lime Absorption.

Soil CO_2 flux was measured for approximately 24 hours two times: July 6 -7, 2009 and September 4 - 5, 2009. Many field studies that measure soil CO_2 flux use an automated portable infrared gas analyzer (IRGA). In this study, my 20 macro-plots were distributed over approximately 10,000 ha with 8 replicates/macro-plot. Because of the spatial distribution of

[8] Because Fort Pickett is an active military training installation access was limited to dates where training activities were not taking place.

macro-plots, measurement of soil CO_2 flux using a portable IRGA would have taken a minimum of 20 days. Because soil CO_2 flux is sensitive to changes in soil temperature and moisture (Davidson et al. 1998), a measurement period of 20 days would have introduced substantial variability due to spatial and temporal differences in air temperature and rainfall. In addition, because of ongoing military training, access to some macro-plot locations would have been difficult. Therefore, I measured soil CO_2 flux using a soda lime absorption technique following the detailed methods tested and modified by Keith and Wong (2006). This method can be applied over large remote areas simultaneously thus limiting variability related to differences in rainfall and temperature. In addition, Keith and Wong (2006) found that soil CO_2 flux measurements, using their modified soda lime absorption technique, were quantitatively similar to measurements using an IRGA with a correlation coefficient of 82%.

Specifically, soil CO_2 flux was measured using non-flow-through steady-state chamber with alkali absorption of CO_2 by soda lime. The soda lime granules were comprised of NaOH and $Ca(OH)_2$ and about 20% H_2O with carbonate formation calculated from the weight gain of the granules (Keith and Wong 2006). Chambers were polyethylene plastic white buckets with the base removed. Chamber dimensions used in my study had a top diameter of 19.8 cm, exterior height 18.9 cm, and bottom diameter 16.2 cm. Chambers were sealed with a well-fitting lid and the rim was coated with vacuum grease to ensure a tight seal (vacuum grease was reapplied whenever the chambers were opened). Chambers were inserted into the ground in the approximate center of each subplot (n = 160) approximately 2 months before the initial measurements were collected to avoid effects of soil disturbance and were left uncovered and in place for the entire course of the experiment when data were not being collected. Chambers were inserted into the litter and surface soil to provide a good seal and anchorage but not deep enough to sever the fine root mat and staked into the ground for stability. All live vegetation inside the chamber was removed to prevent CO_2 uptake or evolution. One blank chamber was used at each macro-plot and consisted of the same bucket and volume with sealed lid but with base remaining intact and not exposed to the soil.

In the lab 50 g of soda lime was placed into petri dishes (160) and oven dried at 105 ^{0}C for a minimum of 14 hours. Oven dry weight of the soda lime-petri dish was recorded and the petri dish tightly sealed with electrical tape. In the field, the tape was removed from the petri dish and the soda lime rewetted and placed in the sealed chambers for 24 hours. Petri dishes were collected from the chambers and resealed with electrical tape for transport back to the lab. The petri dishes were dried and reweighed. The weight gain represented soil CO_2 flux and through a series of calculations (Keith and Wong 2006) was converted to gram C m^{-2} day^{-1}. Blank chambers not exposed to soil were sampled in the same manner in order to account atmospheric CO_2 absorbed during the drying and weighing of the petri dishes.

Available N-NH_4^+

I used an anaerobic incubation method to determine available N-NH_4^+ (Binkley and Hart 1989). Soil samples used to measure available N-NH_4^+ were collected during the same sample period as the soil CO_2 flux measurements. In each subplot 5 subsamples were collected with a 2.5 cm diameter soil augur from the top 20 cm of the mineral soil profile. All 5 sub-samples were homogenized in a bucket onsite to obtain a single 25-g sample. Samples were placed in plastic bags stored in coolers and returned to the lab. All samples were oven dried for 24 hours at 105 ^{0}C and sieved with a 2-mm soil sieve. Two, 5-g soil samples from each subplot were placed in vials, completely filled with distilled water, and incubated at 40 ^{o}C for 7 days. A 3M KCL solution was used to extract mineralized N from the soil. Leachate from the soil and KCL suspension was collected, filtered, and analyzed using Perkin-Elmer Model 1100 Atomic Absorption Spectrophotometer to determine available N-NH_4^+ ppm.

Chlorophyll Fluorescence.

