

Competition between cyanogenic and acyanogenic morphs of *Trifolium repens*

B. Noitsakis¹ and P. Jacquard^{2,*}

¹ Laboratoire de Range Science, University of Thessaloniki, 54006 Thessaloniki, Greece

² Centre Louis Emberger, CNRS, BP 5051, 34033 Montpellier Cedex, France

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Summary. To investigate the cost of the dimorphic cyanogenic system in *Trifolium repens* L., genotypes of the cyanogenic (T_c) and acyanogenic (T_a) morphs were grown in mixtures over a range of ratios and in pure stands at two levels of total density (low in a first experiment, high in a second experiment). The principles of the competition analysis employed were those related to the inverse linear model response. The morphs were compared using two interaction indices, the substitution rate and the relative resource total (RRT). The relative fitness of the two morphs, i.e. biomass and number of flowers per plant, suggests that the T_a morph has a competitive advantage over the T_c morph.

Key words: Competition – Cyanogenesis – *Trifolium repens* – Resource capture – Fitness

Introduction

Natural populations of *Trifolium repens* L. (white clover) contain a variable proportion of individuals that have the ability to release hydrogen cyanide (HCN) from damaged leaves, usually when they are consumed by herbivores. This cyanogenic system, and its polymorphism, has been known about for many years (Ware 1925), and many studies have been published on the frequency and distribution of the genes responsible for the polymorphism and their function (e.g. Burdon 1980; Hughes et al. 1984; Till-Bottreau et al. 1988).

The release of HCN is the result of an interaction between two gene loci, that is between cyanogenic glucoside linamarin and lotaustralin (at the locus *Ac/ac*) and the hydrolysing enzyme linamarase (at the locus *Li/li*).

Two phenotypes can thus be readily distinguished: cyanogenic (genotype *Ac-Li*), and acyanogenic (genotype *ac-Li*, *Ac-li*, or *ac-li*). Moreover, studies of the two genes *Ac* and *Li*, which show incomplete dominance (Hughes and Stirling 1982; Hughes et al. 1984), indicate that they affect not only the occurrence of cyanogenesis but also growth, reproduction and protection against grazing (Kakes 1989). Many authors have already demonstrated that acyanogenic morphs in *Trifolium repens* are selectively grazed by certain herbivores (Dritschilo et al. 1979; Dirzo and Harper 1982), thus favouring the predominance of cyanogenic morphs in a population. In addition, in an analysis of the costs and benefits of the cyanogenic system in *T. repens*, Kakes (1989) found that *Ac* (and possibly *Li*), apart from its influence on the cyanogenic system, may influence the energy balance of individual plants, and so this system should be considered as a “cost” item in biomass production.

The influence of cyanogenesis on reproductive yield has been reported for plants grown in the absence of both intra- and inter-specific competition. Kakes (1989) has demonstrated that *Ac* has such an effect, and that it is not caused by the energy diverted to the production of cyanoglucosides. The understanding of the competitive relationships among the individuals of a binary mixture necessitates an integrated study involving both the intra- and inter-plant competition that occurs within and between individuals. Such relationships result from changes in the proportion of the two morphs when grown in a mixture and variation in the total density. In this paper we report the results of a study designed to examine the effect of competition between cyanogenic and acyanogenic morphs of *T. repens* on biomass accumulation and flower production in order to compare the capture of resources, substitution rates and relative efficiency of the two morphs.

* To whom correspondence should be addressed

Material and methods

Ramets of *T. repens* comprising stolon material and associated roots were collected from a semi-natural pasture at St. Gervais d'Auvergne in the Massif Central, France. Ramets were collected at 1-m intervals along a fertility cline 120 m long. The ramets were tested and grouped according to their cyanogenic reaction (J.-M. Expert and J. Meekel, unpublished). Nine cyanogenic genotypes (T_c), *AcLi* (numbered 6, 8, 21, 34, 49, 102, 108, 109, 118 according to their position on the cline), and nine acyanogenic genotypes (T_a), *acli* (numbered 9, 10, 18, 23, 38, 50, 51, 55, 57) were used in these experiments.

Stolons 3.5 cm in length with their associated root system were combined, in two experiments, in different ratios and total densities (Fig. 1) and without replication.

