Decomposition of Coarse Woody Debris and Microbial Biomass in Tidal Freshwater Forested Wetlands along a River to Estuary Gradient on the Apalachicola River in Florida

by

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Abstract

Decomposition dynamics of mass, carbon (C), nitrogen (N), and phosphorous (P) as well as downed woody debris biomass and microbial biomass were assayed along a river to estuary gradient in wetlands alongside the Apalachicola River in Florida. Decay rates (unitless) ranged from 0.007 to 0.030 for coarse woody debris (CWD) and 0.006 to 0.009 for control wood among plots and was significantly different among plots ($P<0.05$). Differences in decay rates are likely due to hydrological factors. All other parameters measured, such as distance to coast, soil salinity, soil nutrients, and microbial biomass C and N either were not significantly related to decay rates ($P<0.05$) or had very low R^2 values (<0.02). Although C decomposition followed closely with mass loss, N and P did not follow such easily distinguishable trends. Nitrogen and P mineralization/-immobilization patterns varied greatly among plots and collection periods. Average downed woody debris biomass ranged from 1.54 Mg/ha to 5.84 Mg/ha among plots. Downed woody debris biomass in the size class >7.62 cm was significantly related to the parameter, distance to coast, because the three plots farthest from the coast had the highest amounts of downed woody debris biomass. The smaller size class of <7.62cm was statistically related to the parameters of soil C, soil N, and soil P concentrations ($P<0.05$) and showed no real pattern among plots. Microbial biomass C ranged from 0.37 to 0.79 g C/ kg while microbial biomass N ranged from 13.92 to 73.74 mg N/kg among plots. Both microbial biomass C and N were significantly different among plots, although there was no clear pattern in terms of distance to coast. Microbial C and N increased consistently from May - August.

Table of Contents

List of Tables

List of Figures

1. INTRODUCTION

Tidal freshwater forested wetlands are complex systems poised on the fringe between freshwater forests and oceanic bays. Their location as a coastal ecotone makes these wetlands especially susceptible and sensitive to changes in sea level or land use within river basins. This project will help in understanding how these critical ecotones react to the environmental conditions of flooding and the periodic intrusion of saline waters.

Wetlands provide many ecological services and functions to humans and the environment, respectively. Functions such as pollutant removal and retention, carbon sequestration, and reduction of flooding in surrounding areas all directly benefit society. Food and habitat for wildlife such as fish, waterfowl, and black bear (*Ursus americanus*) as well as recreation are also provided by wetlands. (Hopkinson et al. 2008; Park and Polprasert 2008; eds. Mitsch and Gosselink 2000; Kozlowski 2002). Historically, tidal freshwater forested wetlands were seen as ideal lands for the propagation of rice, irrigation for other crops, and timber harvesting. Bald-cypress (*Taxodium distichum*) was very hardy and water resistant, making it attractive for buildings and boats. Wetlands were often drained for farming, and rice fields began to replace native vegetation within the wetlands. Some of the rice fields have evolved to open pond or marsh (Gresham and Hook 1982). Field et al. (1991) performed a nationwide survey inventorying acreages of wetland habitats within coastal counties. This survey conservatively estimated that over 200,000 ha of tidal freshwater forests exist in the Southeastern United States. The author also found tidal freshwater forests to be more abundant than tidal freshwater marshes in the majority of the Southeastern states.

Coastal wetlands are also critical in protecting coastlines from storms as well as aiding in sedimentation to prevent erosion. Unfortunately, tidally influenced freshwater systems represent an understudied type of wetland. Information on carbon cycling is particularly sparse (Doyle et al. 2007). A better understanding of these unique wetlands is vital for preservation and conservation, however, the balance between hydrology and salinity in these distinctive wetlands makes understanding these systems difficult.

Tidal freshwater forested wetlands are not easily classified due to fluctuating factors such as river flow and tidal intrusion (Doyle et al. 2007), and are expected to be among the most susceptible ecosystems to climate change. A change in temperature or precipitation regime as well as land use along coasts would ultimately alter the hydrology, biogeochemistry, biomass production, and biology of wetlands, thus affecting ecosystem functions such as nutrient cycling and flood mitigation (Mulholland et al. 1997). Nutrient turnover rates in brackish areas could potentially be affected by increased microbial decomposition due to an increase in atmospheric CO_2 and warmer temperatures (Keller et al. 2009). Coastal wetlands are also threatened by altered subsidence rates from climate change (Doyle et al. 2007). In particular, wetlands in the Gulf Coast are currently undergoing soil subsidence from various factors such as degradation and hydrological change, and climate change will likely only exacerbate these conditions (Cahoon et al. 1998; Burkett et al. 2002; Morton et al. 2002).

Tidal freshwater forested wetlands may undergo a net loss (Doyle 1998), as well as be affected in a number of other ways due to climate change. Day et al. (2008) stated that coastal and estuarine wetlands, like Apalachicola Florida, will respond to climate related change in four primary ways: shifts in soil or sediment (i.e. sedimentation or soil subsidence), changes in wetland/water area, changes in elevation, and alterations in boundary or edge distribution. The

degree of possible impacts that climate change will have on wetlands differs among wetland type, extent of human involvement, and region, making accurate predictions difficult (Burkett and Kusler 2000; Nicholls 2004; Nicholls et al. 1999).

Wetland function is primarily determined by hydrologic processes (Williams 1998). The manner in which water is transported through or stored within a system defines the type of system. However, wetland complexity increases when salinity and freshwater mix. Day et al. (2007) stated that the hydrology of tidal freshwater forested wetlands has received even less attention than other facets of these wetlands and defining boundaries therein vary in difficulty from upstream to downstream areas.

The flood pulse (i.e. lateral exchange of water between a river channel and adjacent floodplain) plays a vital role in the biogeochemistry of tidal freshwater forested wetlands and is the driving force influencing biota in riverine floodplains (Junk et al. 1998). Furthermore, Junk et al. (1998) suggested that flood pulse duration and frequency can greatly modify the organisms therein. Pulses of longer duration and greater frequency produce an environment where organisms are more adapted to utilize the aquatic/ terrestrial transition zone more efficiently. Similarly, areas with unpredictable pulses of short duration provide environmental conditions where organisms may have difficulty in adapting. Thus, pulsing of river waters with high salinity and sulfate concentrations from adjacent marine systems along with nutrient dynamics associated with an inundated forest causes complexity in biogeochemical processes.

The hydroperiod of tidal freshwater forests is driven primarily by over bank flooding from adjacent rivers and streams as well as tidal surge which fosters flood tolerant plant species such as bald-cypress, tupelo (*Nyssa* spp.), sweetbay magnolia (*Magnolia virginiana*), ash (*Fraxinus* spp.), cabbage palm (*Sabal palmetto*), overcup oak (*Quercus lyrata*), and red maple

(*Acer rubrum*). This type of inundation by river overflow is often referred to as surface water hydrology (Williams 1998). Tidal freshwater forested wetlands occur where tidal influences extend along coastlines and upstream along river banks, and have a significant influence on surface water hydrology. Tidal influences typically range from ~ 10 to 15 km up river along Gulf Coastal rivers, but can range as far as 32 km upriver on the Apalachicola River, although there is no clear evidence of persistent tidal influence that far upriver, and are extremely dependent upon mean regional tidal range (Elder and Cairns 1983).

Tidal bald-cypress swamps usually have hummock – hollow microtopography and relative forest floor elevations near the mean high water level in the adjacent river. Bottomland hardwood species become more dominant as the wetland floor elevation becomes higher relative to the level of mean high water (Day et al. 2007). Species of trees also vary in accordance with microtopography and landscape (backswamp and streamside) (Duberstein and Conner 2009). Tidal freshwater forested areas nearer the coast typically often have relative elevations lower than those of swamps that are farther upstream. The change in relative elevation along the river causes differing inundation periods and changes in tidal connectivity for adjacent swamps.

Forested wetlands along the Apalachicola River in Florida farther from the coast (i.e. non-tidal) exhibit different hydroperiods and hydrographs than forested wetlands nearer the coast (i.e. tidal) (Elder and Cairns 1983). Wetlands up river (> 20 km) tend to have higher flood peaks reaching heights up to 3 – 4 m, and also tend to be flooded for less time throughout the year. The main flood peaks are in winter between January and April (Elder and Cairns 1983), but can flood year round. Up river floodplain topography is also less flat and narrower than down river counterparts. Essentially, water becomes deeper in the low areas and is contained within less land area. Carolina ash (*Fraxinus caroliniana*), water tupelo (*Nyssa aquatica*), and ogeechee

tupelo (*Nyssa ogeche*) are most prevalent within these forested systems while bald-cypress, cabbage palm, swamp tupelo (*Nyssa sylvatica biflora*), and other hardwoods are the dominant canopy cover of forested wetlands closer to the coast.

Forested wetlands near the coast are subjected to both freshwater and saltwater influences while having a lower elevation gradient than wetlands upriver, these tidal wetlands tend to be more frequently inundated for longer periods of time while having lower flood peaks. The saltwater influence near the coast varies over time due to factors such as tides, wind, land gradient, storm frequency, timing, and duration (Doyle et al. 2007; Schroeder 1978). These factors, along with river flow, can establish a salinity gradient in the overlapping riverine and estuarine area (Ward 1978). Low river flows allow saltwater intrusion farther upstream while high river flows push saline waters back toward the ocean. Winds, as well as major climatic events such as tropical storms and hurricanes, may also move salt water upstream. Since river stage, tides, winds, and storms are dynamic in space and time, the salinity gradient also changes continuously along the river channel.

Long term alterations in patterns of salinity exposure could cause changes in the floral and faunal communities. Along with direct salt toxicity from Na^+ and Cl^- ions, salinity exposure increases the osmotic stress on vegetation and may alter the forest community with potential ramifications regarding the occurrence of salt tolerant versus freshwater species (Allen et al. 1998). Some species adapted to the presence of salinity produce compounds that reduce osmotic pressure (osmolytes). The rise in sea level as well as the diversion of water for urban and agricultural needs in the upper portions of the river basins may contribute to the inland movement of tidal waters.

Soils of tidal freshwater swamps accumulate large amounts of organic matter and clay

(Coultas 1984). Generally, high rates of production within tidal freshwater forested wetlands coupled with slow rates of decomposition of woody debris in soil lead to high concentrations of soil organic matter (Wharton 1978). The slow rate of decomposition is commonly associated in areas with prolonged inundation; however, hydrology can have varying effects on decomposition. Cycles of flooding and subsidence can increase or decrease the rate decomposition (Brinson et al. 1981; Mitsch and Gosselink 2007), and it matters if wood is lying on the surface versus buried in the soil. In particular, rates of decomposition may be greatest in areas where single, short-lived flood events take place (Lockaby et al. 1996). Decomposition rates for surface wood are usually greater in floodplains than adjacent uplands, while the opposite would be more accurate for buried wood and senesced roots (Romero et al. 2005).

Coultas (1984) describes soils within the swamps of the Apalachicola estuary as poorly drained and suggests that soils there never fully dry. Cypress swamps in the Apalachicola area of Florida also have low bulk densities (0.18–0.51 Mg/m^3) (Coultas and Duever 1984; Nessel and Bayley 1984). Furthermore, the soils tend to be acidic to neutral (4.9 – 6.6 pH) when moist, but become even more acidic upon drying (up to 2.5 units of pH lower). Soil salinity within these areas generally increases with depth (Coultas and Duever 1984).

There is a lack of knowledge regarding nutrient cycling processes within tidal freshwater swamps. Relatively little biogeochemical research has occurred in these wetlands (Anderson and Lockaby 2007). Decomposition of coarse particulate organic matter, such as coarse woody debris (CWD), is primarily due to the interaction between physical fragmentation and microbial processes (Gessner et al., 1999). CWD is important because of its role in nutrient dynamics. It can release nutrients slowly or rapidly over time, and is an important factor in nutrient transport. The fragmentation of wood is a mechanical process controlled by environmental elements. This

can be due to abrasion by other pieces of debris, but primarily by water flow disintegration of the wood. Physical fragmentation increases the surface area of wood that is available to microarthropods and microbes, thus promoting an increase in microbial colonization. These physical processes can be very important by driving nutrient availability and stimulating a higher rate of decomposition of coarse particulate organic matter (Diez et al., 2002; Gulis et al., 2004). However, distinguishing the effects of fragmentation from microbial breakdown is difficult, but can be important in determining the decomposition microenvironment (Spänhoff et al. 2007).

Tidal freshwater forested wetlands currently remain an understudied ecosystem. Specifically, little knowledge exists regarding the biogeochemistry and soils of these wetlands. The constant interaction of freshwater and saltwater makes these ecotonal wetlands unique and difficult to study. This research project will help in understanding how tidal freshwater forested wetlands cycle nutrients and how they react to differences in hydrology and salinity regimes. With this new information, we will be better enabled to preserve, conserve, and manage these wetlands as well as aid in monitoring climate change effects.

2. DECOMPOSITION AND BIOMASS OF COARSE WOODY DEBRIS IN TIDAL FRESHWATER FORESTED WETLANDS ALONG A RIVER TO ESTUARY GRADIENT ON THE APALACHICOLA RIVER IN FLORIDA

2.1 ABSTRACT

Woody debris decomposition in terms of mass, carbon (C), nitrogen (N), and phosphorous (P) as well as downed woody debris biomass were examined along a river to estuary gradient alongside the Apalachicola River in Florida. The nine plots used were placed in freshwater forested wetlands that varied primarily by distance to the coast. Decay rates (unitless) ranged from 0.007 to 0.030 for coarse woody debris (CWD) and 0.006 to 0.009 for control wood among plots and was significantly different among plots ($P<0.05$). Plot 9 (closest to the coast) had the fastest rate of decay for CWD, while plots 4, 5, and 9 had the fastest decay rates for control wood. Observed differences in decay rates are likely due to hydrological factors. The wetland at plot 9 was drained by nearby sloughs which probably allowed for brief non-flooded periods not experienced by other plots. These intervals of at least somewhat aerated soil conditions may have resulted in the faster decay rates. Also, plots 4 and 5 had the fastest recorded flow rates and had relatively high decay rates as a result of mechanical disintegration. All other parameters measured such as distance to coast, soil salinity, soil C, soil N, soil pH, microbial biomass C, and microbial biomass N either were not significantly related to decay rates ($P<0.05$) or had very low R^2 values (<0.02).

Although C decomposition followed closely with mass loss, N and P did not follow such easily distinguishable trends. Nitrogen and P mineralization and immobilization patterns varied greatly among plots and collection periods. Nitrogen mineralization/-immobilization oscillations

observed during our study most likely occurred because of microbial deficiencies and demands that were not measured for every CWD collection period. We expected N to be consistently immobilized based on CWD and microbial biomass C/N ratios. Phosphorous values exhibited a high amount of variation during the study period. Phosphorous seemed to have undergone some relatively short duration immobilization events, and P remaining at 14 months ranged from 20 – 60% among plots. The immobilization stages of P indicate some periods of microbial P deficiency, and that decomposition may be P limited during short intervals of decomposition. However; the overall loss of P during the observed 14 months suggests that CWD decomposition is not on the whole P limited.

Average downed woody debris biomass ranged from 1.54 Mg/ha to 5.84 Mg/ha among plots. Downed woody debris biomass in the size class >7.62 cm was significantly related to distance to the coast because the three northernmost plots (farthest from the coast) had the highest amounts of downed woody debris biomass. This is likely because the trees tend to be larger in those areas as opposed to areas closer to the coast. The smaller size class of <7.62cm was statistically related to the parameters of soil C, soil N, and soil P concentrations ($P<0.05$) and showed no real pattern among plots (i.e. distance to coast).

2.2 INTRODUCTION

The role of coarse woody debris (CWD) in nutrient cycling is a complex function that varies among locations due to several factors. The function of CWD in nutrient cycling is generally as an immobilization/-mineralization repository for nutrients. Nutrients such as N, C, and P may either be stored in CWD and are unavailable to plants, or CWD may release these nutrients making them plant accessible. Coarse woody debris is broadly defined as downed dead wood. Some common forms of CWD include branches, sections of tree stem wood, and snags;

though snags are also considered standing dead wood. Most studies typically use wood with >2.5cm diameter, but CWD may be much larger (Harmon et al. 1986).

Accumulation of woody debris in an area is a result of the balance between four processes: in situ production, transport of litter from outside into system, decomposition and destruction of litter, and transport of litter out of a system (Facelli & Pickett 1991). In situ litter production may happen for a variety of reasons which include tree mortality and breakage of limbs (Stevens 1997). CWD transport via water can be enhanced by flood and storm events. Large amounts of woody debris can potentially be moved about on a floodplain during high water/ high flow events. This flux of CWD causes changes in habitat quality and nutrients throughout a floodplain.

Forest stand age, disturbance regime, amount of soil organic matter, as well as management and disturbance histories are important vectors that directly affect quantity and quality of CWD in a system (Woldendorp and Keenan 2005; Clark et al. 1998). The proportion of total aboveground biomass in CWD has been recorded from ~1% to as high as ~45% depending upon these factors (Duvigneand and Denaeyer-DeSmet 1970; Grier et al. 1981). However, most studies have focused on upland coniferous forests (Polit and Brown 1996; Brown and Peterson 1983; Harmon et al. 1986). About 12% of the total organic matter found in coastal plain, blackwater swamps is contained in woody debris (Benke and Wallace 1990). Quantity and quality of CWD also differs due to species, edaphic conditions, litterfall, stage of decomposition, microbial activity, fungal presence/absence, leaching, and fragmentation.

The kinds and amounts of nutrients in CWD range widely among ecosystems and can be a potentially critical nutrient sink or source for floodplain ecosystems (Harmon et al. 1986). In some systems, the CWD represents a large pool of C and other nutrients. This C sink in woody

debris can help offset a loss of soil C from land use change (Guo et al. 2006). In ecosystems that undergo large scale disturbances such as hurricanes, CWD represents the largest litter component (Everham and Brokaw 1996). CWD producing events are often key in regulating turnover and storage of C, N, and P (Romero et al. 2005). For instance, Hafner et al. (2005) found that N concentrations were higher in CWD than in the soils directly below.

Percentage of total aboveground storage in CWD of P and N can range from 1-16.5% and 2-21% respectively (Greenland and Kowal 1960; Sollins et al. 1980; Duvigneand and Denaeyer-DeSmet 1970). In general, N concentrations stored in CWD are very low when compared to total N of a system. Soils and living biomass typically contain much higher concentrations of N compared to CWD (Harmon et al. 1986). The concentration of P, however, is much more similar between CWD and soils. Although CWD contains a small proportion of ecosystem total N, it is important since it can potentially alter N availability for plants. The CWD may also drive patterns of N spatial heterogeneity as well as influence the extent of N exported from temperate forests (Hafner and Groffman 2005).

A fraction of the nutrients held within CWD are transported within the CWD as it is moved via water flow. This can either disperse or concentrate the nutrients throughout a watershed. After a major disturbance, these nutrients can be vital for the regrowth of vegetation as they represent a pool of nutrient resources already on site. Pettit and Naiman (2005) found that forest soils associated with large piles of woody debris after a flood had much higher concentrations of nutrients than reference plots without large woody debris. The plots with woody debris present had 19% more total N, 51% more available P, and 36% more total C when compared to the reference plots without large woody debris. This resource pool can considerably influence the onset of riparian vegetation growth. In a small Oregon watershed, woody debris

constituted ~50% of the N pool (Triska et al. 1984). However, this retention of nutrients in woody debris can reduce nutrient supply for surrounding plant growth since the woody debris may immobilize nutrients during decomposition and release it very slowly to the plants (Kuehne et al. 2008).

Laiho and Prescott (2004) stated that the nutrient (N or P) immobilized at the beginning of decay often will show source activity later. Therefore, N or P may increase during decomposition depending on the initial N/P ratio of woody debris. The N/P ratio typically moves toward steady state equilibrium at about 20 (Laiho and Prescott 2004, 1999). One study along the Satilla River in Georgia found that decomposing fallen litter in wet sites within a blackwater floodplain tended to assimilate P at high levels (187% of original P), while N content dropped to 50% during the 2 year study. Based on their results, the authors suggested that the microbial communities in these wet areas were not N limited (Schilling and Lockaby 2005). Conversely, Brinson (1977) found that twigs exhibited a rapid loss of P, and that N was immobilized in an alluvial coastal plain swamp forest in North Carolina. This study also showed a seasonal difference in decomposition rates as well as between river, natural levee, and swamp floor sites.

Rice et al. (1997) studied woody debris decomposition in a forested wetland of Louisiana and found that decomposition rates differed due to orientation (wood was either in contact with the ground or suspended above) for both fine and coarse woody debris. Woody debris in contact with the ground decomposed faster than suspended debris. They also found that light and heavy canopy disturbance regimes were not different in terms of decomposition rates. Nutrient dynamics within the CWD of the study showed that P was released during decomposition and N was accumulated. Mass remaining in CWD was around 70% and 50% at 18 and 30 months respectively. Decay rates for CWD in this study were rapid when compared to other studies

elsewhere in the United States using deciduous CWD.

Romero et al. (2005) studied decomposition of woody debris in a south Florida mangrove forest and found differing rates between species and placement on site. Buried wood decayed more slowly than wood on the soil surface because of the differences in tidal flushing and oxygen availability, and some species decomposed faster than others due to differences in concentrations of labile components in the wood. Also, P was consistently mineralized, while N tended to be immobilized. However, the authors found no significant differences in decomposition rates along a freshwater-to-marine gradient. Elder and Cairns (1983) reported faster leaf litter decay in estuary sites when compared to lower and upper river sites along the Apalachicola River in Florida. They attributed these differences to higher temperatures, wave and tidal action, and large numbers of microbial decomposers, even though they did not quantify microbial populations. This suggests that microenvironment may be more conducive for decomposition closer to the coast, opposite our hypothesis.

Day (1982) found that differences in litter quality had a greater effect on decomposition than the effects of differing hydrologies within four communities of the Great Dismal Swamp in Virginia. However, Baker et al. (2001) found decay rates for leaf litter among four floodplain communities of the Southeastern United States to be primarily affected by hydroperiod, as opposed to litter quality. They suggested that litter quality appears to be more important in driving decomposition in areas with similar edaphic conditions, and that the extent to which litter quality affects decay diminishes as hydroperiods diverge. Another study suggests that pH may influence decomposition rates more than total available soil N, % soil organic matter, or even electrical conductivity (Neher et al. 2003).

Some studies have examined effects on decomposition along a salinity gradient using

maize and pea straw. Muhammad et al. (2006) found that microbial biomass C and biomass N were negatively affected with increased salinity while there was no effect on microbial biomass P. They also found that an increase in salinity did not have a depressive effect on the decomposition of the straw. The soils in this study, however, had high pH (> 8.2). Another study found that increased levels of salinity lead to slower decomposition using maize straw (Wichern et al. 2006). Sometimes increasing salinity levels also comes with an increase in inorganic N, primarily NH□ □, as well as lower microbial biomass and soil respiration.

Another study by Rejmánková and Houdkova (2006) examined effects of salinity, litter quality, and edaphic conditions on *Eleocharis* spp. decomposition. Salinity differences among sites were measured as conductivity and ranged from low (0.2 mmhos/cm) to high (5 mmhos/cm). They attributed the salinity differences among sites to dissolution of parent materials as these were inland sites. They found significant decomposition differences along a salinity gradient among differing sites and litter qualities, with the difference in site (in terms of soil nutrients) effect being stronger. They found that P was the nutrient most important for the differences in decomposition. Material on sites with soils lower in P decomposed more slowly and had lower amounts of microbial biomass. Rejmánková and Houdkova (2006) also stated that the salinity effect was masked by the differences in site and litter nutrient quality, but that decomposition rates were significantly slower at higher salinity sites. They stated that microbial activity may be lower at higher salinities. Li et al. (2006) suggests that the salinity effects on decomposition depended heavily on the interaction of three important variables: phase of decomposition, salinity level, and soil water content. The authors also stated that after an initial lag period from salts being added, microbial communities shifted from salt intolerable to salt tolerable species and respiration from decomposition generally increased. Tidal freshwater

forested wetlands likely have salt intolerable and tolerable microbial communities present that shift in dominance as tidal influence ebbs and flows.

Contradictions remain involving the role of N and P in decomposition within wetlands. There is particularly little known about the role of these nutrients in tidal freshwater forested wetlands. Some studies previously mentioned have shown that CWD acts as more of a P sink than N, while other studies have shown the opposite. Reasons for such discrepancies could be differing hydroperiods, litter quality, and edaphic conditions such as pH, soil fertility, or salinity. Consequently, results vary among studies. Some state that litter quality is the most important factor of decomposition; still others reported hydroperiod or pH to be the most important. Perhaps the reason for such discrepancies for decay rates among the literature is primarily a function of geographic location. These studies were performed in various parts of the world with different climates. Since soil properties such as temperature and moisture are primary drivers of decomposition along with litter quality and microbial populations (Swift et al. 1979), conceivably the differences within studies may be driven by climatic conditions.

An information gap also remains concerning the role of salinity in decomposition. Some studies have found that decomposition was not significantly different between freshwater and saltwater sites, while other studies report differences. Perhaps the high salinity waters produce an environment with high osmotic stress levels causing decomposition in these areas to be slower. However, the high concentrations of sulfate in saline waters could provide ample electron acceptors for microbial communities adapted to live in reduced conditions, thus allowing a higher rate of decomposition. Nutrient cycling roles such as N and P immobilization/-mineralization dynamics during decomposition in tidal freshwater forested wetlands particularly remain unclear.

The objectives of this study were to: (1) determine decomposition dynamics of carbon (C), phosphorous (P), and nitrogen (N) along a river to estuary gradient; (2) ascertain rates of mass loss for CWD along the river to estuary gradients; (3) estimate mass per unit area of CWD across the gradient; and (4) determine nutrient source/ sink relationships in CWD. We hypothesized that: (1) decomposition rates will be slower in areas with higher salinity; (2) plots with higher salinities will accumulate a higher amount of CWD due to slower rates of decomposition; and (3) P and N will exhibit source and sink activities, respectively, during decomposition.

2.3 METHODS

2.3.1 STUDY SITE DESCRIPTION

The Apalachicola River Basin (ARB) is composed of three major rivers and drains an area of about 50,800 km² with an average discharge of 870 m³/s at the Jim Woodruff Dam (Elder and Cairns 1983). The Apalachicola River is approximately 171km long and is formed by the merging of the Flint and Chattahoochee Rivers at the Jim Woodruff Dam on the Georgia/Florida state line. During its course from the Jim Woodruff Dam at the Georgia and Florida state line to the coast, the river falls only 12m in elevation. The Chipola River joins the Apalachicola near Wewahitchka, Florida, approximately 50 km from the coast. The watershed area of Apalachicola and Chipola River is around 12% (6,200 km²) of the entire ARB. The Apalachicola River's floodplain occupies approximately 454 km^2 and broadens to more than 10 km wide near the mouth of the river while narrowing to 2 km wide farther upstream (Elder and Cairns 1983). There is very little development along the southern portion of the Apalachicola River after it and the Chipola River merge; however, there is substantial development within the Apalachicola's watershed farther north (e.g. Atlanta, GA).

Extensive swamps line the floodplain of the Apalachicola River until it transitions into an estuary and flows into the Gulf of Mexico. There are over 40 species of trees that occur within these areas (Elder and Cairns 1983). Bald-cypress (*Taxodium distichum*) and tupelo (*Nyssa* spp.) occur in the uppermost swamps of the river. Other species found in these reaches of swamp are ash (*Fraxinus* spp.), sweetbay magnolia (*Magnolia virginiana*), water elm (*Planera aquatica*), red maple (*Acer rubrum*), and overcup oak (*Quercus lyrata*). However, as the river moves south, cabbage palms (*Sabal palmetto*) become more prevalent while other tree species become stunted and scarcer from the stress related to the higher salinities. Many blackwater creeks feed into the main river stem along its entirety.

This study was performed on 9 plots in freshwater tidal swamps lining the Apalachicola River in Florida (Figure 2.1). These plots ranged from about 7km from the coast to approximately 28 km upstream. The three uppermost plots were placed within cypress-tupelo swamps of the Apalachicola National Forest while the remaining six plots were placed within the Apalachicola River Wildlife and Environmental Area.

All plots consisted of microsites containing one of three soil series: Brickyard (Typic Endoaquepts), Chowan (Thapto-histic Fluvaquents), and Kenner (Fluvaquentic Haplosaprists). The USDA National Resource Conservation Service (NRCS) classifies these soil series as very poorly drained, poorly drained, and very poorly drained respectively (Schuster et al. 2001). Soil texture of plots 1 – 3 (the furthest from the coast) was classified as clay loam. Plot 4 and 5 were silty clay loam and sandy loam, respectively, while plots 6 and 7 were classified as loam. The remaining plots 8 and 9 were considered to be loamy sand and silt loam respectively (Table 2.1).

2.3.2 EXPERIMENTAL DESIGN AND FIELD COLLECTION

To obtain CWD for this study, branches were cut from freshly felled red maple (*Acer rubrum)* trees that occurred near all nine plots. Red maple was chosen because it was one of the few common species across all the study sites, also the red maple wood had slightly lower densities than other common species found within the floodplain. All CWD pieces were cut the same length (~25 cm) and within a set diameter range (~20-40 mm). CWD placed on a plot for the duration of the research was collected near that plot. Thirty two pieces were collected near each plot and brought back to the lab, for a total of 288 pieces of CWD. Each piece of CWD was air dried for two weeks, and weighed as initial air dried weight. Diameters were also measured at each end and in the middle of each piece in order to provide a backup way to measure wood mass. Each piece was individually numbered in order to track it through the course of this study.

Three sticks of CWD not used for decomposition analysis were also collected at each plot in order to determine moisture content. These pieces were air dried then weighed, and then weighed again after being oven dried. Percentage of moisture content was calculated: (1 – (oven dried weight/air dried weight)) x 100. To obtain initial oven dried weights for each piece of CWD, moisture content was subtracted from the air dried weight.

After each piece of CWD was weighed, tagged, and diameters measured, they were returned to the field and placed on the plot from which they were collected. Two sets of CWD were placed on each plot. A set consisted of 18 pieces of wood. Each set of CWD was bound together by running a small rope through the zip ties that held the numbered tree tags on each piece of CWD. The rope was then tied to a nearby tree and staked in the ground using pin flags. This held the CWD in place and kept it from washing away during flood events. The pair of sets was placed within close proximity to each other on the plot on similar micro-topographical features. Four pieces of CWD were collected (two from each set) from each plot per collection

interval.

Sets of wooden dowels made from white pine (*Pinus strobus*) were also deployed and collected from each plot every collection. This wood was also air dried and weighed the same as the red maple. These sticks represented a homogonous substrate. The wooden dowels acted as a control substance so that the influence of site quality could be separated from litter quality. Each stick was 2.5cm x 5cm and approximately 30cm long. The sticks were also held in place in a similar fashion as the CWD. Each CWD piece and wooden stick was separated by a few centimeters and individually marked with tags.

2.3.3 CWD AND CONTROL DECOMPOSITION

To determine decomposition, CWD and control wood were periodically collected over a 14 month period. There were 7 collections: time 0, 1, 3, 5, 7, 11, and 14 months. Collections were more frequent at the beginning of the study period in order to capture the rapid change in the mass loss due to rapid initial decomposition of labile materials within the wood. Handling loss was thought to be minimal for all CWD due to the nature of the bark, which was thin and tightly attached to the wood.

After each collection, the CWD and control wood were oven dried to a constant mass at 70□ C for 6 days, cooled, weighed to the nearest hundredth of a gram, and then ground to pass a 20-mesh sieve (0.85 mm). Percent ash was calculated using 0.25 g of sample and with the formula: (sample mass after ignition/ sample mass before ignition) x 100%. Percent ash was subtracted from the oven dried weight after collection. This corrected weight was then compared to initial oven dried, ash corrected weight to determine percent mass loss due to decomposition.

Percent mass, N, P, and C remaining were calculated for every collection period. Only CWD was assayed for N, P, and C. Total C and N concentrations were determined by thermal

combustion using a Perkin-Elmer 2400 series II CHNS/O analyzer (Perkin-Elmer Corp., Norwalk, CT.). Total P was determined by the vanadomolybdate procedure using HCl extract after dry ashing at 500□C for 4 hours (Jackson 1958).

2.3.4 DOWNED WOODY DEBRIS BIOMASS

The line-intercept method (Brown 1974) was used to estimate the mass of CWD on an area basis at each study site. At each plot, 20 subplots were distinguished by using 4 transects with 5 subplots on each. Transects were spaced 40 meters apart, and each subplot on each transect was spaced 20 meters apart. A 20 meter line in a random direction was extended from the center of each subplot. All woody debris that intersected the line was put into a diameter size class category of 0 - 0.64, 0.64 - 2.54, and 2.54 – 7.62 cm. Also, all wood bigger than 7.62 cm diameter was placed into a decay class category (I – IV) and measured for diameter and length. Decay class category was determined visually by preset characteristics such as presence/absence of bark, fragmentation, and shape of bole. Samples were also taken from the downed woody debris in order to convert volume to mass.

2.3.5 SOIL ANALYSIS

Soil was collected in May, June, July, and August of 2010 in order to evaluate soil nutrient status. Two bags of soil within the top 15 cm of the surface were collected at each plot (one at each CWD pack) and composited to obtain soil nutrient information. Soil parameters analyzed were total C and N, electrical conductivity (mmhos/cm), extractable Ca, K, Mg, Mn, P, and Zn, and soil pH. Total C and N were analyzed on a LECO CNS-2000, soluble salts were analyzed using an Orion model 162a conductance-resistance meter, analysis of extractable P, K, Ca, Mg, Mn, Zn by Mehlich I extract method, and soil pH was obtained by using a LabFit AS-3000 pH analyzer.

Soil textural analysis was also performed on samples from each plot. Fifty mL of a dispersing agent that contained sodium metaphosphate ($(NaPO_3)$ x Na_2O) and sodium carbonate (Na_2CO_3) was thoroughly mixed with 40g of soil and filled to volume with water in a 1000 mL cylinder. Hydrometer readings were recorded at time of initial mixture and at 24 hours. Percent sand, silt, and clay were determined per Gee and Bauder (1986).

2.3.6 HYDROLOGY

A regression formula was created for plots 1, 2, 6, and 9 relating average daily plot water level to average daily gauge height of a nearby USGS gauge (#02359170**)** station near Sumatra, Florida. These four plots had transducers previously placed from another study to record water level data (Anderson, unpublished data). Relative elevation was corrected for differences between the transducer and plot. Using Minitab 14 (Minitab Inc., 2003) a regression line equation was fitted to the data in order to use Sumatra gauge river levels to predict water levels for each plot. Duration and frequency of flooding were the primary parameters assayed. Flow was also measured at each plot during one instance at a low river stage using a Marsh McBirney Flo-Mate flow meter. Flow was measured at three depths in the water column: top 3rd, middle, and lower 3rd. These flows were averaged to obtain the reported flow for each plot.

2.3.7 STATISTICAL ANALYSIS

Statistical analyses were conducted using the GLM (General Linear Model) process to fit non-linear regression to litter mass loss curves. All statistical analysis was performed using the SAS 9.1 program. Nonlinear regression parameters were obtained by using PROC NLIN to predict mass loss. A negative exponential model was applied to the CWD mass loss data. ANOVA was used to compare mean decay rates (k), % C remaining, and % N remaining at 14 months among plots. ANOVA and regression statistical tests (type 1 sum of squares) using

proximity to coast, soil nutrients, and salinity as independent variables were used to evaluate relationships between decomposition metrics of decay rates, % C, % N, and % P remaining. Significant differences among mean decay rates were tested using Tukey's Honestly Significant Difference test at $P < 0.05$.

2.4 RESULTS

2.4.1 CWD DECOMPOSITION

For CWD, *k* ranged from 0.007 to 0.030 among plots (Table 2.2). ANOVA tests showed that there was a significant difference of decay rate among plots ($P<0.05$) with plot 9 (closest to the coast) having the fastest decay rate (k =0.030), while plot 7 had the slowest (k = 0.007). Plots 3, 6, and 7 had significantly slower decay rates than all other plots, and plot 9 had significantly greater decay rate than all other plots (Figure 2.2). Plots 1, 2, 4, 5, and 8 had intermediate decay rates. Control wood also showed significantly different decay rates among plots ($P<0.05$), with decay rates ranging from 0.006 to 0.009. Decay rates of control wood ranked as follows among plots: 6=7 < 3=8 < 2 < 1 < 4=5=9 (Figure 2.3). Percent mass remaining at 14 months followed the same general trend as decay rates.

Distance to coast, soil salinity, soil pH, and soil phosphorous were not significantly related to decay rates ($P>0.05$) for CWD. Conversely, soil carbon and nitrogen were significantly related with percent mass remaining ($P<0.05$) for CWD. However, these relationships all had very low R^2 values (< 0.02). For control wood, all parameters of distance to coast, soil salinity, soil carbon, soil nitrogen and soil pH were not significantly related to percent mass remaining.

2.4.2 C, N, AND P DYNAMICS

ANOVA results of % C remaining at 14 months showed significant differences among plots ($P<0.05$) (Table 2.3). Percent C remaining at 14 months was significantly lower nearest the

coast (plot 9) than all other plots (Figure 2.4). Percent C remaining generally declined during the study period and followed a similar trend to mass loss (Figure 2.5).

Percent N remaining at 14 months did not vary significantly among plots (Figure 2.6). All plots initially mineralized N and tended to have alternating immobilization/-mineralization events thereafter (e.g. Figure 2.7) which varied in magnitude among plots.

Percent P remaining at 14 months also showed no significant differences among plots (Figure 2.8). All plots followed an overall trend of mineralization, with one immobilization event at around 5-7 months (January – March) (e.g. Figure 2.9).

C/N ratios at 14 months varied significantly among plots (Figure 2.10) with plot 5 having significantly greater C/N values than plots 2 and 9. The remaining plots had intermediate C/N ratios. Ratios of N/P and C/P ranged from 10 – 150 and 1,000 – 22,000 respectively and did not vary significantly among plots. Although plots 8 and 9 (closest to the coast) had very high N/P and C/P values when compared to other plots, they were not significantly different.

2.4.3 DOWNED WOODY DEBRIS BIOMASS

Downed woody debris biomass for the size class >7.62cm ranged from 1.61 - 9.16 Mg/ha across plots (Table 2.4; Figure 2.11).The second farthest plot from the coast, plot 2, had the highest values and was significantly different from plots 4 – 9 ($P<0.05$). Plots 1 and 3-9 were not statistically different from each other ($P<0.05$). Plot 2 had a substantially greater woody debris biomass in the biggest size class (>7.62 cm) that was two to three times greater than any other plot. Downed woody debris in this size class was not significantly related to the parameters of soil carbon concentration, soil nitrogen concentration, soil pH, and soil salinity ($P>0.05$); however, distance to coast was significant ($P<0.05$).

Downed woody debris biomass for the size class <7.62cm ranged between 0.51 – 3.27

Mg/ha across plots (Figure 2.12).The four plots closest to the coast, plots 6, 7, 8, and 9, as well as plots 1, 2, and 4 had intermediate amounts of downed woody debris. Plot 3 had a significantly greater amount of woody debris than plots 1, 5, and 6. Plot 5 had the least amount of downed woody debris biomass and was significantly different from plots 2, 3, 7, and 8.

Downed woody debris in the size class <7.62cm was not significantly related to soil pH, soil salinity, and distance to coast ($P>0.05$). However, the parameters soil carbon, soil nitrogen, and soil phosphorous concentrations were significantly related to downed woody debris biomass <7.62cm ($P<0.05$).

2.4.4 SOIL ANALYSIS

Plot 8 had greater values of % total C, % total N, salinity, P, and C/P than any other plot (Table 2.5). Organic matter was thickly intermixed with the mineral soil for the top 15-30 cm, also there seemed to be very little flow at this plot which may account for the high accumulation of C. Plot 5 tended to have the lowest nutrient values and was predominately sand (78%) and exhibited one of the fastest water flows. These conditions provided more potential for nutrient export.

