Sand Abrasion Injury and Biomass Partitioning in Cotton Seedlings

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ABSTRACT

Wind blown soil particle abrasion negatively impacts millions of hectares of crops annually. The goal of this study was to examine the effects of wind and wind blown sand abrasion damage on cotton (Gossypium hirsutum L.) seedling biomass partitioning to leaves, stems, and roots. Seedlings of three cotton cultivars were exposed to no wind (untreated controls) or sand abrasive flux densities of 0, 0.1, 0.25, 0.35, and 0.5 g cm\(^{-1}\) width s\(^{-1}\) at a wind velocity of 13.4 m s\(^{-1}\) in a suction-type laboratory wind tunnel. Plants were destructively sampled at the time of the sand abrasion treatment and at approximately 2 and 4 wk after exposure. These three sampling dates provided two time intervals for assessing the amount of plant damage and regrowth using classical growth analysis. With increasing sand, abrasive flux density, whole plant, leaf, stem, and root biomass, as well as leaf area, were all reduced in both harvest intervals (\(p \leq 0.05\)). Net assimilation rate (NAR) accounted for 96 and 75% of the variability in relative growth rate (RGR) in the first and second harvest intervals, respectively, with small but significant differences in leaf area ratio (LAR). Increasing plant damage caused by sand abrasion treatment resulted in preferential biomass partitioning to the damaged stems rather than roots during the first harvest interval, while a much more stable allometric allocation of biomass among plant organs was observed in the second harvest interval.

METHODS

Plant Culture

Three cotton cultivars, FM 5013, FM 800 (FiberMax, Bayer CropScience, RTP, NC), and PM 2145 (Monsanto, St. Louis, MO) were seeded into 100 1.7-L pots filled with a local sifted Amarillo fine sandy loam (fine-loamy, mixed, thermic Aridic Paleustalfs) top soil and grown in a greenhouse in each of three repeated experimental runs. Following emergence, plants were

Abbreviations: \(\Sigma Tu\) accumulated thermal units; NAR, net assimilation rate; LAR, leaf area ratio, RGR, relative growth rate; S/R, shoot-to-root biomass ratio; Tu, thermal units.
Cotton plants were grown in the greenhouse, exposed to sand abrasion treatments, and then returned to the greenhouse. Sand abrasion treatments were applied using the suction-type laboratory wind tunnel described by Fryrear (1971). The wind tunnel has a test section measuring 0.4 m tall, 0.6 m wide, and 2.4 m long, with a trap door in the bottom to accommodate two potted plants with the top of the pot level with the wind tunnel floor. Wind velocity was measured at 15 cm above the floor immediately upwind of the plants with a pitot tube and static ports connected to a pressure transducer (Setra, Inc., Model 239, Boxborough, MA). A constant wind velocity of 13.4 m s⁻¹ was maintained in the wind tunnel during sand abrasion treatments, which is the same velocity used in previous experiments (Armbrust et al., 1974; Baker, 2007). In West Texas, minimum wind velocity threshold for salinity is often ~10 to 13 m s⁻¹ (Stout and Zobeck, 1997; Zobeck and Van Pelt, 2006), while wind speeds of 11 to 18 m s⁻¹ during dust storms are not uncommon. A washed sand (Silica Sand #3, Oglebay Norton Industrial Sands, Inc., Brady, TX) with a particle size < 0.3 mm was used as the abrasive material. Very similar particle sizes have been used in previous experiments (Baker, 2007; Armbrust et al., 1974; Precheur et al., 1978). A gravity-fed sand-hopper supplied sand into the wind stream through six drop tubes with holes of different diameters to generate different sand abrasive flux density treatments. Treatments in this study were no wind and no sand abrasion (untreated controls), wind with no sand abrasion (0 g cm⁻¹ width s⁻¹) and wind with sand abrasion (0.10, 0.25, 0.35, and 0.50 g cm⁻¹ width s⁻¹). The cross-sectional area of the wind tunnel was 0.24 m². Eight cotton seedlings from each of the three cultivars were exposed to each of the six treatments. Plants were treated inside the wind tunnel for 20 min based on Baker (2007). To treat all the plants in this fashion required about 2.5 d. The entire experiment was repeated three times (n = 3, Table 1).

**Growth Analysis**

For each cultivar × treatment combination, groups of four plants were sampled on three sampling dates. The first destructive sampling was collected at the time of the application of the sand abrasion treatments on untreated plants only. Thereafter, at ~2 wk intervals, the second and third destructive samples were collected. Thus, there were four pots per cultivar sampled on the first sampling date plus four pots × six treatments for both second and third sampling dates, yielding a total of 52 pots per cultivar (e.g., 4 + 4 × 6 + 4 × 6 = 52 pots per cultivar). The three samplings provided two growth time intervals for performing growth analysis. The sand abrasion treatments damaged leaves and stems to varying degrees, and resulted in the drying, death, and shedding of leaf material. The 2-wk interval between the first and second sampling dates provided sufficient time for the drying and shedding of damaged leaves, along with some regrowth. The second interval, between the second and third sampling dates, consisted of regrowth and recovery of the plants.

