Seed production in weedy Setaria spp.-gp

M. J. Haar
Iowa State University

Jack H. Dekker
Iowa State University, newweedbiolab@gmail.com

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Disciplines
Agricultural Science | Agriculture | Agronomy and Crop Sciences | Weed Science

Comments
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INTRODUCTION
The success of the Setaria species group [S. faberi Herm., giant foxtail; S. viridis (L.) Beauv., green foxtail; S. pumila (L.) Beauv., yellow foxtail] as weeds is due in part to seed production [the seed rain] under a wide range of environments and to high reproductive output under favorable conditions. The production of many dormant seed disperses germination over time and soil seed pools allow Setaria to persist at a locality. These adaptive traits provide Setaria the ability to seize and exploit opportunity in local agroecosystems.

Seed production is an emergent property of Setaria reproductive morphology. Seed numbers produced by a Setaria are a function of differences in plant architecture: shoot tillering-panicle formation, panicle-fascicle branching, and fascicle spikelet-floret development. Inherent plastic differences in these reproductive structures among Setaria species determine the reproductive responses of species and populations to available opportunity in its immediate environment.

Setaria panicle inflorescences develop at the terminal ends of shoot tillers. Panicles that develop at the end of the main shoot are referred to as primary panicles [1°; Figure 1]. Secondary panicles [2°] arise at the nodes of the primary tiller, and tertiary panicles [3°] are those that branch laterally from secondary tillers. Developmentally, primary panicles flower first on a plant, followed by secondary, then tertiary. Setaria spp., panicles are composed of fascicles, which consist of spikelet [with florets] and bristle [seta only] shoots [Narayanaswami, 1956; figure 1]. The fascicle-spikelet structure differs among Setaria species. In S. faberi or S. viridis the number of fascicles within each panicle varies, a plastic response to a plant's immediate environment [Clark and Pohl, 1996]. Longer, earlier developing S. faberi or S. viridis panicles often have the most extensive fascicle branching, as well as more spikelets per fascicle [typically 4-6 or more per fascicle]. The plastic response of S. faberi or S. viridis to its immediate environment is also revealed in the number of spikelets-florets

Keywords: seed rain, tillering, panicle, plasticity, prediction, fecundity

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Abstract

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that fully mature, which determines the seed number per panicle length [seed density]. Under favorable conditions more spikelets are able to develop into seeds, while under unfavorable conditions spikelets may abort. S. pumila panicle morphology is different from that of S. faberi or S. viridis. Only a single, terminal, spikelet-floret is found in each S. pumila fascicle [Clark and Pohl, 1996]. This stable, fixed morphology limits the ability of S. pumila to respond in a plastic way to its environment in terms of seed number relative to that of S. faberi or S. viridis.

In addition to morphological traits, genotype and environmental interact to influence the productivity of individual Setaria plants. Weedy Setaria species contain a relatively low degree of genetic variation compared to other species, but there exists significant genotypic and biotypic variation within and among S. viridis and S. pumila which may be associated with differences in seed production [Hubbard, 1915; Norris and Schoner, 1980; Santelmann and Mead, 1961; Schoner, 1978; Schreiber and Oliver, 1971; Wang et al., 1995a; Wang et al., 1995b]. The local environment also affects Setaria growth and seed production [Lee and Cavers, 1981; Nadeau and Morrison, 1986; Santelmann and Meade, 1961; Santelmann et al., 1963; Schreiber, 1965; Van den Born, 1971].

Assessment and prediction of Setaria seed production, additions to the local agricultural soil seed pool, is of considerable importance to weed management systems [Freckleton and Stephens, 2009; Holst et al., 2007; Dekker, 2011]. Rapid estimation of seed production of weedy infestations has stimulated considerable research to discover the relationship of panicle size and seed numbers. The relationship between seed number and panicle length has been described for three Setaria species as stable across environments [Barbour and Forcella, 1996; Forcella et al., 2000] and has been used to estimate Setaria seed production [Defelice et al., 1989; Fausey et al., 1997]. This relationship has also been shown to be stable in E. crus-galli [Norris, 1992]. The values reported for Setaria seed production may not be reliable due to both the methodologies used to determine seed production and environmental variability. Although Setaria panicles and seeds develop over a period of time [e.g., ca. 60 d; Haar and Dekker, 1995], it is common to find reports of seed production based on a single or periodic harvests [Biniak and Aldrich, 1986; Defelice et al., 1989; Fausey et al., 1997; Kawano and Miyake, 1983; Knake, 1972; Nadeau and Morrison, 1986; Santelmann and Meade, 1961; Schreiber, 1965; Wall, 1993]. Values determined by such methods represent only a fraction of total seed production. There is little consistency in the degree of maturity of plants from which seed is harvested or the units of measure for Setaria seed production. Seed production has been reported on per panicle [Biniak and Aldrich, 1986; Santelmann et al., 1963], per panicle length [Fausey et al., 1997], per plant [Kawano and Miyake, 1983; Nadeau and Morrison, 1986; Schreiber, 1965; Wall, 1993] or per area basis [Defelice et al., 1989]. The relationship between panicle length and seed number may also be compromised by the lack of information about whether this relationship pertains under a variety of environmental conditions.

