Rapid changes in simple mixtures of Townsville stylo (Stylosanthes humilis) lines differing in flowering time and growth habit

D. F. Cameron and R. L. McCown

Summary—The ecological adaptation of Townsville stylo (*Stylosanthes humilis*) lines was studied by following changes in the composition of mixtures of the lines. At Weipa, a high rainfall site in north Queensland, the composition of a mixture of four maturity types changed rapidly in favour of the later flowering lines, and the earliest line was almost eliminated by the end of the second year. In binary mixtures at "Lansdown" near Townsville, defoliation every six weeks favoured erect lines but the proportion of prostrate lines was almost doubled at the three week cutting frequency. Changes in mixture composition could not be related to the dry matter yield or pod yield of the monocultures at either site.

The capacity of late flowering lines to increase rapidly in populations growing in high rainfall areas, as demonstrated at the Weipa site, could pose problems for the commercial seed production of earlier flowering lines in such areas.

The two experiments reported in this paper form part of a program designed to study the ecology and genetics of naturalized populations of Townsville stylo (*Stylosanthes humilis*). In earlier studies of these populations significant variation in flowering time and growth habit was observed (Cameron 1965) and the mean flowering time of populations was correlated with rainfall and latitude (Cameron 1967*b*). With infrequent defoliation, selections with an erect growth habit yielded more than prostrate selections of similar flowering time, and late flowering selections yielded more than early selections when moisture stress did not cause early termination of the growing season. Following confirmation in regional evaluation of the roles of flowering time and growth habit in the dry matter production of Townsville stylo selections (Cameron *et al.* unpublished data), three erect cultivars, Paterson (early flowering), Lawson (mid-season) and Gordon (late), were released for commercial use.

Further improvement of Townsville stylo will probably require a more detailed understanding of characters contributing to the ecological adaptation of the species. In its natural distribution the low frequency of late flowering lines in lower rainfall areas probably results from frequent termination of the growing season before the late lines have set seed. However, in higher rainfall areas the seed production of early lines should be favoured by good moisture availability, so that the predominance of late flowering lines in these areas (Cameron 1967*b*) cannot be readily explained. An understanding of this selective advantage for late flowering lines might be useful in defining selection criteria for the species.

In high rainfall areas the rate of change in the composition of mixtures heterogeneous for flowering time could also be of considerable practical importance for commercial seed production. With commercial seed production becoming a more specialized activity, early flowering cultivars and predominantly early flowering populations are being grown in the higher (more reliable) rainfall areas to reduce between season variability in seed yields. Since late lines can be expected to enjoy a selective advantage under these conditions the rate of increase of such late lines will determine how long such areas can be used to provide seed suitable for sowing at lower rainfall locations.

Although erect types have been more productive than prostrate types with infrequent defoliation, their

The Authors—Dr. D. F. Cameron and Dr. R. L. McCown, C.S.I.R.O., Division of Tropical Crops and Pastures, St. Lucia, Queensland.

relative performance also needs to be studied under more frequent defoliation. The prostrate growth habit is obviously well adapted and competitive in native pastures since prostrate lines are widespread and many populations contain mixtures of erect and prostrate lines (Cameron 1965). Environmental conditions, defoliation and fertilizer use are factors that could all affect the composition of such natural populations, and in fertilized pastures defoliation may be the most important management variable.

In the first experiment, the selective advantage for late flowering in the higher rainfall areas was studied by following changes in the composition of a mixture of four lines of different maturity type at Weipa in Cape York Peninsula. In the second experiment, the influence of defoliation frequency on the composition of mixtures of erect and prostrate lines was studied. Dry matter yield and pod yield were chosen for measurement as attributes that might be related to the selective advantage of successful lines.

Materials and methods

Experiment 1

This experiment was located in Cape York Peninsula at Weipa (12°43'S, 142°07'E), annual rainfall 1747 mm, on an area which had been mined for bauxite and then refilled. The virgin soil is a bauxitic laterite and mining operations consist of removal and stockpiling the top soil to reveal the bauxite. The bauxite is mined and the washings of sand and clay material are returned by pipeline. The previously stockpiled soil is then spread over the back-filled area to a depth of 50–100 cm. In previous experimentation by one of us at this site, Townsville stylo had exhibited normal growth and development. Another high rainfall site undisturbed by mining operations would have been preferred but conditions of access and experimental supervision dictated the choice of this Weipa site.

