HERBAGE ACCUMULATION, NUTRITIVE VALUE AND TILLERING DYNAMICS OF BAHIAGRASS GENOTYPES UNDER GRAZING INTENSITIES

By

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1
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To my parents, Paulo and Rita
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# TABLE OF CONTENTS

ACKNOWLEDGMENTS ........................................................................................................... 4

LIST OF TABLES .................................................................................................................. 7

LIST OF FIGURES ............................................................................................................... 8

ABSTRACT .......................................................................................................................... 9

CHAPTER

1 INTRODUCTION ............................................................................................................. 11

2 LITERATURE REVIEW ................................................................................................. 14

   Origin and Characteristics of Bahiagrass ..................................................................... 14
   Taxonomy and Botanical Description .......................................................................... 14
   Center of Origin and Reproductive Behavior .............................................................. 14
   Uses of Bahiagrass in Florida ..................................................................................... 15
   Seasonal Yield Distribution .......................................................................................... 16
   Bahiagrass Tillering Characteristics .......................................................................... 21
   Size-Density Compensation Theory ........................................................................... 24
   Summary and Project Objectives ................................................................................. 27

3 BAHIAGRASS GERMPLASM YIELD AND NUTRITIVE VALUE UNDER TWO GRAZING INTENSITIES ............................................................................................................ 29

   Background .................................................................................................................. 29
   Material and Methods ................................................................................................... 30
   Experimental Site .......................................................................................................... 30
   Experimental Design and Treatments ......................................................................... 31
   Environmental Conditions and Pasture Management .................................................. 32
   Herbage Nutritive Value .............................................................................................. 36
   Statistical Analyses ...................................................................................................... 36
   Results and Discussion ............................................................................................... 37
      Herbage Accumulation .............................................................................................. 37
      Total-season .............................................................................................................. 37
      Seasonal .................................................................................................................... 39
      Total-season Herbage Harvested .............................................................................. 40
   Conclusions .................................................................................................................. 44

4 TILLERING DYNAMICS OF BAHIAGRASS GERMPLASM UNDER GRAZING INTENSITIES ......................................................................................................................... 47

   Background .................................................................................................................. 47
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-1</td>
<td>Weekly average weekly maximum and minimum air temperatures and total precipitation</td>
<td>33</td>
</tr>
<tr>
<td>3-2</td>
<td>Number of grazing events per treatment and year</td>
<td>34</td>
</tr>
<tr>
<td>3-3</td>
<td>Bahiagrass total-season herbage accumulation as affected by year x height x genotype interaction</td>
<td>39</td>
</tr>
<tr>
<td>3-4</td>
<td>Bahiagrass total-season herbage harvested as affected by year x height x genotype interaction</td>
<td>41</td>
</tr>
<tr>
<td>3-5</td>
<td>Bahiagrass weighted total season crude protein as affected by the year x genotype interaction</td>
<td>42</td>
</tr>
<tr>
<td>3-6</td>
<td>Bahiagrass weighted total season crude protein as affected by the stubble height x genotype interaction</td>
<td>43</td>
</tr>
<tr>
<td>3-7</td>
<td>Bahiagrass total season weighted digestibility (IVDOM) as affected by year x height x genotype interaction</td>
<td>44</td>
</tr>
<tr>
<td>4-1</td>
<td>Bahiagrass tiller density (tillers per 200 cm$^2$) as affected by the stubble height X cultivar interaction</td>
<td>51</td>
</tr>
<tr>
<td>4-2</td>
<td>Bahiagrass tiller mass (size) as affected by cultivar</td>
<td>52</td>
</tr>
<tr>
<td>4-3</td>
<td>Bahiagrass leaf-stem ratio as affected by cultivar x stubble height interaction</td>
<td>58</td>
</tr>
<tr>
<td>A-1</td>
<td>Coefficients of the herbage mass double sampling equations</td>
<td>67</td>
</tr>
<tr>
<td>B-1</td>
<td>Entrance height applied by treatment and year</td>
<td>68</td>
</tr>
<tr>
<td>C-1</td>
<td>Sources of variation for bahiagrass variables</td>
<td>69</td>
</tr>
</tbody>
</table>
### LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Illustration of the multiphase mass-density compensation in defoliated swards.</td>
<td>26</td>
</tr>
<tr>
<td>3-1</td>
<td>Herbage accumulation at each grazing event for five bahiagrass genotypes during 2009 and 2010.</td>
<td>40</td>
</tr>
<tr>
<td>4-1</td>
<td>Bahiagrass population density as affected by year and genotype.</td>
<td>55</td>
</tr>
<tr>
<td>4-2</td>
<td>Bahiagrass genotype tiller mass (g DM tiller(^{-1})) as affected by year and genotype.</td>
<td>57</td>
</tr>
<tr>
<td>4-3</td>
<td>Relationship between tiller mass (size) and tiller population density of bahiagrass cultivars.</td>
<td>60</td>
</tr>
</tbody>
</table>
Grown on more than one million ha, bahiagrass (*Paspalum notatum* Flügge) is the main pasture for horses (*Equus caballus*) and cattle (*Bos* sp.) in Florida. One of the limitations to its use is its strong summer dominant herbage production pattern. Breeding efforts have now resulted in the development of less photoperiod-sensitive bahiagrass cultivars that produce more forage for livestock during the cool season. Early evaluation of less photoperiod-sensitive (PCA) bahiagrass genotypes raised concerns regarding their persistence under grazing. The objectives of this study were: i) measure herbage accumulation and nutritive value responses of PCA genotypes to grazing management strategies; and ii) describe the relationships among tiller density, tiller mass, and tiller size-density compensation with bahiagrass persistence and herbage accumulation.

Experiments were conducted in 2009 and 2010 in Gainesville, Florida. Two photoperiod-sensitive diploid genotypes (Pensacola and Tifton 9) and three PCA genotypes (UF-Riata, Cycle 5, and Florida Hay) were evaluated at two grazing intensities (post-graze stubble heights of 8 and 16 cm, with grazing initiated for all
treatments at a 30-cm height). Herbage accumulation in Year 1 was generally greater for the 16- vs. the 8-cm treatment for PCA types Cycle 5 and UF-Riata, but in Year 2 there was no effect of stubble height for any genotype. The new bahiagrass cultivar, UF-Riata, had as great, or greater herbage accumulation than any genotype at all stubble height x year combinations. Lack of stubble height effect in Year 2 was likely due to acclimation to the grazing treatments, and clearly demonstrated no negative carryover effects from Year 1. UF-Riata had crude protein and in vitro digestible organic matter concentrations that were generally as great, or greater than the other bahiagrasses.

Tiller density varied relatively little among three diploid cultivars (Pensacola, Tifton 9, and UF-Riata) in 2009, however, by the end of the 2010 grazing season, Pensacola had more tillers than the others for both stubble height treatments. Tiller mass was greatest for Tifton 9 by October 2010 for both stubble heights. Greatest impact of close grazing on tiller mass occurred in Year 1, but by Year 2 the plants had adapted to the grazing treatments. The expected slope for the tiller size/density compensation (SDC) phenomenon was not observed for any of the cultivars. This may have been due to the relatively small range in grazing stress associated with the treatments imposed.

For these grazing treatments, PCA type UF-Riata was as productive and often higher in nutritive value than existing cultivars. In addition, tiller responses provided no reason for major concerns for persistence under grazing of any cultivar evaluated. Establishment of larger pastures and imposition of a broader range of grazing treatments is recommended so that the range of grazing management strategies that will be successful with PCA plants can be more clearly defined.
CHAPTER 1
INTRODUCTION

It is common in particular regions throughout the world that a single species contributes the bulk of forage production for livestock. This holds true for the state of Florida, southern USA, where approximately one million beef cows (*Bos* sp.), 120,000 dairy cows (*Bos taurus*), and 500,000 horses (*Equus caballus*) are fed, at least in part, from more than one million hectares of the rhizomatous warm-season perennial, bahiagrass (*Paspalum notatum* Flüggé) (Chambliss and Adjei, 2006). Bahiagrass is widely adapted throughout Florida. Because of its tolerance of heavy grazing and productivity in low fertility soils of varying drainage characteristics, it is the species of choice for most beef cattle producers. Grazing tolerance and ability to withstand animal traffic also make it the most widely used grass for equine pastures.

One of the limitations to the use of bahiagrass in Florida is its strong summer dominant herbage production pattern. Bahiagrass yield is concentrated between April and September and its growth during the cool-season (October to April) is minimal (Mislevy and Everett, 1981). Herbage accumulation rates of bahiagrass can be as low as 10 kg.ha\(^{-1}\).d\(^{-1}\) from October to April. Various factors contribute to the low herbage accumulation rate of bahiagrass in the cool season including low nighttime temperatures (Mislevy, 1985), freeze damage to tissue (Breman et al., 2008), and sensitivity to photoperiod. The latter response was documented by Sinclair et al. (2001, 2003) and led to initiation of breeding programs with the goal of developing less photoperiod sensitive bahiagrass cultivars (Blount et al., in review). Plants developed in this breeding program were selected visually for phenotype and inter-mated afterward in
the greenhouse, a breeding approach that is considered to be more than three times as efficient as traditional recurrent mass selection (Burton, 1992).

Early evaluation of less photoperiod-sensitive bahiagrass genotypes raised concerns regarding their long-term persistence. Interrante et al. (2009a) imposed clipping treatments on experimental lines and released cultivars of bahiagrass and found that plant responses related to sward persistence (stem N content and stem base and rhizome mass) were lower for less photoperiod-sensitive vs. standard entries. Such differences were most pronounced under close (4 cm stubble) or frequent (7 days rest period) defoliation. An important question is whether genotypes that are more productive later into autumn and earlier in spring, i.e., the less photoperiod-sensitive types, produce this cool-season growth at the expense of reserves that otherwise would be stored for winter survival and spring regrowth (Hirata et al., 2002; Interrante, 2008). If so, sward persistence or vigor of spring regrowth may be imperiled.

Although carbohydrate reserve status plays an important role, bahiagrass persistence is also a consequence of high tiller, rhizome, and root densities (Hirata, 1993, 2001a). Thus, the detailed study of the dynamics of tiller characteristics should provide information on the mechanisms of sward persistence. One established theory that relates these variables is the size-density compensation (SDC) theory. The SDC theory, or “self-thinning rule”, states that the mass (size) and abundance (density) of live entities in an environment are not related in a linear but in an exponential fashion (Kays and Harper, 1974). Numerous studies in the past 25 yr have shown that this phenomenon is also active in grazed swards (Sackville-Hamilton et al., 1995; Yu et al., 2008). Hirata and Pakiding (2002), for example, found minimal variation in tiller
population density throughout the growing season, but were still able to prove the rule to be true for grazed bahiagrass pastures. Because there are substantial data describing the tillering pattern of persistent cultivars of bahiagrass (Hirata, 2001), major deviations from the theoretical expectations may indicate genotypes prone to stand deterioration and lack of grazing tolerance.

Based on the bahiagrass literature, and in particular the data indicating that less photoperiod-sensitive bahiagrass types may be less persistent under defoliation than existing cultivars, there is need to evaluate the responses of these novel bahiagrass genotypes to grazing. Evaluation of tiller dynamics is also warranted because this information may provide a mechanistic understanding of the effect of defoliation on responses of novel bahiagrasses to grazing. Therefore, experiments were conducted with the objectives of: i) measuring herbage accumulation and nutritive value responses of new bahiagrass genotypes to grazing management strategies; and ii) describing the relationships among tiller density, tiller mass, and tiller size-density compensation with bahiagrass persistence and herbage accumulation. Research exploring herbage accumulation and nutritive value responses is described in Chapter 3 of the thesis, and characterization of tiller dynamics and relationships with persistence and production responses are described in Chapter 4.
CHAPTER 2
LITERATURE REVIEW

Origin and Characteristics of Bahiagrass

Taxonomy and Botanical Description

Bahiagrass (*Paspalum notatum* Flüggé) is a perennial grass with shallow rhizomes [also referred to as stolons (Sampaio et al., 1976; Beaty et al., 1977)], glabrous leaves with blades varying from 3 to 30 cm in length and 3 to 12 mm in width, and a characteristic inflorescence with two racemes.

