Reproductive Allocation of Cotton in Response to Plant and Environmental Factors

V. O. SADRAS*, M. P. BANGE and S. P. MILROY

CSIRO Plant Industry, Locked Bag 59, Narrabri, NSW 2390, Australia

Received: 28 October 1996 Accepted: 23 January 1997

We measured the responses of cotton reproductive allocation (reproductive dry matter/total shoot dry matter) to environmental and plant factors in five field experiments. A wide range of growing conditions were generated by manipulation of sowing date, nitrogen fertilizer, and plant density. Plant factors that varied included phenological development (short- vs. long-season cultivars), and leaf morphology (normal- vs. okra-leaf types). We quantified the relationships between reproductive dry matter and shoot dry matter using allometric analysis, and calculated the daily rate of increase in reproductive allocation. Shoot dry matter ranged from 4 to 235 g per plant, and reproductive dry matter from negligible to 138 g per plant. Within these ranges, the linear regression between log₁₀ reproductive dry matter and log₁₀ shoot dry matter had an $r^2 = 0.81$ ($P = 0.0001$). Differences among experiments were significant, but they accounted for only a small proportion of the variance of reproductive dry matter (8%). The dynamics of reproductive allocation followed a logistic pattern. The rate during the linear phase of increase in reproductive allocation was fairly stable across experiments (± 0.006 d⁻¹). The effect of experiments was significant, but it accounted for only 7% of the variance in the rate of reproductive allocation increase. Analysis of treatment effects on both allometric coefficients and on the rate of increase in reproductive allocation showed that: (a) few of the sources of variation included in these experiments caused significant changes in reproductive allocation; and (b) when significant changes occurred, their magnitude was comparatively small. The relative stability of cotton reproductive allocation suggests that for some applications simple models can be developed on the basis of a fixed rate of increase in reproductive allocation.

Key words: Gossypium hirsutum L., cotton, reproduction, allometry, harvest index, allocation, nitrogen, plant density, okra leaf, phenology.

INTRODUCTION

Reproductive allocation (reproductive dry matter/total shoot dry matter) is an important component of plant fitness (Bazzaz et al., 1987). Chiarello and Gulmon (1991) examined the responses of reproductive development to environmental stresses and highlighted the strong coupling that exists between the reproductive and vegetative growth of plants. As they pointed out, the coupling is implicit when reproduction is viewed as a form of resource partitioning.

Reproductive allocation is also a major determinant of economic yield in seed crops (Gifford et al., 1984). Increased partitioning of dry matter to reproductive organs accounts for much of the progress in breeding for high yield potential in wheat (Triticum aestivum L.), barley (Hordeum vulgare L.), oat (Avena sativa L.), rice (Oryza sativa L.), maize (Zea mays L.), and sunflower (Helianthus annuus L.) (Slafer, 1994).

In grain crops, harvest index (seed dry matter/total shoot dry matter) is a measure of reproductive allocation. In reviewing the concept of harvest index and its application in plant breeding and crop physiology, Hay (1995) pointed out that in the absence of severe stress, major environmental factors have little influence on harvest index. Hay (1995) also emphasized the high heritability of this trait in several species. The dynamics of harvest index have usually been described with a logistic function and a number of studies have concentrated on the stability of harvest index increase during the linear phase of seed growth. Effects of genotype and/or environmental conditions on the rate of harvest index increase during this phase have been investigated in soybean [Glycine max (L.) Merr.] (Spathe and Sinclair, 1985), sorghum [Sorghum bicolor (L.) Moench] (Muchow, 1990), barley (Goyne et al., 1996), wheat (Moot et al., 1996) and sunflower (Chapman, Hammer and Meinke, 1993). The relative stability of the rate of harvest index increase found in some of these studies implies that ‘grain yield accumulation can be estimated from crop biomass at any stage of grain growth without knowledge of grain number or the rate of grain growth’ (Muchow, 1990). For some applications this simple approach to modelling crop yield could be useful, as illustrated by the models of Chapman et al. (1993) and Goyne et al. (1996).

