

## Altruism and Movement of Plants

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Received November 26, 1984; February 15, 1985

**ABSTRACT:** If different individual plants of the same species can alter their phenotypes in opposite directions when subjected to the same environmental change the effect is as if these individuals had moved to different locations within the population. When the phenotype involved is concerned with the defence of the plant against herbivores, the overall advantage of this process to the plants may be to disrupt the learning of a habitat by an intelligent herbivore and thereby escape, if only partly, from herbivory. Furthermore, some of these plants may change from an advantageous to a disadvantageous phenotype (with respect to herbivory) and thereby simulate altruistic behaviour. It appears that *Lotus corniculatus* (bird's-foot trefoil) behaves exactly in this way with respect to the genetic polymorphism for leaf cyanogenesis.

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Leaf cyanogenesis in *Lotus corniculatus* L. depends on the degradation of the cyanoglucosides linamarin and lotaustralin by the  $\beta$ -glucosidase linamarase, when the leaf tissue is damaged. Two loci are involved in the system and in many populations four phenotypes can be distinguished; plants with cyanoglucosides and the  $\beta$ -glucosidase (+ +), those with cyanoglucosides but no enzyme (+ -), those with enzyme but no cyanoglucosides (- +), and those with neither cyanoglucosides nor enzyme (- -). Only + + plants are cyanogenic. Further details of the system are given in Jones (1977).

There is evidence, however, that some plants can change phenotype both quantitatively (Jones, 1962b; Ogilvie, 1970) and qualitatively (Ellis, Keymer & Jones, 1977a) when subjected to changes in temperature. Other plants do not change phenotype in response to the same temperature changes. The effects of this genotype x environment interaction on the apparent distribution of plants in natural populations and on herbivory are described in this report. We will concentrate on the qualitative changes of phenotypes because the consequences are more easily explained and understood, although the quantitative changes are also relevant to the discussion.

## CYANOGENESIS AND THE MOVEMENT OF PLANTS

Using 152 plants derived as stem cuttings from one population at Porthdafarch, Holy Island, Anglesey, Ellis, Keymer & Jones (1977a) found that there was a positive association between the per cent expression (arcsine transformed) of the cyanoglucoside phenotype and minimum temperature in the glasshouse over an 18 month period. In addition there was a positive association between  $\beta$ -glucosidase production and the maximum temperature in the glasshouse. Forty plants lost the ability to produce cyanoglucosides in their leaves as the mean ambient temperature in the glasshouse was lowered from 14°C towards 4°C. Of these 40 plants, 16 that were cyanogenic became acyanogenic. Two other plants, however, gained the ability to synthesize cyanoglucosides under these conditions (e.g. - + or - - to + +). On the other hand, there was a tendency for plants to gain the ability to synthesize linamarase as the temperature was raised towards 25 - 30°C (e.g. + - to + +). Again, 3 plants lost the ability to synthesize the  $\beta$ -glucosidase under

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Evolutionary Theory 7: 143-148 (March, 1985)

The editors thank P. Coley and another referee for help in evaluating this paper.

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these conditions (i.e. they changed from + + to + -). The transitions observed and their effect on the numbers of plants of each phenotype are given in Table 1.

Table 1  
Phenotypic changes in cyanogenic and acyanogenic *Lotus corniculatus*

25 <sup>0</sup> + Towards				From 14 <sup>0</sup> C		Towards + 4 <sup>0</sup> C			
+ +	+ -	- +	- -	+ +		+ +	+ -	- +	- -
62	3	1	0	+ +	66	43	7	15	1
12	23	0	1	+ -	36	2	10	2	22
8	0	5	0	- +	13	1	0	9	3
3	11	0	23	- -	37	1	0	1	35
85	37	6	24		152	47	17	27	61

We chose 14<sup>0</sup>C as base line for these comparisons because it was the mean temperature measured at plant level in the original habitat in May and September (Ellis, Keymer & Jones, 1977b & unpublished observations). The temperatures of 25<sup>0</sup>C and 4<sup>0</sup>C are within the range normally experienced by the plants in the original habitat.

Similar changes of phenotype have also been observed with these plants and with plants from other populations when they were grown outside the glasshouse in the experimental field. Finally, 72 of the original 152 individuals have retained a consistent phenotype when subjected to these treatments in the glasshouse and have continued to do so over a period of 8 years.

Twelve of the plants with stable phenotype were chosen as the parents for a formal breeding programme (Ramnani & Jones, 1984). It was subsequently discovered (Ramnani, 1980) that 8 of these individuals gained the ability to synthesize the cyanoglucosides or linamarase when subjected to winter temperatures in the experimental field at Hull, particularly following a frost (i.e. + - to + +, - - to - + and - - to + -). Transitions from - + to + +, - - to + - and - - to + + were also observed among plants collected from Porthdafarch in 1980 and 1981. Ramnani and Jones (1985) found that these changes of phenotype took less than three days to effect and we were also able to demonstrate the segregation of a temperature sensitive regulatory gene in the progeny of some crosses.