We have made the relationship between seed number and panicle length the subject of further investigation, in particular its validity and consistency among Setaria species, panicle types and environments. An accurate measure of seed production could improve the understanding of Setaria population dynamics and assist in the development of more efficient weed management systems. Conversely, highly variable relationships between Setaria panicle length and seed production may provide us some understanding of stability and plasticity in Setaria reproduction.

The first objective of this study was to provide an accurate measure of Setaria seed production by collecting the entire seed output of individual panicles throughout the seed rain period. Secondly, seed production and panicle length were compared among the three Setaria species, developmental panicle types and sites. We hypothesized that although differences in seed production and panicle length may exist among Setaria species, panicle types and sites, the relationship between seed number and panicle length would be stable across environments. Evaluating this hypothesis was the third objective.

MATERIAL & METHODS
Species and sites
The three weedy Setaria species in this study frequently occur together in Iowa agricultural fields; their presence and relative proportion varies widely by locality [Wang et al., 1995a; Wang et al., 1995b]. S. faberi, S. viridis and S. pumila were selected for experimental study at three sites near Ames, Iowa, in 1995. Site selection criteria included a diversity representative of central Iowa agricultural production, and a representative sample of
individual plant sizes occurring at those sites [table 1].

**Seed Collection**

Panicle type was determined at anthesis and bagged. Bagging occurred between July 25 and September 8, 1995 when the panicles were covered with 7.6 by 25.4 cm mesh pollination bags [Delnet non-woven fabrics, Applied Extrusion Technologies Inc. Middletown, DE 19899, USA] held in place with wire. No more than two bags were attached to a plant. Panicles were harvested on October 10 and 12, 1995. A killing frost on September 21 prevented a few late tertiary S. glauca panicles from completing maturation.

**Data Collection**

Panicles and seed were removed from bags after harvest, and length was determined by measuring from the panicle tip to the point of attachment for the most basal fascicle [Norris, 1992]. Seed that remained attached to the panicle was removed. Seed was cleaned with an air flow cleaner to remove aborted and sterile spikelets and debris, weighed, and electronically counted.

**Statistical Analysis**

Means were calculated for seed number per panicle, panicle length and seed density [seed number per unit panicle length] for *Setaria* species, panicle types and sites. Paired t-tests [\(\alpha=0.05\)] were used to separate means and slopes for all parameters among panicle types within a species and site, among sites within a species and panicle type, among species within a site and among sites within a species. Linear models best described [highest R² value] the relationships between panicle length and seed number, and of panicle length and seed number per panicle length. The linear regression procedure of SAS [1989] was used for analysis.

**RESULTS**

**Setaria Species**

*Setaria faberi*. *S. faberi* seed number [SN], panicle length [PL] and seed density [SPD] was greater for primary [1°] than for tertiary [3°] panicles, with a single exception in SPD at a site A [Tables 2, 3, 4; comparison 1]. For all parameters, secondary [2°] panicles were either similar to or greater than 3°. When differences occurred among sites within a panicle type, SN, PL and SPD were greater at site B than at the other sites, with the exception of 3° panicles, which usually did not differ among sites [Tables 2, 3, 4; comparison 2]. Averaged over all panicle types, SN, PL and SPD were similar at all sites, with a single exception in which seed density was greater at site B than C [Tables 2, 3, 4; comparison 4].

The ability of the linear model to describe the relationship between PL and SN or SPD [R²] varied widely among sites and panicle types. The change in SN with PL was greater in 2° panicles than that observed for 3° panicles at two of the three sites [Table 5, comparison 1]. The secondary and 3° panicles at site C did not show a change in SN with panicle length. No difference in the relationship between SN and PL was observed between 1° and 2° panicle types at any of the three sites. Differences in the SPD per panicle length relationship were not found among panicle types at any site.