*Paspalum* is a large genus of the Poaceae family, comprising approximately 400 species. One of the Poaceae tribes, Paniceae, is characterized by grasses with single spikelets and glumes resembling lemmas. Within this tribe is the genus *Paspalum*, to which the closest genus is *Axonopus*. Plants in *Axonopus* differ subtly from ‘*Paspalums*’ in terms of spikelet shapes and position of the upper lemma (Zuloaga et al., 2004).

There are two botanical varieties of *P. notatum*. One is strong-rooted, with larger leaves and slower spread, and is a tetraploid. Common bahiagrass is an example of this type, and it is classified as *P. notatum* var. *notatum* (Zuloaga et al., 2004). The other form is a diploid and is taller, with longer and narrower leaves, and faster rate of spread. These latter types are classified as *P. notatum* var. *saurae* Parodi, often referred to as Pensacola types (Gates et al., 2004) because ‘Pensacola’ is the cultivar name of the most widely used bahiagrass in the Southeast USA. Plants used in the experiments described in this thesis belong to var. *saurae*.

Center of Origin and Reproductive Behavior

Bahiagrass is a morphologically diverse species indigenous to South America, where it is found growing on light-textured soils and is widely used in lawns, sports turf,
Bahiagrass was first introduced into the USA by the Bureau of Plant Industry and grown by the Florida Agricultural Experiment Station in 1913 (Burton, 1967). The center of origin of Pensacola bahiagrass types is believed to be the region to the north of the Berduc Island, in the Paraná River near Santa Fe, Argentina. It is believed that a sea-borne cargo ship, prior to 1926, brought bahiagrass to the region of Pensacola, Florida (Quarín, 1974; Gates et al., 2004).

Most *Paspalum* species have a base chromosome number of $x = 10$, and known ploidy levels in the wild range from diploid to pentaploid (Burton, 1955). The regular diploid races, including Pensacola types, are sexual and highly cross-pollinated because most plants are self incompatible (Burton, 1948). The tetraploid races reproduce by obligate apomixis (Gates et al., 2004).

**Uses of Bahiagrass in Florida**

The uses of bahiagrass in Florida include turf, pasture, crop rotation, and hay. Pensacola types generally are not preferred for residential turf because they have rapid seedhead emergence following cutting which makes them less attractive. Bahiagrass is used as low maintenance turf because it is very persistent under close mowing and requires minimal nutrient and pesticide inputs. Highway rights-of-way have been planted with bahiagrass throughout the southeastern USA because the sod provides complete cover, limits erosion, and persists under low fertilizer inputs.

Most of the agricultural land area planted to bahiagrass is used for pasture in extensive cow-calf production systems (Gates et al., 2004). Bahiagrass is particularly well suited to this use because of its persistence, even under low soil fertility, and tolerance of environmental stresses and severe grazing by livestock. Bahiagrass forage energy concentration decreases substantially as the season progresses, thus it is not
considered well suited to meet the nutritional requirements of young, growing animals or lactating cows (Gates et al., 2004). Bahiagrass can also be utilized as hay, but it tends to have low nutritive value when dry matter (DM) yield is sufficiently high to make a hay harvest practical (Kalmbacher, 1997).

Recent research has documented the value of bahiagrass as a component of crop rotations. Inclusion of bahiagrass in a crop rotation increased earthworm population and subsequent cotton (*Gossypium hirsutum* L.) crop yields due to improved rooting (Katsvairo et al., 2007). Including bahiagrass in the crop rotation reduced incidence of stem rot of peanut (*Arachis hypogaea* L.) and increased peanut yield (Franzluebbers, 2007).

**Seasonal Yield Distribution**

In the southeastern USA, bahiagrass is most productive from April to October (Mislevy and Dunavin, 1993; Ball et al., 2002). In Florida, 85 to 90% of bahiagrass forage was produced from April through September (Mislevy and Everett, 1981, Kalmbacher, 1997). Stewart et al. (2007) reported herbage accumulation rates of 30, 62, and 15 kg ha\(^{-1}\) d\(^{-1}\) in May, mid-July, and October, respectively, for continuously stocked Pensacola bahiagrass pastures receiving 120 kg N ha\(^{-1}\) yr\(^{-1}\). Similarly in subtropical Japan, above-ground bahiagrass pasture productivity decreased as daylength decreased in autumn (Hirata et al., 2002).

Low productivity of bahiagrass pastures during the cool season necessitates purchase of costly supplements and is a major obstacle to profitability of livestock enterprises. As a result, development of new genotypes that overcome the seasonal shortfall of forage is a primary objective of bahiagrass genetic improvement programs (Blount et al., 2003).
Understanding the cause of this reduction in growth is important to facilitate the development of cultivars that are more productive in cooler months. Pasture productivity in subtropical Japan decreased during short-day months in part because plants allocated a greater proportion of nonstructural carbohydrates to storage organs (Hirata et al., 2002). In the USA, decreased bahiagrass forage growth in autumn was observed even when soil moisture, soil fertility, and temperatures were adequate for much more rapid growth (Sinclair et al., 1997; Gates et al., 2004), implicating plant responses to daylength in the observed yield decrease.

To address the question of the relative role of daylength in the reduction in yield, Sinclair et al. (2001) artificially extended daylength during the winter months and measured the effect on forage yield of Pensacola bahiagrass, ‘Tifton 85’ bermudagrass (Cynodon spp.), ‘Florakirk’ bermudagrass [Cynodon dactylon (L.) Pers.], and ‘Florona’ stargrass (Cynodon nlemfuensis Vanderyst). Yields of these grasses under extended daylength increased up to 6.2-fold vs. that under natural daylength. In another study with these four grasses, growth increased in an extended photoperiod treatment that was imposed during short-daylength months (Sinclair et al., 2003). Pensacola bahiagrass exhibited the greatest increase, with forage yield for many harvests under the extended-daylength treatment being more than double that of the natural daylength treatment (Sinclair et al., 2003). Thus daylength sensitivity appears to be a critical component of the observed low productivity of bahiagrass during short-daylength months (Blount et al., 2003).

This observation led to efforts to select less photoperiod sensitive bahiagrass genotypes that extend growth into the cool season. Although this approach has
potential to address a critical problem in the forage-livestock industry, one possible
problem it may create is that by extending growth into cooler months, carbohydrate
reserves may be reduced. This could result in reduced persistence of less photoperiod
sensitive genotypes. In a 2-yr study, Pensacola bahiagrass, Tifton 85 and Florakirk
bermudagrasses, and Florona stargrass were heavily fertilized (67, 15, and 56 kg ha\(^{-1}\)
harvest\(^{-1}\) of N, P, and K, respectively) and defoliated three times a year (Sinclair et al.,
2003). They reported 1) no decrease in growth following the extended photoperiod
treatment in either season, 2) no difference in below-ground tissue mass throughout the
season between extended and natural daylength treatments, and 3) no influence of
extended daylength on total nonstructural carbohydrate (TNC) concentration of below-
ground tissue. Thus, in that study, extending daylength for daylength-sensitive types
improved seasonal distribution of DM without negative effects on persistence, at least in
the short term.

There is some research, however, that suggests that these improvements in
forage yield may be detrimental to pasture persistence. For example, Tifton 9
bahiagrass is a taller, more erect, higher yielding bahiagrass cultivar that produces
forage earlier in spring and later in fall than the industry standard cultivars, Pensacola
and Argentine. Tifton 9 was selected from populations of Pensacola bahiagrass, a
prostrate cultivar that partitions a large proportion of its dry weight to rhizomes (Beaty
and Tan, 1972). Pedreira and Brown (1996) reported that the selection process that led
to Tifton 9 “resulted in increased allocation of dry matter to harvestable foliage and
possibly a greater production of non-root biomass” and “…resulted in taller plants with
fewer rhizomes, a greater tendency for winter injury, and a greater susceptibility to
population shifts under close, frequent mowing.” This research indicates that it may be
difficult to maintain the same level of pasture persistence in bahiagrasses selected for
improved cool-season forage yield as in the cultivar Pensacola, and that testing of
potential cultivars should include evaluation of persistence under grazing.

**Bahiagrass Response to Defoliation**

**Productivity**

Forage production of bahiagrass is generally thought to be lower than that of other
regionally adapted grasses including bermudagrass and stargrass. Chambliss (2003)
reported total average annual yield of Pensacola, Argentine, and Tifton 9 bahiagrasses
to be approximately 10 Mg DM ha⁻¹. Mislevy (2005) reported 3-yr annual dry biomass
yields ranging from 10.3 Mg ha⁻¹ for Pensacola to 12.1 Mg ha⁻¹ for Tifton 7 (a non-
released breeder’s line) in central Florida when harvested monthly and fertilized with 56
kg N ha⁻¹ harvest⁻¹. For bahiagrass cultivars fertilized once annually with 56, 28, and 56
kg ha⁻¹ of N, P, and K, respectively, and cut to a 5-cm stubble every 35 d in Southwest
Florida, Muchovej and Mullahey (2000) reported annual DM yields ranging from 3 Mg
ha⁻¹ for ‘Paraguay’ to 4 Mg ha⁻¹ for Tifton 7.

Hirata (1993) reported greater yields of Pensacola with increasing stubble heights
in the summer (8 Mg ha⁻¹ at 22-cm stubble vs. 4.5 Mg ha⁻¹ at 2 cm), but greater yields
with decreasing stubble heights in the fall (2 Mg ha⁻¹ at 2-cm stubble vs. 1 Mg ha⁻¹ at 22
cm) when harvested every 2 to 4 wk. Gates et al. (1999) reported bahiagrass DM yields
were greater at a short (1.5 cm) than tall cutting height (10 cm) at 2- or 4-wk regrowth
intervals over 2 yr.
There has been rather limited research done to evaluate the effects of defoliation management on productivity of less photoperiod-sensitive bahiagrass entries. Recent work has shown that an upright-growing, less photoperiod-sensitive entry (Cycle 4, subsequently released as UF-Riata) was generally no more productive during the May through October grazing season than other current cultivars of bahiagrass (Interrante et al., 2009a). However, it was considerably less productive when harvested frequently (7 d), suggesting that its upright growth habit makes it less tolerant of frequent defoliation. Data from other research has shown that yield of Cycle 4 in the cool season was superior to that of Pensacola and Argentine (Blount et al., in review).

**Persistence**

Bahiagrass is valued for excellent persistence under severe grazing (Gates et al., 2004). Pensacola bahiagrass forms a dense sward that contributes to its grazing tolerance (Hirata, 1993). It also maintains stable tiller density in terms of space and time, which contributes to its high persistence under grazing (Hirata and Pakiding, 2004). Gates et al. (1999) reported that bahiagrass cover was not influenced by cutting interval (2, 4, and 8 wk) throughout 3 yr of the experiment and was not influenced by cutting height after the first year. In a 2-yr grazing experiment, Pensacola maintained cover under continuous stocking of yearling heifers, while Tifton 9 cover was reduced after 2 yr.

