Nitrogen accumulation, partitioning, and remobilization by diverse sesame cultivars in the humid southeastern USA

Annie Couch¹, Arun Jani², Mike Mulvaney², George Hochmuth¹, Jerry Bennett³, Romain Gloaguen³, Ray Langham⁴, and Diane Rowland³

¹University of Florida, Soil and Water Sciences Department, PO Box 110290, Gainesville, FL 32611

²University of Florida, West Florida Research and Education Center, 5988 Hwy. 90, Milton, FL 32583

³University of Florida, Agronomy Department, 3105 McCarty Hall B, Gainesville, FL 32611

⁴Sesame Research LLC, 7350 Seidel Rd, San Antonio, TX 78209.

Keywords: sesame (*Sesamum indicum* L.), nitrogen accumulation, partitioning, roots

Abstract

Sesame (*Sesamum indicum* L.) yield response to nitrogen (N) application has been well documented, but the temporal dynamics of N accumulation and partitioning by sesame are poorly understood. Such knowledge is needed to better inform fertilization decisions and improve N use efficiency (NUE). The objective of this study was to characterize N and biomass accumulation, partitioning, and remobilization among diverse sesame cultivars grown in the humid southeastern USA. A two-year field study was conducted at the University of Florida Plant Science Research and Education Unit in Citra, Florida in 2013 and 2014. Four commercially available cultivars (S30, S32, S36, and S39) with variable maturity and branching characteristics were sampled at multiple growth stages and divided into vegetative (stalks plus leaves), reproductive (capsules plus seed), and root (only S30 and S36) components to determine biomass and N accumulation. Medium-maturing cultivars (S30 and S32) reached peak aboveground biomass accumulation at late-bloom stage and accumulated $\sim 5100 \text{ kg biomass ha}^{-1}$ by dry down, while peak aboveground biomass accumulation for late-maturing cultivars (S36 and S39) was reached at physiological maturity and amounted to $8242 - 8739 \text{ kg biomass ha}^{-1}$ at dry down. Cultivars reached peak N accumulation at mid-bloom (S30), late-bloom (S32 and S39), and physiological maturity (S36). Total N accumulated by cultivars ranged from 70 to 99 kg N ha^{-1} in aboveground biomass, of which 33 – 60% was taken up during the reproductive growth phase. It was also estimated that 31 – 66% of aboveground vegetative N was remobilized to capsules and seed during reproductive growth. Root N accumulation peaked at mid-bloom stage, at which point S30 and S36 had accumulated approximately 4 kg N ha^{-1} . Removal of N with harvested seed amounted to $29 - 49 \text{ kg N ha}^{-1}$, with S36 removing more total N with harvest than both medium-maturing cultivars. This pattern of N accumulation suggests that plant

available N has the potential to impact sesame reproductive nutrient allocation, but additional research is needed to determine if the impact of the timing of N fertilization differs among more diverse sesame maturity classes.

1. Introduction

Despite the important role of sesame as a rotational component in tropical and subtropical cropping systems, fertilizer nitrogen (N) management of the crop has not been thoroughly investigated compared to other major agronomic crops. Moderate application of mineral N fertilizer has been shown to enhance sesame seed quality and yield parameters. For example, split-application of 40 – 80 kg N ha⁻¹ increased seed oil content by up to 8% (Ali et al., 2015; Malik et al., 2003), and seed yields by 26 – 52% (Malik et al., 2003; Patel et al., 2014). Nayek et al. (2014) reported that sesame can accumulate 59 – 116 kg N ha⁻¹ depending on fertilizer management practices, but the temporal dynamics of in-season N accumulation, partitioning, and remobilization have not been documented. A more comprehensive understanding of sesame N accumulation patterns is needed to better inform fertilization decisions, which may lead to greater N use efficiency (NUE).

Considering that sesame is typically grown on light-textured soils under weather conditions characterized by intense rainfall events, poor fertilizer management may result in substantial N losses to the environment. For example, Atta and van Cleemput (1988) reported that single application of 238 kg N ha⁻¹ one month after planting on a sandy loam in Egypt resulted in 12% fertilizer N recovery by sesame, while a split-application of 75 kg N ha⁻¹ on a loamy sand in India led to improved (23%) fertilizer N recovery (Patel et al., 2014). Synchronizing N application with crop demand is critical for optimizing NUE. For example, Kalaiselvan et al. (2002) found that application of 26 kg N ha⁻¹ at planting followed by 26 kg N ha⁻¹ from 20 to 40 days after planting (DAP) resulted in higher seed yields compared to a single pre-plant application of 52 kg N ha⁻¹. A better understanding of sesame N accumulation patterns

should improve N fertilization practices and enhance synchrony between N supply and crop demand.

Crop growth stage plays an important role in determining total N accumulation. For example, maize (*Zea mays* L.) has been shown to accumulate 65 – 74% of total N by silking, or the R1 stage (Bender et al., 2013; Ciampitti et al., 2013); while 62% of total N accumulation by winter wheat (*Triticum aestivum* L.) can occur by erect leaf sheath stage, or Feekes 5 (Girma et al., 2010). These studies indicate that the timing of N accumulation is crop dependent, and accumulation by an indeterminate crop like sesame, that has at least partial overlap between vegetative and reproductive stages, may differ from these and other crops. Previous research has shown that 80 – 95% of aboveground sesame biomass is accumulated during reproductive growth beginning 35 – 55 DAP (Mulkey et al., 1987; Narayanan and Reddy, 1982; Reddy and Narayanan, 1987). This rather delayed pattern of biomass accumulation during reproductive stages is somewhat unique to most agronomic crops. However, considering advances in sesame cultivar development since these studies were conducted, additional research is needed that uses modern cultivars to characterize patterns of sesame biomass and N accumulation.