In order to test the experimental effects of disturbance and functional group removal on chlorophyll fluorescence, a phytometer, representing the same plant species, must be present in every treatment. However, no species occurred in all removal plots. Therefore, only the effect of the disturbance class on chlorophyll fluorescence could be measured. From field observations and data collected in 2005, I identified a single woody species, sweetgum (*Liquidambar styraciflua* L.), that occurred at all macro-plot locations with vegetative cover > 10% to use as a chlorophyll fluorescence phytometer. Because the macro-plots were located within a grassland shrubland matrix, none of the sweetgum individuals were > 2.5 meters in height which allowed for relatively easy access to all of the leaves.

There are several parameters of chlorophyll fluorescence related to the efficiency of PSII. I chose to measure the dark-adapted values of the maximum quantum yield of PSII (F_v/F_m) because it is considered a sensitive indicator of photosynthetic performance (Maxwell and Johnson 2000). At each macro-plot location, 10 sweetgum individuals were randomly chosen within 20 meters of plot center. From each of these individuals, 3 healthy (i.e. no obvious signs of insect feeding, chlorosis, or other apparent damage) leaves were selected, 1 each from the top, middle and ground level of the individual. These were placed in double-bagged, black heavy-duty garbage bags to dark-adapt the leaves. After 20 minutes of dark adaptation, the F_v/F_m

chlorophyll fluorescence of each leaf was measured using an OS5p Multi-Mode Chlorophyll Fluorometer (Opti-Sciences 2008).

Data Analysis

I used a blocked, split plot two-way mixed model analysis of variance (ANOVA) to compare treatment main effects (disturbance, plant functional group composition) and interactive effects on soil CO_2 flux (g C m^{-2} day^{-1}) and available N-NH_4^+ (ppm). Prior to statistical analyses, I used a Shapiro-Wilks Test to test for normality of all data. All response data (i.e. soil CO_2 flux, available N-NH_4^+) exhibited non-normal distributions. Each variable was log transformed prior to analysis following the recommendations of Gotelli and Ellison (2004). The two sampling periods (i.e. July 2009 and September 2009) were analyzed and reported separately. I used a one-way ANOVA to compare effect of disturbance on chlorophyll fluorescence of sweetgum (F_v/F_m). Differences among treatment effects for the two-way ANOVA and one-way ANOVA were evaluated using Tukey's HSD test. All statistical analyses were performed using Systat 13.0 (Systat 2009).

RESULTS

Soil CO_2 Flux

There were no statistically significant ($P < 0.05$) independent effects of disturbance on soil CO_2 flux during the July or September sample periods (Table 4-2). However, there were conspicuous, though non-significant at $P < 0.05$ level, differences detected in soil CO_2 flux among disturbance classes in the July sample period. The highest soil CO_2 flux measured during the July sample period was in the 'low' (9.230 g C m^{-2} day^{-1}) disturbance class followed by the 'fire' (6.357 g C m^{-2} day^{-1}), 'moderate' (6.272 g C m^{-2} day^{-1}), and 'high' (4.324 g C m^{-2} day^{-1}) disturbance classes (Table 4-3). In the September sample period, all soil CO_2 flux values declined from their July values and there were no distinct differences among disturbance classes. Functional group composition also had no significant effect on soil CO_2 flux in either the July or September sample period (Table 4-2). In contrast to disturbance class, there were no conspicuous differences in mean soil CO_2 flux attributable to functional group composition (Table 4-4).

The interaction between disturbance class and functional group composition on soil CO_2 flux was significant (*F-ratio = 1.68, P = 0.04)* during the July 2009 sample period (Table 4-2 and Fig. 4-2). Mean soil CO_2 flux ranged from high of 14.66 g C m^{-2} day^{-1} in the *low disturbance x woody removal* treatment to a low of 1.69 g C m^{-2} day^{-1} in the *high disturbance x woody, C_4, and legume removal* treatment (Table C.1,Appendix C).

Table 4-2. Effect of disturbance and plant functional group composition on soil CO_2 flux (g C m^{-2} day^{-1}). F-values are from blocked split plot ANOVA.

Effect	**July 2009**			**September 2009**		
	df	*F-ratio*	*P-value*	*df*	*F-ratio*	*P-value*
Disturbance Class	3	2.30	0.11	3	0.54	0.65
Functional Group Composition	7	1.40	0.21	7	0.47	0.84
Disturbance Class x Functional Group Composition	21	1.68	**0.04**	21	1.03	0.42

Table 4-3. Mean values and standard errors for soil CO_2 flux (g C m^{-2} day^{-1}) among disturbance classes by sample period.

