ABSTRACT

OAKES, JOSEPH CARROLL. Improving Soybean Yield by Identifying Mechanisms and Varieties that Facilitate the Translocation of Starch from Leaves and Stem to the Seed During Periods of Stress. (Under the direction of Drs. Ronnie W. Heiniger, E. James Dunphy, and Thomas E. Carter, Jr.).

To meet the increasing demand for soybean products, yield must increase at a pace that exceeds the current rate. However, soybean yield in North Carolina has not improved substantially over the last twenty years (United States Department of Agriculture, 2012). The average soybean yield in North Carolina in 1992 was 1816 kg ha\(^{-1}\), while the average yield in 2011 was only 2018 kg ha\(^{-1}\). This lack of yield increase can likely be attributed to the impact of environmental factors reducing translocation of assimilates from leaves to the pod. Two separate studies were conducted in North Carolina in 2010 and 2011 to evaluate the effects of shading, defoliation, and seeding rate on pod growth and weight, as well as source-sink interactions.

The first study looked at the effect of shading, defoliation, and seeding rate on pod growth and weight. Treatments were applied to two determinate and two indeterminate cultivars and consisted of three different seeding rates, shade at two different periods during reproduction, and manipulation of the canopy during the reproductive period. Biomass of the entire plants and individual pods were measured along with pods per plant. Harvest yields were used to determine how these plant components affected yield. The high seeding rate of 741,000 plants ha\(^{-1}\) resulted in the highest yield of 2623 kg ha\(^{-1}\). Defoliation resulted in a 33% yield decrease when compared to the non-defoliated low seeding rate as it reduced the amount of assimilate available per pod, and caused a reduction in pod number. The effect of shading depended largely on when the shade was applied. While early shading (R1-R5)
caused a drop in yield, it was not as dramatic as late shading (R5-maturity) which reduced yield by 29% compared to the same seeding rate without shade.

The second study examined the effect of shading, defoliation, and seeding rates on source and sink reactions. Treatments were applied to two determinate and two indeterminate cultivars and consisted of three different seeding rates, shade at two different periods during reproduction, and manipulation of the canopy during the reproductive period. Five plants from each treatment were taken at intervals from R5 to maturity. Biomass of entire plants and individual pods were measured along with pods per plant. Asgrow AG5605 was the least source limited at all locations. Treatments that were source limited varied some by locations; however, both the defoliated and non-defoliated low seeding rate, the high seeding rate, and the medium seeding rate shaded late all exhibited source limitations at each location.
Improving Soybean Yield by Identifying Mechanisms and Varieties that Facilitate the Translocation of Starch from Leaves and Stem to the Seed During Periods of Stress

by
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A thesis submitted to the Graduate Faculty of North Carolina State University in partial fulfillment of the requirements for the degree of Master of Science

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DEDICATION

This thesis is dedicated to my parents, Carroll and Kathryn Oakes, and to my girlfriend Krista Casper. Each of these individuals has provided me much encouragement and support throughout this journey, and has admonished me to trust in God and put him first in all things. I would also like to thank my Lord and Saviour Jesus Christ for without Him I could do nothing.
BIOGRAPHY

Joseph Carroll Oakes was born in Kinston, North Carolina to Carroll and Kathryn Oakes on February 4, 1987. He was raised in the small town of Grifton, North Carolina, where he was home-schooled. In 2002, Joseph accepted Jesus Christ as his personal saviour. He graduated from high school in May, 2005. Throughout his high school years, Joseph enjoyed working many hours with his father at a research farm, where developed a love and a passion for agriculture. Joseph graduated from Bob Jones University in May, 2010 with a Bachelor’s degree in Biology and a minor in Business. In the summer of 2010, he began graduate school at North Carolina State University where he began to pursue a Master’s of Science degree under the direction of Dr. Ronnie Heiniger. Upon the completion of his Master’s degree, Joseph plans to continue his education by pursuing a Doctor of Philosophy in Crop Science.
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CHAPTER ONE

The Influence of Shading, Defoliation, and Seeding Rate on Pod Growth and Weight in Determinate and Indeterminate Soybean Cultivars

JOSEPH C. OAKES and RONNIE W. HEINIGER

ABSTRACT

To meet the increasing demand for soybean products, soybean yield must increase substantially over the next several years. Soybean yield is directly related to the number, size, and growth of soybean pods and seeds. Pod growth and size can be influenced by a variety of factors including light, competition for water and nutrients, and defoliation due to disease or insect pests. The objective of this research was to examine the relative effects of shading, defoliation, and seeding rate on pod growth and weight. A two-year study was conducted at three locations in eastern North Carolina to determine the effects of these three factors. Treatments were applied to two determinate and two indeterminate cultivars and consisted of three different seeding rates (49,400, 296,400, 741,000 plants ha\(^{-1}\)), shade at two different periods during reproduction (R1-R5 & R5-R8), thinning the high seeding rate at R5, and defoliating the low seeding rate at R5. Five plants from each treatment were taken at intervals from stage R5 (early seed set) to maturity. Biomass of the entire plants and individual pods were measured along with pod counts. The low seeding rate treatments consistently resulted in the highest weight per plant, pods per plant, and weights per pod. At the high seeding rate, thinned or non-thinned, and at the medium seeding rate, shaded early
or shaded late, there were no differences in weight per plant at any of the locations. While the medium and high seeding rate treatments rarely exhibited differences in pods per plant, there were differences between shading before and after R5. When shading occurred after R5, pods per plant were significantly reduced compared to shading before R5. Weight per pod did not differ significantly between the medium and high seeding rates, or between shading before or after R5. The high seeding rate that was thinned showed an increase in weight per pod at three of the four locations. Harvest yields were used to determine how closely these plant components associated with yield. Even though the high seeding rate of 741,000 plants ha$^{-1}$ resulted in the highest yield of 2622 kg ha$^{-1}$, it consistently had the lowest weights per plant and pods per plant. Defoliation resulted in a 33% yield decrease when compared to the non-defoliated low seeding rate as it reduced the amount of assimilate available per pod, and caused a reduction in pod number. The effect of shading depended largely on when the shade was applied. While early shading (R1-R5) caused a drop in yield, it was not as dramatic as late shading (R5-maturity) which reduced yield by 29% compared to the same seeding rate without shade.

**INTRODUCTION**

Soybean (*Glycine max*) yield in North Carolina has not improved substantially over the last twenty years (United States Department of Agriculture, 2012). The average soybean yield in North Carolina in 1992 was 1816 kg ha$^{-1}$, while the average yield in 2011 was only 2018 kg$^{-1}$. This lack of yield increase can likely be attributed to the impact of environment reducing pod set and seed fill (Egli, 1985). Pod size is directly influenced by assimilate
availability during seed fill which can be affected by a number of different factors including defoliation, competition for light, and seeding rate. While previous research (Fuellman et al., 1994, Egli et al., 1980, Dunphy et al., 2006) showed that defoliation, shading, and seeding rate all had a substantial impact on yield, the objective of this study is to improve the understanding of how these factors impact yield by examining these factors simultaneously under similar growing conditions.

**Soybean Growth Stages**

An understanding of pod set and seed fill starts with a clear understanding of soybean growth and development. Soybean plants can be divided into two major growth stages – the vegetative stage and the reproductive stage (Fehr & Caviness, 1992). The period between emergence and first flower is known as the vegetative stage. This normally takes six to eight weeks (Hoeft et al., 2000). Soybean reproductive development is divided into eight stages, which is based on flowering, pod development, seed development, and maturation. The appearance of a flower anywhere on the plant marks the start of reproductive stage, and is called R1. The plant is in R2 stage when there is an open flower on any of the top four nodes of the main stem (Fehr & Caviness, 1992). At R3 stage, pods are beginning to form, and are 3/16 inch long. The R4 stage is signified by a full pod, and measures ¾ inch long (Fehr et al., 1981). At R5, seed is beginning to form with in the pod and seeds are 1/8 inch long (Fehr & Caviness, 1992). R6 is when the pod has reached full sized seed; the pod contains green seed that fills the pod capacity. The amount of time that it takes from R4 to R6 can be as long as 46 days (Fehr et al., 1977). Pod color is a visual indicator of physiological maturity. When the seed is completely yellow, it is physiologically mature.
R8 – the final stage – is reached when 95% of the pods have their mature color (Fehr et al., 1977). Assimilatory capacity is more important to yield during the reproductive period (R1 to R8) than it is during the vegetative period (Jiang & Egli, 1993). Brun (1978) notes that yield is influenced more by changes in source strength during the pod filling period compared with the emergence to R1 period.

Influence of Cultivar Type on Pod Set and Seed Fill

One of the key differences in soybean cultivars is the growth habit (Fehr & Caviness, 1992). Cultivars which continue to produce vegetative growth after the start of the flowering period are known as indeterminate cultivars; while those that stop growing vegetatively once flowering begins are known as determinate cultivars. There is a general relationship between soybean maturity groups and whether the plant is determinate or indeterminate. Maturity groups 00 through IV generally fall into the indeterminate class, while maturity groups V through IX are generally determinate types (Fehr & Caviness, 1992). Pod development differs dramatically between determinate and indeterminate cultivars. Indeterminate plants have not reached their final height once flowering begins, and continue to grow while the plant is flowering and developing pods (Fehr & Caviness, 1992). Pod and seed development are more advanced on the lower part of the indeterminate plant compared to the upper part. In comparison, determinate cultivars generally reach their full height once flowering begins, and grow little taller after that. Flowering occurs at the same time at both the top and bottom of the plant; thus, pod and seed development are the same throughout the plant.
Defoliation

Adverse growing conditions during critical development phases of soybean can substantially affect yield. One such adverse growing condition is defoliation. There can be several causes of defoliation, but two of the most prominent are hail damage and insect damage. Yield loss from defoliation depends on when the defoliation occurs and the amount of defoliation. Previous research has shown that a specific percentage of defoliation before flowering has less effect on yield than does the same level of defoliation during pod and seed development. Soybeans are capable of withstanding 33-53% defoliation before flowering (R1) with little yield loss (Todd & Morgan 1972). Likewise, Turnipseed (1972) reported that 33% defoliation at flowering (R1) did not result in any significant yield losses. Insects often consume a high percentage of leaves in August and September (Turnipseed, 1972), which is often when the plant is flowering or setting pods. Defoliation from insects or hail during flowering results in a reduced supply of assimilates per pod in the plant (McAlister & Kroeber, 1958). Both 40% and 80% leaf removal at R1 has been shown to cause a definite decrease in the number of mature pods per plant (McAlister & Kroeber, 1958). The 80% leaf removal treatment resulted in many flat pods with aborted seeds, which was undoubtedly due to the reduction in leaf area.

Both indeterminate and determinate cultivars are sensitive to defoliation from the beginning of pod formation (R3) until the seeds have developed their full size (R6) (Fehr et al., 1981). The extent of yield loss depends largely on when the damage is inflicted on the plant. Fuelleman (1944) studied hail damage in soybeans, and found that severe yield reductions resulted from all rates of defoliation during pod formation and filling. However,
as with studies mentioned above, light defoliation during early growth periods and flowering did not suppress yields. Fehr et al. (1981) found that R5 is the most sensitive growth stage for both determinate and indeterminate cultivars in terms of defoliation, and that 100% defoliation resulted in an 80% yield loss. Their results show that yield loss at R4 and R6 were both considerably less than yield loss at R5 (Fehr et al., 1981). In addition, (Fehr et al., 1977) determined that maximum yield loss from 100% defoliation occurred at R5. Turnipseed (1972) looked at defoliations of 17, 33, 50, and 67%. Sixty-seven percent defoliation at R5 caused the greatest loss. Reductions in seed weight were also substantial, but generally corresponded with the yield reductions. These data are inconsistent with those of Thomas, Ignoffo, Biever, & Smith (1974), who determined that maximum yield loss from 100% defoliation occurred at R4. Defoliation of any level once the plant reaches maturity does not cause substantial reductions in yield because the plant is physiologically mature by this point (Thomas et al., 1974). All studies indicate that maximum yield loss is inflicted when defoliation occurs between R4 and R6.

