

ON THE POLYMORPHISM OF CYANOGENESIS IN *LOTUS CORNICULATUS* L. IX. SELECTIVE HERBIVORY IN NATURAL POPULATIONS AT PORTHDAFARCH, ANGLESEY

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SUMMARY

The *L. corniculatus* populations at Porthdafarch are polymorphic for the characters of leaf cyanogenesis, petal cyanogenesis and keel petal colour. Plants with cyanogenic leaves and petals occur less frequently on the sea cliffs than inland and previous studies have obtained circumstantial evidence of a link between the cline in leaf cyanogenesis and the distribution of selectively grazing molluscs. Counts of leaf and petal damage have confirmed that plants on the cliffs are grazed less heavily than those growing inland and have demonstrated that individuals with acyanogenic leaves or petals are liable to be chewed more heavily than their cyanogenic neighbours. Most of the damage was attributable to feeding by molluscs and it is concluded that herbivorous insects have only a minor role in the maintenance of the clines.

1. INTRODUCTION

The population of *Lotus corniculatus* L. on the cliff along the S. W. facing coast of Porthdafarch, Holy Island, Anglesey contains a lower proportion of plants with cyanogenic leaves than two nearby populations less than 200 metres inland (Jones, 1962). Because this cline appeared to have been stable for several years and the two inland sites had essentially the same proportions of cyanogenic plants, in spite of being topographically very different, Ellis *et al.*, (1977) sought those environmental factors common to the inland sites by which they differed from the cliff site. They determined that the distribution of molluscs known to graze the acyanogenic form preferentially (Jones, 1966, Crawford-Sidebotham, 1972), together with "exposure" to wind and salt spray from the sea, were the principal factors involved. As there was a clear relationship between the distribution of the molluscs and exposure, they then looked for pairs of sites (in which *L. corniculatus* was growing) to the N.W. and S.E. of Porthdafarch, one site being exposed and the other member of the pair not exposed. They found that molluscs were confined almost exclusively to the unexposed sites, even on the two occasions when these were closer to the sea than the exposed sites. The plants were then tested for leaf cyanogenesis and without exception the proportion of cyanogenic plants was higher in each mollusc occupied site. They concluded that acyanogenic *L. corniculatus* were at a disadvantage in some areas of Holy Island because they were liable to suffer from disproportionately high levels of mollusc grazing and that differential herbivory was responsible for the pattern of distribution of the leaf cyanogenic individuals in that study area.

Most European populations of *L. coniculatus* are also polymorphic for the characters of petal cyanogenesis and the colour of the keel petals. Cyanogenesis in the leaves and petals appears to segregate independently, but in the only native population that has been examined in sufficient detail there was a significant excess of individuals sharing the same phenotype (Jones and Crawford, 1977). Using cultivated material, Buzzell and Wilsie (1963) and Bubar and Miri (1965) have detected a locus which is involved in the control of both leaf cyanogenesis and keel colour and which results in an excess of acyanogenic light keeled plants. No such excess has been detected in natural populations (Jones and Crawford, 1977; Ramnani, 1979).

L. corniculatus supports an extensive insect fauna (Compton, 1983), several species of which display a preference for feeding on acyanogenic leaves and flower petals (Compton *et al.*, in preparation). Ellis *et al.* (1977) were unable to include an assessment of the importance of insects in their study of *L. corniculatus* at Porthdafarch and it is clearly important to determine whether insect herbivores could be influencing the frequency of cyanogenesis in these populations.

This report describes the results of scoring plants growing at Porthdafarch for all three phenotypes and also for petal and leaf damage. The objectives of this research were to answer four questions. Is *L. corniculatus* less heavily grazed on the cliff tops? Do acyanogenic plants suffer greater damage from herbivory than their cyanogenic neighbours? Are insect herbivores influencing the distribution of cyanogenic plants? And is the cline for leaf cyanogenesis paralleled by similar clines in the frequencies of petal cyanogenic and dark keeled individuals?