Overall, these results mean that within a polymorphic population of *L. corniculatus* we can find the following situations:

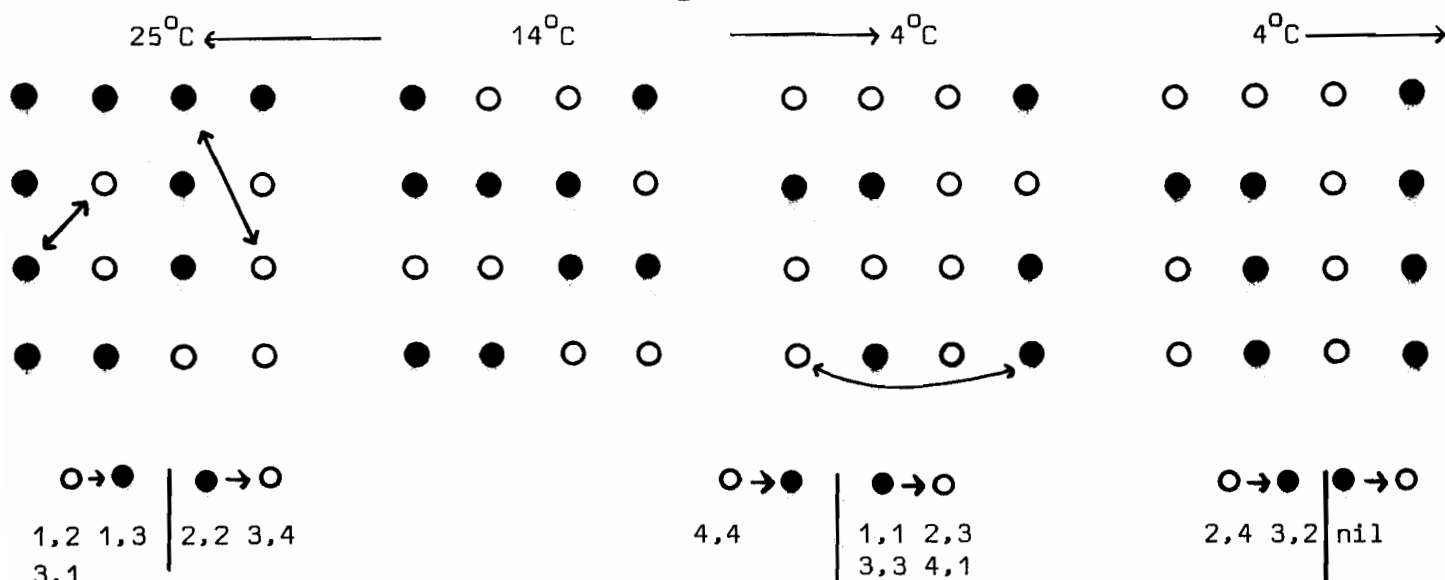
- a) as the temperature rises, some plants become cyanogenic while a few become acyanogenic,
- b) as the temperature falls, some plants become acyanogenic while a few become cyanogenic, and
- c) as the temperature falls below 4<sup>0</sup>C some plants become cyanogenic.

Consequently, at different seasons of the year, both the distribution and the proportion of the cyanogenic forms within a population can change without there being any recruitment or death of individual plants. Because some plants will have changed phenotype in opposite directions these plants will appear to have exchanged positions within the populations. This effect is shown diagrammatically in Figure 1. For example, as the temperature rises from 14<sup>0</sup>C to 25<sup>0</sup>C plant 3,1 becomes cyanogenic while 2,2 becomes acyanogenic. Thus these plants have effectively exchanged places.

#### HERBIVORES AND PLANT ALTRUISM

There can be little doubt that cyanogenesis in plants acts as a chemical defence against herbivores (Jones, 1962a, 1971; Crawford-Sidebotham, 1972a; Ellis, Keymer & Jones, 1977b; Dirzo & Harper, 1982; Compton, 1983). For *L. corniculatus* leaves, however, two classes of herbivores are involved. There are those which have

Figure 1



A model to explain the effect of temperature on the distribution of cyanogenic plants. acyanogenic plants, cyanogenic plants. The arrows indicate pairs of plants that appear to have changed positions within the square. Note that some plants (e.g. 1,4; 2,1; 4,2 and 4,3) retain the same phenotype irrespective of the temperature.

*L. corniculatus* as a preferred foodplant, for example, *Zygaena filipendulae* (L.) and *Polyommatus icarus* (Rott.). These animals show no preference for acyanogenic over cyanogenic leaves and, where appropriate tests have been made, they have been shown to detoxify the HCN released from a cyanogenic plant when it is damaged (Jones, Parsons & Rothschild, 1962; Parsons & Rothschild, 1964; Beesley, Compton & Jones, 1985; Compton & Jones, 1985). Thus it is of no importance to the specialist herbivores whether a plant is cyanogenic or acyanogenic and consequently the changes of phenotype by some plants have little or no relevance to herbivory by these specialists. The other group of herbivores consists of non-specialist, casual feeders and it is these that prefer the acyanogenic form and against which cyanogenesis is a defence. It appears that the selection exerted by these animals is sufficient to be responsible for different proportions of cyanogenic to acyanogenic individuals of *L. corniculatus* in different habitats (Ellis, Keymer & Jones, 1977b; Compton, Beesley & Jones, 1983), but the selection pressure is insufficient to eliminate the acyanogenic form from the majority of habitats. There is some evidence that mammals are among the selective herbivores involved, rabbits (*Oryctolagus cuniculus* L.) (Corkill, 1952), voles (*Microtus agrestis* L.) (Jones, 1962b) and lemmings (*Lemmus lemmus* L.) (Compton, Newsome & Jones, 1983) in particular.