2.4.5 HYDROLOGY

Hydrological equations (Table 2.6) for the four monitored plots showed that for the majority of the study period, the plots remained flooded. Flooding duration was calculated as the number of days during the study period at which water level was at or above ground level. Flooding frequency represented the number of times that water level was above ground level during the study period. For the majority of this study (85% of the time during study), all plots remained under flooded conditions. Due to high rainfall in the river basin, daily discharge recorded at the USGS water gauge near Sumatra Florida was higher than the 36 year mean

during the period from late September 2009 to March 2010 (Figure 2.13). During a more average year, wetlands nearer the coast should be flooded more frequently and have longer flood duration with lower flood peaks than wetlands farther upriver. However, there was very little variation in hydroperiod among plots during the study period. Our observed flooding conditions for plots closest to the coast (plots 7, 8, and 9) were supported by hydrological data obtained from another study for wetlands in this area and during our study period (Jamie Duberstein, unpublished data). Also, flow was highest at plots 4 and 5 and negligible at remaining plots, though flow data was based on a single observation (Figure 2.14).

2.5 DISCUSSION

2.5.1 CWD DECOMPOSITION

Decay rates for this study were very low when compared to other CWD studies. Rice et al. (1997) found decay rates of 0.075 – 0.088 for woody debris 0.5 – 2.5 cm and 7.5 - 20 cm in the Atchafalaya River Basin of Louisiana. The authors used fresh woody debris along with felled wood from a hurricane 12 months earlier in order to construct a decomposition time sequence from 0 – 30 months. Likewise, Cheung and Brown (1995) found a decay rate of 0.089 for silver maple (*Acer saccharinum*) in a central Illinois floodplain forest by means of a chronosequential design using fresh, intermediate, and rotten decay classes. Cheung and Brown (1995) also stated that inundation periods within their study sites lasted only a few weeks and reported that 90% of their mass loss was attributable to microbial activity and leaching. A decay rate for downed maple species of 0.045 was reported for a non-flooded old-growth, mixed hardwood Indiana forest (MacMillan 1988). Onega and Eickmeier (1991) reported a decay rate of 0.11 for fallen dead maple species in an upland deciduous Tennessee forest. Day (1982) found high decay rates of 0.179 – 0.305 for downed red maple (*Acer rubrum*) in the Great Dismal Swamp of coastal

Virginia and North Carolina. Day (1982) suggested that hydrologic regime may have been very conducive for decomposition with alternating flooding and drying. He also noted that although the soil may be temporarily anoxic, the water remained fairly aerobic, allowing at least some oxygen to diffuse to the soil even in flooded conditions. Since our plots remained flooded for the vast majority of the study period, oxygen levels in the soil were likely very low. Also, the woody debris used in Day's study was collected from a tree felled 4 months earlier, which could render faster decay rates than wood collected from a live tree.

Decomposition rates are primarily influenced by microenvironment, litter quality, and microorganisms (Swift et al. 1979). Our decay rate values were likely low as a result of the fresh condition of the material used and the amount of inundation of the plots during the study period. From August 1 to December 1 of 2009, there were six tropical storms and three hurricanes that impacted the area. Although brief flooding events can stimulate decomposition (Lockaby et al. 1996), longer flooding events decrease the amount of oxygen in the soil and can slow rates. If the decomposition environment is anaerobic, microorganisms must rely on other elements besides oxygen as their electron acceptor in order to decompose organic matter. Consequently, the process is not as efficient and requires more time in order to break down organic matter.

Decay rates for CWD did not suggest a trend among plots. The only exception was plot 9 (closest to the coast), which had the fastest decay rate recorded, more than twice that of most of the other plots. The reasons for this remain uncertain, although plot 9 did have the lowest C/N and % P remaining, as well as the second highest % N remaining at 14 months, though not significantly so. Percent C remaining was the only other parameter assayed that was significantly different at plot 9 than the other plots, and this also reflects the high decay rate. Plot 9 also had only intermediate levels of microbial biomass C and N and C/N when compared to the other

plots. Another possible reason for the fast decay rate at plot 9 could be the plot's microtopographical effect on the hydrology. Plot 9 was drained by a couple of nearby sloughs, and the plot was located between these sloughs. Perhaps the plot underwent more aerobic periods (pulsing hydrology) than our hydrological equations accounted for such that it may have drained faster than some of the other plots.

Decay rates for the control wood also showed similar trends to that of the CWD decay rates among plots. There may be some reasons why plots 4, 5, and 9 had significantly faster decay rates than all other plots. Control wood at plot 9 may have had higher decay rates as discussed above for CWD decay rates at that plot. It is important to reiterate that decay rates for control wood only ranged from 0.006 to 0.009 and that some reported statistical differences among plots only varied by 0.001. Also, control wood decomposition showed no significant relationship with any of the soil nutrient or microbial biomass data. This may mean that decomposition of control wood was linked primarily to hydrology. Our hypothesis that decay rates would be slower in areas with higher salinity closer to the coast was not supported. One reason for this could be our low range of measured salinity. Since river flow was so high during the course of our study, the saline waters of the bay were likely prevented from moving up the river channel to our plots, keeping soil salinity measurements low at our plots.

Decay rate patterns for control wood were similar to those of CWD among plots. Both control and CWD rates maximized at plot 9 (closest to coast) followed by plots 4 and 5. This suggests that these plots may have the most conducive microenvironment for decomposition. Since decay rates for control wood and CWD had similar trends among plots suggests that litter quality influence was overridden by factors in the decay environment such as direct influences of hydrology.

2.5.2 C, N, AND P DYNAMICS

Carbon dynamics closely followed rates of mass loss as expected. Percent C remaining was significantly lower at plot 9 (closest to the coast) than all other plots, which coincides with the most rapid decay rates.

C/N ratios at 14 months varied from 140 -210 for CWD. These values are below the 350 – 500 C/N range found for most woody species (Cheung and Brown 1995). Cheung and Brown (1995) also state that N is typically immobilized when the C/N ratio of the substrate is higher than that of the microbial community. The microbial biomass C/N ratio ranged from 10 – 30 among all our plots, so N should have been immobilized consistently; however, there was no clear trend. Nitrogen mineralization and immobilization patterns varied greatly among plots and collections periods possibly due to variation in inundation. Consistent sink activity was not observed for N as we had hypothesized.

Although our P data exhibited a high amount of variation, P content reflected some relatively brief immobilization events, and %P remaining at 14 months ranged from 20 – 60% among plots. The immobilization stages of P indicate some periods of microbial P deficiency and/or high P input from flooding, and that decomposition may be P limited during short intervals of decomposition. However; the overall loss of P during the observed 14 months suggests that CWD decomposition is not P limited. Similar results were found by Cheung and Brown (1995) and Rice et al. (1997). These studies, conversely, had collection intervals of 6 months and could have missed short duration P immobilization events that we observed during early stages of decomposition. Our data may corroborate Brinson's (1977) suggestion that P may be conserved in the forest litter during the winter and released at tree growth initiation in early

spring. Although P represented overall source activity as we expected, P source and sink activity seems to alternate readily depending on hydroperiod and other environmental conditions.

2.5.3 DOWNED WOODY DEBRIS BIOMASS

Average downed woody debris biomass ranged from 1.54 to 5.84 Mg/ha. Downed woody debris in the large size class (>7.62cm) was significantly related to distance from coast. This was because the three northernmost plots (farthest from the coast) had the highest amounts of downed woody debris biomass. The reason for higher amounts of large woody debris in the northernmost plots is likely that the trees tend to be larger in those areas, also decay rate was not related to distance from coast. Trees nearer the coast are generally shorter due to the moisture stress afforded by higher salinities. The salinity may not have been statistically related to downed woody debris biomass because most of the 14 months of the study period were in a wetter than average year. The high river water levels could have pushed the salinity gradient towards the ocean and decreased our measured soil salinity in the more tidal wetlands.

The smaller size class of <7.62cm was statistically related to the parameters of soil carbon, soil nitrogen, and soil phosphorous concentrations ($P<0.05$). Smaller woody debris may represent more rapid release of nutrients than larger woody debris because of the faster decomposition of smaller wood and the higher surface area to volume ratio (Stevens 1997). This quick release of nutrients is likely an explanation for the significant relationship of smaller woody debris with soil carbon, nitrogen, and phosphorous. The amount of smaller woody debris quickly and directly contributes to the amount of carbon and nitrogen in the soil. This suggests that there may be a relatively tight transference of nutrients from smaller woody debris to the soil. Meaning nutrients are transferred quickly into the soil from the small woody debris without much loss during this transaction.

There was no clear pattern of woody debris biomass <7.62cm along the gradient. Plot 3 had the highest values (3.27 Mg/ha) and plot 5 the lowest (0.51 Mg/ha). Plot 5 did have one of the fastest flows of all the plots, which likely flushed out smaller woody debris. Overall, biomass in woody debris <7.62cm was similar among plots. Our hypothesis that plots with higher salinities will accumulate a higher amount of CWD was not supported. However, a potential factor not accounted for could be productivity differences of forest in these areas of varying salinity. A forest with higher productivity may produce larger amounts on downed woody debris and override the differences of woody debris accumulation produced by differing salinities.

The downed woody debris biomass values fell close to the range of 3.8 - 22.5 Mg/ha for a natural floodplain forest (Ellis et al. 1999). Similar to our results, these authors reported that most of their woody debris biomass was in the form of larger sticks and logs. Polit and Brown (1996) reported downed woody debris biomass to represent 42% (6.6 Mg/ha) of the dead wood in a silver maple (*Acer saccharinum*) dominated central Illinois floodplain forest, a level which is very close to our values. Allen et al. (2000) found biomass of downed wood on three Micronesian islands to average 20.9 Mg/ha. They also stated that downed wood biomass did not vary between riverene, interior, or fringe hydrogeomorphic zones.

Overall our estimates fell below or at the low end of the range of 4 – 40 Mg/ha downed woody debris biomass for mature deciduous temperate forests (Gore and Patterson 1986; Lang and Forman 1978; Macmillan 1981; Muller and Liu 1991; Tritton 1980). However, these values are primarily from upland forests which likely have slower decomposition rates as well as different woody debris input/output dynamics. After hurricane disturbances in mangrove forests, downed woody debris can accumulate in amounts as high as 141 to 160 Mg/ ha (Smith *et al.* 1994; Krauss *et al*. 2005). A floodplain forest accumulates wood through deposits within the

floodplain and from outside the floodplain via water flow. Likewise, woody debris can decompose on site or be exported from the floodplain through sheet flow. An upland forest obviously lacks the capacity of woody debris movement via water, so the woody debris in these areas is autochthonous.

2.6 CONCLUSIONS

Most studies involving woody debris decomposition occur in coniferous forest (Harmon et al. 1986). Of the studies performed in a temperate deciduous forest, only a handful have been in wetlands. Our decay rate values were very low when compared to these studies. Hydrology seemed to be the primary driver of decomposition differences among plots. The plot closest to the coast (plot 9) was drained by nearby sloughs which may have allowed for occasional, short interval non-flooded periods. These periods likely lead to the observed increase in decomposition at this plot. Percent C remaining tracked well with percent mass remaining; however, trends of N and P mineralization/-immobilization were greatly varied among plots and collection periods. Patterns of N and P mineralization/-immobilization are likely due to plot specific parameters of microbial population nutrient demands and hydrology. Also, oscillations of N and P mineralization/-immobilization trends seem to occur frequently, but for short intervals during decomposition of CWD in these tidal freshwater forested wetlands.

Average downed woody debris biomass ranged from 1.54 - 5.84 Mg/ha among plots. Downed woody debris biomass in the size class >7.62 cm was significantly related to the parameter distance to coast. This is due to the fact that the three northernmost plots (farthest from the coast) had the highest amounts of downed woody debris biomass. This may be simply because the trees tend to be larger in those areas (i.e. higher productivity) as opposed to areas closer to the coast where the moisture stress is greater due to higher salinities. The smaller size

class of <7.62cm was statistically related to the parameters of soil carbon, soil nitrogen, and soil phosphorous concentrations ($P<0.05$) and showed no real pattern among plots. This suggests that there could be a relatively tight transference of nutrients from smaller woody debris to the soil.

Table 2.1. Soil texture class and particle size percentages by plot and distance to coast.

Plot	Sand	Clay	Silt	Texture Class	Distance to Coast
	----------%----------				(km)
1	34.0	28.5	37.5	Clay Loam	28.0
2	23.0	35.5	41.5	Clay Loam	27.0
3	23.0	38.5	38.5	Clay Loam	20.7
4	10.0	33.5	56.5	Silty Clay Loam	18.3
5	78.0	8.5	13.5	Sandy Loam	15.8
6	41.0	23.0	36.0	Loam	13.3
7	40.5	24.5	35.0	Loam	9.8
8	78.5	4.5	17.0	Loamy Sand	8.3
9	27.5	22.0	50.5	Silt Loam	7.3

Table 2.2. Mean decay rates (k) for both CWD and control wood among plots. Significant (alpha=0.05) differences are indicated by different lowercase letters, and standard errors are presented in brackets.

	Decay Rate (*k*)	
Plot	CWD	Control
1	0.012cd [0.002]	0.008b [0.003]
2	0.013bc [0.001]	0.008c [0.002]
3	0.008d [0.001]	0.006d [0.003]
4	0.013bc [0.002]	0.009a [0.004]
5	0.016b [0.003]	0.009a [0.002]
6	0.009d [0.001]	0.006e [0.002]
7	0.007d [0.001]	0.006e [0.003]
8	0.010bc [0.002]	0.007d [0.002]
9	0.030a [0.004]	0.009a [0.002]

Table 2.3. Percent C, N, and P remaining, and C/N in CWD at 14 months. Significant (alpha=0.05) differences are indicated by different lowercase letters, and standard errors are presented in brackets.

	% Remaining			
Plot	C	N	P	C/N
1	85.71a	66.03a	46.20a	151.13ab
	[1.96]	[3.17]	[18.60]	[10.06]
2	84.50a	92.36a	57.21a	137.51b
	[0.87]	[9.23]	[9.47]	[9.86]
3	89.73a	72.48a	33.25a	180.41ab
	[1.08]	[2.43]	[0.66]	[18.27]
4	81.95a	63.93a	33.20a	161.70bab
	[0.69]	[5.07]	[1.13]	[16.34]
5	79.47a	58.44a	27.72a	210.51a
	[1.36]	[4.34]	[1.10]	[4.50]
6	89.24a	66.28a	31.83a	193.74ab
	[1.33]	[4.58]	[5.18]	[13.27]
7	92.20a	96.78a	40.66a	174.16ab
	[2.34]	[9.18]	[2.77]	[13.53]
8	88.05a	67.55a	30.59a	170.55ab
	[4.63]	[2.39]	[15.53]	[3.33]
9	58.16b	88.95a	19.51a	128.88b
	[6.55]	[19.77]	[10.98]	[10.60]

Table 2.4. Mean downed woody debris biomass for both size classes <7.62 cm and >7.62 cm by plot. Significant (alpha=0.05) differences are indicated by different lowercase letters and standard error presented in brackets.

Plot	Size Class <7.62 cm	Size Class >7.62 cm
1	1.29 bc	5 ab
	[0.27]	[1.65]
2	2.51 ab	9.16 a
	[0.41]	[2.77]
3	3.27 a	4.07 ab
	[0.61]	[1.38]
4	1.67 abc	1.62 b
	[0.35]	[0.66]
5	0.51 c	2.57 b
	[0.18]	[1.24]
6	1.26 bc	2.58 b
	[0.23]	[1.21]
7	2.19 ab	2.19 b
	[0.49]	[0.64]
8	2.32 ab	1.65 b
	[0.29]	[0.47]
9	2.04 abc	2.25 b
	[0.35]	[0.68]

Table 2.5. Soil nutrient data for all plots, C and N are in % total (g/kg), salinity in mmhos, and P in ppm (mg/kg).

Plot	pH	% Total C	% Total N	Salinity (mmhos)	P (ppm)
1	5.06	6.40	0.44	0.19	10.52
2	4.78	7.51	0.53	0.20	11.80
3	4.55	8.04	0.58	0.23	10.86
4	4.97	3.58	0.26	0.13	11.67
5	4.63	1.15	0.07	0.08	8.82
6	4.73	12.75	0.89	0.23	12.00
7	5.16	11.61	0.73	0.38	12.74
8	5.13	28.77	1.78	1.33	19.95
9	4.94	5.54	0.37	0.17	11.20

Table 2.6. Wetland water level equations (derived from Anderson, unpublished data) for four plots based off of USGS Apalachicola River water level recorder near Sumatra, Florida. X is the water level at the USGS gage, and y is the wetland water level.

Plot	Hydrologic Equation
1	$y=0.9395x-99.132$
2	$y=1.0667x-153.7$
6	$y=-0.000001x^3+0.0027x^2-0.376x+4.211$
9	$y=-0.00000001x^3+0.0013x^2-0.327x+3.42$

Figure 2.1. Site map of plots lining southern portion of Apalachicola River in Florida. (Map adapted from Darst and Light 2008.)

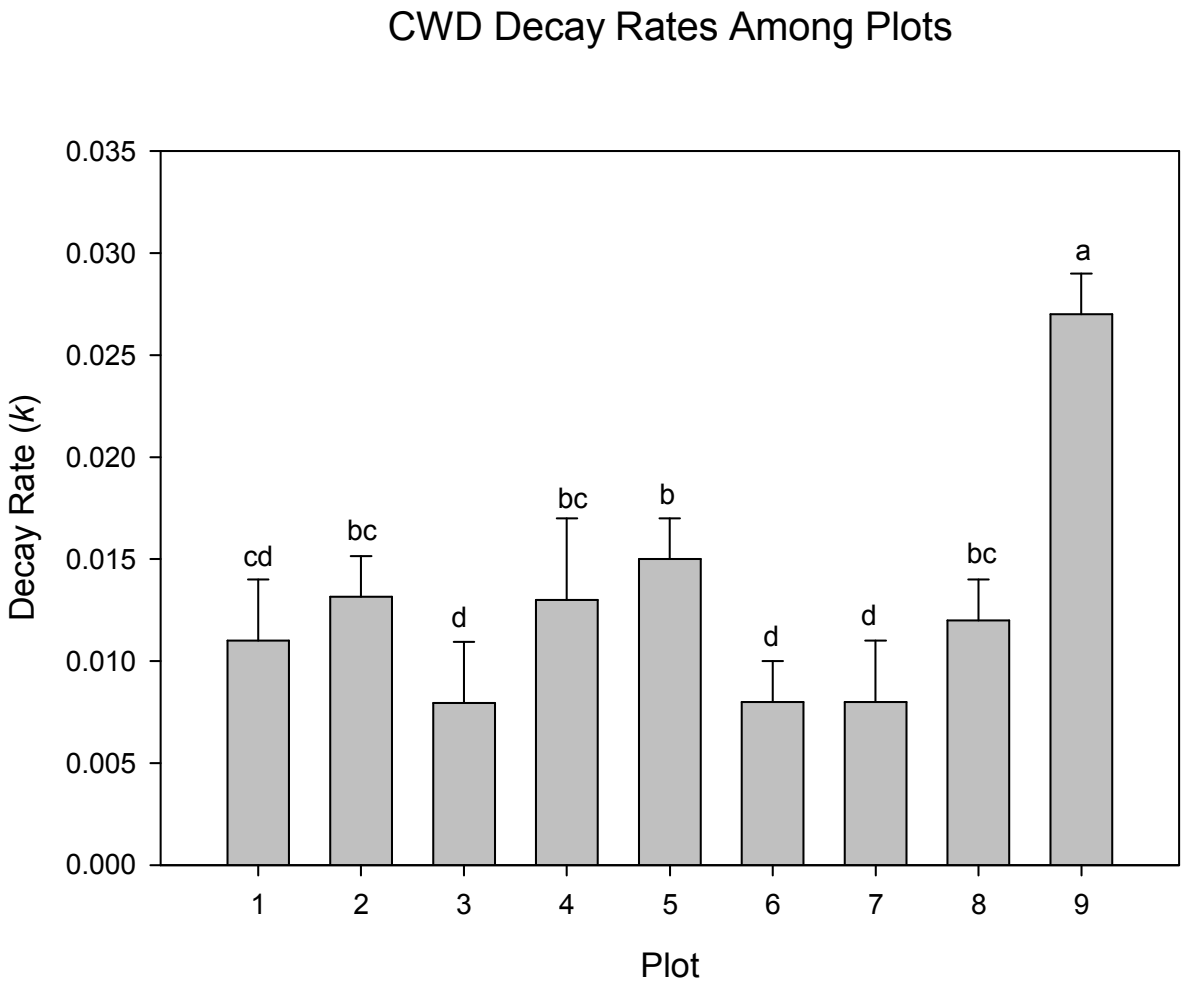

Figure 2.2. Mean CWD decay rates (± SE) among plots. Significant differences at the 0.05 level are indicated by different letters.

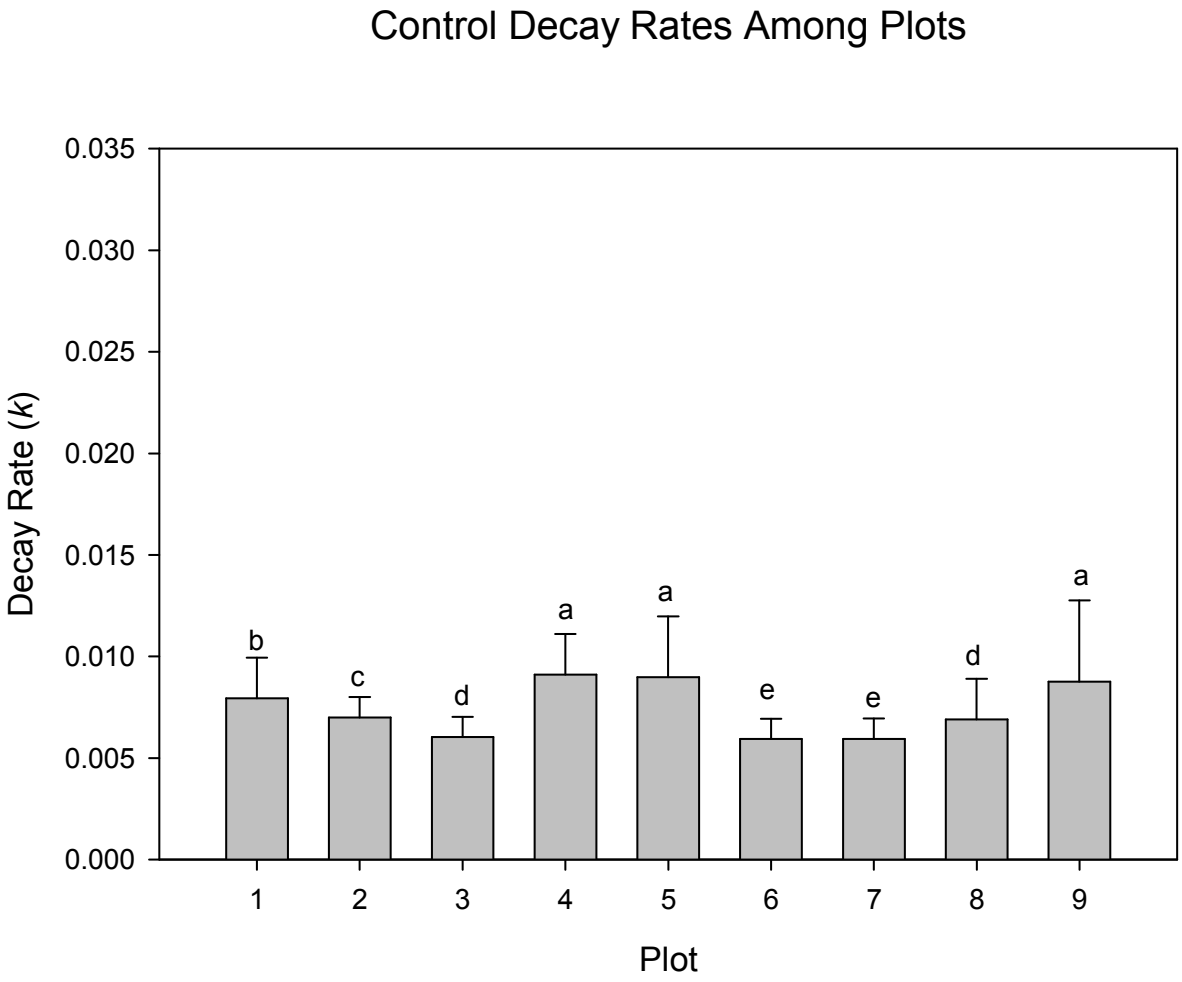

Figure 2.3. Mean control wood decay rates (± SE) among plots. Significant differences at the 0.05 level are indicated by different letters.

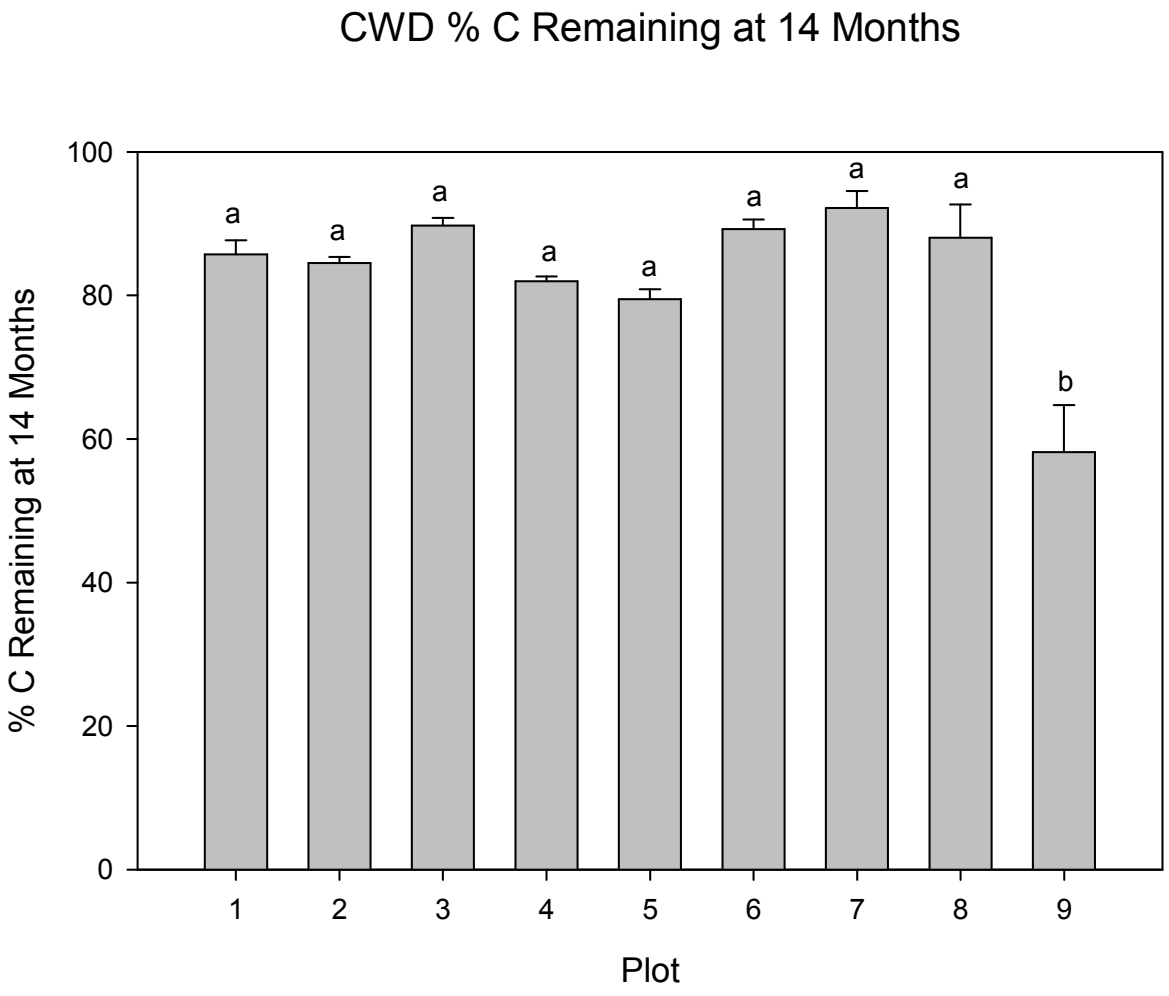

Figure 2.4. Mean percent C remaining (± SE) in CWD at 14 months among plots. Significant differences at the 0.05 level are indicated by different letters.

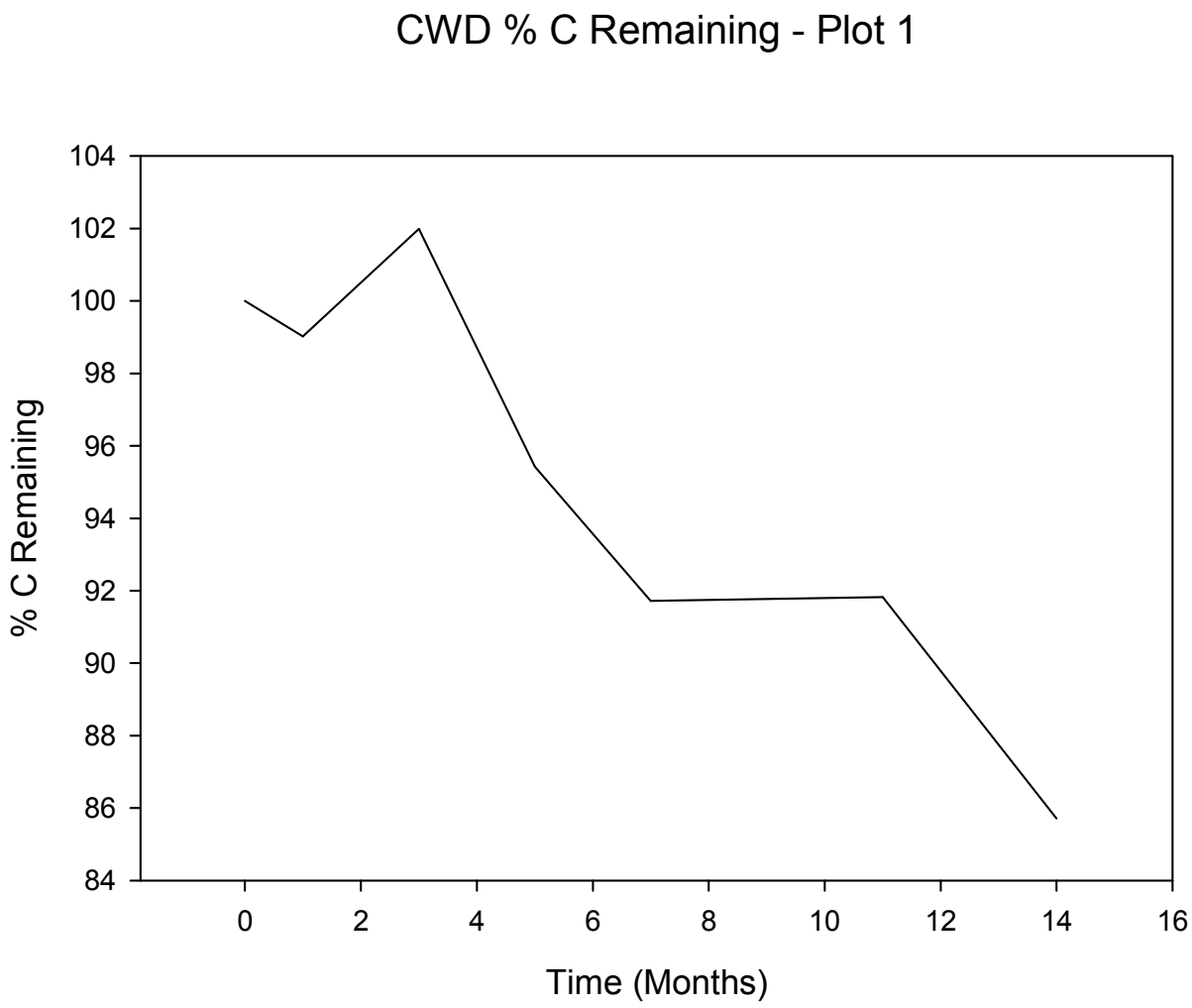

Figure 2.5. CWD percent C remaining up to 14 months for plot 1.

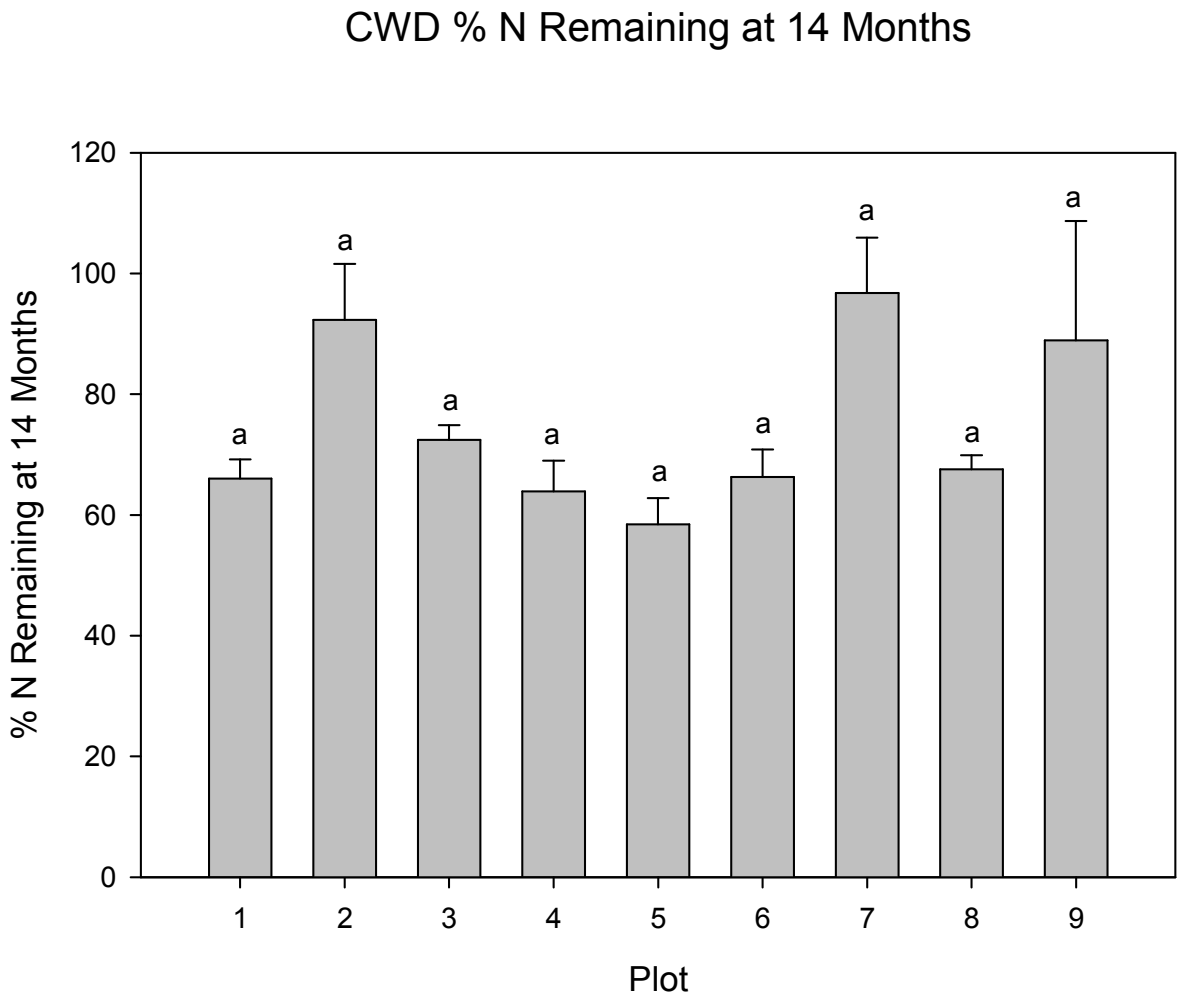

Figure 2.6. Mean percent N remaining (± SE) in CWD at 14 months among plots. Significant differences at the 0.05 level are indicated by different letters.

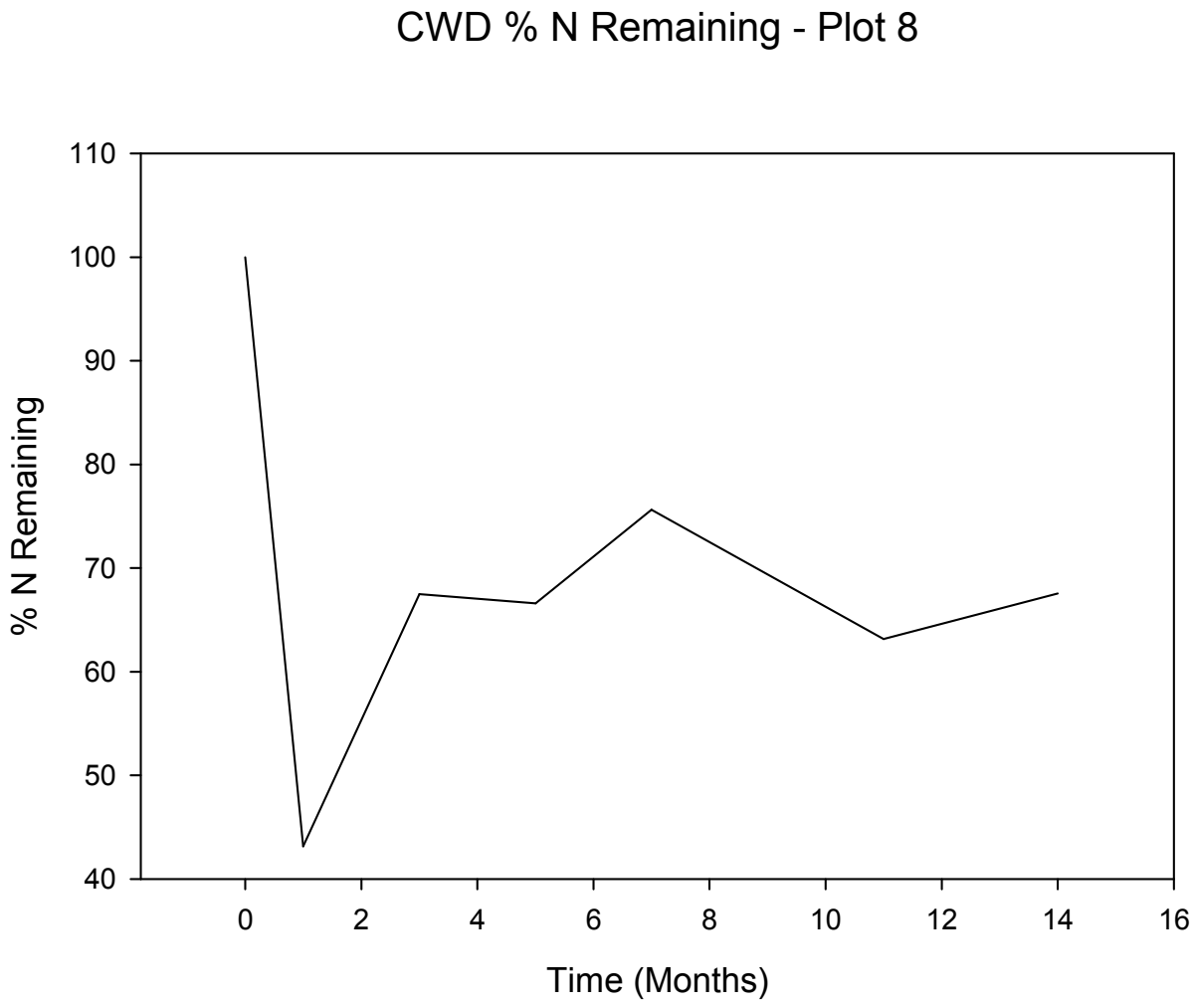

Figure 2.7. CWD percent N remaining up to 14 months for plot 8.

