

MANAGEMENT EFFECTS ON HERBAGE RESPONSES, SIZE OF NUTRIENT POOLS,
AND LITTER DYNAMICS IN GRAZED 'TIFTON 85' BERMUDAGRASS (*CYNODON*
SPP.) PASTURES

By

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To my parents and wife, for all their support and encouragement through the year.

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Abstract of Dissertation Presented to the Graduate School
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SPP.) PASTURES

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Appropriate management is important to ensure efficient nutrient cycling and pasture sustainability. Two experiments were conducted to determine the effect of management strategies of Tifton 85 bermudagrass (*Cynodon* spp.) pastures on herbage characteristics, size of important nutrient pools, and litter dynamics. In Experiment 1, herbage accumulation, nutritive value, and persistence responses were measured from nine treatments that included all combinations of three post-graze stubble heights (SH; 8, 16, and 24 cm) and three lengths of grazing cycle (GC, <10h grazing time plus rest period; 14, 21, and 28 d). Pastures were fertilized with 250 kg N ha⁻¹ yr⁻¹. In Experiment 2, effects of N fertilization (50, 150, and 250 kg N ha⁻¹) and SH (8, 16, and 24 cm) on size of nutrient pools and plant litter dynamics were measured on rotationally stocked Tifton 85 bermudagrass pastures. Experiment 1 showed that Tifton 85 bermudagrass is tolerant of a wide range of grazing management, making it a good candidate for grazed grasslands in warm climates. Greatest herbage accumulation was associated with close grazing (8-cm SH) followed by a relatively long rest period (28 d) or with lax grazing (24-cm SH) followed by a short GC (14 d). Persistence data showed that a 24-cm SH should not be used because of greater incidence of stand loss. If the 24-cm SH is ruled out, then grazing to 8-cm SH

every 28 d is recommended to maximize herbage accumulation, or to 16-cm SH every 14 to 21 d for greater nutritive value without negative impact on persistence or a major reduction in herbage accumulation. Nutrient pools in live herbage, plant litter, root-rhizome, and soil pools increased with taller SH, while increasing N fertilization increased N accumulation in live herbage, plant litter, and root-rhizome pools, but did not affect N content in soil. Carbon content in live herbage and soil pools increased with increasing N fertilizer rate. These data suggest that lower grazing intensity (i.e., taller stubble heights) and greater N fertilization increase C sequestration. Thus, grassland management has potential to increase C sequestration in soils, but the changes are likely to be relatively small. Considering litter dynamics, increasing SH increased existing litter mass and litter mass deposition rate. Nitrogen fertilization had little effect on litter mass, but it had an important effect on litter quality and decomposition. In grasslands in which the proportion of herbage mass consumed is low, grass litter plays a major role in nutrient dynamics, particularly nutrient immobilization and slowing release for plant uptake. Immobilization can have negative effects on grassland productivity and persistence by reducing quantity of nutrients available for plant growth. High levels of N fertilization are thought to increase litter quality and nutrient release, but based on results with Tifton 85 bermudagrass, there was little difference in short-term nutrient contribution from litter of low- and high-input pastures. Although litter quality is greater under high N inputs, it remains sufficiently low that nutrient immobilization continues to occur. In conclusion, Tifton 85 bermudagrass thrives under a wide range of grazing management allowing producers to choose a strategy that fits their objectives. Pasture management has a significant but relatively small effect on C sequestration, but the effect of grazing and fertilization on litter mass and decomposition is significant and can impact long-term pasture sustainability.

CHAPTER 1 INTRODUCTION

Grasslands are one of the world's major ecosystems, and comprise about 40% of the earth's land surface (Scurlock et al., 1998). In the USA, the grassland area is approximately 336 million hectares, nearly 37% of total land area (Schuman et al., 2002). Grassland ecosystems play numerous important roles. They are the backbone of many livestock industries, supplying forage for animals and indirectly, food for human consumption. Grasslands provide a broad array of ecosystem services. They can act as a significant carbon (C) sink, and C sequestration by grasslands is often mentioned as one option for reducing atmospheric CO₂ concentration (Sanderson et al., 2004). Grasslands also protect soil from erosion, provide food and habitat for wildlife, and legumes fix atmospheric N₂ (Wedin and Pastor, 1993; Sanderson et al., 2004).

Rapidly increasing human populations and their subsequent encroachment into agricultural lands are reducing grassland area globally. In addition, improper grassland management is occurring in many regions, decreasing the vigor of grassland species leading to degradation and further loss of grassland area (Boddey et al., 2004). As a result, management practices that enable sustainable grassland ecosystems are of increasing importance worldwide. Sustainable systems are characterized by a balance among species and the efficient cycling of nutrients, water, and energy (Kemp et al., 2001, 2002; Weiner, 2003). From a systems perspective, the products (including energy and nutrients) removed from grassland ecosystems must be less than the internal flows of energy and nutrients, and in order to sustain production the ecosystem needs to be managed optimally (Weiner, 2003). Many components (soils, plants, animals, and the abiotic environment) are part of this system and the impact of management on the interaction of these components affects grassland sustainability (Burke et al., 1989; Hobbie, 1992; Frank et al., 1995; Drewry et al., 2008).

The primary focus of the research reported in this dissertation is the effect of management on nutrient pools and fluxes in grazed grassland, and specifically planted pastureland. Management plays a major role in influencing grassland agronomic and environmental performance (Jarvis et al., 1995; Follett, 2001; Lal, 2002; Bustamante et al., 2006). In low-input pasture systems, efficient management and cycling of scarce and expensive nutrients are inextricably linked to economic and sustained livestock production (Boddey et al., 2004). In high-input systems, nutrient management has a key role in avoiding excessive loss of nutrients to the environment. Vlek et al. (1997) have called for improved recycling of soil nutrients to maintain the nutrient balance in agriculturally managed tropical soils, so that producers can become less dependent on external inputs. Today, nutrient management under grazing has evolved from optimizing manure and fertilizer applications for high herbage yield to a focus on improving nutrient-use efficiency at the farm level while maintaining productivity (Oenema et al., 2006). Whole-farm nutrient budgets are becoming increasingly accepted as a way of describing nutrient flows within farming systems (Stockdale et al., 2001). The ultimate nutrient-management challenge is to achieve a better balance between nutrient inputs and crop requirements. A successful nutrient management plan begins with an understanding of how nutrients cycle (Beegle et al., 2000). To understand nutrient fluxes among different nutrient pools is an important step in developing optimal management strategies.

In grasslands, nutrients released from senescent plant litter, animal excreta, fertilizer, and soil are taken up by plants and are subsequently transferred to grazing animals. Plant species provide feedback to nutrient cycling within the grassland ecosystem directly through uptake, use, and loss of nutrients, and indirectly by influencing microbial activity and herbivore activity (Hobbie, 1992). Khalid et al. (2007) reported that the presence of plants significantly increases

the size of a number of nutrient pools (e.g., C and N) in comparison to the unplanted soil. The behavior of animals changes the type and density of tissues present to carry out photosynthetic and respiratory functions, the amount of plant litter deposition, soil condition, and the sizes of the nutrient pools present in the grassland (Coleman, 1992; Holland et al., 1992; Bari et al., 1993; Frank et al., 1998; Rezende et al., 1999). These changes are due in large part to management practices that affect animal behavior and plant characteristics. Much research has documented the effect of management strategies on grassland ecosystems. For instance, grazing management affects plant community structure (Frank et al., 1995; Schuman et al., 1999), soil chemical and physical properties (Frank et al., 1995), the distribution and cycling of nutrients (Schuman et al., 1999; Wilsey et al., 2002), and grassland productivity and environmental quality (Mathews et al., 1994a, 2001; Franzluebbers et al., 2004a ,2004b).

Grazed tropical pastures are generally low-input systems, often receiving low rates of inorganic fertilizer. Nutrients in these systems are primarily cycling in plant litter and animal excreta (Thomas, 1992; Dubeux et al., 2007). Plant litter plays a large role in nutrient cycling in many warm-climate grasslands because grasslands are often underutilized during the rainy season to stockpile forage for the dry season, resulting in significant senescence of herbage. The accumulation and decomposition of plant litter have long been considered complex and important factors controlling vegetation structure (Facelli and Pickett, 1991), herbivory, hydrology, and energy budgets (Weltzin et al., 2005), as well as influencing herbage biomass, herbage nutrient concentration, and biochemical properties of soils (Dutta et al., 2001). Therefore, understanding the dynamics of litter accumulation, litter mass, and litter decomposition is an important step in managing nutrient flows in warm-climate grasslands. Grazing management has been shown to influence litter accumulation and depletion (Naeth et

al., 1991), its rate of decomposition, litter quality (Shariff et al., 1994; Seneviratne, 2000), and nutrient release from litter (Dubeux et al., 2006a), but there are relatively few studies of nutrient pools and litter dynamics in planted warm-climate grasslands.

Assessing the impact of grazing management practices on nutrient cycling within a pasture system and the dynamics of plant litter are very important to making better use of the pasture resource. Recent studies by Dubeux et al. (2006a and b) have demonstrated the importance of litter as a buffer to minimize nutrient loss in intensively managed bahiagrass (*Paspalum notatum* Flüggé) pastures, and as a potential contributor to pasture degradation in extensively managed swards by virtue of nutrient immobilization. The studies included in this dissertation project broaden the work of Dubeux et al. (2006a and 2006b) by including ‘Tifton 85’ bermudagrass (*Cynodon* sp.), another important species in planted grasslands in Florida, as well as a greater range of grazing strategies (a range of rotational stocking methods while Dubeux et al. evaluated continuous stocking only). This research will inform efforts to build sustainable grazing systems, and develop a strong understanding of the principles behind good grazing management.

The bermudagrass hybrid studied, Tifton 85, was released by USDA and Dr. Glenn Burton in 1992 (Burton et al., 1993a). It has become widely grown for hay and grazed pasture in the southern USA and in tropical and subtropical countries. When compared with other bermudagrasses, Tifton 85 has higher digestible dry matter yield, greater in vitro digestible dry matter concentration, higher digestible neutral detergent fiber, and lower concentrations of lignin and ether-linked ferulic acid (Hill et al., 1993, 1996; Mandebvu et al., 1998). It is important to clearly define the effects of grazing and nutrient management on nutrient dynamics and plant responses of Tifton 85 bermudagrass pastures.

To achieve this goal, experiments were conducted with the objectives of i) determining the effect of grazing intensity and frequency on herbage accumulation, nutritive value, and stand persistence of Tifton 85 bermudagrass pastures; ii) evaluating the size of the most important nutrient pools in Tifton 85 pastures at different times of the year as affected by N fertilization and intensity of defoliation; and iii) quantifying litter production, litter decomposition, and nutrient release from litter in Tifton 85 bermudagrass pastures managed at different intensities.

This research was conducted during the grazing seasons of 2006, 2007, and 2008. Information gathered in these studies will contribute to improved producer management practices, enable lessened detrimental environmental impact of grassland agriculture, and provide a data set that will contribute to whole-farm nutrient budget modeling of nutrient dynamics of grazed grasslands.

CHAPTER 2 LITERATURE REVIEW

Bermudagrass

Bermudagrass [*Cynodon dactylon* (L.) Pers.] is one of the important C₄ perennial grasses used for pasture and hay production in warm climates. In the USA, bermudagrass is grown on approximately 12 million ha and is the most widely used perennial forage in the southern states (Redfearn and Nelson, 2003). It is grown widely in tropical and subtropical regions throughout the world including Africa, Asia, Australia, and the Americas. The popularity of bermudagrass is due to ease of establishment, high biomass production potential, and palatability. Bermudagrass is generally more tolerant of heavy grazing than stargrass (*Cynodon nlemfuensis* Vanderyst). Bermudagrass has rhizomes and associated protected bud sites and reserve storage, while stargrass relies on stem bases and stolons for reserve storage, plant parts that can be removed under frequent, close defoliation (Pitman, 1991). Bermudagrass requires significant soil nutrient inputs to perform at optimal levels and persist long term. Thus, as the cost of N fertilizer increases, it is important to consider the sustainability of current production systems using bermudagrass.

Origin and Characteristics of ‘Tifton 85’

‘Tifton 85’ bermudagrass (*Cynodon* spp.), developed by Dr. Glen Burton (Burton et al., 1993a), is a hybrid produced from the crossing of a South African bermudagrass (PI290884) and ‘Tifton 68’ stargrass, a very highly digestible but cold susceptible hybrid. Tifton 85 is a sterile pentaploid ($2n=5x=45$). It has larger stems and broader leaves than most other bermudagrass cultivars (Burton et al., 1993a). Tifton 85 doesn’t produce seeds, and it is propagated by above-ground stems or below-ground rhizomes. Tifton 85 has much greater cold tolerance than its

parent Tifton 68. Burton et al. (1993b) reported that Tifton 85 survived temperatures as low as -16°C in the southeastern USA.

Tifton 85 is more productive and digestible than most other bermudagrass cultivars including 'Coastal', 'Tifton 44', and 'Tifton 78' (Burton et al., 1993a; Hill et al., 1993; Mandebvu et al., 1999). Hill et al. (1993) reported Tifton 85 produced an average of 26% more dry matter (DM) and was 11% more digestible than Coastal bermudagrass in a 3-yr trial in Georgia. They found that steer (*Bos* sp.) grazing days per hectare were 38% higher and gain per hectare was 46% higher for Tifton 85 than for Tifton 78. Sollenberger et al. (1995) compared Tifton 85 to 'Florakirk' bermudagrass. Tifton 85 had a longer grazing season (160 vs. 141 d), higher average stocking rate (8 vs. 5.8 heifers ha⁻¹), and greater gain per hectare (652 vs. 447 kg). Fike et al. (2003) found that lactating dairy cows fed supplement while grazing Tifton 85 produced 61% more milk per unit land area when stocking rate was 10 vs. 7.5 cows ha⁻¹ (119 vs. 80 kg ha⁻¹ d⁻¹, respectively), illustrating the high productivity and nutritive value of Tifton 85.

Due to its relatively high nutritive value, Tifton 85 also can be used for grazing by early weaned calves (Vendramini et al., 2007). Calves gained 0.6 to 0.7 kg d⁻¹ during summer when grazing 14-d regrowth of Tifton 85 bermudagrass and receiving concentrate supplement at a rate of 15 g kg⁻¹ of body weight (BW) d⁻¹. The high nutritive value of Tifton 85 can be attributed in part to relatively low concentrations of ether-linked ferulic acid and decreased ether bonding in lignin, which result in greater cell wall and total forage digestion (Mandebvu et al., 1999; Hill et al., 2001a). For these reasons, Tifton 85 bermudagrass is valued as forage for grazing livestock and for hay production in warm climate areas.

Tifton 85 Response to N Fertilization

There is extensive literature documenting herbage accumulation responses of *Cynodon* species to N fertilizer (Taliaferro et al., 2004). Early studies conducted by Prine and Burton

(1956) in Georgia showed that increasing N rate from 0 to 300 kg ha⁻¹ yr⁻¹ increased annual yield of Coastal bermudagrass cut every 4 wk from 2.7 to 17.9 Mg ha⁻¹. In Florida, Vendramini et al. (2008a) showed that monthly herbage accumulation of Tifton 85 increased from 1.6 to 2.6 Mg ha⁻¹ as N rate per 4-wk growth period increased from 0 to 80 kg ha⁻¹. In that study, herbage accumulation rate increased linearly from 57 to 93 kg ha⁻¹ d⁻¹ as N rate increased. Throughout a grazing season with herbage allowance maintained at ~ 1.0 kg forage dry matter kg⁻¹ animal liveweight, this increase in herbage accumulation would allow stocking rates to increase from 3.5 to 5.7 animal units (AU) ha⁻¹, where an AU is 500 kg liveweight. In a study conducted in Brazil, greater tiller density and tiller mass explained greater herbage accumulation of Tifton 85 as N rates increased (Premazzi et al., 2003).

Nutritive value of Tifton 85 is responsive to N fertilization. In vitro digestible organic matter concentration increased linearly, from 480 to 530 g kg⁻¹, and herbage crude protein (CP) concentration increased linearly, from 140 to 190 g kg⁻¹ (2-wk regrowth) and 115 to 135 g kg⁻¹ (4-wk regrowth), as N fertilization increased from 0 to 80 kg ha⁻¹ (Vendramini et al., 2008b). In a companion study, N fertilization level did not affect the concentration of Fraction A (rapidly degradable) CP in Tifton 85, however, there was a linear increase in Fraction B (potentially degradable in the rumen) and a linear decrease in Fraction C (rumen undegradable) CP as level of N fertilization increased (Vendramini et al., 2008a). Thus, not only is total CP lower when N fertilizer rates are low, but rumen-degradable protein in Tifton 85 is also reduced, potentially limiting performance of ruminants with high CP requirements.

Tifton 85 Response to Grazing

Mandebvu et al. (1999) evaluated defoliation frequency effects on Tifton 85 and Coastal bermudagrass herbage accumulation and nutritive value. Herbage accumulation increased with increasing regrowth interval for both cultivars, and Tifton 85 outyielded Coastal by 34%. In vitro

digestibility of Tifton 85 was greater than Coastal although Coastal herbage had lower neutral (NDF) and acid detergent fiber (ADF) concentrations. This was attributed in part to greater lignin and ether-linked ferulic acid concentration in Coastal than Tifton 85, factors that contributed to lower NDF and ADF digestibility for Coastal.

Mislevy and Martin (1998) evaluated herbage accumulation and persistence responses of Tifton 85 and Florakirk bermudagrass and 'Florona' and 'Florico' stargrass to defoliation frequency in South Florida. The herbage accumulation response was similar among grasses, increasing linearly as length of regrowth period increased. Of perhaps greater significance was the pattern of response across years. In particular, herbage accumulation was very consistent across years when grazing occurred every 6 wk, but when grazing occurred every 2 wk, herbage accumulation declined from year to year suggesting loss of stand vigor over time. The response to grazing frequency is likely to be affected by grazing stubble height, but there are no data assessing the interaction of these factors for Tifton 85.

Mechanisms of bermudagrass response to defoliation have been assessed in studies of tiller dynamics. Defoliated grasses exhibit tiller mass/density compensation in response to grazing intensity and this self-regulation is a means by which pastures regulate leaf area index in response to changes in grazing intensity (Matthew et al., 1995). There are limits to this compensation, or phenotypic plasticity, associated with particular plant species and environments (Chapman and Lemaire, 1993). Tifton 85 bermudagrass swards were continuously stocked by sheep (*Ovis aries*) to maintain sward heights of 5, 10, 15, and 20 cm during one growing season in Sao Paulo state, Brazil (Sbrissia et al., 2003). During the early to mid-summer, tiller population density decreased with increasing sward height. Tiller mass increased by nearly a factor of six from the shortest to the tallest sward height (23 to 124 mg tiller⁻¹). Although tiller

density declined across this range, the proportional decline in density was much less than the increase in tiller mass, resulting in a doubling or tripling of herbage mass as sward height increased. Thus one likely mechanism for the often-observed response of increasing herbage accumulation with longer regrowth intervals (i.e., taller swards) is an increase in tiller mass.

Sbrissia et al. (2003) suggested that there are limits to plasticity depending on grass species and growing environment. They indicated that during reproductive growth in autumn, a 5-cm grazing height was below the plasticity limit for Tifton 85, i.e., both tiller number and mass were lowest for the 5-cm grazing height. During that time of year tiller mass/density compensation did not occur. This is likely associated with responses observed in other *Cynodon* studies where sustained close grazing negatively impacted sward persistence.

Grazing Systems and Grazing Management

Grazing Systems

Grazing system is “a defined , integrated combination of animal, plant, soil, and other environmental components and the grazing methods by which the system is managed to achieve specific results or goals” (FGTC, 1991). Grazing systems are complex because multiple factors are active within them, including the biotic environment, the grassland resource, the animal resource, and varied management strategies.

Grazing Management

Grazing management is defined as the process that manipulates the interactive complex of soil, forage plant, and grazing animal to achieve long-term production goals (Sollenberger and Newman, 2007). Proper grazing management often will increase plant productivity (Pedreira et al., 1999; Garay et al., 2004), minimize the cost of livestock production, and mitigate soil erosion and run-off of nutrients from surface-applied fertilizer and manure (Franzluebbers et al., 2000; Wilsey et al., 2002; Wright et al., 2004). Inappropriate grazing management may cause adverse

effects, including grassland degradation and reduced grassland persistence (Wu and Tiessen, 2002; Newman and Sollenberger, 2005).

Grazing management is described in terms of grazing intensity, grazing frequency, and the timing of grazing relative to plant growth stage or season of the year. Other management practices, e.g., fertilization, supplementation, forage conservation, and fire, can be used in conjunction with grazing management to optimize the grazing system and achieve long-term production goals.

Grazing intensity

Grazing intensity relates to the severity of grazing (Sollenberger and Newman, 2007). It can be described in terms of stocking rate (number or weight of animals per unit land area over a period of time), stocking density (number or weight of animals per unit land area at a point in time), grazing pressure (number or weight of animals per unit of forage), carrying capacity (stocking rate at a near-optimal grazing pressure), or herbage allowance (weight of herbage per unit of animal live weight). It is the most important grazing management decision because the level of grazing intensity strongly impacts plant productivity, quality, and persistence (Waller and Sale, 2001; Newman and Sollenberger, 2005; Patton et al., 2007), soil conditions (compaction, moisture and temperature, microbe and fauna activity, and nutrient cycling and availability) (Baron et al., 2002; Zhao et al., 2007; Ingram et al., 2008), animal performance (Newman et al., 2002), and grazing area long-term sustainability (Biondini et al., 1998).

Grazing frequency

Grazing frequency is affected by choice of grazing methods, i.e., continuous and rotational stocking, and the interval between grazing events. The choice of grazing frequency impacts uniformity of pasture defoliation (Mathews et al., 1994c; Sollenberger and Newman, 2007), grazing efficiency (Oenema et al., 2006), animal and forage production, pasture persistence, and

distribution and recovery of nutrients in animal excreta and plant litter (Pedreira et al., 1999; Mathews et al., 1994a; Dowling et al., 2005).

In the following sections, research will be reviewed that describes the effect and relationship of grazing management on forage productivity and nutritive value, the dynamics of nutrient pools, and litter deposition and decomposition.

Plant Responses to Grazing Management

Grazing Intensity

Herbage accumulation

The effect of grazing intensity on herbage accumulation is variable. A recent review summarized the effect of grazing intensity on herbage accumulation in 16 studies (Sollenberger et al., in review). Herbage accumulation was not affected by grazing intensity in three studies, was negatively affected by increasing grazing intensity in eight studies, was positively affected by increasing grazing intensity in four studies, and in one study was positively affected by increasing grazing intensity for 2 yr followed by no effect for 2 yr. All but one study showing no effect or a positive effect of increasing grazing intensity on herbage accumulation included one or more temperate species with a decumbent growth habit. In contrast, herbage accumulation decreased with increasing intensity in studies including stargrass in Florida (Mislevy et al., 1989) and Jamaica (Garay et al., 2004), orchardgrass (*Dactylis glomerata* L.)-legume mixtures in Pennsylvania (Carlassare and Karsten, 2002) and California (Hull et al., 1961; 1965), rhizoma peanut (*Arachis glabrata* Benth.) in Florida (Ortega et al., 1992), and bermudagrass in Florida (Pedreira et al., 1999). Herbage accumulation of species in the *Cynodon* genus was generally negatively affected by increasing grazing intensity.

Interaction of grazing intensity and frequency may occur for herbage accumulation. In a study with rhizoma peanut, Ortega et al. (1992) indicated that this interaction occurred. The

effect of grazing intensity was more pronounced when rest periods between grazing events were short rather than long. They also noted that herbage accumulation was not affected by treatments in the first year, attributable to mobilization of energy from rhizomes in intensively grazed pastures. By the second year, when rhizome mass had been depleted in intensively grazed pastures, herbage accumulation decreased as grazing intensity increased. The response to intensity is likely to be greatest when the intensities imposed are high. For example, stargrass herbage accumulation increased linearly as stubble height increased from 5 to 20 cm, but further increases in stubble height above 20 cm had no effect on herbage accumulation (Mislevy et al., 1989). These reports provide clear evidence that the effect of grazing intensity cannot be predicted in isolation; it is also a function of forage species, grazing frequency, and the environment.

The mechanism of grazing intensity effects on herbage accumulation can be complex. Grazing intensity affects canopy structure (i.e., the amount of photosynthetic leaf area, and total forage and plant part bulk density), resource allocation, status of plant reserves, presence of growing points, and distribution of nutrients throughout the canopy (Chapman and Lemaire, 1993; Richards, 1993; Sollenberger and Newman, 2007). Effects of grazing intensity on canopy structure impact light interception. Post-graze canopy light interception increased as defoliation height increased (Chaparro et al., 1996; Pedreira et al., 2000). Pedreira et al. (2000) evaluated Florakirk bermudagrass pastures and found light interception was as low as 22% following grazing to a stubble height of 8 cm, but it was 78% or greater when stubble height was 24 cm. Light interception after a grazing event affects the ability of the plant to carry out photosynthesis and the extent to which plant reserves will need to be mobilized for regrowth. The effect of grazing intensity on presence of active meristems following defoliation is also important. These

meristems provide a strong sink for C and N in the days following a defoliation event, increasing the rate of restoration of leaf area compared to situations when growing points were removed (Chapman and Lemaire, 1993).

Reserve status and persistence

Carbohydrate reserves were actively involved in plant regrowth when grazing intensity was high (Saldivar et al., 1992; Peterson et al., 1994). When plants are grazed, instantaneous reduction of photosynthesis occurs due to a reduction in leaf area. If the supply of current photosynthate is sufficiently low it leads to the mobilization of carbohydrate reserves in order to rebuild leaf area and maintain existing organs (Dankwerts, 1993). For this reason, carbohydrate reserves have been used by many researchers to estimate plant persistence under different management strategies.

Along with influencing the degree of dependence on reserves, grazing intensity affects the quantity of stored carbohydrate reserves (Adjei et al., 1988; Mowrey and Matches, 1991; Newman et al., 2002). High grazing intensity caused total nonstructural carbohydrate (TNC) concentration to decline in roots of sainfoin (*Onobrychis viciifolia*; Mowrey and Matches, 1991). They reported that average TNC for a high grazing intensity (130 g kg^{-1}) was less than for low and moderate grazing intensity (155 g kg^{-1}) when low, moderate, and high intensities averaged 52, 69, and 87% removal of pre-graze herbage mass, respectively.

In Florida, a mixture of rhizoma peanut and common bermudagrass (90% peanut at initiation) was stocked rotationally at a range of grazing intensities (residual herbage mass of 500, 1500, and 2500 kg ha^{-1}) and lengths of rest period (7, 21, 42, and 63 d) (Ortega et al., 1992a, b). The effect of grazing intensity on peanut percentage in pregraze herbage mass after 2 yr was most pronounced for short rest periods (7 d), ranging from 9 to 90% for intensities of 500 to 2500. In contrast, when rest period was 42 d, the range in percent legume was 45 to 90% across

the intensities. Decreasing peanut rhizome mass was associated with changes in percent peanut and likewise reflected the intensity by frequency interaction. When rest period was 7 d, rhizome mass was ~ 500, 1400, and 4000 kg ha⁻¹ for residual herbage mass treatments of 500, 1500, and 2500 kg ha⁻¹, but when rest period was 42 d, rhizome mass was 1500, 3300, and 4000 kg ha⁻¹, respectively. These data illustrate that for persistence responses grazing frequency interacts strongly with intensity.

Nutritive value

The nutritive value response to increasing grazing intensity was described in a recent literature review (Sollenberger et al., in review). Thirty-five of 36 studies summarized reported that increasing grazing intensity had either no effect (12 out of 36) or a positive effect (23 out of 36) on nutritive value. Only one of the 36 studies reported a negative effect of increasing grazing intensity on nutritive value (Ackerman et al., 2001).

There are many examples of positive effects on nutritive value of increasing grazing intensity in both temperate and tropical environments and for C₃ and C₄ species. Coastal and Callie bermudagrass pastures in Texas were stocked with 3.6 to 12.7, 220-kg steers ha⁻¹ (Guerrero et al., 1984). In vitro digestibility increased with increasing stocking rate from 497 to 568 g kg⁻¹ for Coastal and 581 to 675 g kg⁻¹ for Callie. In Brazil, ‘Tanzania’ guineagrass (*Panicum maximum* Jacq.) leaf percentage increased linearly from 47 to 59% as target stubble height of continuously stocked pastures decreased from 80 to 20 cm (do Canto et al., 2008). In tropical Australia, digitgrass (*Digitaria erianthus* Steud.) was stocked continuously at 5.2, 6.3, 8.9, 11.5, and 12.6 steers ha⁻¹ (Jones and LeFeuvre, 2006). As stocking rate increased, herbage N concentration increased linearly from 6 to 15 g kg⁻¹, P increased quadratically with from 1 to 2.2 g kg⁻¹ at a low N fertilizer rate and from 0.7 to 1.4 g kg⁻¹ at a high N rate, sulfur (S) response was

similar to that for P, and in vitro digestion increased linearly from 445 to 475 g kg⁻¹ with increasing stocking rate.

Initially, the increase in herbage nutritive value with greater grazing intensity may seem counterintuitive because at greater intensities herbage mass is less and grazing is occurring at lower strata in the canopy. Nutritive value generally decreases from top to bottom of a canopy, particularly for C₄ grasses (Holderbaum et al., 1992; Fisher et al., 1991). This generalized response may not apply when canopies are grazed intensively over an extended period of time because greater stocking rates imply more frequent visits by grazing animals to a particular patch and lower levels of maturity of the herbage regrowth being grazed (Newman et al., 2002; Garay et al., 2004; Dubeux et al., 2006c). As an example, regrowth herbage of more closely grazed Florakirk bermudagrass had a greater proportion of leaf and greater nutritive value than did canopies grazed to taller stubble heights (Pedreira et al., 1999).

Grazing Frequency

Herbage accumulation

Decreasing grazing frequency has potential to increase pasture production (Motazedian and Sharrow, 1990; Green and Detling, 2000; Mislevy et al., 2008). In a northern mixed-grass prairie at Wind Cave National Park, South Dakota, USA, Green and Detling (2000) found above-ground production was significantly reduced at weekly and biweekly defoliation frequencies compared to monthly and bimonthly frequencies. Mislevy et al. (2008) found a similar trend for stargrass and bermudagrass. They observed that production of these grasses increased linearly as grazing frequency decreased from 2 to 7 wk. Herbage accumulation of Tifton 85 increased from 7.8 (2 wk) to 17.2 Mg ha⁻¹ (7 wk). For rhizoma peanut, average crop growth rate increased from ~ 1.5 to 3.5 g m⁻² d⁻¹ when interval between defoliation events increased from 7 to 49 d and postgraze herbage mass was 500 kg ha⁻¹. There was frequency by intensity interaction, however and the

increase for the same defoliation intervals was only from 3.6 to 4.2 g m⁻² d⁻¹ when postgraze herbage mass was 1500 kg ha⁻¹, and from 4.3 to 4.9 g m⁻² d⁻¹ when postgraze herbage mass was 2500 kg ha⁻¹ (Ortega et al., 1992).

Persistence

An advantage cited for longer regrowth intervals and particularly for rotational vs. continuous stocking is superior persistence (Sollenberger and Newman, 2007). There are numerous examples of this in the literature. Callie bermudagrass was grazed by dairy replacement heifers in northern Florida (Mathews et al., 1994) under continuous stocking. Treatments were three grazing methods, two rotational stocking options and continuous stocking. Percentage Callie bermudagrass declined from 90 (Year 1) to 62% (end of Year 2), while the rotational pastures had total declines of 4 to 7 percentage units. The component of the pastures that increased over time was primarily common bermudagrass. Common bermudagrass is a low-growing species that is shaded during a significant portion of the regrowth period when associated with the taller growing Callie under rotational stocking. Continuous stocking resulted in regular removal of Callie herbage, reduced shading of the lower-growing common bermudagrass, and allowed it to be more competitive with Callie.

Growth habit of the forage plays a role in the persistence response. ‘Florigraze’ and ‘Arbrook’ rhizoma peanut were compared under continuous stocking (Hernández Garay et al., 2004). The percentage of the more upright growing Arbrook in herbage mass decreased from 89 to 82 to 66 over 3 yr compared to 90, 89, and 87 for Florigraze. The lower growing Florigraze persisted better than Arbrook under continuous stocking, and by the third year of grazing average daily gain of cattle grazing Florigraze was superior to that of cattle grazing Arbrook because of the greater percentage of high nutritive value legume in the Florigraze pastures.

Grazing frequency interacts with grazing intensity in affecting persistence responses. Rhizoma peanut was stocked rotationally and grazed at different frequency-intensity combinations (Ortega et al., 1992). Percentage peanut in the herbage DM increased with increasing interval between grazings when post-graze herbage mass was 500 or 1500 kg ha⁻¹, but when post-graze herbage mass was 2500 kg ha⁻¹ there was little effect of interval between grazings.

Nutritive value

Relatively long intervals between defoliation events reduce forage CP and IVDOM. Because the process of plant maturation involves a decline in leaf:stem ratio as well as the quality of stem (Minson, 1990), timely grazing that minimizes the proportion of stem issue will positively influence forage nutritive value (Green and Detling, 2000; Fales and Fritz, 2007). Pedreira et al. (1999) observed that lower concentrations of CP and IVDOM were associated with longer interval between grazing events in Florakirk bermudagrass pastures. A similar response was reported for tall fescue [*Lolium arundinaceum* (Schreb.) S.C. Darbyshire] (Burns et al., 2002), ryegrass (*Lolium perenne* L.) (Motazedian and Sharrow, 1990), bahiagrass (*Paspalum notatum* Flügge), limpograss (*Hemarthria altissima* Stapf et C.E. Hubb.), and stargrass (Mislevy et al., 1989; Adjei et al., 1989).

Nutrient Pools in Grasslands

Nutrient pools are where organic and inorganic nutrients are temporarily stored. In grassland ecosystems, the most important nutrient pools are: (1) live plants, including above- and below-ground tissues; (2) plant litter (dead, undecomposed plant tissues); (3) soil; and (4) live animal biomass, including the grazing animal, the above- and below-ground invertebrates, and microbial populations (Wedin and Russelle, 2007). Carbon, N, P, and K are important nutrients

in grassland ecosystems, and where they reside is discussed in the portion of the review that follows.

Carbon

Grasslands account for more than 10% of the total biosphere C store (Eswaran et al., 1993), and soil is the largest C pool in grassland ecosystems. Thomas and Asakawa (1993) and Stevenson and Cole (1999) reported that the organic matter (OM) of terrestrial soils contains 30 to 50 x 10¹¹ Mg C compared to 7 x 10¹¹ and 4.8 x 10¹¹ Mg in the atmosphere and plant/animal biomass, respectively. Tropical grasslands and savannas contain only 6% of global terrestrial biomass (Schlesinger, 1997) but about 15% of global soil organic C (Jobbagy and Jackson, 2000). Worldwide, approximately 22% of global soil organic C is below grasslands (Jobbagy and Jackson, 2000).

Although vegetation and grazing animal pools contain less C than the SOM, they play an important role in the cycling of C within pasture systems through surface litter deposition and decomposition, excreta return, and methane emission. The extent of pasture utilization (C consumption) by herbivores determines whether litter or excreta is the main source of above-ground C (Thomas, 1992). Dubeux et al. (2006b) reported plant litter deposition of 4540 kg OM ha⁻¹ during a 168-d grazing season of 'Pensacola' bahiagrass. Thomas and Asakawa (1993) measured from 2830 to 11 800 kg DM ha⁻¹ of litter deposited from May to December in creeping signalgrass [*Brachiaria humidicola* (Rendle) Schweick.] and gambagrass (*Andropogon gayanus* Kunth) pastures. Castilla (1992) estimated fecal C return of 3900 kg ha⁻¹ yr⁻¹ in a creeping signalgrass-desmodium [*Desmodium heterocarpon* (L.) DC. subsp. *ovalifolium* (Prain) Ohashi] pasture, and, compared to leaf litter, it was the main source of above-ground C in that system.