Do these animals learn the microgeography of a habitat? We cannot find an explicit statement that they can, although territorial and home range behaviour would not be possible if the animals involved were unable to recognise where they were. Habitat learning is implied in studies of small mammal populations even when territorial behaviour is explicitly ruled out (e.g. Kikkawa, 1964) and home range behaviour is normal (e.g. Nygren, 1980). The ability of some mammals to take consistent evasive actions when frightened or when threatened by a predator can only be based on a knowledge of the home range. We know that small mammals have the ability to learn which foods are unpalatable (Morse, 1980); it seems not unreasonable to argue that they may well be able to remember the location of palatable foods.

The ability of *L. corniculatus* to change phenotype from cyanogenic to acyanogenic and *vice versa* means that the distribution of cyanogenic individuals

in a habitat is in a state of dynamic flux, presumably confusing small mammalian herbivores and impeding the ability of these animals to learn the distribution of palatable plants. A plant which changes from being cyanogenic to acyanogenic may be at some physiological advantage having done so, but it does place itself at a selective disadvantage with respect to other cyanogenic individuals when mammalian (and molluscan) herbivores are present. The effect of a phenotypic change from cyanogenic to acyanogenic would be to increase the mean palatability of *L. corniculatus* locally. The area could then be more attractive to selective herbivores and they could move in. As the selective herbivory by *Microtus agrestis*, for example, is shown when alternative food is present (Jones, 1966) an increase in the proportion of acyanogenic *L. corniculatus* material would increase the probability that plants would not be excessively grazed. In this way the plant that changed phenotype would improve the chances of other acyanogenic individuals surviving and reproducing, thereby simulating some forms of altruistic behaviour.

There is some evidence that small mammals, including *M. agrestis*, show increasing preferences for more familiar diets (Partridge, 1981). Clearly the learning involved in this behaviour must depend upon reinforcement and consequently the selection imposed on a variable food source will be frequency dependent. Thus the ability to change phenotype from palatable to unpalatable (e.g. Compton, Beesley & Jones, in preparation), and *vice versa*, when other sources of food are available (Jones, 1966) may well enable *L. corniculatus* to escape the attention of these microtine mammals in natural populations. There would, therefore, be selection in favour of an ability to change phenotype in some plants.

Such a system would, however, require a trigger, and preferably one that is effective independently of herbivory. Because there is a positive correlation between ambient temperature and the activity of molluscs showing selective herbivory of acyanogenic *L. corniculatus* (Jones, 1966; Crawford-Sidebotham, 1972a,b) it is not surprising to find that the changes in cyanogenic-acyanogenic phenotypes are responses to changes in temperature. The overall effect is an increase in the proportion of cyanogenic plants as the ambient temperature rises and, conversely, a decrease as it falls.

It is not known whether there is a positive correlation between the activity of the small rodents and temperature, but there is evidence that some species are active at temperatures below 0°C (Kikkawa, 1964) whereas, in northern Sweden, Nygren (1980) has trapped *M. agrestis* in November and January. At these low temperatures, acyanogenic *L. corniculatus* would be vulnerable in the presence of active herbivorous rodents. Thus our observations that some plants can become cyanogenic at low temperatures may be the response by the plant to selective grazing during the winter. We have circumstantial evidence supporting this argument, because in Norway the home range of the lemming *Lemmus lemmus* is normally very close to the edge of retreating glaciers and it is precisely within this home range that the *L. corniculatus* is almost exclusively cyanogenic whereas further down the valley the plants are commonly acyanogenic (Compton, Newsome & Jones, 1983).

When frequency dependent selection is being exerted, a phenotypic change in one direction could reduce the frequency of a common morph and *vice versa*. This would enable more rapid adjustment of the equilibrium frequencies in a genetic polymorphism than is possible in an organism where the genotype x environment interaction response is not possible. This method has the added advantage of being effective without the need for the elimination of any individuals and so is very conservative of biomass and energy.

Although Wilson (1975) did not include plants in his definition of altruism and Grant (1978) omits discussion of plants from all three types of altruistic behaviour which he lists in his critique of kin selection, the idea that plants may show altruistic behaviour is not entirely new (Nakamura, 1980). It appears, however, that the polymorphism of cyanogenesis in *Lotus corniculatus* does provide

an example of altruism in plants and, at the same time, demonstrates how plants can seemingly move about a habitat on a relatively short time-scale (a few days).

## ACKNOWLEDGMENTS

We thank Valerie Fairhurst and Ian Taylor for technical assistance and the SERC, the NERC and the University of Sind for financial support. We also thank W.F. Grant for supplying the copy of Ogilvie's thesis.

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