2. MATERIALS, METHODS AND LOCALITIES

The bay at Porthdafarch is situated on the S.W. coast of Holy Island, Anglesey (Grid Reference SH 234 799) and has been described and illustrated by Ellis *et al.* (1977). There are three clearly defined areas, termed the cliff, the hollow and the mound, with the cliff separated from the mound by a distance of approximately 150 metres. The vegetation on the cliff forms a short turf, while the hollow supports a taller sward and the mound a heathland vegetation. Over a 16 year period Ellis *et al.* reported mean leaf cyanogenic frequencies of 25.7 per cent on the cliff, 74.2 per cent in the hollow and 68.0 per cent on the mound.

The *L. corniculatus* population in the hollow is relatively small and was not included in the sampling programmes during the present study. In 1979 the plants on the cliff and mound were sampled at intervals of at least one metre by removing a flower umbel and its associated leafy stem. The areas sampled on the cliff and the mound were essentially the same as those previously sampled (Ellis *et al.*, 1977). The sampling method used has been described earlier (Jones, 1977) although it should be emphasised that the sampling points were distributed throughout each area. Keel colour was scored as either light and dark and damage to the petals was scored on a presence or absence basis. The insects found inside the flowers were also recorded. All the leaflets collected were scored either as chewed or undamaged.

Leaflets were scored because, as Harper (1980) has argued, the food supply of herbivores is usually better defined in terms of food plant units such as leaves or buds rather than as the number of plants that are present. This point is particularly relevant for *L. corniculatus* which clones readily thereby making it often difficult to distinguish between individual genets. In 1982 two further samples were collected, but on these occasions only 20 leaflets (four leaves) per stem were examined whereas the number of absent leaflets was also counted. Outside the flowering season only leafy stems were available. Leaves and petals were tested for cyanogenesis using the sodium picrate test described by Jones (1977) and were scored as either cyanogenic (++) or acyanogenic (-). The three acyanogenic phenotypes (+- have cyanoglucoside, but no β -glucosidase; -+ have β -glucosidase but no cyanoglucoside; -- have neither) were not separated. *L. corniculatus* petals require a longer incubation period than the leaves and were scored after 48 hours, rather than 24.

3. RESULTS

The frequencies of leaf cyanogenic, flower cyanogenic and dark keeled individuals in the samples taken at Porthdafarch are given in table 1. Leaf

TABLE 1

The frequencies of cyanogenic and keel colour phenotypes in two sites at Porthdafarch, Anglesey

A. Leaf Cyanogenesis						
Date	Cliff			Mound		
	++	N	%	++	N	%
11 June 1979	15	55	27.3	53	56	94.6
22 May 1982	28	92	30.4	49	65	75.4
3 September 1982	20	60	33.3	40	60	66.6
Means			30.4			78.4
B. Flower Cyanogenesis						
Date	Cliff			Mound		
	++	N	%	++	N	%
11 June 1979	27	52	51.9	38	39	97.4
22 May 1982	31	93	33.3	58	65	89.2
Means			40.0			92.3
C. Keel Colour						
Date	Cliff			Mound		
	Dark	N	%	Dark	N	%
11 June 1979	6	56	10.7	3	56	5.4
22 May 1982	12	93	12.9	13	65	20.0
Means			12.1			13.2

++ = number of cyanogenic plants, N = sample size, % = frequency of cyanogenesis (tables A and B) or dark keel colour (table C).

cyanogenic frequencies are generally higher than those obtained between 1959 and 1975 (Ellis *et al.*, 1977), but the cliff has retained a lower proportion of cyanogenic individuals. Within each site there is considerable variation between the proportions of cyanogenic plants recorded on different sampling dates. While this may reflect variation in phenotype frequencies between different sections of the cliff and mound habitats, the spring samples

included only plants in flower and hence differential flowering time could be responsible. These differences within the two habitats do not vilify the large and consistent differences in the proportions of leaf cyanogenic individuals between the cliff and the mound and it is this latter difference that is the subject of this report. Flower cyanogenic plants are also more numerous on the mound than the cliff while at both sites cyanogenesis is more common in the flowers than in the leaves. The distribution of the keel colour morphs does not follow that of the cyanogenic polymorphisms and there is no significant difference between the mound and the cliff for keel colour (in 1979 $\chi^2_{(1)} = 1.09$, in 1982 $\chi^2_{(1)} = 1.04$, $P > 0.05$).