Nitrogen

In grazed grassland ecosystems, the major N pools are the soil, vegetation (herbage and plant litter), grazing animals, and the atmosphere (Dubeux et al., 2007). Considering all terrestrial ecosystems, the atmospheric N pool is 16 000 times greater than the sum of the soil and biotic N pools (Russelle, 1996). The atmosphere contains 78% N₂ gas, but this N can not be directly used by plants. It must be fixed through the activity of symbiotic (e.g., rhizobia bacteria) or free-living soil organisms (Whitehead, 2000). The energy requirement for N₂ reduction, either by biological or industrial fixation, is the major reason why N is considered the most limiting nutrient in many agricultural ecosystems (Wedin, 1996).

In grasslands, the soil (not including the earth's mantle and crust) is the second largest N reservoir, behind the atmosphere N pool, and is affected by soil OM, soil microbial biomass, fixed NH₄⁺, and the plant-available inorganic N (Stevenson and Cole, 1999). The below-ground soil mesofauna are important components of the soil pool, and the rhizosphere may contain from 4500 to 24 000 kg N ha⁻¹ (Henzell and Ross, 1973). These amounts are far greater than the range of 20 to 300 kg N ha⁻¹ estimated in live herbage of most forages (Henzell and Ross, 1973). Usually, more than 95% of the total soil N is bound in soil OM. The rest (0-5%) occurs in the inorganic forms, ammonium, nitrite, and nitrate (Whitehead, 2000).

Vegetation is an important N pool. The N in plants is used for amino acid and protein synthesis, the formation of nucleic acids, and the construction of the chlorophyll molecule for photosynthesis. Herbage (grass and legume) N concentration is usually between 10 and 50 g kg⁻¹ of plant DM (Whitehead, 2000). The actual concentration in vegetation is impacted by available N in soil, plant species and cultivar, and the stage of maturity of the herbage. When herbage senesces and becomes plant litter, most N is mobilized from this older to live tissue, but some N remains. Therefore, plant litter is an important N pool, especially for low-input tropical grassland

ecosystems where N inputs and forage utilization are often low (Thomas and Asakawa, 1993; Dubeux et al., 2006a).

Phosphorus

Phosphorus is used for energy transfer and reproduction within cells and is essential for plant growth. It is often the second-most-limiting mineral nutrient to plant production, not only because it is critical for plant growth, but also because the eroded and weathered soils of the southeastern USA, in general, are low in available P, with applied P quickly fixed into unavailable forms (Anderson et al., 1996). In contrast to N, there is no atmospheric or gaseous P pool to replenish grassland ecosystems. Rainfall, together with some dry deposition, usually provides only 0.2 to 1.5 kg P ha⁻¹ yr⁻¹ (Newman, 1995). The P sources for cycling in grasslands are weathering of rock, P fertilizer, animal excreta, and plant residues.

Low P:N ratios in both plant and animal tissues combined with high soil P sorption capacity result in soil being the largest and most important P pool in grassland ecosystems (Haynes and Williams, 1993; Rao et al., 1999). Soil P retention by amorphous and microcrystalline Fe and Al oxides coupled with microbial P demand make most of the inorganic P unavailable (Novais and Smyth, 1999; Olander and Vitousek, 2005). For soils receiving little or no P fertilizer, organic P is considered to be the most important P source for plants and this P pool may be used to increase efficiency of P recycling (Novais and Smyth, 1999; Oberson et al., 1999).

Plant litter and the excreta of animals are important P pools. Whitehead (2000) reported that only 100 to 250 g P kg⁻¹ of P in the diet is converted into live-weight gain or milk. The rest is recycled to grassland soils through plant residues and animal excreta. Because this P is primarily associated with organic compounds in plant litter and animal dung, P mineralization is an important process in grasslands. At a plant-residue P concentration of 2 g kg⁻¹ DM, a balance

between the mineralization and immobilization processes is maintained. Below that concentration, immobilization predominates. Typical P concentration in tropical grasses is $< 2.0 \text{ g kg}^{-1}$ (Minson, 1990), thus high rates of net P immobilization from grass litter are expected.

Potassium

Potassium is the major cation required for plant growth and reproduction. Potassium is involved in activating enzymes and catalyzes several physiological reactions in plants. The K cycle in pastures is simpler and faster than N and P cycles, mainly because K is not part of organic compounds, and the chemistry of K in soils is almost solely based on cation exchange reactions. Potassium is required by plants in higher concentration than any other mineral element besides N (Robinson, 1996). Robinson (1996) reported that at least $200 \text{ to } 400 \text{ kg K ha}^{-1}$ is required annually for sustainable high production of Coastal bermudagrass.

The soil is the greatest reservoir of K. Most of it is in non- or slowly-exchangeable forms (Ayarza, 1988), and only a small amount ($< 2\%$) is available to plants over the growing season. Available K is held on cation exchange sites and in the soil solution. As solution K is removed or taken up by plants, the K on the cation exchange sites reacts to establish a new equilibrium with soil-solution K (Snyder and Leep, 2007).

Plant litter and the animal excreta are important K pools. Whitehead (2000) estimated that K return in dead herbage and dead roots was up to $84 \text{ and } 29 \text{ kg ha}^{-1} \text{ yr}^{-1}$, respectively, assuming $7000 \text{ kg dead herbage and } 5000 \text{ kg dead roots ha}^{-1} \text{ yr}^{-1}$. Animals represent a relatively small K pool, yet they have a critical role in recycling because of the large amount of K ingested and excreted. In New Zealand, Williams et al. (1990) estimated that animals were directly or indirectly responsible for 74 to 92% of all K losses in pastures grazed by dairy cows over a 30-yr period. Total K amount in urine and dung was 128 kg ha^{-1} when dairy cattle grazed at a density of $700 \text{ cow-days ha}^{-1} \text{ yr}^{-1}$ (Whitehead, 2000).

Nutrient Cycling in Grasslands

Nutrients cycle among pools within the grassland ecosystem. Losses of nutrients to the environment accompany transfers from pool to pool. Efficient recapture of nutrients by plants is critical in low-input grasslands if these swards are to persist. In intensively managed systems, an important contribution of efficient recapture of nutrients is minimizing loss of nutrients to the environment (Dubeux et al., 2007). Regardless of management intensity, grassland management decisions should be informed by an understanding of the dynamics of nutrient cycling.

The C, N, P, and K cycles are the most important nutrient cycles in grazed grassland systems. The cycling of these nutrients involves a network of pools. Each cycle has an associated complex set of interactions and transformations, and there are also interactions with other nutrient cycles. For instance, plant nutrients such as N and P are chemically bound to C in organic material. The amount of C in these materials has an effect on the availability of these nutrients for plants. If the amount of C is very high compared to other nutrients, nutrient release will be slow because more bonds need to be broken by microorganisms and a small amount of nutrients is made available to the plant from mineralization (Bellows, 2001; Parton et al., 2007). If the ratio of C to other nutrients is low, fewer bonds need to be broken and nutrient release will be relatively rapid.

The following section includes a general description of the C, N, P, and K cycles in grazed grasslands. More detailed descriptions can be found in Dubeux et al. (2007).

Carbon

The C cycle begins with plants taking up carbon dioxide from the atmosphere in the process of photosynthesis. Plants are eaten by grazing animals which return organic C to the soil in manure. Dead plant matter is also deposited on the soil. Easily broken-down forms of C in manure and plant litter are released as carbon dioxide through respiration of decomposers. Forms

of C that are difficult to break down become stabilized in the soil as humus. This material increases soil aggregation, limits soil erosion, decreases release of other nutrients, and increases cation exchange and water holding capacities (Cambardella et al., 1992).

Nitrogen

Nitrogen enters the cycle primarily through atmospheric N fixation by rhizobia or N application via fertilization or addition of organic amendments. Plants can take up either ammonia or nitrate for growth. Nitrogen in living plants is consumed by animals and a high percentage is returned to the soil in feces or urine. Some proportion of N is not consumed and is returned directly to the soil in plant litter. Soil organisms decompose organic N in soil, plant litter, or animal excreta and release it in inorganic forms. Plants take up the N to start the cycle again.

Phosphorus

The P cycle is mainly affected by microbial and chemical transformations. Phosphorus is chemically bound to Fe and Al in acid soils, and to Ca in alkaline soils. Soil microorganisms mineralize or release P from OM. Efficient cycling of inorganic P is not expected because competition between the soil and the plant for orthophosphate (H_2PO_4^- and HPO_4^{2-}) in solution is such that the soil makes most of the inorganic P unavailable (Novais and Smith, 1999). This rapid geochemical immobilization means that P leaching in most soils is negligible, although some sandy soils are exceptions to this general rule (Smil, 2000). Geochemical sorption and biological demand control P retention and availability in soils. This is true because the biota predominantly utilize the same inorganic form of P, from the same soil pool, and on the same time scale as geochemical sorption, and thus are likely to compete for P as it flows through the available pool (Olander and Vitousek, 2005).

Potassium

Potassium, similar to other nutrients, is cycled through plant uptake, animal consumption, and plant litter and animal manure deposition. The availability of K is greatly affected by the soil parent-material. Whitehead (2000) found that soils derived from granite contain on average nine times more K than soils derived from basalt. Sandy soils have limited ability to retain K, and the susceptibility of K to loss by leaching necessitates relatively frequent applications.

Effects of Management Practices on Nutrient Cycling Among Pools

Nutrient flux dynamics in grazed grassland ecosystems are related to the interactions between plant species, plant tissue quantity and quality, size and availability of soil nutrient pools, and the timing, intensity, and frequency of animal disturbance. In grazed grassland ecosystems, grass is an intermediate product. Only a fraction of the nutrient elements in grass offered to animals ends up in milk or meat products; the majority of nutrients is returned via animal excreta and plant litter, and recycled within nutrient pools (Dubeux et al., 2007). Plants create positive feedbacks to nutrient cycling directly through uptake, use, and loss of nutrients, and indirectly by influencing microbial activity and herbivore behavior (Holland and Detling, 1990; Hobbie, 1992; Frank and Groffman, 1998; Van der krift and Berendse, 2001; Dubeux et al., 2006c). Herbivores impact nutrient cycling through their waste products and their effect on plant species proportion and plant composition (Holland et al., 1992; Shariff et al., 1994; Hobbs, 1996; Frank and Evans, 1997). Management practices impact plant and animal performance and soil condition (Beegle et al., 2000; Conant et al., 2001). Thus, they directly or indirectly influence the interactions and transformations of nutrient elements within and among these pools.

Grazing Management

Carbon. Grazing management alters C storage in grassland ecosystems by modifying the magnitude and relative allocation of C to above- and below-ground biomass, altering microclimate and the availability of light, water, and nutrients in systems, and modifying the functional diversity of plants (Hobbie, 1992; Hobbs, 1996; Frank and Groffman, 1998; Ingram et al., 2007). There is a large amount of variation in rates and the length of time that C may accumulate in soil. Factors that affect C accumulation include the productivity of the vegetation, physical and biological conditions in the soil, and the past history of soil organic C inputs and physical disturbance (Post and Kwon, 2000). The amount of C sequestered in soil is determined by the rate of input of OM and the rate of decomposition of the OM (Jones and Donnelly, 2004). Management practices affect these processes in grassland ecosystems (Burke et al., 1989; Frank et al., 1995; Franzluebbbers et al., 2000; Jones and Donnelly, 2004).

Grazing management practices can increase C accumulation in soil (Derner et al., 1997; Schuman et al., 1999, 2002; Conant et al., 2003). Lal (2002) has reported that properly managed grasslands have the potential to sequester large quantities of C in plant biomass and soil OM. Soil C storage on USA rangelands has been estimated to increase from 0.1 to 0.3 Mg C ha⁻¹ yr⁻¹, and new planted grasslands have been shown to store as much as 0.6 to 1.9 Mg soil organic C ha⁻¹ yr⁻¹ (Trumbore et al., 1995; Schuman et al., 2002; Franzluebbbers, 2007). Derner et al. (1997) also found increased soil C storage under grazed compared to ungrazed shortgrass steppe in northeastern Colorado. They found 1980 g m⁻² in the grazed compared to 1320 g m⁻² in the ungrazed treatments in the 0- to 15-cm soil depth. Reeder and Schuman (2002) reported similar results in a mixed-grass prairie (grazed 12 yr) and a short-grass steppe (grazed 56 yr). They found that significantly greater soil C (0–30 cm) was measured in grazed pastures compared to non-grazed exclosures. Likewise, Franzluebbbers (2005) reported that grazed pasture accumulated

soil organic C at a rate of 1.4 compared to 0.6 Mg ha⁻¹ yr⁻¹ for ungrazed. This pattern of response is thought to be caused by a higher turnover in the form of aboveground biomass, manure, and root material during grazing (Post and Kwon, 2000; Conant et al., 2001; Reeder and Schuman, 2002; Franzluebbers et al., 2000b, 2003). It has also been explained in part because grazed fields had significantly lower ecosystem respiration rates than did ungrazed fields (Wilsey et al., 2002).

The accumulation of C may vary with changes in grazing intensity. Dubeux et al. (2006c) reported that greater stocking rate and N fertilization of bahiagrass pastures resulted in accumulation of C in the light density soil OM fraction, the fraction that is most responsive to management changes in the short term. Reeder and Schuman (2002) showed that soil C content was greatest in USA mixed-grass and short-grass rangelands at the highest stocking density. In an alpine meadow environment on the eastern Tibetan Plateau, Gao et al. (2007) measured soil organic C content under three different grazing intensities by yaks (light: 1.2, moderate: 2.0, and heavy: 2.9 yaks ha⁻¹). They showed that soil organic C at a 0- to 30-cm depth and total plant C increased from light grazing (9800 and 800 g m⁻²) to moderate grazing (10 160 and 1090 g m⁻²) to heavy grazing (11 730 and 1150 g m⁻²).

However, the mass of C in above-ground vegetation decreases with increasing grazing intensity. Schuman et al. (1999) examined the plant–soil C balance in a mixed-grass rangeland (55% cool-season species and 23% warm-season species) under three livestock stocking rates: non-grazed exclosures, a light stocking rate (20 steer-days ha⁻¹), and a heavy stocking rate (59 steer-days ha⁻¹). They found that total above-ground C mass was 1620, 1280, and 750 kg ha⁻¹ for non-grazed exclosures, light stocking rate, and heavy stocking rate, respectively.

Therefore, the amount of C represents the balance of primary productivity and decomposition and as such is an integrated function of management strategies. Quantifying the

effects of forage management on soil C cycling improves our understanding of changes in soil quality in pasture ecosystems.

Nitrogen. Management strategies play important roles in N sequestration. Grazing management, to some degree, can increase N deposition in soil (Schuman et al., 1999). Franzluebbers et al. (2000) observed that grazed tall fescue-common bermudagrass pastures (20-yr-old) had greater total N (34%), and particulate organic N (2.4 fold) at a depth of 0 to 200 mm than adjacent land in conservation-tillage cropland (24-yr-old). Wright et al. (2004) also found that increasing soil organic N was observed up to 32 yr after establishment of bermudagrass pastures.

Grazing also leads to spatial heterogeneity in N mineralization rates and N availability to vegetation (Mathew et al., 1994; Baron et al., 2001; Rossignol et al., 2006). On grassland of the northern winter range of Yellowstone National Park, Frank et al. (1998) reported that average net N mineralization among grazed plots ($3.8 \text{ g N m}^{-2} \text{ yr}^{-1}$) was double that of fenced, ungrazed plots ($1.9 \text{ g N m}^{-2} \text{ yr}^{-1}$). Baron et al. (2002) indicated that the rate of N cycling through the soil-plant-animal system increases with grazing intensity because N excreted by livestock is in a more readily mineralized form than N in herbage. During the grazing process, livestock stimulate the mineralization of N by depositing N-rich, readily decomposable excreta, changing litter quality, and also incorporating vegetation litter into the soil by trampling (Haynes and Williams, 1993; Hobbs, 1996; Hatch et al., 2000; Rossignol et al., 2006).

Phosphorus. Phosphorus cycling and distribution are also affected by grazing practices. Phosphorus is excreted primarily in the feces, and cattle dung is an important pathway for P return to the pasture. Dubeux et al. (2004) estimated that in grazed bahiagrass pastures the dung pool contained more P than the sum of above-ground litter, plant, and urine pools. Chaneton et

al. (1996) proposed that plant P pools were mainly located in below-ground organs, to the extent of 80 to 90% in grazed and 63 to 75% in ungrazed vegetation. On a smooth bromegrass (*Bromus inermis* Leyss.), quackgrass (*Elytrigia repens* L.), and Kentucky bluegrass (*Poa pratensis* L.) mixed pasture in the humid western Canadian parkland, Baron et al. (2001) observed that extractable-P concentration in soil was greater in the 0- to 15-cm depth of heavy (154 mg kg⁻¹) than in medium (138 mg kg⁻¹) or light-grazed (127 mg kg⁻¹) paddocks. This occurs because heavy grazing results in greater forage utilization, increasing the proportion of nutrients being returned to the pasture in excreta compared to plant litter (Thomas, 1992). Redistribution of soil P can occur due to grazing. During 3 yr of grazing bahiagrass in Florida (Dubeux et al., 2009), changes in soil P concentration were greater in magnitude close to the shade and water locations and near the paddock gate. Proportionally greater amounts of time spent near shade and water lead to greater excreta deposition indices in those areas, resulting in greater P concentration changes.

Potassium. Compared with N and P, the effects of grazing management on K cycling and distribution have received relatively little attention in research. Under grazing, animals play a key role in the cycling of K through the return of excreta. Only a small proportion of ingested K is retained within animals; proportionately up to 90% of K is excreted in dung and urine (Haynes and Williams, 1993; Whitehead, 2000). Grazing management can cause soil K accumulation in high traffic areas. On Callie bermudagrass pastures, Mathews et al. (1994b) observed that ranges of extractable K within a pasture were as great as 13-fold (14-181 mg kg⁻¹) after 2 yr of grazing. The effects of three bahiagrass pasture management intensities on soil K concentration were evaluated in Florida (Dubeux et al., 2009). Soil K concentration in the 0- to 8-cm depth was greater for the treatment with the highest stocking rate. Nutrients in excreta are relatively

available in comparison to those in plant litter, and the greater forage utilization that occurred due to greater stocking rate likely increased nutrient return through excreta. Accumulation of K, as also observed for N and P, is usually greater close to shade, water sources, and supplement feeders (lounging areas where cattle tend to congregate or rest) under grazing (Mathews et al., 1994a).

Fertilization

In grassland ecosystems, nutrients must be replaced to maintain grassland sustainability. These nutrients can be replaced through fertilization. The amount, strategies, and types of fertilization affect nutrient cycling and distribution (Evers, 2002; Baer and Blair, 2008).

Insufficient nutrient supply is expected to limit ecosystem-level C uptake and storage in many systems (Rastetter et al., 1997). Appropriate fertilization can increase nutrient deposition in grassland systems (Rice, 2000; Franzluebbbers et al., 2005). Reeder et al. (1998) showed increases in soil C in the surface 10 cm of soil after 4 yr as a result of annual applications of 34 kg N ha⁻¹ on conservation reserve lands seeded to a mixture of cool-season grasses. In a 5-yr study of bermudagrass pastures, Franzluebbbers et al. (2002) observed that Mehlich-I extractable soil P increased from 0.8 to 1.6 mg kg⁻¹ yr⁻¹ at a depth of 0 to 6 cm with inorganic N fertilization.

Johnson et al. (2004) have reported that broiler litter applied to pastures in the southeastern USA results in the buildup of soil P due to the difference in N-P-K ratio of the broiler litter and forage crop requirements. In a 2-yr study with Coastal bermudagrass in eastern Texas, Evers (1998) observed that poultry litter application (9 Mg ha⁻¹ yr⁻¹) raised extractable-soil nutrient levels (0- to 15-cm depth) 43% for K, 32% for Ca, and 73% for Mg compared with inorganic fertilization.

The cycling of nutrients is critical for pasture productivity and sustainability. However, knowledge about how management of grazed grasslands affects the flux of nutrients among

important nutrient pools is still lacking. The research in this dissertation was designed to help to further understand the components of the C, N, P, and K cycles and how these cycles interact with different nutrient pools. This information will help to identify and implement pasture management practices to optimize the efficiency of nutrient cycling.

Litter Dynamics in Grazed Grasslands

Role of Litter in Grassland Ecosystems

Plant litter is an important component of grassland ecosystems. The accumulation and quality of litter can have direct or indirect effects on seedling germination, structure and function of the plant community, grassland productivity, nutrient cycling, and soil condition (Hamrick and Lee, 1987; Naeth et al., 1991; Tian et al., 1997; Lavelle et al., 1997, 2001; Xiong and Nilsson, 1999; Rees et al., 2001). The accumulation of litter affects the composition of the plant community by affecting temperature, nutrient availability, and light availability (Weltzin et al., 2005). Plant litter removal significantly increased non-native plant species richness (Patrick et al., 2008). Raich et al. (2000) found that soil respiration rates correlated positively with litter fall rates and with aboveground net primary productivity in grasslands. Plant litter quality affects ecosystem functioning by changing the balance between nutrient release and uptake by decomposers (Semmartin et al., 2004).

Plant litter deposition and its decomposition accelerate the activity of soil biotic components as labile material provides an available source for the decomposers, and nutrients released by decomposers enter different nutrient cycles. For example, internal recycling of N from litter decomposition provides a key resource for ecosystem productivity (Parton et al., 2007). The litter decomposition process also plays a critical role in maintaining the OM level in soil (Kumar and Goh, 2000). Hence, quantification of the litter deposition and decomposition

processes under management strategies in a grassland ecosystem is of vital importance in understanding the function of grassland ecosystems.

Management Effects on Litter Responses

Litter deposition

The amount of litter deposition is related to pasture management practices (Rzende et al., 1999; Dubeux et al., 2006b). Naeth et al. (1991) assessed impacts of long-term cattle grazing (from light to very heavy intensities) on litter and soil OM in mixed prairie, parkland fescue, and foot-hills fescue grasslands of Alberta, Canada. Results showed that heavy intensity and/or early season grazing had greater negative impacts on litter deposition and soil OM mass accumulation than did light grazing intensity and/or late season grazing. In continuously stocked Pensacola bahiagrass pastures with three management intensities: Low ($40 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $1.4 \text{ AU ha}^{-1} \text{ SR}$), Moderate ($120 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ and $2.8 \text{ AU ha}^{-1} \text{ SR}$), and High ($360 \text{ kg N ha ha}^{-1} \text{ yr}^{-1}$ and $4.2 \text{ AU ha}^{-1} \text{ SR}$), Dubeux et al. (2006b) observed that greater management intensity resulted in less litter mass on the pasture early in the growing season, due to greater disappearance of high quality litter during the cool season, and more litter mass later in the season, due to higher rates of litter production during the warm season. Rate of litter deposition was generally greatest for High and ranged between 23 and $40 \text{ kg OM ha}^{-1} \text{ d}^{-1}$ compared with 13 to $30 \text{ kg OM ha}^{-1} \text{ d}^{-1}$ for Low and Moderate management intensities.

Fertilization may also play a role in increasing litter deposition and quality (Beare et al., 2005). Higher nutrient uptake and greater availability of soil nutrients in fertilized systems may increase litter turnover (Reeder et al., 1998; Rice et al., 2000). Foster and Gross (1998) reported that additions of N fertilizer to experimental plots over two growing seasons increased both living plant biomass and litter biomass.

Litter chemical composition

Litter C:N ratio is accepted as a general index of decomposition rate and nutrient mineralization rate. Lower C:N ratio promotes nutrient release, whereas higher ratios induce microbial immobilization (Semmartin et al., 2004). At low C:N ratios (e.g., high N concentrations), decomposers meet their N requirements directly from the litter, with any excess N released to the soil in available mineral forms. At higher initial C:N ratios, net immobilization typically occurs when microbes access N exogenous to the litter and convert it to microbial biomass (Parton et al., 2007). Parton et al. (2007) suggested that net N release occurred when the average C:N ratio of the leaf litter was less than 40.

Lignin has also been considered an important constituent of litter. Lignin contributes to the recalcitrance of plant litter. The early stages of decomposition are dominated by the easily decomposable carbohydrates, while lignin exerts greater control on decomposition rate at the later stages (Corbeels, 2001). Lignin concentration in litter has been used as an indicator for predicting litter turnover in different climates (Meentemeyer, 1978). The lignin and N concentration of litter can cause large changes in the rate of decomposition and N dynamics (Aber et al., 1982). Litter with high C:N (> 109) and lignin:N ratios (> 25) can cause immobilization of N (Dubeux et al., 2006a). Of a number of chemical ratios in litter that were studied, the lignin:N and (lignin + polyphenol):N ratios were linearly correlated with the loss of OM from grass and legume litter (Thomas et al., 1993). So, lignin:N ratio has been used as a predictor of litter decomposition. Parsons et al. (2008) also reported that the initial lignin:P ratio exerted significant control on decomposition rates.

Litter decomposition and nutrient release

Many factors affect the dynamics of litter decomposition and nutrient release. Physical and chemical features of leaf litter cause marked interspecific differences in decomposition rate

(Anderson, 1991; Cornelissen, 1996, 1997). Cornelissen et al. (1997) reported that grasses had physically tougher leaves with higher silica concentration than did herbaceous dicots, resulting in slower grass litter decomposition. Litter decomposition has been negatively correlated with precipitation (Thomas et al., 1993; Semmartin et al., 2004). In the Cerrado region, Nardoto and Bustamante (2003) found that the rates of net N mineralization increased with the onset of the rainy season, likely associated with greater microbial activity. Austin and Vivanco (2006) observed that photodegradation is a dominant control on above-ground litter decomposition in a semi-arid ecosystem. Parton et al. (2007) thought that net N release from litter was predominantly driven by the initial tissue N concentration and mass remaining regardless of climate, edaphic conditions, or biota. In their study, patterns in net N immobilization and release were clearly delineated into four categories based on the initial leaf litter N concentrations: high N (19.8 g N kg^{-1}), intermediate N (10.2 g N kg^{-1}), low N (6.9 g N kg^{-1}), and very low N ($< 3.9 \text{ g N kg}^{-1}$). They found that leaf litter with intermediate to high initial N concentrations showed little or no net N immobilization during the experimental period. Substantial net N release started when $\sim 40\%$ of the mass was lost for the low initial N concentration. The maximum fraction of original N immobilized increased as the initial N concentration decreased to low and very low levels. On average, 170% of the initial N was immobilized (net) in the litter with very low initial N, and net N release occurred only after 60% of the mass had been lost.

Litter decomposition is also related to the types and population of microorganisms. Smith et al. (2003) manipulated the soil community composition using different mesh sizes (0.1, 2, 2.8, and 4.7 mm) to constrain access of specific soil fauna to the litter on the basis of body size. They found that whether litter quality was a significant determinant of litter decomposition rate was dependent on both the soil community composition and length of field exposure. After 30 d

incubation, there was a significant positive relationship between litter quality and decomposition for the most complex community (coarsest mesh size). The strength of this relationship declined with decreasing mesh size, and, for the most restricted community (smallest mesh size), no quality–decomposition relationship was apparent. In contrast, after 60 d incubation, decomposition was most strongly related to litter quality in the smallest mesh size bags and the relationship between quality and decomposition in the two coarsest mesh bags was non-significant.

More frequent defoliation may cause higher rates of net N mineralization and increase the quantity of N available to plants growing in grassland (Holland and Detling, 1990). Shariff et al. (1994) found that a moderate grazing treatment (45% of annual above-ground growth removed) resulted in higher decomposition and soil N mineralization rates, and lower N releases via decomposition than the long term not grazed and heavy grazing treatments (77% of annual above-ground growth removed). Annual litter decomposition rates in the moderate grazing treatment averaged 55% for 1989-1990 and 63% for 1990-1991, while the long term ungrazed and heavy grazing treatments had rates for the same periods of 13 and 19%, respectively. Annual N release from litter and root decomposition in the heavy grazing and long term ungrazed treatments averaged 70 and 38% respectively during the 1989-1990 incubation period, and 51 and 23% during 1990-1991. Hobbie (1996) thought that keeping grasses short increased soil temperature to some degree, and as soil temperature increased, so did nutrient mineralization by soil organisms. This response is likely environment specific and may not be as important in warm as in colder climates.

Fertilization also impacts litter decomposition. In a typical steppe of Inner Mongolia, Liu et al. (2006) reported that additions of N alone or in mixture with P stimulated the rate of litter

decomposition of two grassland species. Nitrogen and P concentrations in litter increased in response to increases in the rates of fertilizer N or mixed N and P additions. Nutrient limitations for decomposition are suggested by positive correlations between decomposition and litter nutrient concentrations (Taylor et al., 1989; Enriquez et al., 1993). Numerous studies have shown that fresh litter may contain insufficient nutrients to support microbial use of the C contained within that litter (Staaf and Berg, 1981). Fertilization could offset the negative effects of low-quality organic materials and accelerate their decomposition (Palm et al., 1997). The results illustrate that inorganic nutrient application can enhance decomposition and increase total available nutrients for subsequent plant uptake, however in many low input systems this option may not be available. Halvorson et al. (1999) studied residues of 11 crops and found that the amount of crop residue returned to the soil increased with increasing N rate. This resulted in increased soil organic C and total soluble N levels in the 0- to 7.5-cm soil depth.

Summary

Management of grassland ecosystems has an important impact on forage production, animal performance, nutrient cycling, and grassland sustainability. The responses of plant, animal, and soil need to be linked with management strategies in order to find the most appropriate management practices for specific grassland ecosystems.

Therefore, research was conducted to understand the effect of a wide range of pasture conditions and management treatments on 1) productivity, nutritive value, and persistence of Tifton 85 bermudagrass pastures, 2) the size of various nutrient pools in Tifton 85 bermudagrass pastures, 3) the fluxes of nutrients through these pools, and 4) the rates of litter accumulation and decomposition and nutrient release from Tifton 85 bermudagrass plant litter.

CHAPTER 3
GRAZING MANAGEMENT EFFECTS ON PRODUCTIVITY, NUTRITIVE VALUE, AND
PERSISTENCE OF 'TIFTON 85' BERMUDAGRASS PASTURE

Introduction

Bermudagrass [*Cynodon dactylon* (L.) Pers.] is one of the most important forage grasses in the southeastern USA. 'Tifton 85' bermudagrass (*Cynodon spp.*) is an interspecific hybrid between a bermudagrass and a stargrass (*Cynodon nlemfuensis* Vanderyst) released in 1992 (Burton et al., 1993). The potential of this grass for use in forage-livestock system has been verified in tropical and subtropical areas (Mislevy et al., 1998). Dry matter (DM) yield and forage nutritive value of Tifton 85 are greater than other bermudagrass cultivars, including 'Tifton 78', 'Coastal', and 'Florakirk' (Hill et al., 1993, 1997, 2001a; Sollenberger et al., 1995; Mandebvu et al., 1999). As a result, Tifton 85 is increasingly used for hay production and grazed pasture in Florida.

Grazing management affects forage production, dry matter intake, and digestibility, as well as grazing behavior of ruminants (Wright et al., 1990; Prigge et al., 1997; Newman et al., 2002). In selecting grazing management strategies, a balance must be sought between the quality and quantity of forage produced. Generally, infrequent grazing, which maximizes forage production, reduces crude protein (CP) concentration and digestibility of the forage produced (Motazedian and Sharrow, 1990; Burns et al., 2002; Mislevy et al., 2008). Studies have reported the individual effects of grazing frequency (Biondini and Manske, 1996; Green and Detling, 2000; Mislevy et al., 2008) or intensity (Burns et al., 2002; Haan et al., 2007; Patton et al., 2007) on yield and nutritive value of a range of forage grasses. However, much less is known about forage productivity and nutritive value responses when grazing frequency and intensity factors are combined; this is especially the case for C₄ grasses. When evaluating grazing management strategies, persistence is an important response variable to be considered. Regardless of the

production and nutritive value of forage under a particular management practice, if the forage does not persist, the strategy being recommended is of little value to the end user.

There have been several studies evaluating grazing management of Tifton 85. Mandebvu et al. (1999) measured defoliation frequency effects on Tifton 85 and Coastal bermudagrass herbage accumulation. Herbage accumulation increased with increasing regrowth interval for both cultivars, and Tifton 85 outyielded Coastal by 34%. Mislevy and Martin (1998) evaluated herbage accumulation and persistence responses of Tifton 85 and Florakirk bermudagrass and 'Florona' and 'Florico' stargrass to defoliation frequency in South Florida. Herbage accumulation of all grasses increased linearly as length of regrowth period increased. Continuously stocked Tifton 85 bermudagrass swards were grazed to maintain sward heights of 5, 10, 15, and 20 cm in Brazil (Sbrissia et al., 2003). Tiller mass increased and tiller density declined across this range. The proportional decline in density was much less than the increase in mass, resulting in a doubling or tripling of herbage mass as sward height increased. Thus one likely mechanism for the often-observed response of increasing herbage accumulation with longer regrowth intervals (i.e., taller swards) is an increase in tiller mass.

In the study by Mislevy and Martin (1998), the herbage accumulation response was consistent across years when grazing occurred every 6 wk, but when grazing occurred every 2 wk, herbage accumulation declined from year to year suggesting loss of stand vigor with very frequent grazing over time. The response to grazing frequency is likely to be affected by grazing stubble height (Pedreira et al., 2000), but there are no data assessing the interaction of these factors for Tifton 85.

As more land area is established with Tifton 85, research evaluating the interaction of grazing intensity and grazing frequency on performance of this grass is needed. The objectives of

this experiment were to evaluate the effects of a range of grazing frequencies and intensities on herbage accumulation, nutritive value, and persistence of Tifton 85 bermudagrass pastures.

Materials and Methods

Study Site

The study was conducted in 2006, 2007, and 2008 at the University of Florida Beef Research Unit, northeast of Gainesville, FL (29°43' N lat; 82°16' W long) on well-established 14-yr Tifton 85 bermudagrass pastures. Soils are classified as Ultisols from the Plummer (loamy, siliceous, thermic Grossarenic Paleaquults) and Spar series (loamy, siliceous, hyperthermic Grossarenic Paleudults). At the beginning of the study, average soil pH was 6.2 and Mehlich I extractable P, K, Mg, and Ca concentrations were 71, 23, 93, and 732 mg kg⁻¹, respectively. Monthly rainfall at the research site for these 3yr is shown in Table 3-1.

Table 3-1. Monthly rainfall at the University of Florida Beef Research Unit, Gainesville Florida during 2006, 2007, and 2008 and the 30-yr average for Gainesville.

Month	Rainfall			30-yr average
	2006	2007	2008	
	-----mm-----			
January	107	90	72	91
February	317	45	78	84
March	63	39	86	107
April	87	27	46	76
Pre-experimental total	574	201	281	358
May	16	64	10	71
June	144	187	210	173
July	60	115	229	147
August	77	113	236	163
September	52	116	36	135
October	65	79	69	64
Grazing period total	414	675	790	753
November	19	15	54	58
December	87	37	21	69
Annual total	1093	929	1147	1238

Experimental Design

The nine treatments were the factorial combinations of three post-graze stubble heights (SH; 8, 16, and 24 cm) with three different lengths of grazing cycle (GC; 14, 21, and 28 d), and were arranged in a randomized complete block design with two replications. A grazing cycle consisted of a grazing period (1-10 h) plus the rest period between grazing events. Each experimental unit was 8 x 50 m.