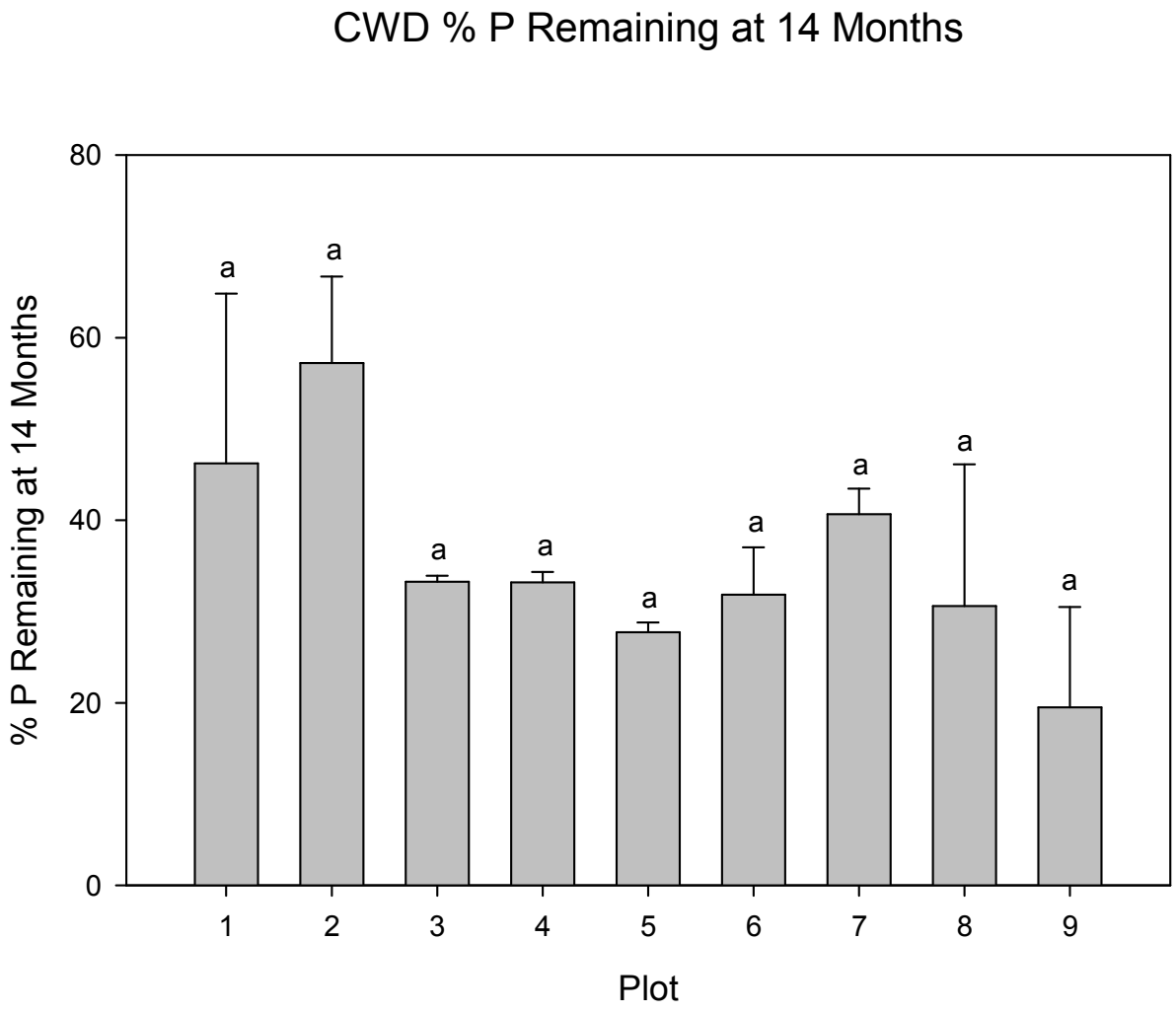

Figure 2.8. Mean percent P remaining (± SE) in CWD at 14 months among plots. Significant differences at the 0.05 level are indicated by different letters.

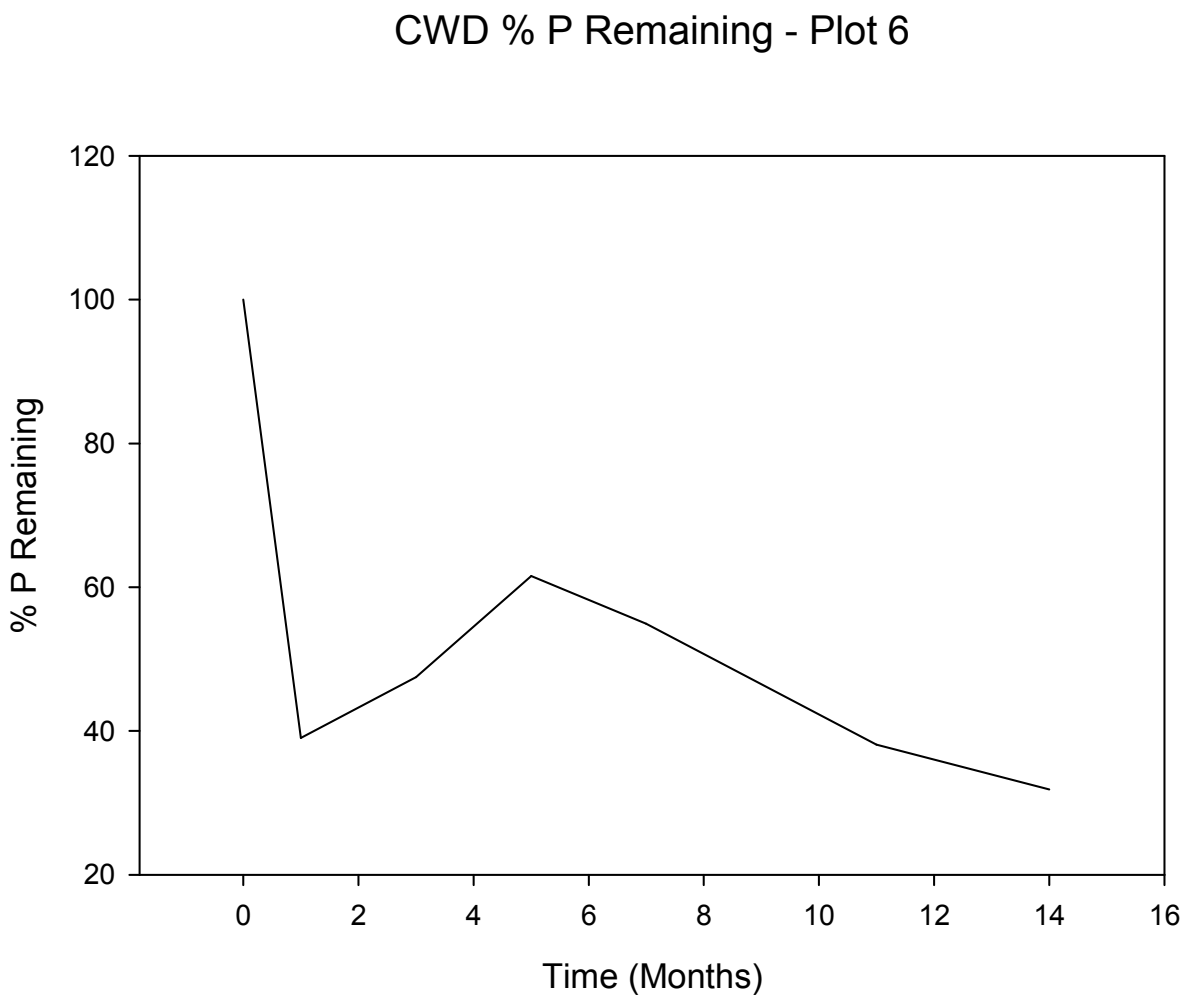

Figure 2.9. CWD percent P remaining up to 14 months for plot 6.

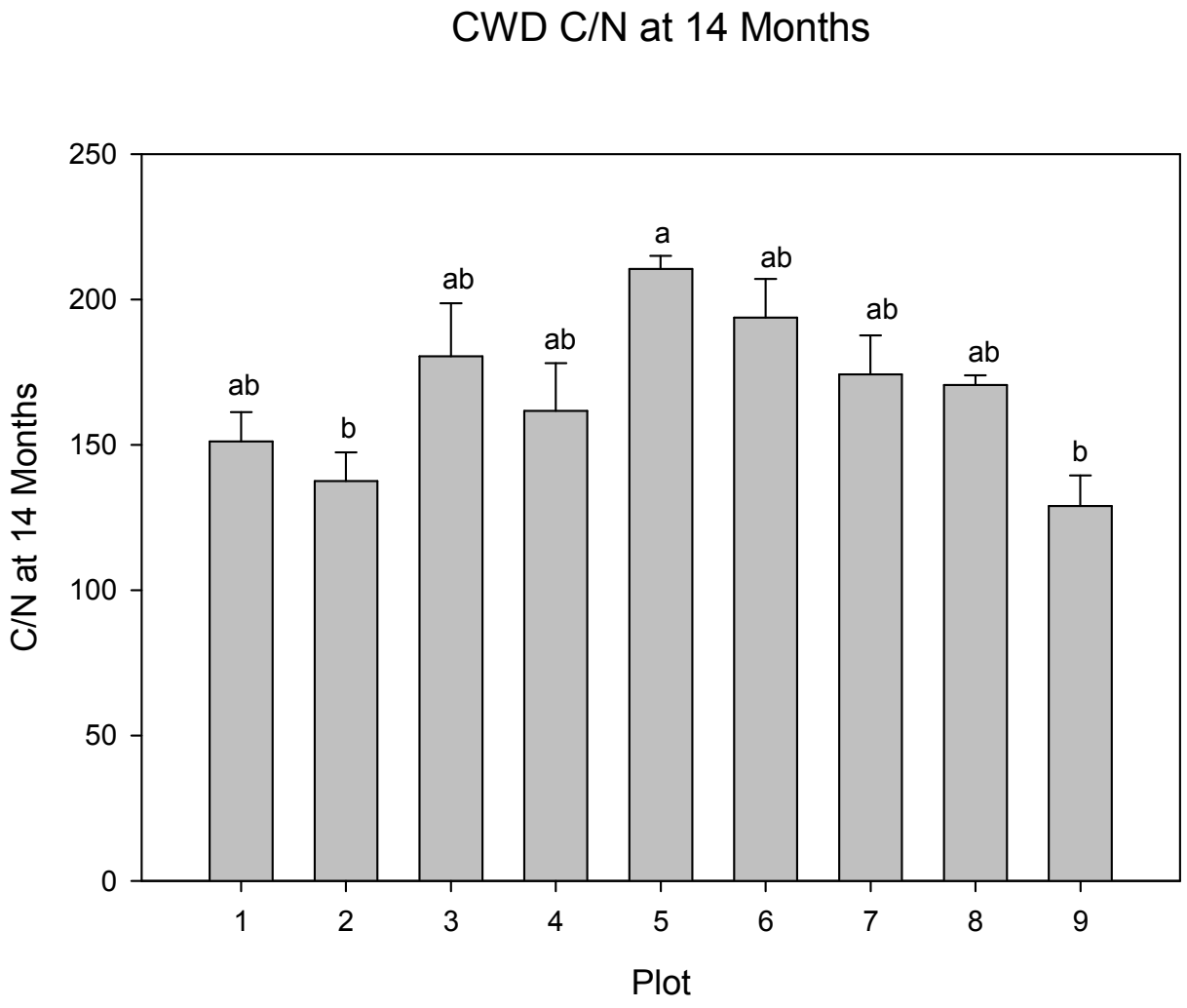

Figure 2.10. Mean C/N ratio (± SE) in CWD at 14 months among plots. Significant differences at the 0.05 level are indicated by different letters.

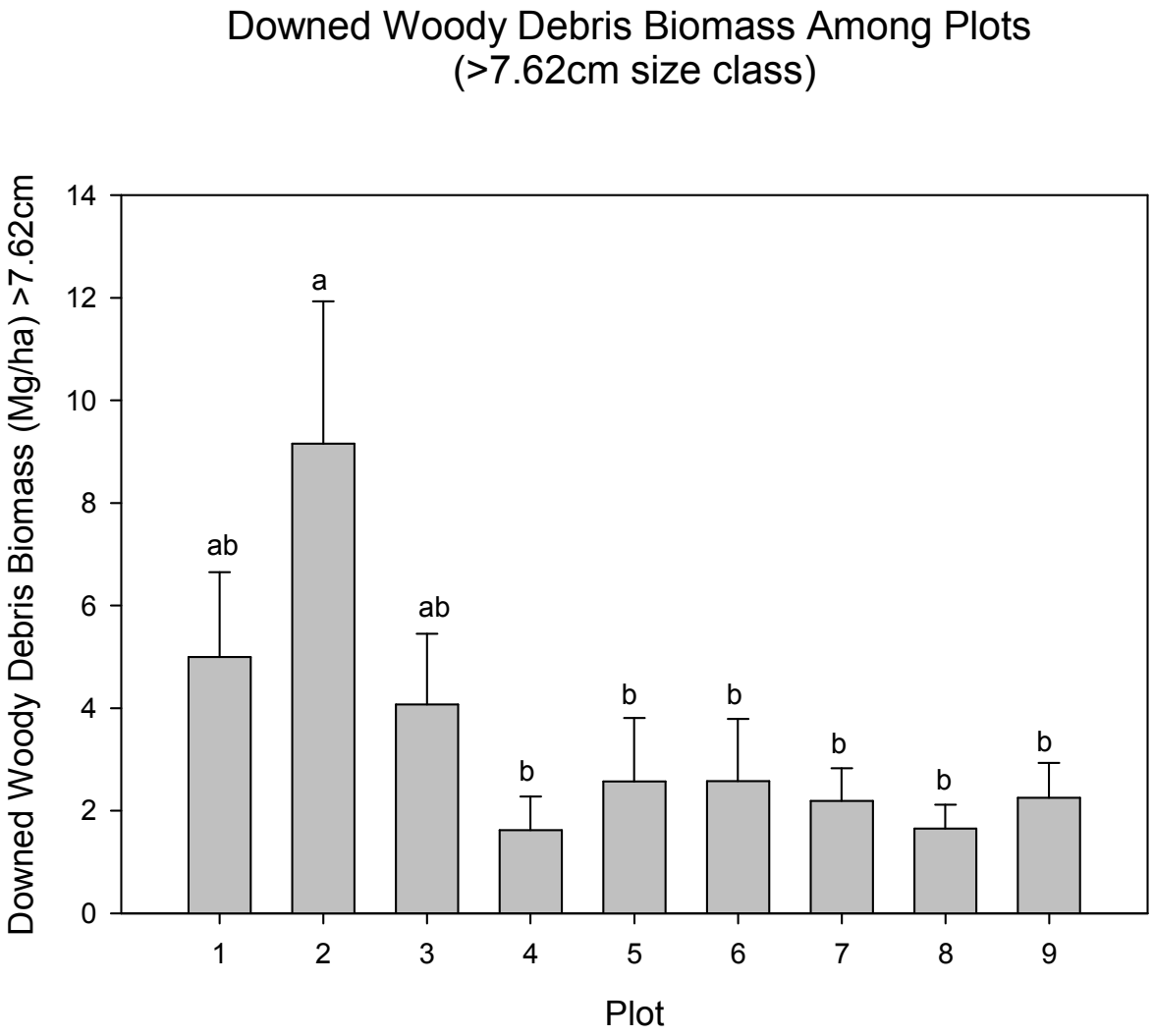

Figure 2.11. Mean (± SE) downed woody debris biomass in the size class >7.62cm by plot. Significant (alpha=0.05) differences are indicated by different letters. Values recorded in Mg/ha.

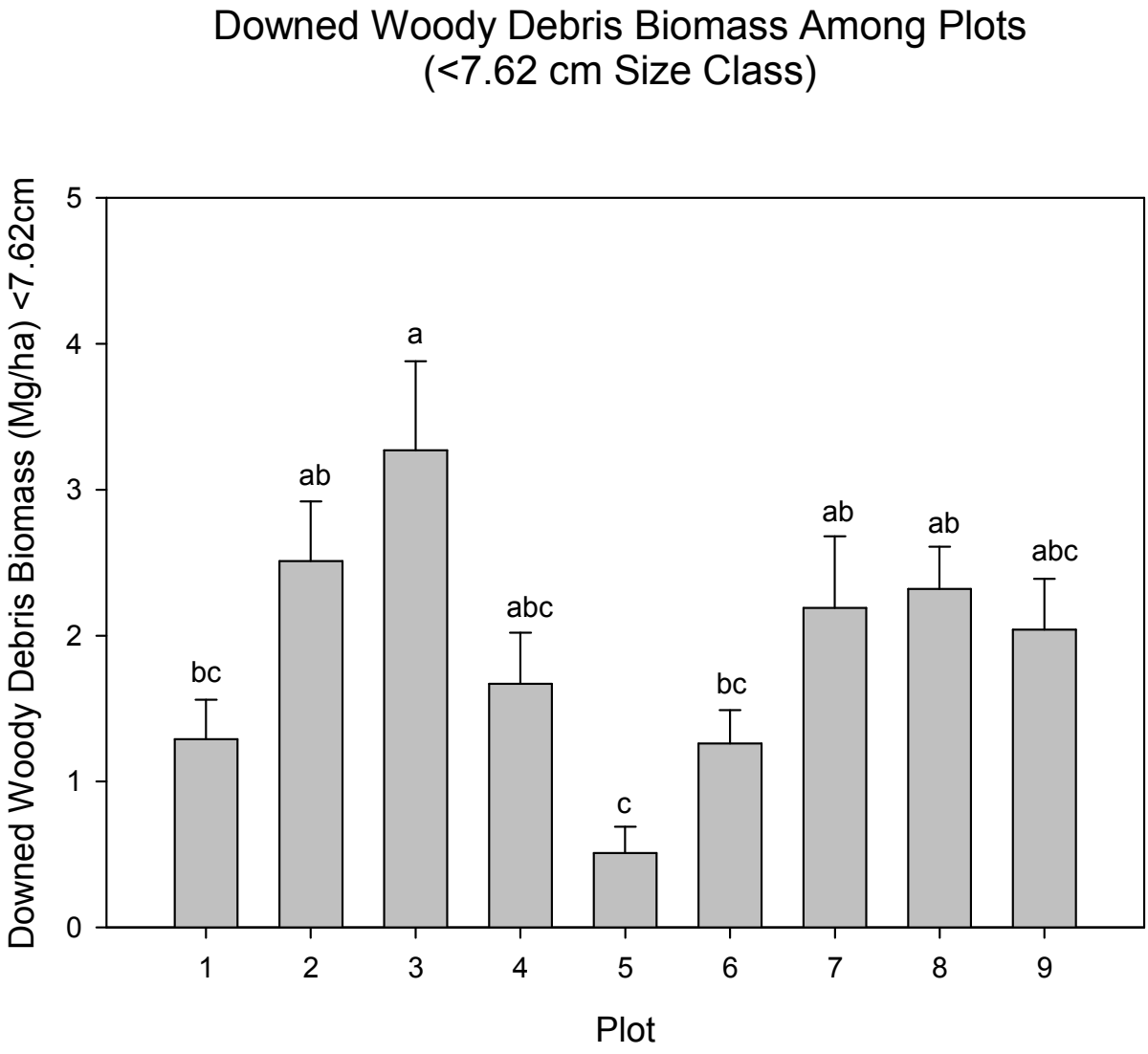

Figure 2.12. Mean (± SE) downed woody debris biomass in the size class <7.62cm by plot. Significant (alpha=0.05) differences are indicated by different letters. Values recorded in Mg/ha.

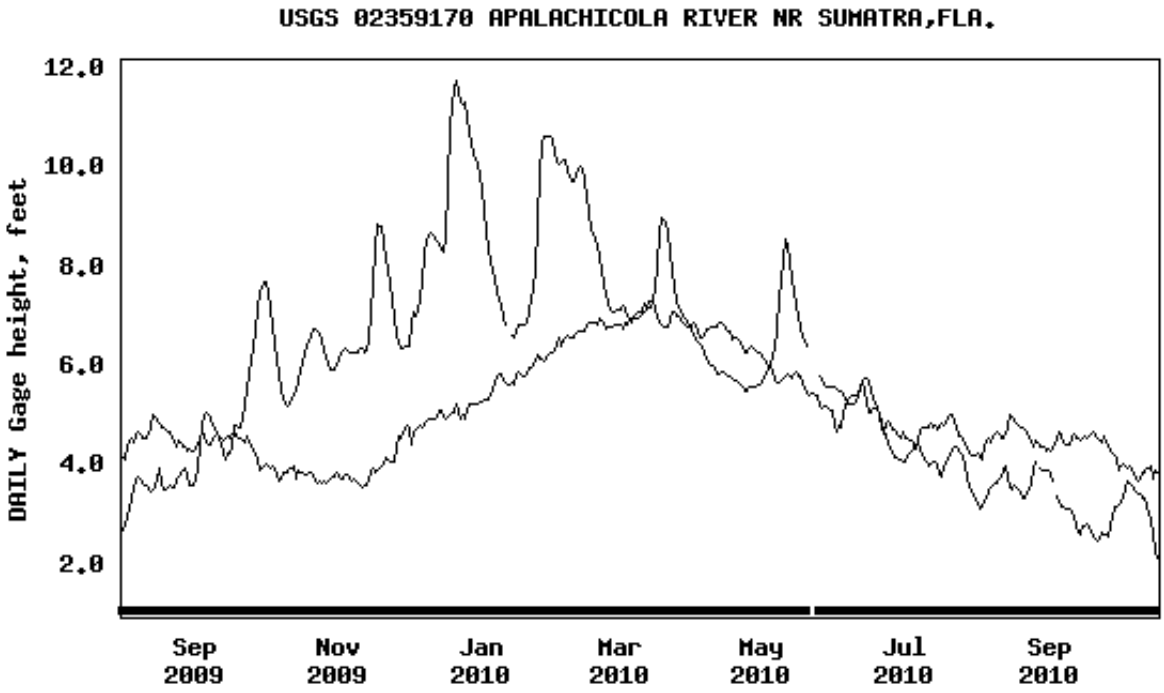

Figure 2.13. Daily gage heights at the USGS water station on the Apalachicola River near Sumatra, Florida. The line of greater gage height from October 2009-March 2010 represents water levels during the study period. The lower line represents the 36 year mean for this water station. Graph adapted from http://waterdata.usgs.gov.

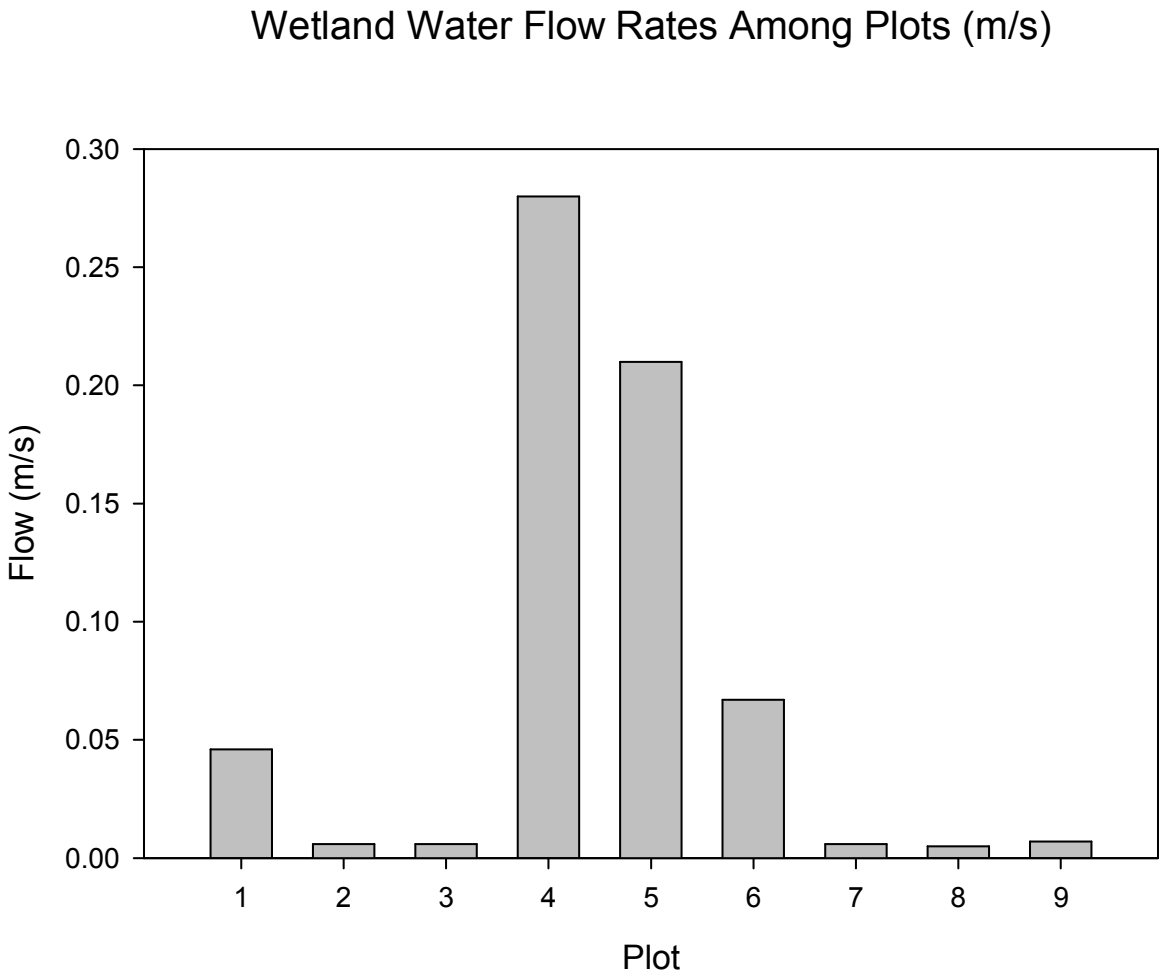

Figure 2.14. Mean wetland water flow rates among plots (m/s) measured at river stage of 2 m.

3. MICROBIAL BIOMASS C AND N IN TIDAL FRESHWATER FORESTED WETLANDS ALONG A RIVER TO ESTUARY GRADIENT ON THE APALACHICOLA RIVER IN FLORIDA

3.1 ABSTRACT

Microbial biomass C and N were estimated on nine plots in tidal freshwater forested wetlands that varied in terms of distance from the coast. Sampling was conducted during the summer of 2010. A chloroform fumigation-incubation technique was used to obtain microbial biomass concentrations. Microbial biomass C ranged from 0.37 to 0.79 g C/ kg of soil while microbial biomass N ranged from 13.92 to 73.74 mg N/kg of soil among plots. Both microbial biomass C and N were significantly different among plots, although there was no clear pattern with distance from coast. Plot 5 accounted for the least microbial biomass C and N, and also had the lowest levels of almost all parameters assayed: microbial biomass C and N, soil carbon, soil nitrogen, soil salinity, and soil phosphorous. Plot 5 also had one of the fastest water flow and second highest sand percentages among plots. Microbial biomass C showed a significant relationship with soil nitrogen concentrations. Microbial biomass N showed a significant relationship with distance to coast. However, R^2 values for these relationships were very small, indicating that these relationships are weak. Microbial C and N increased consistently from May - August collections.

3.2 INTRODUCTION

Bacteria play an important role involving nutrient dynamics and wetland functions, and are very abundant in wetlands compared to other ecosystems. For example, Boon (1991) found

that bacteria in the water column of floodplain wetlands in Australia can reach numbers as high as 10 to 100 x 10^{10} L^{-1}. In contrast, numbers of bacteria in the water column of nearby rivers were an order of magnitude lower. Bacteria can also differ in abundance and richness along environmental gradients or be ubiquitous across such gradients (Crump et al. 2003; Pedros-Alio et al. 2000; Bernhard et al. 2005). In a study that involved mapping bacterial assemblages along a river - bay - ocean gradient in Australia, bacterial abundance ranked as follows: river > bay > ocean. However, only 44 of 76 operational taxonomic units (OTU) were habitat specific. Likewise, 12 OTU were present along the entire gradient and 14 OTU could be considered as occurring in pairs of habitat types (river/ bay or bay/ ocean) (Hewson and Fuhrman 2004). This suggests that a variety of microbes are adapted to the differing environmental conditions within and surrounding estuary systems.

Wetland food webs are significantly detrital, meaning that bacteria probably decompose more organic matter than any other types of organisms (such as fungi), and play a major role in all nutrient cycling processes (Batzer and Sharitz 2006). Bacteria breakdown particulate organic matter, and prepare it for use by other bacteria along with additional types of organisms such as invertebrates. Wetzel (1995) considered bacteria the key organisms in wetlands in regard to wetland function because of their capability to assimilate dissolved organic carbon, which is a dominant organic carbon source in aquatic systems. Bacteria in the upper surface water of estuaries can number from 10^5 to 10^7 cells ml^{-1} and can account for 70% of the total carbon biomass (Hewson and Fuhrman 2004). Zahran (1997) considered that halophilic bacteria play a central role in saline environments based on their ability to degrade plant residue, fix nitrogen, and produce active metabolites under such environmental conditions.

Since bacteria are very numerous and tightly tied to biogeochemical functions in

wetlands, discernable relationships should be evident between decay rates of coarse woody debris (CWD) and microbial biomass. However, little is known about bacterial populations in the majority of marine environments such as the ocean, bays, and estuaries (Hewson and Fuhrman 2004). Also, little information exists particularly regarding relationships between salinity and microbial dynamics in low pH (<5) conditions (Sardinha et al. 2003). Most studies that have reported the effects of salinity on microbes have been performed at high pH in soils of arid regions. These studies have also found that salinity has a depressive effect on microbial biomass (Sardinha et al. 2003; Sarig et al., 1996; Batra and Manna, 1997; Rietz and Haynes, 2003). Conversely, Weston et al. (2006) reported that mineralization of organic matter switched from primarily methanogenesis in freshwater to sulfate reduction in saline water. Tidal freshwater sediments with salinity intrusion had double the amount of organic matter mineralization, increased nutrient release, and shifted rapidly to sulfate reduction as opposed to methanogenesis. Understanding the relationships between microbes and their environment, especially in such a variable ecosystem that is susceptible to climate change, may better equip us to understand how alterations in these systems might affect biogeochemical processes. This information would be pertinent to climate change, nutrient loading, and global carbon budgets.

The purpose of this study was to compare microbial biomass C and N in tidal freshwater forested wetlands along a river to estuary gradient on the Apalachicola River in Florida. The primary objectives of this study were to: (1) assay microbial biomass C and N along a river to estuary gradient, and (2) assess whether a relationship exists between microbial biomass pools and decay dynamics of CWD along the same gradient. We hypothesized that microbial biomass C and N will be inversely related to distance from the coast (i.e. increases inland), and that decomposition rates will be directly related to microbial biomass. The reasoning behind these

hypotheses are that plots closer to the coast (higher salinity plots) tend to be flooded more continually and exhibit a different pulsing hydrology than plots farther upstream. This more frequent inundation coupled with the osmotic stresses associated with higher concentrations of salt water may create a less hospitable environment for microbes.

3.3 METHODS

3.3.1 STUDY SITE DESCRIPTION

The Apalachicola River Basin (ARB) is composed of three major rivers and drains an area of about 50,800 km² with an average discharge of 870 m³/s at the Jim Woodruff Dam (Elder and Cairns 1983). The Apalachicola River is approximately 171km long and is formed by the merging of the Flint and Chattahoochee rivers at the Jim Woodruff Dam on the Georgia/Florida state line. During its course from the Georgia and Florida state line to the coast, the river falls only 12m in elevation. The Chipola River joins the Apalachicola near Wewahitchka, Florida, approximately 50 km from the coast. The watershed area of Apalachicola and Chipola River is around 12% (6,200 km²) of the entire ARB. The Apalachicola River's floodplain occupies approximately 454 km^2 and broadens to more than 10 km wide near the mouth of the river while narrowing to 2 km wide farther upstream (Elder and Cairns 1983). There is very little development along the southern portion of the Apalachicola River after it and the Chipola River merge; however, there is substantial development within the Apalachicola's watershed farther north (e.g. Atlanta, GA).

Extensive swamps line the floodplain of the Apalachicola River until it transitions into an estuary and flows into the Gulf of Mexico. There are over 40 species of trees that occur within these areas (Elder and Cairns 1983). Bald-cypress (*Taxodium distichum*) and tupelo (*Nyssa spp*.) occur in the uppermost swamps of the river. Other species found in these reaches of swamp are

ash (*Fraxinus spp*.), sweetbay magnolia (*Magnolia virginiana*), water elm (*Planera aquatica*), red maple (*Acer rubrum*), and overcup oak (*Quercus lyrata*). However, as the river moves south, cabbage palms (*Sabal palmetto*) became more dominant, and trees become stunted and scarcer from the stress related to the higher salinities. Many blackwater creeks feed into the main river stem along its entirety.

This study was performed on 9 plots in freshwater tidal swamps lining the Apalachicola River in Florida (Figure 2.1). Plot 9 was closest to the coast while plot 1 was the farthest. These plots ranged from about 7 km from the coast to approximately 28 km upstream. The three uppermost plots were placed within the cypress-tupelo swamps of the Apalachicola National Forest while the remaining six plots were placed within the Apalachicola River Wildlife and Environmental Area.

All plots consisted of microsites containing one of three soil series: Brickyard (Typic Endoaquepts), Chowan (Thapto-histic Fluvaquents), and Kenner (Fluvaquentic Haplosaprists). The USDA National Resource Conservation Service (NRCS) classifies these soil series as very poorly drained, poorly drained, and very poorly drained respectively (Schuster et al. 2001).

3.3.2 MICROBIAL BIOMASS C AND N

Soil samples for microbial analysis were collected monthly from May to August 2010. Water levels were too high (as high as 3 – 4 meters) to collect soils during other times of the year. Soil samples were taken from the top 10 cm of soil since microbes in that layer will have direct contact with the samples of wood set out to measure decomposition. Soil samples were collected on similar microsites as those where the decomposing wood samples were placed. Two soil samples were collected from each plot for each collection, and once collected; soil samples were brought back to the lab the same day, stored in a refrigerator at 4°C, and processed the

following day.

The chloroform fumigation-incubation technique was used to obtain microbial biomass carbon and nitrogen (Joergensen 1995; Vance et al. 1987). After soil was taken out of the 4°C refrigerator, it was passed through number 10 sieves (2 mm). The same amount of soil (18.5 g) was used for both the fumigated and non-fumigated samples. Another 10 g of soil was used to estimate moisture content. Fumigated samples were placed in desiccators and fumigated with ethanol free $CHCl_3$ for 24 hours in a darkened hood at room temperature. Fumigated and non-fumigated samples were extracted using 125 mL of 0.5 mol L^{-1} K_2SO_4 and shaken for 30 minutes on an automatic shaker. The resulting soil suspensions were filtered through Whatman #5 (55mm) filters with a vacuum aspirator system and immediately frozen at 0°C for analysis. After being thawed, remaining liquid was analyzed for C and N in a Shimadzu TOC-V and total nitrogen combustion analyzer (Riverwood Drive, Columbia, Maryland).

3.3.3 MICROBIAL BIOMASS CALCULATIONS

Calculations for microbial biomass C and N involved subtracting unfumigated masses from fumigated estimates and dividing by a carbon extraction coefficient. For example: microbial biomass C = $(C_F - C_{UF})/ K_{EC}$; where C_F = fumigated sample extract, C_{UF} = unfumigated sample extract, and K_{EC} = carbon extraction coefficient (i.e. microbial carbon proportion extracted from the soil). A K_{EC} value of 0.45 was used for microbial biomass C calculations and a K_{EN} (nitrogen coefficient) value of 0.54 was used for microbial biomass N calculations as suggested by Vance et al (1987) and Brookes et al. (1985) respectively.

3.3.4 STATISTICAL ANALYSIS

All data were analyzed using SAS version 9.1. The ANOVA procedure was performed to compare mean microbial biomass C and N among plots and collection dates. Proc REG was used

to determine whether soil carbon concentration, soil nitrogen concentrations, soil salinity, soil pH, soil phosphorous concentration, or distance to coast affected microbial biomass. Shapiro-Wilk test was used to verify normality. Significant differences among mean biomass estimations were tested using Tukey's Honestly Significant Difference test at $P < 0.05$.

3.4 RESULTS

3.4.1 MICROBIAL BIOMASS C AND N DYNAMICS

Microbial biomass C ranged from 0.37 to 0.79 g C/-kg among plots (Table 3.1) and showed a significant relationship with soil nitrogen concentrations ($P<0.05$), but exhibited a low R^2 value (0.06). There was no significant relationship between microbial biomass C and distance to coast, soil salinity, carbon, phosphorous, pH, or CWD decay rates. Differences of microbial biomass C was significant among plots ($P<0.05$) (Figure 3.1). Plot 5 had significantly lower microbial biomass C values than plot 6, while all other plots had intermediate values.

Microbial biomass C showed significant differences through time ($P<0.0001$) (Figure 3.2). Averages of all plots by collection date ranged from 0.39 to 0.93 g C/kg (Table 3.2). The last collection date in August had significantly higher amounts of microbial biomass C than each of the previous 3 collections. The middle two collections in June and July were not significantly different from each other, but were lower than August and higher than May collections. Also, the May collection was significantly lower than the last three collections.

Microbial biomass N ranged from 13.9 to 73.7 mg N/kg across plots (Table 3.1) and showed a significant relationship with distance to coast ($P<0.05$). However, as was the case with microbial biomass C, the R^2 value was very low (0.07). Soil salinity, carbon, nitrogen, phosphorous, pH, and CWD decay rates were not significantly related to microbial biomass N. ANOVA analysis showed that microbial biomass N values were significantly different among

plots ($P<0.0001$) (Figure 3.3). Plots 1 and 6 had the highest values and were significantly different from plots 4, 5, 7, 8, and 9. Plot 5 had the lowest recorded value and was significantly different from every other plot except plot 4.

Microbial biomass N was not significant over time ($P=0.054$), but showed a somewhat similar pattern as that of microbial biomass C (Figure 3.4). The August collection was significantly different from the May collection, but not from June and July. Likewise, May collection values were not significantly different from June and July collection values (May=June=July < June=July=August). Averages of all plots by collection date ranged from 39.2 to 58.5 mg N/kg (Table 3.2).

Microbial Biomass C and N both were not significantly related to CWD decay rates ($P>0.05$). Microbial biomass C/N ratios ranged from 10.5 to 29.0 and were significantly different among plots ($P<0.05$) (Figure 3.5 and Table 3.1). Plot 5 had C/N values significantly greater than all other plots. C/N ratios did not vary significantly through time ($P>0.05$).

3.5 DISCUSSION

3.5.1 MICROBIAL BIOMASS C

Microbial biomass C levels varied considerably among only two plots. Plot 6 had significantly higher values than plot 5. Plot 1 is farthest from the coast and plot 9 closest. Plot 5 had the lowest levels of almost all parameters assayed: microbial biomass C and N, soil carbon, soil nitrogen, soil salinity, and soil phosphorous. This plot had one of the highest measured flows, lowest recorded biomass of downed woody debris, and a high sand concentration of 78%. The ground surface there was bare sand suggesting active scouring. The only other plot with sand percentages as high was plot 8, although very high levels of organic matter occurred there. The low levels of organic matter and soil nutrients at plot 5 may explain the low levels of

microbial biomass there since microbial biomass C is strongly linked to organic matter and carbon content of soil (Wardle 1992; Chang et al. 1995).

Microbial biomass C seemed to have a similar pattern across all plots with the exception of plot 5. Groffman et al. (1996) suggested that variation of microbial biomass in red maple swamps of New York is primarily due to hydrology and organic matter. This supports our results since organic matter at plot 5 was so low and it had the fastest flow of all plots during a wetter than normal year. However, other important interactions between microbes and microsite variables such as temperature, microtopographic features, and micro nutrients may also be important (Wardle and Parkinson 1990). This does not support our hypothesis that microbial biomass C would be lowest on plots closest to the coast.

The fact that microbial biomass C showed a statistical significance with relation to soil nitrogen ($P<0.05$) but had a low R^2 value (0.061) is due to the inclusion of plot 5. Plot 5 had low levels of soil N and microbial biomass C. If plot 5 is excluded, then microbial biomass C is not statistically related to soil nitrogen ($P=0.20$).

Amounts of microbial biomass C consistently became greater through time. Concentrations ranged in the order of May < June < July < August, and this order was likely linked to hydrology. Water levels generally decreased from May to August. Although plots were still inundated for most of this time, periods of non-flooded, aerobic conditions became more frequent later in the summer. Also, the general trend of increasing temperatures from May to August may have been a part of the measured increase in microbial biomass through time, although we did not determine air or soil temperatures for this study.