Disturbance Class	**Soil CO_2 Flux (g C m^{-2} day^{-1})**			
	July 2009		**September 2009**	
	$\bar{x}$	*SEM*	$\bar{x}$	*SEM*
Low	9.23	1.19	3.53	0.34
Moderate	6.27	0.40	5.92	0.74
High	4.18	0.65	3.98	0.64
Fire	6.35	0.57	5.79	1.10

Table 4-4. Mean values and standard errors for soil CO_2 flux (g C m^{-2} day^{-1}) among functional group composition treatments by sample period.

Functional Group Composition	Soil CO_2 Flux (g C m^{-2} day^{-1})			
	July 2009		September 2009	
	$\bar{x}$	*SEM*	$\bar{x}$	*SEM*
No removals	6.28	0.85	3.82	0.59
Woody removal	7.49	1.91	4.44	1.05
Legume removal	8.29	1.33	5.06	1.09
C_4 removal	6.70	1.02	5.76	1.27
Woody and Legume removal	5.61	0.72	6.23	1.77
C_4 and Woody removal	6.58	1.30	3.49	0.41
C_4 and Legume removal	6.67	0.83	6.07	1.38
Woody, C_4 and Legume removal	5.77	1.06	4.35	0.62

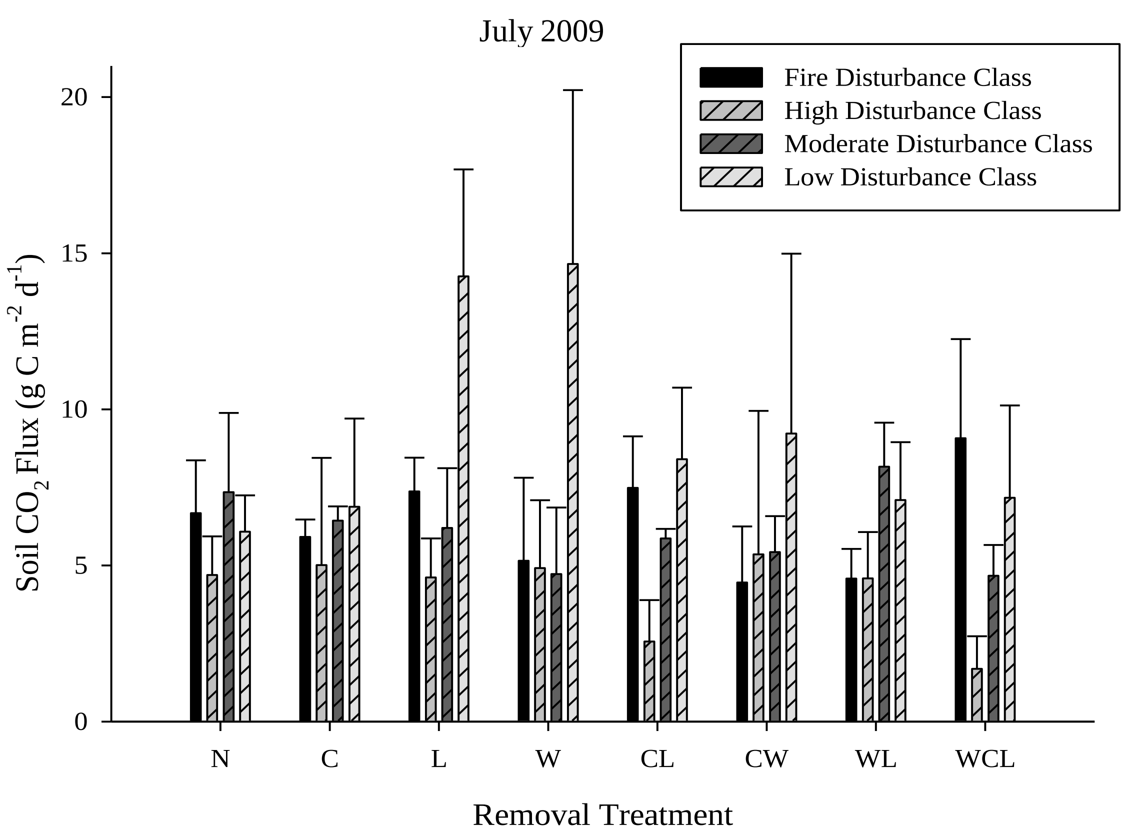

Fig.4-2. The response of soil CO_2 flux (g C m^{-2} day^{-1}) to the significant ($P < 0.05$) interaction of disturbance and plant functional group removal during the July 2009 sample period. Abbreviations for the different functional group removal treatments are: N = no removals, C = C_4 removal, L=legume removal, W = woody removal, CL = C_4 and legume removal, CW = C_4 and woody removal, WL = woody and legume

Available N-NH_4^+

Disturbance class had no significant effect on available soil N-NH_4^+ (ppm) during the July or September sample period (Table 4-5). However, as with soil CO_2 flux there were noticeable though non-significant differences in available soil N-NH_4^+ during the July sample period. Mean available soil N-NH_4^+ was highest in the 'moderate' disturbance class with a value of 10.60 ppm while the 'fire' disturbance class was substantially lower with a mean value of 6.84 ppm (Table 4-6).