While the timing of N accumulation has been quantified in previous studies, the remobilization of N during sesame growth is poorly understood. Atta and van Cleemput (1988) reported that approximately 55 and 45% of total N accumulated by sesame was partitioned into reproductive and vegetative components, respectively; however, the study did not provide information about N remobilization during reproductive growth. Likewise, Kundu and Singh (2006) observed that sesame seed contained 42% of total accumulated N, but that study did not explore N remobilization. Pawar et al. (2003) reported peak leaf tissue N content at 45 DAP for 10 sesame genotypes followed by a 50% reduction over the next 30 days, but N remobilization

from stem biomass, which can account for 38% of sesame dry weight (Atta and van Cleemput, 1988), was not included. Remobilized N from vegetative components as well as N accumulation during reproductive growth are both potential sources of N for reproductive components. From a fertilizer N management perspective, it is important to quantify how these N sources contribute to sesame reproductive structures.

Crop maturity characteristics can impact N allocation and remobilization as well. For example, Heckman (2007) found that late-maturing maize cultivars removed 87% more N with harvested seed than early-maturing cultivars. Modern sesame cultivars are also characterized by maturity, with classes consisting of early (85 – 94 days), medium (95 – 104 days), late (105 – 114), and very late (> 114 days) maturing cultivars (Langham, 2007). There is also variability in morphological characteristics, including ranges of 2 – 51 branches and 138 – 261 leaves on genotypes grown under irrigated conditions (Pham et al., 2010). However, it is not clear if this variability in maturity and morphology impacts sesame N accumulation, partitioning, and remobilization. The objective of this study was to characterize N and biomass accumulation, partitioning, and remobilization among non-dehiscent, diverse sesame cultivars grown in the humid southeastern USA.

2. Materials and Methods

2.1. Field site and experimental design

A two-year field study was conducted at the University of Florida Plant Science Research and Education Unit (PSREU) in Citra, Florida (29.41° N, 82.18° W, 20.7 m above sea level) on a Gainesville loamy sand (Hyperthermic, coated Typic Quartzipsamment) in 2013, and a Candler sand (Hyperthermic, uncoated Lamellic Quartzipsamments) in 2014 (Table 1). Four non-

dehiscent cultivars, S30, S32, S36, and S39 (Sesaco, Austin, TX), representing two maturity classes, medium- (S30 and S32) and late-maturing (S36 and S39), were utilized in the study. These cultivars also represented diverse branching morphologies with either single-stemmed (S30) or branched (S32, S36, and S39) characteristics. Cultivars were selected based on commercial availability in the region and past performance under similar humid, subtropical environmental conditions in Sesaco nurseries in coastal South Texas (personal communication).

Field preparation included two initial disking passes, moldboard plowing followed by harrow disking, and a final field cultivation to form a seedbed. Planting occurred on 30 May 2013 and 18 June 2014; the later planting date in 2014 was due to poor stand establishment with two earlier plantings, the likely cause of which was herbicide injury. Immediately following planting both years, the pre-emergent herbicide (S)-metolachlor (Dual Magnum[®], Syngenta Crop Protection, Greensboro, NC) was applied at 1.47 kg a.i. ha⁻¹ and irrigated into the soil. In 2014, after the first sesame planting and (S)-metolachlor application, heavy rainfall occurred within a few days after planting which likely moved the herbicide through the light-textured soil into direct contact with seed causing poor germination. Heavy rainfall also occurred after the second planting and (S)-metolachlor application in the new location as well, likely causing poor stand establishment. For the third planting, (S)-metolachlor was not used and stand establishment was successful. Sperry et al. (2016) also reported poor sesame stand establishment with (S)-metolachlor application at planting on light-textured soils in Florida. Additional weed control consisted of manual weeding with a scuffle hoe as needed, and cultivation 14 and 28 DAP in 2014 with a tractor-driven field cultivator. In both years, 28 kg N ha⁻¹, 12.4 kg P₂O₅ ha⁻¹, and 23.3 kg K₂O ha⁻¹ was broadcast within 7 DAP; with a second application of 39 kg N ha⁻¹, 17.2 kg P₂O₅ ha⁻¹, and 32.5 kg K₂O ha⁻¹ broadcast ~ 30 DAP to coincide with flower initiation. Plots

were irrigated utilizing center pivot irrigation and scheduled using a general irrigation schedule for crops grown on these soil types. Supplemental irrigation amounted to 120 and 100 mm in 2013 and 2014, respectively. Weather data were collected through the Florida Automated Weather Network utilizing the Citra weather station. Cultivars were planted in a randomized complete block design with four replications. Plots measured 4.2 x 12.2 m with 38 cm row spacing. Sesame was planted at a rate of 5.6 kg ha⁻¹, and plots were harvested by hand when grain moisture content measured below 6%. Capsules were mechanically threshed and grain was weighed for each plot.

2.2. *Sesame biomass sampling*

Plants were destructively sampled 28, 49, 77, 91, and 112 DAP both years. Sampling dates corresponded to different growth stages (Table 3). Physiological maturity was determined using methods described by Langham (2007). Briefly, the concept of physiological maturity in sesame was developed to determine the earliest possible date that sesame could be harvested and still achieve over 95% of potential yield. Physiological maturity in sesame occurs when at least 75% of capsules on the main stem have seed with final color (cultivar-dependent), a darkened tip, and a longitudinal black line on one side. Cultivars used in this study have a buff color at maturity. Several representative plants in each plot were sampled to determine physiological maturity and immature seed was differentiated from mature seed by the former's white to off-white color, lighter-colored, less distinguishable tip, and absence of a longitudinal black line.