The importance of storage organs in defoliation tolerance response has been well-documented in several C₄ grass species (Chaparro et al., 1996; Macoon et al., 2002). When subjected to continuous severe defoliation, bahiagrass tillers depend considerably on storage organs for energy for maintenance and growth of new leaves.
(Hirata and Pakiding, 2003). They reported that bahiagrass swards degraded when all regrowing laminae were removed every 1 to 4 d, resulting in a reduction of laminae production, mass of stubble, and rhizome mass. They concluded that rhizomes play a key role in bahiagrass defoliation tolerance. Gates et al. (1999) reported greater spring reserves (as estimated by total etiolated initial spring growth) for bahiagrass from plots cut every 8 wk the previous growing season than in those cut every 2 or 4 wk. After 3 yr of grazing every 2 wk, bahiagrass stem base TNC concentration during August to early September averaged less than 90 g kg\(^{-1}\), which was 40 g kg\(^{-1}\) lower than the overall average for 3-, 5-, and 7-wk grazing frequencies.

Interrante et al. (2009a) evaluated persistence-related responses of several bahiagrass entries to clipping defoliation every 7 or 21 d to a stubble height of 4 or 8 cm. Across defoliation treatments, stem base mass of Pensacola and Argentine averaged 60% greater than less photoperiod sensitive Cycle 4, while at 4- and 8-cm stubble heights, the numbers were 86 and 41%, respectively. Similarly, when defoliated every 7 d, average stem base mass of Pensacola and Argentine was 125% greater than for Cycle 4, while the difference was only 23% for the 21-d treatment. Pensacola and Argentine also averaged 27% greater root + rhizome mass than Cycle 4; at 4- and 8-cm stubble heights the values were 32 and 21%, respectively. When defoliated every 7 and 21 d, Pensacola and Argentine root + rhizome mass was 38 and 14% greater, respectively, than Cycle 4. These plant responses could result in the photoperiod-insensitive type being less persistent than Argentine and Pensacola under defoliation, particularly frequent or close defoliation. In the same experiment, harvesting every 21 d to an 8-cm stubble height resulted in greatest cover for both Tifton 9 and Cycle 4 (83
and 77%, respectively), while cover for both entries was less than 40% if harvested every 7 d to 4 cm.

Interrante et al. (2009a) reported that Cycle 4 often had less root + rhizome N and TNC content than Argentine and Pensacola. These differences also were most pronounced when the entries were harvested closely or frequently. They concluded that defoliation management of Cycle 4 will likely be more critical than for Pensacola and Argentine bahiagrass and that longer regrowth intervals (21 d or longer) and taller residual heights (8 cm or taller) may be required to ensure its persistence.

**Nutritive Value**

Another important plant response to defoliation is nutritive value. Published differences in nutritive value among bahiagrass cultivars are generally small and inconsistent (Kalmbacher, 1997; Mislevy and Dunavin, 1993; Chambliss and Adjei, 2006). Muchovej and Mullahey (2000) found no differences in in vitro digestible organic matter (IVDOM) concentration among bahiagrass cultivars during summer while Mislevy et al. (2005) likewise reported few differences. Interrante et al. (2009b) found that herbage CP of Cycle 4 was comparable to that of other bahiagrasses, and it was at least as digestible and sometimes more digestible than the existing bahiagrass cultivars. Differences in IVDOM among cultivars were relatively small (< 25 g kg⁻¹); however, and their impacts on cattle gains are not known.

**Tillering and the Size-Density Compensation Theory**

**Bahiagrass Tillering Characteristics**

Research in Japan showed that density characteristics of Pensacola bahiagrass, such as tiller number and rhizome length, tended to increase when cutting heights decreased from 22 to 2 cm (Hirata, 1993). When Pensacola was defoliated daily to
remove all regrowing laminae from an initial 2-cm cutting height, initial tiller density was maintained for 4 to 6 wk before declining (Pakiding and Hirata, 2002). In Japan, Pakiding and Hirata (2003) reported that Pensacola responded to low N (50 kg ha$^{-1}$ yr$^{-1}$) and intense defoliation (2-cm stubble at monthly harvest intervals) with increased tiller longevity, tiller appearance rate, and tiller density compared to high N (20 g m$^{-2}$ yr$^{-1}$) and 12- and 22-cm stubble heights. Pensacola tiller formation was stimulated with high N (20 g m$^{-2}$ split applied annually) in May through June in a Japanese study on plots harvested monthly to a 3-cm stubble when compared to plots receiving 5 g N m$^{-2}$ split applied annually (Islam and Hirata, 2005).

Interrante et al. (2010) evaluated tiller responses of a several bahiagrass entries to clipping defoliation every 7 or 21 d to a stubble height of 4 or 8 cm. Tifton 9 and Cycle 4 decreased tiller number across treatments in the first year of defoliation, likely indicating less rapid morphological adaptation to defoliation by these upright-growing types than the more decumbent Pensacola. All cultivars showed a positive change in tiller number from the beginning of the first to the end of the second year, and the authors concluded that over longer time frames phenotypic plasticity was possible even for the upright-growing types. Less photoperiod-sensitive Cycle 4 generally had the least or not different from the least tiller mass.

In Florida, bahiagrass tiller appearance rate was greatest in spring and least in autumn, and tiller death rate was least in spring and greatest in mid-summer through autumn and was not affected by entry (Interrante et al., 2010). Net tiller appearance rate was greatest and positive in the spring or early summer and tended to be close to zero or negative throughout the remainder of the growing season. The authors concluded
that the documented persistence of Pensacola bahiagrass under defoliation was explained in part by its ability to sustain a high number of tillers across a wide range of defoliation treatments. Tifton 9 and Cycle 4, which were shown to be less tolerant of frequent, close defoliation (Interrante, 2009a), increased tiller number under this type of management, but tiller mass was the least or not different from the least among the entries. Small tillers may be indicative of a weakening stand and entries that are not as tolerant of frequent, close defoliation. This observation led the authors to the conclusion that choice of defoliation management is more critical for Tifton 9 and Cycle 4 than for more decumbent Pensacola.

**Size-Density Compensation Theory**

Plant communities can optimize their LAI in response to defoliation by varying their morphology. This phenomenon, known as phenotypic plasticity (West-Eberhard, 1989; Schlichting, 2002), is reversible and occurs in pastures mainly through three sward characteristics: leaf size, number of leaves per tiller, and tiller population density (Matthew et al., 2000).

Of these three sward characteristics, tiller density is the most important, since leaf number per tiller is relatively constant for a given species (Chapman, 1983) and leaf size is heavily dependent on leaf length which is controlled by defoliation intensity – therefore dependent on grazing management. As a consequence, for short defoliation heights (or low leaf individual area), a higher population density of small tillers maximizes leaf area index, and conversely, lower populations of larger tillers maximizes leaf area index when defoliation height is taller (Matthew et al., 1995). This process of compensation between plant population density and plant size, termed SDC, was first
described by Japanese researchers for tree stands (Yoda, 1963), and later recognized in grasslands (Kays and Harper, 1974).

Over the past three decades, many have attempted to explain the SDC rule through geometric, allometric, and dynamic growth arguments (Kikuzawa, 1999; Li et al., 2000). Among other things, the discussion revolved around the validity of self-thinning as a universal ecological rule, and whether the slope of a size by density logarithmic plot is constant. Some authors have proposed a slope of -3/2 (Hernández-Garay et al., 1999; Bahmani et al., 2000; Matthew et al., 2000; Sbrissia, 2000, 2004), and others found -5/2 to more closely represent the observed response (Davies, 1988). Matthew et al. (2000) proposed a dynamic solution for pastures under defoliation. According to those authors, a four-phase diagram of SDC is more appropriate to explain the tiller dynamics of swards under defoliation.

The four phases (Figure 2-1) represent different states of a pasture maintained at constant herbage mass levels. The first phase is where tiller appearance rate is insufficient for tiller population to reach the SDC boundary line. The second phase represents a condition where self-thinning occurs, but leaf area is kept constant at a slope steeper than -1.5. The third phase is where the self-thinning occurs at the -3/2 boundary line, and at the fourth, self-thinning occurs at a slope of -1.
Figure 2-1. Illustration of the multiphase mass-density compensation in defoliated swards. 1. Shoot size-density relations undefined. 2. Variable leaf area self-thinning with log size: log density slope near -3. 3. Constant leaf area self-thinning along the population boundary line at slope near -1.5. 4. Constant herbage mass self-thinning at slope -1. d and s denote shoot population density and size (mass). Adapted from Matthew et al. (1995) and Scheneiter and Assuero (2010).

Independent of the SDC slope value, there is a consensus that the mechanism operates in plant stands and that the main factor affecting SDC is light competition. Populations of few large tillers appear as a consequence of the death of young tillers, which are usually located at the bottom of the canopy, not receiving enough radiation to thrive (Sbrissia, 2004). Therefore, light may be the main determinant of the position of
the SDC line. White (1981) showed that reductions in light level resulted in lower values for the intercept of the SDC line, and proposed that nutrients do not alter its position directly, but can influence it through their effect on photosynthesis and maintenance of foliar area.

Within this resource competition context, plants with a greater proportion of tissue mass invested in leaves rather than stems are expected to be favored. Hence the use of the R ratio (foliar area: tiller volume) helps to explain the size-density dynamics in a plant population, giving an idea of the plant morphological changes. Matthew et al. (1995) found higher R values for perennial ryegrass (*Lolium perenne* L.) swards grazed to 160 mm when compared to 120 mm. This indicates a mechanism through which large shoots competitively exclude small shoots by changes in tiller geometry. Hernández-Garay et al. (1999) explained that the observed increase in R is a consequence of increased length of individual leaves, because at taller cutting heights there are fewer live leaves per tiller and reduction in leaf number per tiller would tend to decrease R. Those authors also suggested that the 160-mm defoliation height led to a situation where the formation of new leaf tissue was accompanied by senescence of old leaves, with reduced tiller density. Hirata and Pakiding (2002) and Hirata (2002), when assessing the validity of the SDC rule in bahiagrass, did not report R-ratio values, but their results suggest the existence of the self-thinning rule in bahiagrass.

**Summary and Project Objectives**

Based on this review of the literature, it was determined that information was needed on productivity, nutritive value, and tiller dynamics of less photoperiod-sensitive bahiagrass types. The objectives of these studies were 1) to characterize herbage accumulation and nutritive value of new and existing diploid bahiagrass genotypes
under grazing (Chapter 3), and 2) to describe tillering responses of these genotypes and evaluate the relationship between the mechanism of size-density compensation, persistence, and forage production in bahiagrass (Chapter 4).
CHAPTER 3
BAHIAGRASS GERMPLASM YIELD AND NUTRITIVE VALUE UNDER TWO GRAZING INTENSITIES

Background

Bahiagrass (Paspalum notatum Flügge) is used throughout Florida as forage for cattle (Bos sp.) and horses (Equus caballus) because of its tolerance of heavy grazing and productivity in low fertility soils of varying drainage characteristics. A limitation of the most widely used bahiagrass cultivar ‘Pensacola’ is that annual herbage accumulation occurs primarily from April to September (Mislevy, 1985), necessitating the feeding of costly supplements or hay to livestock during the cool season.

Various factors contribute to the low herbage accumulation rate of bahiagrass in the cool season including low nighttime temperatures (Mislevy and Everett, 1985), freeze damage to tissue (Breman et al., 2008), and prioritization of C to storage instead of top-growth under reduced daylength (Sinclair et al., 2001). The latter response was documented by Sinclair et al. (2001, 2003), and led to initiation of breeding programs with the goal of developing less photoperiod-sensitive bahiagrass cultivars (Blount et al., in review).

