Seed production of Stylosanthes guyanensis

1. Growth and development

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Summary—The pattern of growth and development of seed crops of stylo (*Stylosanthes guyanensis*) was derived from measurements made on experimental and commercial crops in north Queensland. The three cultivars Cook, Endeavour, and Schofield differed appreciably only in the timetable of their development. Each had distinct successive phases of vegetative and reproductive development culminating in total annual seed production of 700–800 kg ha^{-1} from a healthy closed canopy, the main recorded cause of reduced production being the disease *Botrytis* sp. In a healthy crop of Cook, the peak quantity of standing seed represented almost 90 per cent of the total accountable seed, and the rise to and decline from this peak proceeded at rates of the order of 3–4 per cent per day.

It is deduced that, although there appears to be little potential for either increase in overall production or improvement in synchronization or retention characteristics beyond that currently attained by a closed canopy of healthy plants, there is scope for an increase in the efficiency of recovery of standing seed. Maximum recovery will be achieved through attention to choice of time of harvest, presentation of a minimum amount of extraneous vegetation to the harvester, and improvement in harvester separation.

Cultivation of the perennial pasture legume stylo (*Stylosanthes guyanensis* cvv. Cook, Endeavour and Schofield) for seed has become a significant component of the agricultural economy in parts of the wet coastal lowlands and adjacent elevated hinterland of north Queensland. Seed crops are generally grown without irrigation, and develop on wet season rainfall to a single annual harvest by an all-crop header-harvester in about the July-September period. Seed production of stylo has been beset with many problems, and overall yields are low.

It was planned, therefore, to make a rational assessment of the potential of stylo for seed production, so that avenues of yield improvement might emerge. In order to set a background of crop growth and development in relation to production and loss of seed, two field experiments were combined with opportunistic sampling of numerous commercial crops. This paper reports the results of these investigations and the deductions drawn from them. The field experiments had as their primary function the provision of this information, but this was combined with an investigation of the effects of defoliation on crop development and yield, the results of which appear in the second paper in this series. So far as is possible, the complications of defoliation have therefore been excluded from the present record, and the results used are those from the plots of minimum defoliation.

Crop morphology

An established seed crop of stylo consists of a variable depth of leafless basal stem supporting a leafy layer of about 30–50 cm depth. Flowering appears to be a response to short days (Mannetje 1965), the development of inflorescences on each shoot starting in the region of the terminal shoot apex and proceeding basipetally, and individual florets on each inflorescence developing acropetally in the order of their initiation. Inflorescences are sessile spikes, subtended by unifoliate or bifoliate bracts, and are borne together in clusters. The pod is a glabrous lomentum with one fertile segment and an insignificant beak; it

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is this fertile segment, with or without the flimsy pod, that is popularly known as "seed". Mature seed is eventually expressed from the spike as additional seeds develop, and is usually held for a time by the viscid hairs on the spike before being shed to the ground.

Experiment 1

The two field experiments were carried out on Walkamin Research Station (see table 1) on a red friable earth (Gn 3.11–Northcote 1971) of basaltic origin in 1970/71 and 1971/72.

Methods

S. guyanensis cv. Cook was sown in 91 cm rows in February 1970 with 250 kg superphosphate and 60 kg ammonium sulphate ha^{-1}. A light seed crop was harvested in August 1970, and the regrowth was mown at about 22 cm height on December 4, 1970 to improve uniformity.

Within this crop, an experimental area of approximately 0.18 ha was then divided into five blocks, each of which was further divided to accommodate four defoliation treatments (of which only the "no further defoliation" one is considered in this paper) in a completely randomized block design. Sampling positions (1.83 m × 0.91 m) were allocated at random within each plot, a single 0.4 m^2 area being sampled from each plot on each of 27 occasions. Sampling began on December 8–9, 1971 and ended on August, 24–25, 1972. A subsampling technique (involving repeated halving of cut material after sorting to approximately 1/8 to 1/16 of the sample) was used to reduce the work involved in counting numbers of leaves, growing points, and spikes; this procedure was checked and found to introduce negligible errors. Measurements included height of surface of crop canopy, numbers of visible (i.e. emerged from stipule sheath) growing points, numbers of visible floral spikes, numbers of unfolded living leaves, leaf areas (by the comparison method of Williams, Evans and Ludwig 1964), and dry weights (dried at 70–80°C), although not all measurements were made on every occasion.