For each sampled plant, the number of mainstem nodes were counted acropetally, with the cotyledonal node designated Node 0 and the node associated with the first true leaf being Node 1, etc. A node was considered to have appeared when its associated leaf was >=3 cm in length (Baker, 2007). Green or living leaves and petioles were separated from the shoots and leaf area was measured with a leaf area meter (LI-COR, LI-3100, Lincoln, NE). At the time of sampling, pots containing intact root systems were placed in a freezer for storage and later processing. Pots were later thawed, and each root system was hand washed and sieved to separate roots from the soil. Dry masses for leaves, stems, petioles, and roots were determined after oven drying at 70°C for 48 h.

Growth analysis requires the determination of specific time intervals between successive plant harvests. Growth analysis is often conducted for plants grown in growth chambers where environmental variables are controlled and chronological time is easily determined. Because of the different planting dates, air temperatures inside the greenhouse varied among the three experimental runs. Differences in plant growth and development due to temperature or harvest timing were accounted for

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**Table 1. Greenhouse planting dates, sand abrasion treatment dates, dates for the first, second, and third destructive samplings, and chronological and thermal time intervals between the first and second destructive sampling date (Interval 1) and the second and third sampling dates (Interval 2).**

<table>
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<th>Exp.</th>
<th>Planting date</th>
<th>Sand abrasion treatment date</th>
<th>First sample</th>
<th>Second sample</th>
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by use of growing degree days or thermal units (Tu, °C) substituted for chronological time. Thermal units were calculated as

\[ Tu = \frac{(T_{\text{max}} + T_{\text{min}})}{2} - T_b \]  \[1\]

where \( T_{\text{max}} \) and \( T_{\text{min}} \) are the maximum and minimum daily air temperatures, respectively, and \( T_b \) is the base temperature considered here to be 15.5 °C (Hake et al., 1996; Oosterhuis, 1990). Accumulated thermal units (ΣTu) were then summed over the time intervals of interest (Table 1).

Growth analysis was used to examine patterns of biomass loss and regrowth among the cultivars and sand abrasion treatments. Relative growth rate (mg g\(^{-1}\) Tu\(^{-1}\)) was calculated as

\[ RGR = \frac{\ln(M_2) - \ln(M_1)}{(\Sigma Tu_2 - \Sigma Tu_1)} \]  \[2\]

where \( \ln(M_2) \) and \( \ln(M_1) \) are the mean ln-transformed dry masses (Fisher, 1921; Hoffmann and Poorter, 2002) at thermal times \( \Sigma Tu_2 \) and \( \Sigma Tu_1 \). Net assimilation rate (g m\(^{-2}\) Tu\(^{-1}\)) was calculated as

\[ NAR = \frac{(M_2 - M_1)(\Sigma Tu_2 - \Sigma Tu_1)}{(\ln(A_2) - \ln(A_1))(A_2 - A_1)} \]  \[3\]

where \( A_2 \) and \( A_1 \) are total leaf area at thermal times \( \Sigma Tu_2 \) and \( \Sigma Tu_1 \). Leaf area ratio (m\(^{-2}\) kg\(^{-1}\)) was calculated as

\[ LAR = 0.5 \times \left[ (A_1/M_1) + (A_2/M_2) \right] \]  \[4\]

The RGR, NAR, LAR and biomass increments of the whole plant (ΔMTota l), leaves (ΔMLeaf), stems + petioles (ΔMStem) and roots (ΔMRoot) were calculated for the first and second harvest time intervals.

The data were pooled for each of the three experimental runs. The three experimental runs were then treated as replicates in a randomized complete block design, and data analysis and mean separation was performed using the MIXED procedure with the Tukey adjustment for mean separation provided by the SAS Institute (SAS Institute, 2002). Random effects included experimental run, experimental run × cultivar and experimental run × sand abrasion treatment. Regression analysis was used to describe the trends in whole plant biomass, RGR and NAR across sand abrasion flux density treatments.

RESULTS

As expected, visible differences in plant damage were apparent following sand abrasion treatments (Fig. 1). Differences among cultivars and cultivar × treatment interactions were not significant for shoot, root, and total plant biomass and leaf area on any of the three harvest dates (Fig. 2, Table 2). Averaged across cultivars, total plant dry biomass decreased with increasing sand abrasion flux density treatment for the second and third destructive samples (Fig. 2). Total plant dry biomass decreased with increasing sand abrasion flux density for the second and third destructive samples (Fig. 2). The decrease was detected in the shoot and root dry mass and leaf area (Table 2).