Comparisons within individual *S. faberi* panicle types among sites revealed that differences were largely due to changes in secondary and 3° but not 1° panicles [Table 5, comparison 2]. Changes in SN and SPD with panicle length were similar in 1° tillers at all three locations. Changes in 2° *S. faberi* SN and SPD with panicle length were greater at site B compared to both other sites. Changes in 3° *S. faberi* SN and SPD with panicle length were greater at site B compared to site C.

When averaged over all three panicle types [Table 4, total] *S. faberi* SN per panicle was correlated with panicle length. Greater change in SN with changes in PL were observed at site B compared to the other two sites [Table 5, comparison 3]. Site B also revealed a greater change in SD with PL. Unlike at sites A and C, *S. faberi* SD at site B increased as PL increased.

*Setaria viridis*. Primary panicles were greater in SN, PL and SPD than 3° tillers at both sites and secondary panicles were either greater or similar to tertiary panicles [Tables 2, 3, 4; comparison 1]. Whether averaged over all panicle types or compared by individual panicle type, SN, PL and SPD in green *Setaria* were similar at both sites [Tables 2, 3, 4; comparisons 2 and 4].

Changes in SPD with panicle length were similar for all panicle types [Table 4 comparison 1] at site C, but lower for 3° panicles at site A. Comparisons within individual *S. viridis* panicle types between sites revealed differences for 3° panicles, but not 1° or 2° panicles [Table 5, comparison 2]. The change in SN or SPD with 3° panicle length was greater for site A than site C. *S. viridis* SN and SPD changed with panicle length at both sites when averaged over all three panicle types [Table 5, comparison 3]. The rates of increase were similar at both sites for either the SD or SN to panicle length relationship.
Setaria pumila. Seed number, PL and SPD in 1° S. pumila tillers were either greater than or similar to those in 2° tillers, depending on the site in which the comparison was made [Tables 2, 3, 4; comparison 1]. Differences between 1° and 2° panicles were not observed in S. pumila at site C. For all three parameters, 1° and 2° panicles at site B were either greater than or similar to comparable types at the other sites. Tertiary S. pumila panicles, however, were similar for all parameters at all sites in which they were sampled [Tables 2, 3, 4; comparison 4]. Inferences about S. pumila were compromised because no 3° panicles occurred at site A. High plant density is thought to be responsible for the absence of S. pumila 3° panicles. When averaged over panicle types, the SN, PL and SPD for S. pumila at site B were either similar to or greater than those at the other sites [Tables 2, 3, 4; comparison 4]. Comparisons among sites for individual S. pumila panicle types revealed no differences in terms of changes in SN or SPD with changes in panicle length [Table 5, comparisons 1 and 2]. Seed number did not change with PL in 1° S. pumila panicles at sites B and C, in 2° at site C, or in 3° at either site [Table 5]. The only change in SD with changes in PL occurred in 2° panicles at site A. When averaged over all three panicle types, the number of S. pumila seed per panicle increased with PL at all three sites, while SD increased at two sites, [Table 5 comparison 3]. The degree of change was similar at all three sites for both parameters.

Setaria Species-Group
Relative differences in mean PL, SN per panicle and SPD between species often changed among sites. When averaged over panicle types, variation was large; however, some consistent.

DISCUSSION

Setaria Seed Production
Previous reports of Setaria seed production may have underestimated the seed rain. We found a higher number of seed per panicle at each site [Table 2] compared to that previously reported for S. faberi, [Biniak and Aldrich, 1986: 207 seeds seeds per panicle] or [Defelice et al., 1989: 110 to 280 seeds per panicle]; for S. viridis, [Wall, 1993: 437 to 577 seeds per panicle] or [Van den Born, 1971: 350 to 500 seed per panicle]. The mean number of S. faberi seed per panicle in this study is greater than that reported for the entire S. faberi [220, 730 and 2,423 seeds per plant], S. viridis [234] or S. pumila [199] plant in two studies by Kawano and Miyake [1983]. These differences in seed number could be due to differences in collection technique, duration of time over which seed was gathered, genotypic responses or differences in resource availability and conditions at individual sites. Conversely, our data may still be an underestimate because the pollenation bags used to capture seed may have decreased the final seed yield by shading the panicle.