Fifteen randomly drawn floral spikes per sample were dissected under magnification for measurement of numbers and stage of development of individual florets. Five stages were distinguished: "pre-seed" (buds with visible subtending bracteoles and all floral parts), "aborted" (corolla withered without seed set), "green", "ripe", and "dropped" seed. Calculation of percentage seed set took account of only the last four "post-flowering" stages.

Standing and fallen seed fractions (the latter initially swept from the ground) were dried at 40°C, threshed in a stationary peg-drum thresher, and cleaned by conventional screening and winnowing; fallen seed was finally separated from dirt by flotation on perchlorethylene (S.G. = 1.62) and hand-sorting.

TABLE 1

Location of sites and meteorological data. Sites without meteorological records have been placed immediately below their nearest relevant meteorological station.

Site	Longitude	Latitude	Elevation	Year	Total rainfall Jan.-Apr.	Total rainfall May-Aug.	Mean temperature January Max.	January Min.	July Max.	July Min.
	(°*E*)	(°*S*)	(*m*)		(*mm*)		(°*C*)		(°*C*)	
Walkamin	145°25′	17°10′	550	1971	790	41	31.3	19.9	22.4	12.3
Walkamin	145°25′	17°10′	550	1972	1030	50	29.7	19.6	22.9	11.8
Turkinje	145°25′	17°05′	450							
Kairi	145°35′	17°15′	650	1972	1450	160	28.2	18.4	20.4	10.2
Yungaburra	145°35′	17°15′	650							
Cardwell	150°00′	18°10′	<50	1972	2040	150	32.3	22.4	25.9	11.8
Murray River	150°00′	18°05′	<50							
Cooktown	145°15′	15°30′	<50	1972	1780	210	32.5	23.9	25.6	19.2

All seed was dried to a uniform moisture content at 40°C and weighed, subsamples of about 200 seeds also being weighed for determination of mean individual seed weight.

Results

Recovery from the December defoliation proceded steadily through an adequate wet season (table 1). The crop reached a maximum height of about 1 m during April, subsequently subsiding gradually to about half that height. Dry weight of aerial parts rose from about 6,000 kg ha^{-1} after defoliation to a peak of over 12,000 kg ha^{-1} in February (day 47), accompanied by commensurate rises in leaf population density and LAI (figure 1). The earlier attainment of an almost steady state in the density of vegetative growing points (figure 1*a*) and the gradual rise in mean size of individual leaves (figure 1*b*) suggest the development of a stable shoot population bearing a canopy of leaves of increasing average age.

After about day 50 and long before flower initiation occurred, a progressive decline in the thickness of the vegetative canopy became apparent, with LAI and its two determinants (i.e. number and mean size of leaves) all falling. No appreciable rain was received after the close of the wet season during April, and the crop matured on stored soil moisture without visible signs of water stress.

First flower initiation was recorded in late March (on day 85) followed by first blooming some 3–4 weeks later in late April. The great structural changes, however, occurred during May: a proliferation of new growing points accompanied the transition from vegetative to floral development, multiple inflorescence buds arising on former simple vegetative shoots (figure 1*a*). Few, if any, retained the vegetative state, the discrepancy between numbers of floral spikes and growing points reflecting the presence of young—and hence macroscopically undeterminable—shoots rather than vegetative ones. The absence of sites for new leaf production accentuated the downward trend in leaf numbers, and mean leaf size continued to fall; the decline in LAI consequently continued. Although bracts and sepals would have taken over some of the photosynthetic function, one may still legitimately infer from the data a progressive senescence of the vegetative canopy.

The population of floral spikes initially increased and later fell as death and disintegration of spikes occurred.