Apparently, wind alone without sand abrasion had little effect on measured plant attributes in this experiment since the effects of wind (e.g., control with no wind vs. 0 g cm\(^{-1}\) width s\(^{-1}\) with wind) were small and nonsignificant.

Using the data in Fig. 2 and Table 2, we calculated RGR, NAR (Fig. 3), and LAR (Table 3). Both RGR and NAR declined with increasing sand abrasion damage in the first harvest interval, while RGR and NAR reached peak values at the 0.25 g cm\(^{-1}\) width s\(^{-1}\) treatment in the second harvest interval, which also had the largest standard error measurements. While significant differences were detected in LAR among cultivars and sand abrasion treatments in the second but not the first harvest interval, RGR depended mainly on NAR rather than LAR. The LAR was poorly correlated with RGR while linear regression of NAR against RGR yielded \( R^2 \) values of 0.96 and 0.75 for the first and second harvest intervals, respectively.

Poorter and Nagel (2000) and Körner (1994) provided convincing arguments for analyzing biomass allocation patterns in plants using at least a three compartment model: leaves, stems, and roots rather than simple S/R. A problem with S/R is that combining leaves and stems into a single shoot compartment ignores the functional difference between these two plant organs. Whereas, a three-compartment model can be interpreted functionally with leaves for light interception and an assimilate source for the plant, stems as providing structural support for leaves, and roots providing water and nutrient uptake. Accordingly, total biomass increment (ΔMTota l) are given in Table 3 and for each of these three compartments (ΔMLeaf, ΔMStem, and ΔMRoot) as well as the net percentage
of $\Delta M_{\text{Total}}$ partitioned to each compartment over both the first and second harvest intervals.

None of the biomass increment measurements in either harvest interval were statistically significantly affected by cultivar while $\Delta M_{\text{Total}}$ was significantly reduced with increasing sand abrasion treatments in both harvest intervals (Table 3). In the first harvest interval, with increasing sand abrasion treatment, percentage of total biomass increment partitioned to the stems increased from 35 to 52%, while that partitioned to leaves and roots appeared to decline. Percentage of biomass allocation among the three compartments was much more stable across sand abrasion treatments during the second harvest interval, with approximately 36, 45, and 18% going to the leaves, stems, and roots, respectively (Table 3).

**DISCUSSION**

A problem with interpretation of these results for the first harvest interval is that during this period, following the sand abrasion treatments, damaged leaves began to exhibit completely desiccated areas that became necrotic, and many of the more heavily damaged leaves were ultimately shed from the plant. Almost invariably this also involved shedding the associated petiole of these leaves. Thus, the first harvest interval represents biomass losses in the leaf and stem compartments as well as regrowth of new plant material. The results presented here represent the net effect of these sand abrasion treatments over the first harvest interval.

The reduction in total plant biomass with increasing abrasive flux density treatments (Fig. 1) is very similar in pattern to shoot biomass reductions measured in a previous
study on cotton seedlings where abrasive flux density was held constant and exposure time varied (Baker, 2007). In that experiment, plants responded to increasing sand abrasion treatment time with a slight but significant increase in the number of main-stem nodes. In the current study, main-stem node number was unaffected by cultivar or sand flux density treatment and averaged 9.6 ± 0.8 nodes by the end of this experiment.

Since RGR is the product of LAR and NAR, variation in RGR is often analyzed by examining changes in LAR and NAR. The LAR is a morphological trait, whereas NAR is more of a physiological trait. The NAR is not exactly the same as net photosynthesis, but the two are usually correlated (Körner, 1994). Thus, growth rate is dependent on leaf area as well as average net assimilation on a leaf area basis. Differences among plant species in RGR are often associated with concomitant changes in LAR rather than NAR (Poorter, 1989; Poorter et al., 1990). Conversely, Villar et al. (2005) found that under a fluctuating environment in the field, the relative importance of NAR vs. LAR in determining RGR depended on the time frame under consideration. In that experiment, the NAR predominated over short time intervals while LAR became more important over longer time intervals. This was attributed to NAR being sensitive to short-term environmental fluctuations (light, temperature, etc.). During longer time intervals, the plant integrates environmental variability and so morphological features such as LAR predominately determine RGR (Villar et al., 2005).