Studies of reproductive allocation are therefore important in understanding both the adaptation of wild plants to their natural environments and the physiology of yield determination. Quantitative relationships to account for the effects of plant and environmental factors on reproductive allocation are essential components of crop simulation models. In cotton (Gossypium hirsutum L.), lint yield is closely related to fruit production (e.g. Hearn, 1975).
The objective of this study was to evaluate the variation in cotton reproductive allocation caused by environmental and plant factors. A range of contrasting growing conditions was available through manipulation of sowing date, nitrogen fertilizer and plant density. Plant factors that varied included leaf morphology, viz. normal- vs. okra-leaf, and phenological development, viz. short- vs. long-season cultivars. The okra-leaf trait is linked with a high rate of flowerbud production (Thomson, 1995), and this could cause differences in reproductive allocation between normal- and okra-leaf types. Likewise, short season cultivars are expected to have earlier reproductive growth and/or greater rates of increase in reproductive allocation (Spaeth and Sinclair, 1985; Chiarello and Gulmon, 1991).

In this study we used two analytical methods: firstly, allometric analysis of the relationship between reproductive dry matter and shoot dry matter was used to separate changes in partitioning related to plant size or ‘ontogenetic drift’ (Evans, 1972) from changes in partitioning related to other sources of variation (Coleman, McConnaughay and Ackerly, 1994). Secondly, we calculated the rate of increase in reproductive allocation with time, a method that allows comparisons with other species.

**MATERIALS AND METHODS**

**Crops and treatments**

Five experiments were conducted at Narrabri, a semi-arid environment in NW New South Wales, Australia (30°13’ S, 149°47’ E). Crops were furrow-irrigated at approx. 14 d intervals; weeds were controlled with pre-sowing herbicides and manually through the season, arthropod pests were monitored twice weekly and controlled with chemicals following the guidelines in entomoLOGIC, a pest management package used in commercial cotton farms (McKewen et al., 1994).

Treatments are summarized in Table 1. Experiment 1 compared two short season cultivars of different leaf morphology (Siokra S324, okra leaf vs. CS7S, normal leaf) grown under contrasting availability of resources: low, resulting from high plant density and no nitrogen fertilization; and high, resulting from low plant density and high nitrogen rate. No attempt was made to separate the effects of plant density and fertilization, which would have required a fully factorial experiment, but rather the treatments were designed to generate extreme growing conditions, as described in Sadras (1996). Experiment 2 compared two plant population densities. Experiment 3 combined two cultivars of contrasting leaf morphology (Siokra 1–4, okra leaf vs. Deltapine 90, normal leaf) and two rates of nitrogen application at high plant density. Experiment 4 compared normal and okra-leaf cultivars. Experiment 5 compared short- (Siokra S324) and long-season (Siokra L22) cultivars at three sowing dates.

All experiments included four replicates per treatment. Treatments were laid out in completely randomized blocks (expts 1, 2, 4 and 5) or a split-plot design with nitrogen rate as main plot and cultivar as sub-plot (expt 3). Individual plots comprised 5 rows × 17 m (expts 1 and 2), 6 rows × 17 m (expt 3), 6 rows × 25 m (expt 4), and 4 rows × 75 m (expt 5). In all experiments inter-row distance was 1 m.

**Measurements**

Dry weights of shoots and of reproductive organs (flowerbuds, green fruit and mature fruit) were obtained

---

**Table 1. Summary of treatments in five field experiments at Narrabri and reproductive allocation measured at the end of the growing season**