Schilling and Lockaby (2006) reported microbial biomass C concentrations of 0.32 – 0.54 g C/kg in a blackwater floodplain system in Georgia's coastal plain. Our values fell very close to

this range which may reflect similarities in system type (blackwater), and similar climates in the southeastern United States. Schilling et al. (1999) also reported concentrations of 1.6 – 2.5 g C/kg in the Pearl River Mississippi floodplain, a brown water system. According to Schilling et al. (1999), microbial biomass C concentrations decreased on clear cut and partial cut plots thought to be due to a decrease in soil moisture from the increased soil temperature/-evaporation. Red maple swamps of New York had microbial biomass C concentrations reported at 2.0 – 3.5 g C/kg (Groffman et al. 1996). Sardinha et al. (2003) found microbial biomass C concentrations ranging from 0.16 – 0.57 g C/kg in a salt affected, low pH floodplain in Germany. These values fall close to, but on the lower end, of our reported values probably because of very similar soil pH and salinity. However, Sardinha et al. (2003) values may by slightly lower than ours because of lesser organic matter. Although the authors did not access amounts of organic matter, they felt that their sites had reduced vegetation, and subsequently microbial biomass, due to the presence of salinity, albeit low. In general, microbial biomass C concentrations in the Apalachicola River floodplain are similar to values reported by other studies in similar conditions (i.e. system type, pH, salinity, and climate).

3.5.2 MICROBIAL BIOMASS N

Microbial biomass N concentrations ranged considerably among plots and were also significantly related, although weakly, to distance from the coast. The reason for this remains unclear since microbial biomass N was not significantly related to any other soil parameter. However, R^2 values for distance to coast are very low, so the relationship between microbial biomass N and distance to coast is highly variable. High concentrations of microbial biomass N at plot 6 and extremely low concentrations at plot 5 could have accounted for many of the significant differences among plots. Therefore, no clear trend in microbial biomass N was found.

Although not significant, microbial biomass N data suggested a trend (P=0.054). In general, microbial biomass N concentrations trended positively through time for each of the four collections, although the difference was only significant among the first and last collections. Any change through time is likely related to water levels as previously described.

Gallardo and Schlesinger (1994) reported microbial biomass N concentrations of 52 mg N/kg without fertilization to 73 mg N/kg with fertilization in a temperate upland forest in North Carolina. These forests were positioned on a slope that consisted mainly of red maple as well as upland oak and hickory on the Duke University campus. Our values may have been similar to values reported by Gallardo and Schlesinger (1994) due to similar climates (Southeastern United States) and substrate quality although ecosystem types were different. Schilling et al.(1999) and Schilling and Lockaby (2006) reported values of 155 mg N/kg in the Pearl River floodplain of Mississippi, and 41 – 65 mg N/kg in a Georgia blackwater swamp. As with microbial biomass C, our values fell closest to the Schilling and Lockaby (2006) study likely because of a similar system type (blackwater) and climate. Sardinha et al. (2003) reported microbial biomass N values ranging from 20 - 96 mg N/kg in a salt affected, low pH floodplain in Germany. These values are very close to ours likely because of very similar soil pH and salinity.

3.5.3 MICROBIAL BIOMASS C/N

Microbial biomass C/N ratios showed no discernable pattern among plots or through time. With the exception of plot 5 (previously described), our C/N ratios fell very close to the range reported by Schilling and Lockaby (2006) and Schilling et al.(1999) for floodplain forests in the Southeastern United States. Sardinha et al. (2003) found C/N values lower than ours. Perhaps due to reduced amounts of vegetation and organic matter thought to be present. A lower

amount of organic matter substrate could effectively lower the C/N ratio. Also, the soil C/N ratio reported by the Sardinha et al. (2003) was lower than our soil C/N ratio.

3.6 CONCLUSIONS

Microbial biomass C and N were highly variable among plots. Plot 5 differed from the others and exhibited significantly lower levels of microbial C and N than other plots, as well as the lowest levels of almost all soil variables: soil carbon, nitrogen, salinity, and phosphorous. This plot also had one of the fastest flows, lowest recorded biomass of downed woody debris, and a high sand concentration of 78%. These low levels of soil nutrients and organic matter likely cause for such low microbial biomass concentrations at plot 5. Our hypotheses that microbial biomass C and N would be inversely related to distance from the coast and directly related to CWD decomposition rates were not supported. Salinity did not vary in a discernable pattern along our river to estuary gradient. Also, water levels were above average for the duration of the study. Therefore plots along the gradient were in similar conditions for most of the study period. These similar conditions could be why there was no clear trend in microbial biomass along the gradient. Microbial biomass C and N varied significantly through time with both generally increasing from May – August 2010. This was likely related to water levels, which dropped from May through August. Although the plots were inundated for most of this time, the frequency of non-flooded conditions increased.

Table 3.1. Mean microbial biomass C, N, and C/N by plot. Significant (alpha=0.05) differences are indicated by different lowercase letters, and standard errors are presented in brackets. Microbial biomass C reported in g/kg, and microbial biomass N reported in mg/kg. Plot 1 is farthest from the coast and Plot 9 the closest.

Plot	C	N	C/N
1	0.78ab	73.74a	10.63a
	[0.09]	[7.79]	[0.75]
2	0.61ab	52.05abc	11.47a
	[0.08]	[3.60]	[1.10]
3	0.53ab	62.23ab	10.5a
	[0.08]	[9.69]	[0.96]
4	0.54ab	33.24cd	16.44a
	[0.07]	[3.07]	[1.44]
5	0.37b	13.92d	28.97b
	[0.08]	[2.69]	[7.36]
6	0.79a	68.7a	11.54a
	[0.08]	[3.82]	[1.1]
7	0.6ab	39.3c	18.76a
	[0.13]	[5.74]	[3.00]
8	0.67ab	41.66bc	16.3a
	[0.10]	[3.52]	[2.54]
9	0.47ab	45.61bc	13.41a
	[0.07]	[2.88]	[3.17]

Table 3.2. Mean microbial biomass C, N, and C/N by collection month. Significant (alpha=0.05) differences are indicated by different lowercase letters, and standard errors are presented in brackets. Microbial biomass C reported in g/kg, and microbial biomass N reported in mg/kg.

Month	C	N	C/N
May	0.4c	39.23b	11.3a
	[0.03]	[4.02]	[1.24]
June	0.62b	44.27ab	18.29a
	[0.05]	[4.75]	[3.78]
July	0.65b	45.97ab	14.13a
	[0.06]	[5.95]	[1.59]
August	0.93a	58.49a	17.62a
	[0.05]	[5.09]	[1.65]

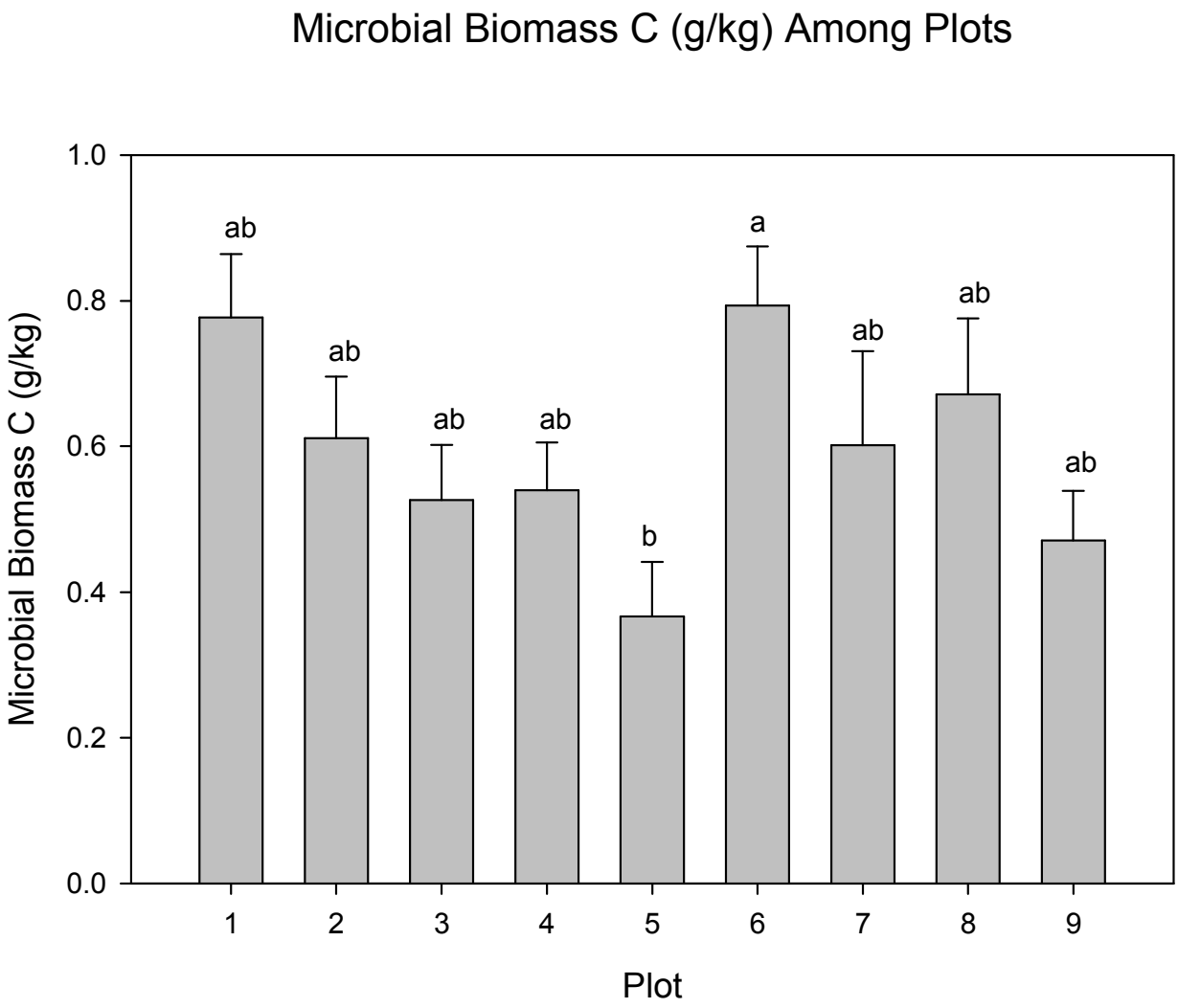

Figure 3.1. Mean microbial biomass C (±SE) by plot. Significant (alpha=0.05) differences are indicated by different letters.

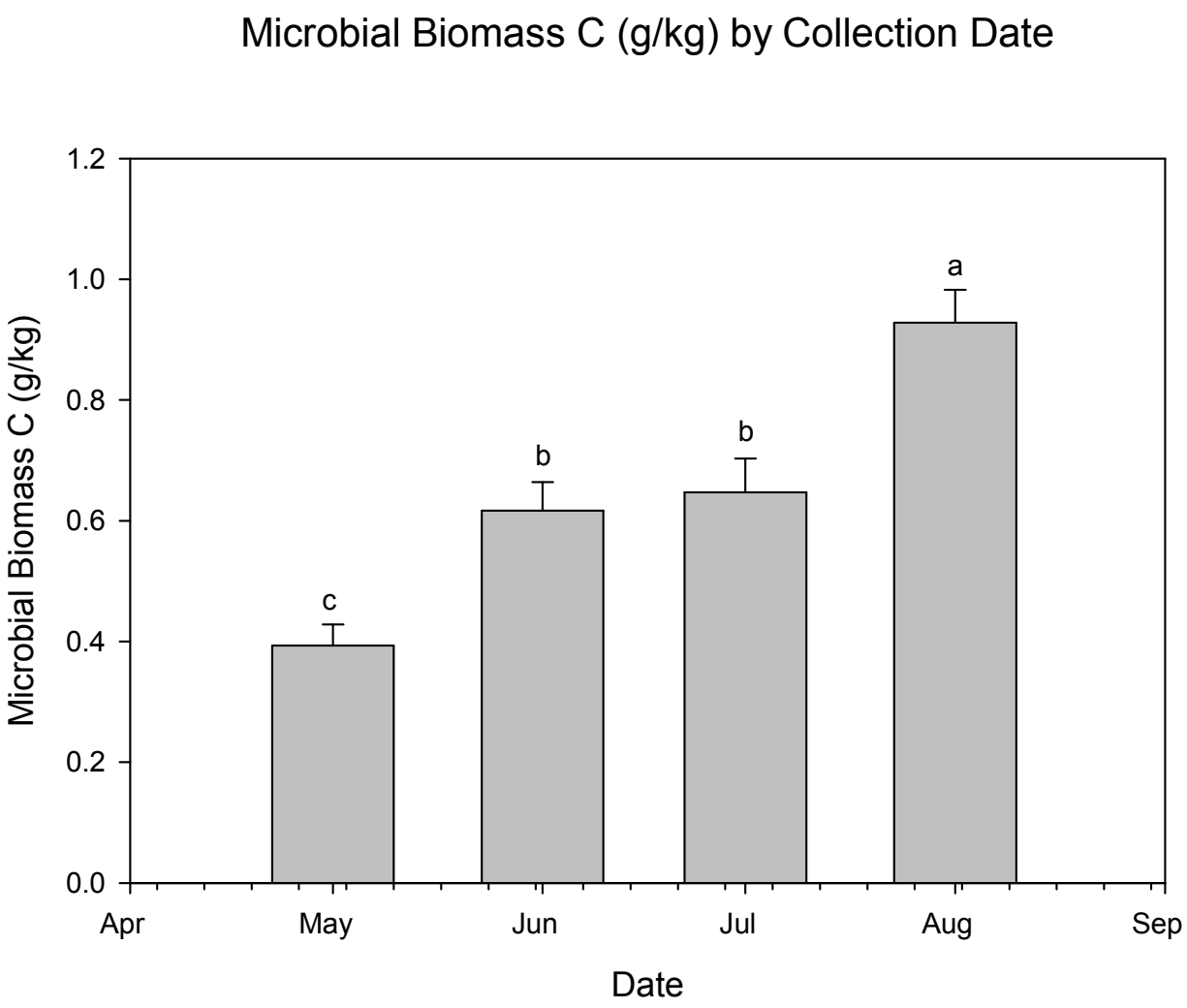

Figure 3.2. Mean microbial biomass C (±SE) by each collection time (May, June, July, and August 2010). Significant (alpha=0.05) differences are indicated by different letters.

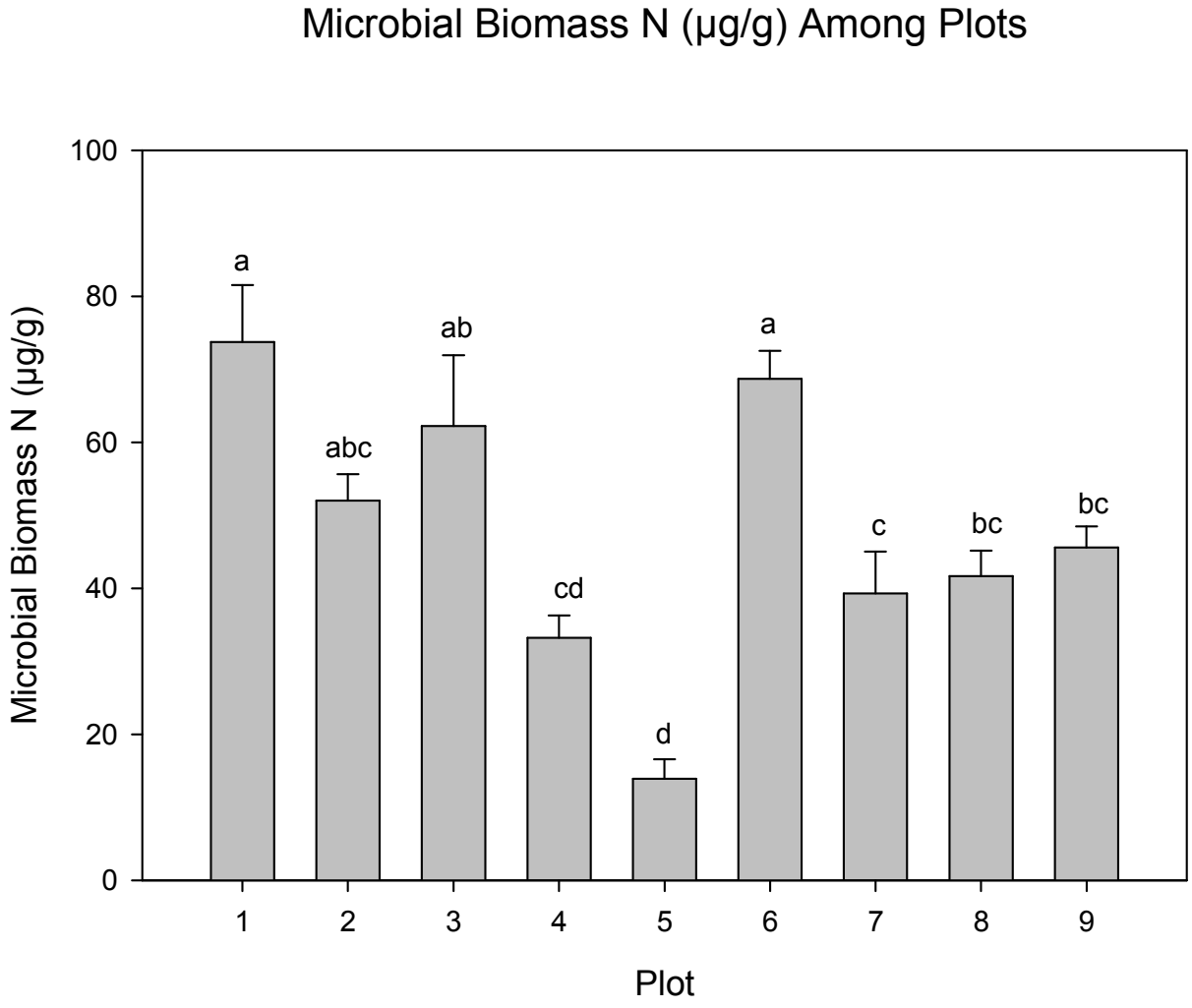

Figure 3.3. Mean microbial biomass N (±SE) by plot. Significant (alpha=0.05) differences are indicated by different letters.

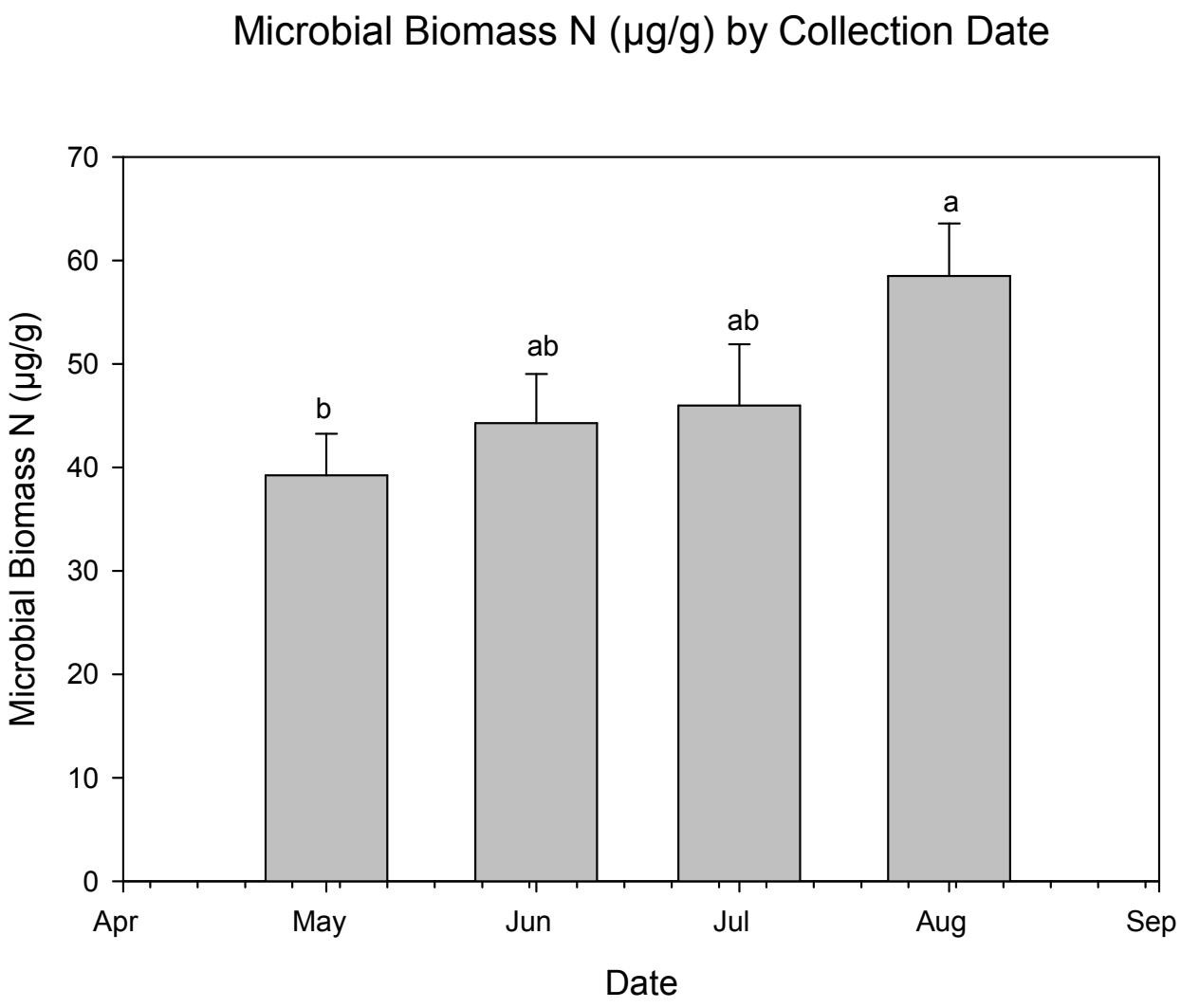

Figure 3.4. Mean microbial biomass N (±SE) by each collection time (May, June, July, and August 2010). Significant (alpha=0.05) differences are indicated by different letters.

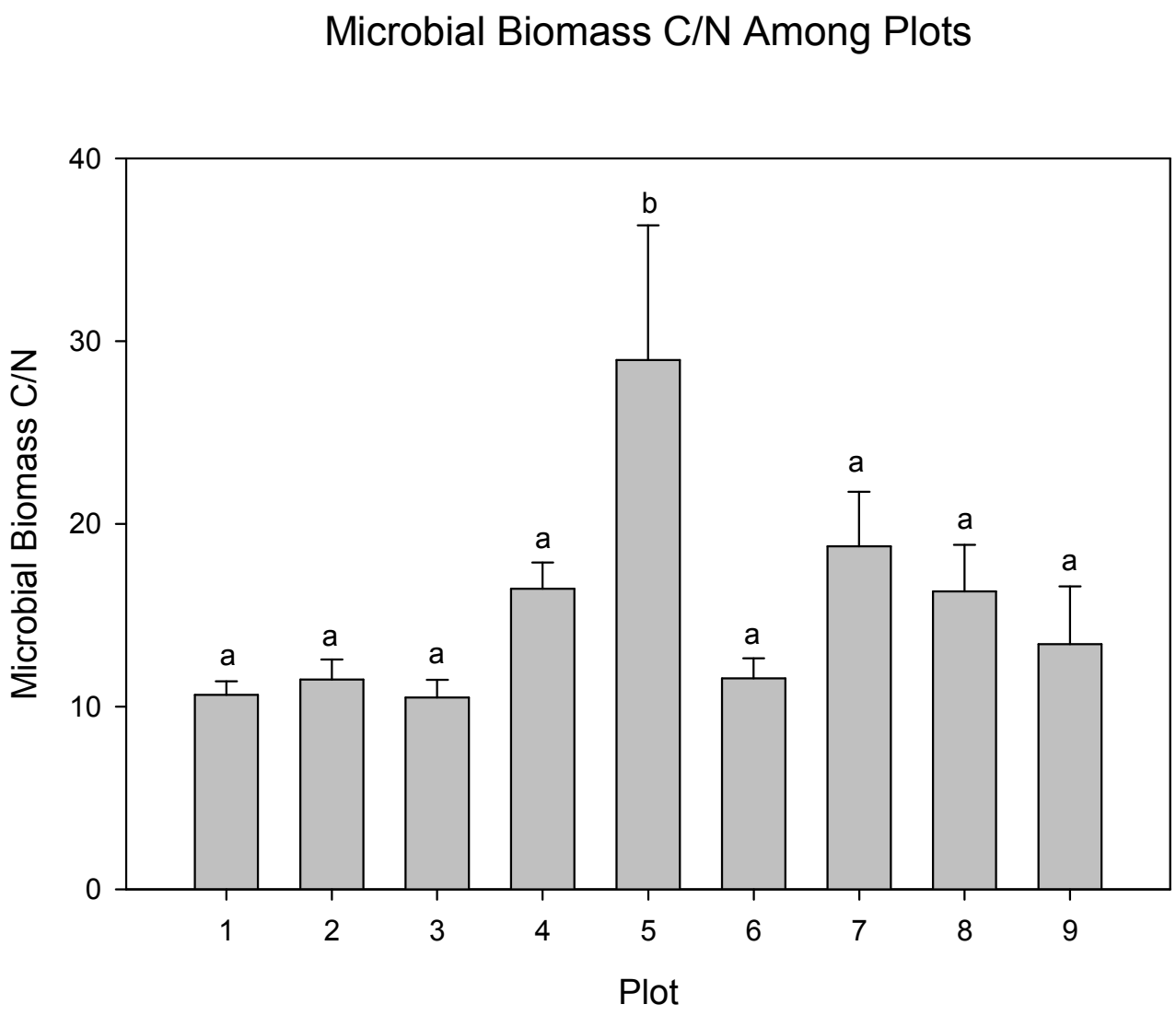

Figure 3.5. Mean microbial biomass C/N (±SE) by plot. Significant (alpha=0.05) differences are indicated by different letters.

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APPENDIX 1: CWD % MASS REMAINING FOR ALL PLOTS TO 14 MONTHS

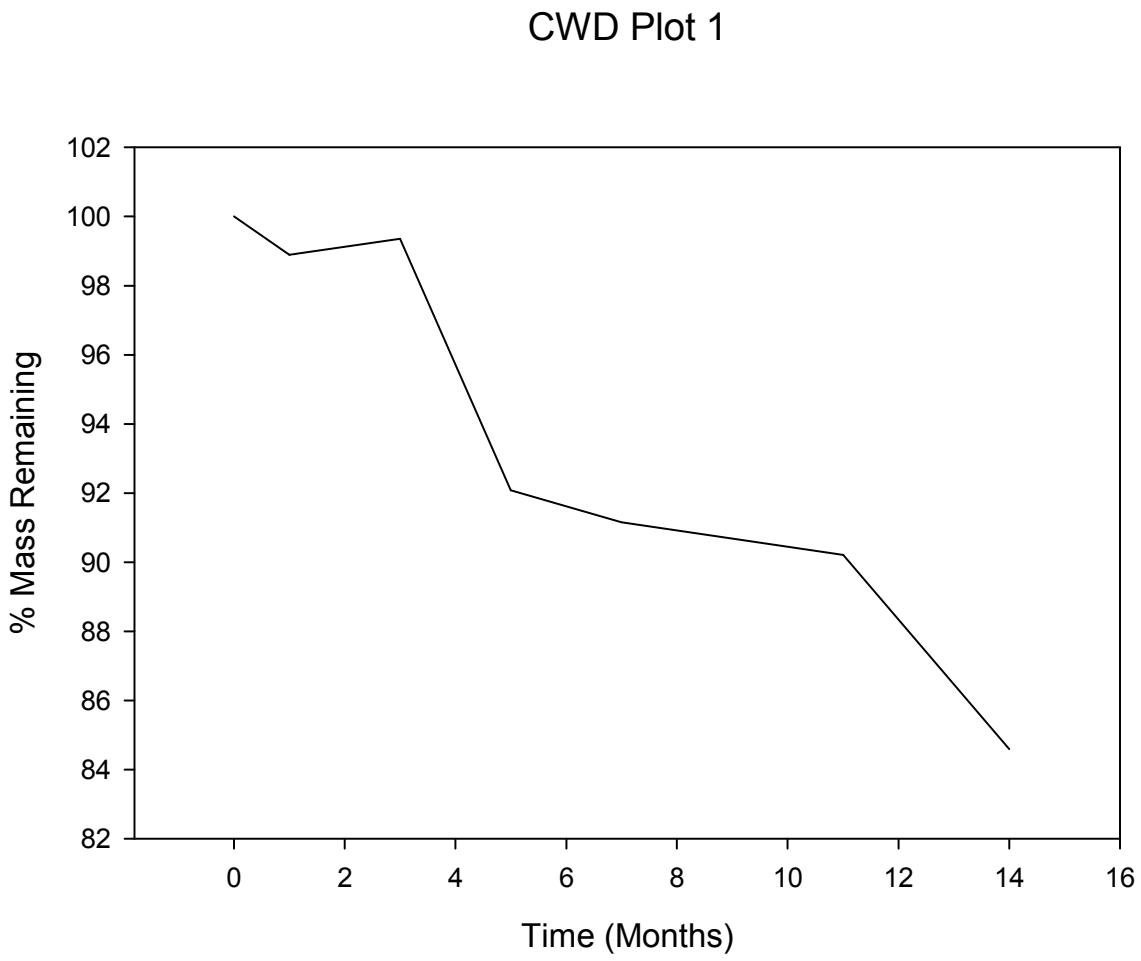

Figure A1.1. CWD percent mass remaining up to 14 months for plot 1.

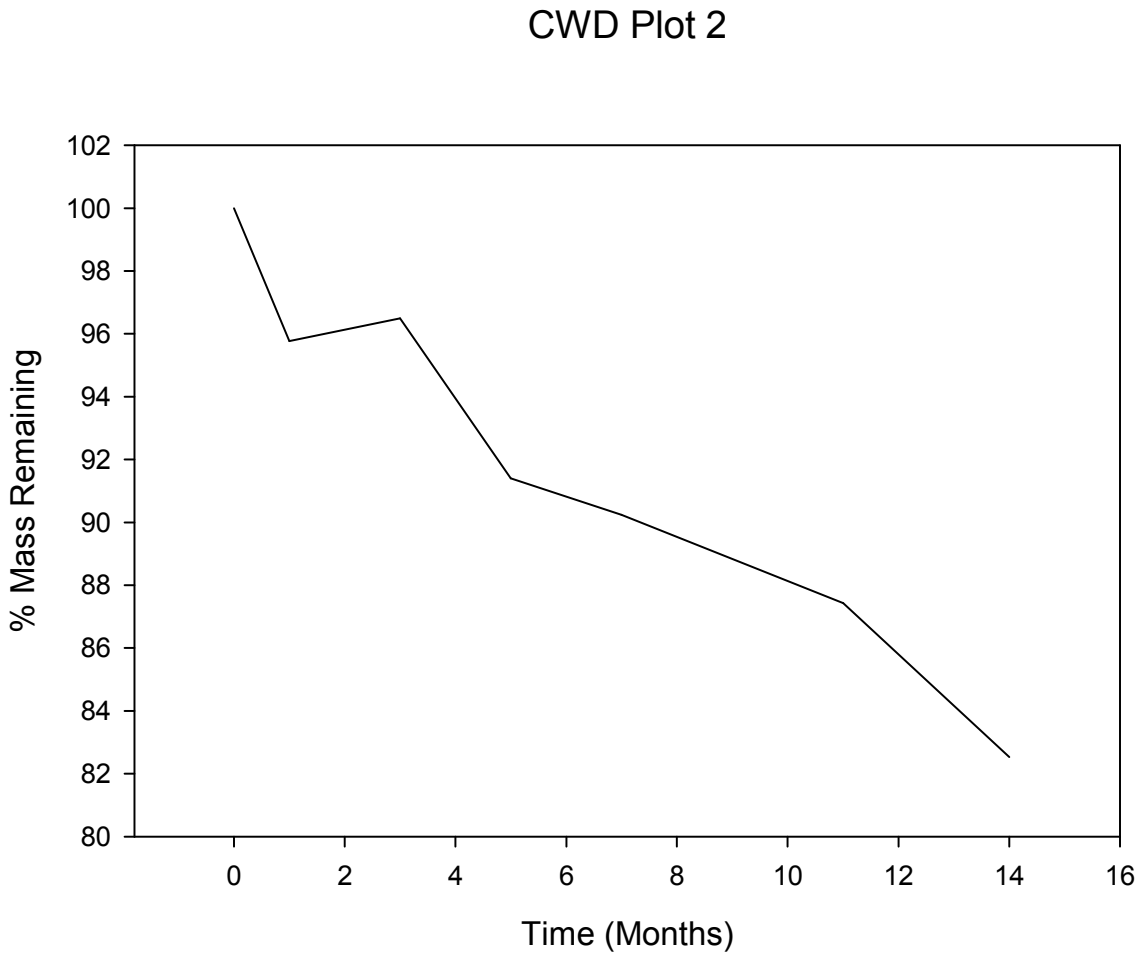

Figure A1.2. CWD percent mass remaining up to 14 months for plot 2.

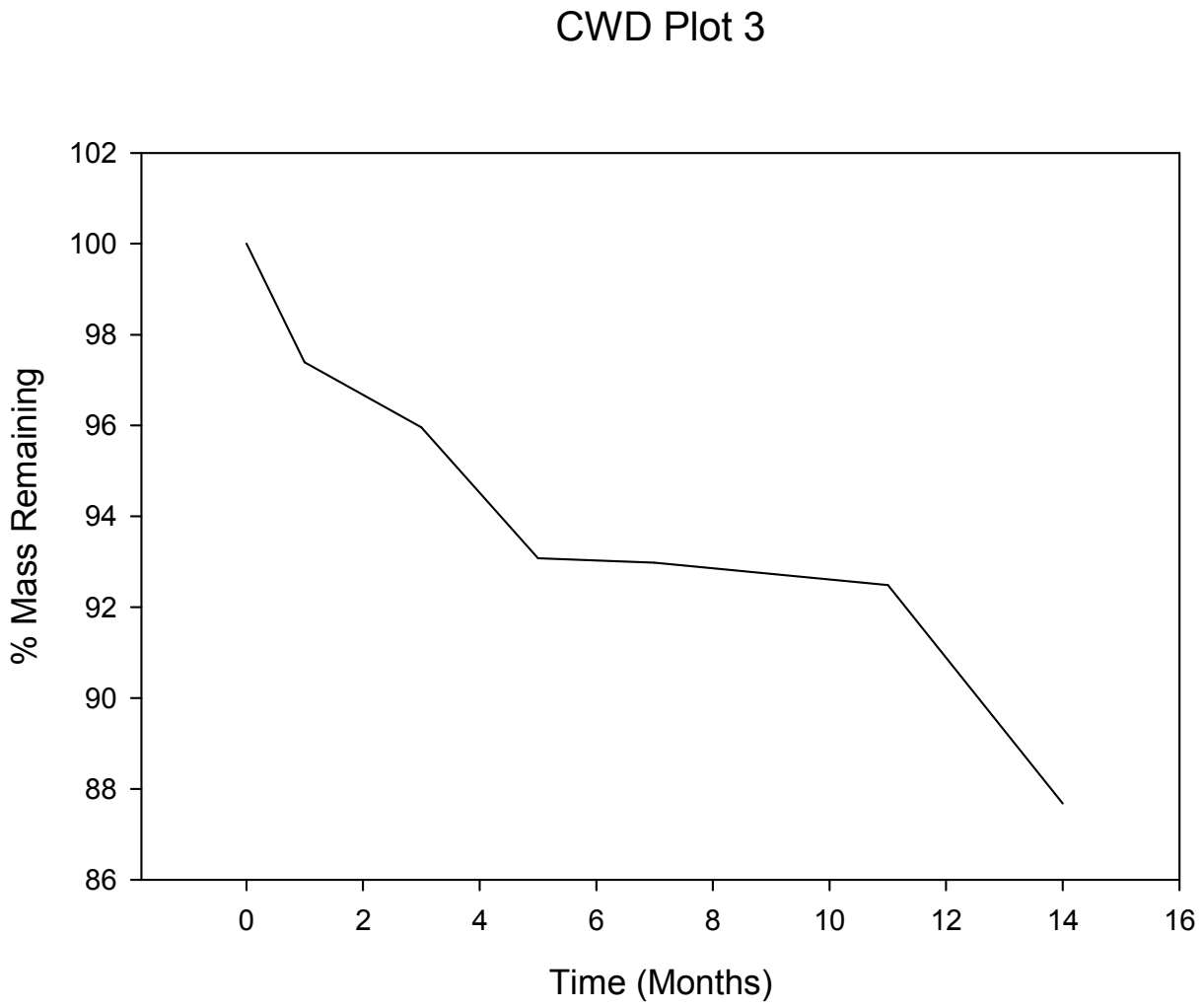

Figure A1.3. CWD percent mass remaining up to 14 months for plot 3.

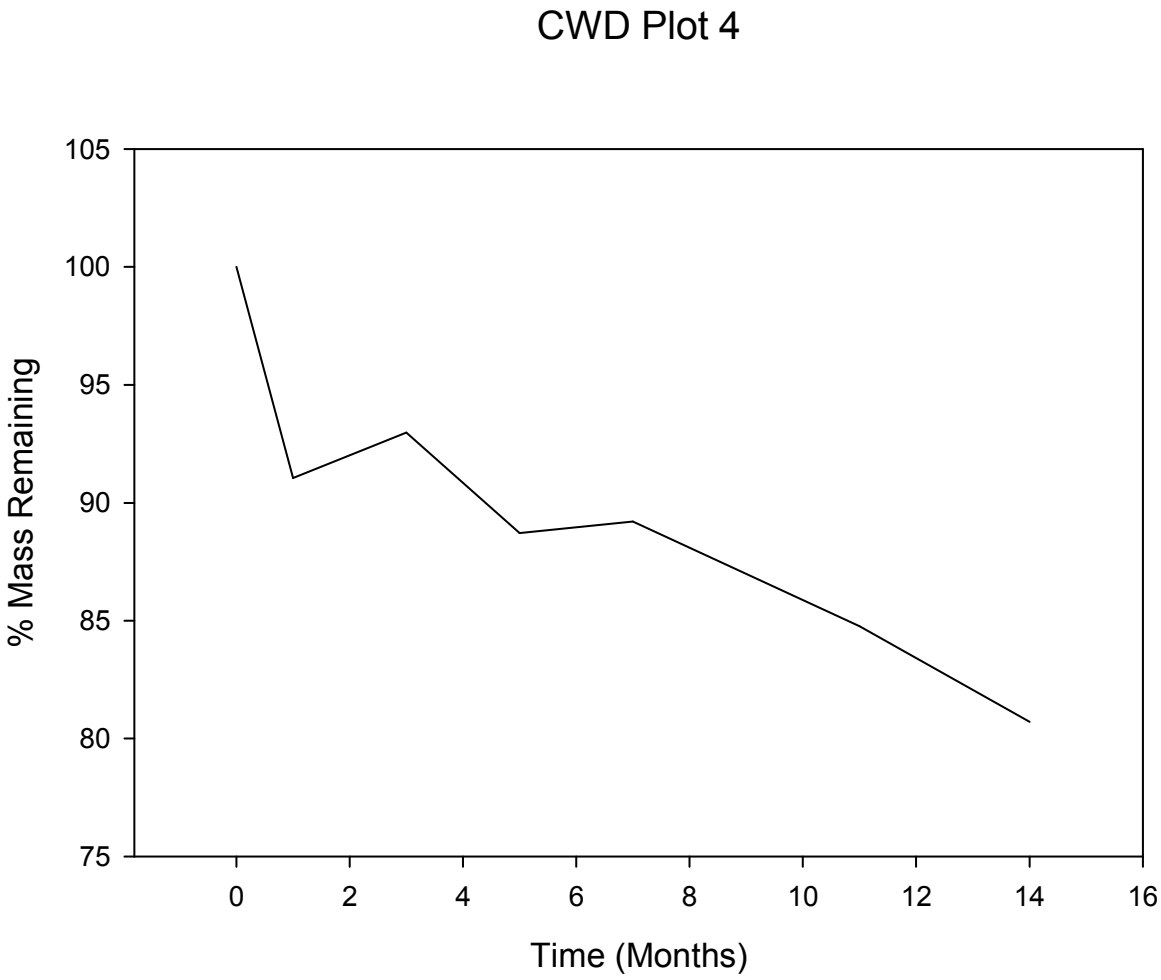

Figure A1.4. CWD percent mass remaining up to 14 months for plot 4.