Table 2a shows that there is a clear excess of individuals either with both leaves and petals cyanogenic or with neither cyanogenic, whereas there

TABLE 2

The relationship between leaf and flower cyanogenesis and keel colour in plants scored for combinations of characters

A. Flower and Leaf Cyanogenesis							
(1) Cliff							
Date	Leaf	Flower				$\chi^2_{(1)}$	P
		++	-	++	-		
11th June 1979		15	11	0	25	20.43	<0.001
22 May 1982		22	9	6	55	36.28	<0.001
(2) Mound							
Date	Leaf	Flower				$\chi^2_{(1)}$	P
		++	-	++	-		
11 June 1979		37	1	0	1		
22 May 1982		47	11	2	5	9.26	<0.01
B. Flower Cyanogenesis and Keel Colour (mound and cliff sites combined)							
Date	Keel Colour	Flower				$\chi^2_{(1)}$	P
		++		-			
		Dark	Light	Dark	Light		
11 June 1979		4	22	4	61	1.97	>0.05
22 May 1982		17	72	8	61	1.64	>0.05
C. Leaf Cyanogenesis and Keel Colour (mound and cliff sites combined)							
Date	Keel Colour	Flower				$\chi^2_{(1)}$	P
		++		-			
		Dark	Light	Dark	Light		
11 June 1979		4	64	5	38	1.17	>0.05
22 May 1982		15	62	10	70	1.43	>0.05

is no relationship between the keel colour phenotype and either of the cyanogenic polymorphisms (tables 2b and 2c). The degree of association between the leaf and flower cyanogenic phenotypes did not differ significantly between the cliff and mound ($\chi^2_{(1)} = 0.99$, $P > 0.05$). It should be noted that it was not possible to score all specimens for all three polymorphic characters and consequently the sample sizes in table 2 are not consistent.

The data in table 3a show that leaflet damage was greater on the mound than on the cliff in early summer ($\chi^2_{(1)} = 91.86$, $P < 0.001$) although no

TABLE 3

Comparisons between the levels of damage sustained by *L. corniculatus* plants growing on the mound and cliff at Porthdafarch

A. Leaf Chewing							
Date	Leaflets	Chewed	Cliff Total	%	Chewed	Mound Total	%
11 June 1979		205	4002	5.1	568	4552	12.5
22 May 1982		276	1835	15.0	236	1275	18.5
3 September 1982		154	1136	13.6	131	1152	11.4
B. Petal chewing							
Date	Flower umbels	Chewed	Cliff Total	%	Chewed	Mound Total	%
11 June 1979		27	56	48.2	36	56	64.3
22 May 1982		35	93	37.6	32	65	49.2
C. Absent leaflets							
Date	Leaflets	Absent	Cliff Present	% Missing	Absent	Mound Present	% Missing
22 May 1982		25	1835	1.3	25	1275	1.9
3 September 1982		64	1136	5.3	48	1152	4.0

significant difference was recorded in September 1982 ($\chi^2_{(1)} = 2.5$, $P > 0.05$). This pattern of leaf damage broadly corresponds with the different mollusc densities recorded at Porthdafarch by Ellis *et al.* (1977), but it appears that damage levels may not be greater on the mound throughout the whole year. The levels of petal damage in the samples (table 3b) also indicate that herbivore activity is typically greater on the mound. More leaflets were absent in September than in May (table 3c), but the numbers that were missing did not differ significantly between sites on either occasion.