Experiment 1 comprised three replacement series containing cyanogenic-acyanogenic ratios of (1) 4/0, 3/1, 1/3, 0/4, (2) 6/0, 4/2, 2/4, 0/6, and (3) 9/0, 6/3, 3/6, 0/9 at total densities of 100, 150, and 220 plants per m^2 respectively.

Experiment 2 comprised three replacement series at high total densities: (1) 8/0, 6/2, 4/4, 2/6, 0/8 (200 plants per m^2), (2) 16/0, 11/5, 8/8, 5/11, 0/16 (400 plants per m^2), and (3) 24/0, 17/7, 12/12, 7/17, 0/24 (600 plants per m^2).

The stolons were planted on May 15, 1989 for experiment 1 (low density) and on June 13, 1989 for experiment 2 (high density) in plastic pots ($20 \times 20 \times 18$ cm) filled with soil, and watered regularly. The individuals of each morph planted in each pot (up to 24) were randomly chosen from the genotypes. It is thus possible that differences between genotypes not associated with the *Ac/Li* system may contribute to variation in the results and thereby increase the degree of error. Single ramets of each morph were carefully separated and harvested for dry weight determination over a range of dates (experiment 1: June 10, July 5, August 1; experiment 2: July 7, August 1, August 21). The mean dry weight of a plant, calculated by dividing the total harvested weight for each morph within a pot by the number of individuals of that morph, was used in all data analyses. The number of

flowers per plants was also recorded at each harvest. These two measured traits were used as estimates of fitness.

Competition analyses

Statistically correct methods for assessing the competitive relations of plants mixtures and their dynamic interaction over time have been proposed by Connolly (1987).

Mathematical response model

The response of individuals in pure and mixed stands reflects their interaction with the biotic and abiotic environment (Harper 1977). Such responses, which are relative to the competitive conditions, have been described by several equations (Wiley and Heath 1969), however it is the "inverse linear model" that potentially offers the most powerful approach because it has a logical, mathematical and biological basis (Wright 1981; Spitters 1983; Jolliffe et al. 1984).

Let the mean weight of an individual plant be denoted by W and the density of individual plants by d . In a two-dimensional plane defined by the densities of two morphs (d_1 and d_2), the yield per individual (W_1 and W_2) can be expressed as a function of the mixed density:

$$\begin{aligned} W_1 &= f_1(d_1, d_2) \\ W_2 &= f_2(d_1, d_2) \end{aligned} \quad (1)$$

Here f_1 and f_2 are functions relating yield per individual to the mixed density. This is the general formulation and is applicable to all two-component mixtures. The particular forms of the inverse linear model of these functions are the equations:

$$\begin{aligned} 1/W_1 &= a_{10} + a_{11}d_1 + a_{12}d_2 \\ 1/W_2 &= a_{20} + a_{21}d_1 + a_{22}d_2 \end{aligned} \quad (2)$$

where a_{11} and a_{22} are the intra-morph coefficients that measure the effect of the density of a particular morph on itself, a_{12} and a_{21} are the inter-morph coefficients measuring the effect of the density of one morph on an other and a_{10} and a_{20} are the intercept terms, often interpreted as attributes of spaced plants, although this is not always correct, particularly where the equations are used as a descriptive fit to data over a limited range of mixtures (Connolly 1986). This is a false attribute because these values may actually be negative (see Table 2 "infra"), in which case $1/a_{10}$ bears no relationship to spaced plants.

Morph interaction index

Many indices have been proposed for the interpretation of pure and mixed stand interactions (Trenbath 1978; Mead and Riley 1981). However these methods are all extremely variable because they are based on the performance of individuals in mixed stands as compared to the performance of individuals in pure stands. It is well known, however, that pure stand performance varies as a function of the density over most of its range. Hence, changing the slope of the replacement line (the line joining the pure stand densities in Fig. 1 for example) may have a considerable influence on the reference yield in the pure stand (Connolly 1986).