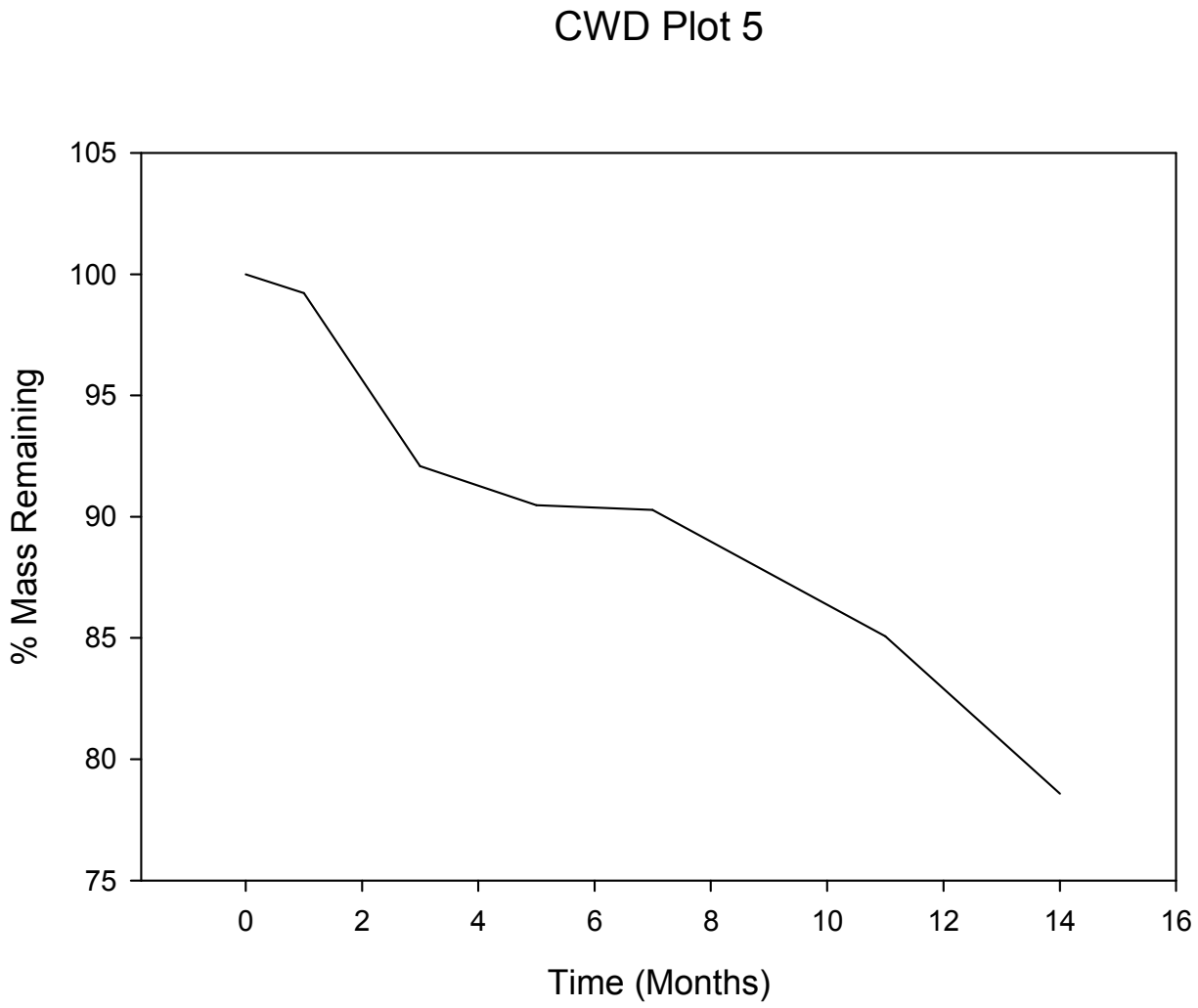

Figure A1.5. CWD percent mass remaining up to 14 months for plot 5.

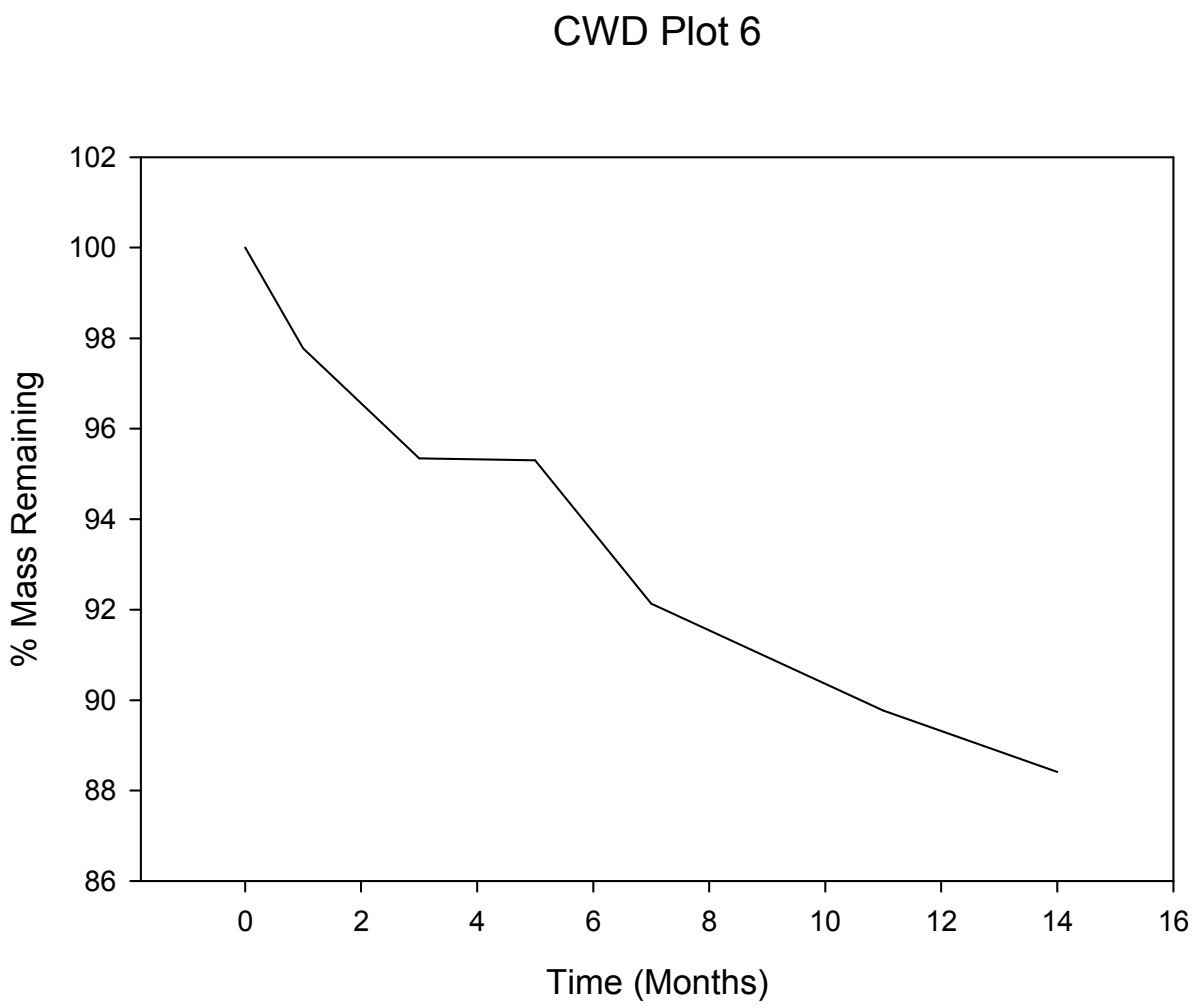

Figure A1.6. CWD percent mass remaining up to 14 months for plot 6.

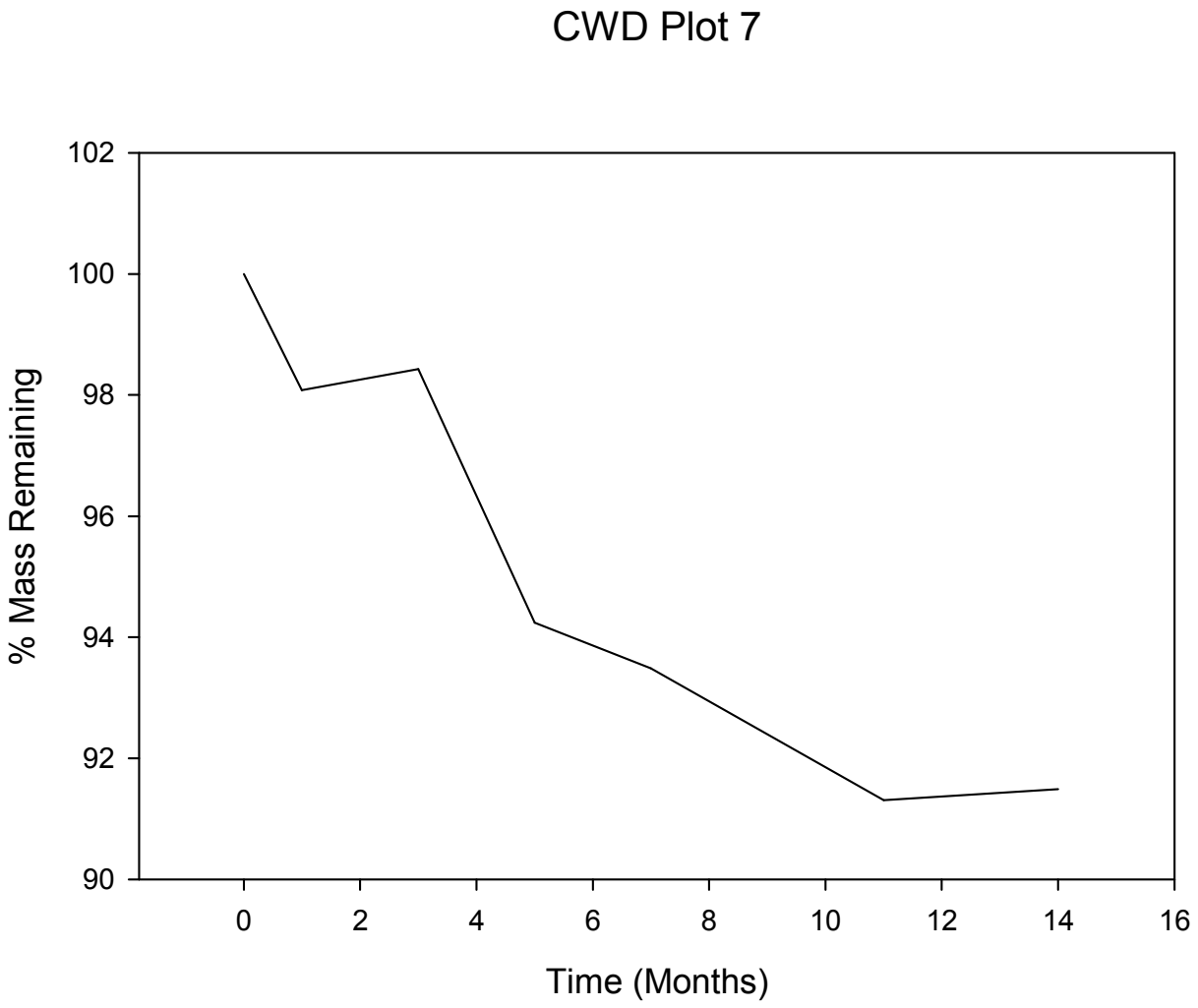

Figure A1.7. CWD percent mass remaining up to 14 months for plot 7.

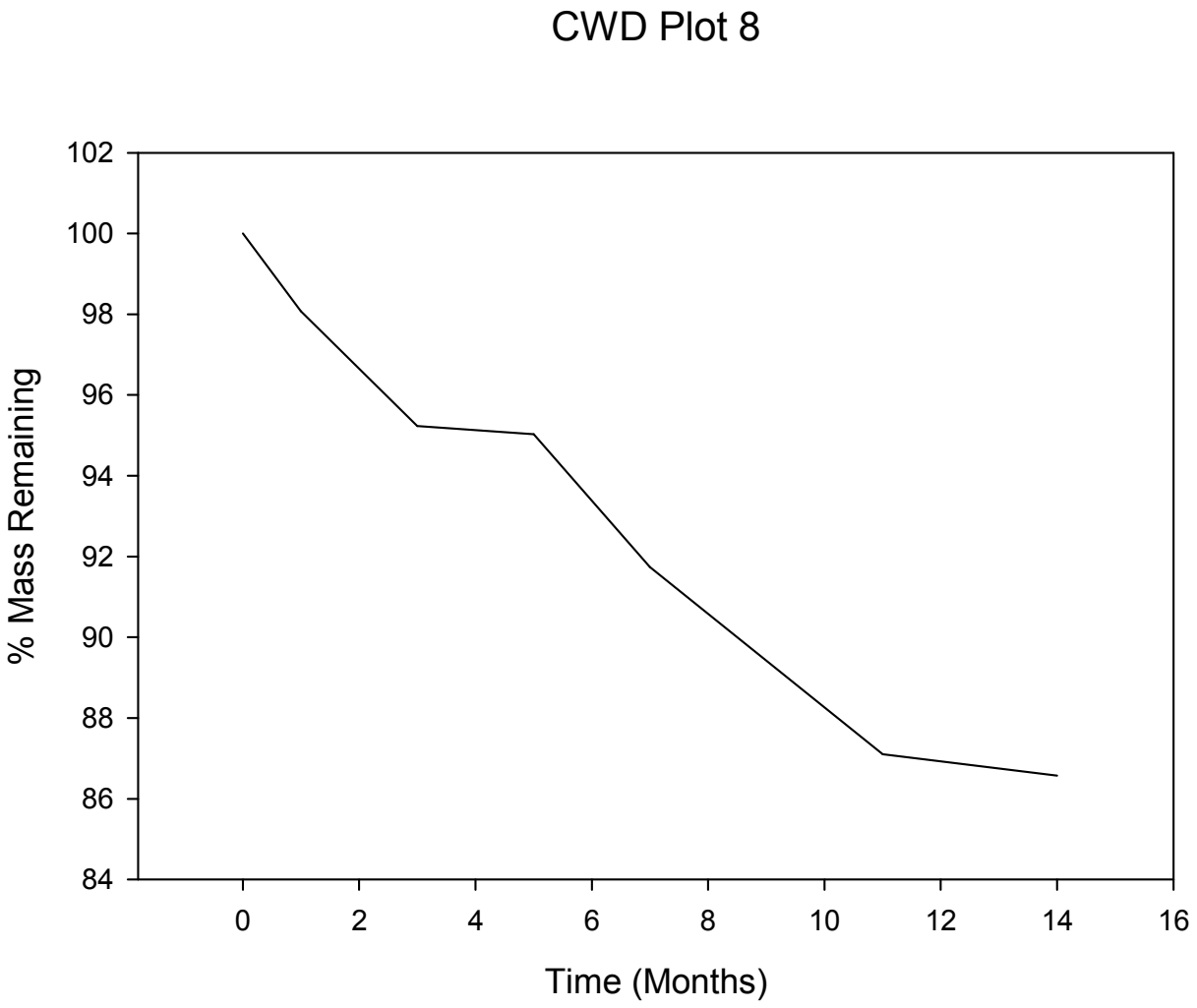

Figure A1.8. CWD percent mass remaining up to 14 months for plot 8.

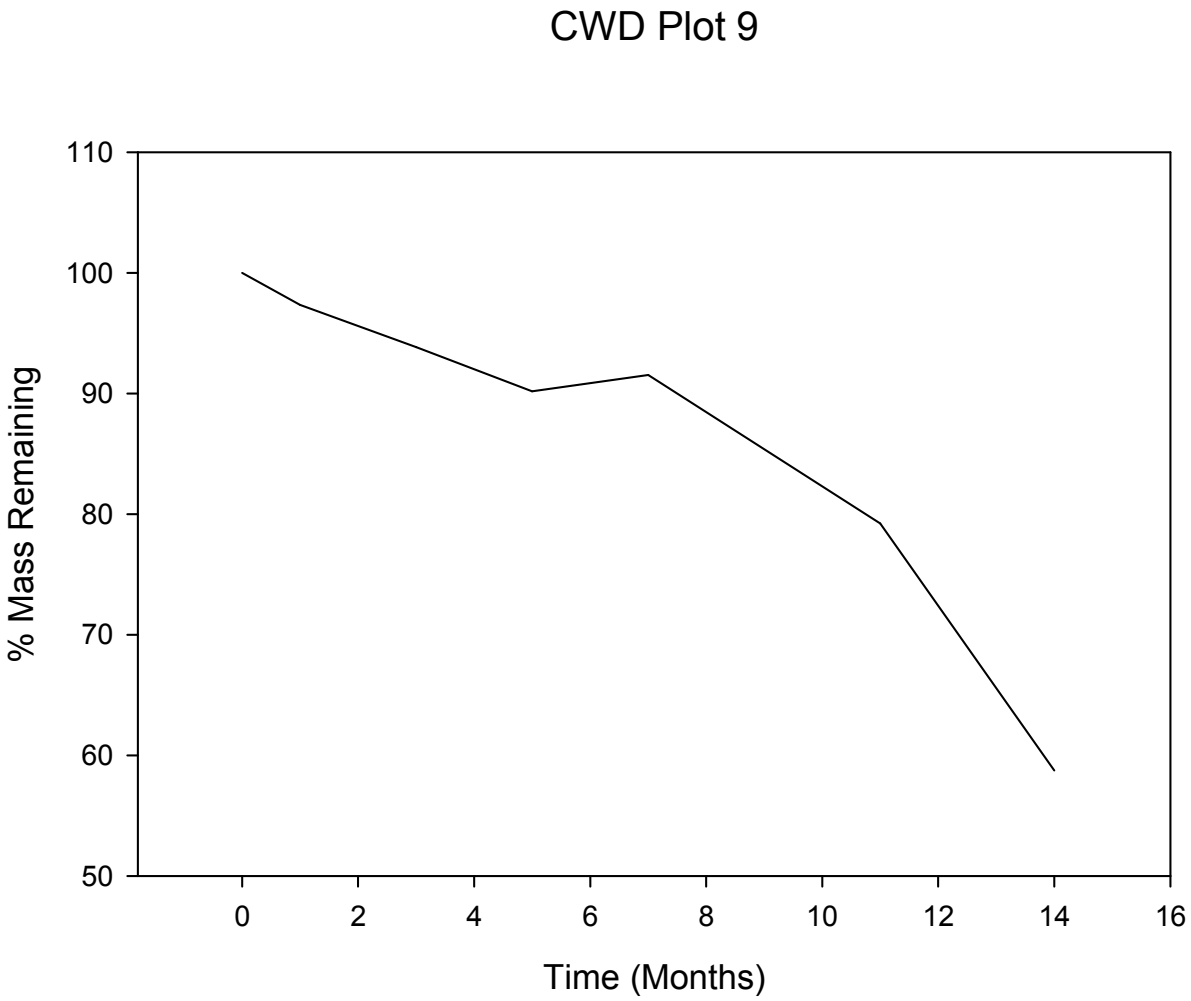

Figure A1.9. CWD percent mass remaining up to 14 months for plot 9.

APPENDIX 2: CONTROL WOOD % MASS REMAINING FOR ALL PLOTS TO 14 MONTHS

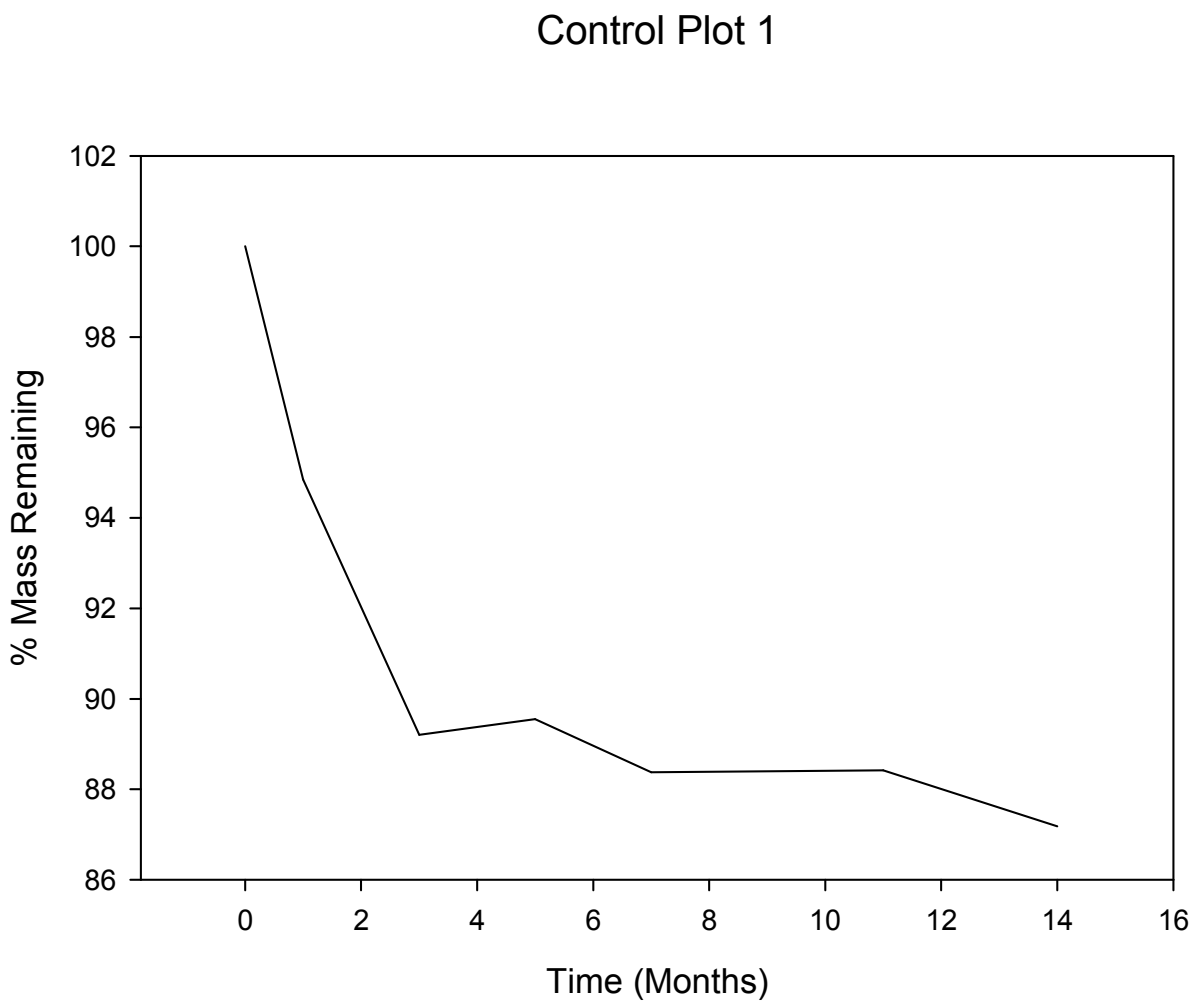

Figure A2.1. Control wood percent mass remaining up to 14 months for plot 1.

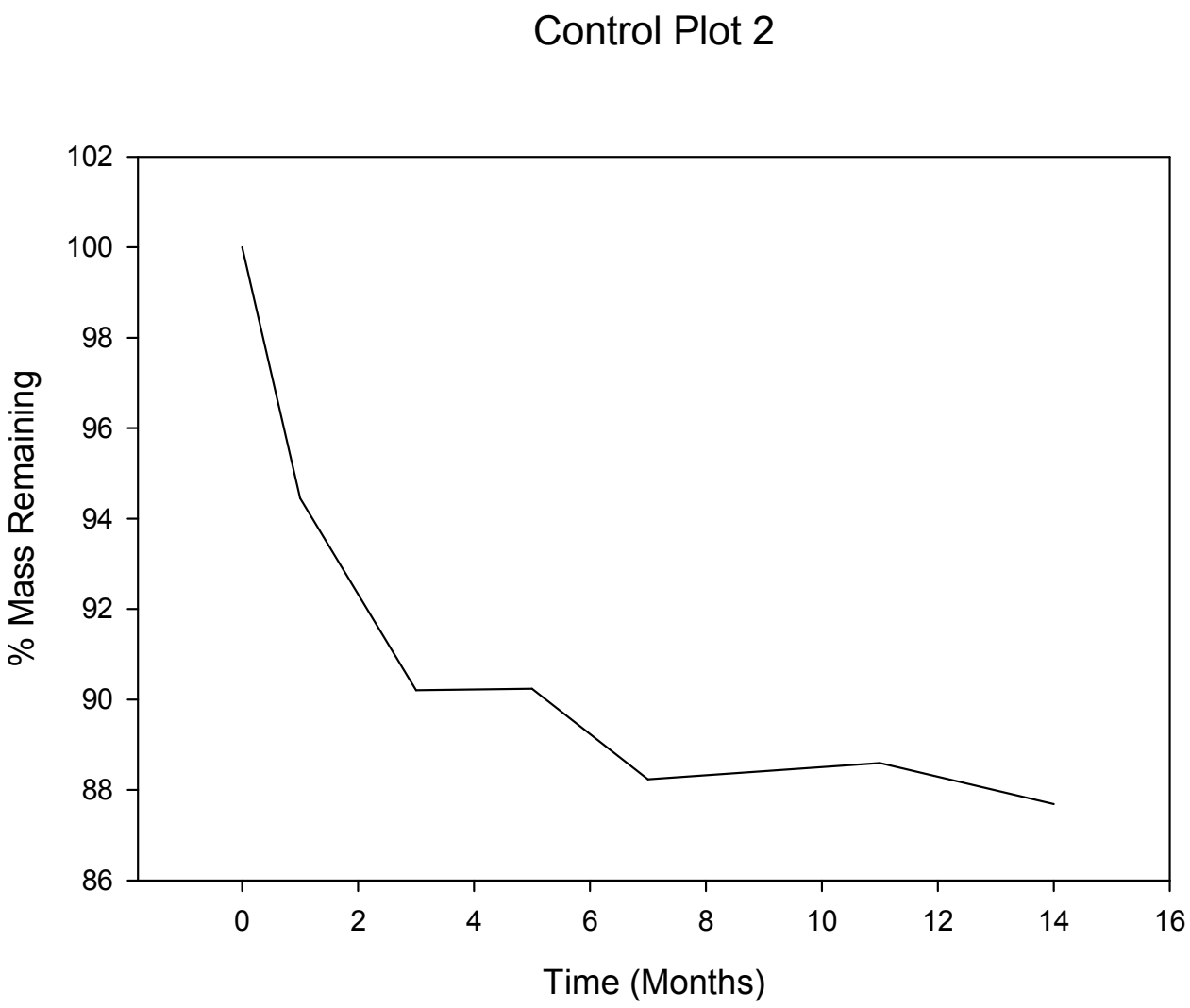

Figure A2.2. Control wood percent mass remaining up to 14 months for plot 2.

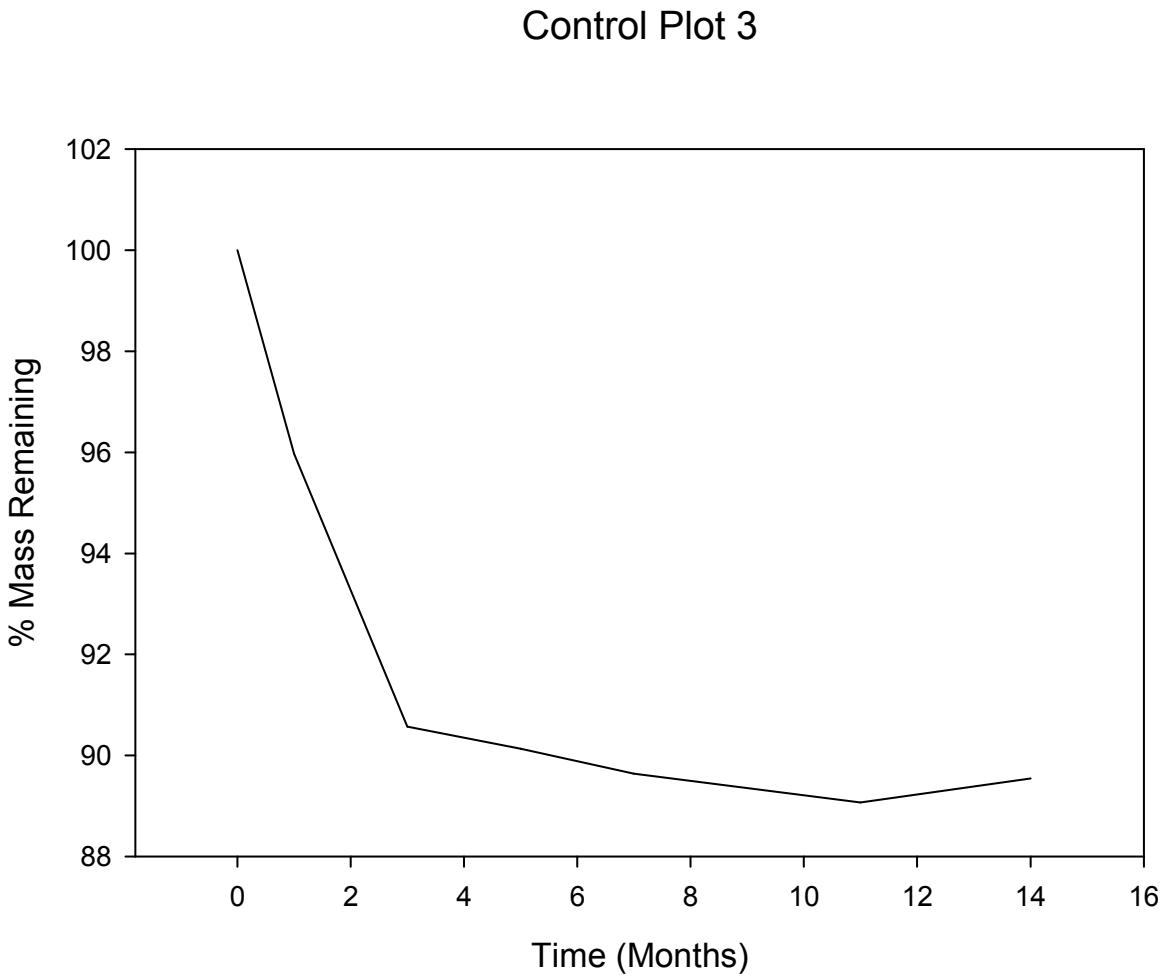

Figure A2.3. Control wood percent mass remaining up to 14 months for plot 3.

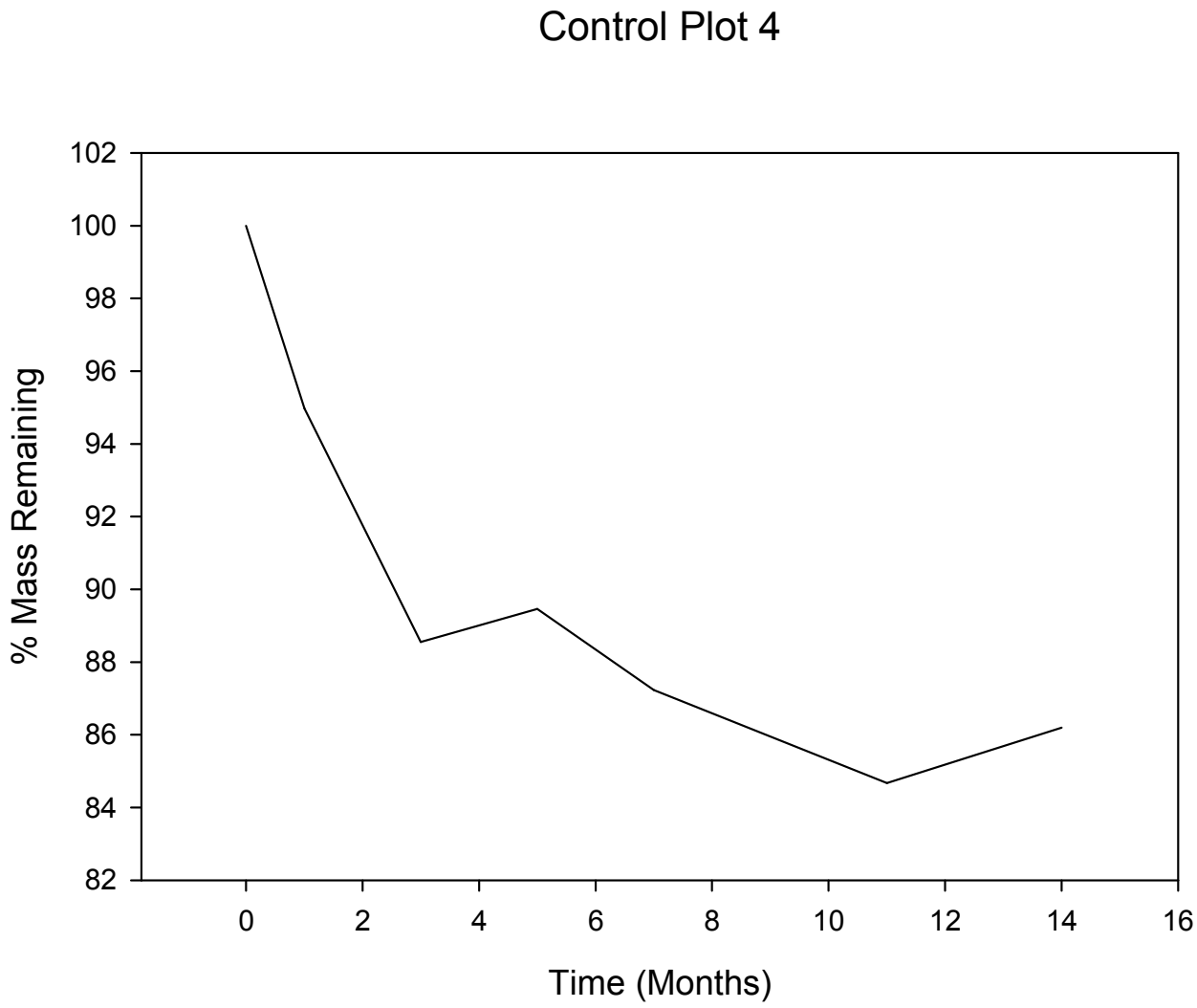

Figure A2.4. Control wood percent mass remaining up to 14 months for plot 4.

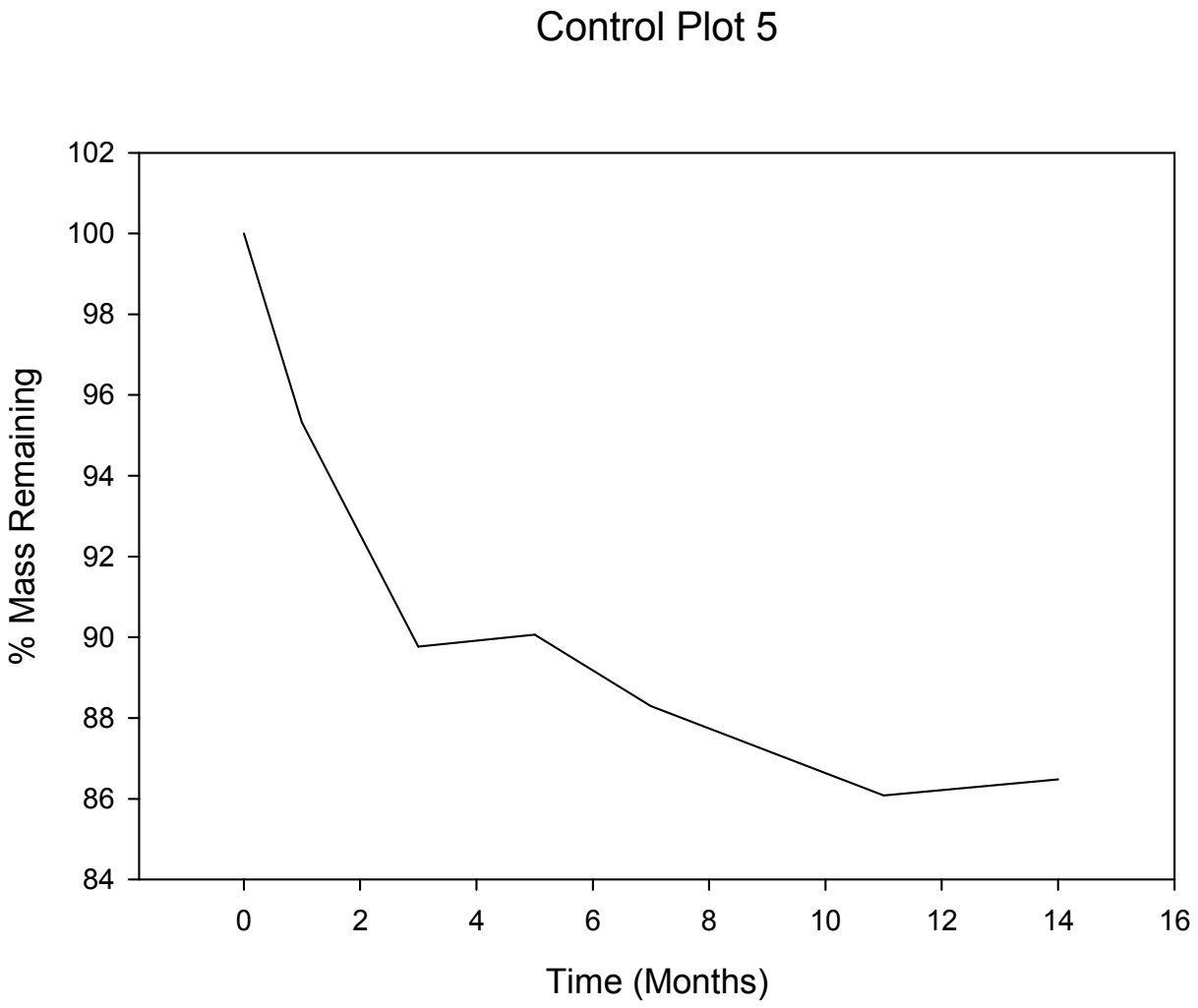

Figure A2.5. Control wood percent mass remaining up to 14 months for plot 5.

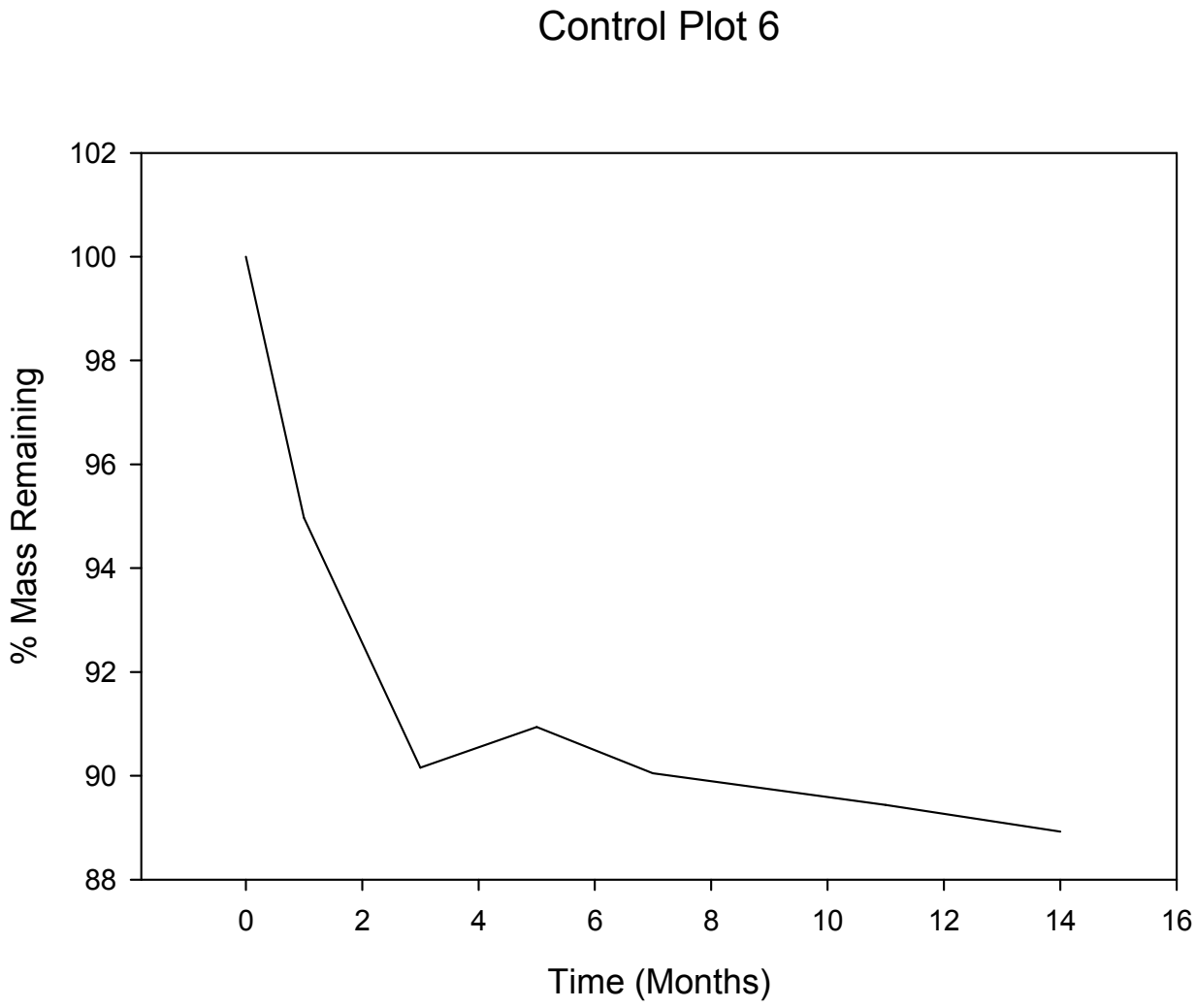

Figure A2.6. Control wood percent mass remaining up to 14 months for plot 6.