Board, Wier, & Boethel (1994) examined the effects of defoliation during mid to late seed filling, after pod formation, on source/sink ratio. Yields from defoliation at R6.3 and R6.6 were significantly lower than the non-defoliated controls. However, yield was reduced 40% when defoliated at R6.3 compared to 20% loss when defoliated at R6.6 (Board et al., 1994). These findings are consistent with Goli & Weaver (1986), who found that yield loss from defoliation at R6 ranged from 37-44%. Defoliation also significantly affected seed size, but did not significantly affect any other yield component (Board et al., 1994). The soybean adjusts to the reduced assimilatory capacity by reducing the seed size. Board et al. (1994)
concluded that once the pod number has been determined, reductions in the assimilatory capacity have little or no effect on pod abortion or seed per pod. Carbohydrate reserves in the leaves, branches, and stems were unable to compensate for the loss of assimilatory capacity from defoliation; therefore, the seeds were not filled to their full potential (Board et al., 1994).

**Shading**

The number of seeds per unit area is a vital component of yield in soybean (Shibles et al., 1975). Likewise, as mentioned when examining defoliation the number of pods and seeds produced by the soybean plant is related to photosynthesis during flowering (Egli, 2010). Shading is a means to induce stress by reducing photosynthesis (Egli, 1997). Thus, shading may have serious consequences on soybean yield and production. Egli, Leggett, & Cheniae (1980) reported that the shading applied at R5 reduced the demand for photosynthesis by reducing the number of seeds. The primary yield component (seeds) is directly influenced by photosynthesis during the flowering and seed fill period (Egli, 1993). This relationship has been confirmed with numerous shade treatment studies, in which shading reduced the number of surviving pods. Egli & Bruening (2005) examined the effects of differing levels of shade. Sixty percent shade from flowering to maturity reduced pods per plant an average of 24%, while 90% continuous shade reduced pods per plant 71% (Egli & Bruening, 2005). The continuous shading also increased pod abortion. Continuous 90% shade caused approximately 80% of the pods to abort before maturity.
Sixty-three percent shading applied at R6 significantly reduced the yield of both early and late cultivars (Egli, 1997). This reduction in seed size is due to the reduced seed weight for all cultivars. Seed weight reductions were 9% larger for early cultivars than for late cultivars. Shading from R5-maturity has resulted in a 32% yield reduction, which was the result of a 16% reduction in seed size and a 19% reduction in seed number (Egli et al., 1980).

Short periods of reduced photosynthesis from shading do not seem to affect pod production (Egli, 2010). However, the effect on pod production seems to depend on how long the soybeans are shaded. Short-term shade periods (4-9 days) just before or just after pod fill had no significant effect on seed number (Egli, 2010). However, the ability to recover from lost photosynthesis is limited (Egli, 2010). In 2007 and 2008, Egli performed shade removal tests to determine the ability of the soybean plant to recover from short-term reductions in photosynthesis. Fourteen days of shading at the beginning of flowering reduced seed number 16%, and reduction from 28-35 days of shading was essentially the same as continuous shade (Egli, 2010). Pods per plant failed to recover from early shading (R1-mid-flowering) because the early shade did not allow sufficient pods to be produced (Egli & Bruening, 2005). Thus, the plant did not have the ability to overcome the photosynthesis loss induced by short term stress during flowering. In summary, short periods of reduced photosynthesis from shading will probably not reduce yield; however, any amount of shading greater than 14 days will begin to affect yield (Egli, 2010).
Seeding rate

Several previous studies have looked at the impact of soybean seeding rates on yield. Dunphy et al. (2006) found that the impact on yield was based on seeding rate as well as planting date. The yields of seven seeding rates ranging from 123,500 through 494,000 seeds per hectare were not statistically different (between 3154 and 3221 kg ha\(^{-1}\)), when planted in May. However, the lowest seeding rate of 59,280 seeds per hectare yielded only 2798 kg ha\(^{-1}\). When planted in June, lower seeding rates resulted in a more decreased yield compared to the higher seeding rates. Seeding rates of 370,500 to 494,000 seeds ha\(^{-1}\) yielded from 2831 to 2851 kg ha\(^{-1}\). Yields at 123,500 seeds ha\(^{-1}\) decreased to 2475 kg ha\(^{-1}\), while 61,750 seeds per hectare decreased to 1963 kg ha\(^{-1}\). Egli (1988) found that an increase in yield was directly proportional to an increase in plant density.

Similarly, many other studies have shown that a lower seeding rate will have a negative effect on yield at later planting dates. Later planting dates of early maturing cultivars cause the length of the vegetative development of the plant to be shortened, which will lower yield (Egli & Bruening, 2000). Ball et al. (2000) found that vegetative periods are shortened when the soybean is planted late or when an early maturing cultivar is used. Shorter growing seasons present serious time limitations on crop growth, which the soybean needs establish canopy coverage to exploit available light (Ball et al., 2000). Because vegetative period is shortened, the branching ability of these plants is limited. Thus, it is not reasonable to reduce seeding rates without sacrificing yield at later planting dates (Akhter & Sneller, 1996). However, at earlier planting dates or for later maturing cultivars, it may be feasible to reduce seeding rates without decreasing yield (Norsworthy & Frederick, 2002). In
order to maintain high yields at low seeding rates, the plant must increase main stem and branch seed yields to compensate for the reductions in the number of plants. Since it is not feasible to plant a short-season crop at low seeding rates, a higher seeding rate density is required for short season cultivars as well as for later planting dates (Ball et al., 2000).

**Fate of Excess Assimilate Supply in Soybean.**

It is not clear that soybean cultivars can store excess assimilate supply for later use in filling seeds. Seeds represent the primary sink for the assimilate (Hume & Criswell, 1973; Lawn & Brun, 1974). Normal soybean growth is characterized by excess sink demand because the roots, nodules and seeds are all competing for a limited supply of assimilate (Egli et al., 1980). In conditions where there is inadequate sink in relation to the amount of assimilate being produced, starch has been shown to accumulate in the leaves (Mondal et al., 1978). Reduced numbers of seeds will result in a reduced sink demand. Thus, the accumulation of starch in the leaves may result from inadequate sink demand (Egli et al., 1980). Egli (1977) observed that reducing photosynthesis by shading caused a 28% reduction of starch in the leaves (Egli et al., 1980). McAlister and Krober (1958) found that removing 80% of the pods increased sugars, starch and nitrogen in the leaves, which indicates that the leaves serve as storage organs in the absence of a sufficient sink. However, they also found decreased carbohydrate levels in the stems. As a result, it is unclear whether starch accumulation is a result of inadequate sink or some other mechanism (Egli et al., 1980).

While previous studies have looked at individual factors of seeding rate, defoliation, and shading, none of these studies have compared the influence of these factors on
determinate versus indeterminate cultivars, nor have they examined the relative influence these factors under similar growing conditions. The objectives of this research were to 1) determine the influence of defoliation, shading, and seeding rate on plant and pod weight and pods per plant at succeeding growth stages during reproduction and 2) to examine the influence of these factors on yield.

**MATERIALS & METHODS**

**Field Experiment**

Research was conducted at three sites over two years: the Tidewater Research Station in Plymouth, NC (2010 and 2011), the Upper Coastal Plain Research Station in Rocky Mount, NC (2010), and the Caswell Research Station in Kinston, NC (2011). Soil at Plymouth was a Portsmouth fine sandy loam (fine-loamy over sandy or sandy-skeletal, mixed, thermic Typic Umbraquults); soil at Rocky Mount was a Goldsboro fine sandy loam (fine-loamy, siliceous, thermic aquic paleudults); and soil at Kinston was Pocalla loamy sand, 0 to 6 percent slopes (sandy, siliceous, thermic, Arenic Paleudults). In 2010, plots were planted on 3 June at Plymouth and on 22 June at Rocky Mount. In 2011, plots were planted on 26 May at Kinston and on 29 June at Plymouth. Conventional management practices were followed at all locations and over both years. Irrigation was applied as needed at Rocky Mount in 2010 and at Kinston and Plymouth in 2011.

Weed and insect control measures were taken at all location over both years. In 2010 at Plymouth, alachlor was applied PRE at 4.49 kg ai ha$^{-1}$. Glyphosate at 1.54 kg ai ha$^{-1}$ and flumiclorac pentyl ester at 0.97 kg ai ha$^{-1}$ were applied POST on 23 June 2010. For insect
control, indoxycarb was applied at 1.40 kg ai \(^{-1}\) on 11 August 2010. In 2011, alachlor was applied PRE at 4.49 kg ai ha\(^{-1}\). At Rocky Mount, glyphosate was applied PRE at 1.54 kg ai ha\(^{-1}\). Spinosad insecticide was applied at 4.49 kg ai ha\(^{-1}\) on 5 August 2010. At Kinston, imazaquin at 38.17 g ai ha\(^{-1}\) and S-metolachlor at 8.56 g ai ha\(^{-1}\) were applied PRE. Clethodim at 2.25 g ai ha\(^{-1}\) and fomesafen at 2.25 g ai ha\(^{-1}\) was applied POST on 6 June 2011. Thiodicarb insecticide was applied on 16 August 2011 at 3.59 g ai ha\(^{-1}\).

The experimental design consisted of a split plot design with four blocks. Main plots consisted of two indeterminate (Syngenta S47-R3 and Syngenta S49-A5) and two determinate (Asgrow AG5605 and Asgrow DP5915) cultivars. Six seeding rate, defoliation, and shade treatments were used as sub-plots. In 2010, each sub-plot was 4.27 by 12.19 m. In 2011, each sub-plot was 3.05 by 12.19 m.

Treatment 1 was a low seeding rate which consisted of 49,400 seeds ha\(^{-1}\). Treatment 2 was a high seeding rate which consisted of 741,000 seeds ha\(^{-1}\). Treatment 3 involved thinning the high seeding rate to 49,400 seeds ha\(^{-1}\) at R5. Treatment 4 consisted of defoliating the low seeding rate at R5. Approximately 50% of the leaf area in the upper canopy was defoliated. Treatment 5 consisted of shading the medium (296,400) seeding rate from R1-R5. Shade cloth was applied over plots and shaded out 50% of the sunlight. Treatment 6 entailed shading the medium seeding rate from R5-maturity.

Treatments were applied at each site within each year according to the following schedule. At Plymouth in 2010, early shade (Treatment 5) was applied on 23 July and 29 July to maturity groups IV and V respectively; while late shade (Treatment 6) was applied on 21
August and 30 August. Both defoliation (Treatment 4) and thinning (Treatment 3) were applied on 10 August and 26 August to maturity groups IV and V respectively. At Rocky Mount in 2010, early shade was applied on 28 July and 9 August to maturity groups IV and V respectively; while late shade was applied on 1 September and 8 September. Both defoliation and thinning were applied on 1 September and 8 September to groups IV and V respectively. At Plymouth in 2011, early shade was applied on 11 August and 2 September to maturity groups IV and V respectively; while late shade and thinning were applied on 2 September and 15 September. At Kinston in 2011, early shade at R5 was applied on 6 July and 14 July to maturity groups IV and V respectively; while late shading, defoliation, and thinning were all applied on 4 August and 18 August to maturity groups IV and V.