In order to develop bahiagrasses that are more cold tolerant and less photoperiod sensitive, recurrent selection was initiated with Pensacola (Blount et al., 2003). Plants developed in this breeding program were selected visually for phenotype and intermated afterward in the greenhouse, a breeding approach that is considered to be at least three times as efficient as traditional recurrent mass selection (Burton, 1992). Through this effort, less photoperiod-sensitive and cold-adapted (PCA) bahiagrass germplasm has been developed in order to extend the grazing season (Blount et al., in review). The PCA types used in the current study are Cycle 4 and Cycle 5, and they
represent the fourth and fifth cycles of selection from Pensacola. Cycle 4 has been released as a cultivar with the name UF-Riata, and it will be referred to by this name throughout the chapter.

Early evaluation of less photoperiod-sensitive bahiagrass genotypes raised concerns regarding plant persistence. Interrante et al. (2009a) imposed clipping treatments on experimental lines and cultivars of bahiagrass. They found that plant responses related to sward persistence (stem N content, stem base and rhizome mass, and cover) were lower for less photoperiod-sensitive vs. standard entries, particularly under close or frequent defoliation. An important question is whether genotypes that are more productive later into autumn and earlier in spring produce this cool-season growth at the expense of reserve storage. If so, sward persistence or at least vigor of spring regrowth and herbage accumulation the following year may be compromised.

Based on the bahiagrass literature, and in particular the data indicating that less photoperiod-sensitive bahiagrass types may be less persistent than existing cultivars when defoliated, there is need to evaluate these novel bahiagrass genotypes under grazing. As suggested by Bouton et al. (1997), the use of grazing animals in cultivar selection and testing should happen as early as possible in the breeding program so pasture potential can be properly assessed. Therefore, an experiment was conducted with the objective of measuring herbage accumulation and nutritive value responses of new bahiagrass genotypes to grazing management strategies.

Material and Methods

Experimental Site

This study was conducted in Gainesville, FL in the U.S. Gulf Coast Region (29°43’ N lat; 82°16’ W long). The climate is humid subtropical (Cfa under the Köppen climate
where the average maximum temperature during the summer is greater than 30°C, and multiple frosts and freezes are common during the winter. Yearly precipitation averages around 1300 mm, of which nearly half occurs in short-duration rainfall events during June through September.

Soil at the location was an Adamsville fine sand (hyperthermic, uncoated Aquic Quartzipsamments). This soil is derived from sandy marine sediment and is described as having moderate drainage and rapid permeability. Average pH was 5.8, and Mehlich-I extractable soil P, K, Mg, and Ca concentrations were 67, 61, 89, and 685 mg kg⁻¹, respectively, in May of 2009, and they were 57, 43, 78, and 669 mg kg⁻¹, respectively, a year later.

Bahiagrass entries used in the study were seeded into a prepared seedbed in September 2007. During the 2008 growing season, prior to the initiation of this study, plots were fertilized and defoliated by clipping three times to encourage tillering and increase cover. Stands were fully established by the start of the experiment in spring of 2009.

Experimental Design and Treatments

Treatments were the factorial combinations of five bahiagrass genotypes and two post-graze stubble heights of rotationally stocked pastures. Experimental units were 36-m² pastures (6 x 6 m), and treatments were arranged in a randomized complete block design with three replications. The five diploid bahiagrass genotypes evaluated were Pensacola, Tifton 9, Florida Hay, UF-Riata, and Cycle 5. Post-graze stubble heights were 8 and 16 cm, and grazing on all treatments was initiated throughout the grazing season when sward canopy height reached 30 cm.
The entrance height of 30 cm is justified on the basis that it corresponds to a leaf area index in the range of four to six, after which forage plant communities are not expected to show an increase in crop growth rate, and should be harvested for maximum efficiency (Bircham and Hodgson, 1984; Gardner et al., 1984). The stubble target of 8 cm was chosen because it corresponds to approximately 1000 kg ha\(^{-1}\) of post-graze herbage mass, a threshold after which cattle intake declines considerably in bahiagrass swards (Hirata et al., 2006).

The five genotypes were selected to include existing cultivars, PCA types, and a range of plant growth habits. Entry UF-Riata is a recently released cultivar (Blount et al., in review) that was selected for greater cool-season production. Cycle 5 is one selection cycle beyond UF-Riata from the same breeding program (Dr. A. Blount, personal communication, 2011). Both UF-Riata and Cycle 5 have a more upright growth habit than Pensacola. Pensacola and Tifton 9 are the industry standard diploid cultivars. Together they occupy approximately 90% of the area planted to bahiagrass in Florida. Pensacola is characterized as decumbent in growth habit, while Tifton 9 has a more erect growth (Pedreira and Brown, 1996). Florida Hay is an experimental line specifically bred for use as a short-rotation crop in integrated row crop-livestock systems in Florida. It is characterized as having upright growth habit, rapid germination, improved resistance to dollar spot (*Sclerotinia homeocarpa*), and ample seed production (Dr. A. Blount, personal communication, 2011).

**Environmental Conditions and Pasture Management**

Grazing was conducted during the growing seasons of 2009 and 2010, with pastures grazed from 2 June to 24 Oct. 2009 and 11 May to 9 Oct. 2010. Weather conditions in both years of experimentation are summarized in Table 3-1. Yearling
Brahman by Angus crossbred heifers (Bos sp.) served as grazing animals. At each grazing event, heifers were allocated to pastures for approximately 1 to 2 h in groups of two to six. Grazing was monitored and when average sward height reached the target stubble, cattle were removed.

Table 3-1. Weekly average weekly maximum and minimum air temperatures and total precipitation at the Beef Research Unit during the experimental period in 2009 and 2010.

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†Week “1” started on 10 May 2009 and 9 May 2010, and Week “24” represents the week beginning with 24 Oct. 2009 and 2010.
The three replicates of each genotype x stubble height treatment were grazed always on the same day during each grazing cycle of each year. Among treatments, number of grazing events per year varied due to level of stubble height and to differences in growth habit and rate of regrowth among genotypes (Table 3-2).

### Table 3-2. Number of grazing events per treatment and year.

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<th>Genotype</th>
<th>Stubble height (cm)</th>
<th>Grazing events</th>
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<td></td>
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Pastures were fertilized three times each year (5 May, 23 June and 9 Aug. 2009, and 20 Apr., 12 June, and 11 Aug. 2010). At each fertilization, 40 kg N ha\(^{-1}\) and 30 kg K ha\(^{-1}\) were applied using ammonium nitrate (NH\(_4\)NO\(_3\)) and muriate of potash (KCl).

**Herbage Accumulation and Harvested**

Herbage mass was measured before and after each grazing event using a double sampling technique, i.e., both a direct and an indirect measure. The indirect measure was a disk meter (Santillan et al. 1979; Michell and Large, 1983), and the direct measure was hand clipping of herbage. Before animals entered the pasture, two 0.25-m\(^2\) 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 10 additional sites within each experimental unit. Sites were selected systematically based on a predetermined number of steps between sites so that the entire experimental unit was represented. Average disk settling height was calculated. After grazing, the same procedure was repeated.

Regression equations were developed that predicted herbage mass from disk settling using the double sampling data. Equations (Table A-1) were generated by grouping the data by genotype since there was no added benefit in looking at pre- and post-graze herbage mass data separately.

Values for pre- and post-graze herbage mass were obtained by entering the average settling height of the 10 disk-height observations for a given pre- or post-graze sampling event into the appropriate equation. The r-square values ranged from 0.67 to 0.75 for the equations used.

Herbage accumulation (HA) was calculated by subtracting post-graze herbage mass at the end of a given grazing cycle from pre-graze herbage mass of the following grazing cycle. Herbage accumulation of Grazing Cycle 1 was considered to be pre-graze herbage mass for this cycle. Seasonal HA was calculated by summing HA across individual grazing cycles within each year.

Herbage harvested by grazing (HH) was calculated by subtracting post-graze herbage mass from pre-graze herbage mass of the same grazing cycle. Seasonal HH was calculated by summing HH across all grazing cycles within a year.
Herbage Nutritive Value

Herbage crude protein (CP) 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. Herbage obtained in a grab sample was removed to the target stubble height at 10 locations per pasture to represent forage grazed by the animals. These samples were composited to a single sample per pasture per grazing cycle. Samples were dried at 60°C in a force-air drying oven 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. Nitrogen concentrations were measured using a modification of the aluminum block digestion procedure (Gallaher et al., 1975). Concentration of CP in herbage DM was calculated as N x 6.25. Herbage IVDOM was determined using a modification of the two-stage technique (Moore and Mott, 1974). Herbage nutritive value for an entire grazing season was the weighted average across grazing cycles.

Statistical Analyses

Statistical analyses were performed using the MIXED procedure of SAS 9.2 (SAS Institute, 2008), where means separation was based on Fisher’s LSD, generated by the PDIFF option of the LSMEANS statement. Assignment of letters for means separation was aided by the PDMIX800 macro (Saxton, 1998). The framework suggested by Crawley (2007) was followed, where the significance level of 5% was adopted. Year, genotype, height, and their interactions were considered fixed effects, and block random. Year was considered fixed because treatments were imposed on the same
experimental unit in both years, and there was reason to expect carryover effects from Year 1 to Year 2. A summary of the analysis of variance is presented in Table C-1.

Results and Discussion

Herbage Accumulation

Total-season

Total-season HA was affected by genotype, year, and genotype X stubble height, genotype X year, and genotype X stubble height X year interactions, thus comparisons were made within year (Table 3-3). Focusing first on stubble height, there was no effect of stubble on Year 2 HA, but in Year 1 the response to stubble height was significant for Cycle 5, UF-Riata, and Pensacola (Table 3-3). There was no effect of stubble height for Florida Hay or Tifton 9 in either year. The more upright growing Cycle 5 and UF-Riata were favored by taller stubble height in Year 1, but the more decumbent-growing Pensacola performed better when grazed to 8 vs. 16 cm.

The first year difference due to stubble height suggests that Cycle 5 and UF-Riata were slow to adapt to close grazing, but the lack of second year response indicates that over time they were able to do so. In the year prior to the start of the study, the plots were mowed approximately every 6 to 8 wk to a relatively lax 15-cm stubble, so the negative effect of an 8-cm stubble in Year 1 likely occurred until plants adapted their growth habit (i.e., phenotypic plasticity) to more intensive defoliation. Evidence of greater adaptation to close grazing can be seen in the year to year changes in HA. For plots grazed to 8 cm, Cycle 5 HA increased 33% and UF-Riata HA increased 34% from 2009 to 2010, while for plots grazed to 16 cm there was essentially no change in HA from year to year. In previous research with UF-Riata, Tifton 9, and Pensacola, there was no effect of clipping stubble height on dry matter yield, but more upright-growing
types like UF-Riata and Tifton 9 performed better with longer regrowth intervals of 21 vs. 7 d (Interrante et al., 2009). In that study, the decumbent Pensacola was not affected by interval between defoliation events.

In evaluating differences among genotypes, UF-Riata had as great or greater HA than any other genotype for each stubble height by year combination (Table 3-3). Greatest differences were between UF-Riata and Penscola (6390 vs. 3310 kg ha⁻¹) in pastures grazed to a 16-cm stubble height in 2009, but by 2010 the differences among genotypes were much less, approximately 1000 kg ha⁻¹. Most genotypes had greater HA in 2010 than in 2009 due to a somewhat longer growing season, and rainfall events that were better distributed throughout the season, which generally resulted in more grazing events per year (Table 3-1) in 2010 vs. 2009. The clipping study by Interrante et al. (2009) showed no differences in HA among diploid genotypes when defoliation occurred every 21 d, but Pensacola and Tifton 9 outyielded UF-Riata when plots were defoliated every 7 d.