Plasticity and Stability in Setaria Seed Production
In this study all observed seed production parameters were plastic. This variability was revealed at several levels of plant organization: Setaria species, tiller branches and individual panicles. In some instances seed production was stable, and independent of the interaction between the biological factors and the site they grew on. More typically, individual Setaria species, tillers and panicles responded to the site they grew on in a plastic way, confounded the formulation of generalizations about panicle length and seed number. Few consistent observations were made about seed productivity between the three Setaria species. Some species and parameters were consistent [stable] in different environments, while others were plastic in response to site conditions. S. faberi and S. pumila seed production usually was greater at site B within each of the individual panicle types. But, S. pumila seed and panicle parameters were usually greater at site B when averaged over types, unlike the other two species. The productivity of tiller panicle types in S. viridis was similar at both sites in which it was evaluated. Earlier-maturing panicle types [e.g., primary] of all species usually were more productive than later maturing panicles [e.g., tertiary].

As conditions changed, each Setaria species adjusted its seed productivity in a plastic manner, but the way this plasticity was expressed differed in each of the individual species. Within individual panicles of any type, seed production plasticity was expressed in two ways. First, the seed number per panicle could change with changing panicle length [Table 5, seed number per panicle length]. Second, seed density could change with changing panicle length [Table 5, seed density per panicle length].

For S. faberi, intra-panicle plasticity among sites was indicated by differences in the relationship [slope] between secondary and tertiary panicle seed number and density with changes in length. For S. viridis, intra-panicle plasticity was only observed in tertiary panicles,
in which the relationship between seed number and density changed with changing panicle length. A stable relationship [slope] between seed number and density with changing panicle length was observed more frequently among primary S. faberi and S. viridis panicles.

S. pumila was more stable than S. faberi and S. viridis in response to changing site conditions, and generalizations about panicle length and seed number may be possible. Changes in S. pumila seed number with panicle length was more stable than in the others, and even less plastic than S. viridis or S. faberi in response to changes in seed density. These species differences may be a function of differences in panicle branching and fascicle organization [Clark and Pohl, 1996]. S. pumila panicle fascicles contain a single fertile spikelet, while in S. viridis and S. faberi fascicles can support one or more fertile spikelets depending on resources and conditions. S. pumila stability also occurs at the level of panicle type. No differences between primary, secondary or tertiary panicles were observed within a site in changes in seed number and density with panicle length.

Plasticity and Prediction in Setaria Seed Production

This study indicates that Setaria traits such as seed number per panicle, panicle length, and seed density possess both stable and variable attributes. These traits were often plastic, but there appeared to be a limit to the range within which these plastic responses occur. The relative differences in panicle length among species, sites and panicle types revealed these limits to plasticity. Although many of these characteristics were variable, some consistent observations occurred. S. faberi had longer panicles than S. viridis. S. viridis panicles had a greater number of seed and higher seed density than yellow. Earlier-developing panicle types were always greater than or similar to the later developing panicle type for each of the parameters measured. Where a difference among sites was found, the values from site B were always the greatest. All other comparisons varied.

The correlation between seed number and panicle length was not constant across environments or panicle types. It is evident that estimates of seed production based on the panicle length must be population and panicle-type specific for S. faberi and perhaps for S. viridis. Comparatively little change in seed density with length for S. pumila was observed, indicating generalizations and predictions of seed rain may be possible in this species as it is in others [Norris, 1992]. The observed degree of variation among these characteristics calls into question the accuracy of estimating seed production based on panicle length for S. faberi or S. viridis as proposed by some [Barbour and Forcella, 1993; Fausey et al., 1997; Forcella et al., 2000].

Plastic responses to changing conditions allows an individual Setaria species, tiller and plant to finely adjust its seed production to highly localized conditions. Although this plasticity confounds our ability to develop quick, accurate predictive tools about the seed rain, it allows the individual weed to exploit the conditions and resources available to maximum advantage. While selection over many generations has resulted in a degree of phenotype stability, plasticity can be highly advantageous to these plants and is preserved [Sultan, 1987].

REFERENCE


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KAWANO, S.; MIYAKE, S., (1983). The productive and reproductive biology of flowering plants X. Reproductive energy allocation and propagule output of
five congeners of the genus *Setaria* (Gramineae). Oecologia., 57, 6-13.


### Table 1. Site cropping (crop, weed control) and weed (species, population size) experimental information.

<table>
<thead>
<tr>
<th>Site</th>
<th>Crop</th>
<th>Weed control</th>
<th>Setaria spp.</th>
<th>Weed population size</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>S. faberi</td>
<td>S. viridis</td>
</tr>
<tr>
<td>A</td>
<td>soyaabean</td>
<td>none</td>
<td>S. viridis</td>
<td>S. pumila large (277-2903 plants per m²)</td>
</tr>
<tr>
<td>B</td>
<td>maize</td>
<td>inter-row cultivation</td>
<td>S. pumila</td>
<td>low</td>
</tr>
<tr>
<td></td>
<td>soyaabean</td>
<td>inter-row cultivation</td>
<td>S. faberi</td>
<td>low</td>
</tr>
<tr>
<td>C</td>
<td>maize</td>
<td>inter-row cultivation</td>
<td>S. viridis</td>
<td>low</td>
</tr>
</tbody>
</table>

### Table 2. Mean (m) seed number and standard error (SE) for *Setaria* species (S. faberi, S. viridis, S. pumila) panicle types (P; 1°, primary; 2°, secondary; 3°, tertiary) and panicle number (n) at three Ames, Iowa sites (A, B, C).