Samples consisted of five plants and were taken from each sub-plot starting at R5. At Plymouth, group IV samples were taken on 9, 20, 27 August, 16 September, and 8 October 2010; group V samples were taken on 20, 27 August, 16 September, and 8 October 2010. In 2011, group IV samples were taken on 6, 20 September, 4, and 25 October 2011; group V samples were taken on 20 September, 4, and 25 October 2011. Rocky Mount group IV samples were taken on 24 August, 8 September, and 8 October 2010. Group V samples were taken 8 September, 8 October, and 20 October 2010. Kinston group IV samples were taken on 8 August, 31 August, and 22 September 2011. Group V samples were taken on 31 August, 8 September, 22 September, and 4 October 2011. Pods were removed from each plant and were counted. Plant biomass and pods were dried for at least 48 hours and weighed. Weight per plant, pods per plant, and weights per pod were calculated for each sample.
In 2010, plots were harvested at Plymouth on 18 October (group IV) and 2 November (group V), and on 15 November at Rocky Mount. In 2011, the plots were harvested at Kinston on 27 October and on 11 November and Plymouth. Plots were harvested using a Gleaner K2 combine equipped with a Harvestmaster Grainage, which measured grain weight, test weight and moisture. Grain weights were adjusted to 15% moisture. Only the front 9.14 meters of the plots were harvested. Samples were taken from the back 3.05 meters of the plots; therefore, this section of the plots and the border rows were removed before harvesting.

**Statistical Procedures**

Differences in the number of samples taken at each location and environmental conditions at the three locations over two years made it impossible to perform a combined analysis across locations. Furthermore, differences in sampling dates precluded performing an analysis across both determinate and indeterminate cultivars at each location. Therefore, at each location, weight per plant, weight per pod, and pods per plant for each treatment within the two determine and two indeterminate cultivars were analyzed using a time series approach with sampling date as the main factor, cultivar as the subplot, and treatment as the sub-subplot. Proc Mixed in SAS was used to identify differences among main, subplot and sub-subplot treatments and interactions with sampling date, cultivar and treatment considered fixed effects and block and all interactions with block considered random effects. When differences were found, Fischer’s protected LSD was used to separate individual differences. Seed yield was analyzed using a split plot approach with cultivar as the main plot and treatment as the subplot. Proc mixed was used to identify significant effects and interactions.
with cultivar and treatment treated as fixed effects and block and all block interactions treated as random effects. Fischers’ protected LSD was used to identify differences among cultivars and treatments.

**Climate 2010 & 2011**

Rainfall amounts and temperature measurements were taken at all locations in each of the two years and recorded by the State Climate Office in North Carolina. Rainfall and temperature data were analyzed for each two week period during sampling. These measurements were compared with the 30 year normal as reported by the State Climate Office of North Carolina.

**Plymouth 2010.** During three of the five two week periods at Plymouth in 2010, the average temperature was two degrees higher than the thirty year average (Table 6). Total precipitation was lower for every period except for two: 15 August to 28 August and 26 September to 9 October. From 15 August to 28 August, the total precipitation was 7.59 cm compared to the 30 year average of 6.43 cm. From 26 September to 9 October, the total rainfall was 40.61 cm while the 30 year average was 5.16 cm.

**Rocky Mount 2010.** At Rocky Mount, the average temperature was higher than the 30 year average at every two week period except for one (Table 7). Total precipitation was lower than the 30 year average from planting to harvest, except for the period from 14 September to 11 October, when rainfall exceeded the thirty year average.
Plymouth 2011. Average temperatures during sampling at Plymouth in 2011 closely resembled the 30 year average except from 19 October to 1 November when the average temperature was below the 30 year average (Table 8). Due to Hurricane Irene, total precipitation from 24 August to 6 September was 35.81 cm compared to the 30 year average of 5.08.

Kinston 2011. There were no striking differences in temperature at Kinston in 2011 (Table 9). Precipitation was generally less than the 30 year average, except during the month of August. From 4 August to 17 August, total precipitation was 14.38 cm compared to the 30 year average of 6.02. Hurricane Irene caused 42.09 cm of precipitation from 18 August to 31 August compared to the 30 year average of 6.30 cm.

RESULTS

Weight per Plant

Indeterminate Cultivars. Plymouth 2010 was the only location with significant date by treatment and variety by treatment interactions for weight per plant. In addition, the date, variety, and treatment main effects were significant (Table 1). Across sampling dates, there were significant differences in weight per plant among both the low seeding rate treatments (Treatments 1 & 4) and the medium and high seeding rate treatments. There were no significant differences among the medium and high seeding rate treatments.

As for the defoliation, shading, and thinning treatments, there was a significant difference between the defoliated and non-defoliated low seeding rate treatment at all but the
first and third sampling dates (Figure 1). In comparison, neither early shading from R1 to R5 nor late shading at R5 of the medium seeding rate resulted in statistical differences in plant weight. Thinning of the high seeding rate at growth stage R5 did not increase weight per plant at any of the sampling dates compared to the high seeding rate treatment alone. Overall, weight per plant did not change across dates except in the low seeding rate and low seeding rate defoliated treatments. At the low seeding rate treatment, weight per plant was significantly higher at the first and fourth sampling date compared to the other three dates. In the low seeding rate defoliated treatment, the second and third sampling date had significantly less biomass than at the first, fourth, and fifth sampling dates.

There were differences between S47-R3 and S49-A5 in the low seeding rate treatments either defoliated or non-defoliated. In both treatments, S49-A5 had more biomass than S47-R3. At the low seeding rate, S49-A5 produced 494 grams per plant biomass compared to 321 grams in S47-R3. In the defoliated low seeding rate, S49-A5 produced 408 grams per plant compared to 310 grams per plant in S47-R3 (Figure 2).

There were no interactions for weight per plant within the indeterminate cultivars at any of the other three locations (Rocky Mount 2010, Plymouth, 2011, and Kinston 2011) (Tables 2, 3, 4). At these locations different combinations of date, treatment and variety main effects were significant. At both Rocky Mount and Kinston, the low seeding rate treatments either non-defoliated (Rocky Mount) or both defoliated and non-defoliated (Kinston) had significantly greater weight per plant than medium or high seeding rate treatments (Table 10). At Rocky Mount there were no differences in weight per plant among the medium and high seeding rate treatments; while at Kinston there was a significant
difference in weight per plant between the low seeding rate shaded early from R1 to R5 and the high seeding rate treatment (124.6 and 62.1 g plant\(^{-1}\), respectively). At both locations, defoliation significantly reduced weight per plant compared to the low seeding rate without defoliation; while shading and thinning did not reduce weight per plant when compared with the corresponding medium or high seeding rate treatments.

The low seeding rate treatments at Plymouth in 2011 were severely damaged by Hurricane Irene. Therefore, the low seeding rate treatments with and without defoliation (Treatments 1 and 4) in all four cultivars were removed from the analysis at this location. Variety, date, and treatment main effects were all significant. There were clear differences in weight per plant between the medium and high seeding rates (Figure 7). Early shading from R1 to R5 had little effect on weight per plant. In comparison, shading from R5 and maturity caused a significant drop in weight per plant. Thinning the high seeding rate did not increase weight per plant.

The date effect at Rocky Mount was caused by a significant increase in biomass between the second and the third sampling periods (Table 13). However, there was no significant difference between the first and second sampling periods.

**Determinate Cultivars.** Maturity group V determinate cultivars showed no interactions of date by variety, variety by treatment, or date by treatment in weight per plant at either location in 2010 (Table 1 and 2). However, in 2011, at Plymouth there were interactions for all three (date by treatment, date by variety, and variety by treatment) and at Kinston in 2011 there was a variety by treatment interaction (Table 3 and 4). The main effects of variety, date,
and treatment were significant at Plymouth both years. Treatment and date main effect were significant at Rocky Mount (Table 2), while at Kinston variety and treatment main effects were significant.

At Plymouth in 2010, differences in weight per plant among seeding rates were mainly due to differences among treatments (Table 10). The low seeding rate treatments (non-defoliated or defoliated) produced more biomass than the medium or high seeding rate treatments (446.5 & 340.9 g plant$^{-1}$, respectively). In turn, medium seeding rate treatments (shaded early or late) had significantly more biomass than the high seeding rate treatments (173.7 & 205.0 g plant$^{-1}$). There was a significant difference between the low seeding rate treatments in which the non-defoliated had significantly more biomass than the defoliated treatment. However, there were no significant differences in the medium seeding rates between shading early and shading late, nor was there any significant difference within the high seeding rates between the plots that were thinned and those that were not. Among dates, there was a significant increase in plant weights at the third sampling date, compared to the other three dates where there was no significant change. The trend suggested that weight per plant increased rapidly between the second and third date and then decreased as leaves started to senesce (Table 13). There was a significant difference in plant weight between cultivars. Asgrow DP 5915 had greater weight per plant compared with AG5605 (251.9 & 214.8 g plant$^{-1}$, respectively).

At Rocky Mount, there was no significant difference in biomass between the medium and low seeding rates (Table 10). However, the high seeding rate treatments had significantly less biomass than either the medium and low seeding rate treatments. Defoliation, shading,
and thinning caused no significant change in biomass. Biomass generally increased across dates (Table 12). There was a significant increase between the first and third sampling periods, but there was no significant increase between the first and second or second and third sampling period.

Differences at Plymouth in 2011 were again the result of seeding rate. The high seeding rate treatments had significantly less biomass compared with the medium seeding rate treatments (Figure 8). Shading from R5 to maturity significantly decreased biomass compared to shading from R1 to R5. Thinning had no effect on biomass.

There was a variety by treatment interaction for biomass among the determinate cultivars at Kinston. The corresponding treatment and variety main effects were also significant. Asgrow DP5915 planted at the low seeding rate had a significantly greater weight per plant (1124 g plant\(^{-1}\)) compared with any other treatment within the same cultivar or with any treatment applied to Asgrow AG5605 (Figure 10). Asgrow AG5605 planted at the low seeding rate and DP5915 where the low seeding rate was defoliated had similar weights per plant and both treatments had significantly greater weights per plant than any other variety by treatment combination other than DP5915 planted at the low seeding rate. Asgrow AG5605 treated by defoliating the low seeding rate had significantly greater weight per plant compared to all of the medium and high seeding rate treatments. However, there were no significant differences in weight per plant among the medium and high seeding rate treatments within either cultivar.
The trend in the variety by treatment interaction aptly describes the pattern in treatments across cultivars with the non-defoliated low seeding rate treatment having significantly greater weight per plant compared to the remaining treatments and the defoliation of the low seeding rate at R5 having significantly greater weight per plant compared to any of the medium or high seeding rate treatments. Again, there were no significant differences among any of the medium or high seeding rate treatments. Asgrow DP5915 had significantly greater weight per plant than the Asgrow AG5605 (375.6 vs. 323.4 g plant\(^{-1}\)).

**Pods per Plant**

*Indeterminate Cultivars.* The date by treatment interactions were significant at Plymouth in 2010 and Kinston in 2011 (Table 1 and 4). Date and treatment main effects were significant at all four locations, and the variety main effect was significant at Plymouth in 2011 (Table 3).

At both Plymouth 2010 and Kinston 2011, the low seeding rate treatments had significantly higher pods per plant at most sampling dates with the exception of Plymouth where there were no differences among treatments at the initial sampling date (Figure 3 &11). However, at Plymouth there was no difference at the initial sampling date. There were no significant differences among the medium and high seeding rate treatments among any of the sampling periods at either location. As expected, defoliation caused a significant drop in the number of pods per plant at the fourth sampling period at Plymouth in 2010. At Kinston, defoliation had no impact on the number of pods per plant.
Across dates, pods per plant at Plymouth 2010 and Kinston increased in the low seeding rate treatments, but not in the medium or high seeding rate treatments. In the low seeding rate non-defoliated treatment, pods per plant increased significantly until the last sampling period. It is unclear why the number of pods per plant declined at this final sampling period. In the defoliated low seeding rate at Plymouth 2010, pods per plant increased from the first through the third sampling period, but then leveled off and remained constant across the last two sampling dates.

At Rocky Mount 2010 (Table 2) and Plymouth 2011 (Table 3), both date and treatment main effects were significant. Across dates, pods per plant generally increased at both locations (Table 13). Between the first and second sampling periods, pods per plant increased significantly at both locations. However, after the second sampling period, pods per plant remained constant and eventually decreased at Plymouth.