In general, as more functional groups were removed, available soil N-NH_4^+ decreased during both sample periods, though the effects were statistically significant only during the September 2009 sample period (*F-ratio =1.89, P =0.07*). The legume removal (10.52 ppm) and woody removal (9.93 ppm) treatments had

Table 4-5. Effect of disturbance and plant functional group composition for available soil N-NH_4^+ (ppm). F-values are from blocked split plot ANOVA.

Effect	July 2009			September 2009		
	df	*F-ratio*	*P-value*	*df*	*F-ratio*	*P-value*
Disturbance Class	3	2.32	0.11	3	0.03	0.99
Functional Group Composition	7	0.95	0.46	7	1.89	**0.07**
Disturbance Class x Functional Group Composition	21	1.19	0.27	21	0.57	0.92

Table 4-6. Mean values and standard errors for available soil N-NH_4^+ (ppm) among disturbance classes and sample period.

Disturbance Class	**Available N-NH_4^+ (ppm)**			
	July		**September**	
	x̄	SEM	x̄	SEM
Low	9.64	0.51	8.66	0.40
Moderate	10.60	0.84	9.76	0.71
High	10.32	0.72	9.19	0.54
Fire	6.84	0.47	8.84	0.52

significantly higher available soil N-NH_4^+ in the September sample period compared to the woody, C_4, and legume removal treatment (8.00 ppm) (Table 4-7). In the treatments where two functional groups were removed, available soil N-NH_4^+ was generally lower than the single functional group removal treatments and higher than the 3 functional group removal treatment though the effects were not statistically significant (Table 4-7).

Table 4-7. Effect of functional group composition on available N-NH_4^+ (ppm) analyzed using a two-way split plot ANOVA. Mean values not connected by the same letter are significantly different at the P < 0.10 level.

Removal Treatment	**Available N-NH_4^+ ppm**			
	July 2009		**September 2009**	
	$\bar{x}$	*SEM*	$\bar{x}$	*SEM*
No removals	9.56	1.16	9.28^{ab}	0.87
Woody removal	9.63	0.93	9.93^{a}	1.02
Legume removal	10.83	1.17	10.52^{a}	0.90
C_4 removal	9.36	1.04	8.78^{ab}	0.67
Woody and Legume removal	9.10	1.02	8.61^{ab}	0.84
C_4 and woody removal	8.18	0.57	8.99^{ab}	0.65
C_4 and Legume removal	9.48	1.09	8.74^{ab}	0.92
Woody, C_4 and Legume removal	8.64	0.75	8.00^{b}	0.65

Chlorophyll fluorescence

Disturbance class had a highly significant effect on chlorophyll fluorescence (F_v/F_m) in the sweetgum phytometers for both August (F = 12.57, P = 0.00) and September (F = 35.48, P = 0.00) (Table 4-8). During the August sampling period, chlorophyll fluorescence was significantly greater in low to moderate disturbance treatments than in the high and fire treatments (Table 4-9). In September, chlorophyll fluorescence was significantly greater in the fire than in all the other treatments.

Table 4-8. Effect of disturbance class on chlorophyll fluorescence (F_v/F_m) analyzed using a one-way ANOVA.

Sample Period	**Treatment**	**df**	**F-Ratio**	**p-Value**
August 2009	Disturbance Class	3	**12.57**	**0.00**
September 2009	Disturbance Class	3	**35.48**	**0.00**

Table 4-9. Comparison of mean treatment effects among 4 disturbance classes at Fort Pickett, VA in 2009. Arithmetic means with different letters are significantly different at the p < 0.05 level within that sampling period.