Recently, Connolly (1987) has proposed the Relative Resource Total (RRT) as an index that can be used to compare the area required to produce the same performance from a pure stand of the components. This RRT represents the total pure stand area required to enable the same performance as a given unit area of the mixture. This can be defined mathematically as:

$$RRT = 1 + \frac{v(a_{22}/a_{21} - a_{12}/a_{11})}{(v + a_{12}/a_{11})(v + a_{22}/a_{21})} \quad (3)$$

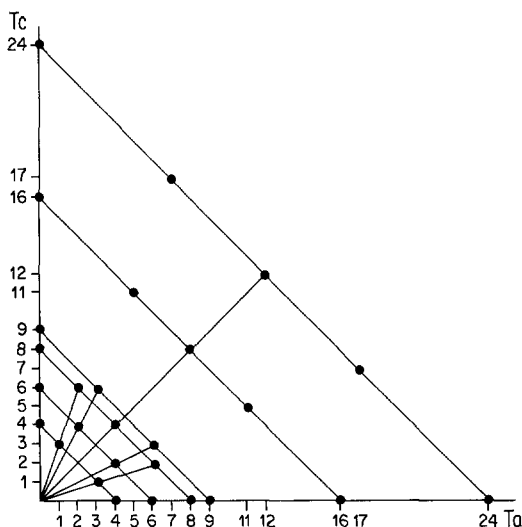


Fig. 1. Diagram of the experimental design showing the combinations of total plant densities and relative frequencies of cyanogenic (T_c) and acyanogenic (T_a) morphs of *Trifolium repens*. The pure stands are presented on both axes

where

$$v = \frac{d_1}{d_2}$$

and a_{22} , a_{21} , a_{12} and a_{11} are the coefficients of Eq. 2 (Connolly 1987). When the $RRT = 1$,

$$\frac{(a_{22})}{(a_{21})} = \frac{(a_{12})}{(a_{11})}$$

This means that the same area would be required in a pure stand to produce the response obtained in mixture, suggesting that the morphs compete for the same resources and that there is no overall benefit accrues to the mixtures. An $RRT > 1$ means that the individuals in mixture exploit more effectively the same resource; an $RRT < 1$ indicates a reduced effectiveness in mixture or the existence of antagonism.

Results

Experiment 1

Biomass. Aboveground biomass per plant data (Table 1) were analysed according to the inverse linear model for

Table 1. Yield (g plant^{-1}) in the replacement series at harvest 1 (C1), harvest 2 (C2), harvest 3 (C3) and cumulative cutting (Cc)

Dens.		C1		C2		C3		Cc	
T_a	T_c	T_a	T_c	T_a	T_c	T_a	T_c	T_a	T_c
Low density									
4	0	0.715	0	1.077	0	0.945	0	2.737	0
6	0	0.586	0	0.671	0	0.565	0	1.822	0
9	0	0.464	0	0.361	0	0.331	0	1.156	0
0	4	0	0.631	0	0.905	0	0.630	0	2.166
0	6	0	0.511	0	0.520	0	0.446	0	1.477
0	9	0	0.386	0	0.183	0	0.238	0	0.807
3	1	0.849	0.667	1.400	0.581	1.246	0.430	3.495	1.678
1	3	0.692	0.666	1.400	0.602	1.330	0.420	3.424	1.688
4	2	0.595	0.538	1.290	0.440	1.140	0.220	3.025	1.198
2	4	0.626	0.506	1.295	0.378	1.050	0.209	2.971	1.093
6	3	0.430	0.413	0.670	0.279	0.495	0.190	1.595	0.882
3	6	0.535	0.385	0.576	0.272	0.493	0.163	1.604	0.820
High density									
8	0	0.765	0	1.080	0	0.448	0	2.293	0
16	0	0.334	0	0.501	0	0.270	0	1.105	0
24	0	0.275	0	0.377	0	0.190	0	0.842	0
0	8	0	0.615	0	0.976	0	0.285	0	1.876
0	16	0	0.420	0	0.455	0	0.160	0	1.035
0	24	0	0.222	0	0.236	0	0.102	0	0.560
6	2	1.062	0.741	1.222	0.546	0.530	0.400	2.814	2.091
4	4	1.656	0.986	1.641	1.165	0.670	0.457	3.967	2.608
2	6	1.415	0.687	1.438	1.019	0.590	0.385	3.443	1.687
11	5	0.739	0.412	0.808	0.356	0.347	0.230	1.894	1.051
8	8	0.757	0.479	1.055	0.440	0.395	0.250	2.207	1.169
5	11	0.759	0.425	0.775	0.401	0.346	0.225	1.880	0.999
17	7	0.417	0.186	0.499	0.259	0.220	0.144	1.136	0.655
12	12	0.458	0.208	0.668	0.373	0.285	0.201	1.411	0.782
7	17	0.427	0.206	0.519	0.299	0.255	0.150	1.201	0.589