Treatment response was nearly identical at both locations (Table 11). Both high seeding rate treatments had fewer pods per plant than did the medium seeding rate treatments. At Rocky Mount 2010, the non-defoliated low seeding rate was not significantly different from the medium seeding rate treatments; but, surprisingly, the defoliated treatments resulted in the highest number of pods per plant compared to the remaining treatments. Shading of the medium seeding rate either early or late and thinning had no impact on pods per plant. Syngenta S47-R3 had more pods per plant compared to Syngenta S49-A5 at Plymouth 2011.
Determinate Cultivars. Date by treatment interactions for pods per plant were found at Plymouth in both years and at Kinston in 2011 (Table 1, 3, and 4). In addition, Plymouth in 2011 had a variety by treatment interaction. All locations had significant date and treatment main effects, except for Kinston which only had a treatment effect. Plymouth 2011 was the only location with a significant variety effect.

At both Plymouth 2010 and Kinston 2011, the low seeding rate had significantly more pods per plant at either most (Plymouth 2010) or all (Kinston 2011) sampling dates. At Kinston, pods per plant did not differ among the medium and high seeding rate treatments. However, at Plymouth 2010, at all except the first sampling date, at least one of the medium seeding rate shade treatment had significantly more pods plant compared to either of the high seeding rate treatments. (Figure 3).

At Plymouth in 2010, defoliation and shading had significant impacts on pods per plant. Defoliation reduced pods per plant at all except for the first sampling date, which occurred before defoliation treatment was applied. Early shading caused an initial drop in pods per plant, while late shading caused a significant drop in the number of pods per plant at the last sampling date. This supports the work of Egli et al. (1980) who reported that shade reduced the demand for photosynthesis by reducing the number of seeds per plant. As in the group IV cultivars, thinning did not have a significant effect on the number of pods per plant. At Kinston, defoliation caused a significant decrease in pods per plant across all sampling dates, but thinning and shading had no effect.
At Plymouth in 2010, pods per plant in the low seeding rate treatments increased across the first three sampling periods but remained constant between the third and fourth period. However, unlike the group IV cultivars, there was a significant increase in pods per plant in the medium seeding rates between the initial and the third sampling period. A key difference across dates occurred in the medium seeding rate treatment where shading was applied at R5. The number of pods per plant declined significantly after the third sampling period compared to the plots that were shaded early in which there was no significant decline. In the high seeding rate treatments, pods per plant increased between the first and second sampling periods but remained constant through the final two sampling periods.

Across sampling dates at Kinston in 2011, there was a significant decrease in pods per plant from the first to the second sampling date in both low seeding rate treatments (Figure 11). Pods per plant did not change significantly among the last three sampling dates in the low seeding rate treatment that was not defoliated, but in the defoliated treatment pods per plant continued to decline significantly between the second and last sampling dates. Pods per plant did not change across sampling dates in the medium and high seeding rate treatments. The extremely dry weather during the first six weeks after planting (Table 5) probably caused significant pod abortion and this effect was magnified by the defoliation of the plants; whereas the medium and high seeding rate treatments started with significantly fewer pods and were not affected by the dry weather.

At Rocky Mount 2010 (Table 2), only the date and treatment main effects for pods per plant were significant. Surprisingly, the defoliated low seeding rate resulted in the highest pods per plant compared with any other treatment (Table 11). There were no significant
differences between the non-defoliated low seeding rate and either of the medium seeding rate treatments. Both the thinned and non-thinned high seeding rates had significantly lower pods per plant than any of the other treatments. Across dates, pods per plant increased significantly between the first and third sampling period (Table 13). However, there was no significant difference between the second and third sampling periods.

At Plymouth 2011, there were date by treatment and variety by treatment interactions for pods per plant and the corresponding treatment, variety, and date main effects were significant (Table 3). In general, across sampling dates, the medium seeding rate treatments of early and late shading had significantly more pods plant$^{-1}$ than the high seeding rate treatments (Figure 9). The two sampling dates with the most pods plant$^{-1}$ were shaded from R1 to R5. However, the early shading treatments at some sampling dates did not differ from the treatments shaded from R5 to maturity. Across dates, there were no significant differences in pods per plant between the high seeding rate and the high seeding rate thinned to the lower seeding rate at R5. While samples taken on 20 September (earliest sampling date) tended to have more pods per plant across most treatments, overall there was not a clear trend among sampling dates nor were there clear differences between cultivars over sampling dates.

A variety by treatment interaction was significant at Plymouth in 2011(Figure 10). In both varieties, the low seeding rate treatments had the lowest pods per plant. Medium seeding rate treatments were significantly higher for both varieties. Asgrow AG5605 shaded early had the highest number of pods per plant.
Weight per Pod

*Indeterminate Cultivars.* Plymouth 2010 was the only location to have any date by treatment and variety by treatment interactions for weight per pod (Table 1). All locations had date and treatment main effects, except for Rocky Mount 2010 which only had a significant date main effect (Tables 2, 3, and 4).

At Plymouth in 2010, significant differences were noted in weight per pod among the three seeding rates at the first three sampling periods (Figure 4). However, at the fourth sampling period, the two medium seeding rate treatments and the non-thinned high seeding rate had significantly lower weight per pod than the other three treatments. At the last sampling period, the late shaded medium seeding rate treatment had the lowest weight per pod. This indicates the negative effect of the late shading. The high seeding rate had the next lowest weight per pod at the last sampling period. Thinning the high seeding rate increased the weight per pod significantly compared to the non-thinned high seeding rate.

In general, weights per pod increased across dates. However, weights per pod did remain constant between the second and third sampling periods at Plymouth in 2010. As expected, weights per pod in late shaded plots increased significantly until the last sampling period. The late shading reduced weights per pod at the final sampling period.

The variety by treatment interaction was mainly the result of differences between cultivars. In both the defoliated and non-defoliated treatments and in the medium seeding rate shaded early, S49-A5 had significantly greater weight per pod than did S47-R3. For the remaining treatments, there were no significant differences between the two cultivars.
Surprisingly, in both cultivars, there were no significant differences in weight per pod between the defoliated and non-defoliated plots. Shading early resulted in a higher weight per pod than shading late when S49-A5 was grown; however, when S47-R3 was grown there were no differences in shading dates. Thinning increased weights per pod in S49-A5, but not in S47-R3.

At Rocky Mount, there was only a date main effect. No significant increase was noted between the first and second sampling periods; however, there was a significant increase in individual weight per pod between the second and third sampling periods (Table 13).

Both Kinston and Plymouth in 2011 had significant date and treatment main effects. At Kinston, both low seeding rate treatments had a significantly higher weight per pod than the remaining treatments (Table 12). There was no significant difference between medium or high seeding rates, and shading or thinning did not have any impact weight per pod. The non-thinned high seeding rate had the highest weight per pod at Plymouth 2011 (Table 12).

Across the first three sampling periods, individual pod weights increased significantly at Plymouth in 2011 (Table 13). However, weights per pod remained constant between the third and fourth sampling period. Weight per pod did not change significantly between the first two sampling dates at Kinston (Table 13). However, weight per pod increased significantly among the first two sampling dates and the last sampling date (0.115 and 0.062 g pod\(^{-1}\) compared to 0.348 g pod\(^{-1}\)).

**Determinate Cultivars:** Both Plymouth 2010 and Kinston 2011 had date by treatment interactions (Tables 1 & 4). Plymouth 2010 also had variety by treatment and date by variety
by treatment interactions. Rocky Mount 2010 had a date by variety interaction and a date main effect, while Plymouth 2011 only had significant date and treatment main effects (Tables 2 and 3).

At both Plymouth 2010 and Kinston 2011, the non-defoliated low seeding rate resulted in the highest weight per pod at the last sampling periods (Figure 4 & 11). At Plymouth, there was no significant difference between any of the other treatments. Defoliation at Kinston caused a significant decline in weight per pod. The high seeding rate and the late shaded medium seeding rate treatments had the lowest weights per pod at Kinston. Weights per pod generally increased significantly across sampling periods at both locations (Figure 4 & 11). However, at Plymouth 2010, Weights per pod remained constant across the first two sampling dates. At both locations, weights per pod in the defoliated plots decreased at the latter sampling periods probably as a result of lack of assimilates due to reduced photosynthesis. The variety by treatment interaction at Plymouth 2010 was the result of both the AG5605 and DP5915 low seeding rate treatments having a significantly greater weight per pod when compared with the rest of the treatments.

Across dates at Rocky Mount in 2010, weight per pod in both varieties generally increased (Figure 6). Weight per pod in both varieties increased significantly between the first and second sampling period. However, AG 5605 remained constant between the second and third sampling period. Weight per pod in Asgrow DP5915 increased significantly across all three sampling periods. The only difference between varieties was at the first sampling period, in which AG5605 had a significantly higher weight per pod. There were no significant differences in weights per pod among most of the treatments (Table 12). Only the
non-thinned high seeding rate treatment had a significantly lower weight per pod compared with the remaining treatments.

Only date and treatment main effects were significant at Plymouth in 2011. The medium seeding rate that was shaded early had the highest weight per pod (Table 12). Late shaded plots had significantly lower weight per pod than did the early shaded plots. The two high seeding rate treatments had the lowest weights per pod, and thinning had no effect. Weights per pod increased significantly across all three sampling periods (Table 13).

**Yield**

There were no variety by treatment interactions at any of the four locations. Only the treatment main effect was significant.

*Plymouth 2010.* The high seeding rate of 741,000 seeds ha\(^{-1}\) resulted in the highest yield compared with the other treatments (Figure 14). In comparison, the high seeding rate thinned resulted in the lowest yield among treatments. This is to be expected because plants were simply removed, and the remaining plants could not compensate by increasing pods per plant or weight per pods. There was no difference in yield between the two medium seeding rate shading treatments; however, both were significantly lower than the highest yielding treatment. As expected, defoliation caused a significantly lower yield than every other treatment except for thinning.

*Rocky Mount 2010.* Yield response at Rocky Mount was comparable to that at Plymouth. However, due to lack of rainfall and poor conditions, overall yields were much
lower. As expected, thinning and defoliation resulted in the two lowest yields (Figure 15).

Surprisingly, early shading yielded the same as both the low and high seeding rate treatments. Unlike Plymouth results, late shading had significantly less yield than did the early shading. Undoubtedly, the lack of rainfall and poor growing conditions at Rocky Mount had an impact on both plant and pod growth. This may explain some of the surprising differences among the treatments.

_Plymouth 2011_. Due to the late planting date, soybean yield at Plymouth was uncharacteristically low (Figure 16). While the high seeding rate resulted in the highest yield, it was not significantly different when compared to the early shaded treatment. However, both the late shaded and thinned plots had significantly lower yields than any of the other treatments applied at this location.

_Kinston 2011_. As with the other locations, the high seeding rate yielded the highest (Figure 17). As expected, thinning and defoliation resulted in the two lowest yields. Late shading resulted in a significantly lower yield than did early shading. The lower yield in the treatment that was shaded at R5 is the result of the lower individual pod weight that was noted previously. The lower weight per pod is a result of the shade being applied during the effective fill period. While thinning did increase weight per pod, the fact that plants were removed reduced yield when compared to the other treatments.
DISCUSSION

Weight per Plant

Several similarities were noted in weight per plant based on the treatment that was imposed. Seeding rate was a key factor in plant weight. As expected, the low seeding rate treatments always had the highest weight per plant, and significant differences at probability level 0.05 were often observed between medium and high seeding rates at all but two locations. Indeterminate cultivars at Plymouth in 2010 and determinate cultivars at Kinston in 2011 showed no significant difference between medium and high seeding rates. Defoliation was the next most important factor affecting plant weight. Defoliated plants were never able to recover from the lost biomass when it occurred at R5. In contrast, shading often had little or no effect on weight per plant. The effect of shading depended on when the shade was applied. Early shading caused had little impact on the final weight per plant. At some locations, early shading caused an initial decrease in plant weight. However, once the shade was removed biomass increased as the plants recovered. Late shading caused decreases in biomass at later sampling dates due to the fact that the plants had no opportunity to recover. Thus, later shading had more of a negative impact on weight per plant than did early shading. Thinning had no effect on weights per plant, except at Plymouth in the indeterminate cultivars in 2010.