Sample Period	**Disturbance Class**	**Chlorophyll Fluorescence (F_v/F_m)**	
		$\bar{x}$	SEM
August 2009	Low	0.724^{A}	0.007
	Moderate	0.728^{A}	0.005
	High	0.748^{B}	0.006
	Fire	0.670^{C}	0.011
September 2009	Low	0.649^{A}	0.007
	Moderate	0.666^{A}	0.006
	High	0.639^{A}	0.008
	Fire	0.734^{B}	0.005

DISCUSSION

Disturbance Effects

Soil CO_2 flux reflects both primary and secondary productivity and thus is an effective measure of ecosystem processes. I detected no statistically significant main effects of disturbance on soil CO_2 flux at Fort Pickett. This result may be related to the heterogeneous nature of disturbance resulting from military training (Demaris et al. 1999). At course spatial scales, disturbance patterns from military training are easily identifiable. However, at relatively fine spatial scales, as in this study, the spatial heterogeneity of disturbance increases, which may have confounded attempts to detect patterns in the response of ecosystem processes to disturbance (Turner et al. 2003). Soil CO_2 flux values during the July sample period did exhibit obvious though differentiation among disturbance classes (Table 4-2). However this differentiation was largely absent during the September sample period.

In the July sample period soil CO_2 flux was conspicuously lower in the 'high' physical disturbance category compared to all other classes (Table 4-3). Lower soil CO_2 flux is consistent with lower vegetative cover (Bremer and Ham 2002), which would be expected in the 'high' physical disturbance class on a military installation (Debusk et al. 2005). However, total vegetative cover did not vary dramatically among the disturbance classes (Fig.4-3) and was in fact lowest in the 'fire' class, which exhibited intermediate soil CO_2 flux values (Table 4-3). High levels of physical disturbance from military training are related to higher soil bulk densities and lower soil macro- porosity at Fort Pickett (see Chapter 3) and at other military installations with maneuver training (Garten et al. 2003, Althoff et al. 2010). Increased soil bulk density and decreased soil macro-porosity limit root penetration, growth, and total root biomass thus negatively affecting root respiration and by extension total soil CO_2 flux (Silveira et al 2010).

Soil microbial biomass and invertebrate communities are also adversely affected by physical disturbance from military training (Peacock et al. 2001, Althoff and Thien 2005) which could result in lower soil CO_2 flux. Debusk et al. (2007) found similar patterns of decreasing soil respiration with increased disturbance at Fort Benning, Ga.

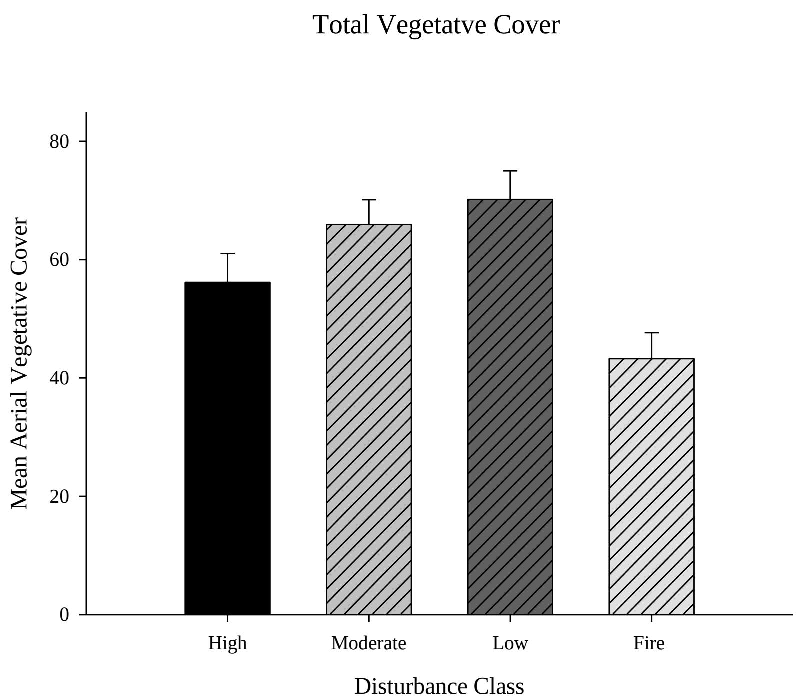

Fig. 4-3. Comparison of total vegetative cover (%) among disturbance classes in the split plot experimental design at Fort Pickett.