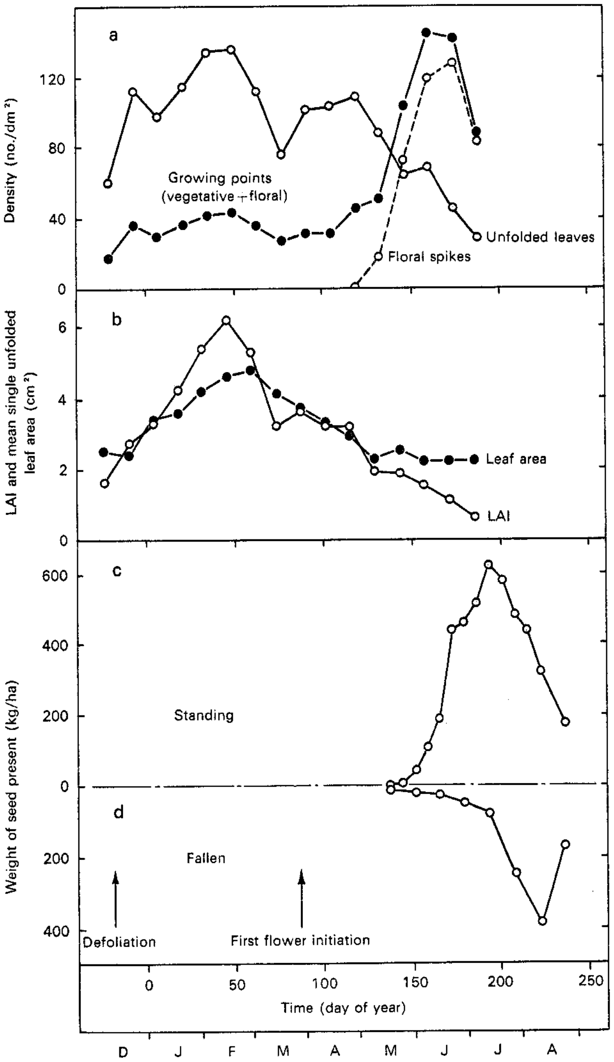

Figure 1—Pattern of development of vegetative canopy and seed crop of 'Cook' stylo (experiment 1). Individual standard errors of means are omitted in order to preserve diagrammatic clarity. Standard errors of each property measured retained reasonable homogeneity over time when expressed as a percentage of the mean. Their average values are: density of unfolded leaves, ±7 per cent; density of growing points, ±7 per cent; density of floral spikes, ±16 per cent; LAI, ±10 per cent; single leaf area, ±5 per cent; standing seed weight, ±20 per cent; fallen seed weight, ±14 per cent.

The increasing overall maturity of the population is illustrated in figure 2*a* by the rising average number of total florets per spike (to a maximum of about 11) and the decreasing number of those in early developmental stages. Seed set, which took account of only the "post-flowering" stages, was relatively uniform (i.e. 71–85 per cent) over the period of measurement, and averaged 79 per cent (table 2).

The peak of standing seed followed some three weeks behind the peak in inflorescence numbers (figure 1*c*). Little loss to the ground had occurred by the time this peak was reached, but over the next 30 days the increase in fallen seed more or less equalled the decrease in standing seed (figure 1*d*), suggesting that little further formation of new seed occurred after mid-July. The rise to and decline from the peak of standing seed proceeded at rates of the order of 3–4 per cent per day.

Experiment 2

This experiment was intended to extend the preceding observations to another season and to two additional cultivars.

Methods

Three stylo cultivars, Cook, Endeavour and Schofield, were combined factorially with three defoliation treatments (of which only the "no defoliation" treatment is considered in this paper) with five absolute replications arranged in randomized blocks.

TABLE 2

Performance of the 1972 crops in comparison with the 1971. Standard errors of means are included where available.