Based on the earlier research of Interrante et al. (2009a), showing less tolerance of frequent, close grazing, it was anticipated that HA of UF-Riata would be reduced with the 8-cm stubble height. However, it is well established that plant response to defoliation is affected by an interaction of defoliation intensity and frequency (Sollenberger and Newman, 2007). In the current study, although UF-Riata was grazed more intensively with the 8-cm stubble height, this treatment was grazed less frequently than the 16-cm stubble treatment. This is reflected in the fact that there were four grazing events each year for the 8-cm treatment but seven grazing events for the 16-cm treatment. Thus, it is concluded that the better than expected performance of UF-Riata
when grazed to an 8-cm stubble is due to the longer regrowth intervals between defoliation events which allowed more time for restoration of leaf area and carbohydrate reserves (Ortega et al., 1992).

Table 3-3. Bahiagrass total-season herbage accumulation as affected by year x height x genotype interaction \((P = 0.0015)\). Data are means of three replicates

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Evaluation year</th>
<th>Stubble height (cm)</th>
<th>2009</th>
<th>2010</th>
<th>P value(\dagger)</th>
<th>2009</th>
<th>2010</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>8</td>
<td>16</td>
<td></td>
<td>8</td>
<td>16</td>
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<td>---------</td>
</tr>
<tr>
<td>Cycle 5</td>
<td></td>
<td></td>
<td>------</td>
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<td>-------------------</td>
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<td>------</td>
<td>---------</td>
</tr>
<tr>
<td>UF-Riata</td>
<td></td>
<td></td>
<td>------</td>
<td>------</td>
<td>-------------------</td>
<td>------</td>
<td>------</td>
<td>---------</td>
</tr>
<tr>
<td>Florida Hay</td>
<td></td>
<td></td>
<td>------</td>
<td>------</td>
<td>-------------------</td>
<td>------</td>
<td>------</td>
<td>---------</td>
</tr>
<tr>
<td>Tifton 9</td>
<td></td>
<td></td>
<td>------</td>
<td>------</td>
<td>-------------------</td>
<td>------</td>
<td>------</td>
<td>---------</td>
</tr>
<tr>
<td>Pensacola</td>
<td></td>
<td></td>
<td>------</td>
<td>------</td>
<td>-------------------</td>
<td>------</td>
<td>------</td>
<td>---------</td>
</tr>
</tbody>
</table>

\(\dagger\) Means within a column followed by the same letter do not differ \((P > 0.05)\).

\(\dagger\) P value for height comparisons within genotype and year.

\(\dagger\) Standard error of the year x height x genotype interaction means.

Seasonal patterns of HA were generally similar among genotypes. Most notable exceptions were the extended fall growth period of UF-Riata for the 8-cm stubble in 2009 and for UF-Riata, Cycle 5, and Florida Hay for the 16-cm stubble in both 2009 and 2010. Interrante et al. (2009) showed that diploid bahiagrass genotypes outyielded tetraploid types in spring but yielded less in summer, however, they found no differences among diploid types in seasonal patterns of HA. Stewart et al. (2005, 2007) plotted seasonal pattern of HA for bahiagrass and showed greatest HA during early summer and lesser HA in spring and fall. Data collection was initiated somewhat later in
the current study and the lower HA in spring reported by Stewart et al. (2005, 2007) was not observed.

![Herbage accumulation graph](image)

Figure 3-1. Herbage accumulation at each grazing event for five bahiagrass genotypes during 2009 and 2010. Error bars denote standard errors of the mean from three replicates.

**Total-season Herbage Harvested**

The general pattern of response for total-season HH (Table 3-4) was similar to that for HA (Table 3-3). As observed for HA, HH of UF-Riata was as great, or greater than that of all other genotypes for each year x stubble height combination. The main
difference between HH and HA responses occurred in 2010. During that year, stubble height affected or tended ($P < 0.10$) to affect the HH for Cycle 5, UF-Riata, and Pensacola, with all having greater levels of HH at the shorter stubble. So even though HA did not differ between stubble heights in 2010, the 8-cm stubble allowed for greater harvest efficiency by grazing and caused the greater HH for three of five genotypes.

Table 3-4. Bahiagrass total-season herbage harvested as affected by year x height x genotype interaction ($P = 0.0008$). Data are means of three replicates.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Evaluation year</th>
<th>Stubble height (cm)</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>16</td>
<td>8</td>
</tr>
<tr>
<td>Cycle 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3500</td>
<td>4760</td>
</tr>
<tr>
<td>UF-Riata</td>
<td></td>
<td></td>
<td>4360</td>
<td>5550</td>
</tr>
<tr>
<td>Florida Hay</td>
<td></td>
<td></td>
<td>4020</td>
<td>4170</td>
</tr>
<tr>
<td>Tifton 9</td>
<td></td>
<td></td>
<td>3870</td>
<td>3200</td>
</tr>
<tr>
<td>Pensacola</td>
<td></td>
<td></td>
<td>3890</td>
<td>2170</td>
</tr>
</tbody>
</table>

| SE§               | 350             |

† Means within a column followed by the same letter do not differ ($P > 0.05$).
‡ P value for height comparisons within genotype and year.
§ Standard error of the year x height x genotype interaction means.

Nutritive Value

Crude protein

There was year x genotype interaction for herbage CP. Interaction occurred because in 2009, Cycle 5 had greatest herbage CP but in 2010 Cycle 5 CP was not different than that of any other genotype (Table 3-5). The CP of UF-Riata was less than only Cycle 5 in 2009 and was as great, or greater than any other genotype in 2010. In research done at the same location as the current trial, CP varied little among three diploid and two tetraploid cultivars of bahiagrass that were harvested by clipping every 7
or 21 d, but UF-Riata CP was as great, or greater than that of the other genotypes (Interrante et al., 2009). In that study, the average CP ranged from 130 to 141 g kg\(^{-1}\) for plants harvested weekly and from 112 to 117 g kg\(^{-1}\) for plants harvested every 3 wk. These values are greater than those observed in the current study for two reasons. First, the defoliation interval in the earlier work was considerably shorter, and secondly the total-season N rate was 160 kg ha\(^{-1}\) in that study vs. 120 in the current research. Stewart et al. (2007) reported herbage CP of Pensacola bahiagrass ranging from 85 to 150 g kg\(^{-1}\) for continuously stocked bahiagrass pastures receiving from 40 to 360 kg N ha\(^{-1}\) yr\(^{-1}\).

Table 3-5. Bahiagrass weighted total season crude protein as affected by the year x genotype interaction (\(P < 0.0001\)). Data are means across two stubble heights and three replicates (\(n = 6\)).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>2009</th>
<th>2010</th>
<th>(P) value(\dagger)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cycle 5</td>
<td>103 (a^\dagger)</td>
<td>86 (ab)</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>UF-Riata</td>
<td>94 (b)</td>
<td>91 (a)</td>
<td>0.4617</td>
</tr>
<tr>
<td>Florida Hay</td>
<td>90 (bc)</td>
<td>84 (b)</td>
<td>0.0743</td>
</tr>
<tr>
<td>Tifton 9</td>
<td>84 (cd)</td>
<td>90 (ab)</td>
<td>0.0979</td>
</tr>
<tr>
<td>Pensacola</td>
<td>77 (d)</td>
<td>86 (ab)</td>
<td>0.0140</td>
</tr>
</tbody>
</table>

\(SE^\S\) 2.6

\(\dagger\) Means within a year followed by the same letter do not differ (\(P > 0.05\)).

\(\dagger\) \(P\) value for year comparisons within genotype.

\(\S\) Standard error of the year x genotype interaction means.

There also was genotype x stubble height interaction for herbage CP (\(P = 0.0084\)). Similar to the data already described, interaction occurred because Cycle 5 had the greatest CP, with the exception of UF-Riata, in 2009, but in 2010 it was greater than only Pensacola and similar to the other genotypes (Table 3-6). Herbage CP of UF-Riata was as great, or greater than all other genotypes in both years.
Based on data from Interrante et al. (2009b), it was anticipated that CP would be greater for the 16- than the 8-cm SH treatment in the current study because of shorter intervals between defoliation events for the 16-cm height. However, there were no differences between stubble heights for any genotypes except Pensacola, where the 8-cm treatment had greater CP than the 16-cm height. Herbage CP occurred over a rather narrow range, such that significant differences in concentration were not detected.

Table 3-6. Bahiagrass weighted total season crude protein as affected by the stubble height x genotype interaction ($P = 0.0084$). Data are means across two stubble heights and three replicates ($n = 6$).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Stubble height (cm)</th>
<th>CP g kg$^{-1}$</th>
<th>$P$ value$^+$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cycle 5</td>
<td>8</td>
<td>97 a$^\dagger$</td>
<td>92 abc</td>
</tr>
<tr>
<td>UF-Riata</td>
<td>90 abc</td>
<td>94 ab</td>
<td>0.2934</td>
</tr>
<tr>
<td>Florida Hay</td>
<td>86 c</td>
<td>87 bc</td>
<td>0.7881</td>
</tr>
<tr>
<td>Tifton 9</td>
<td>87 bc</td>
<td>87 c</td>
<td>0.9527</td>
</tr>
<tr>
<td>Pensacola</td>
<td>89 bc</td>
<td>75 d</td>
<td>0.0003</td>
</tr>
</tbody>
</table>

$^\dagger$ Means within a year followed by the same letter do not differ ($P > 0.05$).

$^+$ $P$ value for height comparisons within genotype.

$^\S$ Standard error of the height x genotype interaction means.

**In vitro digestible organic matter**

Herbage IVDOM was affected by a year x height x genotype interaction ($P = 0.0008$). As with herbage CP concentration, there were few differences between stubble height treatments for IVDOM and no consistent effect of the shorter interval between defoliation events associated with the 16-cm height treatment (Table 3-7). Herbage IVDOM of UF-Riata was greater than any other genotype for both stubble height treatments in 2009. Cycle 5 was next highest in IVDOM for both height treatments and

SE$^\S$ 0.26
was 5.2% less than UF-Riata for the 8-cm treatment and 4.5% less for the 16-cm height. In 2010, UF-Riata was greater in IVDOM than all but Tifton 9 and Pensacola for the 8-cm height and all but Pensacola for the 16-cm height. UF-Riata IVDOM averaged 546 and 562 g kg⁻¹ in 2 yr of defoliation by clipping and was greater than Pensacola in both years and greater than Tifton 9 in 1 of 2 yr. Thus the IVDOM concentrations in the current study occur within the same range as those reported for UF-Riata by Interrante et al. (2009b).

Table 3-7. Bahiagrass total season weighted digestibility (IVDOM) as affected by year x height x genotype interaction (P = 0.0008). Data are means from three replicates

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Evaluation year</th>
<th>Stubble height (cm)</th>
<th>2009</th>
<th>2010</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Stubble height (cm)</td>
<td>8</td>
<td>16</td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>P value‡</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>g kg⁻¹</td>
<td></td>
</tr>
<tr>
<td>Cycle 5</td>
<td>508 b †</td>
<td>515 b</td>
<td>0.5085</td>
<td></td>
<td>519 b</td>
<td>527 b</td>
</tr>
<tr>
<td>UF-Riata</td>
<td>536 a</td>
<td>539 a</td>
<td>0.8106</td>
<td></td>
<td>564 a</td>
<td>571 a</td>
</tr>
<tr>
<td>Florida Hay</td>
<td>506 b</td>
<td>512 b</td>
<td>0.5718</td>
<td></td>
<td>540 b</td>
<td>540 b</td>
</tr>
<tr>
<td>Tifton 9</td>
<td>508 b</td>
<td>513 b</td>
<td>0.6454</td>
<td></td>
<td>577 a</td>
<td>504 c</td>
</tr>
<tr>
<td>Pensacola</td>
<td>471 c</td>
<td>494 b</td>
<td>0.0396</td>
<td></td>
<td>569 a</td>
<td>568 a</td>
</tr>
</tbody>
</table>

SE§ 7.56
† Means within a column followed by the same letter do not differ (p > 0.05).
‡ P value for height comparisons within genotype.
§ Standard error of the year-height-genotype interaction means.