Comparisons of the damage levels sustained by cyanogenic and acyanogenic plants growing in the same areas show that on the cliff the leaflet damage was equally distributed between the two phenotypes (table 4a). This was not the case on the mound, however, where acyanogenic plants suffered a disproportionately high level of leaflet damage (table 4b) and were clearly at a disadvantage in terms of herbivore load.

In the September 1982 sample the extent of damage to each leaflet was also recorded. Analysis of these data on a per plant basis leads to conclusions similar to those based on the presence or absence of leaflet damage (table 5). When scores for absent leaflets are also included in the analysis the acyanogenic plants on the mound are again found to have sustained significantly greater leaf losses (table 6).

The two way analysis of the combined data reveals the complexity of the situation. In neither of the analyses in tables 5c and 6c are the main effects significant although there is a significant phenotype x location interaction in table 6c. The mean damage score for cyanogenic plants on the cliff is not significantly larger than that for the acyanogenic plants (tables

TABLE 4

The proportions of chewed leaves on cyanogenic and acyanogenic L. corniculatus plants growing at Porthdafarch. Damage scores from 13 very weakly cyanogenic plants have not been included

A. Cliff							
Date	Phenotype	Damaged leaflets	Undamaged leaflets	% Damaged	$\chi^2_{(1)}$	P	
11 June 1979	++	61	1088	5.3	0.048	>0.05	
	-	143	2640	5.1			
22 May 1982	++	55	340	13.9	0.381	>0.05	
	-	161	1104	12.7			
3 September 1982	++	45	304	12.9	0.092	>0.05	
	-	104	663	13.6			
Totals	++	161	1732	8.5	0.002	>0.05	
	-	408	4407	8.5			
Heterogeneity $\chi^2_{(2)} = 0.519$ $P > 0.05$							
B. Mound							
Date	Phenotype	Damaged leaflets	Undamaged leaflets	% damaged	$\chi^2_{(1)}$	P	
11 June 1979	++	465	3381	12.1	55.948	<0.001	
	-	103	303	25.4			
22 May 1982	+	163	763	17.6	1.203	>0.05	
	-	63	246	20.4			
3 September 1982	++	76	754	9.2	20.357	<0.001	
	-	54	228	19.1			
Totals	++	704	4898	12.6	62.266	<0.001	
	-	220	782	22.0			
Heterogeneity $\chi^2_{(2)} = 15.242$, $P < 0.001$							

TABLE 5

Analysis of variance of leaflet damage at Porthdafarch, September 1982. Twenty leaflets from each plant were examined, with leaflets that had less than one quarter of their area removed given a damage score of 0.25 and those with greater damage a score of 0.5

A. Between phenotype comparisons on the cliff

Mean damage scores, (++) leaflets 0.91, (-) leaflets 0.88

	d.f.	M.S.	P
Between phenotypes	1	0.01	—
Within phenotypes	57	0.81	
Total	58		

B. Between phenotype comparisons on the mound

Mean damage scores, (++) leaflets 0.54, (-) leaflets 1.08

	d.f.	M.S.	P
Between phenotypes	1	3.27	<0.01
Within phenotypes	56	0.42	
Total	57		

C. Two way analysis of variance

	d.f.	M.S.	P
Between phenotypes	1	2.33	>0.05
Between locations	1	1.27	>0.05
Phenotype \times location	1	0.95	0.62
Within plants	113	0.62	
Total	116		

TABLE 6

Analysis of variance of leaflet damage and absent leaflets at Porthdafarch, September 1982. Twenty leaflets from each plant were examined, with absent leaflets scored as 1.0, leaflets with less than one quarter of their area removed scored as 0.25 and those with greater than one quarter of their area removed scored as 0.5

A. Between phenotype comparisons on the cliff			
	Mean scores, (++) leaflets 2.54, (-) leaflets 1.71		
	d.f.	M.S.	P
Between phenotypes	1	8.94	>0.05
Within phenotypes	57	2.72	
Total	58		
B. Between phenotype comparisons on the mound			
	Mean scores, (++) leaflets 1.24, (-) leaflets 2.28		
	d.f.	M.S.	P
Between phenotypes	1	12.14	<0.01
Within phenotypes	56	1.67	
Total	57		
C. Two way analysis of variance			
	d.f.	M.S.	P
Between phenotypes	1	1.50	—
Between locations	1	6.35	—
Phenotype × location	1	19.59	<0.01
Within plants	113	2.20	
Total	116		

5a, 6a) but in the combined analysis it is sufficient to negate the significantly greater damage to acyanogenic plants on the mound. Clearly we need to know whether the excess damage to cyanogenic plants on the cliff is the result of herbivory or of non-biotic agents.