Pasture Management

All pastures were mowed to an 8-cm SH in March 2006, 2007, and 2008. Grazing was initiated on a given experimental unit each year when sward height was approximately 20 cm taller than the target post-graze SH. Subsequent grazing events occurred according to the established length of GC. At each grazing event, enough yearling beef heifers were assigned to each experimental unit so that within 10 h the herbage could be removed to target SH. Stubble height was measured frequently at 25 locations per experimental unit during each grazing period. When the average of these 25 measurements reached the target SH, that grazing event ended and cattle were removed. The grazing season was from June to October or November each year, and number of grazing events for each treatment in each grazing season is shown in Table 3-2.

All treatments received 250 kg N ha⁻¹ yr⁻¹ in five equal applications of 50 kg ha⁻¹. The N source was NH₄NO₃, and the fertilizer was broadcast on 1 May, 16 June, 14 July, 11 Aug., and 8 Sept. 2006; 2 May, 22 June, 19 July, 17 Aug., and 13 Sept. 2007; and 13 May, 4 July, 4 August, 31 August, and 18 September 2008. Twenty-two kilograms of P and 83 kg K ha⁻¹ were applied with the initial N application each year. The amount of P and K applied was based on soil test recommendations for improved perennial grass pastures.

Table 3-2. Number of grazing events per year for each grazing cycle (GC) by post-graze stubble height (SH) treatment combination during the grazing seasons of 2006, 2007, and 2008.

SH	GC (d)								
	2006			2007			2008		
cm	14	21	28	14	21	28	14	21	28
	----- Number of grazing events -----								
8	10	7	6	9	7	5	9	7	5
16	10	7	6	9	6	5	9	6	5
24	9	7	6	8	6	5	8	6	5

Pasture Sampling

Herbage mass was measured before and after each grazing event using a double sampling technique, i.e., both a direct and indirect measure. The indirect measure used was a disk meter to quantify settling height (Santillan et al., 1979; Pedreira et al., 1999), and the direct measure was hand clipping of herbage. Before animals entered the pasture, two 0.25-m² sites per pasture were selected that represented the range in herbage mass on that experimental unit. Disk settling height was determined at these two sites, and herbage within the 0.25-m² quadrats was clipped to a 5-cm SH, bagged separately, dried at 60°C in a forced-air oven to constant weight, and weighed. Before grazing was initiated, disk settling height was determined at 30 additional sites within each experiment unit. Sites were selected systematically based on a predetermined number of steps between sites so that the entire area of the experimental unit would be adequately represented. Average disk settling height was calculated. After grazing, the same procedure was repeated.

Regression equations were developed to predict herbage mass from the disk settling height. The regression equations used to predict herbage mass and the associated r-square values are

shown in Table 3-3. Pre- and post-graze herbage mass were obtained by entering the average settling height for a given pre- or post-graze sampling event into the appropriate equation.

Table 3-3. Regression equations and associated r-square values for predicting Tifton 85 bermudagrass herbage mass (Mg ha^{-1}) from disk settling height (cm) during the grazing seasons of 2006, 2007, and 2008.

Treatment (SH - GC) [†]	Equation			
	Pre-graze	r-square	Post-graze	r-square
cm - d	2006			
8 - 14	$y = 6.09x - 10.34$	0.85	$y = 6.09x - 19.08$	0.82
8 - 21	$y = 6.36x - 15.62$	0.96	$y = 4.79x - 14.46$	0.94
8 - 28	$y = 6.98x - 22.66$	0.89	$y = 5.39x - 14.33$	0.86
16 - 14	$y = 6.28x - 8.93$	0.91	$y = 6.57x - 12.46$	0.85
16 - 21	$y = 6.67x - 18.52$	0.87	$y = 5.98x - 16.91$	0.89
16 - 28	$y = 6.52x - 14.74$	0.90	$y = 6.46x - 11.51$	0.85
24 - 14	$y = 6.40x - 2.52$	0.83	$y = 5.08x + 12.31$	0.82
24 - 21	$y = 5.69x + 0.99$	0.84	$y = 4.54x + 17.46$	0.84
24 - 28	$y = 5.11x + 14.35$	0.80	$y = 5.66x - 2.74$	0.88
	2007			
8 - 14	$y = 5.74x - 17.51$	0.94	$y = 7.36x - 29.45$	0.93
8 - 21	$y = 5.29x - 14.32$	0.93	$y = 4.39x - 4.26$	0.96
8 - 28	$y = 5.30x - 5.15$	0.91	$y = 3.39x - 1.67$	0.93
16 - 14	$y = 4.75x + 4.15$	0.86	$y = 4.37x + 9.18$	0.84
16 - 21	$y = 3.78x + 9.60$	0.87	$y = 4.68x - 10.25$	0.81
16 - 28	$y = 11.22x - 90.39$	0.95	$y = 6.96x - 18.41$	0.88
24 - 14	$y = 5.91x - 2.71$	0.87	$y = 5.22x + 3.16$	0.92
24 - 21	$y = 5.73x + 13.79$	0.80	$y = 5.59x + 14.07$	0.83
24 - 28	$y = 5.93x - 0.04$	0.88	$y = 6.94x - 13.30$	0.83
	2008			
8 - 14	$y = 5.12x - 9.10$	0.87	$y = 5.0x - 7.52$	0.84
8 - 21	$y = 3.78x + 16.73$	0.82	$y = 5.59x - 8.90$	0.85
8 - 28	$y = 3.03x + 43.11$	0.77	$y = 3.95x + 2.33$	0.92
16 - 14	$y = 6.17x - 13.98$	0.88	$y = 5.84x - 6.96$	0.86
16 - 21	$y = 2.57x + 41$	0.79	$y = 3.85x + 11.30$	0.89
16 - 28	$y = 3.69x + 48.37$	0.88	$y = 6.92x - 6.60$	0.89
24 - 14	$y = 8.91x - 26.57$	0.86	$y = 6.77x + 0.28$	0.85
24 - 21	$y = 7.38x - 22.45$	0.85	$y = 6.0x - 2.70$	0.88
24 - 28	$y = 5.11x + 13.93$	0.90	$y = 8.30x - 24.41$	0.96

[†] SH: post-graze stubble height; GC: length of grazing cycle

Herbage accumulation was calculated by subtracting post-graze herbage mass at the end of a given grazing cycle from pre-graze herbage mass of the following cycle. Herbage accumulation of Cycle 1 was considered to be pre-graze herbage mass of Cycle 1. Seasonal herbage accumulation was calculated by summing herbage accumulation across cycles.

Herbage CP, P, and in vitro digestible organic matter (IVDOM) concentrations were measured to describe forage nutritive value. Hand-plucked herbage samples were collected from each experimental unit during pre-graze sampling of each grazing cycle. This technique attempted to collect a sample representing the forage grazed by the animals by removing grass to the target SH at approximately 20 locations per pasture. These samples were composited to result in a single sample per experimental unit per grazing cycle. Samples were dried for 48 to 72 h at 60°C in a force-air dryer to constant weight and ground in a Wiley mill (Model 4 Thomas-Wiley Laboratory Mill, Thomas Scientific, Swedeboro, NJ) to pass a 1-mm stainless steel screen. Analyses were conducted at the Forage Evaluation Support Laboratory. Nitrogen and P concentrations were measured using modification of the aluminum block digestion procedure (Gallaher et al., 1975). Concentration of CP in herbage DM was calculated as $N \times 6.25$. Herbage IVDOM was determined using a modification of the two-stage technique (Moore and Mott, 1974). Average herbage CP during the grazing season is a weighted average calculated by multiplying CP of the hand-plucked sample and herbage consumed during a given grazing cycle to determine CP content for that cycle. Crude protein content was summed across cycles within a grazing season and divided by the sum of herbage consumed across cycles to arrive at the average herbage CP. Average herbage IVDOM for the total season was calculated similarly but based on organic matter instead of DM.

Herbage persistence was assessed by measuring changes in percent cover of Tifton 85 and in storage organ mass and total non-structural carbohydrate (TNC) and N content and concentration. Percent cover was estimated visually on each experimental unit at initiation of grazing in June 2006 and each year thereafter through 2009. To characterize storage organ traits, four circular core samples (10-cm diameter x 20-cm depth) were taken per pasture after the first and last grazing of the season in 2006, 2007, and 2008. After removing the cores from the soil, they were washed with water and separated into two fractions: above-ground stem base mass and below-ground root + rhizome. Samples were dried at 60°C in a force-air dryer to constant weight, weighed, and ground in a Wiley mill to pass a 1-mm stainless steel screen prior to analysis of N and TNC concentrations.

Storage organ N concentration was determined by using the micro-Kjeldahl technique (Gallaher et al., 1975), and TNC concentration was determined by a modification of the procedure of Christiansen et al. (1988) that was described in detail by Chaparro et al. (1996). This procedure uses invertase and amyloglucosidase to convert starch and oligosaccharides into monosaccharides and measures reducing sugars with a photometric copper reduction method (Nelson, 1944).

Statistical Analysis

To determine the effects of GC and SH on herbage accumulation, nutritive value (CP, P, and IVDOM), and herbage persistence (storage organ mass, N, and TNC), data were analyzed by fitting mixed effects models using the PROC MIXED procedure of SAS (Littell et al., 1996). Year, SH, GC, and their interactions were considered fixed effects. Replication (block) and its interactions with treatment were considered random effects. Year was considered a fixed effect because treatments were imposed on the same experimental unit each year, so there were cumulative effects over time. When treatment x year interaction was significant, data were

analyzed and reported by year. All data are reported as least squares means. Polynomial contrasts were used to evaluate the linear and quadratic effects of GC and SH, and the PDIFF function of the LSMEANS procedure was used to compare year differences when year effects occurred.

Results and Discussion

Herbage Accumulation

There were SH x GC x year interactions for herbage accumulation (Table 3-4), so data were analyzed by year. Herbage accumulation was affected by the interaction of GC x SH in all 3 yr ($P = 0.007$ in 2006, $P = 0.001$ in 2007, and $P = 0.003$ in 2008). Interaction occurred because herbage accumulation increased with increasing GC for the 8- and 16-cm SH treatments, but decreased for the 24-cm SH treatment (Table 3-5). When grazed to an 8-cm SH, herbage accumulation increased linearly from 11.9 to 15.3, 8.7 to 12.0, and 8.7 to 12.4 Mg ha⁻¹ in 2006, 2007, and 2008, respectively, as GC increased from 14 to 28 d. The average increase across the 14- to 28-d range of GC was 3.5 Mg ha⁻¹ (36%) for the 8-cm SH, and the percentage increase was 29, 38, and 43% in 2006, 2007, and 2008, respectively. The increase in relative advantage of the 28- vs. 14-d GC treatment from 2006 to 2008 suggests a cumulative negative impact of close, frequent grazing on Tifton 85 vigor. In contrast, for the 16-cm SH there was a quadratic term in the model each year, and the effect of GC was less pronounced (an average increase of only 0.9 Mg ha⁻¹ or 9% across the range of GC) than for the 8-cm SH. In the third year, the difference in response between the 14- and 28-d GC was only 0.4 Mg ha⁻¹ indicating that the taller SH caused length of GC to be much less important. For the 24-cm SH treatment, as GC increased from 14 to 28 d herbage accumulation decreased 20, 31, and 17% in 2006, 2007, and 2008, respectively. There was a linear pattern to the decline in all years, and the quadratic term was significant in 2006 only. It is quite likely that with tall SH and long GC, average leaf age was considerably greater and photosynthesis less than for shorter SH and GC treatments (Parsons et al., 1988).

This, along with shading and senescence of leaves lower in the canopy is likely responsible for the decline in herbage accumulation with increasing GC when SH was 24 cm.

Table 3-4. Levels of probability (*P*) for the effects of year, post-graze stubble height (SH), grazing cycle (GC), and their interactions on Tifton 85 bermudagrass herbage accumulation, crude protein (CP), in vitro digestible organic matter (IVDOM), and P concentration.

Source of variation	Response variable			
	Herbage accumulation	CP	IVDOM	P
SH	0.013	0.200	0.036	0.075
GC	0.008	< 0.001	0.002	0.006
SH x GC	< 0.001	0.837	0.898	0.448
Year	< 0.001	< 0.001	< 0.001	< 0.001
Year x SH	0.009	0.035	0.019	0.009
Year x GC	0.406	0.330	0.421	0.340
Year x SH x GC	0.036	0.052	0.292	0.370

Research with other forage species has shown greater impact of grazing frequency (the GC variable in the current study) on herbage accumulation when grazing intensity is high. In a grazing study with rhizoma peanut (*Arachis glabrata* Benth.), when residual forage DM after grazing was 500 kg ha⁻¹ (high grazing intensity), total-season average herbage accumulation rate increased from ~ 1.5 to 3.5 g m⁻² d⁻¹ as regrowth interval between grazing events increased from 7 to 49 d, respectively (Ortega et al., 1992). In the same experiment, at a lower grazing intensity, i.e., a residual DM of 1500 kg ha⁻¹, the increase in herbage accumulation rate ranged only from 3.6 to 4.2 g m⁻² d⁻¹ as interval between grazing events increased from 7 to 49 d. ‘Mott’ dwarf elephantgrass (*Pennisetum purpureum* Schum.) clipped to a 10-cm stubble increased herbage accumulation from ~ 6 to 11 Mg ha⁻¹ in one year and 4 to 15 Mg ha⁻¹ in a second year as interval between defoliations increased from 3 to 12 wk (Chaparro et al., 1996). These authors also found that when dwarf elephantgrass was defoliated to 46-cm stubble, defoliation frequency had very little effect on herbage accumulation. Similarly, tall fescue [*Lolium arundinaceum* (Schreb.) S.J.

Darbyshire] annual yields were greater for pastures defoliated to 5-cm SH if subsequent grazings occurred when pasture height was 31 vs. 10 cm (Burns et al., 2002).

In the current study, within a level of GC, increasing SH increased herbage accumulation when GC was 14 d. The response was linear in 2006 and 2008 and had linear and quadratic components in 2007 (Table 3-5). However, herbage accumulation decreased with increasing SH when GC was 21 and 28 d. When GC was 21, the response to SH had both linear and quadratic effects in all years, but when GC was 28 the response to SH was linear in 2006 and 2007 and had linear and quadratic components in 2008. Likewise, dwarf elephantgrass herbage accumulation declined as stubble height increased when interval between defoliation events was long (Chaparro et al., 1996).

The combination of 8-cm SH and 28-d GC had the greatest or equal to the greatest herbage accumulation in the current study. Annual totals were 15.3, 12.0, and 12.4 Mg ha⁻¹ for 2006, 2007, and 2008, respectively. The next greatest herbage accumulation occurred for the 24-cm SH and 14-d GC combination. In 2 of 3 yr of the current study, the lowest herbage accumulation was associated with the 8-cm SH and 14-d GC treatment. When defoliation is frequent and grazing intensity is high, plants may not have sufficient residual leaf area to support photosynthesis and carbohydrate reserves are likely to be depleted over time (Chaparro et al., 1996).

Table 3-5. Herbage accumulation of Tifton 85 bermudagrass pastures as affected by the interaction of length of grazing cycle (GC) and post-graze stubble height (SH) in 2006 ($P = 0.007$), 2007 ($P = 0.001$), and 2008 ($P = 0.003$). Data are means across two replicates ($n = 2$).

SH	2006				2007				2008			
	GC (d)			PC [†]	GC (d)			PC [†]	GC (d)			PC [†]
14	21	28	14		21	28	14		21	28		
cm	-----Mg ha ⁻¹ -----											
8	11.9	12.8	15.3	L	8.7	10.3	12.0	L**	8.7	10.0	12.4	L*
16	12.2	12.0	13.3	L,Q	8.7	8.0	10.0	Q	9.9	9.0	10.3	L,Q**
24	15.0	12.2	12.0	L**,Q*	10.8	8.9	7.4	L**	11.3	9.5	9.4	L*
PC [†]	L	L,Q	L**		L**,Q*	L**,Q**	L		L	L,Q*	L**,Q	
SE [‡]	0.43				0.28				0.39			

[†]PC, polynomial contrast; L = linear and Q = quadratic effects; the letter with no asterisk indicates $P \leq 0.10$ level; *, ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively.

[‡]SE, standard error of a GC x SH interaction mean within year.

Herbage Nutritive Value

There was year x SH x GC interaction for herbage CP (Table 3-4). When analyzed by year, there was SH x GC interaction only in 2006 (Table 3-6). The main effect of GC was significant in 2007 and 2008, but there was no effect of SH in either of those years ($P > 0.346$). Interaction occurred in 2006 because CP decreased with increasing SH for the 14 (149 to 136 g kg⁻¹) and 28-d GC (129 to 108 g kg⁻¹), while for the 21-d GC there was no effect of SH (Table 3-6). Similar results have been obtained for other C4 grasses including stargrass (*Cynodon nlemfuensis* Vanderyst), for which CP increased with increasing stocking rate (Hernández Garay et al., 2004), and limpograss, which had greater CP when grazed to shorter than taller stubble heights (Newman et al., 2002). This pattern of response is probably related to the ratio of young shoots and mature stem in the herbage. Roth et al. (1990) reported that greater defoliation intensity, i.e., shorter SH, resulted in more prostrate growth with predominantly young shoots compared to taller SH with a combination of mature stems and young shoots. Young shoots are greater in CP concentration than mature stems.

Table 3-6. Tifton 85 bermudagrass crude protein (CP) concentration as affected by the grazing cycle (GC) x stubble height (SH) interaction ($P = 0.008$) in 2006. Data are means across two replicates ($n = 2$).

SH	GC (d)			PC [†]
	14	21	28	
cm	-----g kg ⁻¹ -----			
8	149	128	129	L*
16	134	125	111	L*
24	136	135	108	L*, Q
SE [‡]		3		
PC [†]	L	NS	L*, Q	

[†] PC, polynomial contrast; L = linear and Q = quadratic effects; NS = Not significant ($P > 0.10$); a letter with no asterisk following it, $P \leq 0.10$; *, ** indicate significance at $P \leq 0.05$ and 0.01 , respectively.

[‡] SE, standard error of the interaction mean.

Grazing cycle had the most consistent effect on CP. For all three levels of SH in 2006, CP decreased as GC increased (Table 3-6). During 2007 and 2008, CP concentration decreased linearly from 150 to 136 g kg⁻¹ and from 162 to 146 g kg⁻¹, respectively, as GC increased from 14 to 28 d (Table 3-7). This trend is similar to that reported for ‘Florakirk’ bermudagrass (Pedreira et al., 1999), ‘Jiggs’ bermudagrass, and ‘Florona’ stargrass (Mislevy et al., 2008). Longer GC is associated with greater maturity and a smaller leaf:stem ratio (Minson, 1990).

Table 3-7. Tifton 85 bermudagrass herbage crude protein (CP) in 2007 and 2008, and in vitro digestible organic matter (IVDOM) and P concentrations as affected by length of grazing cycle (GC). Data are means across two stubble heights and two replicates for CP (n = 4), and three stubble heights, two replicates, and three years for IVDOM and P (n = 18).

GC	CP		IVDOM	P
	2007	2008		
d	-----g kg ⁻¹ -----			
14	150	162	602	3.1
21	143	152	588	2.9
28	136	146	582	2.8
SE [†]	3	3	4	0.05
PC [‡]	L*	L**	L**	L**

[†] SE, standard error of a grazing cycle mean.

[‡]PC, polynomial contrast; L = linear; *, **, indicate significance at $P \leq 0.05$ and 0.01 .

Herbage IVDOM was affected by a year x SH interaction and the GC main effect (Table 3-4). Only in 2008 was there an SH effect and IVDOM increased linearly as SH increased (Table 3-8). As observed for herbage CP, the main effect of GC had the greatest effect on IVDOM. Averaged across years, IVDOM decreased linearly from 602 to 582 g kg⁻¹ as GC increased from 14 to 28 d (Table 3-7). Decreasing nutritive value with increasing interval between defoliation events is well established in the literature. This has been associated with an increasing stem

percentage and greater lignin concentration in grass cell walls (Akin et al., 1990; Mandebvu et al., 1998).

Table 3-8. Tifton 85 bermudagrass herbage in vitro digestible organic matter (IVDOM) and P concentrations as affected by the interaction of year x post-graze stubble height (SH) ($P=0.19$ and 0.009 , respectively). Data are means across three lengths of grazing cycle and two replicates ($n = 6$).

Year	SH (cm)			PC [†]
	8	16	24	
	IVDOM (g kg ⁻¹)			
2006	623 a [‡]	609 a	615 a	NS
2007	530 c	549 b	547 b	NS
2008	596 b	616a	629 a	L**
SE [§]		7		
	P (g kg ⁻¹)			
2006	2.6 c	2.5 c	2.4 c	L**
2007	3.0 b	2.9 b	2.9 b	NS
2008	3.3 a	3.5 a	3.2 a	L, Q*
SE [§]		0.06		

[†]PC, polynomial contrast; L = linear and Q = quadratic effects; NS = Not significant ($P > 0.10$); a letter with no asterisk following it indicates $P \leq 0.10$; *, ** indicate significance at $P \leq 0.05$ and 0.01 , respectively.

[‡] Means within a response variable and stubble height are not different ($P > 0.10$) if followed by the same letter

[§] SE, standard error of the interaction mean

Similar to the response of IVDOM, herbage P concentration was affected by the year x SH interaction and the main effect of GC (Table 3-4). In 2006, herbage P concentration decreased linearly from 2.6 to 2.4 g kg⁻¹ as SH increased from 8 to 24 cm. There were linear and quadratic effects of SH in 2008 (Table 3-8). The biological significance of the differences in P concentration was likely minimal in all years. The effect of GC was also relatively small. Herbage P concentration decreased only from 3.1 to 2.8 g kg⁻¹ as GC increased from 14 to 28 d (Table 3-7). Belanger et al. (2002) observed that the ratio of young shoots and mature stem has a significant effect on herbage P concentration, with forage containing a greater proportion of young shoots likely to have greater tissue P concentration. Borman (2004) also reported that

herbage P concentration decreases as forage matures. These observations explain the greater P concentration with shorter GC, and suggest that the removal of most residual herbage by grazing to a short SH likely resulted in herbage that had a greater proportion of new leaf tissue.

Herbage P concentration increased 27 to 40% from 2006 to 2008 for the three SH treatments (Table 3-8). Grazing may have increased P cycling and converted more P to available forms in soil (Franzluebbers et al., 2002). In ungrazed pastures in that study, total Mehlich-I extractable soil P at a depth of 0 to 6 cm averaged 427 mg kg⁻¹, however, after 5 yr of grazing total Mehlich-I extractable soil P was 467 and 505 mg kg⁻¹ under low and high grazing pressure, respectively. Therefore, the availability of P for uptake by the plant may increase due to grazing.

Herbage Persistence

Stem base and root-rhizome mass

Stem base mass was affected by the year x SH interaction, but was not affected by GC (Table 3-9). Mass increased linearly with increasing SH in each year (Table 3-10). Stem base mass for the 24-cm SH was nearly six-fold that of 8-cm SH (1430 vs. 240 g m⁻², 1210 vs. 180 g m⁻², and 1260 vs. 230 g m⁻² for 2006, 2007, and 2008, respectively), a function of the fact that total stubble to soil level was considered stem base. Root-rhizome mass was mainly affected by SH (Table 3-11), and mass increased linearly from 623 to 710 g m⁻² as SH increased from 8 to 24 cm (Table 3-12).

The pattern of response observed in the current study is consistent with several previous experiments. Dwarf elephantgrass rhizome mass decreased linearly with both decreasing SH and shorter periods between defoliation events (Chaparro et al., 1996). The bahiagrass genotype, PCA Cycle 4, often had less root-rhizome and stem base mass than more defoliation-tolerant cultivars ‘Argentine’ and ‘Pensacola’ bahiagrass, and these differences were most pronounced when the grasses were defoliated closely or frequently (Interrante et al., in press). After 2 yr of

grazing, rhizoma peanut rhizome mass increased from 500 to 4000 kg ha⁻¹ when post-graze residual herbage mass increased from 500 to 2500 kg ha⁻¹ and grazing frequency was 7 d (Ortega et al., 1992a). Taller post-graze SH or greater residual herbage mass treatments are thought to result in more rapid restoration of positive whole-plant C balance and normal growth patterns, thus plants are dependent on stored C for less time than shorter SH treatments (Chapman and Lemaire, 1993; Richards, 1993).

Table 3-9. Levels of probability (*P*) for the effects of year, post-graze stubble height (SH), grazing cycle (GC), and their interactions on Tifton 85 bermudagrass stem base mass, N content, N concentration, TNC content, and TNC concentration.

Effect	Response variable				
	Mass	N content	N concentration	TNC content	TNC concentration
SH	<0.001	<0.001	0.769	<0.001	0.033
GC	0.123	0.134	0.284	0.581	0.608
SH x GC	0.162	0.321	0.148	0.775	0.368
year	<0.001	<0.001	<0.001	<0.001	0.009
year x SH	0.004	<0.001	0.448	0.001	0.063
year x GC	0.274	0.235	0.109	0.108	0.706
year x SH x GC	0.145	0.404	0.267	0.041	0.007

Table 3-10. Tifton 85 bermudagrass stem base mass as affected by the post-graze stubble height (SH) x year interaction (*P*=0.004) during 2006-2008. Data are means across three lengths of grazing cycle and two replicates (*n* = 6).

Year	SH			PC [†]
	8	16	24	
	-----g m ⁻² -----			
2006	240 a [‡]	970 a	1430 a	L**,Q*
2007	180 b	720 b	1210 b	L**
2008	230 a	1030 a	1260 b	L**,Q**
SE [§]		40		

[†]PC, polynomial contrast; L = linear and Q = quadratic effects; the letter with no asterisk indicates *P* ≤ 0.10 level; *, ** indicate significance at the *P* ≤ 0.05 and 0.01 levels, respectively.

[‡] Means within a column are not different (*P* > 0.100) if followed by the same letter

[§]SE, standard error of a yr x SH interaction mean.

Stem base and root-rhizome N concentration and content

Treatment effects on stem-base N concentration were limited to year effects (Table 3-9), so only stem-base N content will be described. Overall average stem-base N concentration was 13.6 g kg⁻¹.

There was year x SH interaction for stem-base N content (Table 3-9). Stem-base N content increased linearly from 2.1 to 15.4, 2.1 to 12.6, and 4.5 to 25.4 g m⁻² in 2006, 2007 and 2008, respectively, as SH increased from 8 to 24 cm (Table 3-13). The response to SH reflects the large differences in stem-base mass due to SH treatment that were already discussed. For all levels of SH, stem-base N content was greater in Year 3 than in Years 1 and 2.

Root-rhizome N concentration was affected by the main effects of GC, SH, and year (Table 3-11). Root-rhizome N concentration increased linearly from 9.5 to 11.0 g kg⁻¹ as SH increased from 8 to 24 cm (Table 3-12). As GC increased from 14 to 21 to 28 d, root-rhizome N concentration increased from 9.1 to 10.4 to 11.6 g kg⁻¹. Year effect occurred because root-rhizome N concentration increased from 9.2 to 12.2 g kg⁻¹ from 2006 to 2008. Grazing can increase N deposition in soil (Schuman et al., 1999; Franzluebbers et al., 2000; Wright et al., 2004) making more N plant available, increasing N uptake and plant N concentration.

Root-rhizome N content was affected by the main effects of SH, GC, and year (Table 3-11). Root-rhizome N content increased linearly from 5.9 to 7.8 g m⁻² as SH increased from 8 to 24 cm (Table 3-12). When GC increased from 14 to 28 d, root-rhizome N content increased linearly from 5.7 to 8.0 g m⁻². Thus, there was generally greater stored N in rhizomes with taller SH and longer GC.

Table 3-11. Levels of probability (*P*) for the effects of year, post-graze stubble height (SH), grazing cycle (GC), and their interactions on root-rhizome mass, N content, N concentration, total non-structural carbohydrate (TNC) content, and TNC concentration.

Effect	Response variable				
	Mass	N content	N concentration	TNC content	TNC concentration
SH	0.057	0.049	0.148	0.073	0.019
GC	0.571	0.028	0.010	0.521	0.980
SH x GC	0.921	0.495	0.272	0.224	0.092
year	0.542	0.003	0.001	<0.001	<0.001
year x SH	0.866	0.412	0.472	0.362	0.551
year x GC	0.115	0.110	0.226	0.011	0.055
year x SH x GC	0.225	0.123	0.219	0.161	0.176

Table 3-12. Post-graze stubble height (SH) effect on Tifton 85 bermudagrass root-rhizome mass, N concentration and content, and TNC concentration and content during 2006-2008. Data are means across three grazing cycles, two replications, and three years (n = 18).

SH (cm)	Mass (g m ⁻²)	N concentration (g kg ⁻¹)	N content (g m ⁻²)	TNC concentration (g kg ⁻¹)	TNC content (g m ⁻²)
8	623	9.5	5.9	43.1	26.9
16	629	10.7	6.7	53.5	33.2
24	710	11	7.8	42.8	30.6
SE [‡]	40	0.7	0.9	2.4	2.5
PC [†]	L*	L	L*	Q**	Q

[‡]SE, standard error of an interaction mean.

[†]PC, polynomial contrast; L = linear and Q = quadratic effects; a letter followed by no asterisk, *P* ≤ 0.10 level; *, ** indicate significance at the *P* ≤ 0.05 and 0.01 levels, respectively.

Table 3-13. Tifton 85 bermudagrass stem base N content as affected by the interaction of post-graze stubble height (SH) and year (*P* < 0.001) during 2006-2008. Data are means across three lengths of grazing cycles and two replicates (n = 6).

Year	SH (cm)			PC [†]
	8	16	24	
	-----g m ⁻² -----			
2006	2.1 a [‡]	10.3 a	15.4 a	L**
2007	2.1 a	8.0 a	12.6 a	L**
2008	4.5 b	20.8 b	25.4 b	L**
SE [§]	1.1			

[†]PC, polynomial contrast; L = linear; ** indicate significance at *P* ≤ 0.01.

[‡]Means within a column are not different by the LSMEANS test (*P* > 0.10).

[§]SE, standard error of an interaction mean.

Stem base and root-rhizome TNC concentration and content

There were treatment x year interactions for stem-base TNC concentration (Table 3-9), so data were analyzed by year. There were SH x GC interaction effects on stem-base TNC concentration in 2006 ($P = 0.011$) and 2008 ($P = 0.002$), but only a SH main effect in 2007 ($P = 0.049$). The pattern of response was not consistent across years, and there are no specific conclusions that can be drawn regarding effect of defoliation treatments on TNC concentration (Table 3-14).

Stem-base TNC content was also affected by treatment x year interactions (Table 3-9), so data were analyzed by year. In 2006 and 2007, stem-base TNC content was affected by the main effect of SH ($P < 0.001$ in 2006 and $P = 0.002$ in 2007). Stem TNC content increased linearly from 9.7 to 58.2 g m⁻² in 2006 and from 6.0 to 28.9 g m⁻² in 2007, as SH increased from 8 to 24 cm. In 2008, stem-base TNC content was affected by the SH x GC interaction ($P = 0.012$). Within a level of GC, TNC content in stem bases increased with increasing SH, with greatest increase occurring between 8 and 16 cm (Table 3-15).

Table 3-14. Tifton 85 bermudagrass above-ground stem base TNC concentration at the end of the grazing season as affected by the interaction of post-graze stubble height (SH) and grazing cycle (GC) ($P=0.011$ in 2006, 0.354 in 2007, and 0.002 in 2008). Data are means across two replicates ($n = 2$).

SH	2006				2007	2008			
	GC (d)			PC [†]	--g kg ⁻¹ --	GC (d)			PC
	14	21	28			14	21	28	
	-----g kg ⁻¹ -----					-----g kg ⁻¹ -----			
8	32.8	32.9	55.7	L*	35.3	35.1	53.2	30.9	Q**
16	49.8	55.2	47.0	Q*	45.3	40.9	35.0	45.3	NS
24	47.0	40.9	35.3	L	24.1	29.3	38.7	47.8	L*
SE [‡]		5.2			6.1		3.0		
PC	L	Q	L		Q*	NS	L,Q	L	

[†] PC, polynomial contrast; L = linear and Q = quadratic effects; NS = Not significant ($P > 0.10$); a letter not followed by an asterisk, $P \leq 0.10$ level; *, ** indicate significance at $P \leq 0.05$ and 0.01 , respectively.

[‡] SE, standard error of an interaction mean.

Table 3-15. Tifton 85 bermudagrass above-ground stem base TNC content at the end of the 2008 grazing season as affected by the interaction of post-graze stubble height (SH) and grazing cycle (GC)($P=0.012$). Data are the means across two replicates ($n = 2$).

SH	GC (d)			PC [†]
	14	21	28	
cm	-----g m ⁻² -----			
8	8.4	13.3	6.5	Q*
16	42.8	34.5	48.2	NS
24	40.2	43.5	61.5	L
SE [‡]		3.2		
PC	L*,Q*	L**	L**,Q	

[†]PC, polynomial contrast; L = linear and Q = quadratic effects; NS = Not significant ($P > 0.10$); a letter not followed by an asterisk, $P \leq 0.10$ level; *, ** indicate significance at $P \leq 0.05$ and 0.01, respectively.

[‡]SE, standard error of an interaction mean.

Root-rhizome TNC concentration was affected by the interaction of year and GC (Table 3-11). There were no differences among GC treatments in 2006 and 2007, but TNC concentration in root-rhizome increased linearly from 51.5 to 62.9 g kg⁻¹ with increasing GC in 2008 (Table 3-16). Root-rhizome TNC concentration was less in 2007 than in 2006 and 2008, but there is no known reason for this response. There was a main effect of SH on root-rhizome TNC concentration ($P = 0.019$). The response was quadratic (Table 3-12) and was greater for the 16- than the 8- or the 24-cm SH.

Root-rhizome TNC content was affected by the interaction of year and GC (Table 3-11). Variation associated with this response was high. No differences were detected in 2006, but TNC content decreased linearly in 2007 and increased linearly in 2008 as GC increased from 14 to 28 d (Table 3-16). Within a level of GC, root-rhizome TNC content in 2007 was usually less than in 2006 and 2008.

Table 3-16. Tifton 85 bermudagrass root-rhizome TNC concentration and content as affected by the interaction of year and grazing cycle (GC; $P=0.055$ and 0.011 , respectively). Data are the means across three stubble heights and two replicates ($n = 6$).

Year	GC (d)			SE [†]	PC [‡]
	14	21	28		
TNC concentration (g kg ⁻¹)					
2006	53.2 a [§]	57.1 a	50.5 a	3.7	NS
2007	34.4 b	29.0 b	25.3 b		NS
2008	51.5 a	54.3 a	62.9 c		L*
TNC content (g m ⁻²)					
2006	32.9 a	37.7 a	32.6 a	3.3	NS
2007	23.7 b	17.7 b	17.9 b		L
2008	29.7 a	35.8 a	44.0 c		L**

[†] SE, standard error of an interaction mean.

[‡] PC, polynomial contrast; L = linear and Q = quadratic effects; NS = Not significant ($P > 0.10$); a letter not followed by an asterisk, $P \leq 0.10$ level; *, ** indicate significance at $P \leq 0.05$ and 0.01 , respectively.

[§] Means within a column and response variable followed by the letter are not different by the LSMEANS test ($P > 0.10$).

There was a main effect of SH on root-rhizome TNC content (quadratic; $P = 0.057$). The TNC content was 26.5, 33.2, and 30.6 g m⁻² for the 8-, 16-, and 24-cm SH treatments, respectively (Table 3-12). The responses of root-rhizome TNC content were similar, but not nearly as pronounced, as those reported for dwarf elephantgrass (Chaparro et al., 1996). They observed that TNC content was greatly reduced by low SH and short GC and that there was a close positive relationship between rhizome TNC content and persistence. In the current study, the response to SH can be attributed to a greater amount of photosynthetic tissue removed at low SH causing the plant to rely on reserves to greater extent to support regrowth than in the taller SH treatments. The greater rhizome TNC content with increasing GC in 2008 may reflect the benefit of additional time to accumulate and restore carbohydrate reserves prior to subsequent

defoliation (Richards, 1993; Chapman and Lemaire, 1993), but this response was not consistent across years.