Pods per Plant

As was the case with weight per plant, there were clear seeding rate differences in pods per plant with low seeding rates having the highest number of pods per plant and high
seeding rate treatments having the lowest. Only the indeterminate cultivars at Plymouth in 2010 and determinate cultivars at Kinston in 2011 showed no significant difference in pods per plant between medium and high seeding rates. As with weight per plant, defoliation caused a severe drop in pods per plant across all locations. Defoliation consistently caused a 25% or greater drop in pods per plant when compared to the non-defoliated low seeding rate treatment. These observations confirm several previous studies regarding timing of defoliation. Fehr et al. (1981) found that both indeterminate and determinate cultivars are most sensitive to defoliation from the beginning of pod formation until seeds have developed full size.

As was the case with weight per plant, the influence of shading depended on when the shade was present. Early shading had a minimal on final pods per plant. When early shading did cause an initial drop in pods per plant, they recovered once the shade was removed. Late shading caused a significant drop in pods per plant at the later sampling dates. Thus, shade applied during the effective fill period resulted in more negative consequences than did shade applied before pod fill. Only at Kinston in 2011 was there a significant effect from thinning, as it resulted in higher pods per plant in the determinate varieties.

Weight per Pod

Along with pod per plant, weight per pod is a vital factor in determining soybean yield. As with the other plant or yield components, a clear seeding rate difference was observed with the low seeding rate treatments having the highest weight per pod. Defoliation caused weights per pod to be significantly lower than in non-defoliated plots. McAlister &
Kroeber (1958) observed similar results and found many flat pods with aborted seeds on defoliated plants. Across all four locations in both years, early shading had no effect on weight per pod. This is due to the fact that the shade was removed before the effective fill period began. Thinning did show a significant increase in weight per pod at three of the four locations. Removing competition by eliminating neighboring plants explains why weights per pod did increase.

**Yield**

The influence of weight per plant, pods per plant, and weight per pod are important factors in determining yield. However, it is clear from the results of this study that the soybean plant does not always compensate for low numbers of plants per hectare. The high seeding rate treatment had the highest yield at all four locations across both years. Even though the low seeding rate treatment consistently had the highest pods per plant and weight per pod, there was simply not enough compensation within these components to overcome the lack of plants per hectare. As expected, defoliation resulted in the lowest yields at all locations. At Kinston, defoliation resulted in a 53% yield loss. This confirms the findings of Fehr et al. (1981), who noted that R5 was the most sensitive stage for yield loss. The impact of shading depended on when the shade was applied. Early shading had little negative affect on yield, because shade was removed before pod fill began. Shading from R5-maturity caused more of a negative impact on yield, because the shade was present during the pod fill period. At Kinston, the early shaded plots yielded 24% more than did the later shaded plots. However, there was no significant difference between the early shaded treatment and the highest yielding high seeding rate at three of the four locations. Thinning resulted in as much
as a 52% yield loss. Remaining plants were unable to increase the number of pods per plant and weight per pod enough to compensate for the lack of plants.
REFERENCES


Table 1. Analysis of variance for weight per pod, pods per plant, and weight per pod at Plymouth in 2010. *, **, *** indicate significance at the 0.05, 0.01, and 0.001 significance level

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<td>***</td>
<td>12</td>
</tr>
</tbody>
</table>
Table 2. Analysis of variance table for weight per plant, pods per plant and weight per pod at Rocky Mount in 2010. *, **, *** indicate significance at the 0.05, 0.01, and 0.001 significance level

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Maturity Group IV</th>
<th>Maturity Group V</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Weight per Plant</td>
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<tr>
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<tr>
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</tr>
<tr>
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<tr>
<td>variety*treatment</td>
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<tr>
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</tr>
<tr>
<td>block*date</td>
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<tr>
<td>treatment</td>
<td>5</td>
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</tr>
<tr>
<td>date*treatment</td>
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</tr>
<tr>
<td>date<em>variety</em>treatment</td>
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</tr>
<tr>
<td>block*variety (date)</td>
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</tbody>
</table>
Table 3. Analysis of variance table for weight per plant, pods per plant, and weight per pod at Plymouth in 2011. *, **, *** indicate significance at the 0.05, 0.01, and 0.001 significance level

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>DF</th>
<th>Weight per Plant</th>
<th>Pods per Plant</th>
<th>Weight per Pod</th>
<th>DF</th>
<th>Weight per Plant</th>
<th>Pods per Plant</th>
<th>Weight per Pod</th>
</tr>
</thead>
<tbody>
<tr>
<td>date</td>
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<td>*</td>
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<td>*</td>
<td>***</td>
</tr>
<tr>
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<td>*</td>
<td>***</td>
<td>NS</td>
<td>1</td>
<td>***</td>
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<td>NS</td>
</tr>
<tr>
<td>date*variety</td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>2</td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
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</tr>
<tr>
<td>treatment</td>
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<td>***</td>
<td>***</td>
<td>***</td>
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<tr>
<td>date*treatment</td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>6</td>
<td>***</td>
<td>**</td>
<td>NS</td>
</tr>
<tr>
<td>date<em>variety</em>treatment</td>
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<td>NS</td>
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</table>
Table 4. Analysis of variance table for weight per plant, pods per plant, and weight per pod at Kinston in 2011. *, **, *** indicate significance at the 0.05, 0.01, and 0.001 significance level

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Maturity Group IV</th>
<th>Maturity Group V</th>
<th>Maturity Group IV</th>
<th>Maturity Group V</th>
</tr>
</thead>
<tbody>
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<td>DF</td>
<td>Weight per Plant</td>
<td>Pods per Plant</td>
<td>Weight per Pod</td>
</tr>
<tr>
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<td>NS</td>
</tr>
<tr>
<td>date*variety</td>
<td>2</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>variety*trmt</td>
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<td>NS</td>
<td>NS</td>
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<td>***</td>
</tr>
<tr>
<td>block*date</td>
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<td>**</td>
<td>NS</td>
<td>***</td>
</tr>
<tr>
<td>trmt</td>
<td>5</td>
<td>***</td>
<td>***</td>
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<tr>
<td>date*trmt</td>
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<td>NS</td>
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<td>NS</td>
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<td>block*variety</td>
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Table 5. Average temperatures and precipitation over two week periods during the reproductive growth stages at Plymouth in 2010 compared with 30 year normals

<table>
<thead>
<tr>
<th>Period</th>
<th>Average Temp.</th>
<th>30 yr. avg. Temp.</th>
<th>Total Precip.</th>
<th>30 yr. avg. Precip</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 June - 17 June</td>
<td>80.83</td>
<td>74.87</td>
<td>1.59</td>
<td>2.50</td>
</tr>
<tr>
<td>18 June - 2 July</td>
<td>82.13</td>
<td>77.93</td>
<td>1.00</td>
<td>2.55</td>
</tr>
<tr>
<td>3 July - 17 July</td>
<td>80.20</td>
<td>79.87</td>
<td>2.32</td>
<td>2.55</td>
</tr>
<tr>
<td>18 July - 31 July</td>
<td>83.14</td>
<td>80.07</td>
<td>1.01</td>
<td>2.42</td>
</tr>
<tr>
<td>1 August - 14 August</td>
<td>81.82</td>
<td>79.14</td>
<td>1.96</td>
<td>2.52</td>
</tr>
<tr>
<td>15 August - 28 August</td>
<td>79.50</td>
<td>77.57</td>
<td>2.99</td>
<td>2.53</td>
</tr>
<tr>
<td>29 August - 11 September</td>
<td>75.00</td>
<td>75.79</td>
<td>0.48</td>
<td>2.53</td>
</tr>
<tr>
<td>12 September - 25 September</td>
<td>74.89</td>
<td>72.50</td>
<td>0.45</td>
<td>2.38</td>
</tr>
<tr>
<td>26 September - 9 October</td>
<td>66.71</td>
<td>67.57</td>
<td>15.99</td>
<td>2.03</td>
</tr>
<tr>
<td>10 October - 23 October</td>
<td>64.07</td>
<td>62.50</td>
<td>0.61</td>
<td>1.72</td>
</tr>
<tr>
<td>24 October - 5 November</td>
<td>62.08</td>
<td>58.54</td>
<td>1.75</td>
<td>1.43</td>
</tr>
</tbody>
</table>
Table 6. Average temperatures and precipitation over two week periods during the reproductive growth stages at Rocky Mount in 2010 compared with 30 year normals

<table>
<thead>
<tr>
<th>Period</th>
<th>Average Temp</th>
<th>30 yr. avg. Temp</th>
<th>Total Precip</th>
<th>30 yr. avg. Precip</th>
</tr>
</thead>
<tbody>
<tr>
<td>22 June - 5 July</td>
<td>80.33</td>
<td>77.57</td>
<td>0.27</td>
<td>2.04</td>
</tr>
<tr>
<td>6 July - 19 July</td>
<td>82.82</td>
<td>79.29</td>
<td>0.97</td>
<td>2.24</td>
</tr>
<tr>
<td>20 July - 2 August</td>
<td>82.79</td>
<td>79.43</td>
<td>0.68</td>
<td>2.15</td>
</tr>
<tr>
<td>3 August - 16 August</td>
<td>82.64</td>
<td>78.14</td>
<td>1.64</td>
<td>1.89</td>
</tr>
<tr>
<td>17 August - 30 August</td>
<td>79.56</td>
<td>76.36</td>
<td>1.82</td>
<td>2.06</td>
</tr>
<tr>
<td>31 August - 13 September</td>
<td>74.77</td>
<td>74.00</td>
<td>0.42</td>
<td>2.54</td>
</tr>
<tr>
<td>14 September - 27 September</td>
<td>76.76</td>
<td>70.14</td>
<td>3.00</td>
<td>2.49</td>
</tr>
<tr>
<td>28 September - 11 October</td>
<td>64.54</td>
<td>65.07</td>
<td>5.24</td>
<td>1.79</td>
</tr>
<tr>
<td>12 October - 25 October</td>
<td>62.22</td>
<td>60.07</td>
<td>0.62</td>
<td>1.22</td>
</tr>
<tr>
<td>26 October - 8 November</td>
<td>55.79</td>
<td>56.29</td>
<td>0.63</td>
<td>1.18</td>
</tr>
<tr>
<td>9 November - 15 November</td>
<td>50.99</td>
<td>53.43</td>
<td>0.00</td>
<td>0.63</td>
</tr>
</tbody>
</table>
Table 7. Average temperatures and precipitation over two week periods during the reproductive growth stages at Plymouth in 2011 compared with 30 year normals

<table>
<thead>
<tr>
<th>Period</th>
<th>Average Temp.</th>
<th>30 yr. avg. Temp.</th>
<th>Total Precip.</th>
<th>30 yr. avg. Precip</th>
</tr>
</thead>
<tbody>
<tr>
<td>29 June - 12 July</td>
<td>80.95</td>
<td>79.57</td>
<td>2.98</td>
<td>2.38</td>
</tr>
<tr>
<td>13 July - 26 July</td>
<td>81.93</td>
<td>80.07</td>
<td>0.67</td>
<td>2.38</td>
</tr>
<tr>
<td>27 July - 9 August</td>
<td>83.69</td>
<td>79.57</td>
<td>4.49</td>
<td>2.51</td>
</tr>
<tr>
<td>10 August - 23 August</td>
<td>77.89</td>
<td>78.21</td>
<td>2.01</td>
<td>2.52</td>
</tr>
<tr>
<td>24 August - 6 September</td>
<td>76.44</td>
<td>76.50</td>
<td>14.10</td>
<td>2.54</td>
</tr>
<tr>
<td>7 September - 20 September</td>
<td>73.50</td>
<td>73.86</td>
<td>3.70</td>
<td>2.46</td>
</tr>
<tr>
<td>21 September - 4 October</td>
<td>69.53</td>
<td>69.50</td>
<td>4.07</td>
<td>2.17</td>
</tr>
<tr>
<td>5 October - 18 October</td>
<td>65.54</td>
<td>64.21</td>
<td>1.15</td>
<td>1.80</td>
</tr>
<tr>
<td>19 October - 1 November</td>
<td>57.49</td>
<td>59.71</td>
<td>1.28</td>
<td>1.59</td>
</tr>
<tr>
<td>2 November - 11 November</td>
<td>54.00</td>
<td>56.80</td>
<td>1.54</td>
<td>1.10</td>
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</tbody>
</table>
Table 8. Average temperatures and precipitation over two week periods during the reproductive growth stages at Kinston in 2011 compared with 30 year normals