T_a , Acyanogenic morph; T_c , cyanogenic morph

three harvests (Table 2), which gave strong correlations for both the T_a ($R^2 = 0.83$), and T_c ($R^2 = 0.93$) morphs. The slopes of the two regressions indicates that the densities of T_c and T_a have a strong effect on both morphs, that on T_c being stronger than that on T_a . The intra-morph coefficients (a_{ii}), which measure the effect of morph density on itself, were 0.0936 for T_a and 0.1276 for T_c . The inter-morph coefficients (a_{ij}) of 0.1329 for T_a and 0.0520 for T_c show that the effect of T_a as a companion morph is greater than the effect of T_c . The biomass difference between the morphs is partly reflected in the relative size of the coefficients, both inter- and intra-morph, of the cyanotype densities.

The relative effects of the two morphs, as measured by the substitution rates, suggest that the cyanogenic morph is less aggressive than the acyanogenic morph. These substitution rates may, however, be irrelevant to a measure of fitness based on competitive ability. With respect to the relative perception of morphs, the intra-morph perception is greater for the acyanogenic morph. The substitution rates were $S_{T_a} = 0.56$ and $S_{T_c} = 1.04$ for T_a and T_c respectively, indicating that based on the performance of T_a one T_c individual is approximately equivalent to 0.56 individuals of T_a . Conversely, one T_a plant is equal to 1.04 T_c plant if the performance of T_c is examined. Hence, the perceived, or biological densities at (d_{T_a} , d_{T_c}) are, for T_a , $d_{T_a} + 0.56 d_{T_c}$, and, for T_c , $d_{T_c} +$

Table 2. Combined effects of inverse densities of acyanogenic (T_a) and cyanogenic (T_c) morphs: $W_i^{-1} = a_{i0} + a_{iidi} + a_{ijdi}$

Density	Low		High	
	T_a	T_c	T_a	T_c
Mean biomass per acyanogenic and cyanogenic morphs				
a_{i0}	-0.0283	0.0317	0.0492	-0.0712
a_{ii}	0.0936	0.1276	0.0455	0.0698
a_{ij}	0.0520	0.1329	0.0183	0.0630
s_{aii}	0.0124	0.0151	0.0050	0.0074
s_{aij}	0.0144	0.0176	0.0059	0.0088
P_{aii} (%)	0.0004	0.0300	0.0000	0.0000
P_{aij} (%)	0.0115	0.0400	1.2200	0.0100
a_{ij}/a_{ii}	0.56	1.04	0.40	0.90
R^2	0.91	0.93	0.90	0.92
Mean number of flowers per acyanogenic and cyanogenic morphs				
a_{i0}	-0.2381	-0.0756	-0.1631	-0.4262
a_{ii}	0.0801	0.0955	0.0435	0.1263
a_{ij}	0.0900	0.0705	0.0366	0.0643
s_{aii}	0.0230	0.0181	0.0125	0.0230
s_{aij}	0.0269	0.0347	0.0148	0.0273
P_{aii} (%)	1.33	0.21	0.70	0.04
P_{aij} (%)	1.54	8.68	3.48	4.13
a_{ij}/a_{ii}	1.12	0.74	0.84	0.51
R^2	0.72	0.82	0.61	0.77

^a Intracyanotype (a_{ii}) and intercyanotype (a_{ij}) density coefficients and substitution rates (a_{ij}/a_{ii})

1.04 d_{T_a} . The fact that the substitution rates are not reciprocal ($S_{T_a} = 0.56, S_{T_c} = 1.04, 1/S_{T_a} = 1.79$) suggests that the two morphs are at least slightly different in their utilization of available resources.

This is confirmed by the values of the RRT index as a function of the ratio d_T/d_{T_c} for all of the pooled cuttings (Table 3). First, the values of RRT ranged from 1.09 to 1.13, but were always between 1 and 2. Hence, either more resources are being captured, or the same resources are being used more effectively, a fact that indicates a form of synergism between the two morphs. Secondly, the maximum value of RRT (1.13) occurred for the ratio $d_{T_a}/d_{T_c} = 1/2$, which means that a mixed

stand with a relative frequency of 1/2 would require 13% less area than a pure stand in order to produce the same biomass per plant.