At each sampling event, aboveground biomass was collected from representative 38 x 38 cm subplots within each plot. Aboveground biomass was separated into vegetative (stems plus leaves) and reproductive (capsules plus seed) components. Abscised leaves were collected from the ground within subplots weekly, cleaned with a brush to remove soil, and added to the mass of

vegetative structures. Biomass samples were oven-dried at 65°C until constant weights were achieved to determine vegetative and reproductive component dry weight for each sampling date.

Root biomass was collected from S30 and S36 at each sampling date. Due to labor constraints, root biomass collection from all cultivars was not possible; therefore, S30 and S36 were selected due to their diversity in maturity and branching characteristics. To extract root biomass, a volumetric soil root sample (38 x 38 x 120 cm) was taken from a representative section of each plot. Samples were wet-sieved to remove soil from roots utilizing a metal sieve with 1.31 x 1.48 mm openings to minimize loss of fine roots. To better ensure recovery of fine roots, a single sample of soil that had passed through the sieve was collected and processed using the Gottingen method (Böhm, 1979). The method involved adding water to the soil sample and stirring to form a suspension, which was left undisturbed until roots floated. The suspension was then poured through a 30 ASTM (American Society of Testing Materials) sieve and roots were collected. Additional water was added to the soil mixture and the process of suspension, decantation, and sieving was repeated three times. Sieved root biomass was oven-dried as described previously.

2.3. Laboratory analyses

Oven-dried above- and belowground biomass samples were ground to pass a 2 mm mesh screen (Thomas Wiley Laboratory Mill, Thomas Scientific, Swedesboro, New Jersey). Total Kjeldahl N (TKN), organic N, and NH₄-N in plant tissue were quantified by preliminary acid digestion on a block digester following Environmental Protection Agency Method 351.2 standards (US Environmental Protection Agency, 1993). A Bran+Luebbe Technicon AutoAnalyzer II segmented flow analysis system (Norderstedt, Germany) was used to analyze

TKN concentration. Data quality control measures utilized in the analyses included blanks, laboratory control samples, replicates, and continuous calibration verification standards. The quantity of N accumulated by sesame plant components on each sampling date was determined by multiplying the component dry weight by percent N.

2.4. Statistical analyses

Statistical analyses were performed using JMP Pro 11 software (SAS Institute Inc., Cary, NC). Analysis of variance with a linear mixed effects model was used to test the following response variables: above- (total, vegetative, and reproductive) and belowground (root) biomass and N accumulation at different growth stages; seed and N harvest indices; and percent N remobilized. Replication was treated as a random effect, while cultivar, plant component, growth stage, and year were treated as fixed effects. All interactions among fixed effects on relevant response variables were tested. Since measurements were taken throughout the season, a repeated measure first-order autoregressive covariance correlation structure was included in the model. Multiple comparisons for all response variables were made using Tukey's HSD ($p = 0.05$).

Models for total aboveground biomass and N accumulation patterns for each cultivar were fitted to the data over time for the five sampling dates for 2013 and 2014 utilizing both quadratic (1) and sigmoidal (2) equations (Eq.):

$$y = a + (b * DAP) + (c * DAP)^2 \quad (\text{Eq. 1})$$

$$y = \frac{c}{[1 + \text{Exp}[-a * [DAP - b]]]} \quad (\text{Eq. 2})$$

where y is total aboveground biomass or N accumulated (kg ha^{-1}) and DAP is days after planting. In Eq. 1, a , b , and c represent intercept, slope, and the quadratic term, respectively,

while in Eq. 2 these terms represent growth rate, inflection point, and asymptote, respectively. Model selection used to describe aboveground biomass and N accumulation was based on Akaike Information Criterion (AICc) corrected for small samples and coefficient of determination (R^2) values. Models having the smallest AICc and the largest R^2 when fitted to the data were selected to explain the measured data. Root biomass and N data were not included in models because their contribution to total biomass and N was relatively small and did not affect the magnitude or shape of fitted curves. Remobilization of N from vegetative to reproductive components was determined using an adaptation of the “balance approach” described by Ciampitti and Vyn (2013). These authors estimated N remobilization in maize by subtracting stover N at maturity (sum of leaves, stems, shank, cob, and husk N fractions) from vegetative N (cumulative whole plant N at silk emergence). In the current study, N remobilization was determined by subtracting vegetative N content at initial dry-down from vegetative N content at the beginning of mid-bloom (49 DAP).

3. Results

3.1. Environmental conditions and crop development

Atmospheric temperature conditions both years were similar, and closely approximated the 15-year average for the region (Table 2). Total precipitation during the 2013 season was greater than in 2014, and was primarily driven by above average precipitation during July and August 2013 and below average precipitation during June 2014. Precipitation during July and August was 222 mm more in 2013 compared to 2014. While total precipitation in both years was adequate for sesame production (Uçan et al., 2007), in-season variability in rainfall patterns necessitated the use of supplemental irrigation during dry periods to prevent crop moisture stress. Although both medium- and late-maturing cultivars were included in the study, physiological

maturity was reached 91 DAP for all cultivars both years (Table 3). Cultivars also entered growth phases and stages at approximately the same time each year despite a 19-day difference in planting dates between years.