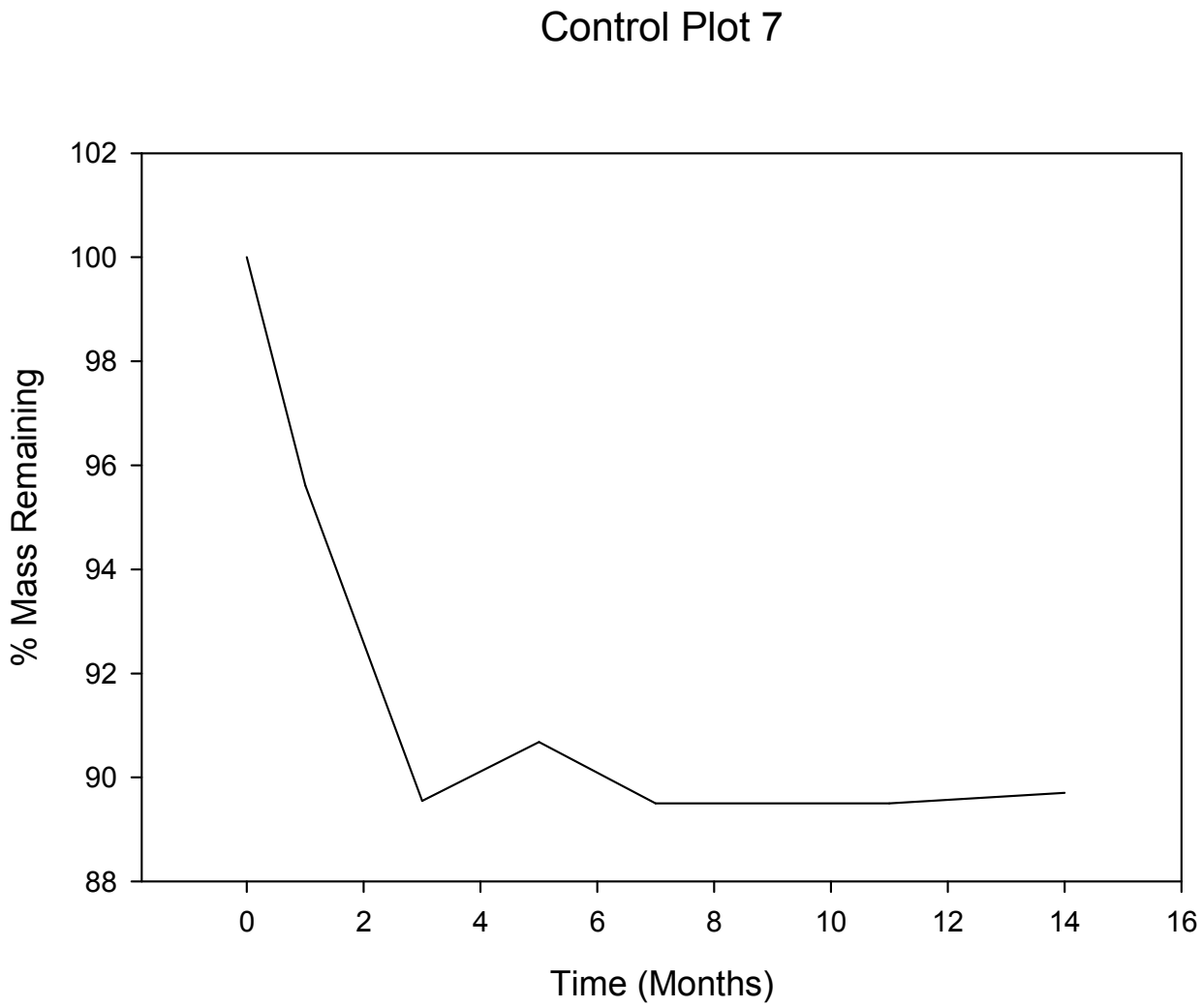

Figure A2.7. Control wood percent mass remaining up to 14 months for plot 7.

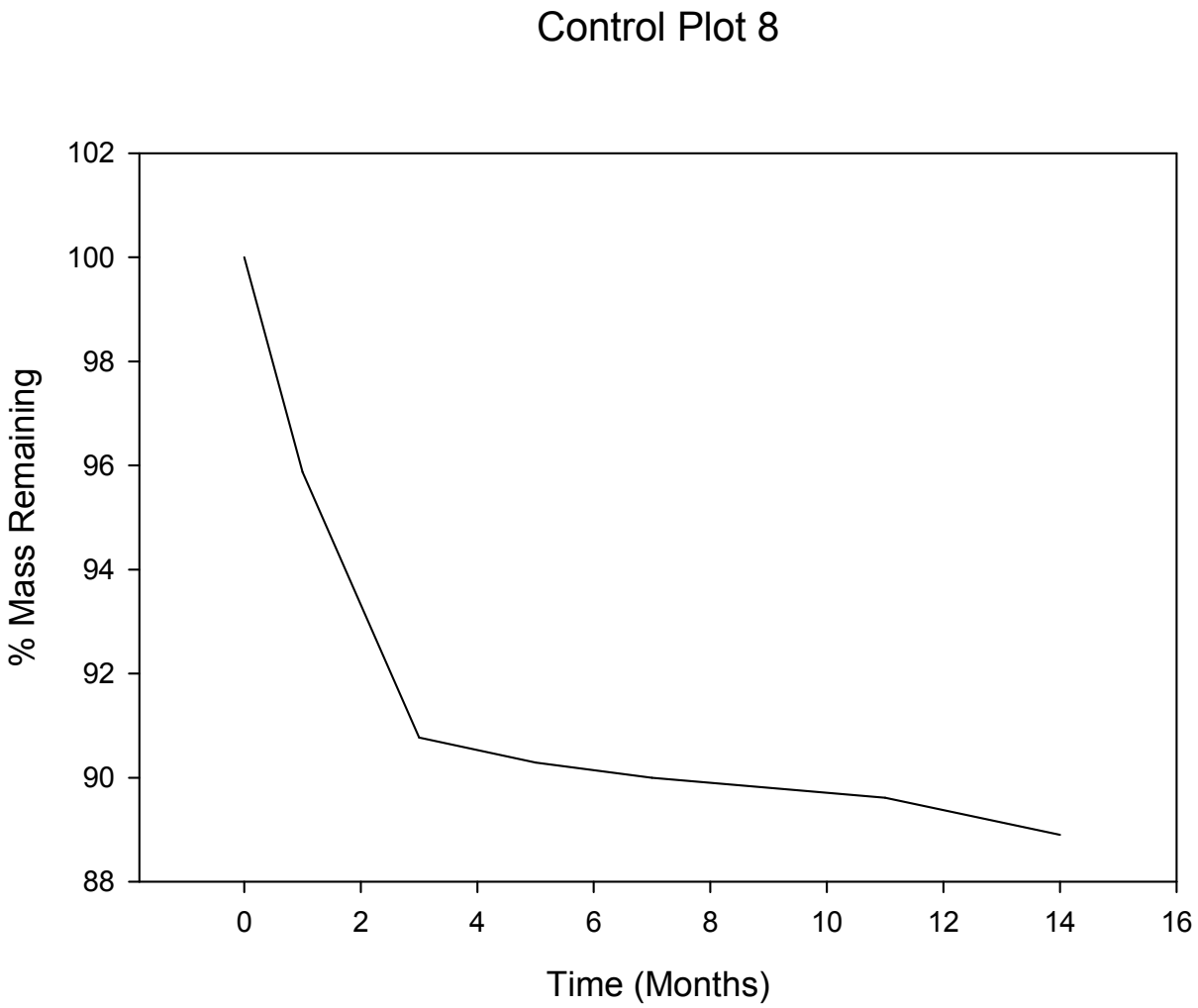

Figure A2.8. Control wood percent mass remaining up to 14 months for plot 8.

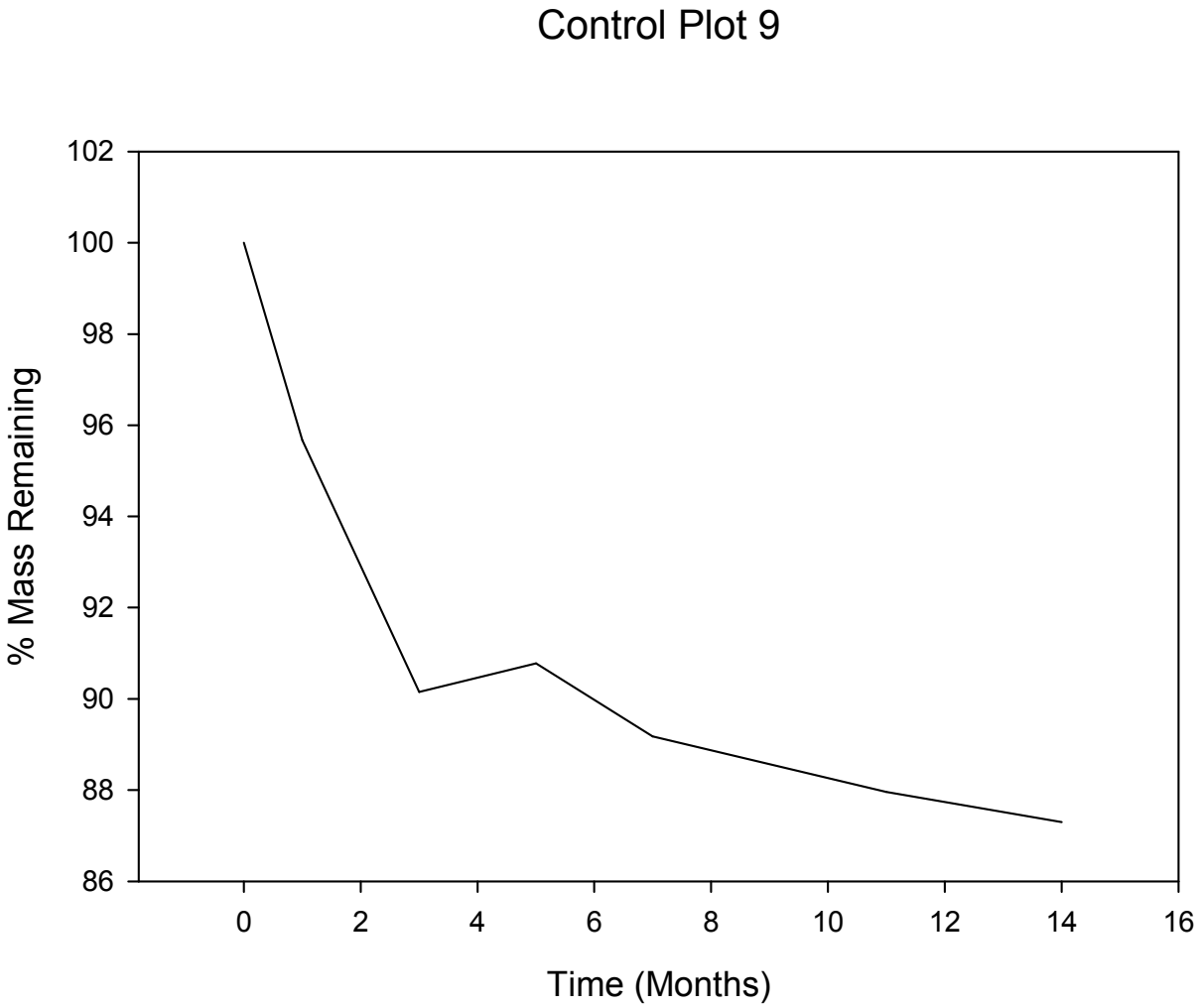

Figure A2.9. Control wood percent mass remaining up to 14 months for plot 9.

APPENDIX 3: CWD 5 C REMAINING FOR ALL PLOTS TO 14 MONTHS

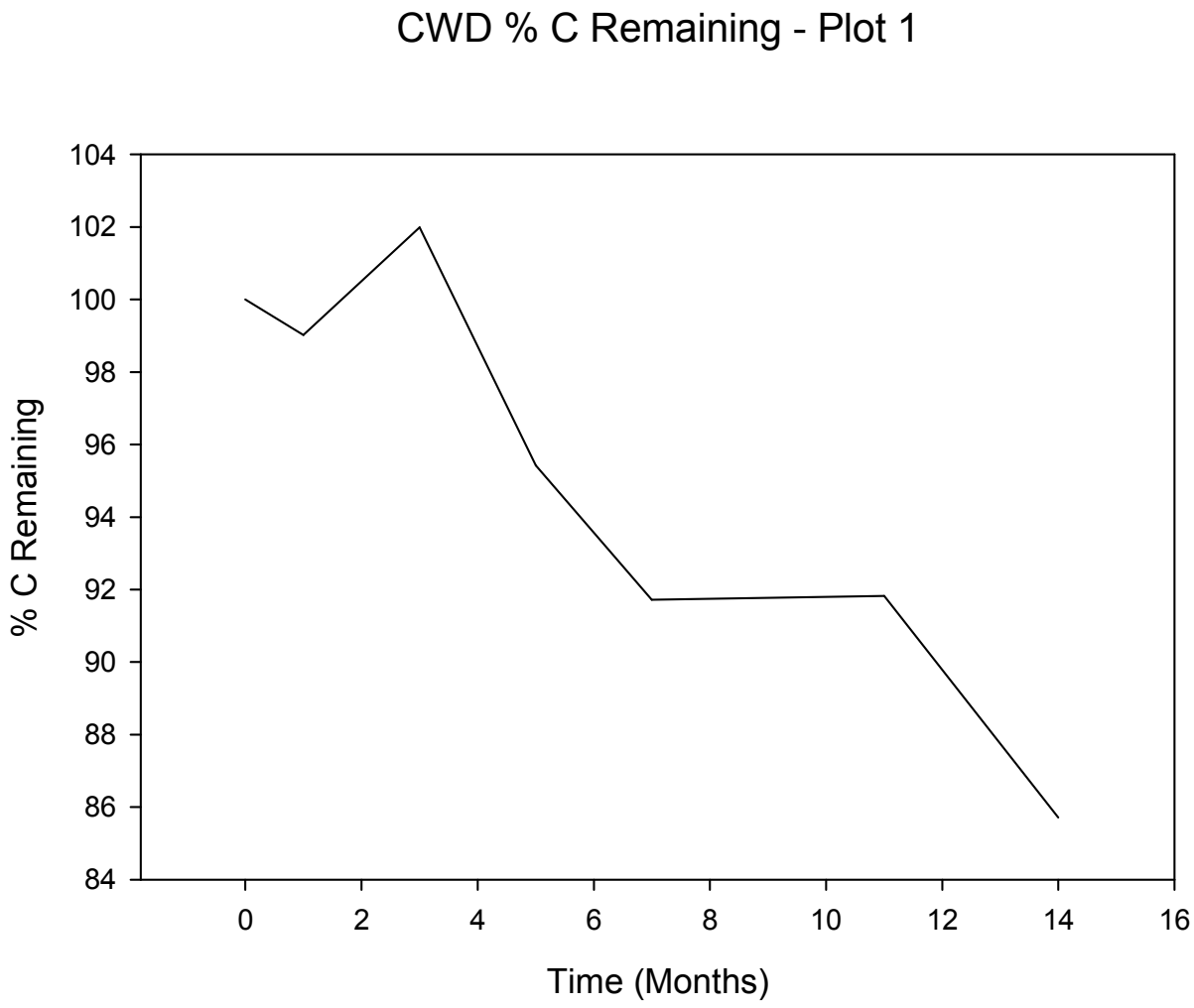

Figure A3.1. CWD percent C remaining up to 14 months for plot 1.

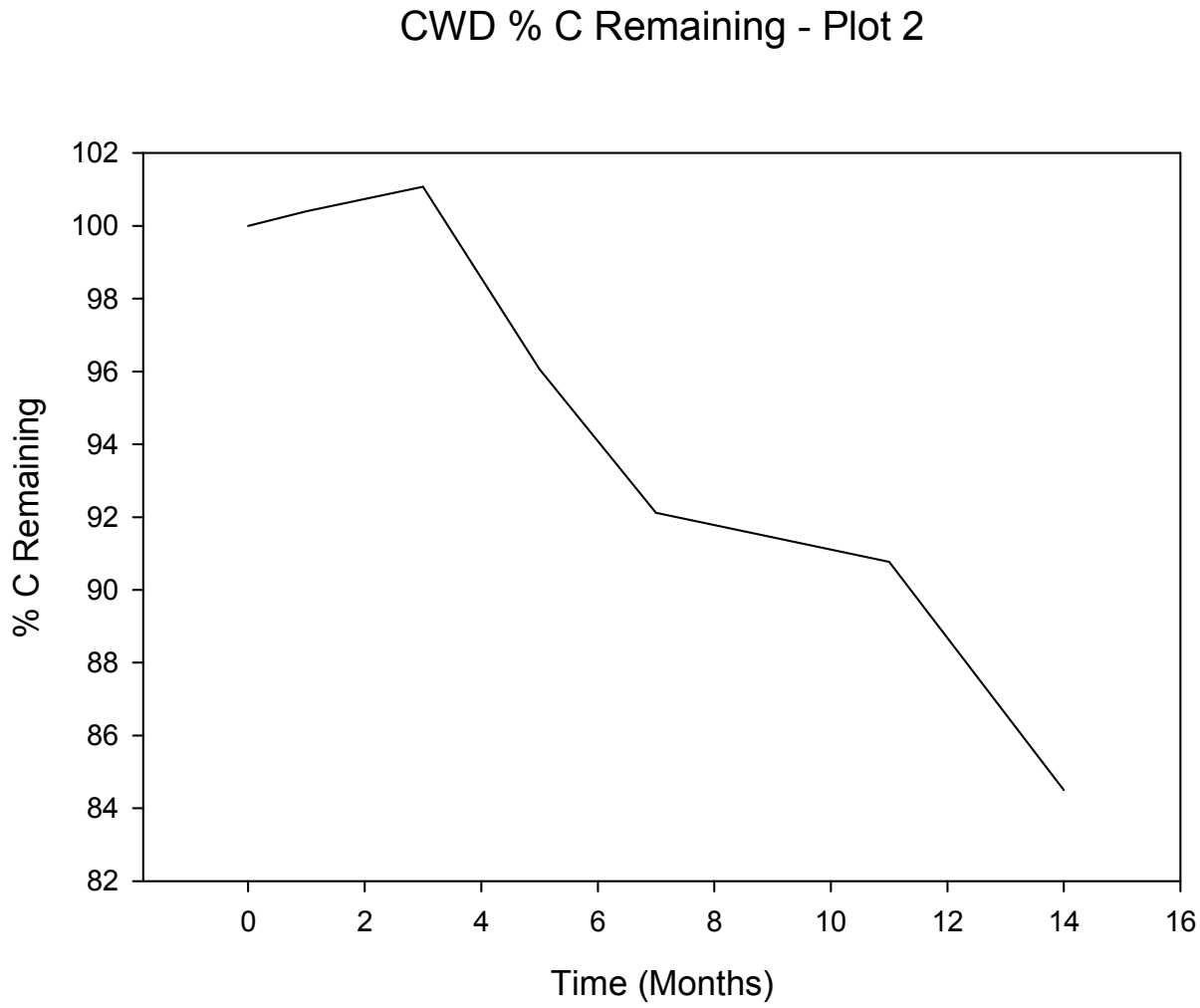

Figure A3.2. CWD percent C remaining up to 14 months for plot 2.

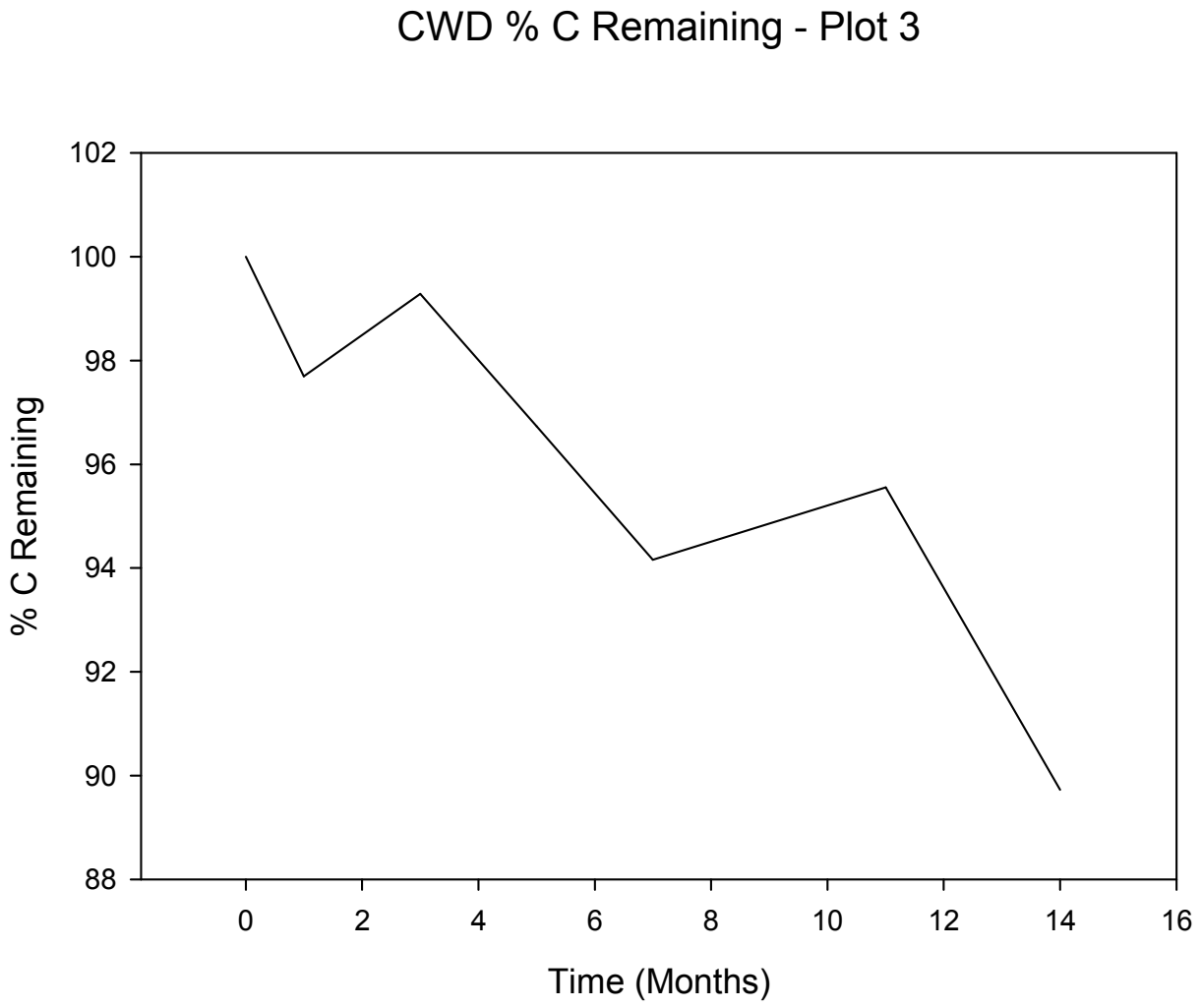

Figure A3.3. CWD percent C remaining up to 14 months for plot 3.

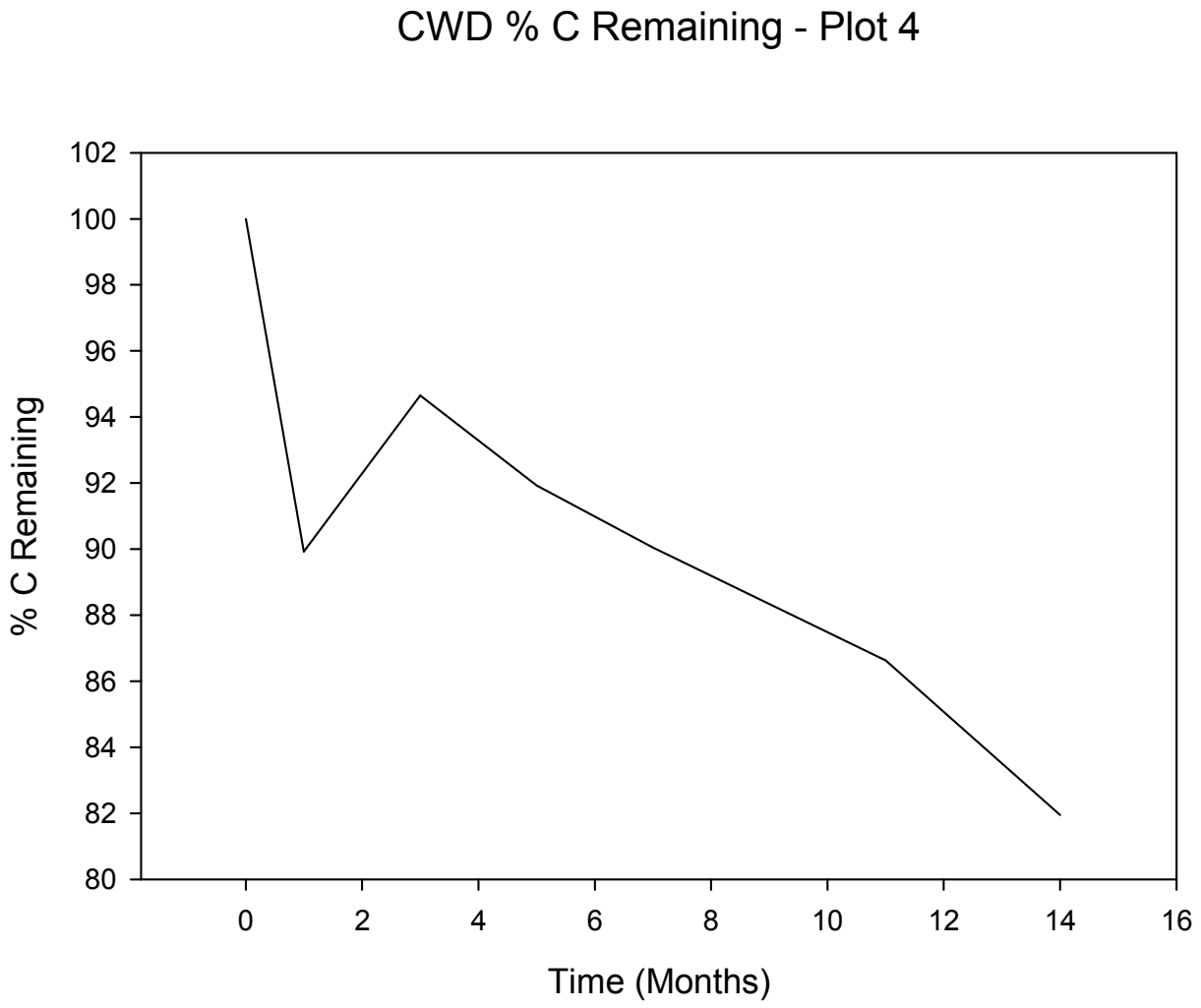

Figure A3.4. CWD percent C remaining up to 14 months for plot 4.

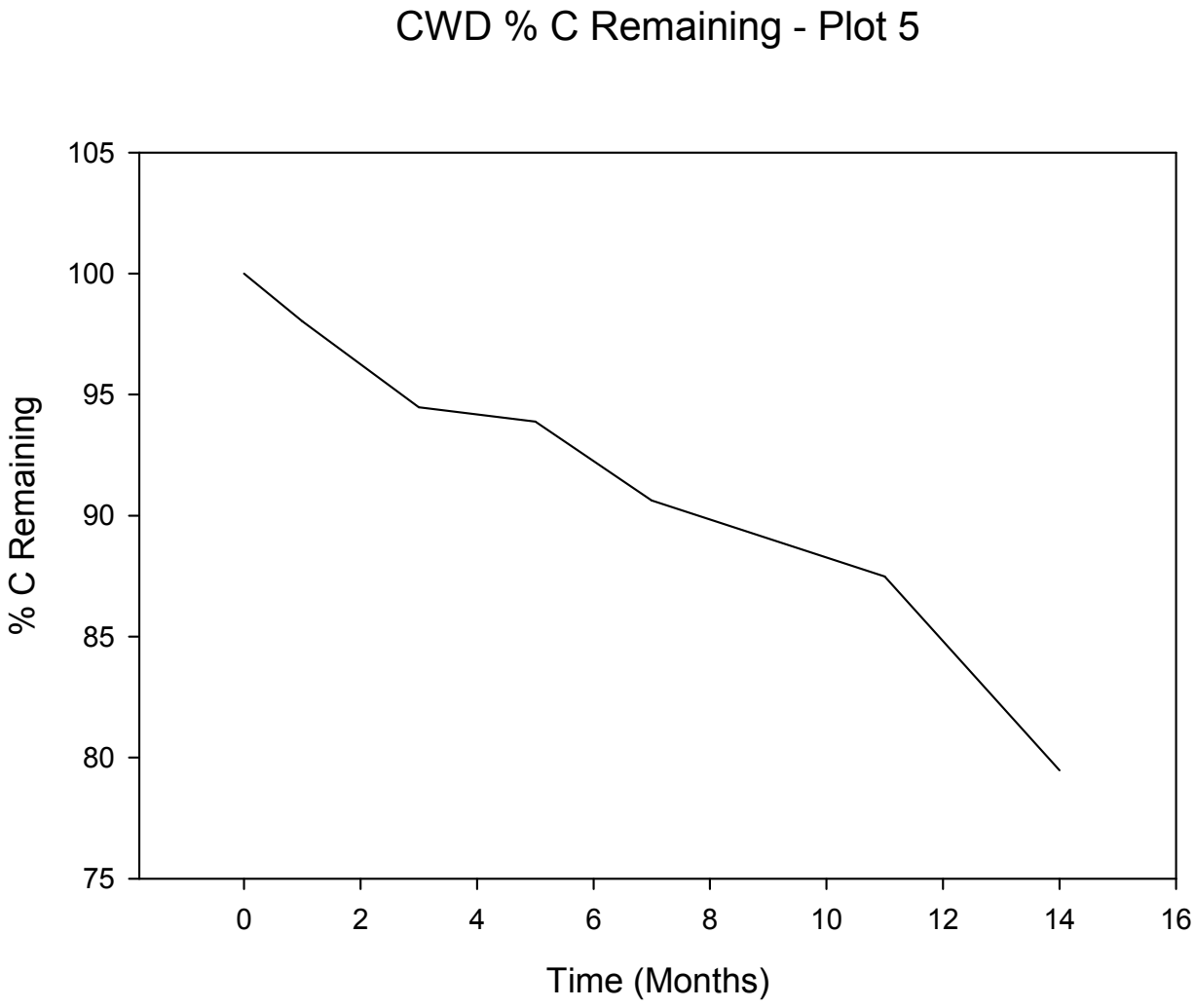

Figure A3.5. CWD percent C remaining up to 14 months for plot 5.

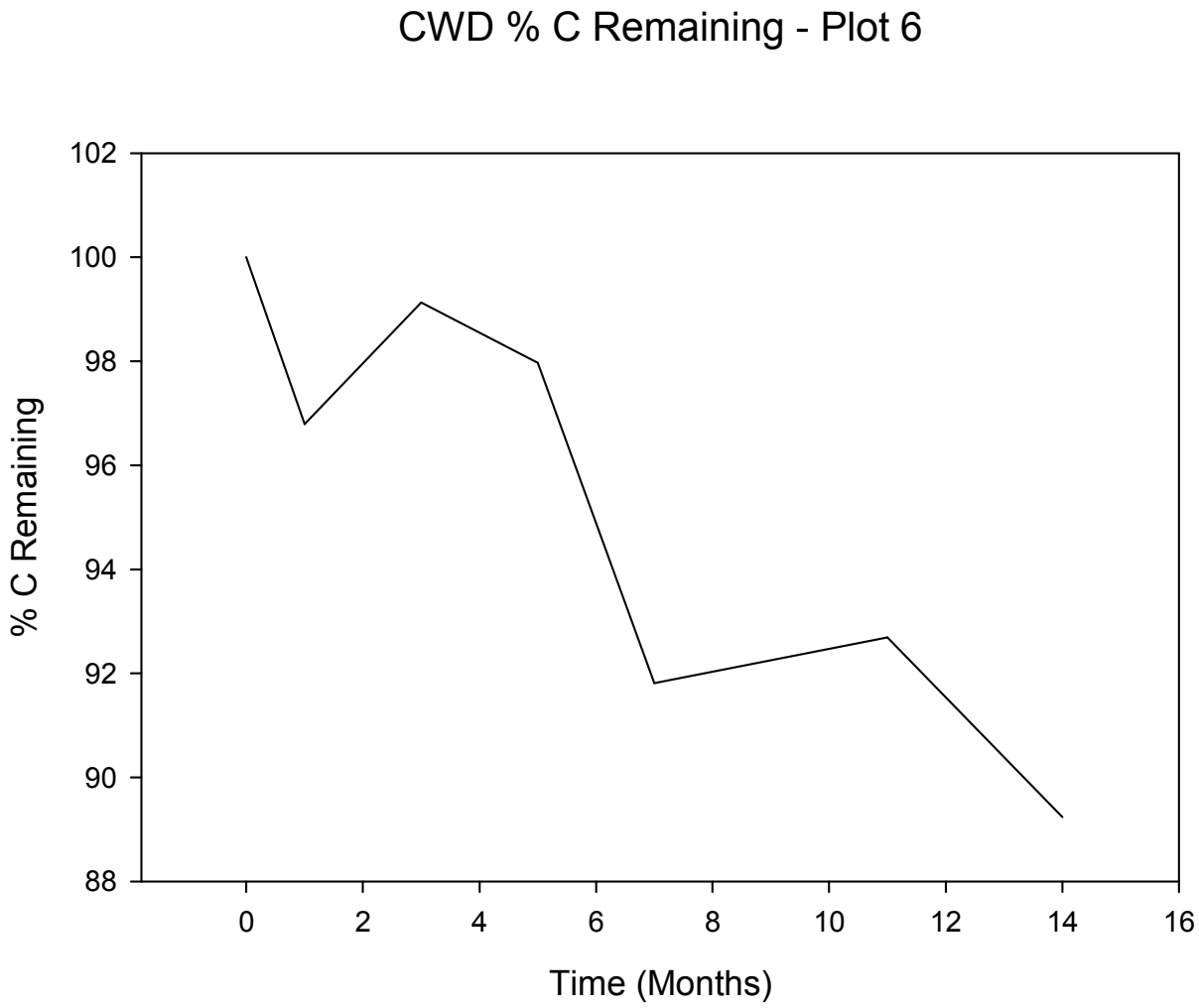

Figure A3.6. CWD percent C remaining up to 14 months for plot 6.

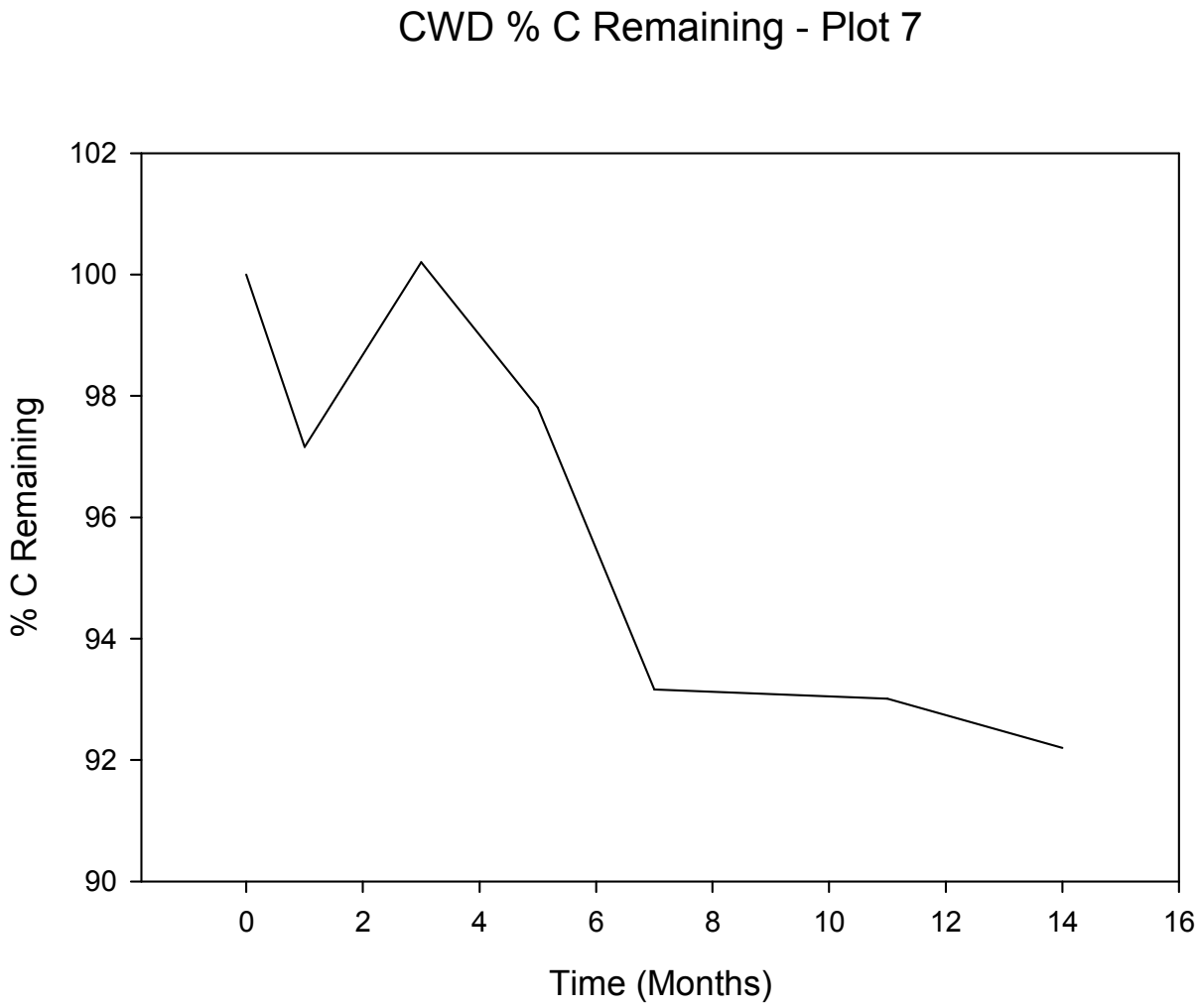

Figure A3.7. CWD percent C remaining up to 14 months for plot 7.