In Fig. 2 the changes in the RRT with respect to the relative frequency ratio are also presented for three cuttings (10/6, 5/7, 1/8/1989). Clearly in the early growth

Table 3. Change in RRT as a function of the ratio d_{T_a}/d_{T_c}

Cumulative harvest data									
d_{T_a}/d_{T_c}	1/3	7/17	5/11	1/2	1	2	11/5	17/7	3
Densities									
Low	1.11			1.13		1.11			1.09
High	1.22	1.24	1.24		1.24		1.18	1.17	1.15

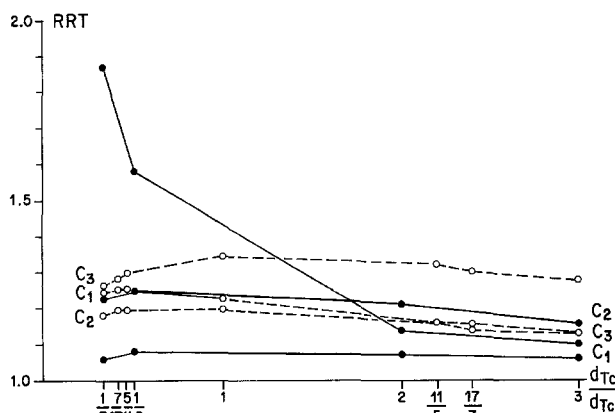


Fig. 2. Change of the Relative Resource Total (RRT) over a range of relative frequencies (ratio d_{T_a}/d_{T_c}) at the low (o) and high (●) densities. C₁, C₂, C₃ cutting 1, 2, 3, respectively

Table 4. Relative weight R_w and cumulated relative efficiency index (REI)

T_a	T_c	C./Cl (R_w)		Ka/Kc (REI)	T_a	T_c	C./Cl (R_w)		Ka/Kc (REI)
		T_a (Ka)	T_c (Kc)				T_a (Ka)	T_c (Kc)	
4	0	3.83	0		8	0	3.00	0	
6	0	3.11	0		16	0	3.31	0	
9	0	2.49	0		24	0	3.06	0	
0	4	0	3.43		0	8	0	3.05	
0	6	0	2.89		0	16	0	2.46	
0	9	0	2.09		0	24	0	2.52	
3	1	4.12	2.52	1.63	6	2	2.65	2.82	0.94
1	3	4.95	2.53	1.96	4	4	2.40	2.65	0.91
4	2	5.08	2.01	2.53	2	6	2.43	2.46	0.99
2	4	4.75	2.16	2.20	11	5	2.56	2.54	1.01
6	3	3.71	2.05	1.81	8	8	2.92	2.44	1.20
3	6	3.00	1.53	1.96	5	11	2.48	2.35	1.06
					17	7	1.57	3.52	0.45
					12	12	1.71	3.76	0.45
					7	17	2.81	1.38	2.04

Combined effects of density

Parameters	K_{T_a}	K_{T_c}	K_{T_a}	K_{T_c}
a_{i0}	5.5400	3.2245	2.4956	2.6125
a_{ii}	-0.3315	-0.0905	0.0316	-0.0183
a_{ij}	-0.1170	-0.2186	-0.0394	0.0389
$s_{a_{ii}}$	0.1171	0.0557	0.0222	0.0301
$s_{a_{ij}}$	0.1367	0.0627	0.0263	0.0357
$P_{a_{ii}}$ (%)	2.95	15.35	18.68	56.26
$P_{a_{ij}}$ (%)	42.89	1.32	16.65	30.43
a_{ij}/a_{ii}	0.35	2.42	1.25	-2.13
R^2	0.59	0.68	0.34	0.20

Table 5. Number of flowers per plant in the replacement series

Low density									
Density		10/6		3/7		1/8		Sum	
T _a	T _c	T _a	T _c	T _a	T _c	T _a	T _c	T _a	T _c
4	0	1.00	0	3.70	0	1.75	0	6.45	0
6	0	1.00	0	3.50	0	1.20	0	5.70	0
9	0	0.50	0	1.50	0	0.50	0	2.50	0
0	4	0	0.50	0	2.50	0	1.60	0	4.60
0	6	0	0.83	0	2.00	0	1.00	0	3.83
0	9	0	0.00	0	0.50	0	0.50	0	1.00
3	1	3.00	1.00	4.20	2.00	1.30	1.00	8.50	4.00
1	3	3.00	1.50	2.00	2.00	2.00	1.00	7.00	4.50
4	2	2.00	1.00	4.30	1.00	0.50	0.50	6.80	2.50
2	4	1.00	0.50	2.00	1.25	1.00	0.50	4.00	2.25
6	3	0.30	0	1.00	0	0	0	1.30	0
3	6	0.60	0	1.00	0.30	0.60	0	2.20	0.30