Attribute	Cook 1971		Cook 1972		Endeavour 1972		Schofield 1972	
Max. density of visible growing points (*no.* dm^{-2})	145±2		121±6		152±25		106±18	
Max. density of floral spikes (*no.* dm^{-2})	128±8		111±9		141±25		82±17	
Date and day of first observed flower initiation†	Mar. 26 (85)		Mar. 28 (88)		Mar. 31 (91)		May 8 (126)	
Max. weight of standing seed (*kg* ha^{-1})	624±98		272±47		213±27		135±61	
Max. weight of fallen seed (*kg* ha^{-1})	382±46		226±21		105±19		67±22	
Overall mean percentage seed set	79		60		26		17	
Overall mean single standing seed weight (*mg*)	2.05		2.10		2.25		2.73	
Overall mean single fallen seed weight (*mg*)	2.25		2.33		2.38		2.75	
Day of year‡	61	89	63	90	75	96	95	130
Density of unfolded leaves (*no.* dm^{-2})	111±8	101±5	95±4	80±5	101±3	101±4	88±5	77±5
Density of visible growing points (*no.* dm^{-2})	36±2	32±1	27±2	27±2	31±1	38±4	30±3	24±2
LAI	5.3±0.4	3.6±0.2	4.8±0.2	3.9±0.2	5.4±0.2	5.0±0.1	4.9±0.2	4.1±0.2
Mean single leaf area (cm^2)	4.8±0.2	3.7±0.1	5.1±0.1	4.9±0.1	5.5±0.1	5.1±0.1	5.7±0.1	5.4±0.2
Total dry weight of tops (*tonnes* ha^{-1})	12.5±0.9	10.5±1.2	5.4±0.3	7.3±0.4	6.1±0.3	8.3±0.5	7.5±0.7	8.7±0.6
Height of drop surface (*cm*)	86±5	102±7	56±2	76±2	71±3	87±4	63±2	80±2

† Day of year shown in parentheses.

‡ The two occasions chosen correspond, in 1972, to the expected time of first flower initiation, and approximately four weeks before that time. The closest comparable 1971 harvest data have been included for comparison.

The experiment was planted in 45 cm rows at sowing rates of about 5 kg ha^{-1} of seed on November 15, 1971, following a dressing of superphosphate of 400 kg ha^{-1}. Early rain and irrigation assured excellent establishment, which combined with a good wet season to produce better first-year growth than is normally obtained. Sampling procedure was as for experiment 1; but the frequency of sampling was greatly reduced, and the 12 sampling times were chosen with reference to reproductive behaviour so that cultivars of differing times of maturity could be compared at common stages of development. Vegetative development of each cultivar was measured by samples taken approximately four weeks before the anticipated date of first flower initiation and immediately following initiation. Reproductive development was recorded from the remaining ten samples which were taken at weekly or fortnightly intervals over a 13-week period commencing approximately six weeks after the date of first blooming.

Results

The vegetative framework in this experiment developed comparably in most respects with that of experiment 1 (table 2). The first-year crop of Cook in experiment 2 never reached the maximum height of the second year stand in experiment 1, and total dry weight of tops at comparable times was lower in experiment 2 (particularly in the early stages), although these differences were due more to the much smaller bulk of old leafless stem in the younger crop than to a thinner leaf canopy. Indeed, LAI values were remarkably uniform at comparable stages of development, and showed the same tendency to decline over the period preceding first flower initiation as in experiment 1.

In experiment 2, leaves of Cook tended to be fewer but individual leaves were larger than those in experiment 1; Endeavour tended to produce more leaves than Cook, and of a slightly greater individual area; and Schofield produced the fewest leaves, but these were of greater mean area than those of Cook or Endeavour. Shoot density of Cook tended to be a little lower in experiment 2, and Schofield never achieved the shoot density of the other two cultivars; but on the whole there was no cause to suspect that the general patterns of vegetative development described for Cook in experiment 1 did not apply to all three cultivars in this second experiment.

