Seed production of Stylosanthes guyanensis

2. The consequences of defoliation

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Summary—The consequences of defoliation on seed production of stylo (*Stylosanthes guyanensis*) were examined in field experiments at Walkamin in north Queensland. The practical aim of defoliation is to present a level uncompacted crop canopy to the harvester without a reduction in the quantity of seed carried at harvest ripeness. It was concluded that the latest date at which defoliation is reasonably certain to achieve its objectives is about four weeks before first flower initiation. In north Queensland, this means late February for cv. Cook and Endeavour and early April for cv. Schofield.

The results suggest that development of the population of individual shoots must be synchronized to produce the highest peaks of standing seed; that this is best achieved by ensuring that a closed crop canopy with a ceiling shoot population exists at the time of first flower initiation; and that poorly synchronized shoot development is a consequence of defoliating too late and a cause of reduced seed production.

The preceding paper in this series (Loch, Hopkinson and English 1976) drew attention to the magnitude of the discrepancy between actual and target seed yields of *Stylosanthes guyanensis* (stylo). One cause of low efficiency in the harvesting of stylo is the large amount of vegetation that must be taken in by the header. Growers commonly slash their crops during the period of vegetative growth in order to produce a canopy that is both level and subject to minimum subsidence. This not only reduces unnecessary intake to a minimum at harvest, but also appears to exercise some measure of weed control.

The practice of slashing has developed without any clear knowledge of its effect on seed production, and doubts exist in particular about the optimum time to slash. To achieve the greatest benefit, this operation should be carried out as late as is possible without also reducing overall seed production.

The experiments described in the earlier paper included a number of cutting treatments with the aim of providing an understanding of the effects of defoliation (used here in the conventional sense implying removal of plant shoots—Humphreys 1966) from which such details as optimum slashing time could be deduced. This paper deals with these treatments and their consequences.

Methods

The conduct of the two field experiments, which included defoliation treatments, is described in the preceding paper. The second (1972) experiment suffered from severe *Botrytis* sp. infection which did considerable damage to the framework of the crop as well as to its seed production. We have, therefore, decided to report in detail only experiment 1 and to omit results from experiment 2 on the grounds that these would serve mainly to confuse this issue, although reference is made to them in the Discussion.

In experiment 1, a regrowing crop of cv. Cook stylo entering its second season was mown at about 22 cm height on December 4, 1970. The following defoliation treatments (applied by hand-cutting) were subsequently imposed, arranged in five randomized blocks:

A — No further defoliation;
B — Defoliated during vegetative growth (February 15–16, 1971);
C — Defoliated soon after first flower initiation (April 1–2, 1971);
D — Defoliated soon after first visible flowering (April 26, 1971).
The immediate effects of treatments B, C, and D are shown in Table 1 and figure 1. Uniformity of treatment in a succession of cuttings is not possible, since the crop structure changes greatly. Reasonable uniformity of reduction in height was achieved, but in terms of the removal of leaf and growing points this rendered the two later cuttings (C and D) rather more drastic than the first (B). Measurements taken were described in the preceding paper (Loch, Hopkinson and English 1976).

Results

Crop height
Defoliated plots never grew to the maximum height reached by treatment A (figure 1); nor did they subside to the same extent. They presented an even, uncompacted canopy at the time of crop ripeness, and thus all fulfilled the primary function of defoliation. Treatment A, on the other hand, resulted in an uneven and badly compacted canopy.

Vegetative growth
Defoliation treatments began at the time of peak LAI (figure 1b). Consequently, all re-growth proceeded during the period of progressively diminishing canopy thickness. In general, recovery took the form of maintenance of, rather than increase in, LAI. Leaf numbers per unit area (not illustrated) rose after each defoliation as did total leaf dry weight (not illustrated), but a rise in LAI was prevented by a progressive reduction of the mean area of individual leaves.

Total dry matter of tops reached a peak at about the same time as LAI, after which it remained, in the absence of defoliation, more or less constant. Defoliated plots never recovered from the reduction brought

TABLE 1
Effects of defoliation treatments in experiment 1. Each value tabulated is that remaining immediately after defoliation, expressed as a percentage of that present immediately before.

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>B</td>
</tr>
<tr>
<td>Height of stand</td>
<td>62</td>
</tr>
<tr>
<td>Density of visible growing points</td>
<td>56</td>
</tr>
<tr>
<td>Density of unfolded leaves</td>
<td>49</td>
</tr>
<tr>
<td>LAI</td>
<td>45</td>
</tr>
<tr>
<td>Stem dry weights</td>
<td>93</td>
</tr>
<tr>
<td>Leaf dry weights</td>
<td>41</td>
</tr>
<tr>
<td>Total tops dry weights</td>
<td>84</td>
</tr>
</tbody>
</table>

Figure 1—Experiment 1, 1971. Changes in crop heights, leaf area indices, and density of growing points in relation to defoliation treatments. Vertical lines connecting A with B, C, and D mark the occasions of defoliation.
about by cutting, total dry matter tending, if anything, to diminish after treatment.