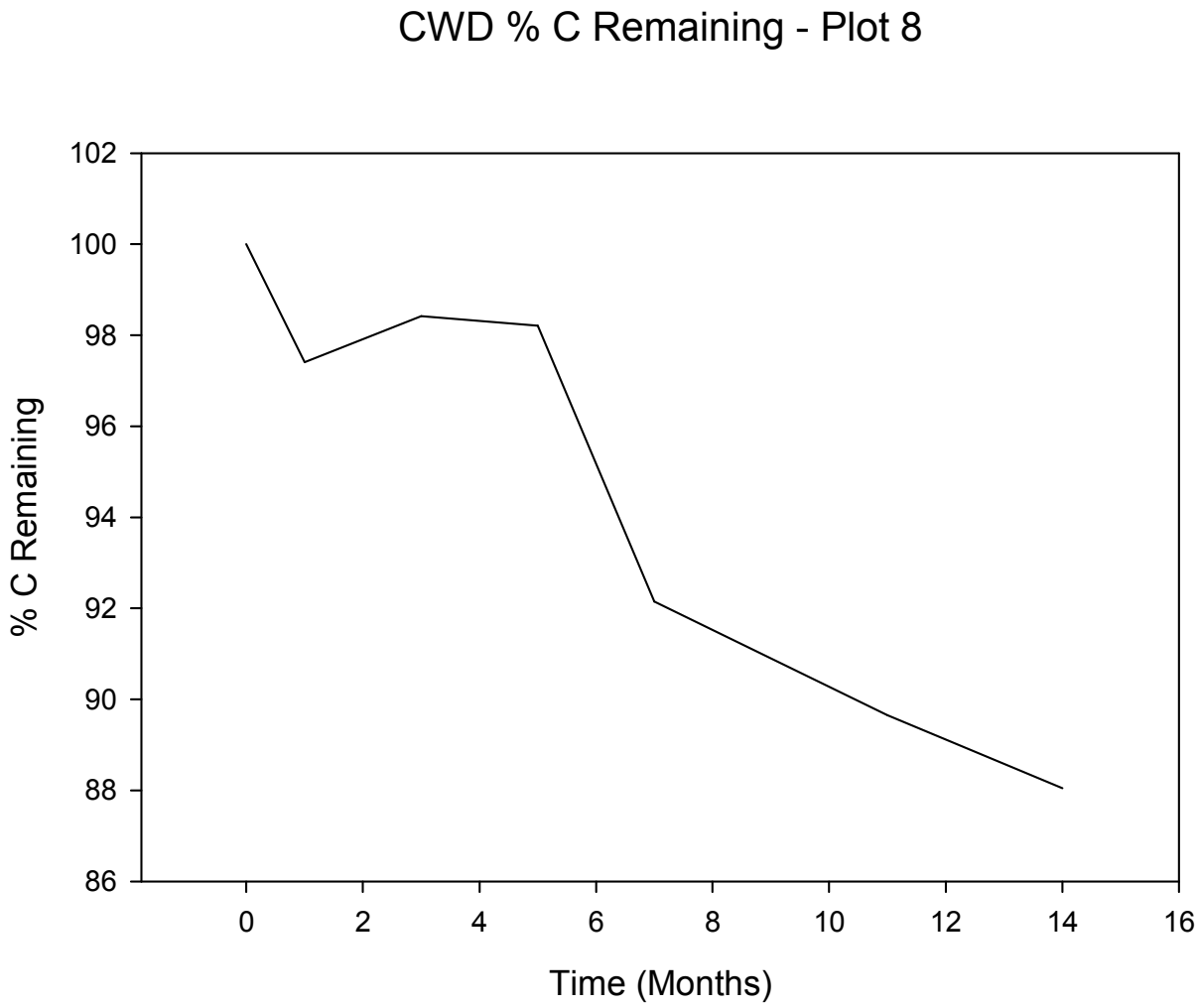

Figure A3.8. CWD percent C remaining up to 14 months for plot 8.

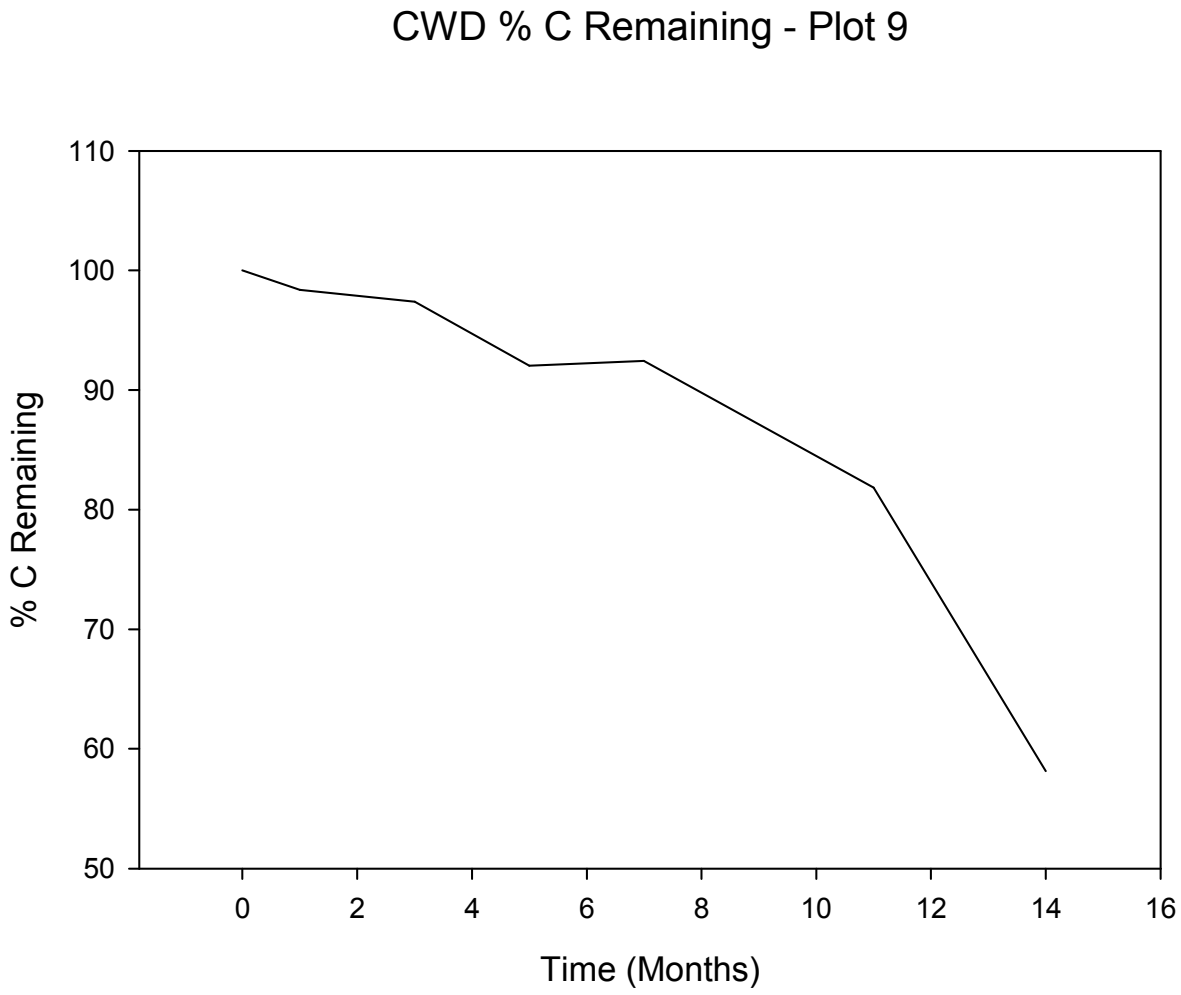

Figure A3.9. CWD percent C remaining up to 14 months for plot 9.

APPENDIX 4: CWD 5 N REMAINING AT ALL PLOTS TO 14 MONTHS

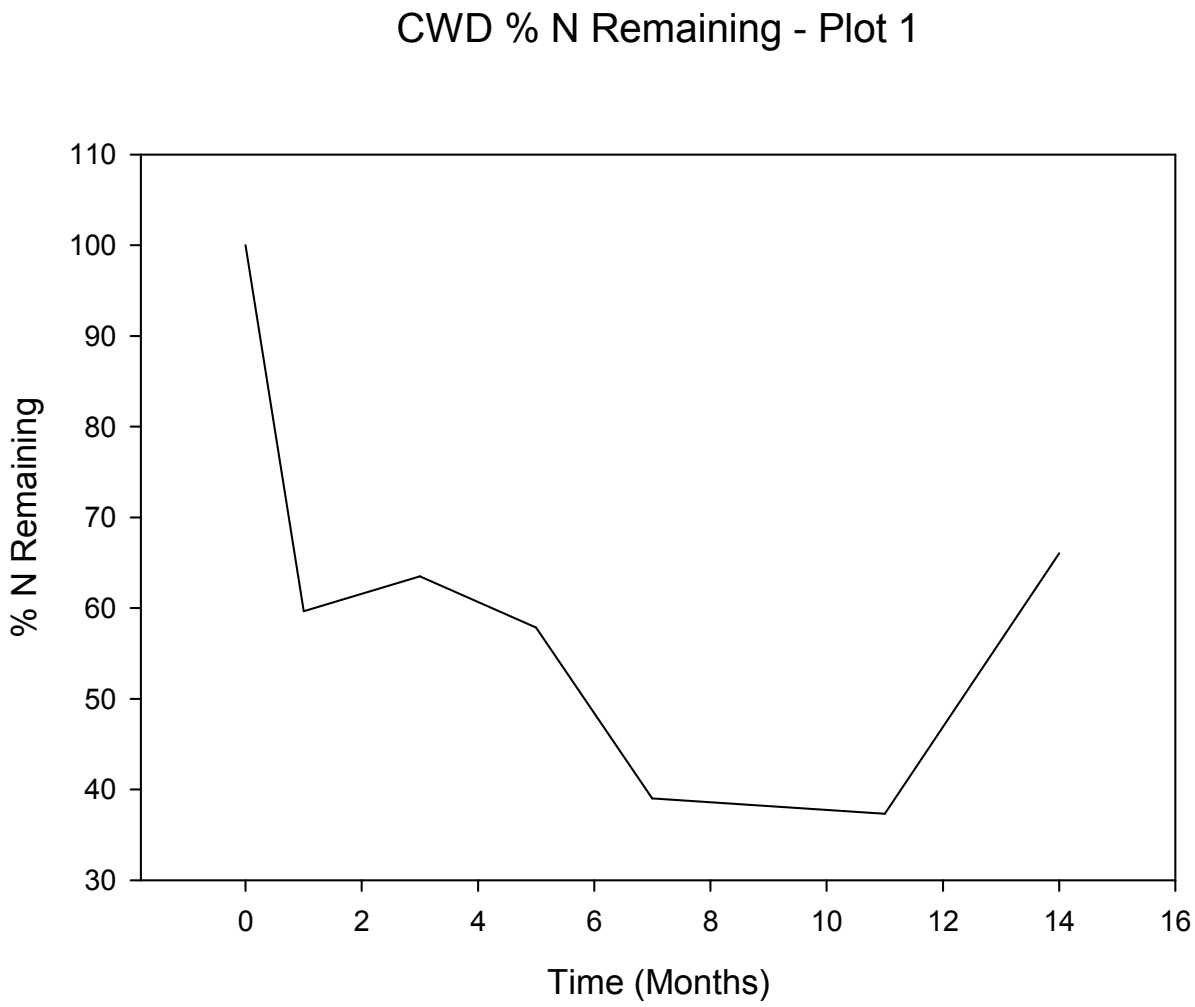

Figure A4.1. CWD percent N remaining up to 14 months for plot 1.

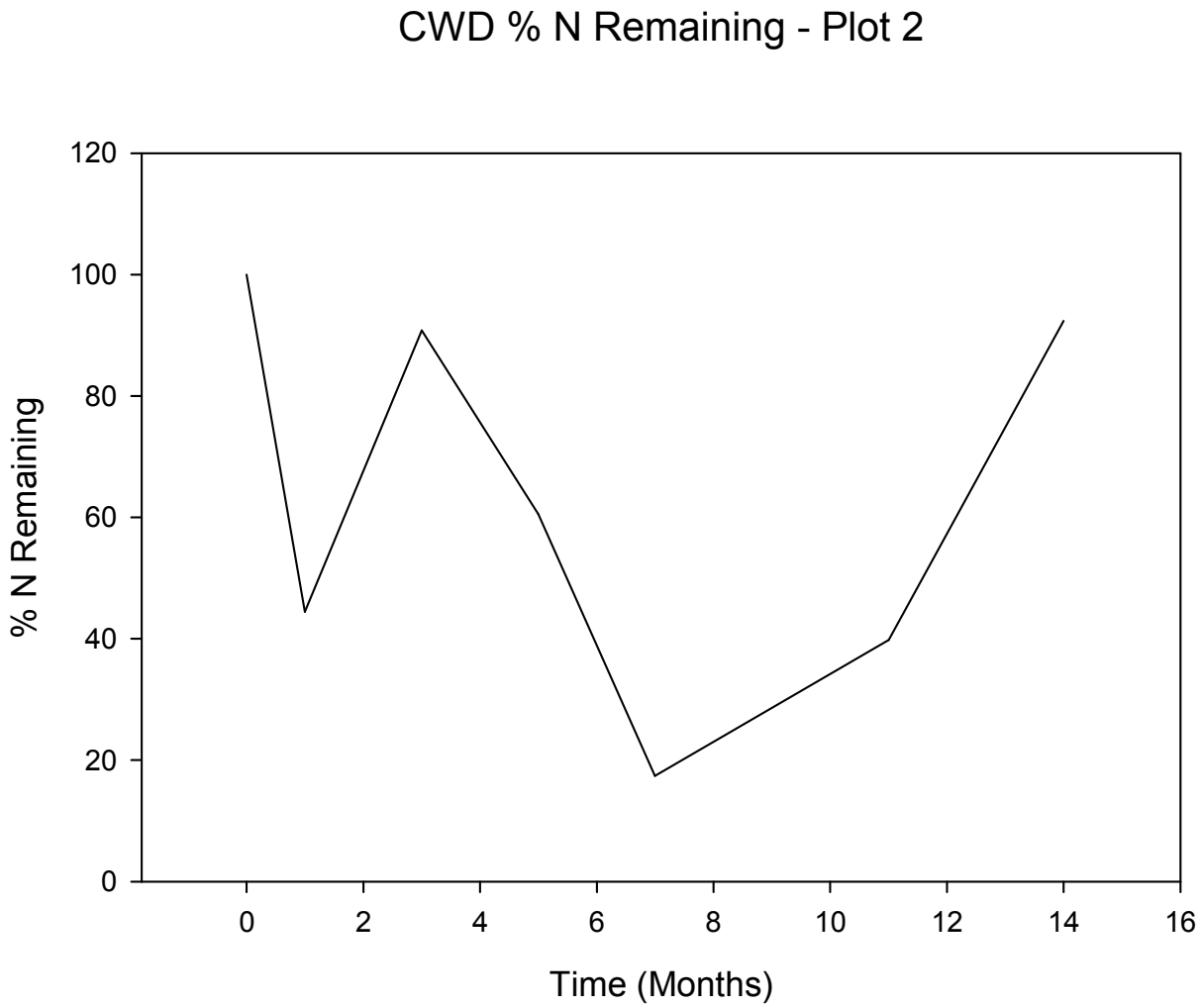

Figure A4.2. CWD percent N remaining up to 14 months for plot 2.

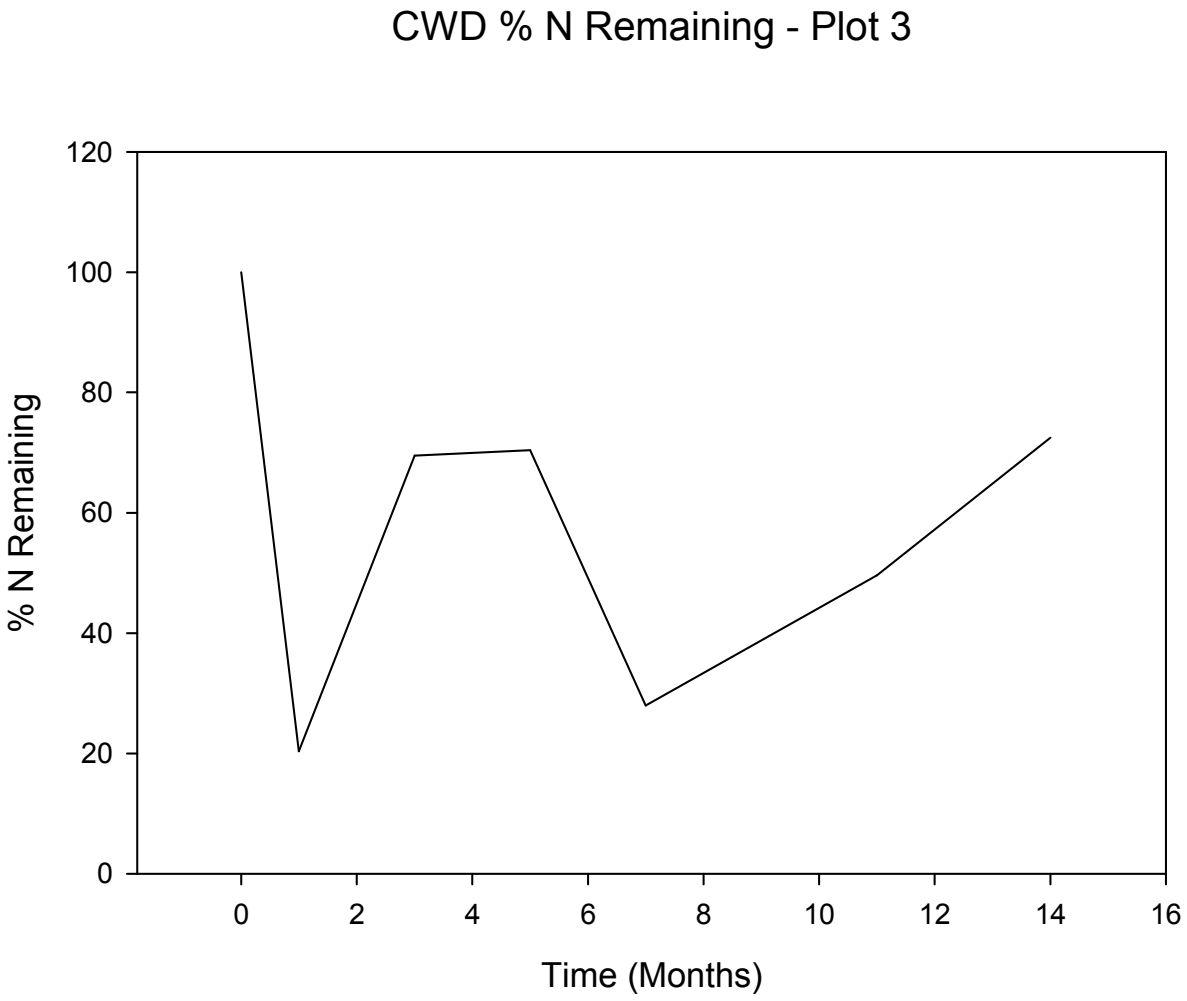

Figure A4.3. CWD percent N remaining up to 14 months for plot 3.

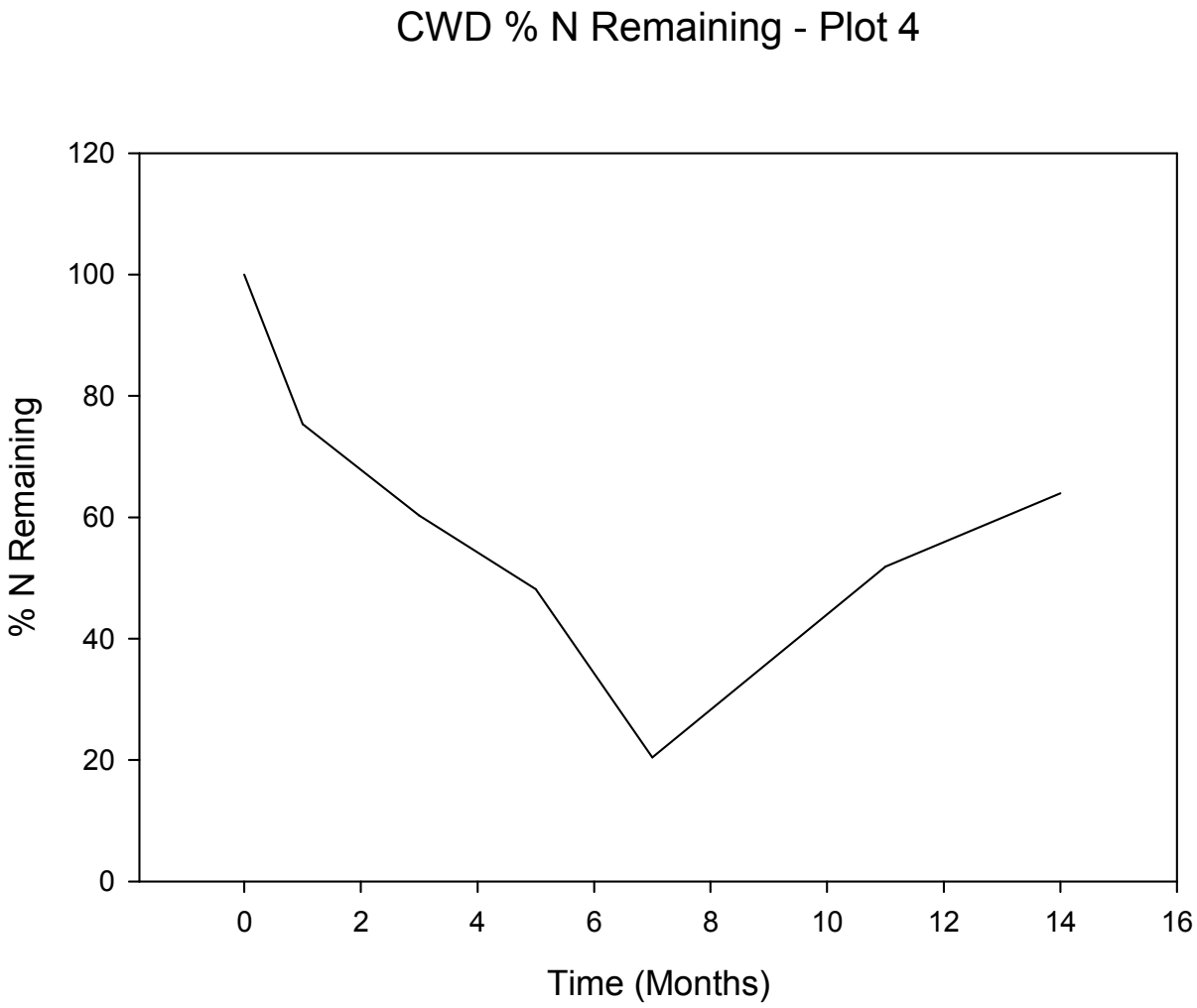

Figure A4.4. CWD percent N remaining up to 14 months for plot 4.

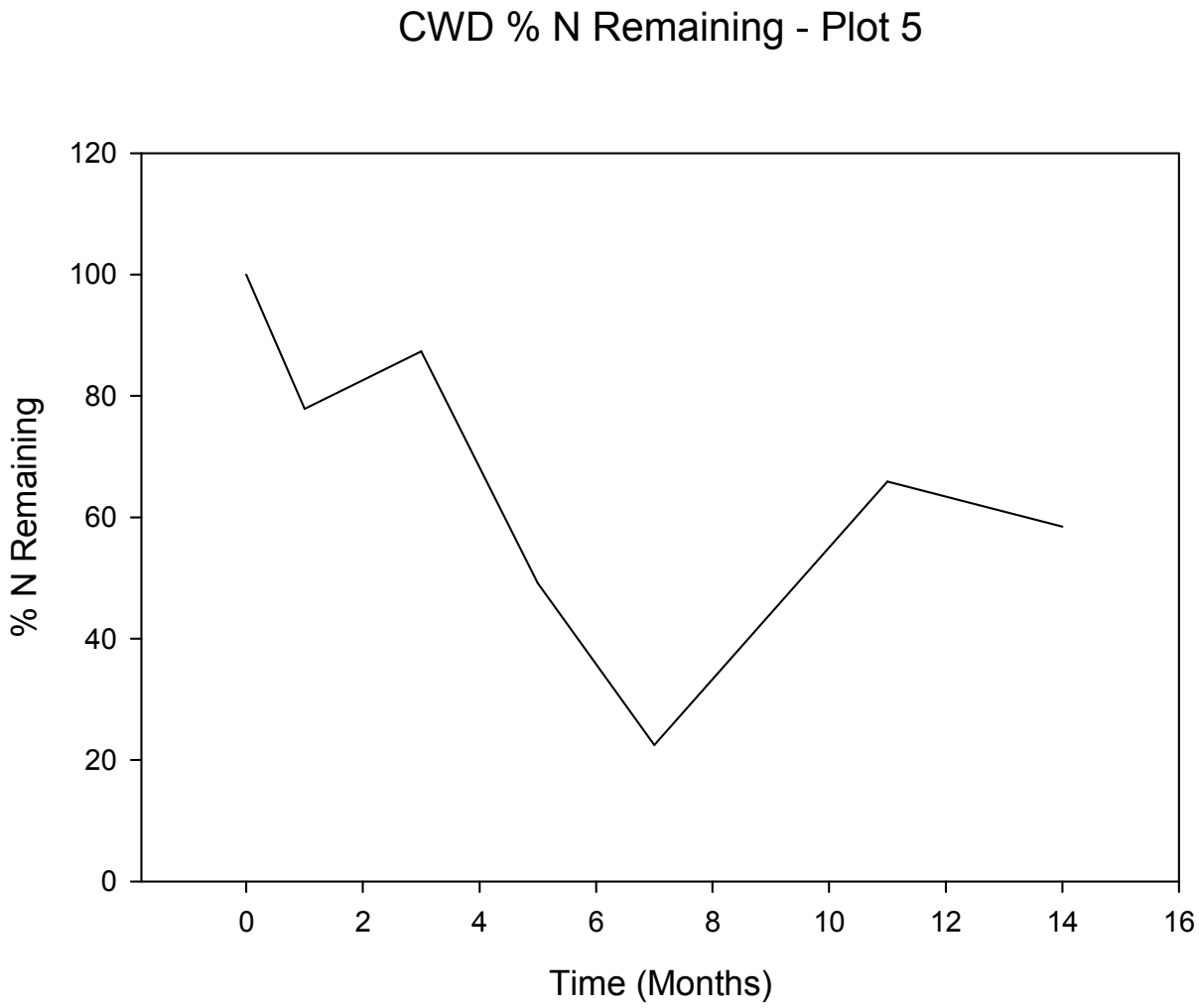

Figure A4.5. CWD percent N remaining up to 14 months for plot 5.

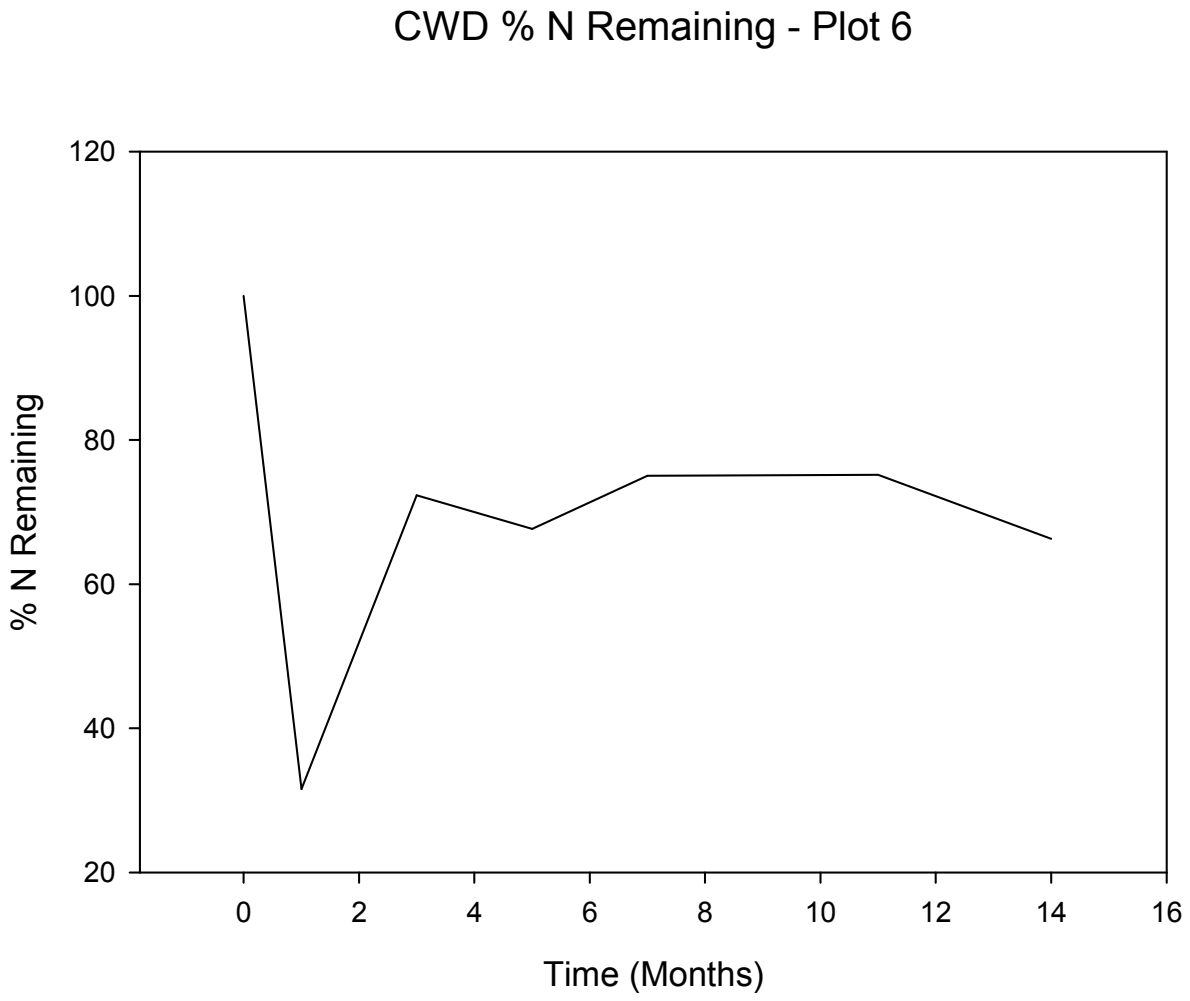

Figure A4.6. CWD percent N remaining up to 14 months for plot 6.

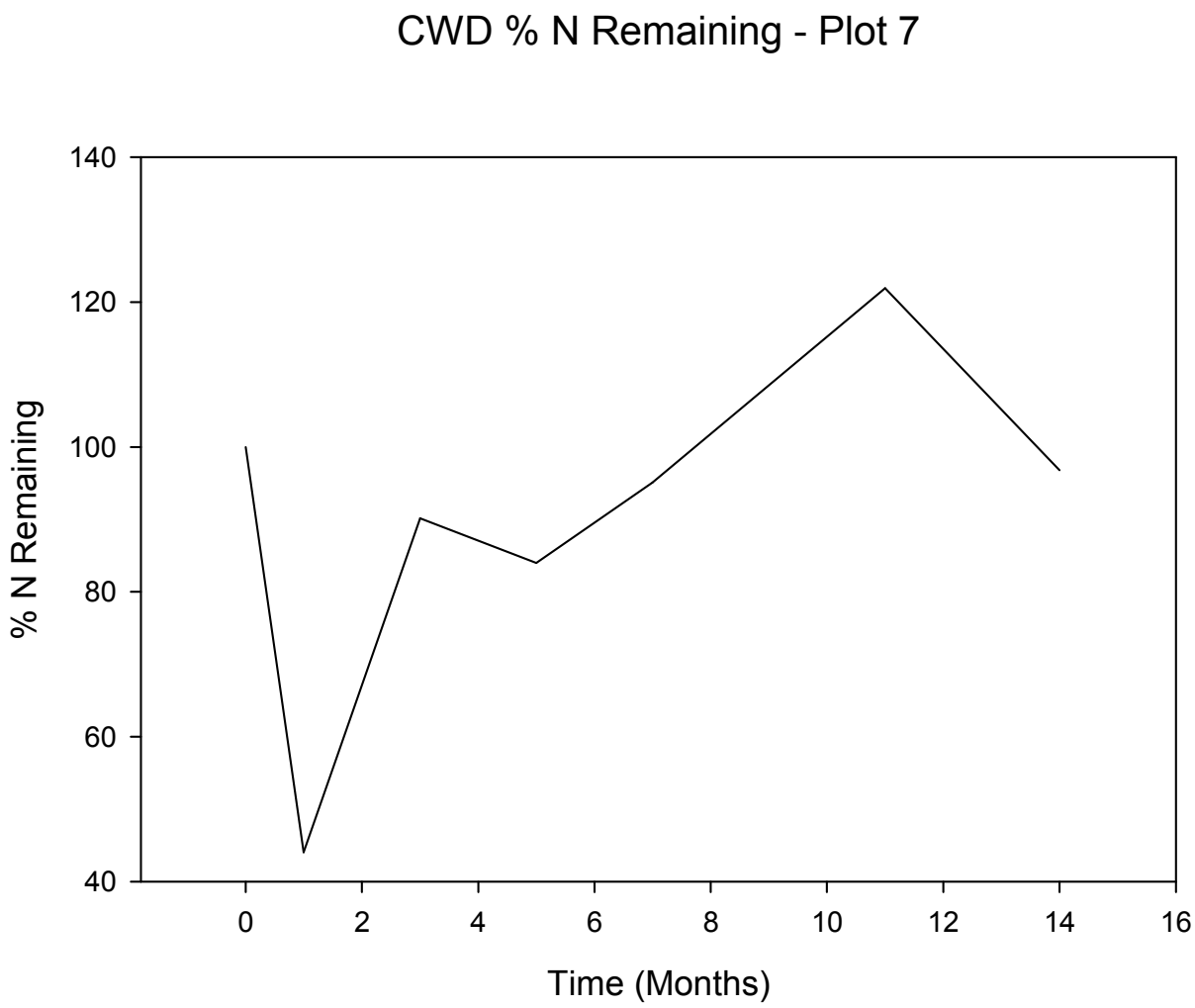

Figure A4.7. CWD percent N remaining up to 14 months for plot 7.

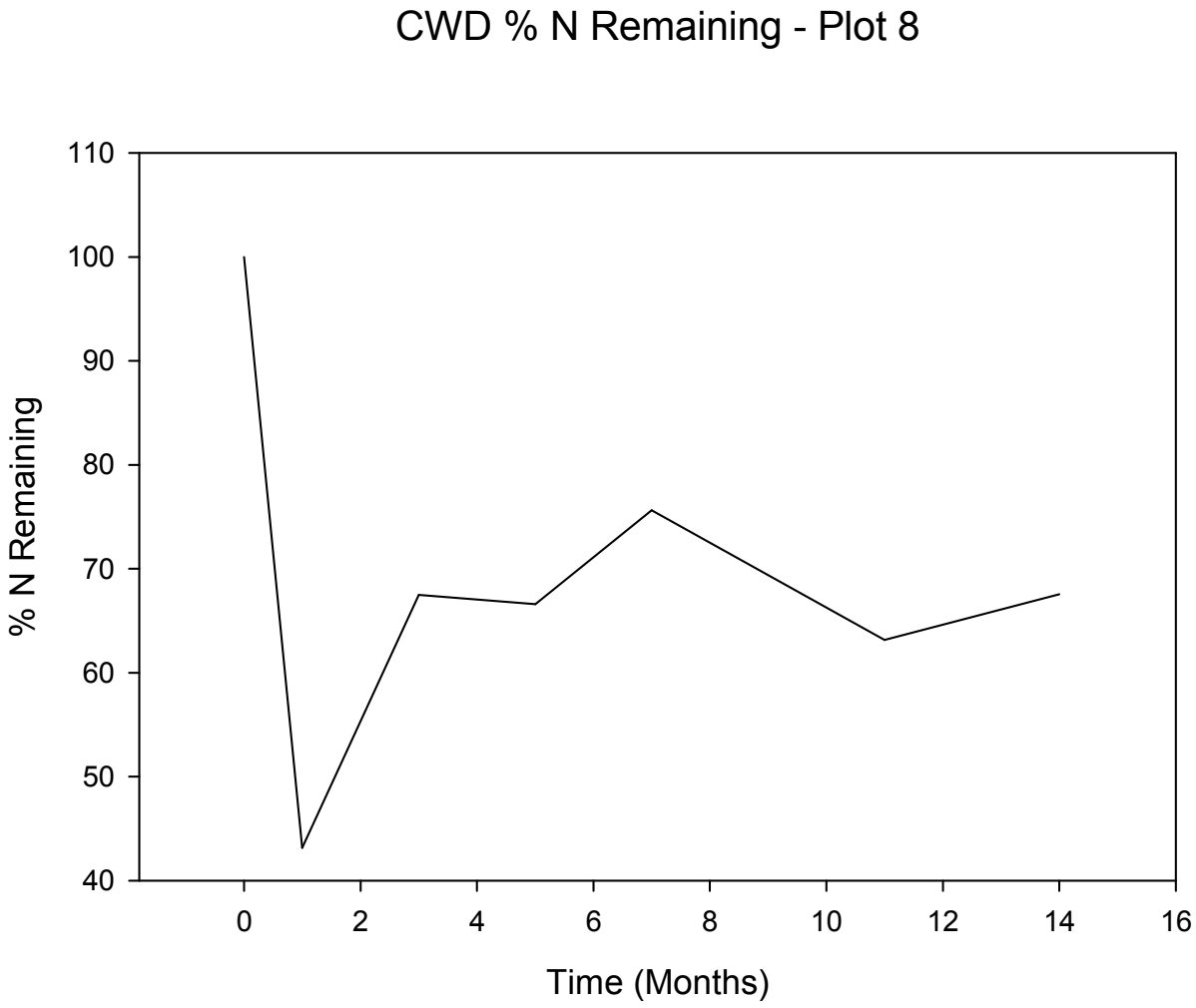

Figure A4.8. CWD percent N remaining up to 14 months for plot 8.

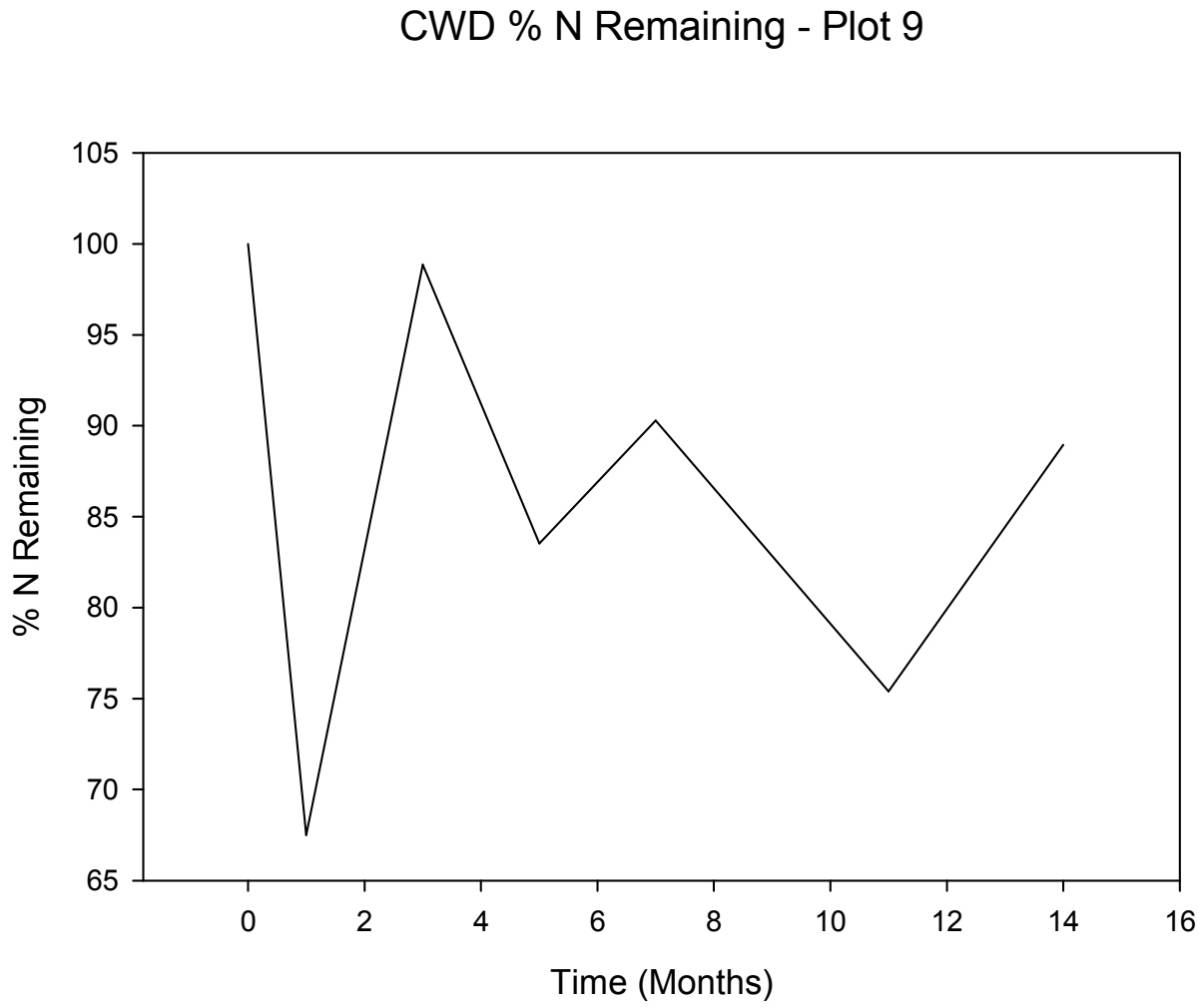

Figure A4.9. CWD percent N remaining up to 14 months for plot 9.