Percent cover after three years of grazing

Percent cover of Tifton 85 and common bermudagrass was assessed at the start of the experiment in June 2006 and after 3 yr of grazing in June 2009. Change in cover over 3 yr and actual cover in June 2009 were affected by the main effect of SH. Initial cover of Tifton 85 ranged from 96 to 98% across treatments. After 3 yr, the cover of Tifton 85 decreased to 78, 78, and 57% for post-graze SH treatments of 8, 16, and 24 cm, respectively (Table 3-17).

There was very little change in percent cover across treatments through the end of the second season of grazing. During the winter after the second year of grazing, there was noticeable plant death leaving open areas in the sward the following spring. These areas were substantially recolonized by Tifton 85 stolons during the third year of grazing, but stand loss recovered during the subsequent winter. As indicated by the data (Table 3-17), the decline in cover was most severe in pastures with the tallest SH. This response has been observed before when residue of grazed Tifton 85 was significant high (Pedreira, 1995; Fike et al., 2003), but it has largely been unexplained. It was associated with presence of *Helminthosporium* sp. (Pedreira, 1995), but this was not determined conclusively to be the causative agent. Tifton 85 stubble height of 20 cm entering winter was found to provide greater early-season growth than a stubble of 2 cm, but there were no differences in sward survival (Reis et al., 2008). Our data do not show any consistent reductions in storage organ mass or N or TNC content for the 24-cm treatment, so reserve status does not explain the greater loss of cover for that treatment. Litter mass was greater with increasing post-graze SH (1725, 2370, 2510 kg ha⁻¹ for 8, 16, 24cm, respectively), and this greater litter layer may have presented some constraints to early-season

growth of Tifton 85, but it seems unlikely to be a major limiting factor. It appears that rotationally stocked Tifton 85, for reasons that are not yet clear, should be grazed to leave a stubble no greater than 16 cm. For common bermudagrass, increasing post-graze SH slightly increased percentage cover in pasture. As the percentage cover of Tifton 85 decreased with increasing SH, common bermudagrass cover increased, likely because of greater light penetration to the base of canopy.

Table 3-17. Change in the percentage cover of pasture component as affected by post-graze stubble height.

Component	Post-graze stubble height (cm)			SE [‡]	PC [†] (P-value)
	8	16	24		
- - Change in percentage cover - -					
Tifton 85	-18	-20	-39	10	L (0.059)
Common bermudagrass	1	5	8	3.5	L (0.111)
Percentage cover at experiment's end					
Tifton 85	78	78	57	10	L (0.060)
Common bermudagrass	1	6	8	4	L (0.174)

[†] PC, polynomial contrast; L = linear effect.

[‡]SE, standard error of an interaction mean.

Florakirk bermudagrass was grazed every 7, 21, and 35 d to postgraze stubble heights of 8, 16, and 24 cm (Pedreira et al., 2000). During 2 yr of grazing, botanical composition was never below 96%. Florakirk responded to close, frequent grazing by assuming a prostrate growth habit and tillering profusely, allowing significant leaf area to remain after grazing and reducing the need for reserves to support regrowth.

Conclusions

Tifton 85 bermudagrass herbage accumulation was strongly affected by the interaction of GC and SH. Greatest herbage accumulation occurred with short SH (8 cm) if GC was long (28 d) or with tall SH (24 cm) if GC was short (14 d). Lowest or nearly lowest herbage accumulation

occurred with frequent grazing (14 d) to low SH (8 cm) or infrequent grazing (28 d) to tall SH (24 cm). At intermediate levels of GC (21 d) or SH (16 cm), the level of the other factors had relatively little impact on herbage accumulation.

Tifton 85 bermudagrass nutritive value (CP, P, and IVDOM) was affected by grazing treatment. When SH affected the response, nutritive value was greatest at 8 cm. The effect of length of GC on nutritive value was more pronounced (generally a linear decline with increasing GC) and more consistent than the effect of SH.

Reduction in percentage cover was most pronounced in the 24-cm SH treatment, and this study and others conducted earlier with Tifton 85 suggest that underutilized pastures may experience significant stand loss. The cause of this reduction has not been determined. It does not appear to be related to loss of storage organ mass or reserve storage capacity because these responses were all quite favorable for the 24-cm SH in the current study. Comparing the other two SH levels, as SH increased from 8 to 16 cm stem base and root-rhizome mass and reserve storage generally increased indicating an advantage in persistence-related responses for the 16-cm SH, although no differences in cover existed between 8 and 16 cm after 3 yr of grazing.

If the 24-cm SH is ruled out for persistence reasons, then our data suggest several options depending on producer goals. Greatest herbage accumulation among the remaining treatments is likely to occur when pastures are grazed to ~ 8-cm SH but relatively infrequently (~ 28 d). Although the current study showed no effect on cover, shorter intervals between grazings to the 8-cm SH, to increase nutritive value, are likely to reduce herbage accumulation in subsequent years, reserve storage, and possibly long-term persistence. If greater nutritive value is needed on Tifton 85 pastures, then the 16-cm SH is likely a good choice because at this height the interval

between grazings can be relatively short (14-21 d) to allow high nutritive value without negative impacts on persistence-related responses.

CHAPTER 4
PASTURE MANAGEMENT EFFECTS ON NUTRIENT DISTRIBUTION AMONG
NUTRIENT POOLS IN ‘TIFTON 85’ BERMUDAGRASS PASTURES

Introduction

Nutrients are the organic and inorganic elements (e.g., C, N, P, and K) that are cycling among various reservoirs or “pools” in an ecosystem. Nutrients reside temporarily in the pools, and in a grassland ecosystem these pools include plants and their residues, grazing livestock, soil fauna and flora, and inorganic and organic compounds other than living tissue (Rotz et al., 2005). Other than the atmosphere, the most important nutrient pools in grazed grassland include: 1) live plants, including above- and below-ground tissues; 2) plant litter (dead, undecomposed plant tissue); 3) soil; and 4) living animal biomass, including the grazing animal, the above- and below-ground invertebrates, and microbial populations (Wedin and Russelle, 2007).

Nutrients cycle among pools due to interactions among plants, animals, and soil in grazed grasslands. Plants affect nutrient cycling directly through uptake from soil, use, and loss of nutrients, and indirectly by influencing microbial activity and herbivore grazing behavior (Holland and Detling, 1990; Hobbie, 1992; Frank and Groffman, 1998; Van der krift and Berendse, 2001; Debeux et al., 2006c). Animals impact nutrient cycling through excreta return, affecting the characteristics of the plants, and influencing the physical and chemical properties of soil (Holland et al., 1992; Shariff et al., 1994; Hobbs, 1996; Frank and Evans, 1997). Haynes and Williams (1993) reported that only a small portion of ingested N is retained by livestock, with the majority returning to the land in the form of feces and urine. Soil directly affects nutrient cycling through nutrient sequestration, storage, and output, and indirectly by influencing plant growth, nutrient uptake, and microbial activity (Jobbagy and Jackson, 2000; Ingram et al., 2007). Frank et al. (1995) observed that the quantity and chemical composition of soil organic matter has a major impact on the storage and distribution of N and C in the plant–soil system. For low-

input tropical grassland ecosystems, plant-available N is usually the most limiting nutrient to grass production, so quantity and chemical composition of soil organic matter is of critical importance to N and C cycling and primary productivity, and thus to overall ecosystem function.

Grassland systems have the potential to sequester soil nutrients (Gebhart et al., 1994; Follet et al., 2001; Franzluebbbers and Stuedemann, 2005). Soil C storage on USA rangelands can increase from 0.1 to 0.3 Mg ha⁻¹ yr⁻¹, and planted grasslands, recently established following extended periods of row-crop production, have been shown to store as much as 0.6 to 1.4 Mg C ha⁻¹ yr⁻¹ (Schuman et al., 2002; Franzluebbbers, 2007). The capacity of grasslands to accumulate nutrients and the size of nutrient pools in grasslands is management dependent (Schnabel et al., 2001). Grazing may cause a higher turnover in above-ground biomass, manure, and root material compared with crop systems and ungrazed grassland ecosystems (Post and Kwon, 2000; Conant et al., 2001; Reeder and Schuman, 2002; Franzluebbbers et al., 2000b, 2003). Wilsey et al. (2002) reported that grazed fields had significantly lower ecosystem respiration rates than did ungrazed fields.

Livestock grazing is one of the most prevalent land uses of the world's grasslands. Management strategies have been developed for grazed grasslands in an effort to sustain efficient use of the forage resource by livestock. Grazing management may also influence plant community structure, animal performance, and soil chemical and physical properties (Beegle et al., 2000; Post and Kwon, 2000; Conant et al., 2001; Dubeux et al., 2009). Grazing management alters nutrient storage in grassland ecosystems by modifying the magnitude and relative allocation of nutrients to above- and below-ground biomass. This can alter microclimate and the availability of light, water, and nutrients in systems and modify the functional diversity of plants to influence the quantity and quality of nutrient inputs (Hobbie, 1992; Hobbs, 1996; Frank and

Groffman, 1998; Ingram et al., 2007). The degree of utilization of grasslands also determines whether plant litter or animal excreta are of greater importance in pasture nutrient cycling (Thomas, 1992). Thus, grazing management directly or indirectly influences the interactions and transformations of nutrient elements within pools and the distribution and cycling of nutrients within the plant–soil system.

In the case of grass swards, N inputs are likely needed to minimize pasture degradation associated with production of low quality litter and subsequent N immobilization by microbes (Boddey et al., 2004). Nitrogen fertilization enhances nutrient cycling, acting as a catalyst of key recycling processes, particularly in low soil fertility environments (Dubeux et al., 2007). Fertilization increases the overall biomass production allowing an increase in stocking rate and causing i) greater excreta deposition (Mathews et al., 2001); ii) litter production and litter decomposition rate; and iii) soil organic matter mineralization rate (Dubeux et al., 2006d).

Therefore, understanding the effects of pasture management on cycling of nutrients is critical for designing productive and sustainable grassland systems. However, knowledge is limited regarding effects of grassland management on distribution and cycling of nutrients among important nutrient pools. This research was designed to further understanding of the C, N, P, and K cycles and how these cycles interact with different nutrient pools. This information will aid in development and implementation of pasture management practices that will optimize the efficiency of nutrient cycling. ‘Tifton 85’ bermudagrass (*Cynodon* spp.) was used for this experiment because bermudagrass is one of the two most important perennial warm-season grasses in North Florida, and Tifton 85 is a widely planted cultivar of bermudagrass.

The objective of this experiment was to measure the effect of different defoliation intensities and levels of N fertilization of Tifton 85 bermudagrass pastures on the nutrient

concentration and content of various nutrient pools. The concentration and content of nutrients were measured in the major nutrient pools, including soil (top 20 cm), live root-rhizome, live herbage, and above-ground plant litter.

Materials and Methods

Study Site

This study was conducted in 2006 and 2007 at the University of Florida Beef Research Unit, northeast of Gainesville, FL, at 29°43' N lat on well established Tifton 85 bermudagrass pastures. The area had been established with Tifton 85 for 14 yr at the start of the trial. Soils are classified as Ultisols from the Plummer (loamy, siliceous, thermic Grossarenic Paleaquults) and Spar series (loamy, siliceous, hyperthermic Grossarenic Paleudults). At the beginning of the study, average soil pH was 6.2 and Mehlich I extractable P, K, Mg, and Ca concentrations were 71, 23, 93, and 732 mg kg⁻¹, respectively. Monthly rainfall at the research site for these 2 yr is shown in Table 3.1 (Chapter 3).

Experimental Design

There were five treatments used to represent a wide range of defoliation intensity and N fertilization of rotationally stocked pastures (Table 4-1). Length of grazing cycle (< 10 h grazing time + rest period) was 28 d for all treatments. Three grazing intensity treatments were established based on differences in post-graze stubble height (SH), with levels being 8, 16, and 24 cm. These treatments all received 250 kg N ha⁻¹ yr⁻¹. The fourth and fifth treatments had 24-cm SH and a 28-d grazing cycle, but they received 150 and 50 kg N ha⁻¹ yr⁻¹. These treatments together provided three N fertilization levels at the same level of grazing intensity (24-cm SH). Each experimental unit was 8- x 50-m, and all treatments were arranged in two replicates of a randomized complete block design.

Table 4-1. Description of the five treatments imposed in the research described in Chapter 4.

SH (cm)	GC (d)	Fertilization (kg N ha ⁻¹ yr ⁻¹)
8	28	250
16	28	250
24	28	250
24	28	150
24	28	50

Pasture Management

All pastures were mowed to an 8-cm SH in March 2006 and 2007. Grazing was initiated on a given experimental unit each year when sward height was 20 cm taller than the target post-graze SH. Subsequent grazing events occurred according to the established treatment description. At each grazing event, enough yearling heifers were assigned to each experimental unit to graze the herbage to the target SH within 10 h. Stubble height was measured frequently at 25 locations per experimental unit during each grazing period. When the average of these 25 measurements reached the target SH, that grazing event ended and cattle were removed. The grazing season was from June to October or November each year, and number of grazing cycles per year for each treatment was six in 2006 and five in 2007.

All treatments received 50 kg N ha⁻¹ on 1 May 2006 and 2 May 2007. For treatments receiving 150 or 250 kg N ha⁻¹ yr⁻¹, the remaining N was applied in four equal applications of 25 (150 kg N rate) or 50 kg N ha⁻¹ (250 kg N rate). The N source was ammonium nitrate, and the four split applications of fertilizer were broadcast applied on 16 June, 14 July, 11 Aug., and 8 Sept. 2006, and on 22 June, 19 July, 17 Aug., and 13 Sept. 2007. Twenty-two kilograms of P and 83 kg K ha⁻¹ were applied with the initial N application each year. The amount of P and K applied was based on soil test recommendations for improved perennial grass pastures.

Pasture Sampling

Samples to characterize nutrient concentration and content in the nutrient pools were taken in June, August, and October (representing spring, summer, and autumn, respectively). Cores were taken immediately after a grazing period ended in each pasture in each season. At each sampling date, four core samples (20 x 20 cm to a 20-cm depth) were taken at randomly selected locations from each pasture. These cores were separated into four pools: live herbage, surface plant litter, root-rhizome, and soil. Above-ground live herbage was removed by clipping the 20-x 20-cm sampling area before the core was removed. Above-ground plant litter was also collected before the cores were removed. These samples were dried at 60°C to constant weight and weighed.

Immediately after removal of the core, it was broken apart and spread out in a large tray and dried at 60°C to constant weight. Soil could not be removed by washing because complete recovery of soil was needed to allow nutrient content to be quantified. The material from the dry core sample was passed through a series of sieves of decreasing mesh size (10, 4, and 2 mm) to aid in separating and allocating material to its appropriate pool. Most root-rhizome fraction did not pass through the 10-mm screen. Small quantities of live herbage, above-ground plant litter, and the remaining root-rhizome that had not been recovered were captured by the 4-mm screen. The live herbage and litter were added to the portion of those fractions collected before the core was removed from the ground. Soil passed through the 2-mm screen. Root-rhizome and soil pool samples were dried again at 60°C to constant weight and weighed. For laboratory analyses, all material within a pool type was composited across the four cores per experimental unit from a given sampling date. All plant tissue samples were ground in a Wiley mill to pass a 1-mm stainless steel screen prior to analysis.

The concentration of C, N, P, and K in each pool was determined. For plant tissue, C and N analyses were done using a Flash EA 1112 NC Analyzer. Phosphorus concentration was measured using a modification of the aluminum block digestion procedure (Gallaher et al., 1975). Potassium was determined by flame atomic absorption spectrophotometry. For soil, C and N were determined using a Flash EA 1112 NC Analyzer. The Mehlich-1 extractant was used for soil P and K, and their concentration was measured by Inductively Coupled Plasma (ICP) with EPA method 200.7.

Statistical Analysis

Although the overall experiment included five treatments, comparisons were limited to two sets of three treatments, i.e., comparisons among the three levels of SH (all of which were fertilized at the same N rate) and among the three levels of N fertilizer application (all were grazed to the same SH at the same frequency). The effects of SH and N fertilization on plant pool mass and plant pool and soil nutrient concentrations (C, N, P, and K) and contents were assessed using a repeated measures ANOVA with the PROC MIXED procedure of SAS (Littell et al., 1996). Season (spring, summer, autumn) was the repeated variable, and each pool (live herbage, plant litter, root-rhizome, and soil) was analyzed using a separate analysis of variance. Year, sampling date, SH or N treatment, and their interactions were considered fixed effects. Replication (block) and its interactions with SH or N fertilization were considered random effects. Year was considered a fixed effect because treatments were imposed on the same experiment unit each year, so there were cumulative effects over time. When treatment x year interaction was significant, data were analyzed and reported by year. Least-significant-difference procedures were used for mean separation when season effects were significant (Steel and Torrie, 1980). Polynomial contrasts were used to evaluate the linear and quadratic effects of SH

or N fertilization and the F test of the year effect was used to compare years. Treatment effects and interactions were considered significant if $P \leq 0.10$.

Results and Discussion

Herbage Accumulation

Although measuring herbage accumulation was not a primary objective of this study, it is an important characteristic of grassland systems that likely impacted other responses of interest in this study. In both 2006 and 2007, herbage accumulation decreased linearly as SH increased from 8 to 24 cm (Table 4-2). The 24-cm SH treatment allowed a large amount of residue, likely increasing the average leaf age of the canopy and the proportion of shaded leaf area, both increasing respiration and having a negative effect on herbage accumulation. Accumulation increased linearly with increasing N rate in both years. This response is consistent with prior observations for Tifton 85 bermudagrass (Vendramini et al., 2008).

Table 4-2. Annual herbage accumulation as affected by post-graze stubble height and N fertilization rate in 2006 and 2007. Means across two replications (n=2).

Year	Stubble height (cm)			SE [†]	PC [‡]
	8	16	24		
	----- kg ha ⁻¹ -----				
2006	15 320	13 340	12 000	201	L**
2007	12 040	10 040	7380	377	L**
	N fertilization (kg N ha ⁻¹)				
	50	150	250		
	----- kg ha ⁻¹ -----				
2006	10 370	11 190	12000	164	L**
2007	6780	6960	7380	162	L*

[†]SE, standard error.

[‡]PC, polynomial contrast; L = linear effect. * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively.

Live Herbage, Plant Litter and Root-Rhizome Mass

Nitrogen fertilization

There were main effects of N rate on live herbage ($P = 0.061$) and root-rhizome mass ($P = 0.093$), but not on litter mass ($P = 0.874$). There also were main effects of season on live herbage ($P = 0.002$), plant litter ($P < 0.001$), and root-rhizome ($P < 0.001$) mass.

Post-graze live herbage mass increased linearly ($P = 0.061$; 6410 to 6880 kg ha⁻¹) with increasing N rate. This difference is relatively small considering the range in N rates applied, but the pattern of response reflects N responses in the literature. Increasing N fertilization rate increased herbage growth rate, tiller density and height (Wilman, 1980), and ultimately herbage mass. Tifton 85 tiller density and mass increased as N rates increased (Premazzi et al., 2003), likely explaining the greater post-graze live herbage mass for greater N rates in the current study.

There was a quadratic effect ($P = 0.093$) of N rate on root-rhizome mass (8740, 10 300, and 9090 kg ha⁻¹ for N rates of 50, 150, and 250 kg N ha⁻¹, respectively). Greater root-rhizome mass for the 150- than the 50-kg N rate likely is associated with superior herbage accumulation of higher N rate treatments (Table 4-2), and greater mass for the 150- than the 250-kg N rate treatment may be associated with greater partitioning to above- vs. below-ground organs associated with the highest N rate. Davidson (1969a) found a linkage between the partitioning of photosynthate and N rate, and in a companion study it was observed that root:shoot ratio decreased from 1.54 to 0.46 for perennial ryegrass (*Lolium perenne* L.) with greater application of N (Davidson, 1969b). Litter mass ranged only from 2620 to 2700 kg ha⁻¹ and was not affected by N rate ($P = 0.874$).

Season affected the responses of live herbage, plant litter, and root-rhizome mass. There were no differences in live herbage mass between spring and summer, but both were greater than autumn (Table 4-3). Herbage accumulation of C₄ grasses in this environment is nearly always

greater in spring and summer, if soil moisture is adequate, than in autumn (Interrante et al., 2009).

Plant litter mass in the current study reached a maximum in summer (3350 kg ha⁻¹), and there was no difference in litter mass between spring and autumn. Increasing litter mass in summer is likely a result of greater herbage accumulation and increasing maturity of post-graze residue. Dubeux et al. (2006b) found that bahiagrass litter deposition was lowest in spring and increased through summer; it remained relatively constant thereafter as herbage accumulation rate decreased. In the current study, root-rhizome mass decreased from 11 200 in spring to 7570 kg ha⁻¹ in autumn.

Table 4-3. Season effect on mass of live herbage ($P = 0.002$), above-ground plant litter ($P < 0.001$), and root-rhizome ($P < 0.001$) pools. Data are means across two replicates, three N rates, and 2 yr ($n = 12$).

Pool	Season			SE [‡]
	Spring	Summer	Autumn	
	----- kg ha ⁻¹ -----			
Live herbage	7040 a [†]	6950 a	5890 b	179
Plant litter	2110 a	3350 b	2500 a	130
Root-rhizome	11 200 a	9380 b	7570 c	554

[†] Season means within a pool are not different ($P > 0.10$) if followed by the same letter.

[‡] SE, standard error.

Grazing intensity

There was an SH x season interaction for mass of live herbage ($P = 0.026$) and plant litter ($P = 0.011$), but there were only main effects of SH ($P = 0.036$) and season ($P = 0.003$) for root-rhizome mass. Within each season, mass of live herbage increased linearly with increasing SH (Table 4-4). In autumn, the mass of live herbage in the 24-cm SH was more than twice as great as the mass of live herbage in the 8-cm SH (6190 vs. 2730 kg ha⁻¹; Table 4-4). Because pool samples were taken after grazing events and post-graze SH varied from 8 to 24, these differences simply reflect the grazing intensities imposed. The mass of live herbage was not different

between spring and summer within a level of SH, but these two seasons were greater than autumn, likely a function of decreasing tiller appearance rate and lower herbage accumulation in autumn (Interrante, 2008).

Plant litter mass increased linearly with increasing SH during summer and autumn but not during spring. The seasonal response is likely due to the shorter time that the SH treatment had been imposed prior to sampling in spring compared to summer and autumn. Increasing litter mass with increasing SH was also observed for bahiagrass in a study conducted in the same environment as the current research (Dubeux et al., 2006a). Thomas (1992) indicated that with increasing grazing intensity, a larger proportion of plant tissue is removed by grazing and the role of plant litter in nutrient cycling decreases, while the role of animal excreta increases. Plant litter mass was greater or tended to be greater in summer compared with spring and autumn for a given SH treatment. Root-rhizome mass decreased from 9810 to 6890 kg ha⁻¹ from spring through autumn and increased linearly from 7080 to 9090 kg ha⁻¹ with increasing SH (Table 4-4).

Nutrient Concentrations in Nutrient Pools

Potassium concentration

Nitrogen rate affected K concentration in all nutrient pools except for root-rhizome. Potassium concentration in live herbage and plant litter increased linearly with increasing N rates (Table 4-5), but there was no difference in root-rhizome K concentration among fertilization treatments. The K concentration increased from 18.5 to 23.1 g kg⁻¹ in live herbage and from 2.8 to 5.1 g kg⁻¹ in plant litter as N rate increased.

In soil, K concentration decreased linearly from 0.059 to 0.046 g kg⁻¹ as N rates increased (Table 4-5). Increasing N fertilization increased herbage accumulation and K concentration in the plant. Greater K uptake by the grass with increasing N rate likely caused a decrease of K in

the soil around the roots, thus explaining the decrease in soil K concentration. Mouat (1983) found that for most plants (including grasses), the cation exchange capacity of the roots increases with increasing N supply, and this may be partially responsible for the greater tissue K concentration. As solution K is removed or taken up by plants, the K on the cation exchange sites reacts to establish a new equilibrium with the soil solution K (Snyder and Leep, 2007).

Table 4-4. Stubble height x season interaction for mass of live herbage ($P = 0.026$), above-ground plant litter ($P = 0.011$), and root-rhizome pools ($P = 0.881$). Data are means across two replicates and 2 yr ($n = 4$).

Pool/Season	Stubble height (cm)			SE [†]	Mean	PC [‡]
	8	16	24			
	-----kg ha ⁻¹ -----					
Live herbage						
Spring	5310 a [§]	5620 a	6870 ab			L**
Summer	5760 a	6310 a	7570 a	261		L**
Autumn	2730 b	4340 b	6190 b			L**
Plant litter						
Spring	1810 a	1960 a	2000 a			NS
Summer	2040 a	2360 b	3580 b	176		L**
Autumn	1780 a	1910 a	2370 a			L*
Root-rhizome						
Spring	8400	10 100	10 900		9810 a [¶]	
Summer	7530	8930	8880	845	8440 b	
Autumn	5320	7890	7450		6890 c	
Mean	7080	8980	9090			L* [#]

[†] SE, standard error

[‡] PC, Polynomial contrast for effect of stubble height within pool and season. L = linear; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

[§] Season means within a pool and stubble height not followed by the same letter are different ($P < 0.10$).

[¶] Season main effect means for root-rhizome mass not followed by the same letter are different ($P < 0.10$).

[#] Main effect of stubble height on root-rhizome mass.

There was a quadratic effect of SH on K concentration in live herbage. This response was associated with a lower K concentration in the 16-cm SH compared to 8- and 24-cm SH treatments, but the difference among treatments was small. In plant litter and root-rhizome, K concentration increased linearly with increasing SH, but SH had no effect on soil K concentration (Table 4-6).

Phosphorus concentration

Nitrogen fertilization affected P concentration of only the plant litter pool (Table 4-5), which increased linearly with increasing N rate. Grazing intensity had very limited impact on plant P concentration, although differences were detected for live herbage and root-rhizome (Table 4-6). There was no consistent directional response of tissue P concentration, and these changes are thought to be of limited biological significance. There was no significant effect of SH on P concentrations of the soil and plant litter pools (Table 4-6).

Nitrogen concentration

Nitrogen fertilization increased N concentration in live herbage ($P < 0.001$), plant litter ($P < 0.001$), and root-rhizome ($P < 0.001$) pools, but there was no effect on N concentration of the soil pool ($P = 0.220$). Live herbage N concentration increased linearly from 7.9 to 13.5 g kg⁻¹ as N rate increased from 50 to 250 kg N ha⁻¹ (Table 4-5). Vendramini et al. (2008) reported in their study that CP concentration in Tifton 85 herbage increased linearly with increasing levels of N fertilization from 0 to 80 kg ha⁻¹ (from 140 to 190 g kg⁻¹ and 115 to 135 g kg⁻¹ for 2- and 4-wk regrowth intervals, respectively). Increasing N fertilization resulted in increased N uptake by the plant and greater plant-tissue N concentration (Haynes and Willams, 1993).

For plant litter and root-rhizome pools, tissue N concentration increased linearly from 11.5 to 18.4 g kg⁻¹ and 7.1 to 10.6 g kg⁻¹, respectively, with increasing N rate (Table 4-5).

Interestingly, the plant litter pool had greater N concentration than the live herbage and root-

rhizome pools. The live herbage N concentration was low (7.9 to 13.5 g kg⁻¹) because it represented post-graze bermudagrass stubble, but that alone does not explain the relative response of live and dead plant material. Dubeux et al. (2006b) studied bahiagrass litter

Table 4-5. Nitrogen rate effect on nutrient concentrations of live herbage, above-ground plant litter, root-rhizome, and soil pools. Data are means across two replicates, three seasons, and 2 yr (n = 12).

Nutrient/Pool	N fertilization (kg ha ⁻¹ yr ⁻¹)			SE [†]	PC [‡]
	50	150	250		
	----- g kg ⁻¹ -----				
Potassium					
Live herbage	18.5	19.1	23.1	0.7	L**
Plant litter	2.8	4	5.1	0.3	L**
Root-rhizome	7.7	7.7	7.8	0.4	NS
Soil	0.059	0.045	0.046	0.003	L*
Phosphorus					
Live herbage	3.1	3	2.9	0.1	NS
Plant litter	1.7	1.7	1.9	0.06	L*
Root-rhizome	2	1.9	2	0.02	NS
Soil	0.080	0.058	0.067	0.009	NS
Nitrogen					
Live herbage	7.9	10.9	13.5	0.4	L**
Plant litter	11.5	14.1	18.4	0.6	L**
Root-rhizome	7.1	8.7	10.6	0.1	L**
Soil	0.68	0.64	0.72	0.06	NS
Carbon					
Live herbage	435	436	439	1	NS
Plant litter	451	454	472	5	L**
Root-rhizome	454	477	501	6	L**
Soil	9	9	10	1	L*

[†] SE, standard error

[‡] PC, Polynomial contrast for effect of N rate within nutrient and pool. L = linear; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.100$.

decomposition from pastures managed at three intensities, including N fertilization ranging from 40 to 360 kg N ha⁻¹ yr⁻¹. Litter N concentration ranged from 15 to 31 g kg⁻¹ and increased during the incubation period for all treatments owing in part to the more rapid disappearance of litter C

than litter N from C₄ grasses (Dubeux et al., 2006b). In addition, microbes access N exogenous to plant litter during litter decomposition causing an increase in litter N concentration (Parton et al., 2007). Thus the higher N concentration of the litter is indicative of the relative recalcitrance of N in litter and the immobilization of soil N by microbes. The litter pool, particularly due to its low quality in warm-climate grasslands, acts as a sink of available soil N (Myers et al., 1986; Thomas and Asakawa, 1993).

Table 4-6. Grazing intensity effect on nutrient concentrations of live herbage, above-ground plant litter, root-rhizome, and soil pools. Data are means across two replicates, three seasons, and 2 yr (n = 12).

Nutrient/Pool	Stubble height (cm)			SE [†]	PC [‡]
	8	16	24		
	----- g kg ⁻¹ -----				
Potassium					
Live herbage	23.1	21.8	23.1	0.6	Q*
Plant litter	3.9	3.9	5.1	0.3	L**, Q
Root-rhizome	6.9	7.1	7.8	0.3	L
Soil	0.045	0.043	0.046	0.002	NS
Phosphorus					
Live herbage	3.0	2.8	2.9	0.06	Q
Plant litter	2.0	2.0	1.9	0.07	NS
Root-rhizome	1.9	1.9	2.0	0.02	L, Q
Soil	0.063	0.078	0.067	0.011	NS
Nitrogen					
Live herbage	15.7	13.8	13.5	0.8	L*
Plant litter	18.0	17.5	18.4	0.8	NS
Root-rhizome	10.8	10.3	10.6	0.2	NS
Soil	0.56	0.7	0.75	0.01	L**, Q*
Carbon					
Live herbage	438	439	439	1	NS
Plant litter	466	471	472	5	NS
Root-rhizome	485	499	500	9	NS
Soil	8.6	9.6	10.6	0.5	L*

[†] SE, standard error.

[‡] PC, Polynomial contrast for effect of stubble height within nutrient and pool. L = linear, Q = quadratic; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. L or Q not followed by asterisk, $P \leq 0.10$, NS = not significant, $P > 0.10$.

Decreasing grazing intensity did not affect plant litter or root-rhizome N concentration, but it did cause a linear decrease in live herbage (15.7 to 13.5 g kg⁻¹) N concentration and an increase in soil N concentration (0.56 to 0.75 g kg⁻¹; Table 4-6). Roth et al. (1990) reported that greater defoliation intensity, i.e., shorter remaining SH, resulted in more prostrate growth with predominantly young shoots compared to taller SH with a greater proportion of mature stems. Young shoots contain higher N concentration than mature stems. Also, taller stubble is associated with more standing dead tissue with lower N concentration (Hoglund, 1985). Increasing grazing intensity increased herbage accumulation (Table 4-2) and N concentration in herbage (Table 4-6), likely resulting in greater N removal from soil. This may explain lower soil N concentration.

Carbon concentration

The C concentration of plant litter, root-rhizome, and soil increased linearly from 451 to 472 g kg⁻¹, 454 to 501 g kg⁻¹, and 9 to 10 g kg⁻¹, respectively, as N rate increased from 50 to 250 kg N ha⁻¹ (Table 4-5). Carbon concentration of live herbage ranged only from 435 to 439 g kg⁻¹ and was not affected by N treatments. In soil beneath bromegrass (*Bromus inermis* Leyss.), Malhi et al. (1997) observed that the concentration of total C in the 0- to 5-cm soil layer increased from 50.3 g kg⁻¹ in the zero-N treatment to 61.6 g kg⁻¹ with 56 kg N ha⁻¹, and to 64.2 g kg⁻¹ with the 112 kg N ha⁻¹.

Carbon concentrations in live herbage, plant litter, and root-rhizome was not affected by grazing intensity, but soil C increased linearly from 8.6 to 10.6 g kg⁻¹ as SH increased from 8 to 24 cm (Table 4-6). Carbon concentration in soil has been reported to be highly related to root turnover and the conversion of litter to soil organic matter (Conant et al., 2003). For the high SH treatment, there was greater plant and root mass than the lower SH treatment (Table 4-4). This was consistent with the increase of C concentration in the soil pool.

Nutrient Content in Nutrient Pools

Interactions of N rate x season and SH x season were significant only for the plant litter pool (K, P, and N content for N rate x season; K, P, N, and C content for SH x season). Because the other pools had only main effects of N rate or SH, the main effects of N and SH are shown for plant litter to provide the complete picture of pool nutrient content (Tables 4-7 and 4-9). The interactions of N x season and SH x season are also described (Tables 4-8 and 4-10).

Potassium content

Potassium content in live herbage and plant litter increased linearly with increasing N rate (Table 4-7). In the plant litter pool, K content at the highest N rate (250 kg N ha⁻¹ yr⁻¹) was almost double that of the lowest N rate (50 kg N ha⁻¹ yr⁻¹), but the total pool size was small (14 vs. 8 kg K ha⁻¹, respectively). Nitrogen fertilization had no effect on K content in the root-rhizome pool. In the soil pool, K content decreased linearly as N rate increased, following the same pattern as soil K concentration.

The manner in which grasses respond to K and the amount needed depends to a large extent on the level of N nutrition. An increasing N supply enhances growth, and consequently, increases the demand for K (Wilkinson et al., 2000; Kayser and Isselstein, 2005). In the current study, the higher rates of N fertilization likely stimulated the plant to absorb more K from soil. The result was an increase in K content in live herbage and a decrease in soil K content as N rate increased.

There was interaction of N rate x season for K content ($P = 0.051$) (Table 4-8). There was no difference among N rates in spring, but K content in plant litter increased linearly in summer and autumn with increasing N rate. Litter K content in summer was more than two-fold greater for the 250 vs. 50 kg N ha⁻¹ treatment (25.6 vs. 11.0 kg ha⁻¹). Within the 50 and 150 kg N

fertilization levels, there was no season effect on K content in plant litter, but for 250 kg N treatment litter, K content was greater in summer than in spring and autumn.

There was a main effect of SH on K content of live herbage ($P < 0.001$), plant litter ($P = 0.014$), and root-rhizome ($P = 0.027$), but no effect on K content of soil ($P = 0.774$). The response of live herbage and plant litter to increasing SH had linear and quadratic terms, but the response of root-rhizome was linear (Table 4-9). Live herbage, plant litter, and root-rhizome K content increased as SH increased from 8 to 24 cm.

There was SH x season interaction for K content of plant litter ($P = 0.005$; Table 4-10). Plant litter K content increased in summer and autumn with increasing SH, but did not differ in spring among treatments. Within the SH treatments, K content in summer was greater than spring and autumn, and there was no difference between the latter seasons.