High density									
Density		7/7		1/8		21/8		Sum	
T _a	T _c	T _a	T _c	T _a	T _c	T _a	T _c	T _a	T _c
8	0	0.75	0	1.60	0	0.55	0	2.90	0
16	0	0.50	0	1.70	0	0.40	0	2.60	0
24	0	0.00	0	1.00	0	0.13	0	1.13	0
0	8	0	0.50	0	0.50	0	0.12	0	1.12
0	16	0	0.13	0	0.40	0	0.06	0	0.59
0	24	0	0.00	0	0.30	0	0.04	0	0.34
6	2	1.33	0.50	2.00	1.50	1.50	1.00	4.83	3.00
4	4	2.00	1.00	3.00	2.00	1.50	1.00	6.50	4.00
2	6	1.00	0.66	2.00	1.50	1.00	0.50	4.00	2.66
11	5	0.54	0.20	1.63	0.60	1.00	0.20	3.17	1.00
8	8	1.00	0.50	2.00	1.00	1.00	0	4.00	1.50
5	11	0.40	0.09	1.40	0.70	0.60	0.20	2.40	0.99
17	7	0.08	0.00	0.30	0.14	0.40	0.28	0.78	0.42
12	12	0.50	0	1.16	0.66	0.80	0.30	2.46	0.96
7	17	0.30	0	0.50	0.30	0.20	0.18	1.00	0.48

stage (first cutting) the situation is slightly synergistic (RRT ranges from 1.06 to 1.08), but in the next two cuttings, the RRT is increasingly greater than 1. The RRT remained relatively high over a wide range of relative frequencies.

In the replacement series (Table 1) the yield per plant of the acyanogenic morph, the morph with the smaller substitution rate ($S_{T_a}=0.56$), is clearly greater, in the overall densities as well as in all relative frequencies, than the cyanogenic morph ($S_{T_c}=1.04$). This implies that the cyanogenic morph of *T. repens* has a poorer performance in mixed stands, at least at the low densities employed here (100; 150 and 220 plants per m²).

Table 4 presents the relative weight (estimated as the ratio cumulated cutting biomass/biomass of cutting 1) and the cumulative relative efficiency index (REI), considered to be a survival component of fitness. The relative efficiency is close to the idea of fitness, performance in

Table 6. Change over time of the combined effects of inverse densities

Low density biomass						
Param- eters	C1		C2		C3	
	T _a	T _c	T _a	T _c	T _a	T _c
a _{io}	0.7249	0.7216	-0.3138	-0.8579	-0.4503	-0.1243
a _{ii}	0.1650	0.2105	0.3020	0.6020	0.3589	0.5116
a _{ij}	0.1348	0.1838	0.1447	0.4683	0.1946	0.7971
s _{aii}	0.0251	0.0073	0.0577	0.1091	0.0508	0.1455
s _{aij}	0.0293	0.0085	0.0673	0.1274	0.0593	0.1698
P _{aii} (%)	0.08	0.00	0.22	0.18	0.06	1.27
P _{aij} (%)	0.40	0.00	7.36	1.06	1.68	0.37
a _{ij} /a _{ii}	0.82	0.87	0.48	0.78	0.54	1.56
R ²	0.88	0.99	0.82	0.84	0.89	0.80

Number of flowers						
Param- eters	10/6		3/7		1/8	
	T _a	T _c	T _a	T _c	T _a	T _c
a _{io}	-1.0833	0.4373	-0.2150	-0.1649	0.3370	-0.1001
a _{ii}	0.3875	0.0694	0.0965	0.1893	0.1199	0.2243
a _{ij}	0.3259	0.1922	0.1559	0.1695	0.0921	0.4022
s _{aii}	0.1065	0.1052	0.0265	0.0382	0.1313	0.0318
s _{aij}	0.1243	0.2019	0.0309	0.0733	0.1533	0.0609
P _{aii} (%)	1.10	53.85	1.09	0.29	39.95	0.06
P _{aij} (%)	3.88	38.04	0.26	5.90	57.44	0.08
a _{ij} /a _{ii}	0.84	2.77	1.62	0.90	0.77	1.79
R ²	0.70	0.15	0.82	0.81	0.12	0.92

mixture being considered to be a measure of the reproductive performance per individual. The relative weight is clearly greater for T_a than for T_c, with the intra-morph perception being significant for the acyanogenic morph and the inter-morph perception for the cyanogenic morph. Consequently, the REI is always at the advantage of the acyanogenic morph.