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Season</th>
<th>Treatment code</th>
<th>Sowing date</th>
<th>Cultivar*</th>
<th>Plant density (m⁻²)</th>
<th>Fertilizer (kg N ha⁻¹)</th>
<th>Reproductive allocation ± s.e. (dimensionless)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1993/94</td>
<td>A</td>
<td>23 Nov.</td>
<td>Siokra S324</td>
<td>5</td>
<td>180</td>
<td>0.63 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>23 Nov.</td>
<td>Siokra S324</td>
<td>12.5</td>
<td>0</td>
<td>0.66 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>23 Nov.</td>
<td>CS7S</td>
<td>5</td>
<td>180</td>
<td>0.68 ± 0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>23 Nov.</td>
<td>CS7S</td>
<td>12.5</td>
<td>0</td>
<td>0.70 ± 0.02</td>
</tr>
<tr>
<td>2</td>
<td>1994/95</td>
<td>A</td>
<td>12 Oct.</td>
<td>Siokra V-15</td>
<td>5</td>
<td>120</td>
<td>0.68 ± 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>12 Oct.</td>
<td>Siokra V-15</td>
<td>10</td>
<td>120</td>
<td>0.66 ± 0.03</td>
</tr>
<tr>
<td>3</td>
<td>1993/94</td>
<td>A</td>
<td>11 Oct.</td>
<td>Siokra 1–4</td>
<td>16</td>
<td>0</td>
<td>0.67 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>11 Oct.</td>
<td>Siokra 1–4</td>
<td>16</td>
<td>105</td>
<td>0.62 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>11 Oct.</td>
<td>Deltapine 90</td>
<td>16</td>
<td>0</td>
<td>0.64 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>11 Oct.</td>
<td>Deltapine 90</td>
<td>16</td>
<td>105</td>
<td>0.55 ± 0.03</td>
</tr>
<tr>
<td>4</td>
<td>1994/95</td>
<td>A</td>
<td>13 Oct.</td>
<td>Siokra 1–4</td>
<td>16</td>
<td>86</td>
<td>0.61 ± 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>13 Oct.</td>
<td>Deltapine 90</td>
<td>16</td>
<td>86</td>
<td>0.61 ± 0.02</td>
</tr>
<tr>
<td>5</td>
<td>1994/95</td>
<td>A</td>
<td>13 Oct.</td>
<td>Siokra S324</td>
<td>8</td>
<td>120</td>
<td>0.60 ± 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B</td>
<td>13 Oct.</td>
<td>Siokra L22</td>
<td>8</td>
<td>120</td>
<td>0.56 ± 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>30 Nov.</td>
<td>Siokra S324</td>
<td>8</td>
<td>120</td>
<td>0.48 ± 0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>30 Nov.</td>
<td>Siokra L22</td>
<td>8</td>
<td>120</td>
<td>0.40 ± 0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td>E</td>
<td>21 Dec.</td>
<td>Siokra S324</td>
<td>8</td>
<td>120</td>
<td>0.20 ± 0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>21 Dec.</td>
<td>Siokra L22</td>
<td>8</td>
<td>120</td>
<td>0.09 ± 0.02</td>
</tr>
</tbody>
</table>

* Siokra S324, Siokra V-15, Siokra L22, and Siokra 1–4 are okra-leaf cultivars while CS7S and Deltapine 90 are normal-leaf cultivars. Siokra L22 is a ‘long’-season, Siokra S324 and CS7S are short-season, and Deltapine 90, Siokra V-15 and Siokra 1–4 are medium-season cultivars (Constable, pers. comm.).
from samples taken from each replicate at approx. 14 d
intervals. Samples were taken at random from the central
crop rows and sample size varied between 0.5 m² (expts 1–4)
and 1 m² (expt 5). No attempt was made to separate seed,
 fibre and other fruit components.

Data analysis
Using values of reproductive dry matter (y) and shoot dry
matter (x), allometric relationships were investigated with
least-squares linear regressions of log-transformed variables
(Coleman et al., 1994). The slope of the regression, b, is an
allometric coefficient or ‘scaling factor’ (Niklas, 1993a) that
expresses the ratio between the relative growth rates of
reproductive structures and shoots (Thornley and Johnson,
1990). Regression analysis was applied to the data pooled
across experiments and differences in b among experiments
were assessed using stepwise procedures (Sokal and Rohlf,
1981). Separate regressions were also calculated for each
experiment and the effects of treatments within each
experiment on b were assessed with stepwise procedures as
before.

Reproductive allocation was calculated as the ratio
between reproductive and total shoot dry matter. The time
course of reproductive allocation followed a logistic pattern
e.g. Fig. 3A). Thermal time (Hodges, 1991) was calculated
using a base temperature of 12 °C (Constable, 1976). The
rate of change in reproductive allocation (y) with time (x)
or thermal time (x) during the linear phase was calculated
using least square regressions; points for inclusion in the
analysis were selected as in Spaeth and Sinclair (1985) and
Moot et al. (1996). Variation in the rate of increase in
reproductive allocation among experiments and in the rate
due to treatments within experiments was analysed statis-
tically as explained above for the allometric coefficient.

To account for the oil-synthesis cost of the cotton seed,
dry matter was converted to glucose equivalents using
production values of fruit and vegetative organs given by
Wall, Amthor and Kimball (1994). The responses of
reproductive allocation to environmental and plant factors,
however, were unchanged by the method used in the
calculations (i.e. dry matter or glucose equivalent) (see also
Sadras, 1997). Thus, for simplicity, and to allow for
comparisons with other studies, this paper presents results
on a dry matter basis.

RESULTS

Allometric relationships

Shoot dry matter ranged from 4 to 235 g per plant and
reproductive dry matter from negligible to 138 g per plant.
Across these ranges, the linear regression of the log-
transformed variables had an $r^2$ of 0.81 (Fig. 1A). The
experiment effect, i.e. the variation in b among experiments,
was highly significant ($P = 0.0001$), and the inclusion of this
effect in the model increased the coefficient of determination
from 0.81 to 0.89.