3.2. Biomass accumulation and partitioning

Total aboveground, vegetative, and reproductive biomass accumulation was affected by the cultivar x growth stage interaction. In addition, there was a growth stage x year effect on vegetative biomass accumulation. (Table 4). Neither year nor an interaction of year with other factors affected total aboveground or reproductive biomass accumulation. The growth stage x year interaction on vegetative biomass accumulation was caused by lower accumulation at late-bloom in 2014 compared to 2013 (data not shown). Differences among cultivars in total aboveground biomass at the end of the growing season were driven by S36 and S39, which had accumulated 8739 kg ha⁻¹ and 8242 kg ha⁻¹, respectively, compared to S30 and S32, which had both accumulated approximately 5100 kg ha⁻¹ (Fig. 1). Differences among cultivars in vegetative biomass accumulation revealed that S36 and S39 had accumulated approximately 2200 kg ha⁻¹ greater vegetative biomass than S30 and S32 by initial dry down.

Interactions between cultivar and growth stage for all three aboveground biomass parameters (total, vegetative, reproductive) revealed differences in the overall pattern of accumulation. Peak total aboveground biomass accumulation was reached at late-bloom for S30 and S32, while total aboveground biomass accumulation peaked two weeks later at physiological maturity for S36 and S39 (Fig. 1). The pattern of vegetative and reproductive biomass accumulation by cultivars followed a similar general trend to total aboveground biomass accumulation: vegetative biomass for S30 and S32 increased through mid-bloom and then plateaued, while S36 and S39 reached peak vegetative biomass four weeks later at late-bloom.

Capsule formation was first observed at early-bloom for all cultivars, and reproductive biomass increased until late-bloom for S30 and S32. However, reproductive biomass for S36 and S39 continued to accumulate until initial dry-down, or five weeks longer than S30 and S32 (Fig. 1). The increase in reproductive biomass from mid- to late-bloom (S30 and S32) or initial dry-down (S36 and S39) was not accompanied by a reduction in vegetative biomass, indicating a lack of evidence for assimilate remobilization from aboveground vegetative components to reproductive structures. Cultivars accumulated similar amounts of reproductive biomass at all growth stages, except for the initial dry-down period when S36 had greater reproductive biomass than S30. Reproductive biomass comprised 42 – 53% of total aboveground biomass at initial dry down.

Roots comprised 6 – 7% of total end-of-season biomass when averaged over years. Root biomass accumulation was affected by all first order interactions including cultivar x growth stage, cultivar x year, and growth stage x year (Table 5). The overall pattern of root biomass accumulation showed the primary increase in biomass occurring between the juvenile and mid-bloom stages: across cultivars, root biomass accumulation between the juvenile and mid-bloom stages increased by 289 and 66% in 2013 and 2014, respectively (Table 6). Averaged across cultivars, root biomass accumulated until late bloom in 2013, but only until mid-bloom in 2014. Both years, S36 accumulated similar amounts of root biomass, while accumulation was greater in 2014 compared to 2013 for S30 (data not shown).

The pattern of total aboveground biomass accumulation for all cultivars was best described by a sigmoidal model (Eq. 2) based on AICc and R^2 criterion. Since total biomass accumulation was not affected by year or an interaction of year with other factors (Table 4), data from both years were combined to generate crop growth rate curves. The sigmoidal model

estimated sesame growth rates of 103 – 115 kg ha⁻¹ day⁻¹ with cultivars accumulating 63 – 79% of total biomass after initiation of reproductive growth (Fig. 2).

3.3. Nitrogen accumulation, partitioning, and remobilization

There was an interaction between cultivar and growth stage for total aboveground and reproductive N accumulation, while the main effect of growth stage affected vegetative N accumulation (Table 4). There was also a growth stage x year interaction on vegetative N accumulation. The interaction between cultivar and growth stage for total N accumulation showed a peak in this parameter for S30 at mid-bloom stage, while S32 and S39 continued to accumulate N through late-bloom stage (Fig. 3). Peak total N accumulation for S36 was not reached until physiological maturity, six weeks after S30. While the temporal pattern of total N accumulation differed between cultivars, quantities at initial dry down did not differ, showing average values across cultivars and years of 81, 21, and 60 kg N ha⁻¹ for total, vegetative, and reproductive N accumulated, respectively. The interaction between growth stage and year for N accumulation in vegetative biomass was limited to a decline in vegetative N content first observed at physiological maturity in 2013 and at late-bloom in 2014 (data not shown).

With the onset of reproductive growth, there was a decline in vegetative N content among all cultivars. It was estimated that 31 – 66% of vegetative N was remobilized to reproductive structures during this time (Fig. 3). However, there was no evidence for cultivar, year, or cultivar x year effects on N remobilization. Nitrogen accumulation by reproductive components peaked at late-bloom for S30 and S32, and at physiological maturity for S36 and S39. By initial dry down, cultivars had accumulated 70 – 99 kg N ha⁻¹ (Fig. 3) of which 29 – 49 kg N ha⁻¹ was removed with seed (Fig. 4).

Root N accumulation was affected by cultivar x growth stage and growth stage x year interactions (Table 5). Root N content increased through mid-bloom stage, and roots from both S30 and S36 contained $\sim 4 \text{ kg N ha}^{-1}$ at peak accumulation (Fig. 3), representing 4 – 5% of total N accumulation for these cultivars. The cultivar x growth stage interaction was driven by different patterns of root N reduction between cultivars after mid-bloom stage (data not shown). Reduction in root N content after mid-bloom was observed at initial dry-down for S30 and at physiological maturity for S36. Averaged across years, root N content was reduced by 58 and 29% from mid-bloom through initial dry-down in S30 and S36, respectively.