The numbers of missing leaflets on the plants growing on the mound and cliff showed different seasonal patterns. On the mound the acyanogenic plants had more missing leaflets in both early and late summer (table 7) and this was presumably related to the greater leaf damage that this phenotype was sustaining (table 4). In contrast, the acyanogenic plants on the cliff did not have a higher proportion of missing leaflets, and in late

TABLE 7

The numbers of absent leaflets on L. corniculatus stems at Porthdafarch

Date	Phenotype	Leaflets		% absent	$\chi^2_{(1)}$	P
		Absent	Present			
Cliff						
22 May 1982	++	5	395	1.25	0.02	>0.05
	-	15	1265	1.2		
3 September 1982	++	31	349	8.2	8.17	<0.01
	-	33	767	4.1		
Mound						
22 May 1982	++	14	926	1.4	4.66	<0.05
	-	11	309	3.4		
3 September 1982	++	30	830	3.5	3.54	>0.05
	-	18	282	6.0		

summer they had significantly fewer losses than the cyanogenic plants growing there (table 7).

On the cliff the plants with acyanogenic petals suffered greater petal damage in both 1979 and 1982 (table 8) and, after combining the damage

TABLE 8

Damage to L. corniculatus petals at Porthdafarch in relation to petal cyanogenic phenotype

Date	Phenotype	Damaged umbels	Undamaged umbels	% damaged	$\chi^2_{(1)}$	P
Cliff						
11 June 1979	++	9	18	33.3		
	-	15	10	60.0	3.71	>0.05
22 May 1982	++	9	22	29.0		
	-	27	35	43.5	1.84	>0.05
Totals	++	18	40	31.0		
	-	42	45	48.3	4.26	<0.05
Heterogeneity $\chi^2_{(1)} = 1.29, P > 0.05$						
Mound						
22 May 1982	++	28	30	48.3		
	-	4	3	57.1	0.20	>0.05

scores from the two samples, it can be concluded that the difference in damage levels was significant. In 1979 only one acyanogenic flower umbel was collected on the mound and so no between-phenotype comparisons of the damage levels can be made. Acyanogenic flowers were also infrequent in the mound samples of 1982 and this may account for the failure to detect significant differences in the damage sustained by the different phenotypes (table 8). Flowers with dark keels were in a minority at both sites and after combining scores from the cliff and mound there is no evidence that damage was associated with keel colour phenotype (table 9).

TABLE 9

Damage to L. corniculatus flowers at Porthdafarch in relation to keel petal colour. Mound and Cliff sites combined

Date	Phenotype	Damaged umbels	Undamaged umbels	% damaged	$\chi^2_{(1)}$	P
11 June 1979	Dark	6	3	66.6		
	Light	60	43	42.0	0.24	>0.05
22 May 1982	Dark	11	14	44.0		
	Light	57	76	42.9	0.01	>0.05

Hand searches and sweep-net sampling of *L. corniculatus* at Porthdafarch failed to find any leaf-chewing insects on the plants growing on the cliff. Leaf chewing insects were also uncommon inland and the lepidopteran *Coleophora discordella* Zell. was the only species detected. In 1979 a survey of the flower feeding insects was carried out. The most abundant inhabitants were found to be larvae of the beetle *Hypera plantaginis* (Degeer) and the eggs and larvae of a second beetle, *Apion loti* (Kirby). Both species were considerably more numerous on the mound, with *A. loti* being virtually