First flower initiation was observed almost simultaneously in Cook and Endeavour, but was recorded much later in Schofield (table 2). For Cook, the 1972 observation (day 88) was only three days later than that made in 1971 (day 85). In spite of simultaneous initiation, floral differentiation proceeded more slowly in Endeavour than in Cook, and a light sprinking of open flowers was first recorded on April 21, May 5, and June 6, 1972, in Cook, Endeavour, and Schofield respectively. Floral spikes proliferated rapidly to peaks of the same order as Cook in experiment 1, with the exception of the consistently smaller populations in Schofield.

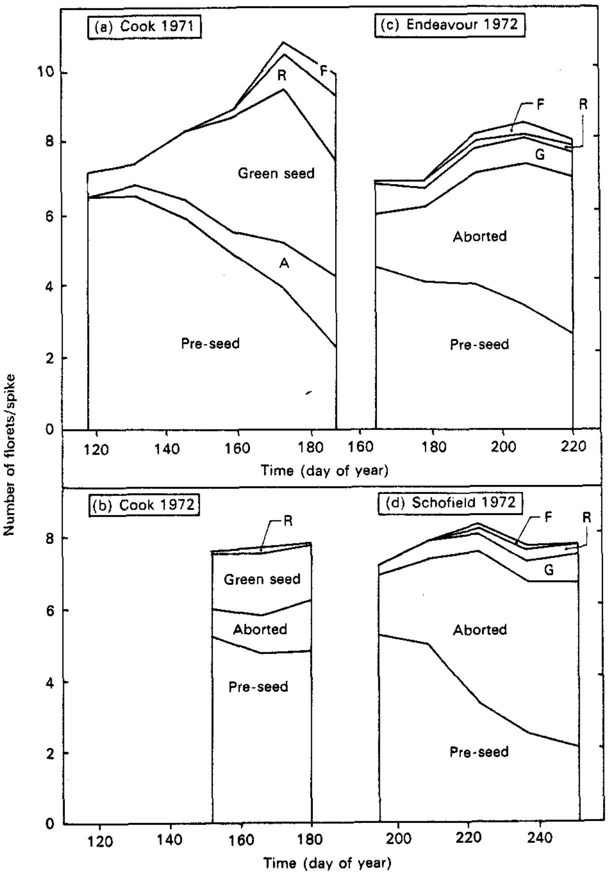

Figure 2—Changes with time in the mean numbers of florets per spike at each stage of development (experiments 1 and 2). Standard errors of means are omitted as in figure 1. Their average values for 'Cook' in 1971, expressed as a percentage of the mean numbers per spike, are: total, ±4 per cent; pre-seed, ±5 per cent; green seed, ±20 per cent; ripe seed, ±25 per cent; fallen seed, ±30 per cent; aborted, ±13 per cent. These values for all cultivars in 1972 are: total ±5 per cent; pre-seed, ±5 per cent; green seed, ±26 per cent; ripe seed, ±27 per cent; aborted, ±12 per cent. Abbreviations: A = aborted, G = green seed; R = ripe seed; F = fallen seed.

At this stage, the fungus disease *Botrytis* sp. struck. Previously unrecorded as a serious pathogen on stylo in the district, though known to have damaged crops on the wet tropical coast, it proceeded to devastate the experiment. Subsequent records are largely a reflection of *Botrytis* damage; consequently, seed yields and subsequent data from the experiment are meaningless, save as a record of the effects of this disease.

Botrytis caused a large increase in the percentage of florets aborting (figure 2). This effect is somewhat masked in the data for Cook, where the ready disintegration of infected spikes led to the recording of an apparent permanently juvenile population (figure 2*b*). In Schofield and Endeavour, the record of damage is far more conspicuous.

District samplings

Methods

In 1972, commercial stylo crops were sampled at about harvest time as the opportunity arose (see tables 1 and 3). Five randomly positioned 0.4 m^2 quadrat cuts were taken from each crop, and standing and fallen seed recovered as in experiment 1.

TABLE 3

Quantities of seed present and percentage seed set in crops sampled in 1972, including standard errors of means where available.