Conclusions

Five diploid genotypes of bahiagrass were compared under grazing to evaluate their herbage accumulation and nutritive value. Of particular interest was the response of the less photoperiod sensitive, cold tolerant genotypes that have been referred to as PCA types. Two defoliation treatments were tested. Grazing was initiated when canopy height reached 30 cm and ended when stubble height was either 8 or 16 cm.
Most productivity and nutritive value responses were affected by two- or three-way interactions. Herbage accumulation in Year 1 was generally greater for the 16- vs. the 8-cm treatment for PCA types Cycle 5 and UF-Riata. This response was anticipated based on previous reports of defoliation sensitivity of the PCA bahiagrasses. However, in Year 2 there was no effect of stubble height for any of the genotypes, as PCA and non-PCA types did equally well with short as with taller stubble. UF-Riata had as great, or greater herbage accumulation than any genotype at all stubble height x year combinations. It seems likely that the lack of stubble height effect in Year 2 was due to acclimation to the grazing treatments and also to the length of the regrowth interval associated with each height treatment. Grass grazed to 8 cm required considerably longer to regrow to 30 cm (an average of 37 d between defoliation events) compared to those plants grazed to 16 cm (average of 25 d between defoliation events). Thus, plants grazed to shorter stubble had longer recovery periods than those grazed to tall stubble, and it is likely that neither treatment imposed high levels of stress on the plants. As a result it is difficult to make conclusive statements about the grazing tolerance of the PCA genotypes, however, based on the work done by Interrante et al. (2009a) it seems likely that PCA types can tolerate moderate levels of defoliation stress, by grazing or clipping, but because of their more upright growth habit they are less likely to perform well under conditions of frequent, close defoliation.

The PCA types had crude protein and in vitro digestible organic matter concentrations that were as great, or greater than other diploid bahiagrasses. Thus, it appears that along with superior cool-season production (Blount et al., in review), they
may increase nutritive value, especially digestibility, over current cultivars. This conclusion is also supported by Interrante et al. (2009b).

With availability of seed of PCA types no longer limiting, it appears that establishment of larger pastures and imposition of a broader range of grazing treatments is warranted to more clearly define the limits of grazing management that will be successful with these plants.
CHAPTER 4
TILLERING DYNAMICS OF BAHIAGRASS GERMPLASM UNDER GRAZING INTENSITIES

Background

Bahiagrass (*Paspalum notatum* Flüggé) is the predominant pasture grass utilized by the beef cattle industry in southern Alabama, southern Georgia, and throughout Florida (Blount, 2003). Its tolerance of heavy grazing and productivity in low fertility soils of varying drainage characteristics makes it the choice for most beef cattle producers.

Sinclair et al. (2001, 2003) showed that bahiagrass responds to photoperiod, resulting in minimal growth during the cool-season. As a consequence, breeding programs were initiated with the goal of developing less photoperiod-sensitive bahiagrass cultivars (Blount et al., 2003). Plants developed in this breeding program were selected visually for phenotype and inter-mated afterward in the greenhouse, a breeding approach that is considered to be more than three times as efficient as traditional recurrent mass selection (Burton, 1992). Because the product of this breeding effort is less photoperiod sensitive, and yields better in the cool season, they are referred as PCA (photoperiod insensitive, cold adapted) types.

Early evaluation of PCA genotypes was made by Interrante (2009a), who imposed clipping treatments on experimental lines and released cultivars of bahiagrass and found that plant responses related to sward persistence (stem N content and stem base and rhizome mass) were lower for less photoperiod-sensitive vs. standard entries. Such differences were most pronounced under close or frequent defoliation. An important question is whether genotypes that are more productive later into autumn and earlier in spring produce this cool-season growth at the expense of reserves that are stored for
winter survival and spring regrowth (Hirata et al., 2002; Interrante, 2008). If so, sward persistence or vigor of spring regrowth may be imperiled.

Although reserve status may play an important role, bahiagrass persistence is also a consequence of high tiller densities (Hirata, 1993, 2001; Hirata et al., 2002). Thus, the detailed study of the dynamics of these tiller characteristics should provide information on the mechanisms of sward persistence. One established theory that relates these variables is the size-density compensation (SDC) theory. The SDC theory, or "self-thinning rule", states that the mass (size) and abundance (density) of live entities in an environment are not related in a linear but in an exponential fashion (Kays and Harper, 1974). Numerous studies in the past 25 yr have shown that this phenomenon is also present in grazed swards (Sackville-Hamilton et al., 1995; Yu et al., 2008). Hirata and Pakiding (2002), for example, found minimal variation in tiller population density throughout the growing season, but were still able to prove the rule to be true for grazed bahiagrass pastures. Because there are substantial data describing the tillering pattern of persistent cultivars of this species (Hirata, 2001), major deviations from the theoretical expectations may indicate genotypes prone to stand deterioration and lack of grazing tolerance.

Tiller dynamics of a PCA type, UF-Riata, was studied by Interrante et al. (2010), but there are no studies evaluating tiller responses of less photoperiod sensitive, cold-adapted bahiagrass under grazing, the most common use of bahiagrass. Therefore, the objectives of this study were i) to determine the effects of grazing intensity (defined in this study by stubble height) on tiller population density, tiller mass, leaf length, and leaf-
stem ratio of three bahiagrass cultivars, and (b) to relate such results with sward persistence of these pastures.

**Material and Methods**

This experiment was conducted on the same experimental units described for Chapter 3. The exception was that only three bahiagrass genotypes were evaluated for tiller responses. All three are released cultivars and will be referred to as such in this chapter. The three chosen were industry standards Pensacola and Tifton 9 and the PCA type UF-Riata.

**Tiller Population Density**

Tiller population density was determined three times (June, August, October) by counting tillers inside 10- by 20-cm quadrats. These times were chosen to show the pattern of tiller density in the early, mid-, and late growing season. More frequent measures are often not useful because no differences in tiller population are expected to be observed in periods shorter than 60 to 90 d (Hirata, 2001a). Ten randomly chosen quadrats (sampling units) were counted in each experimental unit at each date. Because grazing intervals were different for each treatment and tiller populations were assessed at the same date for all treatments, simple interpolation was used to determine tiller populations at a given date.

**Tiller Mass**

Tiller mass was determined before each grazing event. Ten tillers per experimental unit were randomly chosen and cut so that rhizomes and white portions of the sheath were not considered part of the tiller entity. Tillers were placed in plastic bags containing ice, transported to the laboratory, and separated into leaf and stem fractions by cutting at the ligule. Components were dried separately at 60°C until
constant weight. To facilitate presentation of the data and relating of tiller mass and density, some sampling dates were combined for treatments that were grazed more than three times per year. This allowed presentation of the tiller mass and density data for the same three seasons.

**Leaf Number and Length**

Leaf number was determined by counting attached leaves, grazed or not, comprised of more than 50% live tissue on each tiller. Leaf length was measured from the ligule to the tip of leaves with a millimeter scale and dimensions were recorded in centimeters with one decimal place. Both measurements were made before tissues were dried.

**Statistical Analysis**

Statistical analyses were performed using the MIXED procedure of SAS (Saxton, 1998), where means separation was based on Fisher's LSD, generated by the PDIF option of the LSMEANS statement. Assignment of letters for means separation was aided by the PDMIX800 macro (Saxton, 1998). The framework suggested by Crawley (2007) was followed, where the significance level of 5% was adopted. Year, cultivar, height, and their interactions were considered fixed effects, and block random. Year was considered fixed because treatments were imposed on the same experimental unit in both years, and there was potential for carryover effects from Year 1 to Year 2. A summary of the analysis of variance is presented in Table C-1.
Results and Discussion

Tiller Density and Mass

Across seasons

Tiller density and mass of three bahiagrass cultivars were measured during three seasons per year. Initially data will be presented averaged across seasons to describe overall responses to genotype, stubble height, and year.

Across seasons, there was cultivar x stubble height interaction. Tiller density was not affected by cultivar when post-graze stubble height was 8 cm (Table 4-1), but for the 16-cm stubble height Pensacola had 14% more tillers than UF-Riata and 23% more than Tifton 9. More upright-growing cultivars had more tillers (Tifton 9; \( P = 0.0476 \)) or tended to have more tillers (UF-Riata; \( P = 0.1034 \)) when grazed to an 8- than 16-cm stubble, while more decumbent Pensacola tended to have more tillers when grazed to 16 than 8 cm (\( P = 0.0979 \)).

Table 4-1. Bahiagrass tiller density (tillers per 200 cm\(^2\)) as affected by the stubble height X cultivar interaction (\( P = 0.0094 \)). Data are means from three replicates and two years.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Stubble height (cm)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>tillers quadrat(^\ddagger)</td>
<td>tillers quadrat(^\ddagger)</td>
</tr>
<tr>
<td>UF-Riata</td>
<td>17.7 (^a)</td>
<td>16.3 (^b)</td>
</tr>
<tr>
<td>Tifton 9</td>
<td>16.3 (^a)</td>
<td>14.5 (^c)</td>
</tr>
<tr>
<td>Pensacola</td>
<td>17.2 (^a)</td>
<td>18.9 (^a)</td>
</tr>
</tbody>
</table>

\(^\dagger\) Means within a column followed by the same letter do not differ (\( P > 0.05 \)).
\(^\ddagger P\) value for height comparisons within cultivar.
\(^\ddagger\) Standard error of the year-height-cultivar interaction means.

Bahiagrass tiller mass across seasons was affected only by cultivar, with the upright Tifton 9 having greater tiller mass than Pensacola and UF-Riata tiller mass.
being intermediate (Table 4-2). Tiller mass was greater in 2010 than in 2009 (0.458 vs. 0.408 g tiller\(^{-1}\)) across cultivars and stubble heights.

Table 4-2. Bahiagrass tiller mass (size) as affected by cultivar. Data are means from three replicates, two stubble heights, and two years

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>----- g tiller(^{-1}) -----</th>
</tr>
</thead>
<tbody>
<tr>
<td>UF-Riata</td>
<td>0.425 ab</td>
</tr>
<tr>
<td>Tifton 9</td>
<td>0.459 a</td>
</tr>
<tr>
<td>Pensacola</td>
<td>0.416 b</td>
</tr>
<tr>
<td><strong>SE</strong>(^$)</td>
<td><strong>0.025</strong></td>
</tr>
</tbody>
</table>

\(^\dagger\) Means within a column followed by the same letter do not differ (\(P > 0.05\)).

\(^\$\) Standard error of the means.