TABLE 10

Insects present inside L. corniculatus flowers collected at Porthdafarch on 11 June 1979

Species	Cliff			Mound		
	Flowers examined	No. of insects	Density per flower	Flowers examined	No. of insects	Density per flower
<i>Apion loti</i>	167	1	0.006	169	29	0.17
<i>Hypera plantaginis</i>	167	15	0.09	169	72	0.43

absent from the flowers growing on the cliff (table 10). *A. loti* larvae develop inside the immature seed pods of *L. corniculatus* and do not damage the petals. *H. plantaginis* larvae feed on both petals and immature seed pods and were responsible for much of the recorded petal damage. *H. plantaginis* larvae were not present in greater numbers on acyanogenic flowers, however, (table 11) and it is therefore unlikely that this species was responsible for the differential petal damage observed on the cliff (table 7).

TABLE 11

The distribution of Hypera plantaginis larvae in relation to flower cyanogenic phenotype. Porthdafarch 11 June 1979, cliff site only

Flower phenotype		<i>H. plantaginis</i>	<i>L. corniculatus</i>
		larvae	flowers
++		7	79
-		6	62

$\chi^2_{(1)} = 0.02, P > 0.05$

4. DISCUSSION

Ellis *et al.* (1977) concluded that the cline in leaf cyanogenesis at Porthdafarch was probably the result of the cliff area supporting fewer selectively grazing molluscs than the mound. The results presented here have confirmed that the *L. corniculatus* population on the mound is generally more heavily grazed, and have shown that the acyanogenic plants growing there are likely to be at a selective disadvantage because they suffer more leaf damage than their cyanogenic neighbours. The leaves of acyanogenic plants were not more heavily grazed on the cliff, where it can be concluded that neither phenotype is at an advantage in terms of selective herbivory. Leaf feeding insects appear to be infrequent on both the cliff and mound and most of the leaf damage at Porthdafarch was attributable to feeding by molluscs. The difference in damage levels between the two areas is nonetheless smaller than might have been predicted from the considerably higher density of molluscs recorded previously on the mound (Ellis *et al.*, 1977). This may reflect the increased relative palatability of the predominantly acyanogenic cliff population. As the most abundant of the mollusc species found at Porthdafarch are known to display selective feeding (Keymer and Ellis, 1978) and their distribution is correlated with the observed levels of leaf damage, there is now considerable evidence in support of the hypothesis that variation in mollusc density is influencing the frequency of the leaf cyanogenic phenotype in these populations.

Damage to the flower petals was also greater on the mound, but between phenotype comparisons of petal damage are limited by a shortage of acyanogenic individuals at the site and no differential damage was detected. Comparisons between plants growing on the cliff did show that acyanogenic petals were being more heavily damaged and this confirms the defensive capability of cyanogenesis in both the leaves and flowers of *L. corniculatus*.

Flowers on the cliff contained relatively low densities of insects and the distribution of the major petal feeding species (*Hypera plantaginis*) appears to be independent of flower phenotype. The larvae of this species have a limited host range, and *Lotus* spp. are the usual host plants (Compton, 1983). As *H. plantaginis* is also known to contain the cyanide de-toxifying enzyme rhodanese (Parsons and Rothschild, 1964) it is perhaps not surprising that this specialist herbivore should be undeterred by cyanogenesis. Other candidates for the selective flower feeding observed at the cliff site include molluscs and grasshoppers. The snail *Helicella itala* (L.) is known to prefer to feed on flowers rather than leaves (Malan, 1973). This species, together with the slug *Deroceras reticulatum* (Muller), are abundant at Porthdafarch and in laboratory feeding choice experiments they eat significantly more of the acyanogenic petal morph (Compton *et al.* in preparation). Grasshoppers are also present at Porthdafarch (Ellis *et al.*, 1977) and we have found that *L. corniculatus* flowers are much more palatable than leaves to at least three species, all of which display selective eating in the laboratory. Identification of the species that are responsible for the selective feeding at Porthdafarch will require more extensive on-site observations both of the feeding behaviour and of the distribution of each species.