Phosphorus content

Fertilization had no effect on P content in nutrient pools with the exception of plant litter which increased linearly with increasing N rate (Table 4-7). The response observed for plant litter was a function of P concentration (Table 4-5) because litter mass was not affected by N rate. In bermudagrass pastures, Franzluebbbers et al. (2002) also found that Mehlich-I extractable soil P generally was not different among N fertilization treatments.

The interaction of season and N rate also affected plant litter P content ($P = 0.038$) (Table 4-8). During summer and autumn, P content in plant litter increased linearly as N rate increased, but there was no effect of N fertilization in spring. Litter P content was greatest or equal to the greatest among seasons during the summer.

Grazing intensity affected P content of all nutrient pools except soil. For the plant fractions, P content increased linearly as SH increased for litter and root-rhizome pools and there were significant linear and quadratic effects of SH for live herbage (Table 4-9). These responses

reflect the greater pool mass associated with taller SH. Our results were similar to the observation of Chaneton et al. (1996) and Haan et al. (2007) that showed that decreasing grazing intensity caused an increase in P content of above-ground plant parts and the root system.

Table 4-7. Nitrogen rate effect on nutrient content of live herbage, above-ground plant litter, root-rhizome, and soil pools. Data are means across two replicates, three seasons, and 2 yr (n = 12).

Nutrient/Pool	N fertilization (kg ha ⁻¹ yr ⁻¹)				PC [‡]
	50	150	250	SE [†]	
	-----kg ha ⁻¹ -----				
Potassium					
Live herbage	118	128	159	7	L**
Plant litter	8	11	14	2	L*
Root-rhizome	67	77	70	5	NS
Soil	182	143	139	9	L*
Phosphorus					
Live herbage	19.8	20.0	20.2	1.0	NS
Plant litter	4.4	4.5	5.2	0.3	L
Root-rhizome	17	20	18	1	NS
Soil	243	180	203	29	NS
Nitrogen					
Live herbage	50	71	92	3	L**
Plant litter	30	38	49	2	L**
Root-rhizome	63	87	95	4	L**, Q
Soil	2110	2020	2270	171	NS
Carbon					
Live herbage	2790	2870	3020	60	L*
Plant litter	1180	1220	1260	58	NS
Root-rhizome	3980	4980	4580	349	NS
Soil	28 200	29 300	32 100	2220	L**

[†] SE, standard error.

[‡] PC, Polynomial contrast for effect of N rate within nutrient and pool. L = linear, Q = quadratic; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. L or Q not followed by an asterisk, $P \leq 0.10$, NS = not significant, $P > 0.10$.

Table 4-8. Nitrogen rate x season interaction for nutrient content in plant litter. Data are means across two replicates and 2 yr (n = 4).

Nutrient/Season	N fertilization (kg ha ⁻¹ yr ⁻¹)			SE [†]	PC [‡]
	50	150	250		
	----- kg ha ⁻¹ -----				
K content					
Spring	6.4 a [§]	10.3 a	7.6 a		NS
Summer	11.0 a	13.5 a	25.6 b	2.4	L*
Autumn	5.3 a	9.1 a	9.9 a		L**
P content					
Spring	4.1 a	3.5 a	3.7 a		NS
Summer	5.9 b	5.5 b	7.5 b	0.4	L
Autumn	3.4 a	4.6 ab	4.3 a		L
N content					
Spring	24.4 a	27.3 a	30.5 a		NS
Summer	36.1 a	45.8 b	68.0 b	3.7	L**
Autumn	29.5 a	41.5 b	47.5 c		L**

[†]SE, standard error.

[‡]PC, Polynomial contrast for effect of N rate within nutrient and season. L = linear; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. L followed by no asterisk, $P \leq 0.10$, NS = not significant, $P > 0.10$.

[§] Season means within a pool and N rate not followed by the same letter are different ($P > 0.10$).

Plant litter P content also was affected by the interaction of SH and season ($P = 0.006$).

There was no difference among SH treatments in spring and autumn, but P content increased from 3.9 to 7.5 kg ha⁻¹ in summer as SH increased (linear and quadratic effects; Table 4-10).

Within the 8- and 16-cm SH treatments, P content was not different among seasons, but for the 24-cm SH the P content in summer was greater than in spring or autumn. This was due to relatively high litter accumulation in summer.

Nitrogen content

Nitrogen fertilization affected N content of live herbage, plant litter, and root-rhizome, but it had no effect on soil (Table 4-7). Live herbage and plant litter N content increased linearly with increasing N rate. In root-rhizome, N content also increased as N rate increased, but the response had both linear and quadratic terms. In root-rhizome, N content increased up to 50%

when N rate increased from 50 to 250 kg N ha⁻¹ yr⁻¹. Similar or greater responses were observed for live herbage and plant litter. The increase in N content was a function of greater N concentration in plant fractions with increasing N rate (Table 4-5). Nitrogen concentration of soil was not affected by N fertilization, and this resulted in a nearly stable soil N content with increasing N rate.

Table 4-9. Stubble height effect on nutrient content of live herbage, above-ground plant litter, root-rhizome, and soil pools. Data are means across two replicates, three seasons, and 2 yr (n = 12).

Nutrient/Pool	Stubble height (cm)			SE [†]	PC [‡]
	8	16	24		
	-----kg ha ⁻¹ -----				
Potassium					
Live herbage	107	117	159	3	L**, Q**
Plant litter	7.5	8.1	14.4	1.1	L**, Q
Root-rhizome	49	63	70	5	L*
Soil	141	136	139	6	NS
Phosphorous					
Live herbage	14	16	20	1	L**, Q*
Plant litter	3.7	4.1	5.2	0.2	L**
Root-rhizome	14	17	18	1	L*
Soil	200	246	203	38	NS
Nitrogen					
Live herbage	69	71	92	3	L**, Q*
Plant litter	32	36	49	2	L**, Q*
Root-rhizome	80	88	95	2	L**
Soil	1790	2220	2270	57	L**, Q*
Carbon					
Live herbage	2020	2380	3020	63	L**
Plant litter	877	976	1260	57	L**
Root-rhizome	3470	4490	4580	264	L*
Soil	27 400	30 200	32 100	1330	L*

[†] SE, standard error.

[‡] PC, polynomial contrast for effect of stubble height within nutrient and pool. L = linear, Q = quadratic; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. Q not followed by an asterisk, $P \leq 0.10$, NS = not significant, $P > 0.10$.

Table 4-10. Stubble height x season interaction for nutrient content in plant litter. Data are means across two replicates and 2 yr (n = 4).

Nutrient/Season	Stubble height (cm)			SE [†]	PC [‡]
	8	16	24		
	-----kg ha ⁻¹ -----				
Potassium					
Spring	6.6 a [§]	7.2 a	7.6 a	1.9	NS
Summer	9.5 b	9.9 b	25.6 b		L**, Q
Autumn	6.4 a	7.2 a	9.9 a		L**
Phosphorous					
Spring	4.0 a	3.9 a	3.7 a	0.4	NS
Summer	3.9 a	4.5 a	7.5 b		L**, Q*
Autumn	3.3 a	4.0 a	4.3 a		NS
Nitrogen					
Spring	25.3 a	30.2 a	30.5 a	2.8	NS
Summer	39.9 b	42.7 b	68.0 b		L**, Q*
Autumn	31.8 a	34.8 a	47.5 c		L**, Q*
Carbon					
Spring	864 a	918 a	934 a	76.4	NS
Summer	955 a	1100 b	1750 b		L**, Q*
Autumn	813 a	909 a	1090 a		L*

[†] SE, standard error of an interaction mean.

[‡] PC, polynomial contrast for effect of stubble height within nutrient and season. L = linear, Q = quadratic; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. Q not followed by an asterisk, $P \leq 0.10$, NS = not significant, $P > 0.10$.

[§] Season means within a nutrient and stubble height followed by the same letter are not different ($P > 0.10$).

Plant litter N content also was affected by the interaction between season and N rate ($P = 0.025$; Table 4-8). In spring, there was no difference in plant litter N content among N rates, but N content increased linearly with increasing N rate in summer and autumn. Within an N rate, N content in plant litter in summer was always as great as or greater than in spring and autumn.

Grazing intensity affected N content of the nutrient pools. The N content in each nutrient pool increased with increasing SH. The effect was linear for root-rhizome, and there were linear and quadratic effects for live herbage, plant litter, and soil (Table 4-9). The smaller soil N content under high grazing intensity (lower SH) compared to medium and high grazing

intensities is consistent with the findings of other researchers (Derner et al., 1997; Schnabel et al., 2001; Haan et al., 2008), reflecting decreased inputs of both above- and below-ground vegetation and possibly accelerated decomposition of litter and soil organic matter. Wright et al. (2004) indicated that high grazing intensity (low SH) resulted in lower soil N content than low-grazing intensity (high SH) due to faster turnover of animal excreta, relative to plant components, and physical disruption of soil at high grazing pressure, which hastened the loss of soil C and N. Also, there generally was less plant litter mass when SH was low (Table 4-4).

Based on the relatively tight coupling of soil C and N under most conditions, changes in management that drive changes in soil C should result in concomitant changes in soil N (Conant and Paustian, 2001c; Conant et al., 2005). Conant et al. (2005) regressed N sequestration on C sequestration rate, and C sequestration rate explained nearly 60% of the variation in N sequestration rate. In this study, C content in each nutrient pool increased linearly, similar to the increase in N, as stubble height increased (Table 4-9).

The interaction of SH and season affected N content in plant litter ($P = 0.004$; Table 4-10). In spring, there was no effect of SH, but N content in plant litter increased in summer and autumn with increasing SH. The response had both linear and quadratic terms. Litter N content was greater in summer than in spring or autumn for each SH treatment. Greater litter N content in summer was attributable to greater litter mass (Table 4-4) because litter N concentration was not affected by SH (Table 4-5).

Carbon content

Nitrogen fertilization affected C content in live herbage ($P = 0.034$) and soil ($P = 0.006$), but it did not affect plant litter and root-rhizome C content (Table 4-7). Live herbage and soil pool N content increased linearly as N rate increased, and although not significant the general pattern of response of litter and root-rhizome C content were similar. Higher C content in live

herbage was attributed to higher C concentration and greater live herbage mass as N rate increased. Higher C content in soil was associated with greater C concentration at higher N rates.

Many researchers have reported that N fertilization leads to increased grassland soil C stocks (Reeder et al., 1998; Rice, 2000; Conant et al., 2001). In bahiagrass pastures, Dubeux et al. (2006c) observed that soil C accumulation reached higher levels as management intensity (stocking rate and N fertilization level) increased. Fertilization results in increased below-ground root production as well as above-ground herbage production (Russell and Williams 1982), which can both lead to increased soil organic matter. The soil C pool is a function of the C concentration in the SOM and the amount of SOM present. Higher C concentration under higher levels of N fertilization also contributed to greater C content in this study.

Increasing SH increased C content in all nutrient pools (Table 4-9), and the response was linear for all pools. Carbon accumulation increased 50% for live herbage, 43% for plant litter, 32% for root-rhizome, and 17% for soil when SH increased from 8 to 24 cm. This indicates that decreasing grazing intensity is associated with the increase of C accumulation in nutrient pools.

This result was consistent with observations that continuous stocking at high grazing intensities results in the lowest soil C content (Mathews et al., 1994; Manley et al., 1995; Wright et al., 2004; Han et al., 2008). In meadow bromegrass (*Bromus riparius* *Rhem.*) swards, Baron et al. (2002) reported that heavy (grazed to 13 cm) and medium (grazed to 17 cm) grazing intensities produced 87 and 90% as much as above ground C content as the light intensity (grazed to 26 cm). Increasing soil C content in response to grazing intensity is likely to be driven by C inputs to soil due to changes in herbage production, biomass allocation, and reduced losses of C from the plant-soil system (Derner et al., 1997; Schuman et al., 1999; Lal, 2002; Conant et al., 2003; Han et al., 2008). Reduction in above-ground biomass associated with higher

compared to lower grazing intensity is thought to result in lower potential C inputs from both above- and below-ground litter production (Holland and Detling, 1990; Ingram et al., 2007).

Hence, soil C content is strongly related to root C inputs (Gale and Cambardella, 2000).

Increases in root biomass would typically precede increases in total soil C.

Carbon content of plant litter also was affected by SH x season interaction ($P = 0.001$; Table 4-10). Carbon content increased in summer (linear and quadratic effects) and autumn (linear effects) with increasing SH, but it was not affected by SH in spring. Litter C content was greater in summer than spring and autumn due to greater plant litter mass in summer.

Proportion of Nutrients in Various Nutrient Pools

The effect of N fertilization and SH treatments on the proportion of nutrients in various pools was explored. The influence of management on distribution of nutrients to various pools is potentially of great importance, so this topic will be explored for K, P, N, and C in the following section.

Potassium

As N rate increased, the proportion of K that was in live herbage increased linearly from 31 to 42% and the proportion in plant litter increased linearly from 2 to 4% (Table 4-11). In root-rhizome, K proportion was greater at 150 kg N treatment than for the 50 and 250 kg N treatments. Increasing N fertilization caused a reduction in the proportion of K in the soil pool. Among the nutrient pools evaluated, soil contained the greatest proportion of K pool when N rates were 50 and 150 kg ha⁻¹, but live herbage contained the greatest proportion when N rate was 250 kg ha⁻¹. The proportion of K content in root-rhizome was 18 to 22%, and less than 5% of K was found in plant litter.

The proportion of K in live herbage and plant litter pools increased linearly with increasing SH, but there was no effect of SH on the proportion of K contained in the root-rhizome pool

(Table 4-12). Increasing SH caused the proportion of K in the soil pool to decrease. Among the SH treatments, the soil pool had the greatest proportion of K when SH was 8 and 16 cm, but live herbage was the largest K pool when SH was 24 cm. The root-rhizome pool contained 16 to 20% of total K, and the plant litter pool contained around 3 to 4%. These results indicate that both SH and N fertilization can alter the proportion of K contained in specific nutrient pools and in some cases can change the pool rank.

Table 4-11. The proportion of K, P, N, and C contained in specific nutrient pools as affected by N rates. Data are means across two replicates, three seasons, and 2 yr (n = 12).

Nutrient/Pool	N fertilization (kg ha ⁻¹ yr ⁻¹)				PC [‡]
	50	150	250	SE [†]	
	-----%-----				
Potassium					
Live herbage	31	35	42	2	L*
Plant litter	2	3	4	0.4	L*
Root-rhizome	18	22	18	1	Q*
Soil	49	40	36	2	L**
Phosphorous					
Live herbage	7	10	8	1	NS
Plant litter	2	2	2	0.3	NS
Root-rhizome	6	9	7	0.8	NS
Soil	85	79	83	2	NS
Nitrogen					
Live herbage	2	3	4	0.2	L**
Plant litter	1	2	2	0.2	L**
Root-rhizome	3	4	4	0.2	L*,Q*
Soil	93	91	90	0.5	L**,Q
Carbon					
Live herbage	8	8	8	0.5	NS
Plant litter	3	3	3	0.3	NS
Root-rhizome	11	13	11	0.8	Q
Soil	78	76	78	0.9	Q*

[†] SE, standard error.

[‡] PC, Polynomial contrast for effect of N rate within nutrient and pool. L = linear, Q = quadratic; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. Q not followed by an asterisk, $P \leq 0.10$, NS = not significant, $P > 0.10$.

Table 4-12. Post-graze stubble height effects on the proportion of nutrients in specific nutrient pools. Data are means across two replicates, three seasons, and 2 yr (n = 12).

Nutrient/Pool	Post-graze stubble height (cm)			SE [†]	PC [‡]
	8	16	24		
	-----%-----				
Potassium					
Live herbage	35	36	42	1	L**
Plant litter	3	3	4	0.3	L*
Root-rhizome	16	20	18	1.3	NS
Soil	46	41	36	0.9	L**
Phosphorous					
Live herbage	6	6	8	0.8	NS
Plant litter	2	2	2	0.2	NS
Root-rhizome	6	7	7	1	NS
Soil	86	85	83	2	NS
Nitrogen					
Live herbage	4	3	4	0.1	Q**
Plant litter	2	1	2	0.1	L**,Q**
Root-rhizome	4	4	4	0.2	NS
Soil	90	92	90	0.3	Q**
Carbon					
Live herbage	6	6	8	0.2	L**
Plant litter	3	3	3	0.2	NS
Root-rhizome	10	12	11	0.8	NS
Soil	81	79	78	0.9	L*

[†] SE, standard error.

[‡] PC, polynomial contrast for effect of stubble height within nutrient and pool. L = linear, Q = quadratic; *, **, indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

Phosphorus

Nitrogen fertilization did not affect the proportion of P in any of the nutrient pools studied (Table 4-11). Soil is the largest P pool evaluated, containing 79 to 85% of total P. Live plant parts contained 7 to 10% of the P pool, while only 2% of P was stored in plant litter. Similar to the N fertilization effect, the proportion of P in the various nutrient pools did not differ due to SH (Table 4-12). Soil was the largest P pool among the SH treatments, containing 83 to 86% of total P. Plant litter was the smallest P pool, containing around 2% of total P.

Nitrogen

The proportion of N contained by live herbage, plant litter, and root-rhizome pools increased as N rate increased leading to a small reduction in the proportion of N in the soil pool (Table 4-11). The effect was linear for live herbage and plant litter and it had linear and quadratic term for root-rhizome and soil. Within any of the N fertilization levels, soil was the largest N pool, contributing 90 to 93% of total N in the pools studied. Among plant components, the root-rhizome pool was the largest, containing around 50% of total N stored in plant fractions. As a proportion of all N in pools studied, 2% or less of total N was contained in plant litter.

There were quadratic effects of SH on the proportion of total N contained in live herbage and soil pools, and linear and quadratic effects of SH on plant litter pool N (Table 4-12). The proportion of N in the root-rhizome pool was not affected by SH. Within a given SH treatment, soil was always by far the largest N pool, containing 90 to 92% of total N. The next largest pools were the root-rhizome and live herbage pools that contained 3 to 4%. Plant litter contained only 1 to 2% of the total N.

Carbon

The proportion of C contained in the live herbage and plant litter pools was not affected by N fertilization treatments, but there were quadratic effects of N rate on the percentage in the root-rhizome and soil pools (Table 4-11). These responses are largely the result of the quadratic effect of N rate on root-rhizome mass (8740, 10 300, and 9090 kg ha⁻¹ for N rates of 50, 150, and 250 kg N ha⁻¹, respectively) that was described earlier. The soil pool contained 76 to 78% of the total C that was accounted for in these four nutrient pools. Schlesinger (1997) and Jobbagy and Jackson (2000) reported that stored organic C in soil is more than the combination of C in plant and atmospheric pools. In the current study, the root-rhizome pool was the second largest C pool, containing 11 to 13% of total C. The live herbage and plant litter pools contained approximately

8 and 3% of C, respectively. In semi-arid mixed grass and short-grass rangelands, Reeder and Schuman (2002) reported that over 90% of C was in soil organic matter, and less than 10% of system C was in plant components, with 80 to 90% of plant C in below-ground biomass. In this study, 58 to 62% of live plant C was below ground.

The proportion of C contained in the live herbage pool increased linearly with increasing SH, but there was no effect of SH on proportions of C in plant litter or root-rhizome pools (Table 4-12). The proportion of C in the soil pool decreased linearly as SH increased, but the range of the response was small and the soil pool contained 78 to 81% of total C. The root-rhizome pool contained 10 to 12%, while only approximately 3% was stored in plant litter. Regardless of the N rate or grazing SH, the soil C pool had large and fairly similar proportions of total C contained among the four pools studied.

Summary and Conclusions

This study evaluated the effect of three N rates (50, 150, and 250 kg N ha⁻¹) and three postgraze residual SH (8, 16, and 24 cm) of rotationally stocked Tifton 85 bermudagrass swards on mass, nutrient concentration, and nutrient content of four nutrient pools. The nutrient pools were above-ground live herbage, above-ground plant litter, below-ground root-rhizome, and soil, the latter two to a 20-cm depth.

Increasing N fertilization increased live herbage mass, and it increased root-rhizome mass up to 150 kg N ha⁻¹. There was no effect of N fertilization on the mass of the plant litter pool. Decreasing pasture SH caused a decrease in live herbage, plant litter, and root-rhizome pool mass. Greatest mass of above-ground herbage and plant litter generally occurred in summer vs. spring or autumn.

Nutrient concentrations were measured in the four nutrient pools. Nitrogen and C concentration in live herbage, plant litter, and root-rhizome pools increased with increasing N

fertilization. Live herbage N concentration decreased with increasing post-graze residual SH. Stubble height did not affect N and C concentration in plant litter and root-rhizome pools, but increasing SH caused an increase in N and C concentration in soil. Nitrogen fertilization had no effect on soil N concentration, but greater N rates were associated with greater C concentration in soil. Potassium concentration in live herbage and plant litter increased and soil K concentration decreased with increasing N rate. Increasing SH caused an increase in K concentration in plant litter and root-rhizome pools. Nitrogen fertilization had no effect on P concentration in live herbage, root-rhizome, and soil pools, but plant litter P concentration increased as N fertilization rate increased. Stubble had minimal effect on P concentration in the four nutrient pools.

Nutrient content in live herbage, plant litter, and root-rhizome increased with increasing SH. Carbon and N content in soil also increased as SH increased, but soil K and P content didn't differ among SH treatments. Increasing N fertilization increased N content in live herbage, plant litter, and root-rhizome pools, but did not affect N content in soil. Carbon content in live herbage and soil increased with increasing N fertilizer rate, but there was no effect of N fertilization on C content of plant litter and root-rhizome pools. Potassium content in live herbage, plant litter, and soil increased with increasing N rate, while P content was only slightly affected by N fertilization.

Increasing fertilization increased the proportion of K and N contained in live herbage and plant litter pools and decreased the proportion contained in the soil pool. Nitrogen rate did not affect the proportion of P and C contained in live herbage and plant litter pools. The proportion of C, K, and P contained in the live herbage pool increased with taller SH. The proportion of nutrients contained in the root-rhizome pool was not affected by SH.

In conclusion, these data suggest that lower grazing intensity (i.e., taller stubble heights, lower stocking rates) and greater N fertilization increase C sequestration and accumulation of N in nutrient pools. Increasing N fertilization and decreasing grazing intensity of Tifton 85 bermudagrass pastures (taller SH) causes a redistribution of nutrients among pools; this redistribution is greatest for K, not measurable for P, and significant but generally small for C and N.

CHAPTER 5
GRAZING INTENSITY AND NITROGEN FERTILIZATION EFFECTS ON LITTER
DECOMPOSITION AND MINERALIZATION IN 'TIFTON 85' BERMUDAGRASS
PASTURES

Introduction

Tropical grasslands are generally low-input systems, often receiving low rates of inorganic fertilizer. In the absence of large fertilizer inputs, nutrients cycling via plant litter and animal excreta are important sources of nutrients for grass growth (Thomas, 1992; Dubeux et al., 2007). In addition, many warm-climate grasslands are not intensively utilized during the primary growing season because of excess forage mass, thus litter production is high and the proportion of nutrients cycling in plant litter can be disproportionately large (Thomas, 1992). Plant litter has a wide range of impacts in grasslands, affecting vegetation structure (Facelli and Pickett, 1991a), herbivory, hydrology, and energy budgets (Weltzin et al., 2005), plant community structure (Xiong and Nilsson, 1999; Patrick et al., 2008), soil moisture (Hamrick and Lee, 1987; Kumar and Goh, 2000), and nutrient cycling (Dubeux et. al., 2007).

In plant litter, nutrients like N are chemically bound to C in organic materials. For these nutrients to become available for plant use, soil organisms need to break chemical bonds in a process called mineralization. Many factors affect mineralization including precipitation (Nardoto and Bustamante, 2003; Semmartin et al., 2004), litter quality (Anderson, 1991; Cornelissen, 1996, 1997), light intensity (Austin and Vivanco, 2006), initial N concentration (Parton et al., 2007), and the types and population of microorganisms (Smith et al., 2003). The chemical composition of plant litter can be one of the most important determinants controlling mineralization (Thomas and Asakawa, 1993; Paustian et al., 1997).

Pasture management strategies, including defoliation intensity and fertilization, affect plant litter quantity and quality, and as a result they influence plant litter decomposition and nutrient

release from litter (Naeth et al., 1991; Shariff et al., 1994; Seneviratne, 2000; Dutta et al., 2001; Dubeux et al., 2006a). More frequent defoliation and N fertilization increase the N concentration of herbage and associated plant litter and may cause higher rates of net N mineralization and increase the quantity of N available to plants growing in grassland (Holland and Detling, 1990; Boddey et al., 2004; Dubeux et al., 2006a). Defoliation of grassland alone influences tissue dynamics of grazed grasslands. Schuman et al. (1999) reported that shoot turnover was estimated to be 36 and 39% under light and heavy grazing compared to 28% in ungrazed exclosures.

Nutrient limitations to litter decomposition are suggested by positive correlations between decomposition and litter nutrient concentrations (Taylor et al., 1989; Enriquez et al., 1993). Numerous studies have shown that fresh litter may contain insufficient nutrients, especially N and P, to support microbial use of the C contained within that litter (Staaf and Berg, 1981). Fertilization can offset the negative effects of low-quality organic material by increasing nutrient concentration and accelerating decomposition (Palm et al., 1997).

Understanding the dynamics of litter decomposition and nutrient release under different management practices is important to understanding nutrient cycling in grassland ecosystems, but little attention has been given to this topic in C₄ grass pastures. The objective of this study was to determine the effect of pasture management (defoliation intensity and N fertilization) on above-ground plant litter decomposition and nutrient mineralization.

Materials and Methods

Study Site

This study was conducted in 2006 and 2007 at the University of Florida Beef Research Unit, northeast of Gainesville, FL, at 29°43' N lat on well established Tifton 85 bermudagrass pastures. The area had been planted to Tifton 85 for 14 yr at the start of the trial. Soils are classified as Ultisols from the Plummer (loamy, siliceous, thermic Grossarenic Paleaquults) and

Spar series (loamy, siliceous, hyperthermic Grossarenic Paleudults). At the beginning of the study, average soil pH was 6.2 and Mehlich-I extractable P, K, Mg, and Ca concentrations were 71, 23, 93, and 732 mg kg⁻¹, respectively. Monthly rainfall at the research site for these 2 yr is shown in Table 3.1 (Chapter 3).

Experimental Design

There were five treatments selected to represent a wide range in defoliation intensity and N fertilization of rotationally stocked Tifton 85 pastures (Table 5-1). Length of grazing cycle (< 10 h grazing time + rest period) was 28 d for all treatments. Three grazing intensity treatments were established based on differences in post-graze stubble height (SH), with levels being 8, 16, and 24 cm. These treatments all received 250 kg N ha⁻¹ yr⁻¹. The fourth and fifth treatments had a 24-cm SH and a 28-d grazing cycle, but they received 150 and 50 kg N ha⁻¹ yr⁻¹. This provided three N fertilization levels at the same level of grazing intensity. Each experimental unit was 8- x 50-m, and all treatments were arranged in two replicates of a randomized complete block design.

Table 5-1. Description of the five treatments imposed in the study described in Chapter 5.

Post-graze stubble height (cm)	Grazing cycle (d)	Fertilization (kg N ha ⁻¹ yr ⁻¹)
8	28	250
16	28	250
24	28	250
24	28	150
24	28	50

Pasture Management

All pastures were mowed to an 8-cm SH in March 2006 and 2007. Grazing was initiated on a given experimental unit each year when sward height was 20 cm taller than the target post-graze SH. Subsequent grazing events occurred according to the established treatment description. At each grazing event, sufficient yearling heifers were assigned to each experimental unit to

graze the herbage to the target SH within 10 h. Stubble height was measured frequently at 25 locations per experimental unit during each grazing period. When the average of these 25 measurements reached the target SH, that grazing event ended and cattle were removed. The grazing season was from June to October or November each year, and number of grazing cycles per year for each treatment was six in 2006 and five in 2007.

All treatments received 50 kg N ha⁻¹ on 1 May 2006 and 2 May 2007. For treatments receiving 150 and 250 kg N ha⁻¹ yr⁻¹, the remaining N was applied in four equal applications of 25 (150 kg N rate) or 50 kg N ha⁻¹ (250 kg N rate). The N source was ammonium nitrate, and the four split applications of fertilizer were broadcast applied on 16 June, 14 July, 11 Aug., and 8 Sept. 2006, and on 22 June, 19 July, 17 Aug., and 13 Sept. 2007. Twenty-two kilograms of P and 83 kg K ha⁻¹ were applied with the initial N application each year. The amount of P and K applied was based on soil test recommendations for improved perennial grass pastures.

Response Variables

Litter decomposition and nutrient (N and P) disappearance were estimated using a litter bag technique (Dubeux et al., 2006a). For measurement of these responses, litter was defined as the senescent leaves still attached to the plant. The reason for this approach was to avoid collecting litter from the ground that was already partially degraded, but to an unknown extent. Litter was obtained by cutting standing herbage to soil level from each of the 10 experimental units after first two grazing cycles were completed. This timing was chosen so that treatments were fully imposed before sampling began. Senescent herbage was hand-separated from green herbage, and the senescent fraction from each experimental unit was oven-dried (60°C for 72 h). The litter was not ground so that surface area was as similar as possible to the original litter.

Litter from each experimental unit was either stored to be used for analysis to characterize non-incubated material or was placed in bags for incubation. Litter bags were 15 x 20 cm and

were made from 75- μ m mesh polyester (4 g of litter per bag). The bags were heat sealed and placed on the ground in the same pasture from which the litter originated. Bags containing litter were placed in sets of six, and there were four sets per pasture. Incubation times were 4, 8, 16, 32, 64, and 128 d, so each incubation time was replicated four times (i.e., four bags) within each experimental unit, resulting in a total of 24 litter bags per experimental unit. There were also six empty bags placed in each experiment unit, and one empty bag was collected at the end of each incubation time. This empty bag was used to correct the bag weight of the bags containing litter.

The sites in each pasture where litter bags were placed were chosen because they represented the average herbage mass of the pasture at Day zero, based on disk settling height (Chapter 3). After placement on the ground, the bags were lightly covered with litter from that pasture. A wire-mesh exclusion cage was placed over each set of bags to protect them from disturbance by grazing cattle or other animals. Herbage inside the cage was clipped to target treatment stubble height at the end of each grazing period in order to maintain the herbage height inside the cage as close as possible to the average canopy height of the pasture. This clipped material was collected and removed from the cage.

At the end of each incubation time, one litter bag was taken from each of four cages per experimental unit and one empty bag was collected from each experimental unit. The five bags per pasture were oven-dried (60°C for 72 h) and weighed. Contents from the four litter bags per pastures were composited for subsequent laboratory analyses. The composited samples and samples of original litter (non-incubated) were milled individually to pass a 1-mm screen and analyzed for dry matter (DM), organic matter (OM), C, N, P, and acid detergent lignin. Dry matter and OM analyses were performed using the procedure described by Moore and Mott (1974). Carbon and N analyses were done using Flash EA 1112 NC Analyzers. Phosphorous

concentration was measured using a modification of the aluminum block digestion procedure (Gallaher et al., 1975). Acid detergent lignin analysis was run in an ANKOM fiber analyzer (ANKOM Technology, 2003a, 2003b, 2003c). The percentage of remaining nutrient was calculated based on the content of that nutrient prior to and after the incubation period.

Statistical Analysis

Nonlinear models were used to fit the curves of plant litter mass decay and nutrient release by Proc NLIN from SAS (SAS Inst., 1996). Before choosing the model, each data set was plotted to observe the pattern of distribution. According to most research reports, decay curves usually follow the single or double exponential functions (Weider and Lang, 1982; Dubeux et al., 2006b). The single exponential model fit the data well and was used to explain the mass decay curves. It is described by the equation that follows:

$$Y = a + (100 - a) * \exp(-k * t) \quad (\text{Equation 1})$$

Where:

Y = percentage of remaining litter biomass at time t

a = constant

k = decay constant

After solving the above equation, the output parameters (a and k) of each treatment were used to calculate their respective relative decomposition rate (RDR) using Equation 2 described by Weider and Lang (1982):

$$RDR = \frac{-(100 - a) * k * e^{-k*t}}{a + (100 - a) * e^{-k*t}} \quad (\text{Equation 2})$$

For N release, the quadratic polynomial equation was the best fit to describe N release from litter. This equation follows:

$$NR = b_0 + b_1t + b_2t^2 \quad \text{(Equation 3)}$$

Where:

NR= the percentage of total N remaining at time t

b0, b1, and b2 = constants.

For P decomposition and C:N ratio dynamics, the single exponential model fit well and was used. It is described as follows:

$$Y = a + b * \exp(-k * t) \quad \text{(Equation 4)}$$

Where:

Y = percentage of remaining P or the C:N ratio at time t

a and b = constants

k = decay constant

After fitting the appropriate model, the output parameters were analyzed and compared using Proc Mixed from SAS (SAS Inst., 1996) with SH or N, year, and their interactions considered fixed effects and replicate and its interaction random. The SH and N fertilization means were compared using polynomial contrasts to determine the nature of the response to SH or N. Incubation period means were compared using the SAS LSMEANS test.

Results and Discussion

Initial Litter Chemical Composition

Initial litter N and C:N and lignin:N ratios were affected by year x SH interaction. Interaction occurred because SH affected these responses in 2006 but not in 2007 (Table 5-2). In 2006, initial N concentration decreased linearly with increasing SH. Litter N concentration in 8-cm SH treatment was nearly twice as great as for the 24-cm SH treatment (12.6 vs. 6.5 g kg⁻¹). The C:N and lignin:N ratios increased as SH increased because initial C and lignin

concentrations were not different among SH treatments while N concentration was greater with shorter SH. In 2007, initial N concentration and C:N and lignin:N ratios averaged 7.8 g kg^{-1} , 60, and 12, respectively. Initial P concentration and C:P ratio did not differ among SH treatments in either year.

There was year x N rate interaction for initial litter N concentration and C:N and lignin:N ratios. Interaction occurred because there were no differences among treatments in 2006, but there was a treatment effect in 2007 (Table 5-3). In 2006, average litter N concentration and C:N and lignin:N ratios were 6.7 g kg^{-1} , 72, and 14, respectively. In 2007, initial N concentration increased linearly from 5.9 to 8.4 g kg^{-1} with increasing N rate from 50 to $250 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Litter C:N and lignin:N ratios decreased linearly as N rate increased. Greater N concentration was responsible for lower ratios in higher fertilization treatments. Initial P concentration and C:P ratio did not differ among treatments within year, but there was a year effect. The average values for initial P concentration and C:P ratio were 1.3 g kg^{-1} and 374 in 2006, and 1.5 g kg^{-1} and 324 in 2007, respectively.

Litter quality is a key factor controlling litter decomposition and nutrient release (Corbeels, 2001). Chemical quality indices in litter, such as initial N concentration and the ratios of C:N, lignin:N, and C:P, have been used to define plant litter quality in many studies (Dalal, 1979; Heal et al., 1997; Seneviratne, 2000; Dubeux et al., 2006a; Parton et al., 2007). Parton et al. (2007) observed that leaf litter showed little or no net N immobilization when initial N concentration was $> 10 \text{ g kg}^{-1}$. They also observed net N release from leaf litter when C:N ratio of the leaf litter was less than 40 (studied a range of 31 to 48). The literature is not consistent in this regard, as Wanger and Wolf (1999) reported that litter N mineralization predominated when C:N ratio was < 20 , whereas C:N ratio > 30 favored immobilization. For C:P ratio, it has been

Table 5-2. Initial N and P concentrations and C:N, lignin:N, and C:P ratios of Tifton 85 bermudagrass plant litter from rotationally stocked pastures grazed to three different post-graze stubble heights (SH) during 2006 and 2007. Data are means across two replications (n = 2).