<table>
<thead>
<tr>
<th>Date Range</th>
<th>Average Temp.</th>
<th>30 yr. avg. Temp.</th>
<th>Total Precip.</th>
<th>30 yr. avg. Precip</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 May - 8 June</td>
<td>80.02</td>
<td>74.21</td>
<td>0.56</td>
<td>1.95</td>
</tr>
<tr>
<td>9 June - 22 June</td>
<td>79.77</td>
<td>77.07</td>
<td>0.60</td>
<td>2.08</td>
</tr>
<tr>
<td>23 June - 6 July</td>
<td>82.33</td>
<td>79.50</td>
<td>0.99</td>
<td>2.30</td>
</tr>
<tr>
<td>7 July - 20 July</td>
<td>81.08</td>
<td>81.00</td>
<td>2.21</td>
<td>2.39</td>
</tr>
<tr>
<td>21 July - 3 August</td>
<td>85.87</td>
<td>81.07</td>
<td>2.69</td>
<td>2.38</td>
</tr>
<tr>
<td>4 August - 17 August</td>
<td>81.51</td>
<td>79.93</td>
<td>5.66</td>
<td>2.37</td>
</tr>
<tr>
<td>18 August - 31 August</td>
<td>78.47</td>
<td>78.50</td>
<td>16.57</td>
<td>2.48</td>
</tr>
<tr>
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<td>76.89</td>
<td>76.43</td>
<td>1.43</td>
<td>2.77</td>
</tr>
<tr>
<td>15 September - 28 September</td>
<td>73.12</td>
<td>72.79</td>
<td>0.82</td>
<td>2.54</td>
</tr>
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<td>29 September - 12 October</td>
<td>65.36</td>
<td>67.50</td>
<td>0.65</td>
<td>1.84</td>
</tr>
<tr>
<td>13 October - 27 October</td>
<td>64.22</td>
<td>62.60</td>
<td>0.96</td>
<td>1.43</td>
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</tbody>
</table>
Table 9. Treatment main effects for weight per plant for locations and cultivar types where only the main effect was significant. Differing letters represent LSD at p <0.05.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Plymouth 2010 Group V</th>
<th>Rocky Mount 2010 Group IV</th>
<th>Rocky Mount 2010 Group V</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g plant⁻¹</td>
<td>g plant⁻¹</td>
<td>g plant⁻¹</td>
</tr>
<tr>
<td>Low</td>
<td>446.5 A</td>
<td>255.8 A</td>
<td>204.9 A</td>
</tr>
<tr>
<td>Low - Defoliated</td>
<td>340.9 B</td>
<td>165 D</td>
<td>250.3 A</td>
</tr>
<tr>
<td>Medium - Shade Early</td>
<td>205 C</td>
<td>120.3 CDE</td>
<td>189.1 A</td>
</tr>
<tr>
<td>Medium - Shade Late</td>
<td>173.7 C</td>
<td>116.3 CE</td>
<td>194 A</td>
</tr>
<tr>
<td>High</td>
<td>122.2 D</td>
<td>77.6 BC</td>
<td>102 B</td>
</tr>
<tr>
<td>High - Thinned</td>
<td>111.8 D</td>
<td>55.1 B</td>
<td>99.6 B</td>
</tr>
</tbody>
</table>
Table 10. Treatment main effect for pods per plant for locations and cultivar types where only the main effect was significant. Differing letters represent LSD at p <0.05.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Rocky Mount 2010 Group IV</th>
<th>Rocky Mount 2010 Group V</th>
<th>Plymouth 2011 Group IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>Pods plant¹</td>
<td>Pods plant¹</td>
</tr>
<tr>
<td>Low</td>
<td>442.5</td>
<td>A</td>
<td>204.9</td>
</tr>
<tr>
<td>Low - Defoliated</td>
<td>558.5</td>
<td>C</td>
<td>250.3</td>
</tr>
<tr>
<td>Medium - Shade Early</td>
<td>420.3</td>
<td>A</td>
<td>189.1</td>
</tr>
<tr>
<td>Medium - Shade Late</td>
<td>444.9</td>
<td>A</td>
<td>194</td>
</tr>
<tr>
<td>High</td>
<td>228.4</td>
<td>B</td>
<td>102</td>
</tr>
<tr>
<td>High - Thinned</td>
<td>192.5</td>
<td>B</td>
<td>99.6</td>
</tr>
</tbody>
</table>
Table 11. Treatment main effect for individual pod weight for locations and cultivar types where only the main effect was significant. Differing letters represent LSD at p <0.05.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g pod⁻¹</td>
<td>g pod⁻¹</td>
<td>g pod⁻¹</td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0.252</td>
<td>A</td>
<td>0.239</td>
<td>A</td>
</tr>
<tr>
<td>Low - Defoliated</td>
<td>0.246</td>
<td>A</td>
<td></td>
<td>0.254</td>
</tr>
<tr>
<td>Medium - Shade Early</td>
<td>0.255</td>
<td>A</td>
<td>0.228</td>
<td>A</td>
</tr>
<tr>
<td>Medium - Shade Late</td>
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<td>0.237</td>
<td>A</td>
</tr>
<tr>
<td>High</td>
<td>0.206</td>
<td>B</td>
<td>0.271</td>
<td>B</td>
</tr>
<tr>
<td>High - Thinned</td>
<td>0.236</td>
<td>A</td>
<td>0.222</td>
<td>A</td>
</tr>
</tbody>
</table>
Table 12. Date main effects for plant weight, pod counts, and pod weight for locations and cultivar types where only the main effect was significant. Differing letters represent LSD at p <0.05.

### Weight per Plant

<table>
<thead>
<tr>
<th>GDD</th>
<th>Plymouth Group V</th>
<th>Rocky Mount Group IV</th>
<th>Rocky Mount Group V</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g plant⁻¹</td>
<td>g plant⁻¹</td>
<td>g plant⁻¹</td>
</tr>
<tr>
<td>2497</td>
<td>233.2 A</td>
<td>2038 107.7 A</td>
<td>2442 148 A</td>
</tr>
<tr>
<td>2694</td>
<td>220.4 A</td>
<td>2442 112.5 A</td>
<td>3076 171.4 AB</td>
</tr>
<tr>
<td>3189</td>
<td>287.1 B</td>
<td>3076 185.3 B</td>
<td>3246 203.1 B</td>
</tr>
<tr>
<td>3624</td>
<td>225.2 A</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### Pods per Plant

<table>
<thead>
<tr>
<th>GDD</th>
<th>Rocky Mount Group IV</th>
<th>Plymouth Group IV</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>pods plant⁻¹</td>
<td>pods plant⁻¹</td>
</tr>
<tr>
<td>2442</td>
<td>308 A</td>
<td>2105 135.6 A</td>
</tr>
<tr>
<td>3076</td>
<td>415.4 B</td>
<td>2434 169.3 B</td>
</tr>
<tr>
<td>3246</td>
<td>445.6 B</td>
<td>2707 174.3 B</td>
</tr>
<tr>
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### Weight per Pod

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<tr>
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Figure 1: Individual Plant Weights for indeterminate, maturity group IV, cultivars by date at Plymouth in 2010. Differing letters within sample period represent P at <0.05.
Figure 2: Variety by treatment interaction for indeterminate, maturity group IV, cultivars at Plymouth in 2010. Differing letters within sample period represent LSD at P <0.05.
Figure 3: Pods per plant for indeterminate, maturity group IV (A); and determinate, maturity group V (B), cultivars by date at Plymouth in 2010. Differing letters within sample periods represent LSD at $P < 0.05$. 
Figure 4: Individual pod weights for indeterminate, maturity group IV (A), and determinate, maturity group V (B), cultivars by date at Plymouth in 2010. Error bars represent LSD at P < 0.05.
Figure 5: Pods per plant for indeterminate, maturity group IV, cultivars by date at Rocky Mount in 2010. Differing letters within sample period represent LSD at P < 0.05.
Figure 6: Date by variety interaction for determinate, maturity group V, cultivars at Rocky Mount in 2010. Differing letters within sample period represent LSD at $P < 0.05$. 
Figure 7: Treatment main effect for indeterminate, maturity group IV, cultivars at Plymouth in 2011. Differing letters within sample period represent LSD at P < 0.05.
Figure 8: Individual plant weights for determinate, maturity group V, cultivars by date at Plymouth in 2011. Differing letters within sample period represent LSD at P <0.05.
Figure 9: Pods per plant for determinate, maturity group V, cultivars by date at Plymouth in 2011. Differing letters within sample period represent LSD at P <0.05.
Figure 10: Variety by treatment interaction for determinate, maturity group V, cultivars at Plymouth in 2011. Different letters represent LSD at p <0.05.
Figure 11: Variety by treatment interaction for determinate, maturity group V, cultivars at Kinston in 2011. Differing letters within sample period represent LSD at $P < 0.05$. 
Figure 12: Pods per plant for indeterminate, maturity group IV (A); and determinate, maturity group V (B) cultivars by date at Kinston in 2011. Differing letters within sample period represent LSD at P <0.05.
Figure 13: Individual pod weights for determinate, maturity group V, cultivars by date at Kinston in 2011. Differing letters within sample period represent LSD at $P < 0.05$. 

Low Population
Low Population - Defoliated
High Population
Medium Population - Shaded R1 to R5
Medium Population - Shaded R5 to Maturity
High Population - Thinned to Low
Figure 14: Yield at Plymouth in 2010. Differing letters represent LSD at P <0.05.
Figure 15: Yield at Rocky Mount in 2010. Differing letters represent LSD at $P < 0.05$. 
Figure 16: Yield at Plymouth in 2011. Differing letters represent LSD at $P < 0.05$. 
Figure 17: Yield at Kinston in 2011. Differing letters represent LSD at p <0.05.
CHAPTER TWO

The Effect of Shading, Defoliation, and Deeding Rate on Source and Sink Reactions in
Determinate and Indeterminate Soybean Cultivars

JOSEPH C. OAKES and RONNIE W. HEINIGER

ABSTRACT

Research was conducted at three locations in North Carolina in 2010 and 2011 in order to examine source and sink relationships. The objectives of this research are to determine if different cultivars are more likely to overcome source limitations by translocation of starch from the leaves to the seed, and to examine how the treatments imposed enhanced or reduced source limitations or created sink limited conditions.

Treatments were applied to two determinate and two indeterminate cultivars and consisted of three different seeding rates (49,400, 296,400, 741,000 plants ha\(^{-1}\)), shade at two different periods during reproduction (R1-R5 & R5-R8), thinning the high seeding rate at R5, and defoliating the low seeding rate at R5. Five plants from each treatment were taken at intervals from R5 to maturity. Biomass of entire plants and individual pods were measured along with pods per plant. The amount of dry matter produced per pod per growing degree day was compared to the rate of increase in individual pod weight per plant in order to determine source and sink relationships.

If the increase in weight per pod is equal to the amount of dry matter per pod per GDD, this indicates that the total amount of assimilate produced by the plant during this
period is being translocated directly to the pods. If the increase in weight per pod is greater than the rate of plant growth per pod, then remobilization of assimilate must be occurring resulting in source limited situation. In contrast, if the increase in weight per pod is less than the rate of plant growth per pod then the excess assimilate is being stored in organs other than the pod. This indicates a sink limiting situation. To determine whether the plants were source or sink limiting, the rate of increase in weight per pod was divided by the increase in weight per plant per pod per GDD. This ratio was then compared to a ratio of 1 which, as described above, indicates neither a source or sink limiting situation. Proc GLM was used to determine which cultivars and treatments had a ratio that differed significantly from 1. In addition, ratios for each cultivar and treatment were compared with each other to determine significant differences.