125 kg ha^{-1} molybdenized superphosphate and 375 kg ha^{-1} superphosphate were broadcast before sowing in early January 1968, and a further 125 kg ha^{-1} molybdenized superphosphate and 875 kg ha^{-1} superphosphate were applied prior to the 1969 wet season. Five erect lines of Townsville stylo (Greenvale, cv. Lawson, Giru, cv. Gordon and Kalumburu), ranging from early to late maturity type (table 1), and a composite comprising equal proportions by seed weight (seed sizes are similar, 2.1–2.3 mg) of the first four lines, were inoculated with CB 756 *Rhizobium* and sown (28 kg ha^{-1} naked seed) on a clean seed bed

TABLE 1

Dry matter and pod yields of Townsville stylo lines and composite in 1968 and 1969 (experiment 1).

Line or Composite	Maturity type	DM yield Apr. 3, 1968 T.S.†	DM yield May 7, 1968 T.S.	DM yield Mar. 10, 1969 T.S.	DM yield Mar. 10, 1969 O.S.	DM yield Apr. 30, 1969 T.S.	DM yield Apr. 30, 1969 O.S.	Yield of pods Oct. 9, 1968	Yield of pods Sep. 25, 1969
		kg ha⁻¹		*kg ha⁻¹*		*kg ha⁻¹*		*kg ha⁻¹*	
Greenvale (G)	Early	2130	1580	940	2240	920	4110	640	140
cv. Lawson (L)	Mid-season	2500	2730	3440	1480	3520	2020	830	420
Giru (Gi)	Late-mid-season	2590	2630	4670	580	4310	1560	820	160
cv. Gordon (Go)	Late	2310	3490	3850	1200	3870	2300	670	80
Kalumburu (K)	Late	1940	3420	2290	2140	3700	2370	540	60
Composite (G+L+Gi+Go)	Mixed	2740	2590	2680	2270	2810	2910	890	140
L.S.D. $P = 0.05$		n.s.	1170	2290	n.s.	n.s.	n.s.	n.s.	180

† T.S.— Townsville stylo; O.S.— other species.

in plots 4 m × 4 m arranged in a randomized block design with four replicates. Herbage yields were estimated on two occasions in each of the two growing seasons from three samples (0.5 m × 0.4 m) cut at ground level in each plot from previously unsampled positions. Samples were sorted, dried and weighed. Unsampled areas of the plots grew undefoliated throughout the growing season and were mown off at 5 cm in the dry season after sampling for pod yield. Pod yields were estimated from three samples per plot (0.5 m × 0.4 m) collected from the ground surface during the dry season. A simple water balance model developed by McCown (1973) was used to estimate the water climate, assuming a soil water storage capacity of 100 mm. Rainfall was measured at the site and pan evaporation at 5 km from the site.

In the absence of distinctive plant morphological characters, the composition of mixtures could not be determined from the inspection of plants growing in the sward. Accordingly the composition of mixtures was estimated by classifying individual plants grown from seed collected in mixture plots. Seeds were rubbed from the pods collected in the plots of the composite in 1968 and 1969, scarified and germinated in petri dishes. Germinated seeds were planted singly in 15 cm freely draining plastic pots of soil in the open at Townsville (19°15'S, 146°48'E) on December 1, 1969. There were four replicates of the pot experiment with each replicate corresponding to a field replicate of the Weipa experiment. One hundred pots of the composite from each of the 1968 and 1969 pod collections were grown in each replicate, together with 25 pots of the original composite sample (from remnant seed) and five pots of each of the four components of the composite. Weekly observations of flowering time were used to allocate plants from the composite samples to the four maturity type groups of the components.