A relationship between the distribution of molluscs and the frequency of plant characters associated with herbivore resistance has also been demonstrated by Cates (1975) and Dirzo and Harper (1982). The latter have adopted a similar approach to ours in their studies of the interaction between slugs and *Trifolium repens* L., a plant that is also polymorphic for leaf cyanogenesis. Working in a field that is maintained as permanent grassland they have shown that cyanogenic plants were over represented in those areas of the field where mollusc densities were high and that leaflets on acyanogenic plants were being more heavily chewed than those on cyanogenic plants. Cates investigated the relationship between the slug *Agriolimax columbianus* (Gould) and *Asarum caudatum* Lindl., a plant which in North America is polymorphic for an unidentified chemical defence which makes the plant unacceptable to the slug. He found that in those parts of the plant range where slugs were abundant it was the less palatable form of *A. caudatum* which was the dominant morph, whereas elsewhere it was replaced by the palatable form which had a higher growth rate and greater seed production.

The metabolic costs of cyanogenesis are likely to be low, particularly for legumes (McKey, 1979) and there is no evidence that cyanogenic individuals of *L. corniculatus* are at any disadvantage in terms of reproductive output or vegetative growth (Jones, 1963; Keymer and Ellis, 1978). Keymer and Ellis did find that cyanogenic plants from Porthdafarch were less salt tolerant than acyanogenic plants, however, and this may explain the success of the latter on the cliff. In September 1982 the cyanogenic *L. corniculatus* growing on the cliff site had significantly more missing leaves

than the acyanogenic plants. If this sample reflects a general difference in leaf fall then we may have detected the results of physiological stresses, such as salt spray, acting differentially on the two phenotypes.

The cyanogenic ability of *L. corniculatus* petals has been recognised for many years (Guérin, 1929) and the inheritance of this character has been studied by Rammani (1979). Less well understood is the relationship between cyanogenesis in the leaves and the petals. Jones and Crawford (1977) scored an *L. corniculatus* population in the West Midlands and found that although plants with all 16 possible combinations of phenotypes were present there was an excess of those individuals which shared the same phenotype in the leaves and flowers. The populations at Porthdafarch also display this association between phenotypes, but more formal genetic studies will be required before the basis of this relationship can be clarified. At Porthdafarch there is no association between the expression of keel colour and either leaf or flower cyanogenesis, and this agrees with studies in the West Midlands (Jones and Crawford, 1977) and Norway (Compton *et al.*, in preparation) which have also failed to detect the excess of acyanogenic pale keeled plants that was predicted by the findings of Buzzell and Wilsie (1963).

In areas such as the cliff at Porthdafarch an association between the expression of cyanogenesis in the leaves and flowers would appear to be unfavourable because there is evidence that plants with cyanogenic petals may be at an advantage (due to reduced herbivory) while plants with cyanogenic leaves are at a disadvantage (due perhaps to being linked with reduced salt tolerance). If flower cyanogenesis is not also linked with salt tolerance then selection would be expected to favour plants with cyanogenic flowers and acyanogenic leaves and ultimately the independence of these two characters. There is no evidence that this separation has taken place, however, as individuals with different phenotypes for leaf and petal cyanogenesis were no more frequent on the cliff than the mound.

Flower damage is clearly linked with fecundity (both directly through ovule losses and indirectly via a reduction in pollination levels) and the protection evidently afforded by petal cyanogenesis can be assumed to have a significant bearing on reproductive output. Mature plants have a well documented ability to compensate for losses of leaf tissue and Crawford-Sidebotham (1972) and Jones (1972) have argued that leaf cyanogenesis may be of most benefit to *L. corniculatus* during its seedling stage, when individuals are far more vulnerable. *L. corniculatus* is not an ideal subject for demographic studies (Keymer, 1978), but further investigation of the cline in cyanogenesis at Porthdafarch will clearly need to include an appraisal of the significance of cyanogenesis throughout the life history of the plant.

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