There were variety by treatment interactions at all locations. At Plymouth in 2010 and at Kinston in 2011, the most consistent treatments were the low seeding rate which tended to have the highest source-sink ratio when compared to the remaining treatments, and the high seeding rate thinned, which consistently had the lowest source-sink ratio, which was not significantly different from 1. At Plymouth in 2011, the high seeding rate treatment had the highest source-sink ratio, with no consistent differences among the thinned high seeding rate or the medium seeding rate shaded early or late. Among cultivars, the only consistent trend occurred at Plymouth in 2011, where the determinate cultivars had lower source-sink ratios compared to the indeterminate cultivars.
Introduction

Over the last twenty years, soybean (*Glycine max*) yield has not increased substantially in North Carolina. An important part of the yield process in a grain crop is the accumulation of dry matter by the developing seed (Egli et al., 1985). This accumulation of dry matter in the seed is driven by the production of assimilates in the leaves and their translocation to the seed. Without this translocation of assimilates from leaves to seed, yield can be drastically reduced. A better understanding of source-sink limitations in soybean is needed to improve our understanding of the factors limiting yield.

The ability to translocate assimilate from the leaves or stem to the stem has been observed in several grain crops, including Mediterranean durum wheat (*Triticum turgidum* L.), maize (*Zea mays* L) (Daynard et al., 1969), and sorghum (*Sorghum bicolor* L) (Heiniger et al., 1997). Alvaro et al. (2008) found that modern durum wheat cultivars translocate total dry matter from the main stem to the seed. Up to 25% of the main stem biomass in durum wheat has been shown to translocate to the grain. Alvaro et al. (2008) also found that translocation efficiency has improved in modern cultivars when compared to early 20th century cultivars. Several workers have observed that translocation occurs in maize as well. Daynard et al. (1969) studied soluble carbohydrates in maize stalks and found that carbohydrates stored in the stem are translocated during the latter part of the grain filling period. Dry weight of the stem has been shown to increase during the first two or three weeks after silking then to decrease during the grain filling period (Allison et al., 1975). This suggests that the stem weights decrease when the carbohydrates are effectively translocated from the stem to the grain. As in wheat and maize, soybean yield largely depends on
photosynthesis by the leaves during seed fill and the translocation of assimilates to the seed (Egli et al., 1980). A limitation in either the source or the sink could have a negative effect on yield.

Several researchers have observed and studied source-sink relationships and limitations in soybean. The production of assimilates by the leaves (the source) and the subsequent translocation of these assimilates to the seeds (the sink) is an integral factor in soybean yield (Egli, 1999). Source limitations are characterized by a lack of assimilate to meet the demand of the seeds. During the seed fill period, the canopy deteriorates as leaves senesce resulting in a reduction of assimilate availability (Egli et al., 1980). Egli et. al (1980) performed shading tests, and found that shading reduced the seed growth rate. This reduction in seed growth rate is due to the plant being source limited. This indicates that the seed growth rate is dependent on canopy photosynthesis and the ability of the source to supply assimilates to the sink. The close association between environmental variation in soybean yield and seed number, and the fact that seed growth is primarily dependent on canopy photosynthesis, provides evidence that yields are primarily source limited (Egli, 1999). Thus, any increase in canopy photosynthesis should decrease source limitations and increase yield.

Both shading and defoliation serve as ways to limit the source and decrease the amount of assimilate available to the plant. Board et al. (1994) performed several defoliation studies in relation to insect damage. Their data showed that carbohydrate reserves in the leaves and branches were unable to compensate for the loss of assimilatory capacity and carbohydrate reserves in the leaves. Since carbohydrate translocation from the leaves to the seed has been identified as an integral factor in seed fill (Egli et al., 1980), defoliation will
cause a decrease in pod fill and eventually yield. The soybean plant will adjust to the reduced assimilatory capacity and reduce the seed size. The idea that reduced assimilatory capacity will result in decreased yield corresponds with several previous studies. Fehr et al. (1977) found that maximum yield loss from defoliation occurred at R5. R5 is when the seed is beginning to form in the pod and the seed is 1/8 inch in the pod (Fehr & Caviness, 1992). Since R5 is when the seed needs the carbohydrate assimilates the most, and since assimilates are lost, defoliation at this growth period is most critical to seed fill and yield. Like defoliation, shading will induce stress by limiting the source and reducing photosynthesis and assimilate supplies to the seed during the seed fill period (Egli, 1997).

A sink limitation occurs when the assimilate supply from photosynthesis exceeds the ability of the seeds to utilize the assimilate (Egli, 1999). Since seed number is dependent on canopy photosynthesis as mentioned above, it could be assumed that sink limitations are minimal (Egli, 1999). Nevertheless, field conditions are rarely constant and a change in environmental conditions during flowering or seed fill could increase photosynthesis and create a sink limitation. This could possibly happen after the seed number is fixed, when the seed cannot respond to increased assimilate supply. After R6, the seed number can no longer change (Board & Tan, 1995). Since the seed represents the primary sink for assimilates (Hume & Criswell, 1973), the seed can only respond to the increased assimilate supply by increasing the seed growth rate. If the seed growth rate does not increase when the assimilate increases, a sink limitation will occur and starch will begin to accumulate in the leaves (Ackerson et al., 1984). Mondal et al. (1978) found that a reduction of sink relative to the source has been shown to cause an accumulation in starch in the leaves of soybean. Thus, an
accumulation of starch in the leaves suggests that there is an inadequate sink demand and therefore a sink limitation (Egli et al., 1980). This proposition is supported by the data of McAlister and Krober (1958), who found that removing 80% of the pods increased the sugars and starch in the leaves. In the absence of a sink, the leaves of the plant serve as storage organs for food materials. Egli (1999) found that average insolation was less during seed fill than during flowering and pod set. However, this decrease from flowering to seed fill was larger for later cultivars than for early cultivars. This suggests that sink limitations may be less likely to occur when reproductive growth occurs later in the growing season. These limitations in the sink are less likely to occur in well-watered soybean, and are more common in periods of moisture stress.

Borras et al. (2004) examined source and sink relationships in wheat, maize, and soybean. A bilinear plateau model was used to determine whether each species was either source or sink limited. The response of relative seed dry weight (Y) to the relative change in potential assimilate available per seed (X) was used in fitting this bilinear plateau model. Heiniger et al. (1997) used a similar process when examining caryopsis weight in sorghum. Again, relationships between grain fill rate and plant dry matter per seed per growing degree day (GDD) were graphed, with grain fill rate per GDD (X) compared with dry matter produced per seed per GDD (Y). Borras et al. (2004) and Heiniger et al. (1997) used a slope of 1 to determine the source-sink relationship. A ratio above 1:1 indicated a source limitation, while a ratio below 1:1 indicated a sink limitation.

Borras et al. (2004) found that soybean seed dry weight was responsive to increased source per seed. Mean seed dry weight was 46% higher when assimilate availability was
increased. Therefore, it seems that maximum soybean seed dry weights are rarely achieved because of large source limitations for seed growth. Furthermore, when assimilate availability was reduced due to shading and defoliation, soybean seed dry weight decreased. In examining several different research studies, Borras et al. (2004) found that grain fill in soybean is generally source limited.

The objectives of this research are 1) to determine if different cultivars are more likely to overcome source limitations by translocation of starch from the leaves to the seed, and 2) to examine how the treatments imposed enhanced or reduced source or sink limitations.

MATERIALS & METHODS

Field Experiment

Research was conducted at three sites over two years: the Tidewater Research Station in Plymouth, NC (2010 and 2011), the Upper Coastal Plain Research Station in Rocky Mount, NC (2010), and the Caswell Research Station in Kinston, NC (2011). Soil at Plymouth was a Portsmouth fine sandy loam (fine-loamy over sandy or sandy-skeletal, mixed, thermic Typic Umbraquults); soil at Rocky Mount was a Goldsboro fine sandy loam (fine-loamy, siliceous, thermic aquic paleudults); and soil at Kinston was Pocalla loamy sand, 0 to 6 percent slopes (sandy, siliceous, thermic, Arenic Paleudults). In 2010, plots were planted on 3 June at Plymouth and on 22 June at Rocky Mount. In 2011, plots were planted on 26 May at Kinston and on 29 June at Plymouth. Conventional management practices
were followed at all locations and over both years, Irrigation was applied as needed at Rocky Mount in 2010 and at Kinston and Plymouth in 2011.

Weed and insect control measures were taken at all location over both years. In 2010 at Plymouth, alachlor was applied PRE at 4.49 kg ai ha\(^{-1}\). Glyphosate at 1.54 kg ai ha\(^{-1}\) and flumiclorac pentyl ester at 0.97 kg ai ha\(^{-1}\) were applied POST on 23 June 2010. For insect control, indoxycarb was applied at 1.40 kg ai ha\(^{-1}\) on 11 August 2010. In 2011, alachlor was applied PRE at 4.49 kg ai ha\(^{-1}\). At Rocky Mount, glyphosate was applied PRE at 1.54 kg ai ha\(^{-1}\). Spinosad insecticide was applied at 4.49 kg ai ha\(^{-1}\) on 5 August 2010. At Kinston, imazaquin at 38.17 g ai ha\(^{-1}\) and S-metolachlor at 8.56 g ai ha\(^{-1}\) were applied PRE. Clethodim at 2.25 g ai ha\(^{-1}\) and fomesafen at 2.25 g ai ha\(^{-1}\) was applied POST on 6 June 2011. Thiodicarb insecticide was applied on 16 August 2011 at 3.59 g ai ha\(^{-1}\).

The experimental design consisted of a split plot design with four blocks. Main plots consisted of two indeterminate (Syngenta S47-R3 and Syngenta S49-A5) and two determinate (Asgrow AG5605 and Asgrow DP5915) cultivars. Six seeding rate, defoliation, and shade treatments were used as sub-plots. In 2010, each sub-plot was 4.27 by 12.19 m. In 2011, each sub-plot was 3.05 by 12.19 m.

Treatment 1 was a low seeding rate which consisted of 49,400 seeds per hectare. Treatment 2 was a high seeding rate which consisted of 741,000 seeds per hectare. Treatment 3 involved thinning the high seeding rate to 49,400 seeds per hectare at R5. Treatment 4 consisted of defoliating the low seeding rate at R5. Approximately 50% of the leaf area in the upper canopy was defoliated. Treatment 5 consisted of shading the medium (296,400)
seeding rate from R1-R5. Shade cloth was applied over plots and shaded out 50% of the sunlight. Treatment 6 entailed shading the medium seeding rate from R5-maturity.

Treatments were applied at each site within each year according to the following schedule. At Plymouth in 2010, early shade (Treatment 5) was applied on 23 July and 29 July to maturity groups IV and V respectively; while late shade (Treatment 6) was applied on 21 August and 30 August. Both defoliation (Treatment 4) and thinning (Treatment 3) were applied on 10 August and 26 August to maturity groups IV and V respectively. At Rocky Mount in 2010, early shade was applied on 28 July and 9 August to maturity groups IV and V respectively; while late shade was applied on 1 September and 8 September. Both defoliation and thinning were applied on 1 September and 8 September to groups IV and V respectively. At Plymouth in 2011, early shade was applied on 11 August and 2 September to maturity groups IV and V respectively; while late shade and thinning were applied on 2 September and 15 September. At Kinston in 2011, early shade at R5 was applied on 6 July and 14 July to maturity groups IV and V respectively; while late shading, defoliation, and thinning were all applied on 4 August and 18 August to maturity groups IV and V.