Experiment 2

As limited seed supplies precluded the use of cattle for studying the effects of defoliation on mixtures of Townsville stylo lines of different growth habit, a reciprocating mower was used to defoliate the plots. Over the natural distribution range of Townsville stylo in northern Australia, defoliation of pastures during the wet season has to be relatively lenient to allow sufficient accumulation of standing feed for grazing during the long dry season. To simulate this lax grazing system the plots were cut at a height of 8 cm. A companion grass was also sown, as earlier work had suggested that a companion grass could affect the relative yields of lines with different growth habit (Cameron 1967*b*). Adequate fertilizer and irrigation were supplied to ensure vigorous sward growth for the defoliation treatments. Although the erect and prostrate growth habits are clearly expressed in spaced plant conditions, these differences may be largely obscured in high density swards (Torssell 1974) and particularly in defoliated swards. However, some northern Australian populations contain low frequencies of black seeded lines which can be readily distinguished from the normal yellowish-brown seeded lines (Burt, Williams and Compton 1973; D. F. Cameron, unpublished data). This seed colour difference provided a convenient method for following changes in mixture composition.

The experiment was located at the Lansdown Research Station (19°40'S, 146°50'E) on a red podzolic soil, Gn 3.15, which was fertilized with 250 kg ha^{-1} molybdenized superphosphate in December 1969. Four lines of Townsville stylo (Wrotham Park, Bloomsbury, Greenvale and cv. Paterson) differing in growth habit and/or seed colour (table 3) were grown singly and in four binary mixtures (1 : 1 by seed weight), comprising two mixtures of prostrate × erect growth habit and one each of erect × erect and prostrate × prostrate growth habits. Plots of 3 m × 3 m were separated by a border of 1 m and arranged in a split plot design with two replicates. The main plots were cutting frequencies of three or six weeks at a height of 8 cm and the subplots were Townsville stylo lines (single or mixed). Plots were sown on January 8, 1970 on a prepared seed bed with 34 kg ha^{-1} of scarified Townsville stylo seed and 6 kg ha^{-1} of *Urochloa mosambicensis*. Irrigation was used to establish the experiment and, thereafter, as required to prevent moisture stress. Established plants were counted on February 9, 1970 (4 quadrats/plot, 0.4 m × 0.2 m). Yields were estimated on each cutting date by cutting a 90 cm swathe through the centre of each plot at 8 cm height after removal of a 45 cm strip from each end. Subsamples were sorted, dried and weighed to determine yield and botanical composition. Unsampled areas of the plots were cut at 8 cm and raked off after each sampling. Cutting treatments were commenced on February 18 and finished on April 22, 1970. Immediately after the last cut, the yield accumulated below the cutting height was estimated by cutting one quadrat (0.5 m × 0.4 m) to ground level in each plot. Pod yields were estimated by collecting pods from the surface of the ground in two quadrats (1 m × 0.4 m) in August when all pods had been shed from plant residues. At the same time samples of pods were collected from five random sites in each mixture plot; subsequently, the compositions of the mixture plots were estimated by counting the numbers of black and brown seeds in 100 pod subsamples from each site.

Results

Experiment 1

Rainfall for 1967–8 and 1968–9 was 1987 and 1196 mm respectively compared with the long term average of 1747 mm. Calculations using the water balance model showed that the water index (= estimated evapotranspiration/potential evapotranspiration) did not fall below 1.00 in any week of either growing season until after the last rain had fallen. The last rainfall for the growing season was recorded during the first week in May (54 mm) in 1968 and the first week in April (39 mm) in 1969. Calculations from the water balance model show that the estimated soil water storage capacity of 100 mm was fully recharged on both occasions. Adopting McCown's (1973) water index value of 0.50 as indicating severe visible wilting in Townsville stylo, the calculated times for severe water stress in the present experiment were the end of May in 1968, and the end of April in 1969.