As observed with CO_2 flux, treatment effects on available soil N-NH_4^+ were for the most part, not statistically significant. In July, mean available soil N-NH_4^+ was substantially lower in the ‘fire’ disturbance class, but the difference was not statistically significant (Table 4-6). It is possible that fire intensity and frequency were insufficient at the study sites to affect clearer response. Low intensity fire can increase nutrient availability through the partial consumption and subsequent mineralization of above-ground biomass (Wilson et al. 2002). Moderate to severe intensity fire can reduce available soil N through volatilization of mineral N and the reduction or elimination of organic matter inputs (Christensen 1977, Certini 2005). As with fire, low to moderate intensity physical disturbance will increase mineralization of organic matter thus increasing nutrient availability (Thiffault et al. 2007).

Unlike soil CO_2 flux and available soil N-NH_4^+, chlorophyll fluorescence showed a strong and statistically significant response to disturbance in both the July and September sample periods. Chlorophyll fluorescence provides information about the state of PSII and though not a direct measure of photosynthesis is indicative of the rate of photosynthesis with the optimal value for the dark -adapted maximum quantum yield of PSII (F_v/F_m) being approximately 0.8 (Maxwell and Johnson 2000). A reduction from the 0.8 value indicates a stress (light, water, and/or nutrient) on the plant and correlates well with CO_2 assimilation rates (Cavender-Bares and Bazzaz 2004). In the August sample period the ‘fire’ disturbance class showed significantly reduced F_v/F_m values compared to the other disturbance classes indicating heightened stress and by extension reduced CO_2 assimilation rates. Fluorescence data do not pinpoint the precise source of plant stress thus making broad conclusions difficult without supporting data. However, available soil N-NH_4^+ was substantially lower in the ‘fire’ disturbance class during the July sample period possibly suggesting that moderately intense fire may be limiting growth rates by decreasing nutrient availability during the summer growing season. By the September sample period the pattern reversed. The mean F_v/F_m value for the fire disturbance class was significantly higher than the other disturbance classes which corresponded to increased available soil N-NH_4^+

compared to mid-summer values. While these patterns are intriguing, they simply suggest a potential relationship and not conclusive evidence of nutrient limitation.

Plant Functional Group Composition Effects

In my study the effect of functional group composition on ecosystem processes, measured as soil CO_2 flux and available soil $N\text{-}NH_4^+$, were mixed. While there were some indications, particularly during the July sample period, that functional composition affected soil CO_2 flux, none of the effects of removal treatments were statistically significant. In the September sample period two different treatments (i.e. legume removal treatment and woody removal treatment) did have significantly higher available soil $N\text{-}NH_4^+$ than the woody, C_4, and legume removal treatment (Table 4-7). These results were part of a larger pattern where single removal treatments generally increased available soil $N\text{-}NH_4^+$, but as functional diversity (i.e. more functional removals) decreased available soil $N\text{-}NH_4^+$ also decreased.

Functional group composition and diversity has been shown to effect soil nutrient availability (Flombaum and Sala 2008, Symstad and Tilman 2001) most notably in studies where lower functional diversity resulted in higher plant available mineral N (Fonara and Tilman 2008, Davies et al 2007 Reich et al 2004). This effect of increased nutrient availability coupled with lower functional group diversity is considered an example of complementarity (Hooper and Vitousek 1997). In my study, two competing patterns emerged. In the single functional group removal treatments, available soil $N\text{-}NH_4^+$ increased, thus suggesting that plant functional groups were complimentary in this system (Hooper and Vitousek 1997). However, in the removal treatments where 2 and 3 functional groups were removed, available soil $N\text{-}NH_4^+$ decreased, which is inconsistent with a system where nutrient use among plants is complimentary (Table 7).

Regardless of functional group identity, the removal of aboveground plant biomass has been shown to increase mineral N availability due to the decomposition and subsequent mineralization of roots remaining in the soil (Anderson et al. 2006, Davies et al 2007). Conversely, removal of above-ground plant biomass and associated root decomposition can also have the opposite competing effect and immobilize soil N-NH_4^+ and other nutrients by increasing soil C (McLaren and Turkington 2010, Johnson and Machett 2001). In my study, removals of single functional groups (i.e. woody removal and legume removal) increased available soil N-NH_4^+ suggesting that mineralization was the dominant process. However, as the number of functional groups removed increased, root decomposition likely increased soil C to a point where immobilization became the dominant process thus limiting the available soil N-NH_4^+.

The difference among single group removals provided some evidence of an effect of functional group identity on available soil N-NH_4^+. The legume removal treatments were consistently and in the case of the September sample period significantly higher in available soil N-NH_4^+ likely due low C:N ratio of the root biomass. Conversely, the C_4 removal treatment had the lowest available soil N-NH_4^+ of all the single removal treatments, which may be related to the high root to shoot and C:N ratio specific to C_4 grasses (Fonara and Tilman 2008).