Neither year nor an interaction of year with other factors on aboveground N accumulation was observed, therefore, data were combined from both years to generate N accumulation curves (Fig. 5). The relationship between aboveground N accumulation and growth stage across years revealed that a sigmoidal model (Eq. 2) best described this pattern for all cultivars based on AICc and R^2 values. While a sigmoidal model provided the best fit of data, R^2 values describing N accumulation were relatively low compared to values for biomass accumulation (R^2 ranges of 0.66 – 0.91 and 0.46 – 0.71 for biomass and N accumulation, respectively). The sigmoidal model estimated N accumulation rates of $0.84 - 1.47 \text{ kg ha}^{-1} \text{ day}^{-1}$ N with cultivars accumulating 33 – 60% of total aboveground N during reproductive growth.

4. Discussion

This study provided critical data on N and biomass accumulation, partitioning, and remobilization among commercial sesame cultivars grown on light-textured soils in a humid, subtropical climate. Biomass partitioning into vegetative, reproductive, and root components was similar to values reported in earlier studies on sandy loam soils. These earlier studies showed that 50 – 73, 16 – 43, and 7 – 11% of accumulated biomass was allocated to vegetative, reproductive,

and root components, respectively (Atta and van Cleemput, 1988; Narayanan and Reddy, 1982). A relatively small portion of total aboveground biomass (21 – 37%) relative to total N (40 – 67%) was accumulated by cultivars during the vegetative growth phase in comparison to crops such as maize where up to 71% and 59% of total N and biomass accumulation, respectively, has occurred during vegetative growth (Bender et al., 2013; Ciampitti et al., 2013). Soybean has been shown to accumulate 35% of aboveground biomass during vegetative growth, a pattern that more closely resembles sesame. (Bender et al., 2015). The potentially large amount of N accumulated relative to aboveground biomass produced during the sesame vegetative growth phase may relate to the production of robust root systems early in development, thus allowing for efficient soil exploration and likely increased N uptake.

This study also documented critical information, heretofore unknown for non-dehiscent sesame cultivars, about the pattern of belowground biomass and N accumulation. Sesame develops a deep taproot and produces an extensive network of fibrous roots (Langham, 2007). Comparison of root to shoot ratios for S30 and S36 at the end of the vegetative growth phase (0.17 – 0.19) and initial dry down (0.05 – 0.08) show that root production during the vegetative growth phase was disproportionately large relative to aboveground biomass production. Averaging over years, S30 and S36 accumulated 57 and 24% of maximum root biomass produced, respectively, by the juvenile stage. In comparison, only 20 and 12% of total aboveground biomass for S30 and S36, respectively, had accumulated by this stage. These results are in accordance with earlier research that showed ~ 50% of sesame root biomass and 40% of aboveground biomass was produced during the vegetative growth phase (Narayanan and Reddy, 1982). However, evidence suggests that sesame roots do not serve as a long-term sink for plant N. For example, Atta and van Cleemput (1988) found that sesame roots comprised only 4%

of total end-of-season plant N, compared to 2 – 3% in the current study, and that 3% of labeled N fertilizer taken up by the crop was allocated to roots.

Results from this study address an important question about the ability of sesame to support large increases in reproductive biomass concomitant with the senescence of many of the photosynthetically active vegetative structures. Since cultivars produced 63 – 79% of total aboveground biomass during the reproductive phase (Fig. 2), it may be speculated that optimal rates of photosynthesis during this phase were essential for biomass accumulation. Otherwise, remobilization of previously assimilated carbohydrates would be needed. In the current study, leaf senescence and abscission were noted beginning at late-bloom and resulted in little foliar biomass present during later seed fill. Despite a reduction in photosynthetic structures and lack of evidence to support assimilate remobilization, reproductive biomass for S36 and S39 continued to increase through initial dry down (112 DAP; Fig. 1). Bascones and Ritas (1961) reported a similar pattern of growth at a location in Venezuela with similar growing season rainfall and temperature conditions as the Florida location. In that study, leaf biomass decreased by 60% from the start of capsule formation until harvest, but capsule biomass continued to increase during the same time period. However, reproductive growth after physiological maturity has been reached in later-maturing cultivars is generally limited to the top portion of plants. Seed weight at the top of plants is relatively low and would not seriously impact potential yield when excluded from harvest (Langham, 2007).

It is conceivable that assimilate production by capsules, stems, and smaller leaves subtending capsules, which were retained longer than other leaves, may have contributed assimilates to increase late-season reproductive biomass. In field pea (*Pisum arvense* L.), Flinn and Pate (1970) found that up to 75% of assimilates exiting leaves subtending pods were

remobilized to pod and developing seed tissues. The study also showed that pea pods can photosynthesize and accumulate assimilates. Other studies have similarly shown photosynthetic activity in soybean pods (Andrews and Svec, 1975; 1976). It is possible that photosynthesis by sesame capsules, smaller leaves, and stems contributed, at least in part, to the increase in reproductive dry matter during late reproductive growth. However, the photosynthetic capacity of sesame capsules or stems is unknown and warrants investigation.

All cultivars reached physiological maturity approximately 91 DAP, which was not expected since both medium- and late-maturing cultivars were included in the study. Although not commonly reported, similar observations have also been made with cotton (*Gossypium hirsutum* L.) where maturity dates were shown to overlap for cultivars classified as early-medium, medium-late, or late (Bange and Milroy, 2004). Timing of physiological maturity in the current study was also earlier than the timeframe reported by Langham (2007) for medium- (95 – 104 days) and late-maturing (105 – 114 days) cultivars. This discrepancy is likely explained by the fact that sesame maturity class categories were developed under irrigation in Southwest Texas (Langham, 2007), which has a drier climate than the humid southeastern USA. Genotype x environment interactive effects on sesame phenology have been reported elsewhere (Suddhiyam et al., 1992; Morris, 2009; Pham et al., 2010), and suggest that maturity classification systems should be developed for different environments where sesame is grown.