Almost pure stands of Townsville stylo were obtained in the first year. Differences in the flowering time of the four maturity types were clearly evident at both the 1968 harvests. Growth of Townsville stylo declines after flowering and this was reflected in a decline in the yield of the early flowering Greenvale (G) at the second harvest ($P < 0.10$), whereas the yields of the late flowering Gordon (Go) and Kalumburu (K) improved ($P < 0.01$) (table 1). The yield of the composite was intermediate between the early and the late types at the second harvest. Pod yields were high in 1968 with no significant differences between lines. With earlier germination in December of the second season, G gave a very low yield at both harvests but Go and K did not show the same improvement at the later harvest, probably due to dry conditions during April (only 39 mm rainfall). Dry conditions apparently adversely affected pod set of the later lines, with the midseason cultivar, Lawson (L), having a much higher pod yield than the other lines. Substantial yields of invading grass weeds were measured at both harvests in the second year but treatment differences were not statistically significant. However, other species yields were negatively correlated with Townsville stylo yields at both harvests (Harvest 1, $r = -0.89$; Harvest 2, $r = -0.97$).

Although the composite line was formed by mixing equal weights of the four component lines, only 6 per cent of Go was found in the remnant sample of the original mixture (table 2). The pods of each line had been fed separately through a hammermill to remove the pods and scarify the seed and differential damage might have adversely affected the germination of Go. Although good establishment and early growth were obtained in the Go plots, no establishment counts were made and the heavy planting rate of 28 kg ha^{-1} could have compensated for any damage to the Go seed.

Rapid shifts in the composition of the composite were clearly evident in the population grown from the 1968 sample, with the early line G being displaced by Go (table 2). The population shift in favour of the late maturity type continued the following year with a further substantial increase in Go, a decline in G to trace proportions and a substantial decline in L. Inspection of the experiment in late February 1970 confirmed these findings as the G plots were flowering and seeding but no flowering plants could be seen in the plots of the composite.

The selective disadvantage of the G line is consistent with its poor dry matter production but, by contrast, pod production by G was not inferior to that of Go either year. A surprising result was the appreciable decline in L in the composite plots in 1969, a year when the early onset of severe water stress at the end

TABLE 2

Composition of composite line in original, 1968 and 1969 samples (experiment 1).

Year of sampling	Percentage of population			
	Greenvale	cv. Lawson	Giru	cv. Gordon
Original mixture	35	32	27	6
1968	13	25	30	31
1969	1	16	28	54

of April heavily favoured the monoculture pod production of this cultivar over the later flowering lines and did not allow the later flowering lines to show improved dry matter production late in the growing season.

Experiment 2

Establishment of Townsville stylo lines was excellent, ranging from 690–950 plants m^{-2} with no significant differences between lines or mixtures. Germination of *Urochloa* was extremely low and very few plants established. Intermittent use of irrigation prevented moisture stress during the growing season and favoured normal reproductive development and seed production. G, Paterson (P) and Wrotham Park (WP) commenced flowering in the second week of February but Bloomsbury (B) did not flower until the end of March.

Total Townsville stylo yields for the season were not significantly different for lines and mixtures or for the three and six week cutting treatments (table 3). The yields of other species were extremely variable and total yields for the season ranged from 460–1400 kg ha^{-1} with no significant differences. Overall, some 70 per cent of the total yield was accumulated below the 8 cm cutting height, with this yield component for WP being significantly greater than for all other lines and mixtures (table 3). Total yield harvested above the 8 cm cutting height was greater at the six week cutting frequency ($P < 0.05$) but differences between lines were not significant. However, total yield above 8 cm at the end of the first six week cutting cycle (March 11, 1970), expressed as a percentage of final total yield (cut to ground level), was significantly higher for the six week cutting frequency and for the erect lines G and P (table 4). Values for the mixture plots were intermediate between the monocultures. Pod yields for P + G, P and G were significantly higher than for the prostrate B and WP and the other three mixtures (table 3). Cutting frequency did not affect pod yield, which also bore little relation to the yield of dry matter accumulated below the 8 cm cutting height ($r = -0.38$).

Counts of black and brown seed in the pod samples collected from the mixture plots showed that marked changes had occurred in the composition of some mixtures (table 5). Cutting frequency had no effect on the composition of mixtures of erect (P + G) and of prostrate (WP + B) lines. In the mixtures of erect and prostrate lines (WP + G and P + B), however, cutting frequency had a pronounced effect on mixture composition with the proportion of the prostrate lines being almost doubled at the three week frequency. The composition of the mixtures was not related to

TABLE 3

Dry matter and pod yields of lines and mixtures (averaged over 3 and 6 week cutting frequencies) (experiment 2).