Number of flowers/plant. The number of flowers per plant (Table 5) were analysed according to the inverse linear model for three cuttings (Table 2); weaker correlations ($R^2=0.72$ for T_a; $R^2=0.82$ for T_c) than those observed for biomass were found. The slope of the two regressions indicates that the densities of T_c and T_a have a strong effect on both morphs.

The relative effects of the two morphs as measured by the substitution rates suggest that the cyanogenic morph is more aggressive than the acyanogenic morph. With respect to the relative perception of the morphs, intra-morph perception is less for the acyanogenic and greater for the cyanogenic morph. The substitution rates were $S_{T_a}=1.12$ and $S_{T_c}=0.74$ for T_a and T_c, respectively, indicating that one T_c is roughly equivalent to 1.12 T_a individual. Conversely, one T_a is equal to 0.74 T_c's.

The change over time in combined effects is given in Table 6. There is a contrasting trend in the dynamics of morph interaction: for an individual of the T_c morph the area seems more crowded at the third cutting, which it would be were all individuals of the T_a morph to be replaced by an equal number of T_c morph individuals.

Experiment 2

Biomass. The inverse linear model for the total above-ground yield per plant (sum of three cuttings) (Table 1) has given strong correlations ($R^2=0.90$ for T_a and $R^2=0.92$ for T_c). The slopes of the two regressions (Table 2) indicate that the densities of T_a and T_c have a strong effect on biomass. This suggests that competition is primarily inter-morph; the substitution rates were $S_{T_a}=0.40$ and $S_{T_c}=0.90$ for T_a and T_c , respectively. These values indicate that for the performance of the T_a morph, 1 T_c is approximately equal to 0.40 T_a , while for the performance of the T_c morph, 1 T_a is equal to 0.90 T_c . Once again this implies a difference in resource utilization by the two morphs, a fact that is verified by the change in RRT as a function of d_{T_a}/d_{T_c} (Table 3).

A RRT > 1 implies competition between the two lines with overcompensation or reduced performance for one

morph only. The minimum values of RRT (1.15) occurs at $d_{T_a}/d_{T_c}=3$ and means that a mixed stand with a relative frequency of 3 would require 15% less area than the pure stand in order to produce the same yield per plant.

The change in RRT as a function of d_{T_a}/d_{T_c} for three cuttings (7/7, 1/8, 21/8/1989) during the growing season showed a similar pattern at high density (Fig. 2) and at low density. The decrease in RRT (> 1) from harvest to harvest was less, and the overcompensation not as high, as at low density. This may be due to the fact that at high density the nutrients in the soil act as limiting factors, such that nutrient competition influences morph yield.

No effect of density was observed on the relative weight and the cumulative relative efficiency index (REI) (Table 4).

Number of flowers/plant. The number of flowers per plant (Table 5) were analysed according to the inverse linear model for three cuttings (Table 2), which gave weaker correlations ($R^2=0.61$ for T_a ; $R^2=0.77$ for T_c) than those observed for biomass. The slope of the two regressions indicates that the densities of T_c and T_a have a marked effect on T_c .

The relative effects of the two morphs, as measured by the substitution rates, suggest that the acyanogenic