Interaction of Disturbance and Plant Functional Group Composition

The interactive effect of disturbance and functional group removal on ecosystem processes was only significant for soil CO_2 flux in the July sample period. The clearest effect on soil CO_2 flux occurred in the low disturbance class in combination with legume removal and woody removal treatments (Fig. 4-2.). Relatively low physical disturbance related to military training at Fort Pickett likely does not substantially suppress the biologic activity of heterotrophic or autotrophic organisms (Peacock et al. 2001, Althoff and Thien 2005). As discussed previously single functional group removals likely increase mineralization rates, which would be reflected in increased soil respiration. Thus, the combinations of these two treatments were additive resulting in relatively high soil CO_2 flux (Fig. 4-2). The combination of the other disturbance classes and single functional group removal had little effect on soil CO_2 flux. However, as the number of functional groups removed increased (i.e. lower functional diversity) in combination with the 'moderate', 'high' and 'fire' disturbance classes, soil CO_2 flux began to fluctuate substantially (Fig. 4-2). Thus, the combination of disturbance and reduced functional diversity created instability in the system. In other words, the effects of disturbance on key ecosystem processes may be ameliorated by the functional diversity.

Conclusions

Disturbance is a fundamental abiotic process affecting many levels of ecological organization (Laska 2001). Consequently, the most surprising result of my study was the lack of a statistically significant disturbance effect for two of the response variables, soil CO_2 flux and available N-NH_4^+, that have shown strong responses in other studies (Reich et al. 2004, Anderson et al. 2006, Althoff et al. 2010).

The only explicit main effect I was able to detect was that of functional composition on available soil N-NH_4^+. In my study, removals of single functional groups increased available soil N-NH_4^+ suggesting that mineralization was the dominant process. However, as the number of functional groups removed increased root decomposition likely increased soil C to a point where immobilization became the dominant process thus limiting the available soil N-NH_4^+. The interactive effects of disturbance and functional composition on soil CO_2 flux demonstrated how the loss of functional diversity can lead to instability in ecosystem processes in disturbed ecosystems.

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APPENDIX C: Values for CO_2 Flux by Disturbance Class and Functional Group Composition

Table C.1: Mean values and standard errors for soil CO_2 flux (g C m^{-2} day^{-1}) by disturbance class and functional group composition during the July 2009 sample period.

Disturbance Class	**Functional Group Composition**	**Soil CO_2 (g C m^{-2} day^{-1})**	**SEM**
Low	Woody removal	14.66	5.57
Low	Legume removal	14.26	3.43
Low	C_4 and Woody removal	9.22	5.76
Fire	Woody, C_4, and Legume removal	9.08	3.17
Low	C_4 and Legume removal	8.41	2.29
Moderate	Woody and Legume removal	8.17	1.41
Fire	C_4 and Legume removal	7.49	1.65
Fire	Legume removal	7.37	1.08
Moderate	No removals	7.35	2.54
Low	Woody, C_4, and Legume removal	7.17	2.96
Low	Woody and Legume removal	7.10	1.86
Low	C_4 removal	6.88	2.83
High	No removals	6.67	1.70
Moderate	C_4 removal	6.44	0.45
Moderate	Legume removal	6.20	1.92
Low	No removals	6.08	1.16
Fire	C_4 removal	5.92	0.55
Moderate	C_4 and Legume removal	5.86	0.31
Moderate	C_4 and Woody removal	5.43	1.16
High	C_4 and Woody removal	5.36	4.60
Fire	Woody removal	5.15	2.65
High	C_4 removal	5.01	3.43
High	Woody removal	4.92	2.17
Moderate	Woody removal	4.73	2.13
High	No removals	4.70	1.24
Moderate	Woody, C_4, and Legume removal	4.67	0.99
High	Legume removal	4.62	1.25
High	Woody and Legume removal	4.59	1.48
Fire	Woody and Legume removal	4.58	0.95
Fire	C_4 and Woody removal	4.45	1.80

High	C_4 and Legume removal	2.57	1.32
High	Woody, C_4, and Legume removal	1.69	1.05

Chapter 5: Summary and Conclusions

Disturbance is widely recognized as a fundamental factor affecting many levels of ecological organization, from individual species to entire landscapes. Anthropogenic disturbances from military training, because they are well documented and have occurred consistently for decades, provide a unique opportunity to examine effects of disturbance on vegetation dynamics, physicochemical soil properties, and ecosystem processes. In addition plant functional diversity has been suggested as the key to ecosystem processes such as productivity. To investigate the relationship between disturbance, functional composition and diversity, soil physicochemical properties, and ecosystem processes, I developed three general research objectives to guide my research:

1. Identify the relationships between plant community composition and diversity with disturbance.
2. Examine the effects of disturbance on soil chemical and physical properties.
3. Experimentally examine the effect of disturbance and plant community composition ecosystem processes.