Year	SH	N	C:N	Lignin:N	P	C:P
	cm	g kg ⁻¹			g kg ⁻¹	
2006	8	12.6	40	9	1.4	348
	16	8.9	54	12	1.3	355
	24	6.5	72	14	1.3	354
	SE [†]	0.6	4	0.7	0.09	26
	PC [‡]	L**	L*	L*	NS	NS
2007	8	7.1	66	13	1.6	297
	16	7.9	59	12	1.4	331
	24	8.4	56	11	1.5	314
	SE	0.3	3	0.7	0.06	14
	PC	NS	NS	NS	NS	NS

[†] SE, standard error.

[‡] PC, polynomial contrast; L = linear effect; NS = Not significant ($P > 0.10$); *, ** indicate significance at $P \leq 0.05$ and 0.01 , respectively.

Table 5-3. Initial litter N and P concentrations and ratios of C:N, lignin:N, and C:P for rotationally stocked Tifton 85 bermudagrass pastures fertilized at three levels of N during 2006 and 2007. Data are means across two replications (n = 2).

Year	N rate	N	C:N	Lignin:N	P	C:P
	kg ha ⁻¹ yr ⁻¹	g kg ⁻¹			g kg ⁻¹	
2006	50	6.5	75	14	1.2	389
	150	7.1	68	15	1.3	377
	250	6.6	72	13	1.3	354
	SE [†]	0.2	4	0.5	0.05	19
	PC [‡]	NS	NS	NS	NS	NS
2007	50	5.9	84	16	1.5	326
	150	6.8	70	13	1.4	333
	250	8.4	56	11	1.5	314
	SE	0.2	2	0.4	0.05	14
	PC	L*	L*	L**	NS	NS

[†] SE, standard error of mean.

[‡] PC, polynomial contrast; L = linear effect; NS = Not significant ($P > 0.10$); *, ** indicate significance at $P \leq 0.05$ and 0.01 , respectively.

reported that mineralization predominates when C:P ratio is < 200, whereas immobilization predominates when C:P ratio is > 300 (Dalal, 1979; Mclaughlin and Alston, 1986). In the current study, initial N concentrations in most grazing intensity and N fertilization treatments were < 10 g kg⁻¹, and C:N ratios were > 40. These traits suggest that N immobilization is likely during litter decomposition.

Litter Mass Disappearance

Grazing intensity

Post-graze stubble height had no effect on litter decomposition ($P = 0.384$), but litter decomposition was affected by the year x incubation time interaction ($P < 0.001$). Within each year, loss of litter mass decreased with increasing incubation time and followed the same single exponential decay model across levels of SH (Figure 5-1). At each incubation time, litter OM loss was greater in 2007 than 2006, and it resulted in the greater total litter mass loss in 2007 than in 2006 (55 vs. 36%) at the end of the 128-d incubation period. This difference was probably explained in part due to differences in rainfall. There was more precipitation during the incubation period in 2007 than in 2006 (675 vs. 414 mm; Chapter 3, Table 3-1). Several studies have shown that rainfall was positively correlated with litter decomposition rate and litter mass loss (Strojan et al., 1987; Gholz et al., 2000; Salamanca et al., 2003; Reed et al., 2009). These litter mass loss values cover approximately the same range as those reported by Dubeux et al. (2006) in 'Pensacola' bahiagrass pastures at the same location. They observed that litter biomass loss after 128 d of incubation ranged from 40 to 60%.

Over the course of the incubation period, there was no grazing intensity effect on the RDR ($P = 0.392$), but there was year x incubation time interaction ($P < 0.001$). Relative decomposition rate decreased from 0.0070 to 0.0012 g g⁻¹d⁻¹ in 2006 and from 0.0155 to 0.0011 g g⁻¹d⁻¹ in 2007 as the incubation period progressed (Table 5-4). Relative decomposition rate

generally was greater at a given incubation time in 2007 than in 2006. Litter quality and environmental conditions (soil temperature and soil moisture) probably contributed to this difference (Heal et al., 1997), but there was no difference at the 128-d incubation time between 2 years. This likely was associated with there being primarily recalcitrant materials left to decompose at this time and environmental conditions may have minimal effect on decomposition rate of this material.

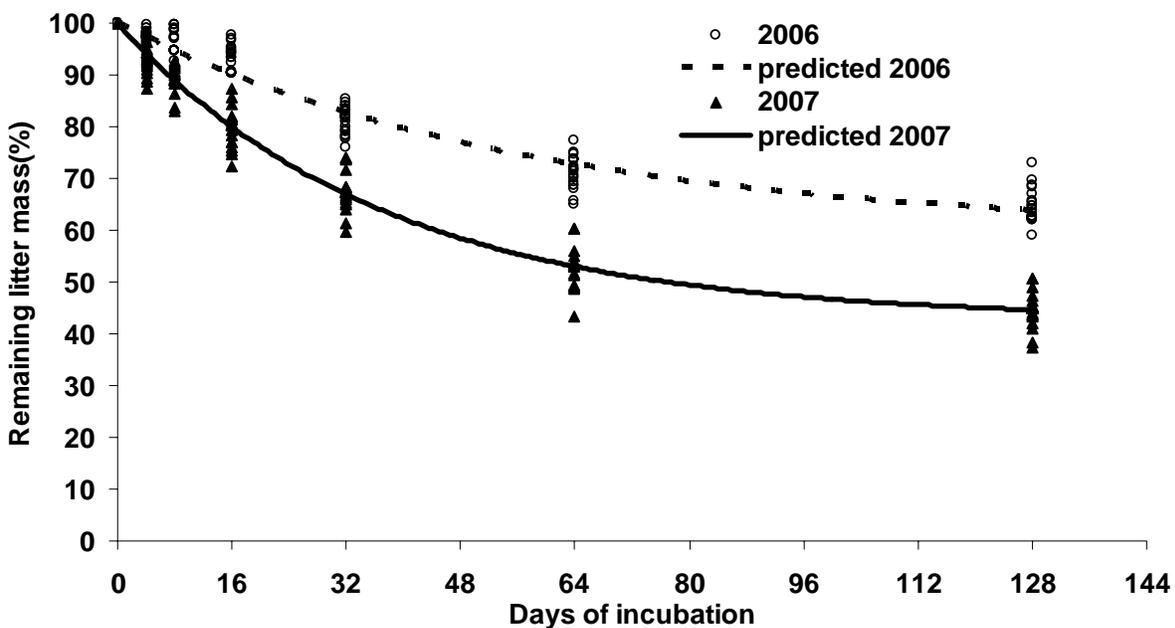


Figure 5-1. Litter mass remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures grazed to three post-graze stubble heights during 2006-2007. There was no stubble height effect, so all three stubble heights are included in the regression for each year. The equations are: for 2006, $y = 59.5 + 40.50 \cdot \exp(-0.018 \cdot x)$, $r\text{-square} = 0.96$; for 2007 $y = 42.9 + 57.15 \cdot \exp(-0.027 \cdot x)$, $r\text{-square} = 0.97$. Year effects were significant ($P < 0.001$) at each day of incubation.

Heal et al. (1997) and Wider and Lang (1982) reported that early in a decomposition period the more soluble compounds rapidly decompose resulting in greater RDR. After that phase, more recalcitrant materials were broken down, but the amount of time involved in their decomposition is large which decreases RDR until it eventually reaches a relatively constant low level. In our

study, RDR was greater at the beginning of the incubation period and decreased over time, becoming nearly constant close to the end of the 128-d incubation period. Approximately 50% of the total litter mass that disappeared during the 128-d incubation period was lost during the first 32 d. In bahiagrass pastures, Dubeux et al. (2006) reported that nearly 15% of total litter biomass was lost after only 8 d; this was approximately one-third to one-fourth of the total litter biomass that disappeared during a 128-d incubation period. Considering the low RDR at 128 d of incubation, the half-life for the remaining litter mass was around 594 d. This value is greater than reported by Dubeux et al. (2006a) using a litter bag technique to estimate bahiagrass litter decomposition. They observed that litter half-life ranged from 231 (high management intensity) to 433 d (low management intensity).

Table 5-4. Relative decomposition rate (RDR) of Tifton 85 bermudagrass plant litter at different incubation times from rotationally stocked pastures grazed to three post-graze stubble heights during 2006 and 2007. Data are averages across the three stubble heights.

Incubation time (day)	Relative decomposition rate		<i>P</i> -value
	2006	2007	
	-----g g ⁻¹ d ⁻¹ -----		
0	0.0070 a [‡]	0.0155 a	< 0.001
4	0.0067 ab	0.0148 b	< 0.001
8	0.0064 b	0.0140 c	< 0.001
16	0.0059 c	0.0126 d	< 0.001
32	0.0049 d	0.0097 e	< 0.001
64	0.0032 e	0.0052 f	< 0.001
128	0.0012 f	0.0011 g	0.179
SE [†]	0.0002		

[†]SE, standard error.

[‡]Means within a year followed by the same letter are not different ($P > 0.10$) by the SAS LSMEANS test.

N fertilization

There was year x incubation time x N fertilization interaction for litter mass disappearance ($P = 0.001$), thus data were analyzed by year. Within year, there was N fertilization x incubation

time interaction for litter decomposition, and the response followed the single exponential model for each treatment (Figures 5-2 and 5-3). At the beginning of the incubation period, litter mass loss was relatively rapid and not affected by fertilization treatment. In 2006, litter decomposition was not different during the initial 16 d among fertilization treatments. In 2007, there was no difference among treatments during the first 8 d of incubation. After this initial phase, greater N fertilization generally resulted in greater litter mass loss than low amounts of N and the effect of N was linear. At the end of the 128-d incubation period in 2006, litter OM loss was 22, 34, and 37% for 50, 150, 250 kg N ha⁻¹ fertilization treatments, respectively. Only the 150 and 250 N rate treatments approached the average OM loss of the three SH treatments, likely due in part because all SH treatments received the 250 kg ha⁻¹ N fertilizer rate. In 2007, the litter mass loss increased from 48 to 55% as N fertilization increased from 50 to 250 kg ha⁻¹ yr⁻¹. Rates of litter decomposition in N-fertilized swards have been reported to be faster than in those receiving less or no N (Hunt et al., 1988; Prescott et al., 1992).

Corresponding to litter mass loss, litter RDR was affected by the year x N rate x incubation time interaction ($P < 0.001$). Within an incubation time, litter RDR generally increased linearly as N rate increased each year (Table 5-5). These results were likely due to N availability for microbial processes. Nutrient limitations for decomposition are suggested by positive correlations between decomposition and litter nutrient concentrations (Taylor et al., 1989; Enriquez et al., 1993). Fertilization can at least partially offset the negative effects of low-quality organic material and accelerate their decomposition (Palm et al., 1997). In the current study, fertilization resulted in relatively higher RDR with high N additions. Within a level of N rate, RDR decreased with increasing incubation time. It was likely due to an increase in the proportion of recalcitrant material in total remaining litter as decomposition proceeded.

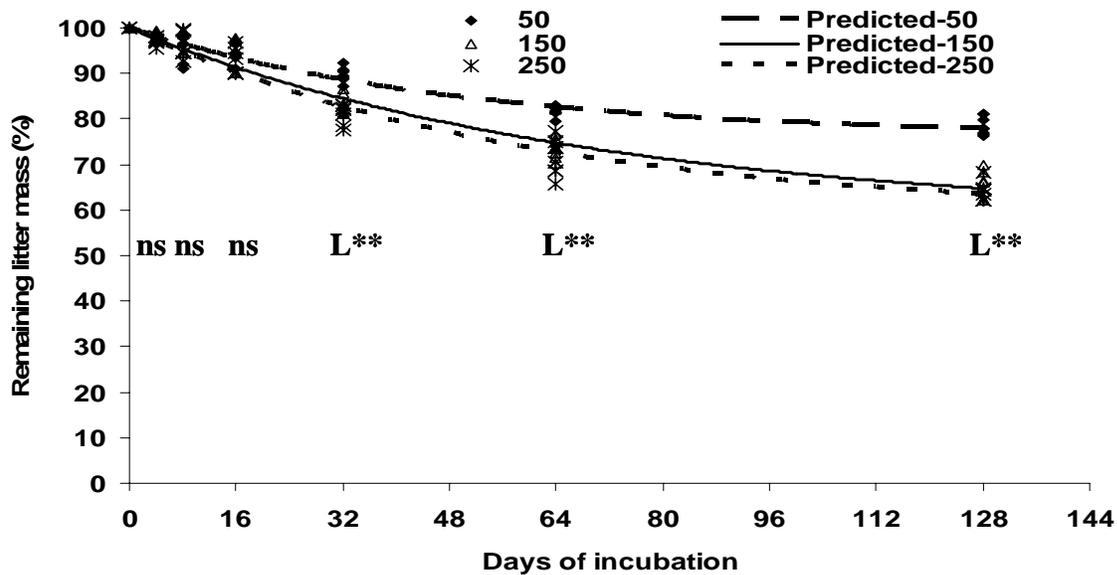


Figure 5-2. Litter mass remaining as a function of incubation time on rotationally stocked Tifton 85 pastures receiving three levels of N fertilization levels in 2006. The equations are: for 50 kg N, $y = 76.0 + 23.97 \cdot \exp(-0.020 \cdot x)$, r-square = 0.92; for 150 kg N, $y = 61.1 + 38.90 \cdot \exp(-0.017 \cdot x)$, r-square = 0.90; for 250 kg N, $y = 61.5 + 38.54 \cdot \exp(-0.018 \cdot x)$, r-square = 0.90. Polynomial contrasts for the N effect within an incubation time: ns = not significant ($P > 0.10$), L = linear effect; ** indicates significance at $P \leq 0.01$.

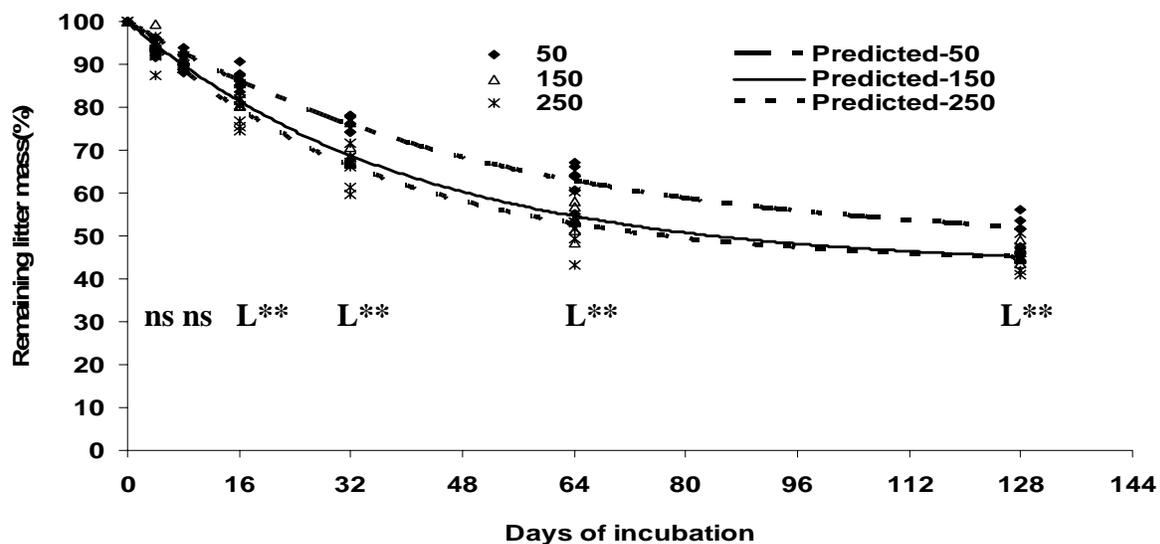


Figure 5-3. Litter mass remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures as affected by three levels of N fertilization in 2007. The equations are: for 50 kg N ha⁻¹, $y = 47.6 + 52.37 \cdot \exp(-0.019 \cdot x)$, r-square = 0.98; for 150 kg N ha⁻¹, $y = 42.8 + 57.21 \cdot \exp(-0.025 \cdot x)$, r-square = 0.99; for 250 kg N ha⁻¹, $y = 43.4 + 56.58 \cdot \exp(-0.028 \cdot x)$, r-square = 0.97. Polynomial contrasts for the N effect within an incubation time: ns = not significant ($P > 0.10$), L = linear effect; ** indicates significance at $P \leq 0.01$.

Table 5-5. Relative decomposition rate (RDR) of Tifton 85 bermudagrass litter at different incubation times from pastures fertilized with different rates of N during 2006 and 2007.

N rate	Incubation time (d)						
	0	4	8	16	32	64	128
kg ha ⁻¹ yr ⁻¹	-----g g ⁻¹ d ⁻¹ -----						
2006							
50	0.0049 a [§]	0.0046 ab	0.0043 b	0.0038 c	0.0029 d	0.0016 e	0.0005 f
150	0.0061 a	0.0059 a	0.0057 ab	0.0053 b	0.0045 c	0.0032 d	0.0015e
250	0.0071 a	0.0067 ab	0.0065 b	0.0059 c	0.0049 d	0.0032 e	0.0012 f
SE [†]				0.0002			
PC [‡]	L*	L*	L*	L**	L**,Q*	L**,Q**	L,Q
2007							
50	0.0102 a	0.0098 a	0.0094 ab	0.0087 b	0.0072 c	0.0047 d	0.0017 e
150	0.0141 a	0.0135 ab	0.0129 b	0.0117 c	0.0093 d	0.0053 e	0.0013 f
250	0.0161 a	0.0153 ab	0.0145 b	0.0129 c	0.0098 d	0.0049 e	0.0010 f
SE				0.0006			
PC	L*	L*	L*	L*	L*	L*,Q**	L

[†]SE, standard error of mean.

[‡]PC, polynomial contrast; L = linear effect, Q=quadratic effect; NS = Not significant ($P > 0.10$); * and ** indicate significance at $P \leq 0.05$ and 0.01 , respectively. L or Q not followed by an asterisk, $P \leq 0.10$.

[§]Means within year and level of N fertilization followed by the same letter are not different ($P > 0.10$) by the SAS LSMEANS test.

Litter N Remaining

Grazing intensity

There was a year x incubation time x grazing intensity interaction for litter N remaining ($P < 0.001$), so data were analyzed by year. Within year, grazing intensity interacted with incubation time affecting N release from plant litter (Figure 5-4, 5-5). Generally, during the first 4 d of incubation, soluble N components were released from litter for each SH level. After 4 d, total N disappearance in litter followed a quadratic model. For these three levels of SH, N remaining in plant litter actually increased from the fourth day each year until incubation time reached at least 70 d, after which N release began (Figure 5-4, 5-5). This response indicates that net N immobilization occurred almost from the beginning of incubation. According to the fit

model, the percentage of total N remaining in plant litter reached its maximum on Days 82 (146%), 77 (129%), and 70 (101%) of the incubation period in 2006 for the 24-, 16-, and 8-cm SH treatments, respectively. In 2007, the greatest amount of N immobilization was predicted to occur on Days 77 (127%), 78 (117%), and 81 (109%) for the 24-, 16-, and 8-cm SH treatments, respectively. As SH decreased from tall to short, N immobilization decreased (Figure 5-4, 5-5). There were linear effects among SH treatments within each incubation time in 2006, but linear effects began after 16 d of incubation in 2007. At the end of the incubation period in 2006, N remaining was 131, 113, and 92% of initial N in the litter bags for the 24-, 16-, and 8-cm SH treatments, respectively. In 2007, N remaining at the end of incubation was 113, 107, and 104% for 24-, 16-, and 8-cm SH treatments. For the treatments in which N immobilization occurred (all but the 8-cm SH in 2006), net N release was predicted to begin on Days 164 and 146 for the 24- and 16-cm SH in 2006 and Days 150, 141, and 145 for the 24-, 16-, and 8-cm SH treatments in 2007.

Similar responses have been reported in other studies with C₄ grasses. In green panic (*Panicum maximum* Jacq. var. *trichoglume*) pastures, Robbins et al. (1989) reported that net N mineralization did not occur until 50 to 100 d after litter deposition because of microbial immobilization. This response was explained based on initial litter N concentration and C:N and lignin:N ratios. Other researchers have reported that initial N concentration in litter has a significant effect on net N immobilization and release (Bargali, 1996; Parton et al., 2007). Parton et al. (2007) observed that litter with high initial N concentration (>10 g kg⁻¹) showed little or no N immobilization, however, low N concentration (<10 g kg⁻¹) in litter caused N immobilization from the beginning of the incubation period. In the current study, the 8-cm SH treatment in 2006 had initial N concentration > 10 g kg⁻¹, but the other SH treatments had less than that

concentration in both years (Table 5-2). The 8-cm treatment was also the only treatment that showed net N mineralization during the 128-d incubation period in 2006.

Initial C:N and lignin:N ratios have been considered to be important factors controlling net N release during litter decomposition due to their close relationship with the activity of decomposers (Dubeux et al., 2007). At low levels of C:N and lignin:N, decomposers can obtain sufficient N from litter directly. However, when these ratios are high, decomposers must access N from sources other than litter, resulting in N immobilization (Frey et al., 2000). Parton et al. (2007) reported that N mineralization occurred when the C:N ratio of the leaf litter was less than 40. In the current study, initial C:N and lignin:N ratios in 2006 increased linearly from 40 to 72 and 9 to 14, respectively, when SH increased from 8 to 24 cm. There was no difference in these ratios in 2007, but all C:N ratios were greater than 40 (Table 5-2).

Other factors that may be associated with the SH effect on litter response are different edaphic conditions and composition of microbial communities under these stubble heights. These factors have been reported to indirectly or directly affect N immobilization and mineralization in litter (Frey et al., 2004; Moore et al., 2006). Low grazing intensity (10% utilization) has been reported to support high microbial biomass compared to higher grazing intensities (50% utilization) in Ascalon and Altvan soils (Ingram et al., 2008). Greater microbial populations will access more external N to litter and cause greater N immobilization.

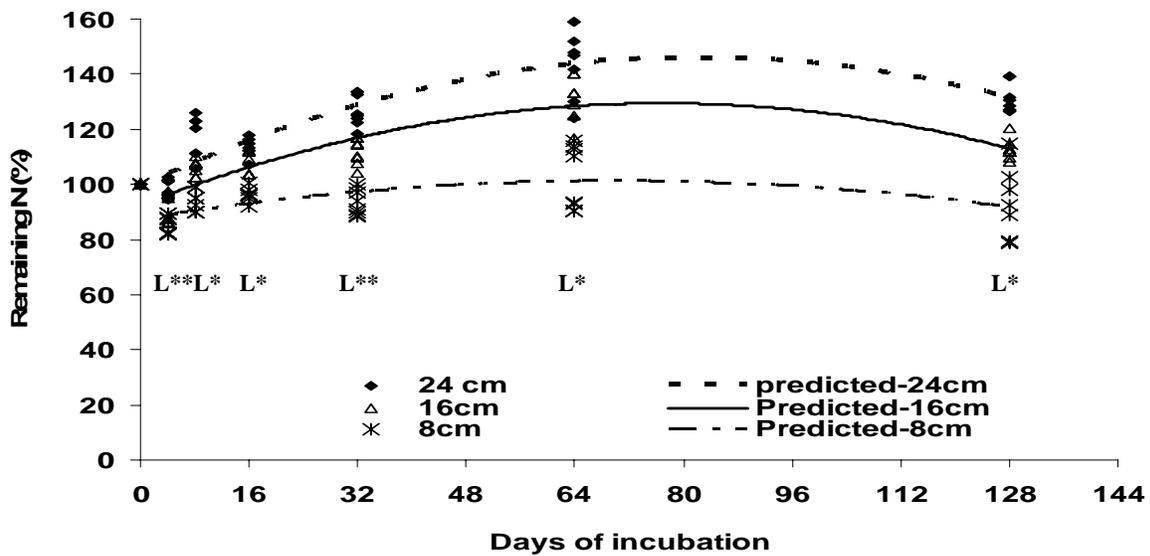


Figure 5-4. Litter N remaining as a function of incubation time on rotationally stocked Tifton 85 pastures grazed to three post-graze stubble heights (SH) in 2006. The equations are: for 24 cm, $y = 99.3 + 1.14x - 0.007x^2$, r-square = 0.91; for 16 cm, $y = 92.4 + 0.96x - 0.006x^2$, r-square = 0.88; for 8 cm, $y = 87.5 + 0.40x - 0.003x^2$, r-square = 0.68. Polynomial contrasts for the SH effect within incubation time: ns = not significant ($P > 0.10$), L = linear effect; *, ** indicate significance at $P \leq 0.05$ and 0.01, respectively.

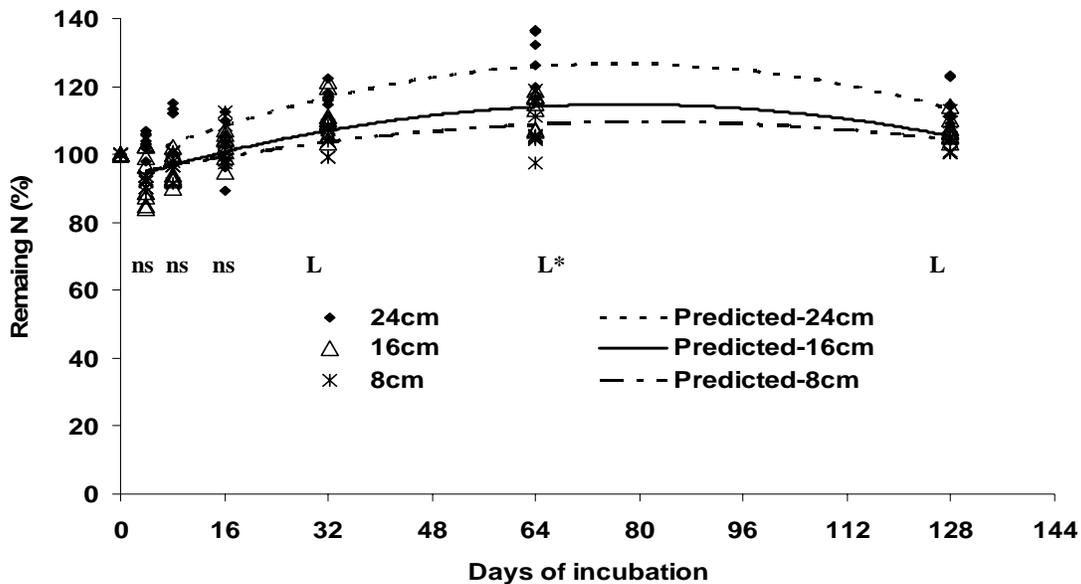


Figure 5-5. Litter N remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures as affected by three post-graze stubble heights (SH) in 2007. The equations are: for 24 cm, $y = 97.4 + 0.77x - 0.005x^2$, r-square = 0.86; for 16 cm, $y = 91.8 + 0.65x - 0.004x^2$, r-square = 0.95; for 8 cm, $y = 93.7 + 0.39x - 0.002x^2$, r-square = 0.82. Polynomial contrasts for the SH effect within an incubation time: ns = not significant ($P > 0.10$), L = linear effect; * indicates significance at $P \leq 0.05$; L followed by no asterisk, $P \leq 0.10$.

N fertilization

There was interaction of year x fertilization x incubation time ($P = 0.028$) on litter N release, so data were analyzed and reported by year. As observed for the SH treatments, N was released rapidly during the first 4 d of the incubation, but over the entire period N release followed a quadratic model (Figure 5-6, 5-7). For all fertilization treatments, N remaining in litter increased after the fourth day, reaching a maximum on Day 82 (146%), 87 (112%), and 100 (105%) for the 250, 150, and 50 kg N treatments, respectively. In 2007, the greatest N remaining occurred on Day 77 (127%) and 87 (107%) for the 250 and 150 kg N treatments, but N remaining kept increasing during the incubation period for the 50-kg treatment. At the end of 128 d of incubation, N remaining was more than at initiation of incubation for all fertilization treatments. This indicated that microbes breaking down plant litter in this C_4 grassland ecosystem accessed N exogenous to litter. As a result, deposition of plant litter in grasslands can result in immobilization of N and limit availability for plant growth (Wedin, 1996; Dubeux et al., 2006a). As reported by Parton et al. (2007) and Hobbie (2000), low initial N concentration ($< 10 \text{ g kg}^{-1}$) and high initial C:N (> 40) and lignin:N ratio in litter probably contributes to immobilization. In this study, initial N concentration for each fertilization treatment was lower than 10 g kg^{-1} and initial C:N ratio was greater than 40 for all treatments in each experimental year (Table 5-2). These characteristics of the original litter likely contributed to the N immobilization that was observed.

Increasing pasture N fertilization actually increased N immobilization in plant litter. Generally this response is unexpected, especially if litter N concentration and C:N ratio follow the anticipated pattern of response to N fertilization as was observed in 2007 (Table 5-3). However the N concentrations and C:N ratios of litter from the N treatments in this study were at levels commonly associated with N immobilization. Thus, the greater immobilization of N with

greater N fertilization may have been caused to a greater extent by the amount of N available in the grassland ecosystem as opposed to the specific characteristics of the litter from these three treatments. Previous work has shown that when more N fertilizer was added to a pasture, it increased the N availability to microbes (Hall and Matson, 1999). Therefore, microbes had greater access to N from the environment in pastures receiving greater levels of N fertilization, and they used that N to produce microbial biomass (Frey et al., 2000). This process resulted in more N content in litter and greater N immobilization under high N fertilization.

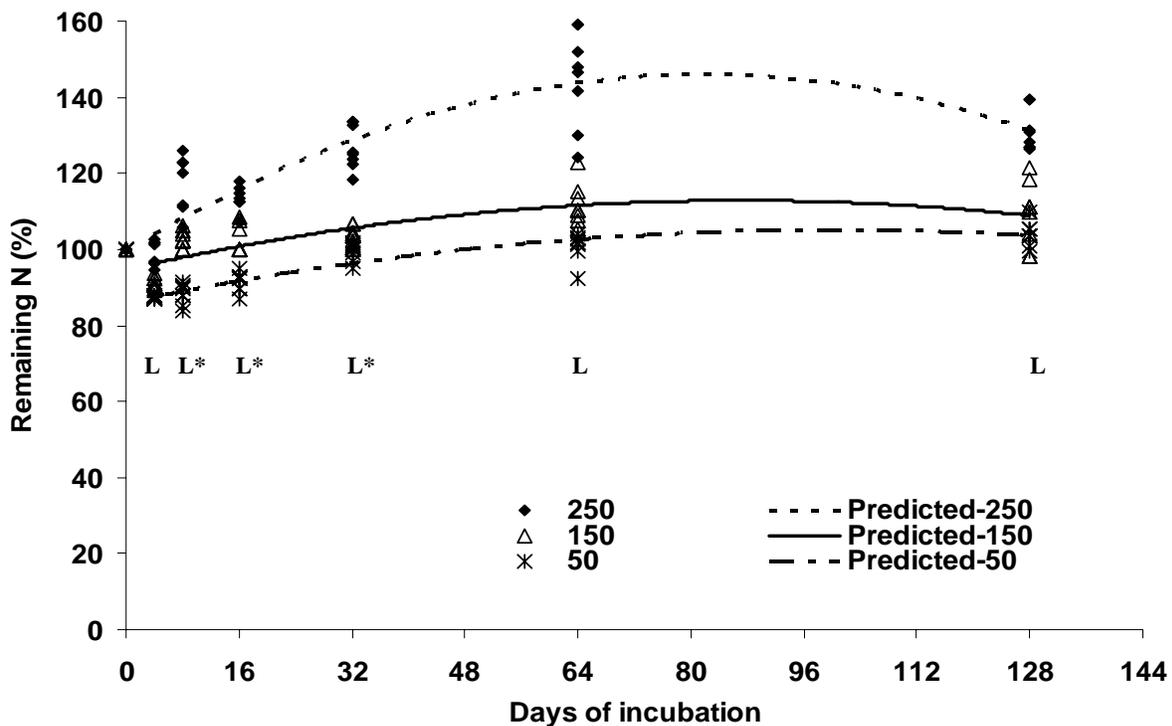


Figure 5-6. Litter N remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three N fertilization levels in 2006. The equations are: for 250 kg N, $y = 99.3 + 1.14x - 0.007x^2$, r-square = 0.91; for 150 kg N, $y = 94.7 + 0.42x - 0.002x^2$, r-square = 0.78; for 50 kg N: $y = 86.15 + 0.38x - 0.002x^2$, r-square = 0.95. Polynomial contrasts for the N effect within incubation time: L = linear effect; * indicates significance at $P \leq 0.05$; L followed by no asterisk, $P \leq 0.10$.

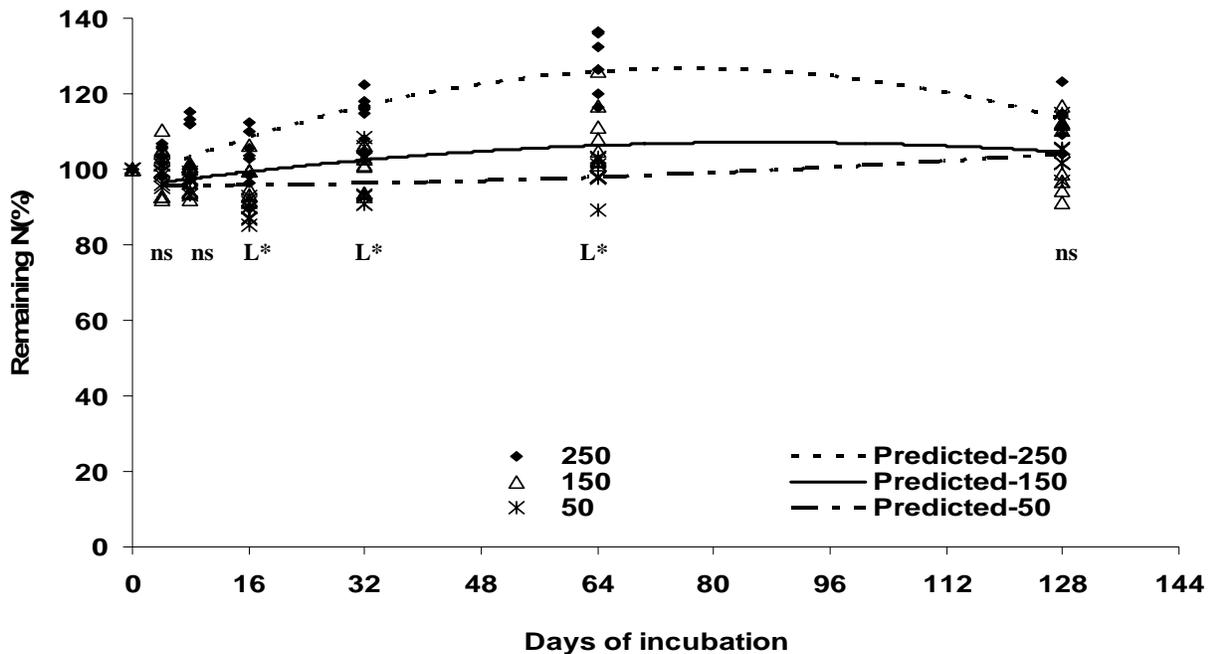


Figure 5-7. Litter N remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by a range of fertilization levels in 2007. The equations are: for 250 kg N, $y = 97.4 + 0.77x - 0.005x^2$, r-square = 0.86; for 150 kg N, $y = 95.4 + 0.27x - 0.002x^2$, r-square = 0.74; for 50 kg N, $y = 95.7 + 0.002x + 0.0005x^2$, r-square = 0.50. Polynomial contrasts for the N effect within incubation time: ns = not significant ($P > 0.10$), L = linear effect; * indicates significance at $P \leq 0.05$.