As noted above, interpretation of the reduction in RGR with increasing sand abrasion treatment during the first

Fig. 3. Relative growth rate (RGR) and net assimilation rate (NAR) averaged over three cotton cultivars vs. sand abrasive flux density treatment. Control treatment (open symbol) was excluded from the indicated regression. Error bars are ± SE.
harvest interval is complicated by the shedding of leaves and petioles along with varying amounts of regrowth among treatments. Surprisingly, LAR was remarkably constant over this first harvest interval (Table 3), while NAR tracked similar trends as RGR (Fig. 3). In a previous study, whole plant photosynthesis of wheat plants was sharply reduced by sand abrasion treatments, but when expressed on a live leaf area basis, photosynthetic rate increased by 8 to 18% while respiration expressed on a live leaf area basis increased by 28 to 35% (Armbrust, 1968, 1982). In the first harvest interval, increased dark respiration rate for plant tissue repair may be an important aspect influencing the reduction in NAR with increasing sand abrasion damage. Planned research at this location will examine the role of the plant gas exchange processes in response to plant injury from sand abrasion. We will test whether whole plant photosynthesis is being regulated via the creation of new sinks or the destruction of existing sources (e.g., defoliation).

As plants age and increase in size, RGR is typically reduced as the plant invests relatively more new biomass into less physiologically active support tissue such as stems and/or petioles. An example of this effect can be seen in Fig. 3 by comparison of untreated controls (open symbols) for the first vs. the second harvest intervals. In this case, RGR of the untreated controls plants was 8.4 ± 0.4 g kg–1 Tu–1 in the first harvest interval, compared with 5.6 ± 0.3 g kg–1 Tu–1 in the second harvest interval.

Following sand abrasion treatment, plants in the 0.5 g cm–1 width s–1 treatment were ultimately defoliated of nearly all leaves and petioles that existed on the plants at the time of sand abrasion treatment. This was followed by regrowth of new plant material during Harvest Interval 1. If we assume instantaneous defoliation at the time of sand abrasion treatment with only stem and root components remaining (e.g., setting the leaf and petiole compartments of the 0.5 g cm–1 width s–1 = 0.0 g on the first destructive sample) and recalculating a theoretical RGR across harvest interval 1 yields different results. In this case, using only root and stem mass for the first destructive sample and all plant material measured on the second destructive sample results in an estimated RGR of 5.6 ± 1.0 g kg–1 Tu–1 compared with 8.4 ± 0.4 g kg–1 Tu–1 for the previously noted untreated control. This difference between these two estimates (5.6 vs. 8.4) points to the importance of viable leaf tissue for light interception and growth, but also suggests the possibility that sand abrasion injury may impact the plant more severely than a comparable reduction in plant leaf area from, for example, pruning alone. In the second harvest interval, RGR of the control (5.5 ± 0.4) and the 0.5 g cm–1 width s–1 treatment (6.3 ± 0.8) were not significantly different (Fig. 3) despite large differences in plant size (Table 2). This, combined with the relatively uniform partitioning of biomass among plant organs (Interval 2, Table 3), points to a remarkable ability of plants to rapidly recover from this type of environmental disturbance and regain stable allometric allocation of biomass among plant organs.

In the second harvest interval, both RGR and NAR reached an apparent peak in the 0.25 g cm–1 width s–1 treatment (Fig. 3). Reasons why this peak occurred at the 0.25 g cm–1 width s–1 treatment are not readily apparent, but may have been associated with differences in the trends in total biomass vs. abrasive flux density between the second and third harvests shown in Fig. 2. Significant differences in LAR were detected among sand abrasion treatments, but these differences were relatively small and showed no consistent trend with sand abrasion treatment (Table 3). Although absolute plant growth was decreased with increasing sand abrasion treatment (Fig. 2), there are previous reports where small amounts of sand abrasion actually stimulated growth (Armbrust, 1968, 1982). Again, measurement of whole plant photosynthetic gains and respiratory losses will be needed to shed further light on the physiological underpinnings of the trends in RGR and NAR reported here. There is a need to identify physiological or
morphological traits that provide resistance to sand abrasion and enhanced recovery of damaged plants.

CONCLUSION

Sand abrasive flux density treatments reduced plant biomass and leaf area. While small significant differences in LAR were detected among sand abrasion treatments, RGR depended mainly on NAR rather than LAR. Differences in RGR and NAR among cultivars were not significant in this experiment. By using a functional three-compartment model of biomass allocation consisting of leaves, stems + petioles, and roots, we found preferential net allocation of biomass to the injured stems following sand abrasion injury during the first harvest interval. By the second harvest interval we observed much more stable allometric allocation of biomass among plant organs. Whole plant measurements of net photosynthesis and dark respiration are needed to gain further insight into the underlying physiological mechanisms of plant injury and recovery reported here. Results of this type should point to physiological traits that could be selected to develop cotton cultivars better able to withstand and recover from sand abrasion injury.

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REFERENCES