Shoot and inflorescence development
Vegetative recovery in treatment B was, in all relevant details, completed by the time of first flower initiation (day 85), and the treatment had no significant effect on populations of growing points and floral spikes during the reproductive phase (figure 2). Treatments C and D, however, both delayed the start and retarded the course of reproductive development, resulting in substantially lower maximum measured densities of growing points and floral spikes.

The effect of treatment on the development and success of individual florets within the floral spikes is
difficult to determine, since it is not always possible to separate the effects. At each harvest, the relative immaturity of spike populations from treatments C and D was apparent, but beyond this, little could be specifically attributed to treatment. The distinct fall in the percentage of successful seed sites measured at the final two harvests (figure 2b), for example, suggests a deteriorating environment for seed setting rather than a direct treatment effect.

Seed production
The production of seed (figure 2c) closely followed the patterns of development previously set by the populations of growing points and floral spikes. Plots of treatments A and B behaved similarly, with high and well defined peaks of standing seed at about day 200, followed some 7–14 days later by peaks of retrievable fallen seed. Seed production was both delayed and depressed as a result of the later defoliations, however, and although the experiment ended before clear peaks were reached in treatments C and D, the seasonal deterioration in conditions for growth precludes any further prospect of substantial recovery.

Discussion
Defoliation performed early enough to permit full recovery of the vegetative framework before flower initiation began had no effect on seed production. Defoliation performed later, however, adversely affected both the quantity produced and the pattern of production. Although admittedly more severe than treatment B in terms of removal of both photosynthetic surfaces and bud sites, the later defoliations produced results that favour the argument that their timing was more critical than their severity in its effects on seed production.

The spread of flowering in time may be viewed as having two components: one due to age differences between florets within each spike and spikes on each shoot, and the other due to age differences between individual shoots. Floral differentiation proceeds in a recognizable sequence in each shoot, the development of inflorescences starting in the region of the terminal shoot apex and proceeding basipetally, and individual florets on each spike developing acropetally in the order of their initiation. This component of spread may be regarded as an ontogenetic inevitability. The other component—that due to differences in shoot age—is manipulable, and is the significant variable in the situation under discussion.

Each new shoot is obliged to pass through a life history similar to that of an individual annual plant; it must make a certain amount of vegetative growth before flowering can occur, but we do not know whether this is due to the duration of induction, a ripeness-to-flower requirement, or other factors. Flowering is succeeded by seeding and senescence in the usual sequence, but on a timetable largely independent of that of its neighbouring shoots.

To produce the best synchronized seed crop, therefore, all individual shoots should be synchronized in their development. In a short-day plant with a predictable date of first flower initiation, the simplest way to achieve optimum synchronization is to ensure that a closed canopy carrying a ceiling shoot population exists by that date. Failure to achieve this state, whether through defoliation, late planting, or sparse establishment, may be expected to result in poorer synchronization of seed production.

To translate this rationalization into a practical recommendation, one must state that a defoliation operation should be carried out no later and no more severely than will permit return to a closed canopy by the time of first flower initiation. Results indicate that during late summer in north Queensland, recovery of a vegetative stand of stylo from a reasonably severe slashing should be completed within about four weeks. With the observed dates of first flower initiation recorded in the preceding paper of this series, the estimated latest safe times for slashing in north Queensland appear as late February for Cook and Endeavour, and early April for Schofield.

A second experiment during 1972 was intended to test these recommendations, an aim largely thwarted by Botrytis. Defoliation of the same order of severity as that of treatment B in 1971 had, if anything, a beneficial effect on the early reproductive framework of crops of all three cultivars when performed at the predicted latest safe date. However, similar defoliations carried out at about first flower initiation did not consistently produce a significant adverse effect, though initially delaying development of the seed crop. These results probably represent borderline cases between adequate and inadequate recovery, since the later cuts in 1972 were less severe than the similarly timed treatment C in 1971 (40–60 per cent removal of growing points, compared with 74 per cent). Our definition of the latest safe slashing date may, therefore, be a little conservative, but should
provide some insurance against such events as over-
zealous slashing and the occurrence of unfavourable
growing conditions in the interval between defoli-
ation and flower initiation.

There is little other available information to enable
us to test either the truth or the extent of our rational-
ization. The defoliation experiment carried out by
Loch and Humphreys (1970) on S. humilis in irrigated
boxes at Brisbane certainly recorded an adverse effect
of defoliation at about first flower initiation, but more
through failure of seed set than through reduction in
numbers of structural elements. Seasonal climatic
deterioration, however, probably influenced the
results of that experiment very strongly, a suspicion
voiced by the authors and subsequently lent support
by the demonstration of failure of the reproductive
processes of S. humilis at low temperatures (Skerman
and Humphreys 1973, 1975; Schoonover and
Humphreys 1974).

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