**Seasonal patterns of tiller response**

Tiller density generally decreased as the grazing season progressed in both 2009 and 2010, with the exception of UF-Riata pastures grazed to 8 cm in 2009 (Fig. 4-1). Based on previous research with bahiagrass, this pattern of response is not considered to be indicative of poor persistence. When several bahiagrass genotypes were defoliated by clipping, net tiller appearance rate decreased throughout the growing season each year, with rates as low as \(-7.4\) tillers m\(^{-2}\) d\(^{-1}\) in August 2005 and \(-2.1\) tillers m\(^{-2}\) d\(^{-1}\) in October 2006 (Interrante et al., 2010). Hirata and Pakiding (2001) and Pakiding and Hirata (2003) reported that net tiller appearance rate in Pensacola bahiagrass was generally positive in May or June, and was usually close to zero or negative in other seasons. These seasonal patterns in net tiller appearance likely explain the general overall decrease in tiller density as the season progressed in the current study.
Tiller density varied relatively little among cultivars in 2009 (Fig. 4-1), however, in 2010 cultivar effects were much more pronounced. In 2010, Pensacola generally had a greater tiller density than the other cultivars (Fig. 4-1). This result is similar to that reported by Interrante et al. (2010) who found that upright-growing bahiagrass genotypes generally had the fewest tillers for four defoliation treatments, while the more decumbent genotypes like Pensacola had the most tillers for each defoliation treatment. In addition, they observed that Pensacola tiller density did not respond to clipping frequency or intensity. In contrast, tiller number of both Tifton 9 and UF-Riata varied widely across defoliation treatments and was greatest when those cultivars were defoliated frequently and closely (Interrante et al., 2010). In 2010 of the current study, Tifton 9 and UF-Riata generally had fewer tillers than Pensacola, and the effect of stubble height on tiller density was more pronounced for Tifton 9 and UF-Riata than Pensacola.

The pattern of response to stubble height described earlier in the across-seasons comparisons (i.e., greater tiller density at 8-cm stubble for UF-Riata and Tifton 9 and greater density at 16-cm stubble for Pensacola) started to emerge in 2009. By 2010, Pensacola had more tillers than the other cultivars by season’s end for the 8-cm stubble height and at all dates for the 16-cm stubble. Tiller density was similar at all 2010 dates for UF-Riata and Tifton 9 when grazed to an 8-cm stubble, but when grazed to a 16-cm stubble it was greater for Tifton 9 than UF-Riata in June and August. The advantage in tiller density of the 16- vs. 8-cm stubble height was evident for Pensacola throughout 2010, while the advantage of 8- vs. 16-cm stubble was pronounced only in June and August for Tifton 9 and UF-Riata.
Previous research showed that Pensacola bahiagrass tiller number increased as cutting height decreased from 22 to 2 cm (Pakiding and Hirata, 2002). They also found that Pensacola responded to intense defoliation with increased tiller longevity, tiller appearance rate, and tiller density compared to 12- and 22-cm stubble heights (Hirata and Pakiding, 2004; Hirata, 2004). In another study, tiller number of highly persistent Pensacola was unaffected by four defoliation treatments and generally greatest among genotypes tested (Interrante et al., 2010).

In the current study, Pensacola tiller density increased with taller stubble instead of with shorter stubble height. This response was unexpected, but it can be explained based on conditions of the experiment. This may be due in part to intervals between grazing events not being consistent across stubble height treatments, i.e., pastures grazed to short stubble (8 cm) required a longer regrowth period to reach a 30-cm height than tall-stubble (16 cm) pastures. Thus, short-stubble treatments had greater recovery time, and the anticipated greater level of defoliation stress, that would lead to more and smaller tillers for the 8-cm stubble treatment, did not materialize. Additionally, the longer regrowth periods increased the time period when the base of the dense Pensacola canopy was shaded, and tiller density is reduced in low-light environments (White, 1981). Tifton 9 and UF-Riata likely responded differently because their growth habit is more bunch-like, and the degree of shading lower in the canopy is likely much less relative to Pensacola.
Figure 4-1. Bahiagrass population density as affected by year and genotype. Error bars denote standard errors.

Tiller mass decreased for the 8-cm stubble height throughout the entire 2009 grazing season (Fig. 4-2). For the 16-cm height, tiller mass increased (UF-Riata and Tifton 9) or remained relatively constant (Pensacola) from August to October after decreasing from June to August. Tiller mass was not different between stubble heights during June and August 2009 (Fig. 4-2), but for all genotypes there was greater tiller mass for the 16- than the 8-cm stubble treatment in October. In 2010, there was less seasonal change in tiller mass and patterns of response were generally similar for the two stubble heights. For example, UF-Riata tiller mass decreased from 0.52 to 0.19 g
from June to October 2009, but in 2010 the decrease was from 0.49 to 0.28 g. For Pensacola, the changes were 0.52 to 0.30 g in 2009 vs. 0.43 to 0.31 in 2010. These data suggest that greatest impact of close grazing on tiller mass occurred in Year 1 and that by Year 2 the plants had adapted to this grazing treatment. Interestingly, although tiller mass for the 8-cm stubble treatments did not decrease as much as the season progressed in Year 2 as in Year 1, the changes in tiller density were more pronounced for UF-Riata and Tifton 9 in 2010 than 2009 (Fig. 4-1), suggesting some mass/density compensation. For the 16-cm stubble in 2010, neither Pensacola nor UF-Riata tiller mass varied widely throughout the year, but mass of Tifton 9 tillers increased from June to October.

Tiller mass was not different among cultivars in June and August 2009, but by October Pensacola had the smallest tillers for the 16-cm stubble. In 2010, June tiller mass for all cultivars approximated that observed in 2009, and again there were no cultivar differences in June and August (Fig. 4-2). At the end of the grazing season each year for each stubble height, Pensacola tillers had the lowest or equal to the lowest mass and Tifton 9 tillers were as heavy, or heavier, than the other genotypes. Mass of UF-Riata tillers in October was generally not different than Pensacola, with the exception of the 16-cm stubble height in 2009 (Fig. 4-2). Interrante et al. (2010) evaluated tiller responses of several bahiagrass entries to clipping defoliation every 7 or 21 d to a stubble height of 4 or 8 cm. They found that Tifton 9 and UF-Riata decreased in tiller number across treatments in the first year of defoliation, likely indicating less rapid morphological adaptation to defoliation by these upright-growing types than the
more decumbent Pensacola. Less photoperiod-sensitive UF-Riata generally had the least or not different from the least tiller mass as well in that study.

Figure 4-2. Bahiagrass genotype tiller mass (g DM tiller$^{-1}$) as affected by year and genotype. Error bars denote standard errors.
**Leaf:stem Ratio and Leaf Characteristics**

There was cultivar x stubble height interaction for tiller leaf:stem ratio (Table 4-3). Leaf:stem ratio was not affected by cultivar for the 8-cm stubble, but when grazed to a 16-cm stubble it was 25% greater for Pensacola than Tifton 9 and 15% greater for Pensacola than UF-Riata (Table 4-3). Leaf:stem ratio was greater for the 8- than 16-cm stubble for Tifton 9 and tended to be greater for UF-Riata, but the reverse was true for the more decumbent Pensacola.

Table 4-3. Bahiagrass leaf-stem ratio as affected by cultivar x stubble height interaction. Data are means across three replicates.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Grazing height (cm)</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>8</td>
<td>16</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>g g⁻¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UF-Riata</td>
<td>1.84 a†</td>
<td>1.46 b</td>
<td></td>
<td>0.0184</td>
<td></td>
</tr>
<tr>
<td>Tifton 9</td>
<td>1.78 a</td>
<td>1.07 c</td>
<td></td>
<td>&lt;.0001</td>
<td></td>
</tr>
<tr>
<td>Pensacola</td>
<td>1.99 a</td>
<td>1.82 a</td>
<td></td>
<td>0.404</td>
<td></td>
</tr>
</tbody>
</table>

SE§ 0.12

† Means within a column followed by the same letter do not differ (P > 0.05).
‡ P value for height comparisons within cultivar
§ Standard error of the year-height-cultivar interaction means.

Leaf characteristics were generally unaffected by treatments with the exception of leaf width (P = 0.0061). Leaf width was marginally greater for Tifton 9 (0.36 cm) than for UF-Riata (0.34 cm) and Pensacola (0.33 cm). There was no effect of stubble height (P = 0.5526) or cultivar (P = 0.3353) on the number of leaves per tiller. Number of leaves ranged from 3.0 to 6.2 and averaged 4.8. There also was no effect of stubble height (P = 0.8162) or cultivar (P = 0.6390) on leaf length. Leaf length ranged from 18 to 44 cm and averaged 32 cm. Neither was there an effect of stubble height (P = 0.4466) or cultivar (P = 0.3444) on leaf area per tiller. Overall values of leaf area per tiller (cm² tiller⁻¹) were in the range 23 to 97 and averaged 53.
Size-density Compensation

Figure 4-3 shows the relationship between tiller mass (size) and tiller population density of the cultivars studied. Each data point in the plot corresponds to one observation from an experimental unit, where the value of tiller mass was determined immediately before a grazing event. For these cultivars grazed in the manner of this experiment, the relationship does not correspond to theoretical expectations of SDC. This is in contrast to results of Hirata and Pakiding (2002) who found the relationship to be present in bahiagrass swards stocked continuously throughout the year. Neither do these results support the theory suggested by Sackville-Hamilton et al. (1995), since none of the slopes is different from zero. Separating the data by year, or seasons (Sbrissia, 2004) does not change the interpretation of these data.

These results may not provide conclusive evidence of whether SDC occurs for the bahiagrass genotypes evaluated. The SDC is best observed across a wide range of grazing management treatments, and in this experiment the range of defoliation stress imposed was relatively narrow due to the structure of the treatments. As indicated in Chapter 3, grass grazed to 8 cm required an average of 37 d between defoliation events, while that grazed to 16 cm required an average of 25 d between defoliation events. Longer recovery time ameliorates the effects of short stubble heights, thus, neither treatment imposed high levels of stress on the plants. Levels of stress imposed were likely quite similar, as reflected in a lack of differences in 2010 herbage accumulation between stubble heights within a cultivar.
Figure 4-3. Relationship between tiller mass (size) and tiller population density of bahiagrass cultivars. The shaded area comprises standard errors of predictions. The dashed line (slope = -1.5; intercept = 2), was plotted to represent what a curve with the expected inclination would be in the neighborhood of the collected data. Each data point corresponds to one observation from one experimental unit.

Conclusions

Tiller density, mass, and leaf characteristics of three diploid cultivars (Pensacola, Tifton 9, and UF-Riata) of bahiagrass were compared to make inference regarding plant persistence under grazing. Two defoliation treatments were imposed during 2009 and
2010, with grazing events initiated when canopy height reached 30 cm and terminated when stubble height was either 8 or 16 cm.

Tiller density generally decreased as the grazing season progressed in both 2009 and 2010, but this response was primarily due to normal seasonal patterns of bahiagrass growth and less a response to treatments. Tiller density varied relatively little among cultivars in 2009, however, in 2010 cultivar effects were much more pronounced. By the end of the 2010 grazing season, Pensacola had more tillers than the other cultivars for both stubble height treatments. Tiller density was similar at all 2010 dates for UF-Riata and Tifton 9 when grazed to an 8-cm stubble, but when grazed to a 16-cm stubble it was greater for Tifton 9 than UF-Riata in June and August. Tiller density was greater for the 16- vs. 8-cm stubble height for Pensacola throughout 2010, while for Tifton 9 and UF-Riata there was an advantage of the 8- vs. 16-cm stubble at two of three dates.

Tiller mass was not different between stubble heights during June and August of the 2 yr, but Tifton 9 had the heaviest tillers in October 2010 for both stubble height treatments. In 2010, there was less seasonal change in tiller mass and patterns of response were generally similar for the two stubble heights. Greatest impact of close grazing on tiller mass occurred in Year 1, and it appears that by Year 2 the plants had adapted to the grazing treatments.