Despite reaching physiological maturity at the same time, medium-maturing cultivars (S30 and S32) generally attained peak aboveground biomass production earlier than late-maturing cultivars (S36 and S39; Fig. 2). Similarly, Narayanan and Reddy (1982) reported earlier peak biomass accumulation and lower total biomass production for early-maturing cultivars compared to late-maturing cultivars. In the current study, all cultivars reached peak

vegetative N accumulation at the same time (mid-bloom), which supports earlier research that found peak leaf tissue N accumulation occurred approximately 45 DAP for 10 sesame genotypes (Pawar et al., 2003). The similar quantity of N partitioned to seed among medium-maturing cultivars in the current study also complements earlier research in Virginia that showed similar amounts of secondary and micronutrients allocated to seed among medium-maturing cultivars, including S30 and S32 (Bhardwaj et al., 2014).

It remains difficult to explain why medium- and late-maturing cultivars had different patterns of biomass and N accumulation when physiological maturity was reached at the same time for all cultivars. Bange and Milroy (2004) reported similar findings for cotton in which an early cultivar accumulated significantly less total biomass than an early-medium maturity cultivar despite just a four-day difference in reaching maturity. Field studies in Texas have shown that sesame can reach physiological maturity 96 – 106 DAP depending on year, while much less variation (40 – 44 days) has been observed for days to flowering (Langham, 2007). It is possible that in-season development and nutrient accumulation patterns are under tighter genetic control than later maturity processes, but additional studies are needed to validate this speculation.

The pattern of total N accumulation during vegetative and reproductive growth phases has important N fertilization management implications for sesame production. The potentially large proportion of total N accumulated during reproductive growth indicates that the supply of plant available N is critical during this period. Additionally, the cultivar x growth stage interaction for N accumulation in this study may have implications for specific N management of different cultivars grown on similar soil types. While Kalaiselvan et al. (2002) found that split N application 20 and 30 DAP compared to 30 and 40 DAP did not affect sesame seed yields, the

study did not provide information about cultivar maturity characteristics, which our study indicates can influence N accumulation patterns. The fact that S36 continued to accumulate N for 9 weeks after N accumulation had plateaued in S30 while also removing more N with harvested seed, indicates that N fertilization practices may need to be tailored for individual sesame cultivars. Under mechanized sesame management, split N applications tailored to sesame maturity classes may be optimal; with the possibility of utilizing slow release N fertilizer sources as well.

5. Conclusions

This study provided evidence for differential patterns of biomass and N accumulation for sesame cultivars among growth stages, thus indicating cultivar differences in partitioning and N remobilization dynamics. The potentially large proportion of aboveground biomass and N accumulated by cultivars during reproductive growth underscores the importance of plant available N beyond the vegetative growth phase. These findings point to the need for additional research focused on sesame response to timing of split-N applications and the utility of slow release N fertilizer sources to improve NUE. Special consideration should be given to conducting such research on a broader array of soil textural classes since conclusions drawn in this study are applicable to light-textured soils. Considering the importance of sesame as a rotational crop on marginally fertile soils in tropical and subtropical cropping systems, similar research focused on other plant essential nutrients is warranted.

Acknowledgements

This work was supported by the USDA National Institute of Food and Agriculture, under HATCH project numbers FLA-AGR-005478 and FLA-JAY-005475 award numbers 2012-04124, 2014-09667, and 1007448. We wish to thank members of the George Hochmuth and

Diane Rowland lab groups for their support with data collection and Sesaco for providing seed and assistance with processing harvested samples.

References

- Ali, S., Jan, A., Sohail, A., Habibullah, M., Zhikuan, J., Khan, A. Z., Akhtar, K. 2015. Agro-management effects on fatty acid composition of sesame (*Sesamum indicm* L.) Pure Appl. Bio. 4 (1), 43-49.
- Andrews, A. K., Svec, L. V. 1975. Photosynthetic activity of soybean pods at different growth stages compared to leaves. Can. J. Plant Sci. 55, 501-505
- Andrews, A. K., Svec, L. V. 1976. Pod and leaf photosynthesis and disease incidence in soybean (*Glycine max* (L.) Merr.) with potassium fertilization. Comm. Soil Sci. Plant Anal. 7 (4), 345-363.
- Atta, S. K. H., van Cleemput, O. 1988. Field study of the fate of labelled fertilizer ammonium-N applied to sesame and sunflower in a sandy soil. Plant Soil 107, 123-126.
- Bange, M. P., Milroy, S. P. 2004. Growth and dry matter partitioning of diverse cotton genotypes. Field Crop Res. 87, 73-87.
- Bascones, L., Lopez Ritas, J. 1961. La nutricion mineral de ajonjoli. II. Extraccion total de nutrientes. Agron. Trop. 11 (2), 93-101.
- Bender, R. R., Haegele, J. W., Ruffo, M. L., Below, F. E. 2013. Nutrient uptake, partitioning, and remobilization, in modern transgenic insect-protected maize hybrids. Agron. J. 105, 161-170.

475 Bhardwaj, H. B., Hamama, A. A., Kraemer, M. E., Langham, D. R. 2014. Cultivars, planting
 476 dates, and row spacing effects on sesame seed yield and mineral composition. J. Agr.
 477 Sci. 6 (9), 1-7.