Table 7. Change over time of the combined effects of inverse densities

High density biomass						
Parameters	C1		C2		C3	
	T_a	T_c	T_a	T_c	T_a	T_c
a_{i0}	0.0086	-0.6718	0.1256	0.0258	0.5629	0.4533
a_{ii}	0.1470	0.2117	0.0997	0.1484	0.1892	0.3468
a_{ij}	0.0467	0.2345	0.0434	0.1456	0.0984	0.1552
s_{aii}	0.0189	0.0254	0.0126	0.0249	0.0149	0.0449
s_{aij}	0.0223	0.0301	0.0149	0.0295	0.0177	0.0532
P_{aii} (%)	0.00	0.00	0.00	0.03	0.00	0.00
P_{aij} (%)	6.41	0.00	1.67	0.09	0.04	1.67
a_{ij}/a_{ii}	0.32	1.11	0.44	0.98	0.52	0.87
R^2	0.87	0.92	0.88	0.83	0.95	0.87
Number of flowers						
Parameters	7/7		1/8		21/8	
	T_a	T_c	T_a	T_c	T_a	T_c
a_{i0}	-1.1645	4.2387	-0.3451	-0.7267	0.8427	0.1733
a_{ii}	0.2118	-0.0361	0.0775	0.1599	0.2514	0.8699
a_{ij}	0.2407	-0.2114	0.0890	0.2122	0.0932	-0.4028
s_{aii}	0.1635	0.1877	0.0364	0.0755	0.0813	0.1757
s_{aij}	0.1938	0.2225	0.0432	0.0895	0.0964	0.2082
P_{aii} (%)	22.6	84.59	6.03	6.13	1.26	0.09
P_{aij} (%)	24.46	36.96	6.72	4.05	36.15	8.26
a_{ij}/a_{ii}	1.14	5.86	1.15	1.33	0.37	-0.46
R^2	0.21	0.09	0.42	0.46	0.51	0.81

morph is more influential than the cyanogenic morph. Intra-morph perception was much less for the acyanogenic than for the cyanogenic morph. The substitution rates of $S_{T_a} = 0.84$ and $S_{T_c} = 0.51$ for T_a and T_c , respectively, indicate that one T_c is approximately equivalent to 0.84 individuals of T_a . Conversely one T_a is equal to 0.51 T_c plants. Changes over time of the combined effects is given in Table 7.

Discussion and conclusion

Connolly (1987) claimed that a smaller substitution rate of a species could not always be interpreted to have a greater contribution to yield than the species with greater substitution rate. The substitution rates, considered by Firbank and Watkinson (1985) to be competition coefficients, should be interpreted in an "effective" sense; that is, a smaller substitution rate represents a greater relative perception. This may, however, bear little relation to either fitness or yield. Nevertheless, at high density, the acyanogenic morph (with an S_{T_a} of 0.40) appears to have greater biomass in the overall density as well as for the all relative frequencies than the cyanogenic morph (with an $S_{T_c} = 0.90$). This suggests that the acyanogenic morph, even at the highest density, appears to have a greater fitness than the cyanogenic morph in terms of its contribution to biomass accumulation in a mixed stand. If, at high density, inter-morphic competition improves the biomass of the acyanogenic morph, such competition augments the number of flowers of the cyanogenic morph.

It is clear from the equations that, in pure stand, the potential yield per unit area for the acyanogenic morph is much greater than for the cyanogenic morph. There was no apparent systematic difference in ramet size between the morphs that could contribute to the difference in final size. Hence, if the experiment had continued, the difference between the morphs, both in pure stand and in mixture, would probably have been maintained.

As *Ac* and *Li* were not distinguished in this study, the results cannot be compared to those of Ennos (1981) and Kakes (1989). The results do, however, provide support for the hypothesis that cyanogenesis acts directly or indirectly on the energy balance, such that its presence increases the cost of biomass production. The greater contribution of the acyanogenic morph to biomass accumulation and flower production per plant may therefore be a result of a more efficient utilization of energy.

The performance of acyanogenic morphs over all densities as well as all the relative frequencies suggest that the substitution rates computed from the inverse linear model can not always be interpreted as competition coefficients that influence the relative fitness of the two morphs.

The different processes occurring at low density (100, 150, 220 plants/m²) and high density (200, 400, 600 plants/m²), which appear to follow the change in RRT as a function of d_{T_a}/d_{T_c} at the third harvest date, may be attributed to an interaction between density and proportion when d_{T_a} forms the minority component of the mixture. The clear change in RRT during the early stage of the experiment at low density is in agreement with the fact that the RRT may change with time (Connolly, 1987).

A difficulty remains, however, in the interpretation of an increasing synergism between the two morphs. It is important to note that the a_{ij} and a_{ji} , and consequently the RRT, can be strongly influenced by the date at which the harvest is performed and by the relative emergence time of the two morphs (Spitters 1983; Kropff et al. 1984; Firbank and Watkinson 1986). However, the cumulative results of RRT for the different harvest times suggest that competition with overcompensation occurs at all levels of density.

The results suggest that, independent of density, the acyanogenic morph has a greater fitness, in terms of relative performance in mixture, than the cyanogenic morph. This seems to be more evident for biomass accumulation than for fecundity.

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