Line or mixture	Growth habit,	and Seed colour	DM yield Above 8 cm	DM yield Below 8 cm	DM yield Total	Yield of pods
				kg ha⁻¹		*kg ha⁻¹*
Wrotham Park (WP)	Pr,†	Bl‡	1040	4870	5910	220
Bloomsbury (B)	Pr,	Br	1100	3310	4410	190
Greenvale (G)	E,	Br	1870	2660	4530	340
cv. Paterson (P)	E,	Bl	1780	2940	4720	390
WP + B	—	—	1370	3250	4620	160
WP + G	—	—	1370	3240	4610	240
P + B	—	—	1630	3120	4750	240
P + G	—	—	1580	3180	4760	440
L.S.D.						
$P = 0.05$			n.s.	1140	n.s.	72

† Growth habit: Pr = prostrate, E = erect. ‡ Seed colour: Bl = black, Br = brown.

TABLE 4

Townsville stylo yield above 8 cm at 6 weeks expressed as a percentage of total yield (cut to ground level) (experiment 2).

Line or Mixture	Percentage of total yield from 2 × 3 weekly cuts	1 × 6 weekly cut
Wrotham Park (WP)	10.7(19.13)†	20.2(26.74)
Bloomsbury (B)	13.8(21.59)	32.3(34.47)
Greenvale (G)	25.4(30.30)	49.1(44.48)
cv. Paterson (P)	21.6(27.56)	43.0(40.95)
WP + B	12.5(20.62)	36.8(37.32)
WP + G	12.8(20.95)	39.5(38.88)
P + B	20.5(26.91)	33.7(35.43)
P + G	24.4(29.63)	33.5(35.18)
L.S.D. $P = 0.05$	9.42	

† arc sin $\surd$ transform.

TABLE 5

Composition of mixture plots at 3 and 6 week cutting frequencies (experiment 2).

Mixture	Frequency of black seeded component 3-week cut	6-week cut
	%	
Wrotham Park (Pr, Bl)† + Bloomsbury (Pr, Br)	50	54
cv. Paterson (E, Bl) + Greenvale (E, Br)	32	28
Wrotham Park (Pr, Bl) + Greenvale (E, Br)	56	30
Paterson (E, Bl) + Bloomsbury (Pr, Br)	34	64
	S.E. ± 2.7	

† Growth habit; Pr = prostrate; E = erect. Seed colour: Bl = black, Br = brown.

the relative pod yields of the component lines as measured in the single line plots ($r = 0.29$). There was strong selection against the black seeded P in the P + G mixtures but the black seeded WP was not at a competitive disadvantage in the WP + B plots.

Discussion

These two experiments have shown that the population structure of Townsville stylo populations can change rapidly, with poor competitors being almost eliminated in only two years. Similar rapid changes in natural populations have been measured by Burt, Williams and Compton (1974) who found an increase from 8 per cent to 33 per cent for a prostrate growth form of Townsville stylo after a single season's growth. Morley *et al.* (1962) observed violent fluctuations in the composition of mixtures of subterranean clover lines with early varieties increasing from 43 per cent to 75 per cent in one year and then declining to only 16 per cent of the mixture in the following.

The strong selective advantage for the later flowering lines in the Weipa experiment is in agreement with the pattern of flowering time observed in the natural populations where all the late flowering populations were derived from sites receiving at least 1150 mm annual rainfall (Cameron 1967 *b*). All plants grown from collections at the adjacent Weipa Mission and at three sites at the northern extremity of Cape York Peninsula were late flowering. In the Lansdown experiment, B flowered some six weeks later than the other lines but did not enjoy a competitive advantage in mixture with the other prostrate line WP. Moreover, the competitive ability of B in the P + B mixture was very similar to that of WP in the WP + G mixture at both cutting frequencies. The relative dry matter yields of the early lines at each site could explain the different competitive ability of this maturity group at Weipa and Lansdown. At Weipa the end of season yields of the early flowering G were low relative to the later flowering lines but at Lansdown the early lines gave similar yields to the later flowering B.