478 Böhm, W .1979. Methods of Studying Root Systems. Ecological Studies 33. Springer-
 479 Verlag, Berlin

480 Ciampitti, I. A., Camberato, J. J., Murrell, S. T., Vyn, T. J. 2013. Maize nutrient accumulation
 481 and partitioning in response to plant density and nitrogen rate: I. Macronutrients. Agron.
 482 J. 105 (3), 783-795.

483 Ciampitti, I. A., Vyn, T. J. 2013. Grain nitrogen source changes over time in maize: a review.
 484 Crop Sci. 53, 366-377.

485 Flinn, A. M., Pate, J. S. 1970. A quantitative study of carbon transfer from pod and subtending
 486 leaf to the ripening seeds of the field pea (*Pisum arvense* L.). J. Expl. Bot. 21 (66), 71-82.

487 Girma, K., Holtz, S., Tubaña, B. Solie, J., Raun, W. 2010. Nitrogen accumulation in shoots as a
 488 function of growth stage of corn and winter wheat. J. Plant Nut. 34, 165-182.

489

490 Heckman, J. R. 2007. Sweet corn nutrient uptake and removal. HortTech 17 (1), 82-86.

491 Kalaiselvan, P., Subrahmaniyan, K., Balasubramanian. 2002. Effect of split application of N and
 492 K on the growth, yield attributes and yield of sesame. Sesame and Safflower Newsletter
 493 17. Center for Agrarian Research and Development, Córdoba, Spain.

494 Kundu, D. K., Singh, R. 2006. Effect of irrigation on yield and nutrient uptake of summer
 495 sesame (*Sesamum indicum* L.) in coastal Orissa. Indian J. Agr. Sci. 76 (9), 531-534.

496 Langham, R. 2007. Phenology of sesame. *In*: Issues in new crop and new uses. Eds. Janick, J.,
 497 Whipkey, A. ASHS Press, Alexandria, Virginia.

498 Malik, M. A., Saleem, M. F., Cheema, M. A., Ahmed, S. 2003. Influence of different nitrogen
499 levels on productivity of sesame (*Sesamum indicum* L.) under varying planting patterns.
500 Int. J. Agric. Biol. 5 (4), 490-492.

501 Morris, J. B. 2009. Characterization of sesame (*Sesamum indicum* L.) germplasm regenerated in
502 Georgia, USA. Genet. Resour. Crop Evol. 56, 925-936.

503 Mulkey, J. R., Drawe, H. J., Elledge, R. E. 1987. Planting date effects on plant growth and
504 development in sesame. Agron. J. 79, 701-703.

505 Narayanan, A., Reddy, B. 1982. Growth, development, and yield of sesame (*Sesamum indicum*
506 L.) cultivars. Field Crop Res. 5, 217-224.

507 Nayek, S. S., Brahmachari, K., Chowdhury, M. D. R. 2014. Integrated approach in nutrient
508 management of sesame with special reference to its yield, quality, and nutrient uptake.
509 Bioscan 9 (1), 101-105.

510 Patel, H. K., Patel, R. M., Desai, C. K., Patel, H. B. 2014. Response of summer sesamum
511 (*Sesamum indicum* L.) to different spacings and levels of nitrogen under north Gujarat
512 condition. Int. J. Agric. Sci. 10 (1), 336-343.

513

514 Pawar, K. N., Chetti, M. B., Koti, R. V. 2003. Variability study in sesame (*Sesamum indicum* L.)
515 for chlorophyll and leaf nitrogen content. Agric. Sci. Dig. 23 (2), 143-145.

516 Pham, T. D., Nguyen, T. T., Carlsson, A. S., Bui, T. M. 2010. Morphological evaluation of
517 sesame (*Sesamum indicum* L.) varieties from different origins. Aust. J. Crop Sci. 4 (7),
518 498-504.

519 Reddy, K. B., Narayanan, A. 1987. Dry matter production and nutrient uptake in sesame
520 (*Sesamum indicum* L.) genotypes. Sesame and Safflower Newsletter 3. Center for
521 Agrarian Research and Development, Córdoba, Spain.

522 Sperry, B. P., Ferrell, J., Leon, R., Rowland, D., Mulvaney, M. 2016. Influence of planting depth
523 and application timing on s-metolachlor injury in sesame (*Sesamum indicum* L.). Weed
524 Technol. In-press.

525 Suddhiyam, P., Steer, B. T., Turner, D. 1992. The flowering of sesame (*Sesamum indicum* L.) in
526 response to temperature and photoperiod. Aust. J. Agric. Res. 43, 1101-1116.

527 Uçan, K., Killi, F., Gençoglan, C., Merdun, H. 2007. Effect of irrigation frequency and amount
528 on water use efficiency and yield of sesame (*Sesamum indicum* L.) under field
529 conditions. Field Crop Res. 101, 249-258.

530 United States Environmental Protection Agency. 1993. Methods for the chemical analysis of
531 water and wastes (MCAWW). EPA/600/4-79/020.

532
533
534
535
536
537
538

Fig. 1. Vegetative and reproductive biomass accumulation for sesame cultivars S30, S32, S36, and S39 averaged over 2013 and 2014 seasons in Citra, FL. Growth stages are as follows: juvenile (Juv.), mid bloom (MB), late bloom (LB), physiological maturity (PM), and initial dry down (DD). For S30 and S32, vegetative and reproductive biomass peaked at MB and LB, respectively. Peak vegetative and reproductive biomass for S36 and S39 was recorded at LB and DD, respectively. Despite apparent visual differences, biomass accumulation after these peaks did not increase based on multiple comparisons testing (Tukey's HSD).