The allometric relationship obtained in our experiments
was compared with data from experiments of Hearn (1975)
in a tropical environment (Fig. 1B). The plants of Hearn’s
experiments were initially well below the allometric re-
liationship obtained for our plants, but differences dimin-
ished as reproductive growth progressed.

Allochronometric analysis for the treatments in each experiment
showed that plants growing under low availability of
resources (low nitrogen supply, high density) had a
significantly greater allometric coefficient than their counter-
parts grown under more favourable conditions (Fig. 2, expt
1). Allometric coefficients were unaffected by (a) leaf type (expts 1, 3 and 4), (b) plant density (expt 2), or (c) phenological development and sowing date (expt 5) (Fig. 2).

Dynamics of reproductive allocation

Changes in reproductive allocation with thermal time followed a logistic curve, as shown in the example of Fig. 3A. The only exception to this pattern was the December sowing of expt 5 (Table 1) in which plants did not reach the linear stage of reproductive allocation increase due to low temperatures which terminated plant growth. Excluding this treatment, the pooled data for the linear stage of the five experiments is shown in Fig. 3B. A linear model with thermal time as the independent variable accounted for 88% of the variation in reproductive allocation, a marginally better correlation than that obtained using time as the independent variable ($r^2 = 0.82$). The average rate of increase in reproductive allocation was $5.45 \times 10^{-4}$ (°C d)$^{-1}$ or $5.98 \times 10^{-3}$ d$^{-1}$. The experiment effect, i.e. the variation in rate among experiments was significant ($P = 0.004$) and the inclusion of this effect in the thermal-time model raised the coefficient of determination from 0.88 (Fig. 3B) to 0.95.

Analysis for the treatments in each experiment showed that in expt 1 plants grown under low availability of resources had a significantly greater rate of increase in reproductive allocation than their counterparts grown under more favourable conditions (Fig. 4). In expt 3, the rate of increase in reproductive allocation was greater in Siokra 1–4 (okra-leaf) than in Deltapine 90 (normal-leaf), but no significant differences between cultivars with different leaf morphologies were found in expts 1 and 4. Rates were also unaffected by plant density (expt 2), phenological development or sowing date (expt 5) (Fig. 4).

DISCUSSION

We used allometric analysis (Figs 1 and 2) and analysis of the dynamics of reproductive allocation (Figs 3 and 4) to explore the effects of plant type and growing conditions (Table 1) on the reproductive allocation of cotton plants. Okra-leaf cultivars have a high rate of flowerbud production compared with normal-leaf types (Thomson, 1995). Although strict comparisons should include isogenic lines for leaf morphology, comparisons between okra- and normal-leaf types with different genetic backgrounds (e.g. Deltapine 90 vs. Siokra 1–4, expt 4) have often had the resolution to detect biologically meaningful differences (e.g. Wilson, 1994). Allometric analysis showed no difference
between normal- and okra-leaf types in three experiments (Fig. 2), and the rate of increase in reproductive allocation was higher in the okra-leaf type in one out of three experiments (Fig. 4).

The rate of harvest index increase of Gokuwasechishima, an early soybean cultivar, was almost twice as high as the average rate of mid-season cultivars (Spaeth and Sinclair, 1985). Also, comparisons of plants grown in contrasting environments indicate that the stress of a shorter growing season may increase partitioning to sexual reproduction (Chiarello and Gulmon, 1991). In our study, a comparison of cultivars of contrasting phenology showed trends in the expected direction: i.e. the short-season cultivar (Siokra S324) had a greater allometric coefficient than the long-season cultivar (Siokra L22) in three sowing dates (Fig. 2, expt 5), and it also had a slightly greater rate of increase in reproductive allocation at two sowing dates (Fig. 4, expt 5). None of these differences, however, were statistically significant.

Plant density, ranging from 5 to 10 plants m⁻², did not affect reproductive allocation of well fertilized plants (Figs 2 and 4, expt 2). In contrast, plants grown under severe stress due to the combination of high population density and no fertilization had a greater reproductive allocation than their counterparts grown under more favourable conditions in expt 2 (Figs 2 and 4). This response is consistent with the high initial rate of fruit setting of nitrogen- and water-stressed cotton plants in comparison with well fertilized and frequently irrigated controls (Constable and Hearn, 1981). The responses of reproductive allocation to stress depend on (a) the resource(s) involved, viz. water, light, space, minerals, (b) interactions between stresses; and (c) plant type, e.g. perennials vs. annuals, wild vs. domesticated (Chiarello and Gulmon, 1991). In general polycarpic perennials reduce their partitioning to sexual reproduction under low availability of resources, but there are many exceptions to this rule including the case of perennials that act as annuals under stress (Chiarello and Gulmon, 1991). In all four species of cultivated *Gossypium*, a genus of perennial shrubs, annual types have been developed under domestication (Evans, 1993) that retain some perennial traits (e.g. Sadras, 1996).