The erect lines P and G were clearly differentiated from the prostrate lines B and WP in the distribution of dry matter yield above and below the 8 cm cutting height (table 4), and WP with the numerically highest total yield and significantly highest yield below 8 cm (table 3) was clearly not inferior to the two erect lines in this experiment. Contrary to expectation, the relative yields of the erect and prostrate groups were not affected by cutting frequency. However, in the WP + G and P + B mixtures the increase in proportion of the prostrate component at the three week frequency suggests that frequent defoliation could be an important factor favouring the prostrate growth habit in natural populations. Moisture stress may also favour this growth habit since Burt, Williams and Compton (1973) observed a strong selective advantage for prostrate and compact growth forms when a heterogeneous population was grown in a number of dry environments.

The ecological significance of dry matter yield and pod yield has not been clarified by the present experiments. The dry matter yield of lines in monoculture did not serve as a reliable guide to competitive ability in the mixtures. At Weipa both L and G declined relative to Go in 1969, when dry matter yields of all three were similar. At Lansdown the higher yield below the 8 cm cutting height of WP compared with B did not give WP a selective advantage at either cutting frequency. Conversely, G dominated the G + P mixture at both cutting frequencies even though the yields of G and P, both above and below the cutting height, were similar.

The competitive ability of subterranean clover lines in mixtures is closely related to their seed production in pure swards (Rossiter 1966) but there was no evidence for such a relationship in the Townsville stylo mixtures. At Weipa, the proportion of the early line in the composite plots was reduced after only one year even though its pod yield in monoculture was similar to that of Go which increased substantially. In the second year the onset of severe water stress was estimated to occur some four weeks earlier than the first year and the pod yields of Gi and Go showed a corresponding decline in the second year. Although the pod production of L in monoculture was clearly superior to all other lines in the second year it formed only 16 per cent of the pods produced by the composite in that year. The low pod yield of the composite in 1969 was consistent with its 82 per cent composition of the later flowering lines Gi and Go. Similarly, the high pod yields of P and G in monocultures in experiment 2 did not confer a selective advantage over the prostrate lines in the mixtures which were defoliated every three weeks.

Torssell, Rose and Cunningham (1975) have explained the population dynamics of the Townsville stylo/annual grass pasture system in the Northern Territory by dividing the pasture life cycle into three phases of germination/establishment, main growth period and seed production. A similar approach may be necessary to identify plant attributes influencing the composition of mixtures of Townsville stylo lines. Nevertheless, in the light of the uniformly high seedling establishment at Lansdown, it is unlikely that the germination/establishment phase would have contributed to mixture changes in that experiment.

As commercial seed production becomes a more specialized activity, the seed growing areas become concentrated in the higher (more reliable) rainfall areas to reduce between season variability in seed yields. The results from the Weipa experiment suggest that later flowering contaminants in early lines could build up very rapidly under these conditions. Apart from the black seed character, no other marker characters have been reported in naturalized Australian populations so that contaminating lines could be very difficult to recognize. Flowering time variants can be quite difficult to identify under sward conditions because even pure lines may continue to produce new flowers over a two month period. Careful selection of areas free of volunteer Townsville stylo and regular grow out checks will be required if selected cultivars are to be kept true to type.

Torssell (1974) has discussed the climatic and edaphic features of the Katherine, N.T. environment favouring genetically heterogeneous populations and Burt, Williams and Compton (1973) have suggested that pure line performance may be inferior to that of more heterogeneous populations of Townsville stylo, but no yield advantage was observed for any mixture in the present experiments. Longer term experiments encompassing greater year-to-year environmental variation might favour mixture performance, and advantages for heterogeneous populations have been associated with stressed environments (Frey and Maldonado 1967). In the drier regions, wide fluctuations in local climate can prevent seed production of later maturity types (e.g. Cameron 1967*b*) so that less productive earlier types will be favoured in some years. Nevertheless, all lines of Townsville stylo tested have a capacity to produce high proportions of hard seed (Cameron 1967*a*), which may serve to reduce potential fluctuations in productivity resulting from the deleterious effects of inter-seasonal variation on the seed production of pure lines.

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