Fig. 2. Fitted sigmoidal crop growth rate (CGR) curves for aboveground biomass of sesame cultivars S30, S32, S36, and S39 grown in Citra, FL. Curves were generated averaging data over years. Growth stages are as follows: juvenile (Juv.), mid bloom (MB), late bloom (LB), physiological maturity (PM), and initial dry down (DD).

Fig. 3. Vegetative and reproductive nitrogen accumulation for sesame cultivars S30, S32, S36, and S39 averaged over 2013 and 2014 seasons in Citra, FL. Growth stages are as follows: juvenile (Juv.), mid bloom (MB), late bloom (LB), physiological maturity (PM), and initial dry down (DD). Vegetative N peaked at MB for all cultivars. Reproductive N peaked at LB for S30 and S32 and at PM for S36 and S39.

Fig. 4. Nitrogen removed (kg ha⁻¹) with harvested seed from S30, S32, S36, and S39. Means with the same letter were not significantly different at $p = 0.05$ according to Tukey's HSD.

Fig. 5. Fitted sigmoidal aboveground nitrogen accumulation rate (NAR) curves for sesame cultivars S30, S32, S36, and S39 grown in Citra, FL. Curves were generated averaging data over years. Growth stages are as follows: juvenile (Juv.), mid bloom (MB), late bloom (LB), physiological maturity (PM), and initial dry down (DD).

Table 1

Initial properties of soils used in 2013 and 2014 in Citra, FL.
Nutrient testing was conducted using the Mehlich 1 extractant method.

Soil property ^a	2013	2014
	Gainesville loamy sand	Candler sand
pH	6.2	6.7
CEC	5.7	3.4
Organic matter (%)	< 1	< 1
P ^b	100	66
K	35.5	29
Mg	32.5	20.5
Ca	749.5	473
S	2	16.5
B	0.2	0.1
Zn	1.2	0.9
Mn	3.6	1.5
Fe	16.5	13
Cu	0.8	0.4

^aCation exchange capacity (CEC) is reported as meq 100 g⁻¹.

^bNutrients are reported in mg kg⁻¹.

Table 2

Monthly means of air temperature (°C) and total precipitation (mm) in Citra, FL in 2013 and 2014. Data were provided by the Florida Automated Weather Network.

Month	2013		2014		15-year mean	
	Temp.	Prec.	Temp.	Prec.	Temp.	Prec.
May	22	44	24	95	24	68
June	26	165	26	103	26	163
July	26	238	26	163	27	158
August	27	202	27	117	27	158
September	25	110	25	117	26	124
October	22	40	21	31	22	72
Total	25	799	25	626	25	743

Table 3

Timing of sesame growth phases and stages observed in 2013 and 2014 in Citra, FL. Growth phase and stage descriptions were provided by Langham (2007)

Growth phase	Growth stage	End point of stage	Days after planting ^a
Vegetative	Seedling	3 sets of true leaves	21
Vegetative	Juvenile	First buds	28
Vegetative	Pre-reproductive	50% open flowers	35
Reproductive	Early bloom	5 node pairs of capsules	42
Reproductive	Mid-bloom	Branches/minor plants stop flowering	49
Reproductive	Late bloom	90% of plants with no open flowers	77
Ripening	Physiological maturity	75% of capsules have final cultivar seed color	91
Drying	Initial dry down	1st field dry capsules	112

^a Biomass was sampled 4, 7, 11, 13, and 16 weeks after planting.

Table 4

Sources of variance and significance of effects for total, vegetative (Veg), and reproductive (Repr) biomass and N accumulation by sesame in Citra, FL in 2013 and 2014.

Source	Biomass accumulation			N accumulation		
	Total	Veg	Repr	Total	Veg	Repr
Cultivar	*	*	NS	NS	NS	NS
Growth stage	***	***	***	***	***	***
Year	NS	NS	NS	NS	NS	NS
Cultivar x growth stage	***	***	***	*	NS	***
Cultivar x year	NS	NS	NS	NS	NS	NS
Growth stage x year	NS	*	NS	NS	**	NS
Cultivar x growth stage x year	NS	NS	NS	NS	NS	NS

* Significant at $p \leq 0.05$

** Significant at $p \leq 0.01$

*** Significant at $p \leq 0.001$

NS, not significant

Table 5

Sources of variance and significance of effects for root biomass and N accumulation by sesame cultivars grown in Citra, FL in 2013 and 2014.

Source	Root biomass accumulation	Root N accumulation
Cultivar	*	NS
Growth stage	***	***
Year	**	*
Cultivar x growth stage	**	***
Cultivar x year	**	NS
Growth stage x year	*	***
Cultivar x growth stage x year	NS	NS

* Significant at $p \leq 0.05$

** Significant at $p \leq 0.01$

*** Significant at $p \leq 0.001$

NS, not significant

Table 6

Root biomass and N accumulation averaged across cultivars (S30 and S36) at different growth stages in 2013 and 2014 in Citra, Fl.

Growth stage	Root biomass		Root N content	
	kg ha ⁻¹			
	2013	2014	2013	2014
Juvenile (first bud)	139c ^a	348b	1.5ab	2.3b
Mid-bloom	541ab	579a	2.7a	5.0a
Late-bloom	644a	659a	2.7a	3.0b
Physiological maturity	480ab	675a	1.4ab	3.3ab
Initial dry down	293bc	647a	0.9b	3.4ab

^aMeans within columns with the same letter are not significantly different at $p \leq 0.05$ according to Tukey's HSD.