The small magnitude of the changes in reproductive allocation of the plants in our experiments contrast with the apparently high responsiveness of wild plants (Chiarello and Gulmon, 1991). This could be, in part, due to intrinsic differences between wild and domesticated plants. However, it could also be that some of the changes in reproductive allocation reported for wild species are not true changes in partitioning, but rather variations associated with plant size that require allometric analysis to be resolved (Coleman et al., 1994). Using allometric analysis, Niklas (1993a, b) found a stable relationship between reproductive biomass and stem diameter for different species in each of three taxa (Pteridophytes, four species; Gymnosperms, six species; Angiosperms, two species). Likewise, allometric analysis showed that significant reductions in reproductive allocation of cotton plants caused by spider-mite (*Tetranychus urticae* Koch) infestation were not due to true changes in partitioning, but rather reflected the effects of mites on plant size (Sadras and Wilson, 1997).

We compared the allometric relationship obtained in our experiment (Fig. 1B) with data from the experiments of Hearn (1975). Hearn’s experiments contrast with ours in three aspects: (a) they included an obsolete cultivar (Deltapine 16); (b) crops were grown in a tropical environment (latitude 15° S); and (c) they were unprotected from insects during the ‘wet’ season. The initial divergence between Hearn’s data and ours is probably due to the relatively high vegetative growth caused by high temperature, and insect-induced fruit shedding (Sadras, 1995).
Once the plants were allowed to set fruit by protecting them with insecticides, they gradually reached allometric proportions similar to the plants in our experiments, which include current cultivars in a temperate environment.

Final harvest index depends on the rate of harvest index increase and the duration of the reproductive growth period. Previous studies with cotton indicate that final harvest index is fairly stable in relation to major environmental factors such as water availability, nitrogen supply and CO₂ concentration (Constable and Hearn, 1981; Orgaz, Mateos and Fereres, 1992; Kimball and Mauney, 1993). In our study reproductive allocation at the end of the growing season consistently showed relatively little variation except for expt 5, in which delaying the sowing date consistently reduced the final value of reproductive allocation (Table 1). This, together with the relative stability of the rate of change in reproductive allocation of cotton found in the present study (Fig. 3), suggests that significant changes in final harvest index are more likely to be found in cases when plant and/or environmental factors affect the duration of reproductive growth.

The stability of the rate of change in reproductive allocation of cotton is comparable to that reported for a number of cultivated species (see Introduction). The average rate of change in reproductive allocation in cotton found in this study (≈0.006 d⁻¹) is much lower than the rates reported for other species, which range from about 0.01 to 0.02 d⁻¹ (soybean, Spaeth and Sinclair, 1985; sorghum, Muchow, 1990; barley, Goyne et al., 1996; wheat, Moot et al., 1996). Given that reproductive allocation in our study included flowerbuds and whole fruits, while only seed was considered in other studies, the differences between cotton and other species are still greater. The low rate of increase in reproductive allocation of cotton, in comparison to cereals, could be related to differences in growth habit: in determinate species there is usually little vegetative growth from shortly after anthesis, while significant vegetative growth is often observed during part of the post-flowering period of cotton. Comparisons between cotton and soybean (Spaeth and Sinclair, 1985), however, indicate that the low rate of increase in cotton reproductive allocation with time cannot be completely attributed to cotton’s indeterminate growth habit. The lack of allometric analyses for other species precludes further comparisons.

In summary, few of the sources of variation included in these experiments caused statistically significant changes in reproductive allocation of cotton, and when significant changes did occur, their magnitude was comparatively small. The relative stability of cotton reproductive allocation suggests that for some applications simple models can be developed on the basis of a fixed rate of reproductive allocation increase.
ACKNOWLEDGMENTS

We thank AB Hearn for use of his unpublished data, JF Angus, GC Constable, AB Hearn and P Wright for comments on the manuscript, and the Cotton Research and Development Corporation of Australia for financial support (grants CSP39C, CSP68C, CSP57C, CSP67C).

LITERATURE CITED