APPENDIX 5: CWD % P REMAINING AT ALL PLOTS TO 14 MONTHS

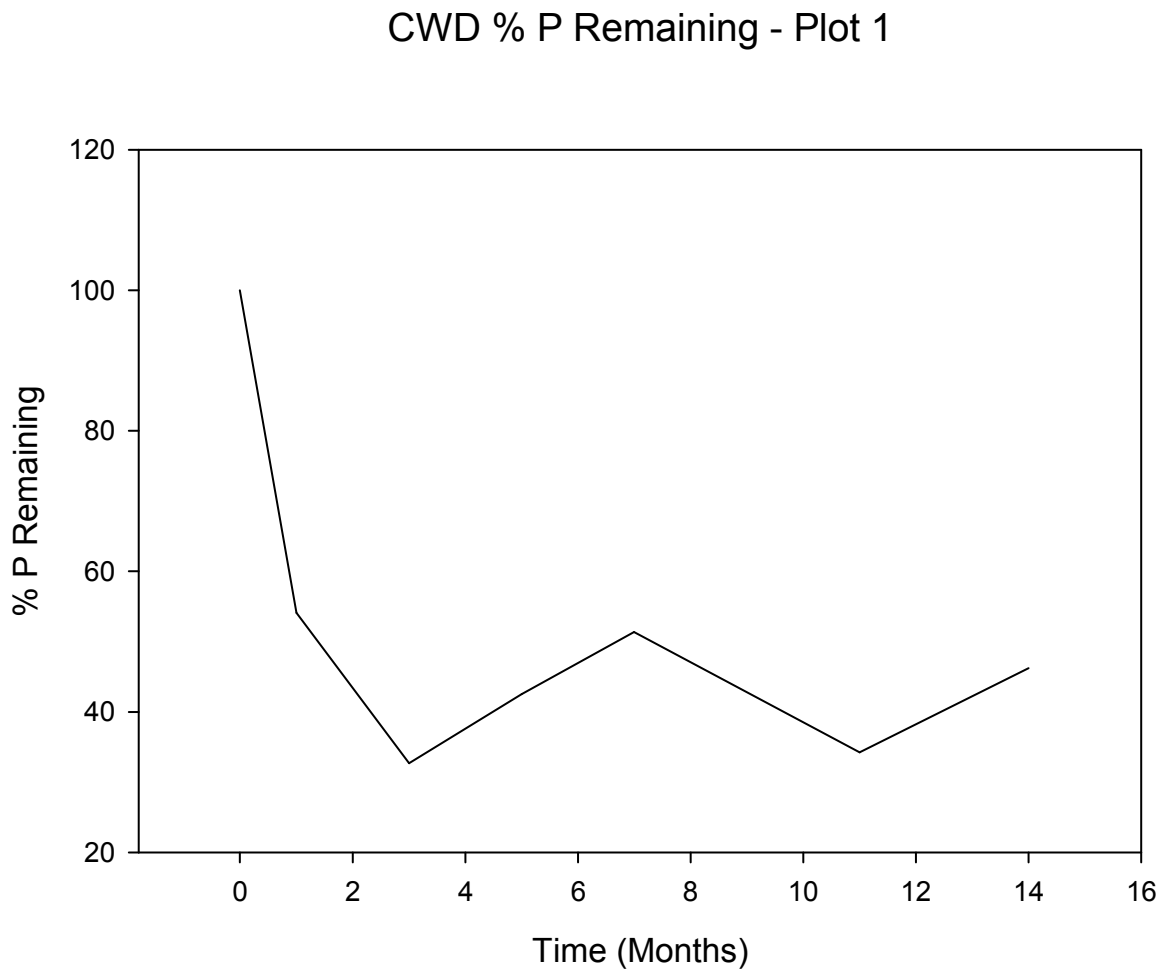

Figure A5.1. CWD percent P remaining up to 14 months for plot 1.

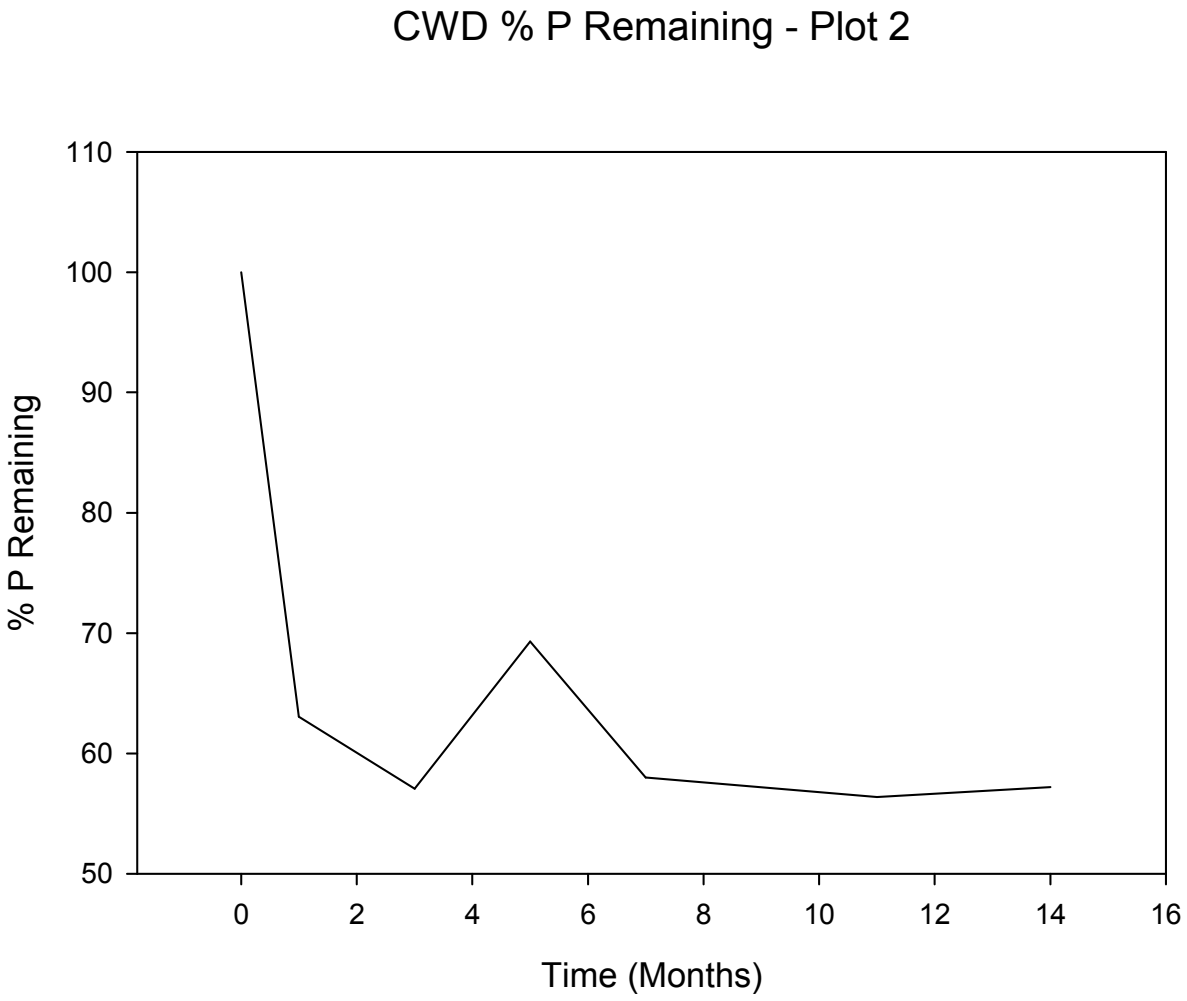

Figure A5.2. CWD percent P remaining up to 14 months for plot 2.

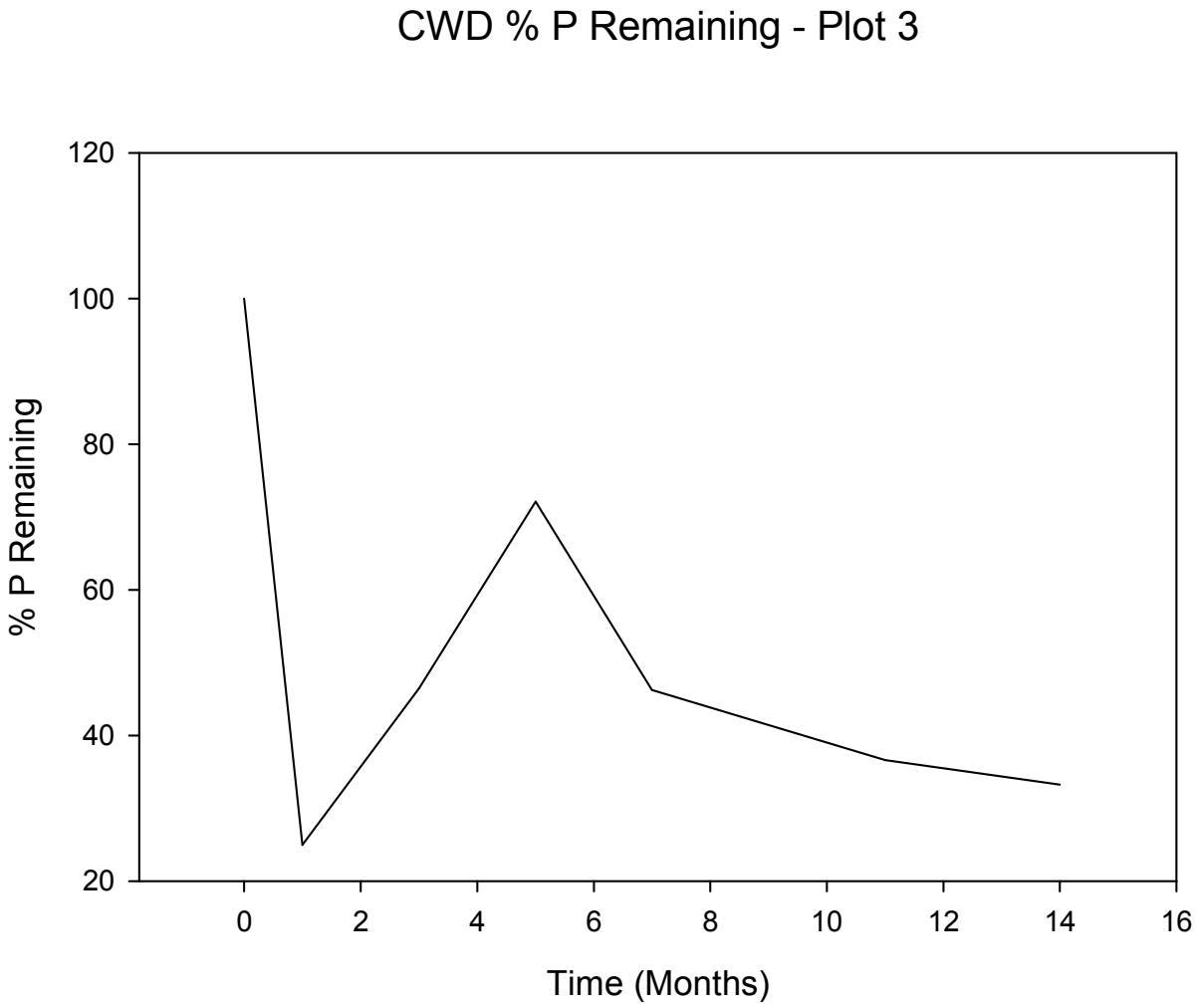

Figure A5.3. CWD percent P remaining up to 14 months for plot 3.

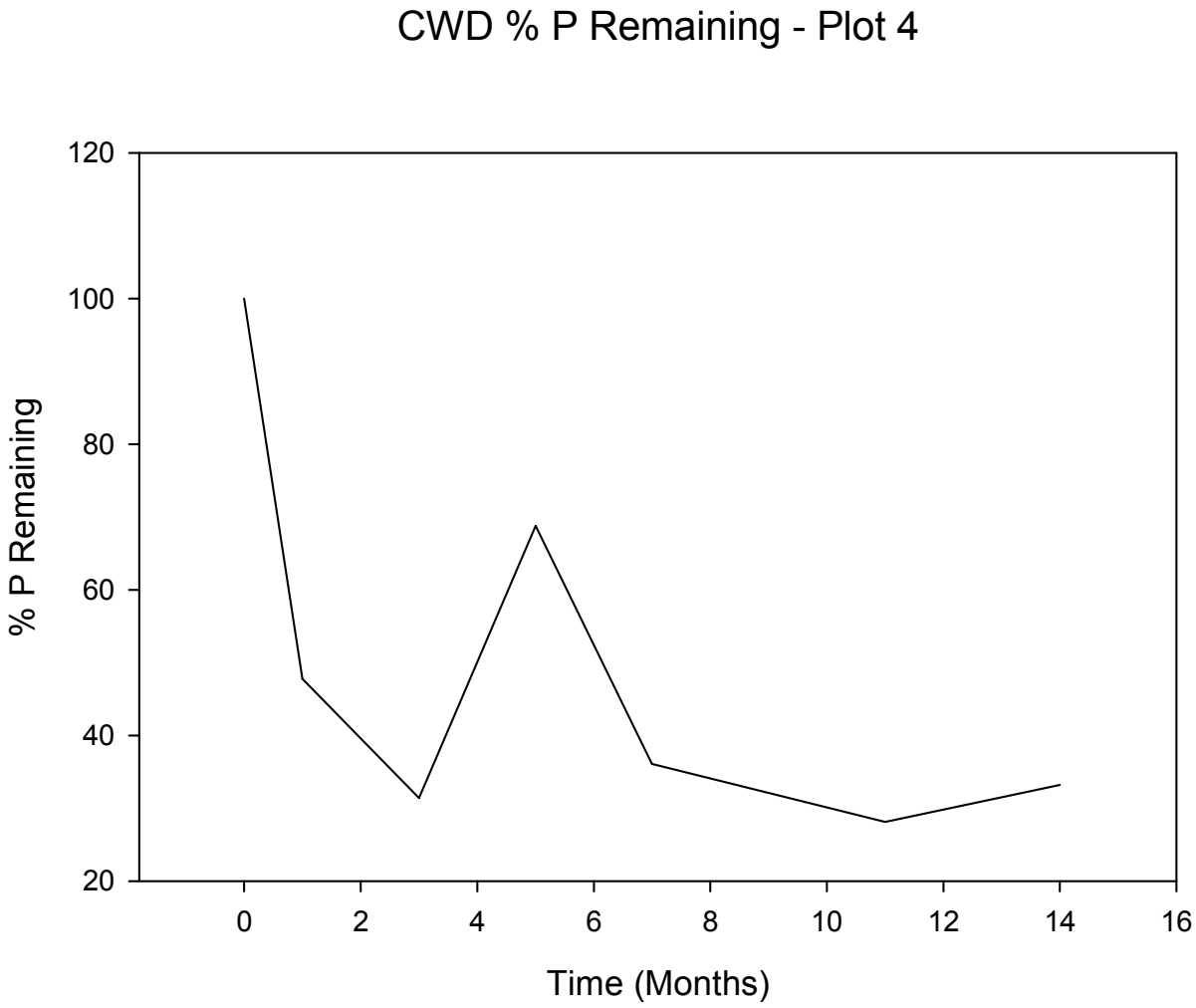

Figure A5.4. CWD percent P remaining up to 14 months for plot 4.

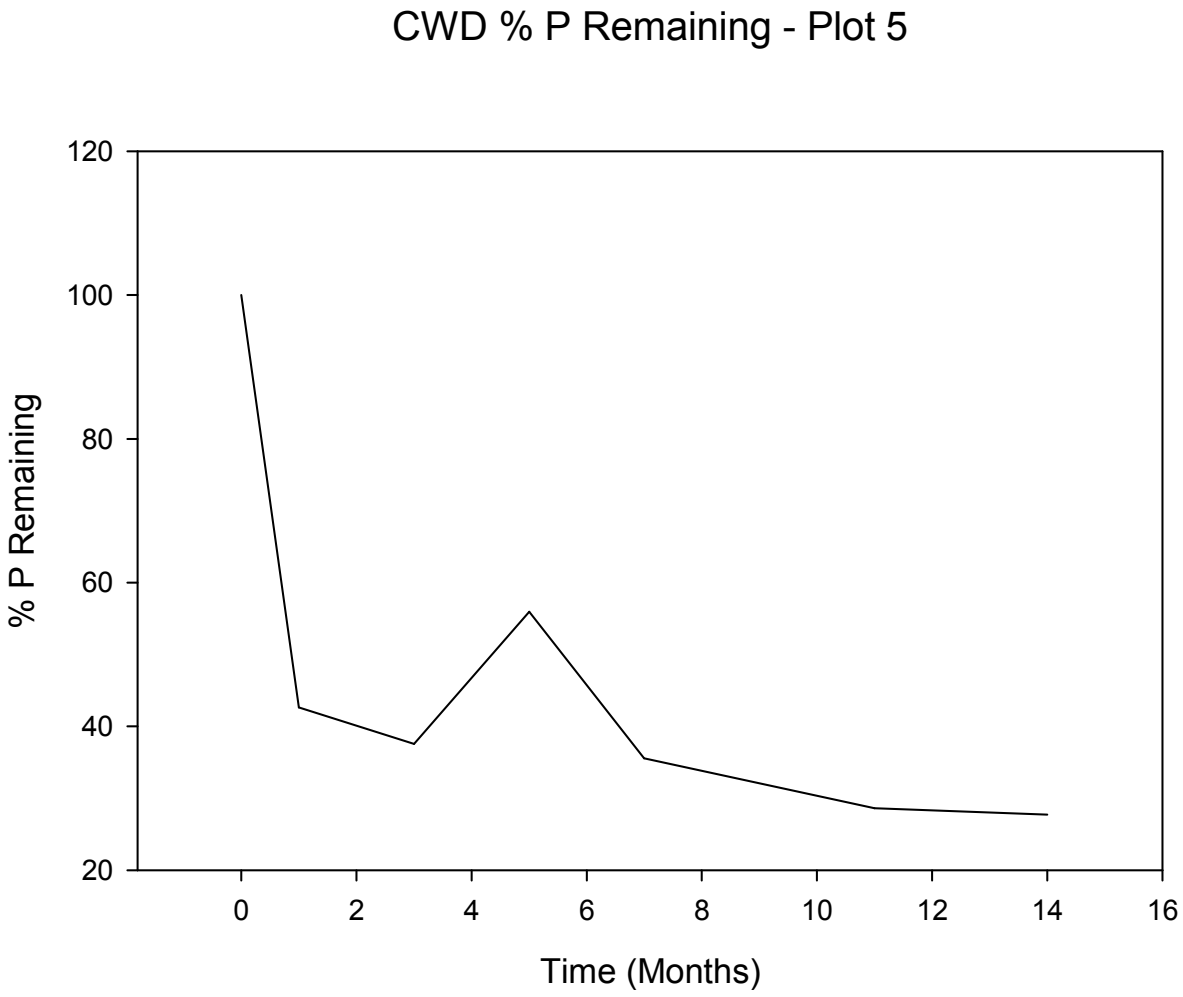

Figure A5.5. CWD percent P remaining up to 14 months for plot 5.

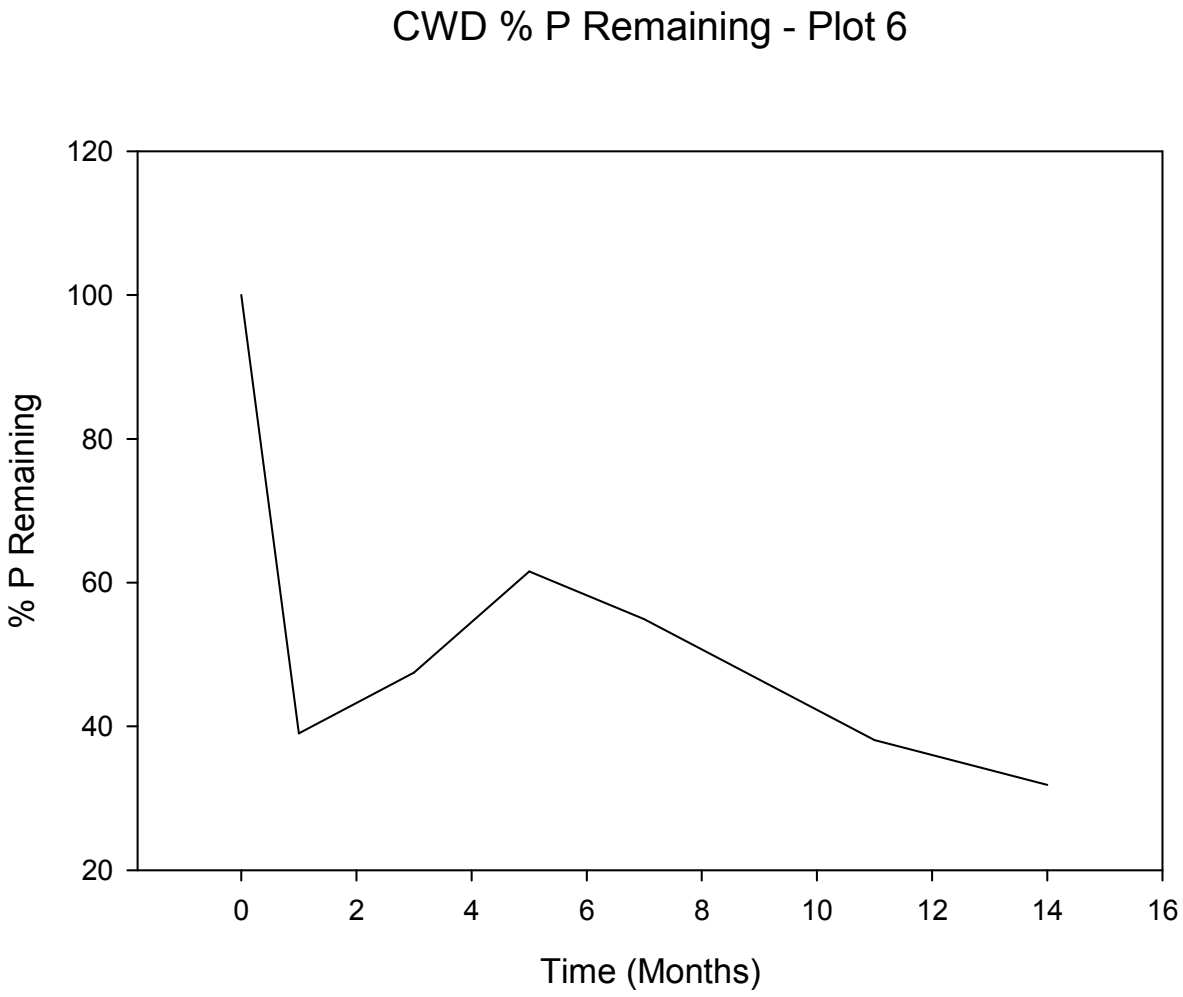

Figure A5.6. CWD percent P remaining up to 14 months for plot 6.

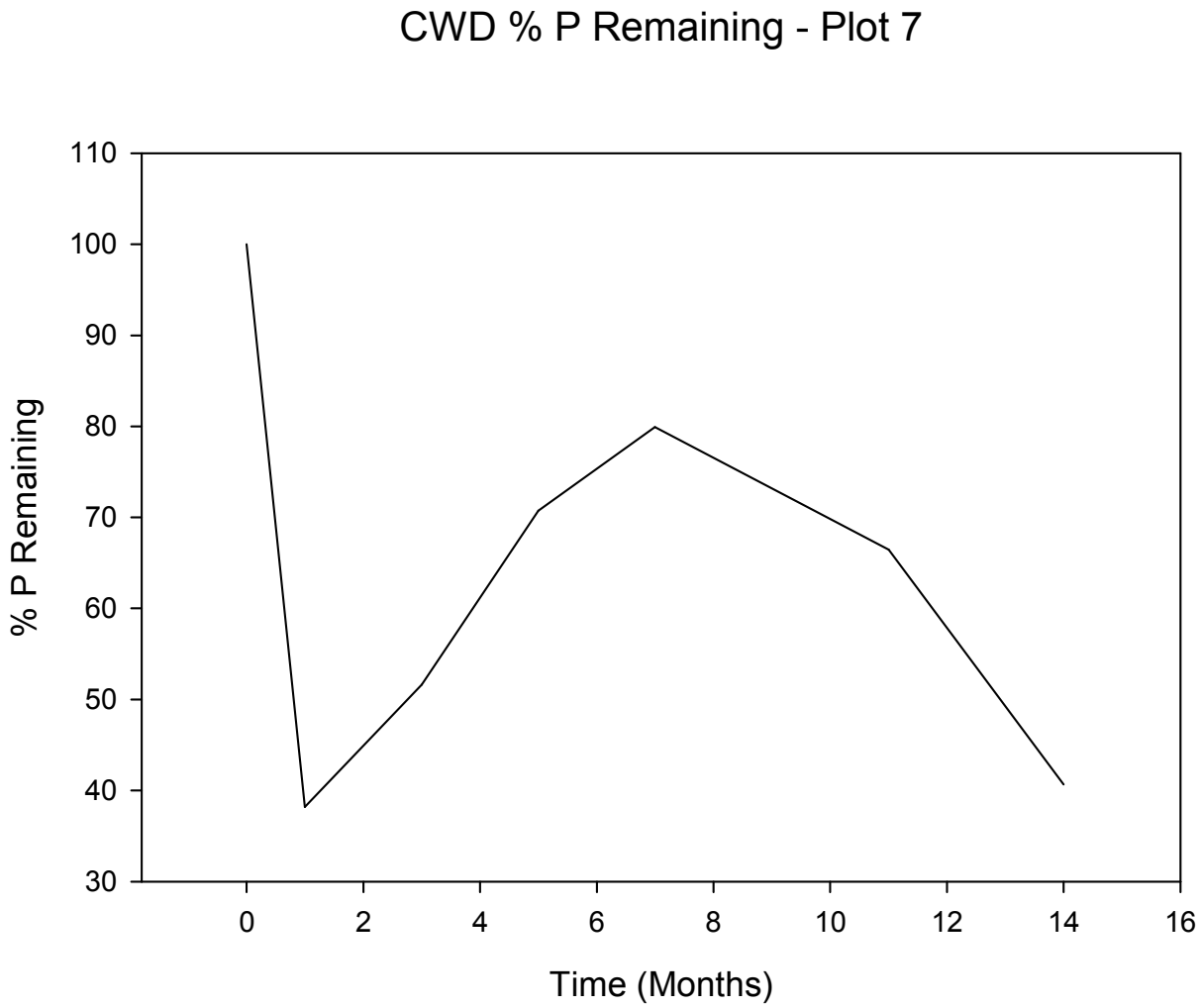

Figure A5.7. CWD percent P remaining up to 14 months for plot 7.

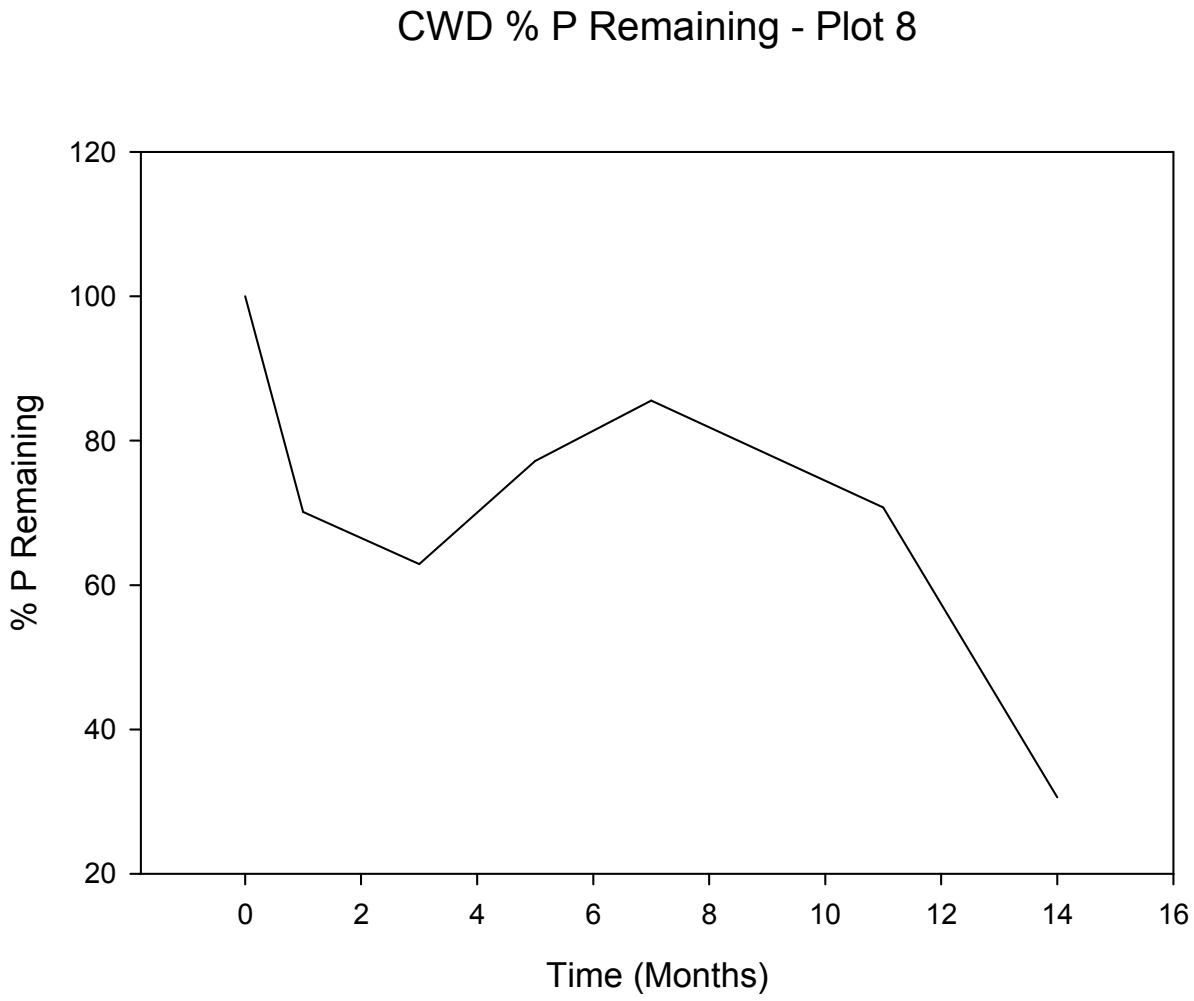

Figure A5.8. CWD percent P remaining up to 14 months for plot 8.

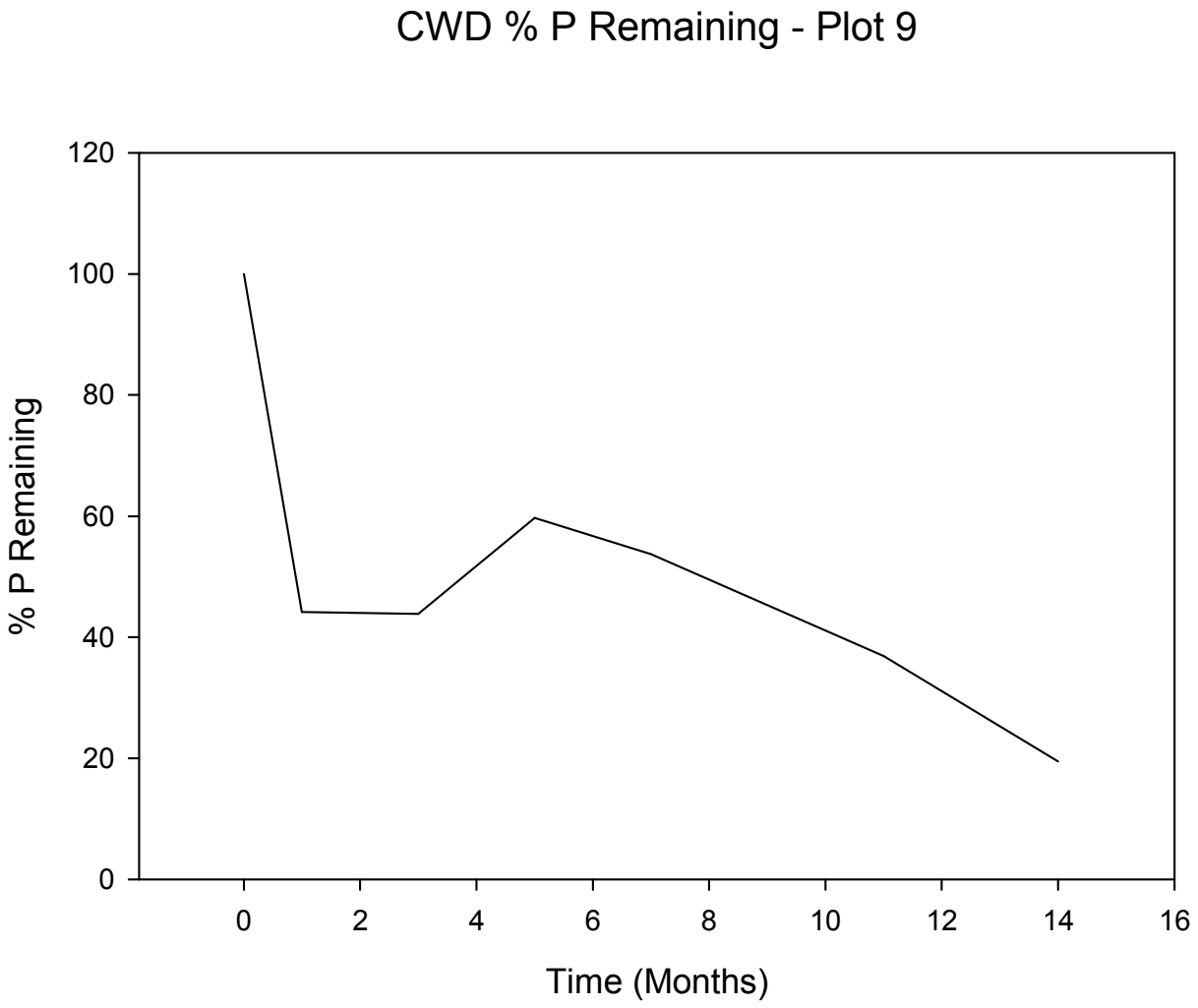

Figure A5.9. CWD percent P remaining up to 14 months for plot 9.

APPENDIX 6: PERCENT MASS (CWD AND CONTROL), C, N, AND P REMAINING FOR ALL PLOTS AND COLLECTIONS.

Table A6.1. Percent mass (CWD and Control), C, N, and P remaining for plot 1. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
1	0	100	100	100	100	100
1	1	98.89	94.85	99.02	59.67	54.07
1	3	99.35	89.2	101.99	63.49	32.66
1	5	92.08	89.55	95.42	57.85	42.52
1	7	91.15	88.38	91.72	39.05	51.37
1	11	90.21	88.42	91.82	37.36	34.22
1	14	84.59	87.18	85.71	66.03	46.2

Table A6.2. Percent mass (CWD and Control), C, N, and P remaining for plot 2. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
2	0	100	100	100	100	100
2	1	95.77	94.45	100.4	44.44	63.06
2	3	96.49	90.21	101.07	90.77	57.08
2	5	91.4	90.24	96.06	60.54	69.3
2	7	90.24	88.24	92.11	17.4	57.99
2	11	87.43	88.6	90.77	39.79	56.39
2	14	82.53	87.69	84.5	92.36	57.21

Table A6.3. Percent mass (CWD and Control), C, N, and P remaining for plot 3. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
3	0	100	100	100	100	100
3	1	97.39	95.97	97.69	20.39	24.97
3	3	95.96	90.57	99.28	69.51	46.47
3	5	93.08	90.13	96.73	70.41	72.11
3	7	92.98	89.64	94.16	28.01	46.23
3	11	92.49	89.07	95.55	49.61	36.62
3	14	87.68	89.54	89.73	72.48	33.25

Table A6.4. Percent mass (CWD and Control), C, N, and P remaining for plot 4. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
4	0	100	100	100	100	100
4	1	91.05	94.97	89.93	75.36	47.78
4	3	92.97	88.55	94.65	60.28	31.38
4	5	88.72	89.46	91.93	48.16	68.79
4	7	89.21	87.23	90.05	20.41	36.08
4	11	84.77	84.67	86.63	51.87	28.12
4	14	80.71	86.19	81.95	63.93	33.2

Table A6.5. Percent mass (CWD and Control), C, N, and P remaining for plot 5. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
5	0	100	100	100	100	100
5	1	99.22	95.32	98.03	77.84	42.65
5	3	92.08	89.77	94.48	87.34	37.56
5	5	90.47	90.06	93.88	49.16	55.95
5	7	90.28	88.29	90.62	22.47	35.56
5	11	85.07	86.08	87.48	65.88	28.62
5	14	78.57	86.48	79.47	58.44	27.72

Table A6.6. Percent mass (CWD and Control), C, N, and P remaining for plot 6. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
6	0	100	100	100	100	100
6	1	97.78	94.97	96.79	31.56	39.05
6	3	95.34	90.16	99.13	72.34	47.5
6	5	95.3	90.94	97.97	67.67	61.56
6	7	92.13	90.05	91.81	75.05	54.89
6	11	89.77	89.44	92.69	75.16	38.09
6	14	88.41	88.92	89.24	66.28	31.83

Table A6.7. Percent mass (CWD and Control), C, N, and P remaining for plot 7. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
7	0	100	100	100	100	100
7	1	98.08	95.61	97.16	44.03	38.19
7	3	98.43	89.55	100.2	90.17	51.64
7	5	94.24	90.68	97.81	83.99	70.73
7	7	93.49	89.5	93.16	95.06	79.92
7	11	91.31	89.5	93.01	121.92	66.44
7	14	91.49	89.7	92.2	96.78	40.66

Table A6.8. Percent mass (CWD and Control), C, N, and P remaining for plot 8. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
8	0	100	100	100	100	100
8	1	98.08	95.87	97.41	43.16	70.14
8	3	95.23	90.77	98.42	67.5	62.91
8	5	95.03	90.29	98.21	66.59	77.18
8	7	91.74	90	92.15	75.63	85.56
8	11	87.1	89.61	89.65	63.16	70.76
8	14	86.57	88.9	88.05	67.55	30.6

Table A6.9. Percent mass (CWD and Control), C, N, and P remaining for plot 9. Time is in months.

		%Mass Remaining				
Plot	Time (Months)	CWD	Control	% C	% N	% P
9	0	100	100	100	100	100
9	1	97.34	95.67	98.38	67.5	44.14
9	3	93.82	90.15	97.39	98.84	43.82
9	5	90.2	90.78	92.03	83.53	59.72
9	7	91.53	89.18	92.44	90.29	53.7
9	11	79.22	87.96	81.84	75.39	36.92
9	14	58.76	87.3	58.16	88.95	19.5