Cultivar and Crop	Date	Total seed	Fallen seed	Seed set	First season crop	*Botrytis* status†
Cook		(*kg ha*$^{-1}$)	%	%		
1—Turkinje	Aug. 7	702±66	32	80	+	—
2—Turkinje	July 25	581±66	26	78	+	—
3—Turkinje	July 26	549±106	45	75	+	—
4—Cooktown	July 22	369±40	28	83	+	—
5—Turkinje	July 16	357±47	17	78	+	—
6—Murray River	Aug. 23	144±37	77	79	+	+
7—Walkamin	July 19	96±25	18	62	+	++
8—Kairi	July 19	13±3	45	14		+++
9—Walkamin	Aug. 4	—	—	75	+	—
Endeavour						
10—Cooktown	July 22	752±95	44	83		—
11—Cooktown	July 21	550±33	21	64		—
12—Turkinje	Aug. 3	282±36	50	50		+
13—Walkamin	Aug. 7	82±24	22	19	+	++
14—Yungaburra	Sep. 7	—	—	19	+	+++
Schofield						
15—Cooktown	Sep. 1	827±139	34	76		+
16—Cooktown	Sep. 1	420±103	26	68		+
17—Walkamin	Sep. 7	158±63	24	20	+	++
18—Cooktown	Aug. 18	—	—	92		—
19—Cooktown	Aug. 18	—	—	77	+	—
20—Cooktown	Aug. 19	—	—	83		—
21—Murray River	Aug. 3	—	—	70		—
22—Murray River	Aug. 23	—	—	56		+
23—Kairi	Sep. 3	—	—	35	+	+++

† *Botrytis* status: — not evident; + present; ++ severe infection; +++ very severe infection.

In addition, flowering branches were collected and their floral spikes stripped, sub-sampled, and used to determine percentage seed set.

Results

Measurements taken before and after the 1971–72 wet season indicated negligible carry-over of seed from one season to the next: the quantity of fallen seed of Schofield at Cooktown, for example, declined from 287 ± 50 kg ha^{-1}, to 6 ± 4 kg ha^{-1} between September 1, 1971 and April 25, 1972. Total production, even from a stand beyond its first season, therefore represents only seed formed during the current season.

The figures presented in table 3 clearly indicate that healthy stands of all three cultivars were capable of producing more than 700 kg ha^{-1} year^{-1}. Furthermore, a reasonable proportion of total production—greater than about two-thirds—was present as standing seed just prior to harvest. *Botrytis* damage was evident in some crops, and was generally accompanied by low seed yields. Only one very low seed yield (crop 6) was not associated with severe *Botrytis* infection, and was largely a consequence of late planting.

Although seed set in healthy crops normally exceeded 70 per cent, the presence of *Botrytis* was almost always accompanied by a reduction in percentage seed set, the extent of reduction and the severity of the disease being closely linked. Below average floret numbers and seed weights were also closely linked with *Botrytis* incidence. The mean numbers of post-flowering florets measured per spike varied from 4.4 to 10.0 (Cook), 5.3 to 6.8 (Endeavour), and 5.8 to 6.3 (Schofield). Mean single seed weight varied from 1.89 to 2.16 mg (Cook standing), 2.32 to 2.71 mg (Cook fallen), 2.11 to 2.45 mg (Endeavour standing), 2.38 to 2.92 mg (Endeavour fallen), 2.56 to 2.84 mg (Schofield standing), and 2.94 to 3.30 mg (Schofield fallen).

Botrytis incidence was related to locality. Severity of attack increased with elevation of the site (see also table 1).

Discussion

The reconstruction of crop development derived in detail from experiment 1 and supported, until the intervention of *Botrytis*, by the results of experiment 2, may reasonably be taken as typical of the behaviour of a healthy closed canopy of stylo. The qualification "closed" is applied here because the consequences of opening the canopy are dealt with in the next paper in this series, and introduce complications best left until then.