Litter P Remaining

Grazing intensity

There were year but no grazing intensity differences on P decomposition in plant litter (Figure 5-8). Phosphorus release from litter followed a single exponential model. The actual data appear to show P immobilization in the first days of the incubation period, but P mineralization began relatively early in the period and the pattern of response corresponded to that of litter OM. High C:P can contribute to P immobilization, and in these cases C:P ratio is often negatively correlated with release rates (Moore et al. 1999). Generally, there is a critical value for this ratio, below which net loss of P from litter begins. According to some reports, critical C:P ratio for

foliar litters ranges from 350 (Rustad and Cronan, 1988) to 480 (Gosz et al., 1973). Sims and Wolf (1994) also reported that P became "fixed" in an immobilized organic form if the C:P ratio exceeded 300. In this study, initial C:P ratio was around 352 in 2006 and 314 in 2007 (Table 5-2), thus it was marginal for both release and immobilization. At the beginning of incubation, there was no difference for P remaining between years, but P release became greater in 2007 than in 2006 after 16 d of incubation (Figure 5-8). At the end of 128 d, approximately 30 and 46% of total initial P in litter was released in 2006 and 2007, respectively.

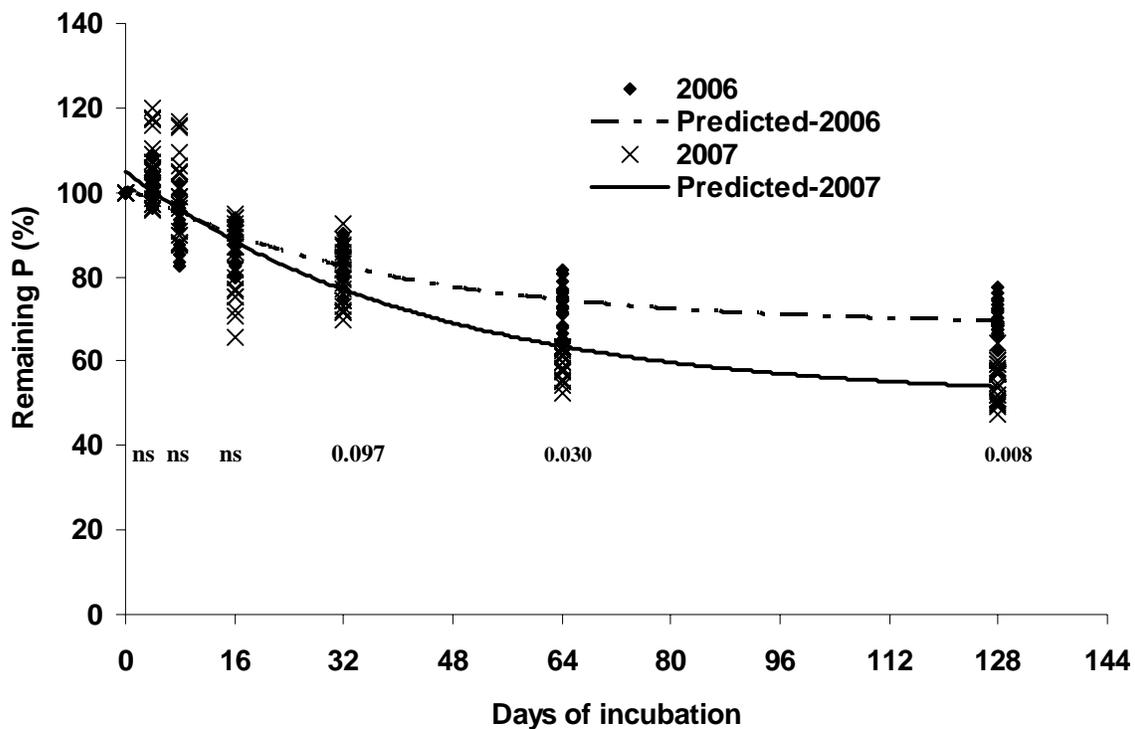


Figure 5-8. Litter P remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures grazed to three levels of post-graze stubble height (SH) in 2006 and 2007. The equations are: for 2006, $y = 68.7 + 32.65 \cdot \exp(-0.03 \cdot x)$, r -square = 0.86; for 2007, $y = 51.1 + 53.78 \cdot \exp(-0.02 \cdot x)$, r -square = 0.86. The P value for the year effect within a specific incubation time is shown: ns = not significant, $P > 0.10$.

N fertilization

There was interaction of year x incubation time x N fertilization on litter P remaining ($P < 0.001$), so data were analyzed and are reported by year. Within each experimental year, N fertilization interacted with incubation time affecting P release from plant litter (Figure 5-9, 5-10). Phosphorus release followed a single exponential model. During the first few day of the incubation period, the actual data suggest P immobilization. After this very short immobilization phase, P mineralization started and continued across the incubation period.

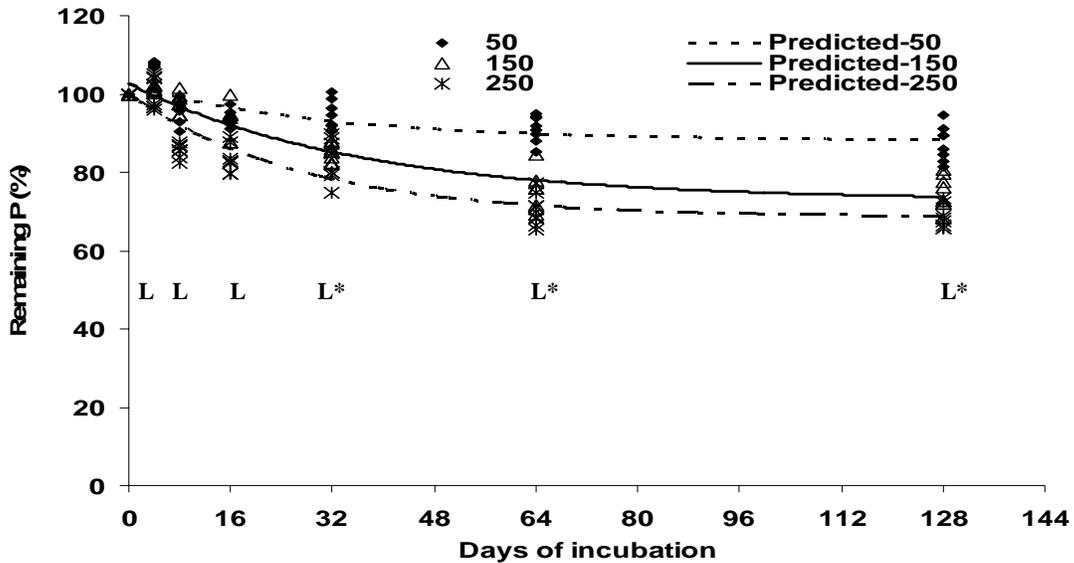


Figure 5-9. Litter P remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three N fertilization levels in 2006. The equations are: for 50 kg N, $y = 88.2 + 14.3 * \exp(-0.03 * x)$, r-square = 0.58; for 150 kg N, $y = 72.9 + 29.69 * \exp(-0.03 * x)$, r-square = 0.90; for 250 kg N, $y = 68.6 + 31.28 * \exp(-0.04 * x)$, r-square = 0.84. Polynomial contrasts for the N effect within an incubation time: L = linear effect; * indicates significance at $P \leq 0.05$; L with no asterisk, $P \leq 0.10$.

Phosphorous release from litter increased linearly as N fertilization increased (Figure 5-9, 5-10). Increasing N fertilization likely increased N availability for decomposers and increased litter decomposition. This can result in increased microbial biomass (Smolander et al., 1994; Fisk and Fahey, 2001), and more microbes will generally result in greater P decomposition. During

the 128-d incubation period in 2006, net P release was 12, 26, and 31% of total initial P for the 50, 150, and 250 kg N treatments, respectively. In 2007, net P release was greater and totaled 37, 41, and 45 for the 50, 150, and 250 kg N treatments, respectively.

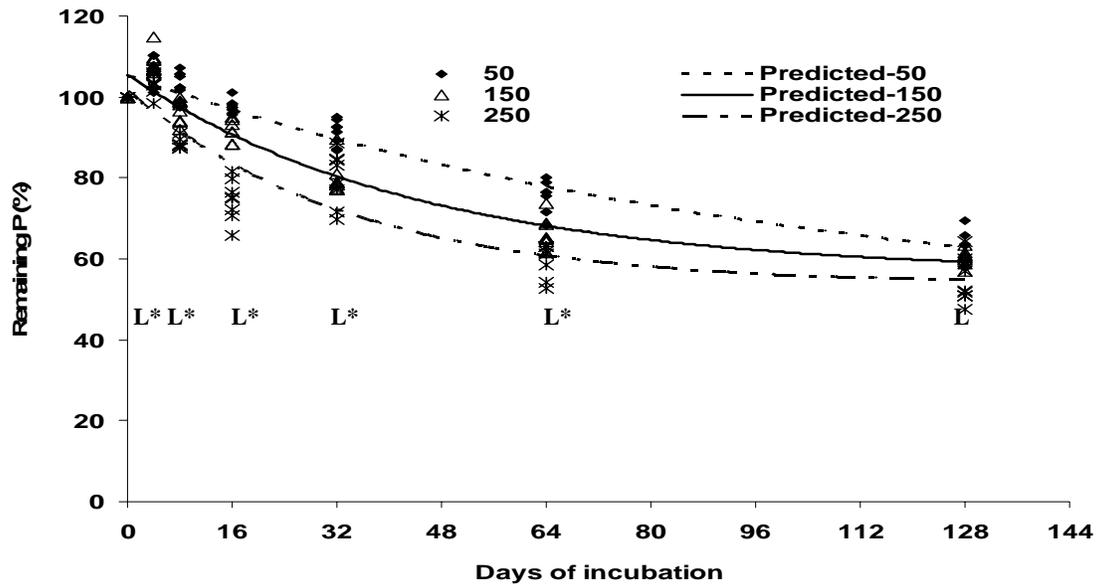


Figure 5-10. Litter P remaining as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three N fertilization levels in 2007. The equations are: for 50 kg N, $y = 44.3 + 60.95 * \exp(-0.009 * x)$, r-square = 0.93; for 150 kg N, $y = 56.5 + 48.96 * \exp(-0.02 * x)$, r-square = 0.93; for 250 kg N: $y = 53.7 + 47.82 * \exp(-0.03 * x)$, r-square = 0.86. Polynomial contrasts for the N effect within an incubation time: L = linear effect; * indicates significance at $P \leq 0.05$; L with no asterisk, $P \leq 0.10$.

Litter C:N ratio

Grazing intensity

There was year x grazing intensity x incubation time interaction ($P < 0.001$) for the C:N ratio in plant litter, so data were analyzed and reported by year. There were differences between years. Grazing intensity interacted with incubation time affecting C:N ratio in 2006 ($P < 0.001$) and 2007 ($P < 0.001$) (Figure 5-11, 5-12). The change in C:N ratio followed the single exponential model. Decreasing C:N ratio over incubation time was related to varying levels of changes in C and N content in litter. Carbon compounds in litter decomposed, as evidenced by

the loss in litter mass, but N immobilization occurred throughout the incubation period, thus C:N decreased throughout the incubation period. The SH response was not consistent across years, with C:N ratio being greater for the tall SH throughout the incubation period in 2006 but greater for the short SH in 2007. The pattern of C:N response to SH during incubation reflected C:N characteristics of initial litter in 2006. In 2007, there were no differences in initial C:N ratio, but the ranking of SH treatments remained unchanged from that of initial litter (Table 5-2).

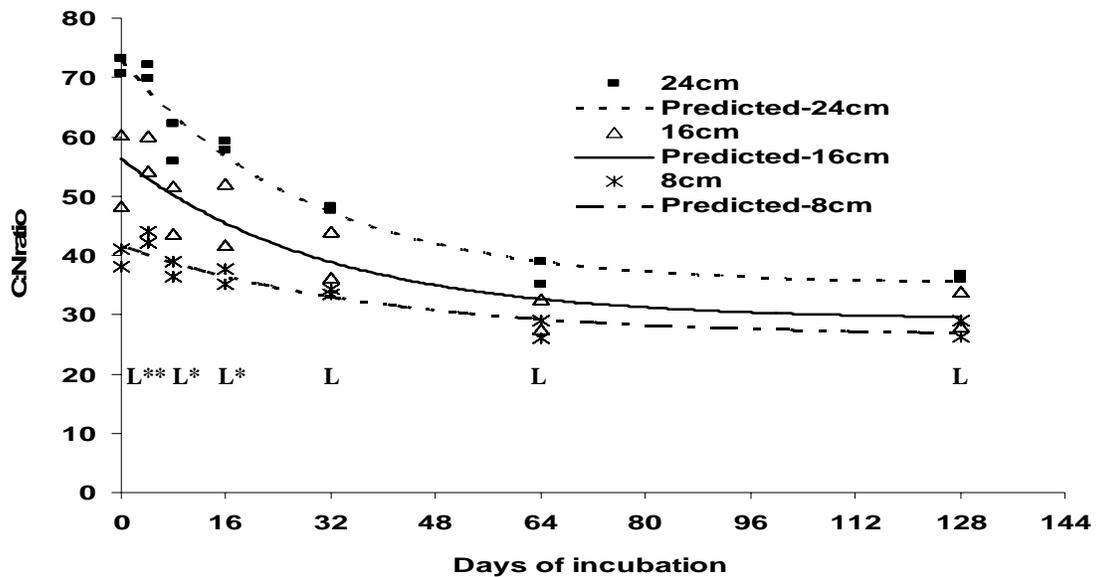


Figure 5-11. Litter C:N ratio as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three post-graze stubble heights (SH) in 2006. The equations are: for 24 cm, $y = 35.1 + 37.80 \cdot \exp(-0.04 \cdot x)$, $r\text{-square} = 0.96$; for 16 cm, $y = 29.2 + 27.13 \cdot \exp(-0.03 \cdot x)$, $r\text{-square} = 0.80$; for 8 cm, $y = 26.3 + 18.22 \cdot \exp(-0.03 \cdot x)$, $r\text{-square} = 0.87$. Polynomial contrast within incubation time among SH treatments: L = linear effect; * and ** indicate significance at $P \leq 0.05$ and 0.01 , respectively; L with no asterisk, $P \leq 0.10$.

After the 128-d incubation, C:N ratios in 2006 were 35, 30, and 27 for the 24-, 16-, and 8-cm SH treatments, respectively. In 2007, the comparable values were 23, 24, and 31 for the 24-, 16-, and 8-cm SH treatments, respectively. It was of interest to explore changes in C:N relative to initiation of N mineralization. Parton et al. (2007) reported that N mineralization occurred when the C:N ratio of leaf litter was < 40 . In the current study, C:N ratio became < 40 after plant

litter incubated around 57, 29, and 1 d for 24-,16-, and 8-cm SH treatments, respectively, in 2006. In 2007, the ratio became < 40 after litter incubated 19, 28, and 42 d for 24-, 16-, and 8-cm SH treatments, respectively. This transition occurred much earlier than the time when N mineralization began in the corresponding treatments, indicating limitation of C:N ratio in predicting net N release from litter, especially when exogenous N is easily accessed by microbes.

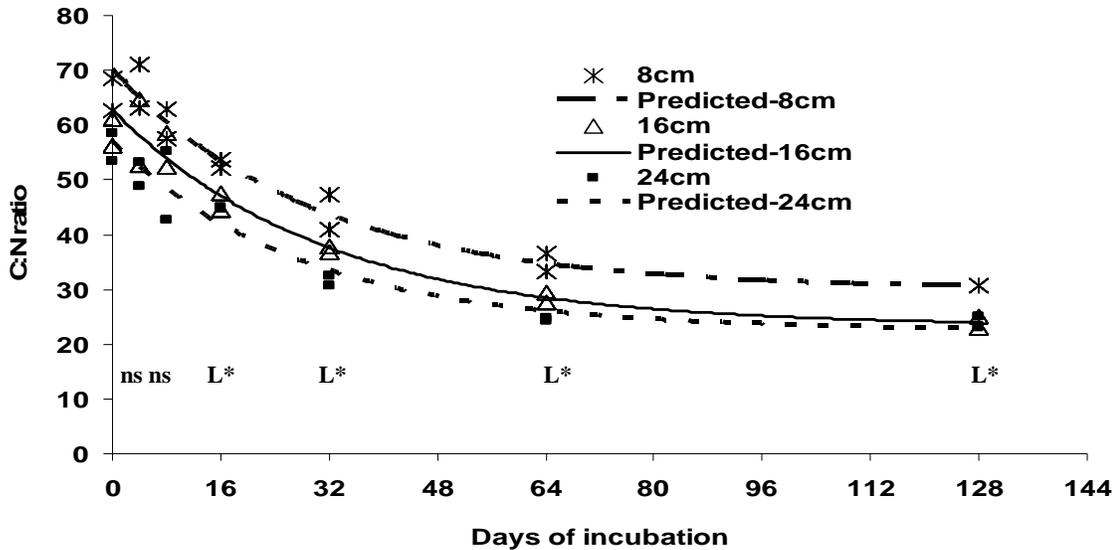


Figure 5-12. Litter C:N ratio as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three post-graze stubble heights (SH) in 2007. The equations are: for 24 cm, $y = 22.55 + 34.47 \cdot \exp(-0.036 \cdot x)$, r-square = 0.92; for 16 cm, $y = 23.32 + 39.46 \cdot \exp(-0.032 \cdot x)$, r-square = 0.95; for 8 cm, $y = 30.06 + 40.12 \cdot \exp(-0.034 \cdot x)$, r-square = 0.96. Polynomial contrasts for the SH effect within an incubation time: ns = not significant, L = linear effect; * indicates significance at $P \leq 0.05$.

N fertilization

There were differences between years and among N fertilization treatments in C:N ratio throughout the incubation period (Figs. 5-13, 5-14). The C:N ratio under each fertilization treatment followed a single exponential decay model and decreased across the incubation period. Generally, the C:N ratio of litter was greater for the low than the high N fertilizer level, except for early in the incubation period in 2006 when there were no differences. There were linear effects of N fertilization level for each incubation time in both years. Litter C:N ratios at the end

of the incubation period in 2006 were 55, 40, and 35 for the 50, 150, and 250 kg N treatments, respectively. In 2007, the values were around 42, 31, and 23 for same treatments. This response was probably related to N availability in the grassland ecosystem in response to N fertilization in 2006, and to both initial litter C:N (declined linearly with increasing N rate in 2007) and N availability in the ecosystem in 2007. As noted earlier in the discussion of N release, addition of N fertilizer has been shown to increase N availability to microbes (Hall and Matson, 1999), increasing microbial biomass (Frey et al., 2000). This process likely resulted in greater N content in litter and greater N immobilization under high N fertilization, leading to the lower C:N ratios observed for high N fertilizer rates in the current study.

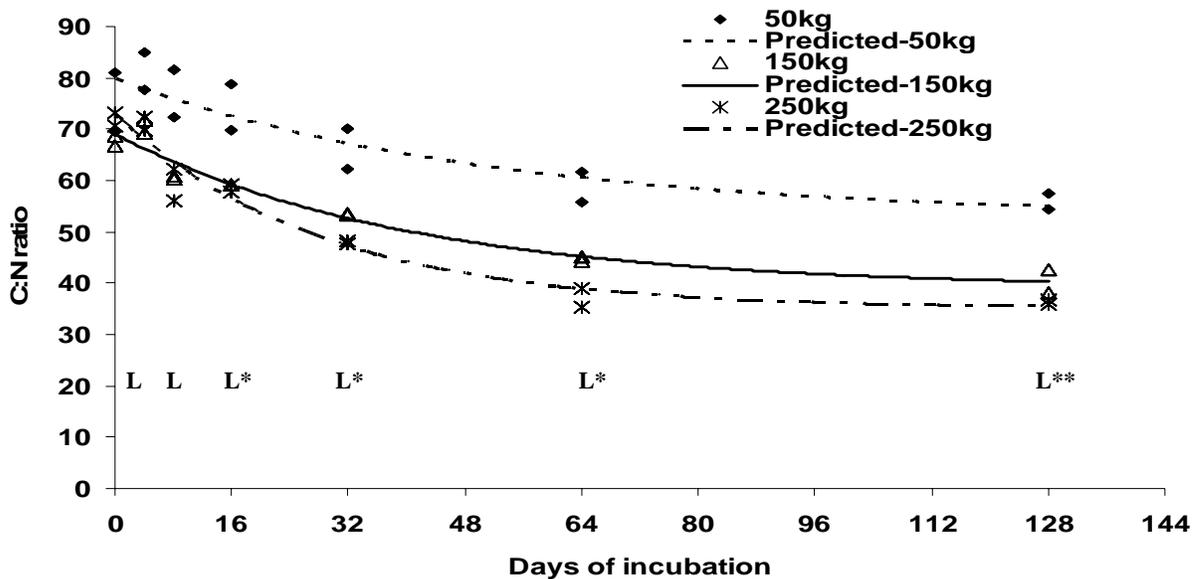


Figure 5-13. Litter C:N ratio as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three N fertilization levels in 2006. The equations are: for 50 kg N, $y = 52.7 + 27.06 * \exp(-0.02 * x)$, r-square = 0.77; for 150 kg N, $y = 39.0 + 29.97 * \exp(-0.02 * x)$, r-square = 0.95; for 250 kg N, $y = 35.1 + 37.80 * \exp(-0.04 * x)$, r-square = 0.96. Polynomial contrasts for the N rate effect within an incubation time: L = linear effect; * and ** indicate significance at $P \leq 0.05$ and 0.01, respectively; L with no asterisk, $P \leq 0.10$.

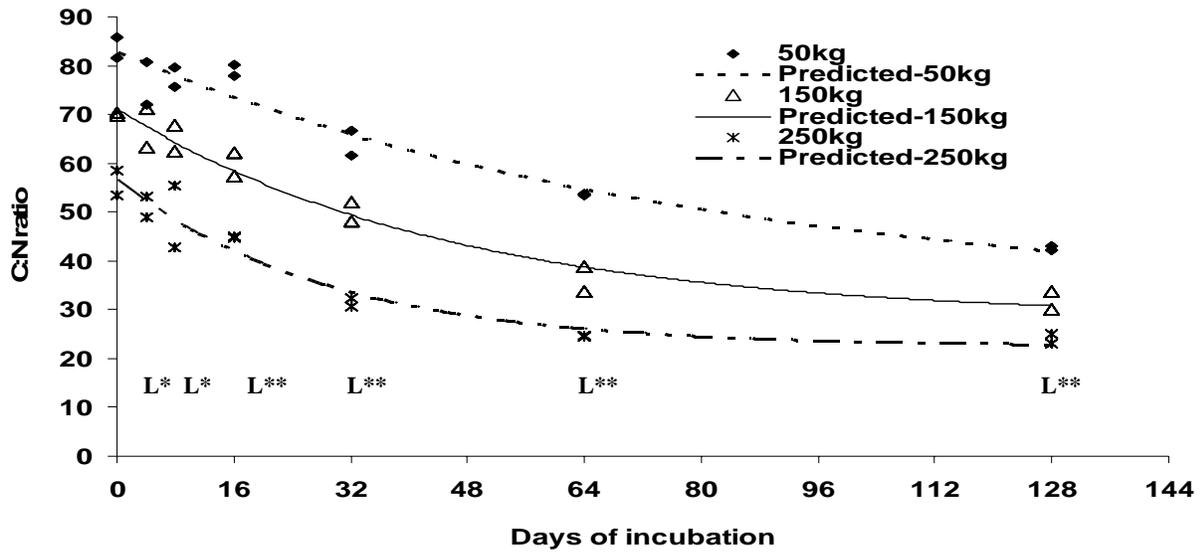


Figure 5-14. Litter C:N ratio as a function of incubation time on rotationally stocked Tifton 85 bermudagrass pastures affected by three N fertilization levels in 2007. The equations are: for 50 kg N, $y = 31.8 + 50.98 * \exp(-0.01 * x)$, r-square = 0.93; for 150 kg N: $y = 28.3 + 42.89 * \exp(-0.02 * x)$, r-square = 0.96; for 250 kg N, $y = 22.5 + 34.13 * \exp(-0.04 * x)$, r-square = 0.93. Polynomial contrasts for the N rate effect within an incubation time: L = linear effect; * and ** indicate significance at $P \leq 0.05$ and 0.01, respectively.

Summary and Conclusions

During litter decomposition, loss of litter mass was rapid early in the incubation period.

Grazing intensity (post-graze stubble height) had no effect on litter decomposition, but increasing N fertilization resulted in litter with faster relative decomposition rate.

Generally, soluble N components in litter were released rapidly within the first few days of the incubation period. Following that very short phase, however, N immobilization began and did not reach its maximum for up to 80 d. Increasing pasture SH and N fertilization resulted in an increase of N immobilization in plant litter. This response indicated that plant litter can act as a buffering pool for N, potentially causing a shortage of N for pasture plant growth or alternatively, reducing N loss to the environment in high N-input grassland ecosystems. Under a range of grazing intensities within the same level of N fertilization, high initial N concentration

and low C:N and lignin:N ratios resulted in greater N mineralization. Under a range of N fertilization treatments, exogenous N appeared to be the key factor controlling N immobilization of litter with a high C:N ratio.

Phosphorus decomposition in plant litter was not different among grazing intensities, but increasing N fertilization caused more P release from litter. This response followed similar patterns to litter OM loss, indicating that the factors controlling break down of litter mass may also be those controlling P release.

From this study, it can be concluded that N fertilization has a greater effect on litter decomposition and nutrient release than grazing intensity. Plant litter of C₄ grasses is not likely to provide significant N for plant growth in the short term due to initial immobilization. Periods of immobilization can last in excess of 128 d, possibly resulting in periods of shortfall of available N to swards without N fertilizer input. In order to more fully understand litter nutrient dynamics in warm climate grasslands, year-round characterization of responses will be needed and longer-term studies will be required. Additional information is also needed regarding the relationship between plant nutrient demand and ecosystem supply.

CHAPTER 6
GRAZING INTENSITY AND NITROGEN FERTILIZATION EFFECTS ON LITTER MASS,
DEPOSITION RATE, AND CHEMICAL COMPOSITION IN ROTATIONALLY STOCKED
'TIFTON 85' BERMUDAGRASS PASTURES

Introduction

The accumulation of plant litter and the availability of nutrients in litter affect grassland community composition and persistence (Robbins et al., 1989; Weltzin et al., 2005; Patrick et al., 2008). Plant litter plays an important role in nutrient return and soil organic matter (SOM) turnover in grassland ecosystems (Drinkwater et al., 1998; Dubeux et al., 2006a, 2006b), and litter can be an important source of nutrients for plants and a source of both nutrients and energy for microbes (Moore and Braswell, 1994).

Pasture management affects litter deposition and the pathways of nutrient return (Rezende et al., 1999; Sangha et al., 2006; Dubeux et al., 2006a). For example, increasing stocking rate decreased litter deposition (Rezende et al., 1999), because of its impact on above-ground herbage mass, and increased the proportion of nutrients returned to the pasture via excreta compared with litter (Thomas, 1992). In general, increasing inputs into a pasture system are associated with greater litter deposition rate (Schuman et al., 1999; Dubeux et al., 2006a). Foster and Gross (1998) reported that addition of N fertilizer over two growing seasons increased both live plant and litter biomass. In addition to increasing litter deposition, fertilization has been associated with greater litter quality (Beare et al., 2005; Li et al., 2007). Higher nutrient uptake by fertilized plants may increase litter turnover and nutrient release (Dubeux et al., 2006a), and greater availability of soil nutrients in fertilized systems may provide critical nutrients for microbial activity and contribute to more rapid release of nutrients from litter (Reeder et al., 1998; Rice et al., 2000).

It is clear from the literature that pasture management decisions affect litter deposition and quality, which in turn impact nutrient dynamics of pastures. Perhaps the two most critical pasture management decisions in terms of nutrient dynamics are grazing intensity (e.g., stocking rate or sward height) and level of fertilization. There is limited information regarding the impact of these management practices on litter responses, particular in sub-tropical and tropical grassland ecosystems. There are no known data on pasture management effects on litter dynamics of bermudagrass (*Cynodon dactylon* [L.] Pers.) pastures. Because bermudagrass is the most important warm-season perennial grass in the southeastern USA (Taliaferro et al., 2004), this information is needed. Thus, the objective of this study was to determine the effect of varied grazing intensity (post-graze sward height) and N fertilization levels on existing litter mass, litter deposition, and litter chemical composition on rotationally stocked ‘Tifton 85’ bermudagrass (*Cynodon* spp.) pastures.

Materials and Methods

Experimental Site

Research was conducted at the University of Florida Beef Research Unit, northeast of Gainesville, FL, at 29°43’ N lat on well-established Tifton 85 bermudagrass pastures. Soils are classified as Ultisols from the Plummer (loamy, siliceous, thermic Grossarenic Paleaquults) and Spar series (loamy, siliceous, hyperthermic Grossarenic Paleudults) with average soil pH of 6.2. Mehlich I extractable P, K, Mg, and Ca concentrations in soil were 71, 23, 93, and 732 mg kg⁻¹, respectively.

Treatments and Design

This experiment was conducted during 2006 and 2007. There were five treatments that were chosen to represent a wide range of grazing intensity and N fertilization of rotationally stocked pastures (Table 4-1). One set of three treatments was designed to study the effect of

grazing intensity, and they were defined in terms of post-graze stubble height (SH). The three levels of SH evaluated were 8, 16, and 24 cm. All three SH treatments had the same length of grazing cycle (28 d, composed of < 10 h grazing time plus the rest period) and the same level of N fertilization ($250 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). The fourth and fifth treatments were grazed to SH of 24 cm with a 28-d grazing cycle, but they differed in amount of N fertilizer applied (50 and $150 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). These two treatments along with one already described, i.e., grazed to 24-cm SH but received $250 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, provided another set of three treatments varying only in amount of N fertilizer applied. Each experimental unit was $8 \times 50 \text{ m}$, and all treatments were arranged in two replicates of a randomized complete block design. There were a total of 10 pastures included in this study.

All pastures were mowed to an 8-cm SH in March 2006 and 2007. Grazing was initiated on a given experimental unit each year when sward height was 20 cm taller than the target post-graze SH. Subsequent grazing events occurred according to the established treatment description. At each grazing event, enough yearling heifers were assigned to each experimental unit to graze the herbage to the target SH within 10 h. Stubble height was measured frequently at 25 locations per experimental unit during each grazing period. When the average of the 25 measurements reached the target SH, the grazing event ended and cattle were removed. The grazing season was from June to October or November each year, and number of grazing cycles per year for each treatment was six in 2006 and five in 2007.

All treatments received 50 kg N ha^{-1} on 1 May 2006 and 2 May 2007. For treatments receiving 150 or $250 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, the remaining N was applied in four equal applications of 25 (150 kg N rate) or 50 kg N ha^{-1} (250 kg N rate). The N source was ammonium nitrate, and the four split applications of fertilizer were broadcast applied on 16 June, 14 July, 11 Aug., and 8

Sept. 2006, and on 22 June, 19 July, 17 Aug., and 13 Sept. 2007. Twenty-two kilograms of P and 83 kg K ha⁻¹ were applied with the initial N application each year. The amount of P and K applied was based on soil test recommendations for improved perennial grass pastures.

Response Variables

Existing and deposited litter mass

Existing and deposited litter mass were measured based on the technique described by Bruce and Ebersohn (1982) and also used by Thomas and Asakawa (1993), Rezende et al. (1999), and Dubeux et al. (2006b). Existing and deposited litter were defined as dead plant material on the surface of the soil, no longer attached to the plant. Existing litter in the pasture was determined during the regrowth period by sampling four circular quadrats (0.25 m²) per pasture in areas that represented the average pasture herbage mass.

Sampling started after completion of the first grazing cycle of each treatment so that treatments were imposed prior to any sampling events. Seven days into the regrowth period following the first and each subsequent grazing event except the last of the season, the existing litter within each quadrat was raked and collected, dried (72 h at 60°C), and weighed. After 14 d (21 d into the regrowth period), the site was sampled again to collect new litter (termed deposited litter) within the cleared quadrats. Deposited litter was collected, dried, and weighed using the same protocol as for existing litter.

The time period, i.e., from Day 7 through 21 of a regrowth period was chosen so that litter deposition was measured during the middle of the regrowth period and represented the average deposition for that treatment. In order to correct for soil contamination, final weights were expressed on an OM basis. If some green material was collected along with the litter, correction for green herbage occurred by hand separating green material from litter. In the next grazing cycle, four new 0.25-m² areas were chosen in each of the 10 pastures for measurement of

existing and deposited litter, and this procedure was repeated four times in each grazing season. Litter, within litter type (i.e., existing or deposited litter), was composited across the four quadrats per pasture for each evaluation date prior to subsequent laboratory analyses.

Litter deposition rate

Litter deposition rate was determined by using the approach described by Rezende et al. (1999) with some modifications in respect to the use of the rate of decomposition (Dubeux et al., 2006b). According to their description, the litter on the ground at any time is a function of the litter deposition minus the litter decomposition that occurred within a given period. Therefore, in the case of litter deposited in an area that had been cleared of litter, the quantity of litter (dX) present after the increment of time 'dt' is:

Litter on the ground = litter deposited – disappeared litter, or:

$$dX = Ldt - KXd t \quad \text{(Equation 1)}$$

Where:

L is the true daily rate of litter deposition in $\text{g m}^{-2} \text{d}^{-1}$.

X is the quantity of litter on the ground at any time (g m^{-2}).

K is the relative decomposition rate.

dt is the period of time after clearing the site of existing litter.

The litter deposition rate was calculated using as X the 14-d deposited litter mass after an area was cleared. The relative decomposition rate, k, used was obtained from the decomposition model for litter bag data (Chapter 5) and using 14 d as the incubation period. Thus, dt in this study was 14 d.

Litter chemical composition

Existing and deposited litter samples were oven-dried and milled to pass a 1-mm screen and analyzed for dry matter (DM), OM, C, N, P, acid detergent fiber (ADF), and acid detergent

lignin. Dry matter and OM analyses were performed using the procedure described by Moore and Mott (1974). Carbon and N analyses were done using Flash EA 1112 NC Analyzers. Phosphorus concentration was measured using the modification of the aluminum block digestion procedure (Gallaher et al., 1975). Litter ADF and acid detergent lignin analyses were run in an ANKOM fiber analyzer (ANKOM Technology, 2003a, 2003b).

Statistical Analysis

The effects of grazing intensity and N fertilization on existing litter mass, litter deposition rate, and litter chemical composition were assessed using a repeated measures ANOVA with the PROC MIXED procedure of SAS (Littell et al., 1996). Sampling date was the repeated variable. Year, sampling date, SH or N treatment, and their interactions were considered fixed effects. Replication (block) and its interactions with SH or N fertilization were considered random effects. Year was considered a fixed effect because treatments were imposed on the same experimental unit each year, so there may have been cumulative effects over time. When treatment by year interaction was significant, data were analyzed and reported by year. Least-significant-difference procedures were used for mean separation when sampling date effects were significant (Steel and Torrie, 1980). Polynomial contrasts were used to evaluate the linear and quadratic effects of SH or N fertilization level, and the F test of the year effect was used to compare years. Treatment effects and interactions were considered significant if $P \leq 0.10$.

Results and Discussion

Existing Litter Mass

There was year x grazing intensity x sampling date interaction for existing litter mass ($P = 0.071$), so data were analyzed and reported by year. Within each year, there was no grazing intensity x sampling date interaction for existing litter mass ($P = 0.436$ in 2006, $P = 0.138$ in 2007), but there was a SH main effect (Table 6-1). Grazing to short SH resulted in less existing

litter mass compared to tall SH. Existing litter OM mass increased from 1790 to 2700 kg ha⁻¹ and 1660 to 2320 kg ha⁻¹ for 2006 and 2007, respectively, as SH increased from 8 to 24 cm, and there were both linear and quadratic effects of SH (Table 6-1). A greater proportion of herbage was consumed by animals when pastures were grazed to short vs. tall SH, leaving less plant mass to senesce. The importance of plant litter as a pool for nutrients cycling through the ecosystem is thought to be smaller when forage utilization rate is high because animal excreta forms a more important nutrient pool under these conditions (Thomas, 1992; Dubeux et al., 2006b). In mixed prairie, parkland fescue, and foot-hills fescue grasslands, Naeth et al. (1991) observed that heavy grazing intensity reduced litter mass relative to light grazing intensity. In the current study, greater existing litter mass for tall SH appears to be a function of greater litter deposition rate (described later in this chapter) than for short SH and no difference in litter decomposition rate among levels of SH (Chapter 5).