Samples consisted of five plants and were taken from each sub-plot starting at R5. At Plymouth, group IV samples were taken on 9, 20, 27 August, 16 September, and 8 October 2010; group V samples were taken on 20, 27 August, 16 September, and 8 October 2010. In 2011, group IV samples were taken on 6, 20 September, 4, and 25 October 2011; group V samples were taken on 20 September, 4, and 25 October 2011. Rocky Mount group IV samples were taken on 24 August, 8 September, and 8 October 2010. Group V samples were taken 8 September, 8 October, and 20 October 2010. Kinston group IV samples were
taken on 8 August, 31 August, and 22 September 2011. Group V samples were taken on 31 August, 8 September, 22 September, and 4 October 2011. Pods were removed from each plant and were counted. Plant biomass and pods were dried for at least 48 hours and weighed. Weight per plant, pods per plant, and weights per pod were calculated for each sample.

**Statistical Procedure**

Differences in the number of samples taken at each location and environmental conditions at the three locations over two years made it impossible to perform a combined analysis across locations. Thus, separate analyses were run at each location.

At each sampling date, weights per plant within each treatment at each sampling date were averaged across the four blocks in order to obtain one value for weight per plant for each sampling date. A regression was fit to the change in weight across the sampling period. The slope of the regression line equaled the change in weight per plant per growing degree day. This value was then divided by the maximum number of pods over the sampling period, in order to obtain the amount of dry matter produced per pod, g GDD$^{-1}$ pod$^{-1}$. To obtain the grain fill rate, the change in weight per pod was analyzed across the sampling period. The period of highest change in weight per pod between was determined. The amount of change was then divided by the growing degree days over the same time period in order to obtain the grain fill rate.

Grain fill rates were plotted against measured plant biomass production (g pod$^{-1}$ GDD$^{-1}$) for each treatment and cultivar at each location (Figures 1, 2, and 3). The x-axis represented the change in biomass per pod over time which measures assimilate supply,
while the y-axis represented the grain fill rate which represents sink demand. The ratio between assimilate supply and sink demand [(grain fill rate) / (weight per plant / pod# / GDD)] for each treatment within each cultivar at each location was compared to a 1:1 ratio, which represents the point at which assimilate supply precisely matches the sink demand. Values over the 1:1 ratio indicate a situation where the plant is source limited (seed growth exceeds the amount of assimilate fixed by the plant), while points below the line indicate a sink limitation (assimilate supply exceeds the growth of seeds). This process is similar to the one used by Heiniger et al. (1997) and Borras et al. (2004). The proc glm procedure in SAS using the ratio (grain fill rate) / (weight per plant / pod# / GDD) was used to examine differences among treatments and cultivars, and to compare the ratio for each treatment or cultivar to the 1:1 ratio. Fisher’s Protected LSD was used to analyze specific differences between cultivars, treatments and the 1:1 ratio.

RESULTS

Figures 1 through 3 display the relationship between pod fill rate and the change in plant weight per pod per GDD for each treatment within the four cultivars at Plymouth in 2010 and 2011 and Kinston in 2011. Points above the 1:1 ratio line indicate a source limitation, while points below the 1:1 line indicate a sink limitation. While it is evident that all treatments within the four cultivars are primarily source limited, the relationship between plant weight per pod per GDD and the rate of pod fill within each cultivar was relatively weak. This was primarily the result of the difficulty in accurately measuring the rate of pod fill based on the limited number of sampling periods used in this study. The lack of strong
regression relationships within each cultivar made it impossible to determine the pattern of source-sink relationships for each cultivar as demonstrated by Borras et al. (2004), and to use regression analysis to compare cultivars. However, it was possible to use the replicated samples to examine differences in the source-sink ratios among treatments and cultivars and a ratio of 1:1 (source = sink) by comparing linear models. Using this approach, only the treatments or cultivars that are significantly greater than one can be designated as source limited. Those significantly less than one can be designated as sink limited, and for those treatments or cultivars that do not significantly differ from one it is impossible to determine whether they are source or sink limited.

Plymouth 2010. At Plymouth in 2010, there was a significant date by variety interaction, as well as, variety and treatment main effects (Table 1). Within the variety by treatment interaction, there were 13 treatments that were significantly different from the 1:1 ratio indicating a source limitation (Figure 5). In Syngenta S47-R3, three of the treatments were significantly different from the 1:1 ratio. These included both the defoliated and non-defoliated low seeding rates and the medium seeding rate shaded late. All treatments in S49-A5, except for the thinned high seeding rate, were significantly different from the 1:1 ratio indicating that they were definitely source limited. Only the defoliated low seeding rate from AG5605 was significantly different from the 1:1 ratio. There were four treatments within DP5915 that were significantly different from the 1:1 ratio. These included both the defoliated and non-defoliated low seeding rate, the non-thinned high seeding rate, and early shaded medium seeding rate.
The variation in treatments across cultivars made it difficult to identify a pattern in differences among cultivars. Within the treatment main effect, all treatments except the thinned high seeding rate were significantly different from the 1:1 ratio. Again, both the defoliated and non-defoliated low seeding rate treatments were the most source limited, with no significant difference between the two. The non-thinned high seeding was the next most source limited treatment. There was no significant difference in source-sink ratio between the medium seeding rate shaded from R1-R5 and from R5-maturity.

_Plymouth 2011._ The low seeding rate treatments at Plymouth in 2011 were severely damaged by Hurricane Irene. Therefore, the low seeding rate treatments with and without defoliation (Treatments 1 and 4) in all four cultivars were removed from the analysis at this location. Both variety and treatment main effects were significant, as well as a variety by treatment interaction (Table 1).

Within all cultivars, there were only five treatments that were significantly different from the 1:1 ratio (Figure 6). There were no treatments within AG5605 that were significantly different from the 1:1 ratio. In S47-R3, the most source limited cultivar, the non-thinned high seeding rate and the medium seeding rate shaded late were both significantly different from the 1:1 ratio. Both the high seeding rate treatments in S49-A5 were significantly different from the 1:1 ratio. In DP5915, only the non-thinned high seeding rate treatment was significantly different from the 1:1 ratio.

The only clear treatment effects at this location occurred in the non-thinned high seeding rate, and in the medium seeding rate treatments. The non-thinned high seeding rate
treatment had a ratio that was significantly greater than the 1:1 ratio in three of the four cultivars. Neither the medium seeding rate shaded early nor the medium seeding rates shaded late were significantly different from the 1:1 ratio. Among cultivars, S47-R3 and S49-A5 tended to have higher ratios than AG5605 and DP5915. AG5605 was the least source limited.

*Kinston 2011.* Hurricane Irene made it impossible to take the last two samples in the group IV cultivars. This made it impossible to properly determine the pod fill rates. Therefore, only maturity group V data was used in this analysis. As in Plymouth in 2010 and 2011, both variety and treatment main effects were significant, as well as a variety by treatment interaction (Table 1).

Within cultivars, there were five treatments that were significantly different from the 1:1 ratio (Figure 7). In AG5605, the non-defoliated low seeding rate and the non-thinned high seeding rate were both significantly different from the 1:1 ratio. They are the only source limited treatments in AG5605. Both the defoliated and non-defoliated low seeding rate and the medium seeding rate shaded after R5 were significantly different from the 1:1 ratio in DP5915. These three treatments are source limited within DP5915.

Across cultivars, the thinned high seeding rate and the medium seeding rate shaded early, were not significantly different from the 1:1 ratio indicating that these treatments were not source limited. The non-defoliated low seeding rate always had a ratio that was greater than 1:1 and was clearly source limited. The variation in ratios among treatments makes it impossible to compare cultivars at this location.
DISCUSSION

At all locations over both years, there were treatments in all cultivars that were source limited (Figures 5, 6, and 7). This source limitation across all cultivars and treatment is primarily due to the adverse growing conditions both years. Throughout the sampling period, it was noticed that the hot and dry weather contributed to reduced plant weight due to a drop in leaves late in the season. The reduction in plant weight is due to reduced photosynthesis caused by the adverse growing conditions. These factors added to the source limitation.

When considering the effects of the treatments applied on the source-sink ratio, the thinned high seeding rate treatments were almost always the least source limited and often had a ratio that was not significantly different from 1:1 at each of the three locations. The fact that the thinned plots are the least source limited is explained by the increased light interception and the limited number of pods that were set prior to thinning. The removal of plants decreased competition for light, water, and nutrients.

In contrast, the non-thinned high seeding rate plots had high ratios at all three locations. While this treatment similar pod numbers when compared to the thinned treatment, there was significant competition for light and water due to the higher number of plants. Generally, only the two low seeding rate treatments were more source limited than the non-thinned high seeding rate.

At Plymouth in 2010 and Kinston in 2011, the low seeding rate treatments tended to be the most source limited treatments. At Plymouth, the two treatments were not significantly different from each other. Most often, the non-defoliated low seeding rate experienced the
highest source-sink ratio due to the fact that the plant set so many pods (sink), that it was unable to provide enough assimilate (source) strength for the large number of pods given the amount of biomass that was produced. In the defoliated treatments, the removal of leaf area further reduced the amount of assimilate available to meet the demands of the pods.

In general, there was no clear trend within the medium seeding rate treatments shaded early or late. At Plymouth in 2010, both were significantly different from the 1:1 ratio. However, neither treatment differed from the 1:1 ratio at either Plymouth in 2011 or Kinston in 2011. It is unclear why the shading caused a source limitation at only one location and not at the other two. According to Egli (1999), shading causes a limitation in canopy photosynthesis, which results in a source limitation. Even though we are unable to determine whether shading causes a source limitation, it is clear that there is not difference between shading early and shading late.

Across the three locations there was only one site in which a clear cultivar difference existed. At Plymouth in 2011, the two indeterminate cultivars tended to have higher source-sink ratios than the determinate cultivars. This pattern makes sense from the standpoint that indeterminate cultivars are continuing to produce vegetative growth during the reproductive period. Therefore, assimilate would be directed to other parts of the plant resulting in a source limitation.

This research confirms the results found Borras et al., (2004) which describe soybean as being primarily source limited. In this study, the only situation where soybean was not primarily source limited was where the number of pods was artificially low and the amount
of light and water available was high (Treatment 3, thinned high seeding rate). In comparison, treatments with high number of pods per plant (Low seeding rate) were almost always source limited. This indicates that the soybean plant typically sets more pods that it can support with the amount of assimilate being produced. In order to increase soybean yield future studies should focus on ways to increase assimilate supply during the grain fill period.
REFERENCES


Retrieved February 6, 2012, from

http://www.nass.usda.gov/QuickStats/PullData_US.jsp
Table 1: Analysis of variance table for source and sink ratios for variety and treatment two locations over two years

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- **Plymouth 2010**
- **Plymouth 2011**
- **Kinston 2011**
Dry Matter Produced Per Pod, g GDD$^{-1}$

Grain Fill Rate, g GDD$^{-1}$

Source Limited

Sink Limited

Figure 1: Relationship between the amount of soybean plant dry matter produced per pod per growing degree day (GDD) and grain-filling rates at Plymouth in 2010. Points above 1:1 ratio line are source limited, while points below are sink limited.
Figure 2: Relationship between the amount of soybean plant dry matter produced per pod per growing degree day (GDD) and grain-filling rates at Plymouth in 2011. Points above 1:1 ratio line are source limited, while points below are sink limited.
Figure 3: Relationship between the amount of soybean plant dry matter produced per pod per growing degree day (GDD) and grain-filling rates at Kinston in 2011. Points above 1:1 ratio line are source limited, while points below are sink limited.
Figure 4: Source-sink ratios for treatment main at Plymouth in 2010. Reference line indicates a source-sink ratio of 1:1. Differing letters represent LSD at P < 0.05.
Figure 5: Source/Sink ratios at Plymouth in 2010 for the variety by treatment interaction.

Reference line indicates a source-sink ratio of 1:1. Differing letters represent LSD at P <0.05.
**Figure 6:** Source/Sink ratios at Plymouth in 2011. Reference line indicates a source-sink ratio of 1:1. Differing letters represent LSD at P <0.05
Figure 7: Source/Sink ratios at Kinston in 2011. Reference line indicates a source-sink ratio of 1:1. Differing letters represent LSD at P <0.05.