<table>
<thead>
<tr>
<th>Site A</th>
<th>Site B</th>
<th>Site C</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. SE</td>
<td>No. SE</td>
<td>No. SE</td>
</tr>
<tr>
<td>1 2 3 4</td>
<td>1 2 3 4</td>
<td>1 2 3 4</td>
</tr>
</tbody>
</table>

- **Comparison**
  - a: within a species and site, among panicle types (within a column)
  - b: within a species and panicle type, among sites (within a row)
  - c: within a site, among species (within a column)
  - d: among sites, within a species (within a row)

Means within a comparison followed by the same letter are not significantly different (P=0.05) as determined by t-tests.
### Table 3

Mean (m) panicle length (cm) and standard error (SE) for Setaria species (S. faberi, S. viridis, S. pumila) panicle types (P; 1°, primary; 2°, secondary; 3°, tertiary) and panicle number (n) at three Ames, Iowa sites (A, B, C).

A = within a species and site, among panicle types (within a column); B = within a species and panicle type, among sites (within a row); C = within a site, among species (within a column); D = among sites, within a species (within a row). Means within a comparison followed by the same letter are not significantly different (P > 0.05) as determined by t-tests.
Seed production in weedy Setaria spp.

Table 4. Mean (m) seed number per panicle length (cm; seed density) and standard error (SE) for Setaria species (S. faberi, S. viridis, S. pumila) panicle types (P; 1°, primary; 2°, secondary; 3°, tertiary) and panicle number (n) at three Ames, Iowa sites (A, B, C).

<table>
<thead>
<tr>
<th>Site</th>
<th>P</th>
<th>n</th>
<th>m</th>
<th>SE</th>
<th>1°</th>
<th>2°</th>
<th>3°</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site A</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Site B</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Site C</td>
<td></td>
<td></td>
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</tbody>
</table>

Means within a comparison followed by the same letter are not significantly different (P>0.05) as determined by t-tests.
Table 5. Linear regression and comparisons of slopes (± s.e.) and coefficients of determination (R²) describing the relationships between panicle length and seed number, and of panicle length and seed number per panicle length, for Setaria species (S. faberi, S. viridis, S. pumila) and panicle types (P; 1°, primary; 2°, secondary; 3°, tertiary) at three Ames, Iowa sites (A, B, C).

<table>
<thead>
<tr>
<th>Site</th>
<th>Panicle length-Seed number</th>
<th>Panicle length-Seed number per length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>SE</td>
</tr>
<tr>
<td>A</td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1°</td>
<td>38.7</td>
<td>95.0</td>
</tr>
<tr>
<td>2°</td>
<td>48.2</td>
<td>19.7</td>
</tr>
<tr>
<td>3°</td>
<td>75.9</td>
<td>23.9</td>
</tr>
<tr>
<td>Tot</td>
<td>56.8</td>
<td>20.4</td>
</tr>
<tr>
<td>B</td>
<td>Setaria viridis</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1°</td>
<td>149.7</td>
<td>113.8</td>
</tr>
<tr>
<td>2°</td>
<td>153.4</td>
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<tr>
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<td>6.0</td>
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<tr>
<td>Tot</td>
<td>172.4</td>
<td>27.6</td>
</tr>
<tr>
<td>C</td>
<td>Setaria pumila</td>
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<td>1°</td>
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<tr>
<td>Tot</td>
<td>39.5</td>
<td>7.2</td>
</tr>
</tbody>
</table>

**Figure 1.** Schematic diagram of weedy *Setaria* species-group reproductive shoot architecture and panicle structure; tiller and panicle types (1°, primary; 2°, secondary; 3°, tertiary): left; fascicle branching (F₁,F₂) on panicle axis: top, right; fascicle structure and arrangement of bristle (seta) shoots (BS) and spikelet shoots (SS) along rachilla axis: *S. pumila* (bottom, middle); *S. viridis* and *S. faberi* (bottom, right).