At Fort Pickett, as with other military installations, disturbance caused by landscape level military training (i.e. vehicle maneuvers and fire) interacts spatially and temporally to create a gradient of disturbance intensity across the landscape. Military training of this nature has been occurring on many installations for a number of years, thus allowing the biological communities time to adjust their distribution and occurrence in response to the unique gradient of disturbance.

In my research, I used the predictable disturbance patterns that occur on military installations to investigate the long-term effect of multiple disturbances on plant functional group abundance and diversity. Because of the unique disturbance regime present on military installations and Fort Pickett specifically, I investigated not only the effects of long-term disturbance but also the effect of their interaction on functional group abundance and diversity. I chose functional groups (C4 grasses, C3 grasses, forbs, legumes, and woody plants) that consisted of species with similar physiology and effects on ecosystem processes. At Fort Pickett the disturbances associated with military training, fire and vehicle maneuvers, have occurred consistently for over 60 years, allowing time for the system to reach a new equilibrium with respect to species distributions and ecosystem processes. My research showed that two distinct disturbances associated with military training, vehicle maneuvers, and fire; do affect functional group abundance, within functional group richness, and total species richness. In general, non- woody functional groups increased in abundance as both types of disturbance increased and within functional group richness, a measure of functional redundancy, generally increased in response to fire and decreased in response to military vehicle disturbance.

Soils are the medium in which many biogeochemical processes occur that affect ecosystem structure and function, and thus soil disturbance can have profound effect on overall ecosystem processes. At Fort Pickett, as with other military installations, disturbance caused by landscape-level military training (i.e. vehicle maneuvers and fire) interacts spatially and temporally to create a gradient of disturbance intensity across the landscape. The most apparent effect of disturbance from military training to ecosystem structure is the destruction of vegetation. I provided clear evidence that military disturbance occurring at Fort Pickett affects the composition and diversity of plant communities. Impacts caused by military maneuvers to the physicochemical properties of soil are less apparent but may still have important effects on ecosystem processes, including a reduction in above- and below-ground productivity.

I used the unique land-use practices that occur on military installations to demonstrate the long-term effect of multiple disturbances on physicochemical soil properties at Fort Pickett. Physical disturbance from military maneuvers adversely influenced physical soil structure by increasing bulk density and decreasing overall porosity and, more importantly, macroporosity. Wildfire from military training also affected physical soil properties through the consumption of above-ground vegetation and resultant reduction in litter inputs to the soil profile. This effect was more pronounced when both types of disturbance co-occur. Both types of disturbance were related to higher stocks of soil cations, presumably through increased mineralization rates of organic matter. However, the strength of these relationships was moderate at best, which may reflect the influence of previous land use. The signatures from years of varied and at times intense land use associated with typical small farms of the Virginia piedmont (e.g. a mosaic of pasture, row crops, and woodlots) are still evident in many of the soils found at Fort Pickett. This historic land use is an underlying source of variation, which complicates attempts to isolate the precise response of soil physicochemical properties to military training.

Disturbance is a fundamental abiotic process affecting many levels of ecological organization. Consequently, the most surprising result of my study was the lack of a statistically significant disturbance main effect for two of the response variables, soil CO_2 flux and available N-NH4+, that have shown strong responses in other studies. The only explicit experimental main effect I was able to detect was that of functional composition on available soil N-NH4+. In my research, removals of single functional groups increased available soil N-NH_4^+, suggesting that mineralization was the dominant process. However, as the number of functional groups removed increased root decomposition likely increased soil C to a point where immobilization became the dominant process, thus limiting the available soil N-NH4+. The interactive effects of disturbance and functional composition on soil CO_2 flux demonstrated how the loss of functional diversity may lead to instability in ecosystem processes in disturbed ecosystems.

In this dynamic ecosystem, I demonstrated that the abundance and diversity of plant functional groups was significantly influenced by the type and intensity of disturbance. These physiologically based functional groups have been shown to influence ecosystem processes. By experimentally altering the abundance and diversity of these functional groups in a disturbance-mediated ecosystem, I showed that functional groups and presumably species influence key ecosystem processes.