Given an adequate population of healthy plants as a starting point, there appears to be no likelihood of increasing overall production. There is ample time before flowering to achieve a closed canopy, at least in a perennating or early planted stand; and this coupled with a total commitment to reproductive development, would seem to ensure the maximum possible density of floral spikes. This commitment also sets an effective time limit on the useful life of the crop by bringing to an end the progressive replacement of the leaf canopy. A developing seed crop is supported by an aging population of leaves in a deteriorating environment (see figure 1*b* and table 1). The combination proves catastrophic, and the aerial framework of the crop lapses into senescent decline. Rejuvenation is possible, through either defoliation or water, but only at the expense of the existing seed crop. Moreover, time is limited owing to the short day flowering response of the species. Mannetje's (1965) conclusion that *S. guyanensis* is a short-day plant is supported by its field behaviour, and there is no serious prospect of a second crop.

Thus, for the circumstances of the seed crop at least, floral spike populations are largely under the control of inevitable ontogenetic factors. Floret numbers per spike are probably under similar control (at least, we know of no way of manipulating them), and percentage seed set is, in the absence of *Botrytis*, already high. We are, therefore, led to the conclusion that the production achieved in experiment 1, and in the best commercial crops examined, was close to the ultimate realistic potential.

The greatest total quantities of seed recorded were of the order of 700–800 kg ha^{-1} for all three cultivars, and probably represent slight under-estimates of total potential annual production since disappearance of early formed seed can be assumed to have occurred before a peak was reached. Nevertheless, they provide a reasonable ceiling on which to base a target for ultimate yield improvement.

These figures indicate that there is considerable potential for a general improvement in recovery of seed. Although Cowdry and Verhoeven (1961) and Gilchrist (1967) report yields of 225 kg ha^{-1} and more, and we have reliable farm records of occasional crop yields of about 300 kg ha^{-1}, commercial yields—even in 1972—were regarded as satisfactory if they exceeded 100 kg ha^{-1}, and as exceptional at 200 kg ha^{-1}. Reliable district averages are not available, but are thought never to have exceeded 100 kg ha^{-1} of saleable seed.

Improved recovery must derive from the more efficient harvest of the standing crop. The commercial recovery of fallen seed by suction harvesting, although not seriously attempted, does not appear feasible. Fallen seed of stylo deteriorates rapidly; it would present serious cleaning problem; and the necessary ground preparation would endanger the survival of the perennial rootstocks.

Of the estimated 700–800 kg ha^{-1} ceiling for total annual seed production, some 600 kg ha^{-1} may be expected to be carried as standing seed at the peak, and this quantity must therefore represent the target for harvest. The discrepancy between actual and target yields has a number of obvious causes, most of which revolve around inadequate separation of seed in the harvester. Although the current trend towards the use of machines with a narrow cut and a high threshing and cleaning capacity will increase the efficiency of recovery, it may also be possible to manipulate the crop to ease the work of the machine. The vast intake of extraneous vegetation is a major cause of inefficiency, and may be much reduced by the presentation of a level, even crop. Stickiness of the green crop is another, and, although diminishing with ripening, is still a serious problem at the seed peak. Choice of harvest time—a compromise between diminishing stickiness and increasing seed shedding—is thus critical.

Obviously, the discrepancy is not wholly due to inefficient recovery. Many crops fail to achieve adequate plant populations, or suffer from weed competition. The removal of certain weed seeds (notably *Sida* spp.) at cleaning involves the sacrifice of much good seed and consequent reduction in effective yield.

Botrytis damage can also seriously reduce the quantity of stylo seed available for harvest, particularly where humid conditions are encountered during flowering (e.g. at elevation in north Queensland). Moreover, such damage may affect seed quality, if it is indeed the cause of the reductions in mean seed size reported earlier. If we can extrapolate from work by Chu Chou and Preece (1968) and Mansfield and Deverall (1971) on the infection of *Fragaria ananassa* and *Vicia faba* by *Botrytis cinerea*, it appears that the presence of pollen is necessary to enable the fungus to overcome the resistance of living tissue to infection by means of access to a certain organic acid in the pollen grains, the active principle of which is effective even when extremely dilute. In the presence of flowers, therefore, it is not uncommon for *Botrytis* to change its role suddenly from that of a universal but insignificant saprophyte to that of a virulent pathogen.

Acknowledgments

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