The tiller SDC was not observed for any of the bahiagrass cultivars in the current study. The relatively small range in grazing stress imposed by the treatments in the study may have been responsible for the lack of measureable SDC.
In conclusion, changes in tiller density and mass generally were more pronounced in the first than the second year of grazing, suggesting that all three bahiagrass cultivars have the ability to adapt to new defoliation regimes, at least within the range of stress imposed by these specific grazing treatments. For these low- to moderate-stress grazing treatments, patterns in tiller density and mass varied among cultivars but did not suggest major concerns for persistence of any of the cultivars evaluated. This is also supported by the absence of grazing treatment effects on herbage accumulation in the second year of the study (2010; Chapter 3). With seed supply of UF-Riata no longer limiting, evaluation of this new cultivar under grazing should continue, and a much wider range of grazing intensities should be imposed to better assess its persistence under defoliation by livestock.
Grown on more than one million ha, bahiagrass (*Paspalum notatum* Flügge) is the main pasture for horses (*Equus caballus*) and cattle (*Bos* sp.) in Florida (Chambliss and Adjei, 2006). One of the limitations to its use is its strong summer dominant herbage production pattern. Bahiagrass yield is concentrated between April and September and its growth during the cool-season is minimal (Mislevy and Everett, 1981).

The reasons for minimal herbage accumulation during the cool-season were established by Sinclair et al. (1997, 2001, 2003), and include the negative response of bahiagrass above-ground herbage productivity to shorter daylength. Such findings led to initiation of breeding programs with the goal of developing less photoperiod sensitive bahiagrass cultivars that would produce more forage for livestock during the cool season (Blount et al., in review).

Early evaluation of less photoperiod-sensitive bahiagrass genotypes raised concerns regarding their long-term persistence, since Interrante et al. (2009a) found that plant responses related to sward persistence (stem N content and stem base and rhizome mass) were lower for less photoperiod-sensitive vs. standard entries. Given that Interrante’s study did not include animals and the response of new entries under grazing is of great interest (Bouton, 1997), the objectives of this study were: i) measure herbage accumulation and nutritive value responses of new bahiagrass genotypes to grazing management strategies; and ii) describe the relationships among tiller density, tiller mass, and tiller size-density compensation with bahiagrass persistence and herbage accumulation.
Experiments were conducted in 2009 and 2010 in Gainesville, Florida. Two photoperiod-sensitive diploid genotypes (Pensacola and Tifton 9) and three cold-adapted, less photoperiod sensitive genotypes (UF-Riata, Cycle 5, and Florida Hay) were evaluated under mob-grazing at two grazing intensities (post-graze stubble heights of 8 and 16 cm, with grazing initiated for all treatments at a 30-cm height). Measurements of interest were herbage accumulation, forage nutritive value, and tiller dynamics.

Herbage accumulation in Year 1 was generally greater for the 16- vs. the 8-cm treatment for PCA types Cycle 5 and UF-Riata. However, in Year 2 there was no effect of stubble height for any of the genotypes. The new bahiagrass cultivar, UF-Riata, had as great, or greater herbage accumulation than any genotype at all stubble height x year combinations. Lack of stubble height effect in Year 2 was likely due to acclimation to the grazing treatments, and clearly demonstrated no negative carryover effects from Year 1. In addition, neither grazing treatment imposed high levels of defoliation stress because plants grazed to the 8-cm stubble had average regrowth periods of 37 d to reach a 30-cm height, and plants grazed to 16 cm had average regrowth periods of 25 d. As a result it is difficult to make conclusive statements about the grazing tolerance of the PCA genotypes. However, based on the work done by Interrante et al. (2009a), it seems likely that PCA types can tolerate moderate levels of defoliation stress, by grazing or clipping, but because of their more upright growth habit they are less likely than existing cultivars like Pensacola and Argentine to perform well under conditions of frequent, close defoliation.
UF-Riata had crude protein and in vitro digestible organic matter concentrations that were generally as great, or greater than other diploid bahiagrasses. Thus, it appears that along with superior cool-season production (Blount et al., in review), it may increase nutritive value, especially digestibility, over current cultivars. This conclusion is also supported by Interrante et al. (2009b).

Tiller density varied relatively little among three diploid cultivars (Pensacola, Tifton 9, and UF-Riata) in 2009, however, by the end of the 2010 grazing season, Pensacola had more tillers than the other genotypes for both stubble height treatments. Tiller mass was not different between stubble heights during June and August of the 2 yr, but Tifton 9 had the heaviest tillers by October 2010 for both stubble height treatments. Greatest impact of close grazing on tiller mass occurred in Year 1, and it appears that by Year 2 the plants had adapted to the grazing treatments.

The tiller size/density compensation phenomenon was not observed for any of the bahiagrass cultivars in the current study. The relatively small range in grazing stress imposed by the treatments in the study may have been responsible for the lack of measureable SDC. Overall, changes in tiller density and mass generally were more pronounced in the first than the second year of grazing, suggesting that all three bahiagrass cultivars have the ability to adapt to new defoliation regimes, at least within the range of stress imposed by these specific grazing treatments. For these grazing treatments, tiller responses did not give reason for major concerns for persistence of any cultivar evaluated.

At the time of establishment of this study, limited seed availability of photoperiod-insensitive, cold-adapted (PCA) types reduced plot area and number of treatments that
could be imposed. With the subsequent release of UF-Riata as a cultivar, availability of seed of this PCA type is no longer limiting, and establishment of larger pastures and imposition of a broader range of grazing treatments is now possible and is warranted to more clearly define the range of grazing management strategies that will be successful with PCA plants.
APPENDIX A

DOUBLE SAMPLING EQUATIONS TABLE

Table A-1. Coefficients of the herbage mass double sampling equations with their respective coefficient of determination and confidence intervals for the slope

<table>
<thead>
<tr>
<th>Genotype</th>
<th>$\beta_0$</th>
<th>$\beta_1$</th>
<th>$r^2$</th>
<th>C.I. ($\beta_1$) †</th>
</tr>
</thead>
<tbody>
<tr>
<td>PEN</td>
<td>-8.1*</td>
<td>4.4 ± 0.3 ***</td>
<td>0.73</td>
<td>(3.8; 4.9)</td>
</tr>
<tr>
<td>T9</td>
<td>-7.6*</td>
<td>4.0 ± 0.2 ***</td>
<td>0.72</td>
<td>(3.6; 4.5)</td>
</tr>
<tr>
<td>FH</td>
<td>-7.3*</td>
<td>3.7 ± 0.2 ***</td>
<td>0.67</td>
<td>(3.3; 4.1)</td>
</tr>
<tr>
<td>C4</td>
<td>-6.9*</td>
<td>3.9 ± 0.2 ***</td>
<td>0.72</td>
<td>(3.5; 4.3)</td>
</tr>
<tr>
<td>C5</td>
<td>-6.7*</td>
<td>3.5 ± 0.2 ***</td>
<td>0.75</td>
<td>(3.2; 3.9)</td>
</tr>
</tbody>
</table>

† Confidence intervals for the slopes are based on a 5% significance level.
Signif. codes: 0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05 ‘.’ 0.1 ‘ ’ 1
## APPENDIX B
### ENTRANCE HEIGHT TABLE

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Stubble height (cm)</th>
<th>Entrance height (cm)</th>
<th>2009</th>
<th>2010</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>2009</td>
<td>2010</td>
</tr>
<tr>
<td>C5</td>
<td>8</td>
<td>33.2 (3.8) †</td>
<td>31.4 (2.3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>32.5 (5.1)</td>
<td>31.4 (2.5)</td>
<td></td>
</tr>
<tr>
<td>C4</td>
<td>8</td>
<td>28.3 (1.7)</td>
<td>31.2 (1.8)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>30.4 (2.5)</td>
<td>32.2 (2.5)</td>
<td></td>
</tr>
<tr>
<td>FH</td>
<td>8</td>
<td>34.7 (4.8)</td>
<td>30.9 (1.8)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>31.8 (6.4)</td>
<td>31.8 (2.4)</td>
<td></td>
</tr>
<tr>
<td>T9</td>
<td>8</td>
<td>31.2 (1.6)</td>
<td>31.6 (1.0)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>30.0 (1.8)</td>
<td>31.1 (2.8)</td>
<td></td>
</tr>
<tr>
<td>PEN</td>
<td>8</td>
<td>31.4 (1.2)</td>
<td>29.7 (1.9)</td>
<td></td>
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<tr>
<td></td>
<td>16</td>
<td>30.6 (1.9)</td>
<td>30.7 (2.4)</td>
<td></td>
</tr>
</tbody>
</table>

† Numbers in parenthesis denote the standard deviation of the mean entrance height.
APPENDIX C

SOURCES OF VARIATION

Table C-1. Sources of variation for bahiagrass variables.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Source of variation</th>
<th>Entry</th>
<th>SSH</th>
<th>Year</th>
<th>Entry X SSH</th>
<th>Entry X Year</th>
<th>SSH X Year</th>
<th>Entry X SSH X Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>HA</td>
<td></td>
<td>$P = 0.0002$</td>
<td>$P = 0.0661$</td>
<td>$P &lt; 0.0001$</td>
<td>$P = 0.0123$</td>
<td>$P = 0.0013$</td>
<td>$P = 0.0201$</td>
<td>$P = 0.0015$</td>
</tr>
<tr>
<td>HD</td>
<td></td>
<td>$P &lt; 0.0001$</td>
<td>$P = 0.0416$</td>
<td>$P &lt; 0.0001$</td>
<td>$P = 0.0201$</td>
<td>$P &lt; 0.0001$</td>
<td>---</td>
<td>$P = 0.0019$</td>
</tr>
<tr>
<td>CP</td>
<td></td>
<td>$P = 0.0001$</td>
<td>$P = 0.0669$</td>
<td>---</td>
<td>$P = 0.0084$</td>
<td>$P &lt; 0.0001$</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>IVOMD</td>
<td></td>
<td>$P &lt; 0.0001$</td>
<td>$P &lt; 0.0001$</td>
<td>$P &lt; 0.0001$</td>
<td>$P = 0.007$</td>
<td>---</td>
<td>$P = 0.0045$</td>
<td>$P = 0.0020$</td>
</tr>
<tr>
<td>Tiller density</td>
<td></td>
<td>$P = 0.0002$</td>
<td>$P = 0.3472$</td>
<td>---</td>
<td>$P = 0.0094$</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Tiller mass</td>
<td></td>
<td>$P = 0.0911$</td>
<td>---</td>
<td>$P = 0.0033$</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Leaf:stem ratio</td>
<td></td>
<td>$P = 0.0016$</td>
<td>$P = 0.1417$</td>
<td>$P &lt; 0.0001$</td>
<td>$P = 0.0894$</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Leaf length</td>
<td></td>
<td>$P = 0.0061$</td>
<td>$P = 0.3664$</td>
<td>---</td>
<td>$P = 0.2659$</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Leaves per tiller</td>
<td></td>
<td>$P = 0.3353$</td>
<td>$P = 0.5526$</td>
<td>---</td>
<td>$P = 0.5813$</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Leaf area per tiller</td>
<td></td>
<td>$P = 0.3444$</td>
<td>$P = 0.4466$</td>
<td>---</td>
<td>$P = 0.0497$</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>
LIST OF REFERENCES


BIOGRAPHICAL SKETCH

Daniel Reis Pereira was born on 29 May 1985 in Brasília, Distrito Federal, Brazil. He moved several times throughout the country, but most of his summer vacations were spent on his family dairy, in the Paraíba valley region, where he developed his interest for agriculture. In 2008 he graduated from the University of São Paulo (Brazil) with a B.S. in Agronomy and in the summer of 2011 he completed his M.S. in Agronomy at the University of Florida.