Nitrogen fertilization had no effect on existing litter mass ($P = 0.558$). Values ranged from 2220 to 2420 kg ha⁻¹ across the N levels imposed. Considering only the three N level treatments, existing litter mass was affected by the interaction of year and sampling date ($P < 0.001$) (Table 6-2). Existing litter mass in 2006 was greater than in 2007 at three of four sampling dates. This response was likely associated with litter decomposition rate. According to litter decomposition results previously reported (Chapter 5), litter decomposition rate was greater in 2007 than in 2006, likely resulting in less existing litter mass in the second year. Existing litter mass was least at the beginning of sampling each year and increased through October 2006. In 2007 the response was less consistent, but it was least in July and greatest in August. This was likely associated with seasonal patterns of herbage accumulation; it is low during the cool season and

early spring and much greater during the warm season. Greater herbage mass generally results in greater litter deposition (Reardon and Merrill, 1976).

Table 6-1. Effect of post-graze stubble height of rotationally stocked Tifton 85 bermudagrass pastures on existing litter organic matter (OM) mass during 2006 and 2007. Data are means across four sampling dates and two replications (n = 8).

SH	Year	
	2006	2007
cm	kg ha ⁻¹	kg ha ⁻¹
8	1790	1660
16	2500	2240
24	2700	2320
SE [†]	70	78
PC [‡]	L**,Q	L**,Q

[†] SE, standard error

[‡] PC, polynomial contrast for effect of stubble height. L = linear, Q = quadratic; L or Q with no asterisk following the letter indicates significance at $P \leq 0.10$; * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

Table 6-2. The effect of year x sampling date interaction on existing litter organic matter (OM) mass ($P < 0.001$) and litter deposition rate ($P = 0.057$) of rotationally stocked Tifton 85 bermudagrass pastures under three levels of N fertilization. Data are means across three N rates and two replications (n = 6).

Year	Sampling date			
	July	August	Sept.	Oct.
Existing litter OM mass				
-----kg ha ⁻¹ -----				
2006	2190d [†]	2430c	2670b	3060a
2007	1880c	2350a	1930c	2200b
SE [‡]			147	
P value	0.048 [§]	0.358	< 0.001	< 0.001
Litter deposition rate				
-----kg OM ha ⁻¹ d ⁻¹ -----				
2006	52a	45a	30b	19c
2007	38a	19b	16c	11d
SE			6	
P value	0.035	< 0.001	0.042	0.021

[†] Means within a year not followed by the same letter are different ($P < 0.10$).

[‡] SE, standard error

[§] P value for year effect within sampling date and response variable.

Litter Deposition Rate

There was year x SH x sampling date interaction for litter deposition rate ($P < 0.001$), so data were analyzed by year. Litter deposition rate was affected by the interaction of SH x sampling date in both years ($P = 0.011$ in 2006 and $P = 0.005$ in 2007) (Table 6-3). Interaction occurred due to the magnitude of differences in the response. Difference between years are likely due to lower pre-experimental period rainfall (Table 3-1) and smaller herbage accumulation (Table 3-5) in 2007 than in 2006. Within a sampling date, litter deposition rate increased with increasing SH in each year. The response had a linear component at all sampling dates, and the quadratic effect was significant in September of 2006 and July and August of 2007. Increasing litter deposition rate with increasing SH was likely associated with greater post-graze herbage mass for the tall SH treatment (Chapter 4) and opportunity for senescence of this residual herbage over the grazing season. Litter deposition rate in the 24-cm SH treatment was at least twice as great as for the 8-cm SH treatment at each date. This consistently high litter deposition rate throughout the experimental period for the 24-cm SH treatment contributed to the observed increase in existing litter mass as SH increased (Table 6-1). Within a level of SH, litter deposition rate decreased as the grazing season progressed from July to October. For example, litter deposition rate in the 8-cm SH treatment decreased from 25 to 4 and 11 to 3 kg OM ha⁻¹ d⁻¹ in 2006 and 2007, respectively, for sampling dates in July and October. Similar trends occurred for 16- and 24-cm SH treatments. Litter deposition rate was always at least twice as great in July as in October. These seasonal patterns in litter deposition are likely a function of post-graze live herbage mass. Live herbage mass was consistently greater following summer than autumn grazings (Chapter 4; Table 4-4). In *Brachiaria* pastures in the Atlantic forest region of the South of Bahia, Brazil, Rezende et al. (1999) observed that the quantity of litter deposited increased

from July to November due to increasing temperature and rainfall, and then decreased due to drier and cooler weather.

Litter deposition rate was not affected by the main effect of N fertilization ($P = 0.951$), but there was year x sampling date interaction ($P = 0.057$) for the fertilization treatments (Table 6-2). Litter deposition rate in 2006 was greater than in 2007 within sampling dates. This was reflected in the relatively greater existing litter mass for 2006 (Table 6-2). As the grazing season progressed, litter deposition rate decreased from 52 to 19 and 38 to 11 kg OM ha⁻¹ d⁻¹ during July through October of 2006 and 2007, respectively. Reasons for the seasonal pattern of litter deposition response were already discussed.

Table 6-3. Litter organic matter (OM) deposition rate in rotationally stocked Tifton 85 bermudagrass pastures as affected by the post-graze stubble height (SH) x year interaction in 2006 ($P = 0.011$) and 2007 ($P = 0.005$). Data are means across two replications (n = 2).

Year/SH (cm)	Sampling date			
	July	August	Sept.	Oct.
	-----kg OM ha ⁻¹ d ⁻¹ -----			
2006				
8	25a [†]	12b	10b	4c
16	38a	26b	32b	13c
24	48a	48a	26ab	22b
SE [‡]			6	
PC [§]	L	L*	L**,Q**	L
2007				
8	11a	9a	7ab	3b
16	14a	13a	10b	4c
24	42a	23b	20bc	11c
SE			2	
PC	L*,Q	L**,Q	L*	L

[†] Sampling date means within a level of SH not followed by the same letter are different ($P < 0.10$).

[‡] SE, standard error

[§] PC, polynomial contrast for effect of SH within sampling date and year. L = linear, Q = quadratic; L or Q with no asterisk following the letter indicates significance at $P \leq 0.10$; * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

Litter Chemical Composition

N concentration

There was no SH x sampling date interaction for N concentration in existing litter ($P = 0.573$), but there was an SH main effect ($P = 0.054$) (Table 6-4). Existing litter N concentration decreased linearly from 20.5 to 19.2 g kg⁻¹ with increasing SH from 8 to 24 cm. Increasing grazing intensity has been associated with greater forage nutritive value (Newman et al., 2004) and greater litter quality (Shariff et al., 1994; Barger et al., 2004). Existing litter N content was approximately 35, 48, and 48 kg ha⁻¹ for the 8-, 16-, and 24-cm SH treatments, respectively, indicating that litter is potentially an important nutrient pool from which N can gradually be released for use by plants and microbes (Dubeux et al., 2006b).

Increasing N rate increased N concentration in existing litter (Table 6-5). Litter N concentration increased linearly from 11.5 to 19.2 g kg⁻¹ as N rate increased from 50 to 250 kg ha⁻¹ yr⁻¹. Litter N concentration for the high N fertilization level was almost twice as great as for the low level, reflecting the impact of greater N fertilization on herbage and subsequent litter N concentration (Dubeux et al., 2006b). Dubeux et al. (2006b) observed that existing litter N concentration of 'Pensacola' bahiagrass (*Paspalum notatum* Flügge) was approximately 50% greater for a high management intensity treatment (360 kg N fertilizer ha⁻¹ yr⁻¹ and 4.2 animal unit ha⁻¹ stocking rate) than low management intensity (40 kg N ha⁻¹ yr⁻¹ and 1.4 animal unit ha⁻¹ stocking rate). In the current study, the interaction of year x sampling date also affected N concentration in existing litter (Table 6-6). There was no difference among sampling dates in 2006, but in 2007 greatest N concentrations occurred later in the season.

Table 6-4. Effect of post-graze stubble height of rotationally stocked Tifton 85 bermudagrass pastures on existing litter organic matter (OM) mass, N and lignin concentrations, and C:N and lignin:N ratios during 2006 and 2007. Data are means across two years, four sampling dates, and two replications (n = 16).

Stubble height	Existing litter			
	N	C:N	Lignin	Lignin:N
cm	g kg ⁻¹		g kg ⁻¹	
8	20.5	24	186	9.2
16	20.4	24	167	8.2
24	19.2	26	148	7.8
SE [†]	0.6	1	4	0.4
PC [‡]	L	L	L**	L*

[†] SE, standard error

[‡] PC, polynomial contrast for effect of stubble height. L = linear, Q = quadratic; L or Q with no asterisk following the letter indicates significance at $P \leq 0.10$; * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

Lignin concentration and lignin:N and C:N ratio

There was no SH x sampling date interaction for existing litter lignin concentration ($P = 0.489$), lignin:N ratio ($P = 0.437$), or C:N ratio ($P = 0.587$), but there was SH main effect (Table 6-4). Lignin concentration and lignin:N ratio in existing litter decreased linearly with increasing SH, but C:N ratio increased linearly as SH increased. Lignin concentration in newly deposited Tifton 85 litter averaged 98 g kg⁻¹ (Chapter 5), but lignin concentration of existing litter was 50 to almost 100% greater than newly deposited litter due to the fact that existing litter had been in the field undergoing decomposition for varying amounts of time. This conclusion is supported by Dubeux et al. (2006a) who showed that lignin:N ratio of bahiagrass litter doubled during a 128-d incubation period. The lower lignin concentration and lignin:N ratio of tall SH treatments in the current study is likely related to rates of new litter deposition. Litter deposition increased markedly as SH increased (Table 6-3), thus the proportion of newly deposited litter in existing litter was greater for taller SH treatments. Newly deposited litter has lower lignin concentration

Table 6-5. The effect of N fertilization level of rotationally stocked Tifton 85 bermudagrass pastures on existing litter organic matter (OM) mass, P, N, lignin, and acid detergent fiber (ADF) concentrations, and C:N, lignin:N, and C:P ratios. Data are means across 2 yr, four sampling dates, and two replications (n = 16).

N rate kg ha ⁻¹	Existing litter						
	N ----- g kg ⁻¹ -----	Lignin	C:N	Lignin:N	ADF ----- g kg ⁻¹ -----	P	C:P
50	11.5	140	43	12.5	508	1.3	409
150	15.6	151	31	9.7	538	1.5	339
250	19.2	148	26	7.8	518	2.0	259
SE	1	18	2	1.4	25	0.1	37
PC	L**	NS	L**	L*	NS	L**	L**

† SE, standard error

‡ PC, polynomial contrast for effect of N fertilization. L = linear; * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

and lignin:N ratio. Carbon concentration (486 g kg⁻¹) did not differ among levels of SH, so the small differences in C:N reflect differences in litter N concentration.

Nitrogen fertilization had no effect on lignin concentration in existing litter, but there were pronounced linear declines in C:N and lignin:N ratios with increasing N rate (Table 6-5). The increase in N concentration in existing litter with increasing N rate was the primary determinant

Table 6-6. Effect of year x sampling date interaction on existing litter N ($P=0.010$), P ($P<0.001$), lignin ($P=0.054$), and acid detergent fiber (ADF; $P=0.001$) concentrations on rotationally stocked Tifton 85 bermudagrass pastures. Data are means across three levels of N fertilization and two replications ($n=6$).

Item/year	Sampling date			
	July	August	Sep.	Oct.
-----g kg ⁻¹ -----				
N				
2006	15.1a [†]	15.5a	15.5a	15.1a
2007	13.3b	14.5b	17.3a	17.3a
SE [‡]		1		
P-Value [§]	0.097	0.34	0.112	0.047
Lignin				
2006	134b	130b	166a	143b
2007	137b	146b	151ab	164a
SE		17		
P-Value	0.893	0.391	0.455	0.259
ADF				
2006	500b	553a	501b	490b
2007	510b	498b	590a	531b
SE		25		
P-Value	0.718	0.060	0.003	0.147
P				
2006	2.3a	1.7b	1.1c	1.6b
2007	1.4a	1.4a	1.5a	1.5a
SE		0.1		
P-value	< 0.001	0.009	0.002	0.626

[†] Sampling date means within a nutrient and year not followed by the same letter are different ($P<0.10$).

[‡] SE, standard error

[§] P value for year effect within sampling date and response variable.

of these changes. There was year x sampling date interaction for existing litter lignin concentration, C:N ratio, and lignin:N ratio (Tables 6-6 and 6-7). Lignin concentration did not differ between years, but increased from the first to later sampling dates. The range of the increase was 134 to 166 and 137 to 164 g kg⁻¹ in 2006 and 2007, respectively. The increase in lignin concentration as the season progresses may reflect the lower litter deposition rate later in the season (Table 6-2), i.e., at later sampling dates a greater proportion of existing litter was litter that was deposited earlier in the season and lignin was more concentrated in this material because the more degradable components had already broken down. Existing litter C:N ratio varied among sampling dates from 31 to 33 and 29 to 39 for 2006 and 2007, respectively, but the sampling date effect was not consistent across years, reflecting primarily the lack of N fertilizer effect on litter N concentration in 2006 and the strong linear effect on N concentration in 2007. The reason for the difference between years is not clear. Lignin:N ratio ranged from 8.4 to 11.2 and from 9.8 to 11.1 for 2006 and 2007, respectively. The sampling date effect was not consistent across years for lignin:N either, again because of the difference in litter N response in the 2 yr.

Litter C:N ratio is accepted as a useful predictor of decomposition and N mineralization rates (Corbeels, 2001). Wagner and Wolf (1999) reported that N mineralization was favored when C:N ratio was lower than 20, but N immobilization dominated when C:N ratio was greater than 30. Parton et al. (2007) observed that net N release occurred when the average C:N ratio of leaf litter was less than 40. In bahiagrass pastures, Dubeux et al. (2006a) found that litter with high C:N (> 109) and lignin:N ratios (> 25) caused immobilization of N. In the current study, C:N ratio ranged from 24 to 26 under the three SH treatments. These are intermediate values indicating potential for N release or N immobilization from existing litter. When N fertilization

was 50 kg ha⁻¹ yr⁻¹, C:N ratio was 43, suggesting that N immobilization was likely. In contrast, C:N ratio decreased to 26 as N rate increased to 250 kg ha⁻¹ yr⁻¹, suggesting greater potential for N mineralization. In reality, there was very little N mineralization during a 128-d incubation period of litter from the 50 kg N fertilizer treatment, and litter from both the 150 and 250 kg N treatments immobilized N over nearly the entire 128-d period (Chapter 5). These results suggest that factors other than litter C:N ratio impact N release and immobilization of Tifton 85 litter. In particular, the amount of N available in the environment, as associated with N fertilizer level, appeared to play a significant role (Chapter 5).

Table 6-7. Effect of year x sampling date interaction on existing litter C:N ($P < 0.001$), lignin:N ($P = 0.006$) and C:P ($P < 0.001$) ratios in rotationally stocked Tifton 85 bermudagrass pastures. Data are means across three levels of N fertilization and two replications (n = 6).

Item/Year	Sampling date			
	July	August	Sept.	Oct.
C:N				
2006	31b [†]	31b	33a	33a
2007	39a	38a	31b	29b
SE [‡]			2	
P value [§]	0.002	0.010	0.361	0.102
Lignin:N				
2006	8.9b	8.4b	11.2a	10.6a
2007	11.1a	11.1a	9.8b	10.0b
SE			1.4	
P value	0.022	0.007	0.328	0.788
C:P				
2006	197d	284c	448a	311b
2007	360a	380a	353a	350a
SE			37	
P value	0.003	0.010	0.005	0.221

[†] Sampling date means within year not followed by the same letter are different ($P < 0.10$).

[‡] SE, standard error

[§] P value for year effect with sampling date and response variable.

ADF concentration

There was year x grazing intensity x sampling date interaction for existing litter ADF concentration ($P = 0.007$), so data were analyzed and reported by year. Litter ADF concentration was affected by the interaction of grazing intensity x sampling date in both experimental years ($P = 0.022$ in 2006 and $P = 0.009$ in 2007) (Table 6-8). The most consistent response was observed for the 8-cm SH treatment for which ADF concentration increased from the beginning to end of the grazing season in both years. Responses were much less consistent for the other SH treatments with no obvious pattern of response. Litter ADF was not affected by sampling date for the 16-cm SH in 2007 and was greatest in September in 2006. For the 24-cm SH treatment, ADF concentration reached a maximum value (577 g kg^{-1}) in August 2006 and September 2007 (567 g kg^{-1}), and there were no differences among other sampling dates. Litter ADF concentration did not differ among SH treatments in July and August 2006, but ADF concentration decreased in September 2006 and September and October 2007 and tended to decrease in July (quadratic, $P = 0.112$) and August 2007 (linear, $P = 0.136$). The reduction in ADF with increasing SH is consistent with decreasing lignin concentration and lignin:N ratio (Table 6-4), and likely occurred for reasons similar to those already described for those responses.

Existing litter ADF concentration was not affected by N fertilization (Table 6-5), averaging 520 g kg^{-1} . There was year x sampling date interaction for litter ADF (Table 6-6). Litter ADF concentration was greater in August than other sampling dates in 2006 and greater in September than other dates in 2007.

Table 6-8. Effect of stubble height (SH) x sampling date interaction on litter ADF concentration on rotationally stocked Tifton 85 bermudagrass pastures during 2006 ($P = 0.022$) and 2007 ($P = 0.009$). Data are means across two replications ($n = 2$).

Year/SH (cm)	Sampling date			
	July	August	Sept.	Oct.
	-----g kg ⁻¹ -----			
2006				
8	482b [†]	516a	528a	513a
16	494b	486b	552a	504b
24	480b	577a	509b	495b
SE [‡]			18	
PC [§]	NS	NS	L,Q*	NS
2007				
8	538c	573b	591b	638a
16	560a	537a	498a	561a
24	496b	487b	567a	518b
SE			21	
PC	NS	NS	Q	L*

[†] Sampling date means within SH and year not followed by the same letter are different ($P < 0.10$).

[‡]SE, standard error

[§]PC, polynomial contrast for effect of post-graze stubble height. L = linear, Q=quadratic; L or Q with no asterisk following the letter indicates significance at $P \leq 0.10$; * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

P concentration and C:P ratio

There was year x SH x sampling date interaction for P concentration and C:P ratio in existing litter ($P = 0.009$ for P concentration; $P = 0.005$ for C:P ratio), so data were reported by year. Within both years, there was no SH x sampling date interaction, but there was a main effect of SH on P concentration and C:P ratio (Table 6-9). Litter P concentration increased linearly and C:P ratio decreased linearly with increasing SH from 8 to 24 cm in both years; P concentration increased from 1.8 to 1.9 and 1.5 to 2.0 g kg⁻¹ in 2006 and 2007, respectively, and C:P ratio decreased from 279 to 240 and 327 to 252 in 2006 and 2007, respectively. Litter C concentration did not differ among grazing intensities, averaging 486 g kg⁻¹, thus changes in P concentration caused the change in C:P ratio. Dalal (1979) reported that P immobilization predominated when

C:P ratio was > 200:1. Therefore, P immobilization would be expected for litter from all SH treatments in both years of the current study.

Table 6-9. Effect of postgraze stubble height (SH) on existing litter P concentration and C:P ratio on rotationally stocked Tifton 85 bermudagrass pastures during 2006 and 2007. Data are means across four sampling dates and two replications (n = 8).

SH -----cm-----	2006		2007	
	P concentration -----g kg ⁻¹ -----	C:P	P concentration -----g kg ⁻¹ -----	C:P
8	1.8	279	1.5	327
16	1.9	256	1.6	312
24	1.9	240	2.0	252
SE [†]	0.02	5	0.05	15
PC [‡]	L	L**	L**	L*

[†] SE, standard error

[‡] PC, polynomial contrast for effect of post-graze stubble height within a response variable and year. L = linear; L or Q with no asterisk following the letter indicates significance at $P \leq 0.10$; * and ** indicate significance at the $P \leq 0.05$ and 0.01 levels, respectively. NS = not significant, $P > 0.10$.

There was no year x N fertilization x sampling date interaction for P concentration ($P = 0.209$) and C:P ratio ($P = 0.10$) in existing litter, but there was an N fertilization main effect (Table 6-5). Increasing N fertilization increased existing litter P concentration linearly and decreased C:P ratio linearly. Litter P concentration increased from 1.3 to 2.0 g kg⁻¹ and C:P ratio decreased from 409 to 259 as N rate increased from 50 to 250 kg N ha⁻¹ yr⁻¹. All treatments received the same amount of P fertilizer, so greater N fertilization likely caused increased litter P concentration indirectly by increasing P availability to the plant or by increasing root mass to access P (Dubeux et al., 2006b). Litter P concentration and C:P ratio in existing litter were also affected by year x sampling date interaction for the N fertilization portion of the study (Tables 6-6 and 6-7). Litter P concentration in 2006 decreased to September, but it did not differ among sampling dates in 2007. Litter C:P ratio increased to September in 2006 and decreased in

October; in 2007 there was no effect of sampling date. There were no differences in C concentration among treatments, so changes in C:P ratio reflected changes in P concentration. The C:P ratio was generally above 200 across sampling dates in both years, implying that P immobilization was likely by litter from all fertilization treatments through these grazing seasons.

Conclusions

Post-graze SH (grazing intensity) affected existing litter mass and litter deposition rate in Tifton 85 bermudagrass pastures. Existing litter mass and litter deposition rate increased as SH increased (grazing intensity decreased). However, N fertilization had no effect on existing litter mass and litter deposition rate. Litter deposition rate decreased as the grazing season progressed likely due to a decrease in post-graze residual live herbage mass from summer to autumn (Table 4-4).

Decreasing post-graze SH increased N, lignin, and ADF concentrations in existing litter and resulted in lower C:N ratio. Existing litter N concentration increased with increasing N fertilization, but N fertilization had no effect on lignin and ADF concentrations. Litter P concentration increased as SH and N fertilization increased. This resulted in lower litter C:P ratios in the tallest SH or greatest N fertilization treatments, suggesting these treatments are least likely to be associated with P immobilization.

Low grazing intensity (tall SH) was associated with greater litter deposition rate and existing litter mass, high nutrient content (primarily a function of greater litter mass), and high C:N ratio. This combination of traits suggests that in grasslands where the proportion of herbage mass consumed is low, grass litter will play a major role in nutrient dynamics, particularly in immobilization and slowing subsequent release of nutrients for plant uptake. This nutrient immobilization can have significant negative effects on grassland productivity and persistence in

low-input systems, primarily by further reducing nutrients available for plant growth. In grasslands receiving high levels of N fertilizer input, litter N and P concentrations and C:N and C:P ratios are higher than in low-input systems. These traits suggest that litter decomposition and nutrient mineralization may be more rapid in high- than low-input systems.

Based on results with Tifton 85 bermudagrass, the difference in short-term nutrient contribution from litter of C₄ grasses of low- and high-input systems may not be as great as expected because although litter quality is greater under high inputs it remains sufficiently low that nutrient immobilization continues to occur. This conclusion is supported in Chapter 5 by evidence of N immobilization, even under N rates as great as 250 kg ha⁻¹ yr⁻¹. Under these conditions, plant litter will likely accumulate significant quantities of nutrients, but as characteristic of lower quality litter, it will release them slowly. Perhaps the greatest benefit from C₄ grass litter in high input systems is slowing nutrient release and perhaps reducing nutrient loss to the environment.

CHAPTER 7 SUMMARY AND CONCLUSIONS

Bermudagrass [*Cynodon dactylon* (L.) Pers.] is one of the important C4 perennial grasses in warm climates. Tifton 85 bermudagrass (*Cynodon* spp.) is widely used for hay and pasture in the southern USA due to its greater productivity and digestibility than most other bermudagrass cultivars. There are no studies reported in the literature that have assessed the interaction of grazing intensity and grazing frequency on performance of Tifton 85 nor has the effect of pasture management on nutrient pools and plant litter dynamics been explored. It is important to clearly define the effects of grazing and nutrient management on pasture performance and nutrient dynamics if Tifton 85 bermudagrass pastures are to be sustainable and utilized efficiently.

To achieve this goal, experiments were conducted with the objectives of i) determining the effect of grazing intensity and frequency on herbage responses of Tifton 85 bermudagrass pastures (Chapter 3); ii) evaluating the size of the most important nutrient pools in Tifton 85 pastures at different times of the year as affected by N fertilization and intensity of defoliation (Chapter 4); and iii) quantifying litter production, litter decomposition, and nutrient release from litter on Tifton 85 bermudagrass pastures managed at different intensities and levels of N fertilization (Chapter 5 and 6).

In order to accomplish these objectives, experiments were conducted from 2006 to 2008 (Experiment 1) and 2006 to 2007 (Experiment 2). In Experiment 1, Tifton 85 herbage responses were determined for nine treatments. They were all factorial combinations of three post-graze stubble heights (SH; 8, 16, and 24 cm) with three different lengths of grazing cycle (GC; 14, 21, and 28 d). These treatments all received 250 kg N ha⁻¹ yr⁻¹. In Experiment 2, five treatments were evaluated. Three treatments were N fertilization levels (50, 150, and 250 kg N ha⁻¹), and all were compared using the same SH (24 cm) and GC (28 d). The other two treatments were SH levels of

8 and 16 cm, with GC (28 d) and N rate (250 kg N ha⁻¹) being the same for both. When these two were combined with the 24-cm SH treatment described earlier, it provided three levels of SH. Thus Experiment 2 allowed comparison of three levels of N fertilization (50, 150, and 250 kg N ha⁻¹) at the same grazing intensity, and three levels of grazing intensity (SH) at the same level of N fertilization.

Herbage Responses

In Experiment 1, the effects of a range of grazing frequencies and intensities on herbage accumulation, nutritive value, and persistence responses of Tifton 85 bermudagrass pastures were evaluated from 2006 to 2008. Tifton 85 bermudagrass herbage accumulation was strongly affected by the interaction of GC and SH. Greatest herbage accumulation occurred with short SH (8 cm) if GC was long (28 d) or with tall SH (24 cm) if GC was short (14 d). Lowest or nearly lowest herbage accumulation occurred with frequent grazing (14 d) to low SH (8 cm) or infrequent grazing (28 d) to tall SH (24 cm). At intermediate levels of GC (21 d) or SH (16 cm), the level of the other factor had relatively little impact on herbage accumulation.

Tifton 85 bermudagrass maintained relatively high nutritive value (crude protein and in vitro digestibility) across a wide range of grazing treatments. When SH affected the response, nutritive value was greatest at 8 cm. The effect of length of GC on nutritive value was more pronounced (generally a linear decline with increasing GC) and more consistent than the effect of SH.

Reduction in percentage cover was most pronounced in the 24-cm SH treatment, and this study and others conducted earlier with Tifton 85 suggest that underutilized pastures may experience significant stand loss. The cause of this reduction has not been determined. It does not appear to be related to loss of storage organ mass or reserve storage capacity because these responses were all quite favorable for the 24-cm SH in the current study. When comparing the

other two SH levels, as SH increased from 8 to 16 cm the year-to-year decrease in herbage accumulation was much less, stem base and root-rhizome mass increased, and reserve storage content generally increased indicating an advantage in persistence-related responses for the 16-cm SH.

If the 24-cm SH is ruled out for persistence reasons, then our data suggest several options depending on producer goals. Greatest herbage accumulation among the remaining treatments is likely to occur when pastures are grazed to ~ 8-cm SH but relatively infrequently (~ 28 d). Although the current study showed no effect on cover, shorter intervals between grazings to the 8-cm SH to increase nutritive value, are likely to reduce reserve storage and possibly long-term persistence. If greater nutritive value is needed on Tifton 85 pastures, then the 16-cm SH is likely a good choice because at this height the interval between grazings can be relatively short (14-21 d) to allow high nutritive value without negative impacts on persistence-related responses.

Nutrient Distribution Among Nutrient Pools

Experiment 2 quantified the effect of three N rates (50, 150, and 250 kg N ha⁻¹) and three SH (8, 16, and 24 cm) on mass, nutrient concentration, and nutrient content of four nutrient pools in rotationally stocked Tifton 85 bermudagrass swards. The nutrient pools were above-ground live herbage, above-ground plant litter, below-ground root-rhizome, and soil to 20-cm depth.

Increasing N fertilization increased live herbage mass, and it increased root-rhizome mass up to 150 kg N ha⁻¹. There was no effect of N fertilization on the mass of the plant litter pool. Decreasing pasture SH caused a decrease in live herbage, plant litter, and root-rhizome pool mass. Greatest mass of above-ground herbage and plant litter generally occurred in summer vs. spring or autumn.

Nutrient content (kg ha⁻¹) in live herbage, plant litter, and root-rhizome pools increased with increasing SH. Carbon and N content in soil also increased as SH increased, but soil K and

P content didn't differ among SH treatments. Increasing N fertilization increased N content in live herbage, plant litter, and root-rhizome pools, but did not affect N content in soil. Carbon content in live herbage and soil increased with increasing N fertilizer rate, but there was no effect of N fertilization on C content of plant litter and root-rhizome pools. Potassium content in live herbage, plant litter, and soil increased with increasing N rate, while P content was only slightly affected by N fertilization.

Increasing fertilization increased the proportion of K and N contained in live herbage and plant litter pools and decreased the proportion contained in the soil pool. Nitrogen rate did not affect the proportion of P and C contained in live herbage and plant litter pools. The proportion of C, K, and P contained in the live herbage pool increased with taller SH. The proportion of nutrients contained in the root-rhizome pool was not affected by SH.

These data suggest that lower grazing intensity (i.e., taller stubble heights, lower stocking rates) and greater N fertilization increase C sequestration and accumulation of N in nutrient pools in Tifton 85 bermudagrass pastures. Increasing N fertilization and decreasing grazing intensity (taller SH) causes a redistribution of nutrients among pools; this redistribution is greatest for K, not measurable for P, and significant but generally small for C and N.

Litter Decomposition and Nutrient Release

In Experiment 2, the effects of N fertilization level and grazing intensity (SH) on litter decomposition and nutrient release from litter were measured. During litter decomposition, loss of litter mass was rapid during the early part of the incubation period. Grazing intensity (post-graze stubble height) had no effect on litter decomposition, but increasing N fertilization resulted in litter with faster relative decomposition rate.

Generally, soluble N components in litter were released rapidly within the first few days of the incubation period. Following that short phase, however, N immobilization began and did not

reach its maximum for up to 80 d. Increasing pasture stubble height and N fertilization resulted in an increase of N immobilization in plant litter. This response indicated that plant litter can act as a buffering pool for N, potentially causing a shortage of N for pasture plant growth or alternatively, reducing N loss to the environment in high N-input grassland ecosystems. Under a range of grazing intensities with the same N fertilization, high initial N concentration and low C:N and lignin:N ratio resulted in greater N mineralization. For a range of N fertilization treatments, exogenous N in the ecosystems appeared to be the key factor controlling N immobilization of litter with high C:N ratio.

Phosphorus mineralization in plant litter was not different among grazing intensities, but increasing N fertilization caused more P release from litter. This response followed patterns similar to those for litter OM loss, indicating that the factors controlling break down of litter may also be those controlling P release.

From this study, it can be concluded that N fertilization has a greater effect on litter decomposition and nutrient release than grazing intensity. Plant litter of C₄ grasses is not likely to provide significant N for plant growth in the short term due to initial immobilization. Periods of immobilization can last in excess of 128 d, possibly resulting in periods of shortfall of available N to swards not receiving fertilizer inputs.

Litter Production and Chemical Composition

In Experiment 2, the effects of N fertilization level and grazing intensity (SH) on existing litter mass and litter deposition were measured on Tifton 85 bermudagrass pastures. Existing litter mass and litter deposition rate increased as SH increased (grazing intensity decreased). However, N fertilization had no effect on existing litter mass and litter deposition rate. Litter deposition rate decreased from summer to autumn likely due to a decrease in post-graze residual herbage mass from summer to autumn.

Increasing post-graze SH decreased existing litter N, lignin, and ADF concentrations and resulted in lower lignin:N ratio. Greater values of these responses at short SH likely reflect litter deposition rates in the three SH treatments and changes in litter composition over time. For example, lignin concentration in newly deposited Tifton 85 litter averaged 98 g kg^{-1} , but lignin concentration of existing litter was 50 to almost 100% greater due to decomposition of more degradable components of litter following litter deposition. In addition, much greater litter deposition rates for tall SH, up to four times greater for 24- vs. 8-cm SH, resulted in a greater proportion of more recently deposited and less decomposed litter in the existing litter fraction of the tall SH treatments. Existing litter N concentration increased with increasing N fertilization, but N fertilization had no effect on lignin and ADF concentrations. Litter P concentration increased as SH and N fertilization increased. This resulted in lower litter C:P ratios in the tallest SH or greatest N fertilization treatments, suggesting these treatments are the least likely to be associated with P immobilization.

Low grazing intensity (tall SH) was associated with greater litter deposition rate and existing litter mass, high existing litter nutrient content (primarily a function of greater litter mass), and high C:N ratio. This combination of traits suggests that in grasslands where the proportion of total herbage mass that is consumed by herbivores is low, grass litter will play a major role in nutrient dynamics, particularly in immobilization and slowing subsequent release of nutrients for plant uptake. This nutrient immobilization can have significant negative effects on grassland productivity and persistence in low-input systems, primarily by further reducing nutrients available for plant growth. In grasslands receiving high levels of N fertilizer input, litter N and P concentrations are higher and C:N and C:P ratios are lower than in low-input systems. Based on conventional wisdom, these traits suggest that litter decomposition and nutrient

mineralization will be more rapid in high- than low-input systems. With bermudagrass and likely with other C_4 grasses, however, the difference in nutrient contribution from litter of low- and high-input systems may not be as great as expected because although litter quality is greater under high inputs it remains sufficiently low that nutrient immobilization continues to occur. This conclusion is supported in Chapter 5 by evidence of N immobilization, even under N rates as great as $250 \text{ kg ha}^{-1} \text{ yr}^{-1}$. Under these conditions, plant litter acted as a buffering pool, immobilizing N, and not a major short-term nutrient provider for plant growth.

Implications of the Research

These experiments have demonstrated that:

1. Tifton 85 bermudagrass performed well under a range of grazing management strategies, but a) tall post-graze stubble heights ($\sim 24 \text{ cm}$) should be avoided, b) herbage accumulation was likely to be maximized with \sim an 8-cm stubble and a 28-d regrowth period, and c) nutritive value was quite high and reduction in within-year and year-to-year herbage accumulation relatively small with a 16-cm SH in combination with a 14- to 21-d regrowth period.
2. Nutrient pools in Tifton 85 pastures were affected by grazing management. Both taller SH and greater N fertilization increase C and N storage in soils, but the changes were relatively small compared to those associated with land-use changes. The economic and environmental benefit of increasing N fertilization to increase soil C storage is highly questionable.
3. In grasslands where the proportion of herbage mass consumed is low, grass litter will play a major role in nutrient dynamics, particularly in immobilization and slowing subsequent release of nutrients for plant uptake. Increasing application of N fertilizer affected litter quality, but even at relatively high levels of N fertilization,

bermudagrass litter decomposed slowly and immobilized N for 4 mo or longer, possibly resulting in periods of shortfall of available N to the sward. In order to more fully understand litter nutrient dynamics in warm climate grasslands, year-round characterization of responses will be needed and longer-term studies will be required. Additional information is also needed regarding the relationship between plant nutrient demand and ecosystem supply.

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BIOGRAPHICAL SKETCH

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