Some effects of associated growth on grass and clover under field conditions

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Summary

A two-year field experiment with pure stands of white clover, perennial ryegrass and cocksfoot, with alternate rows of clover and the grass species, and with separated and unseparated root systems on a nitrogen-deficient soil is discussed.

It is shown that nitrogen transfer from clover to grass takes place through loss of leaves and leaching of nitrogen from the above-ground parts. The mutual effects of the species are analysed.

1. Introduction

Grass grown in association with clover seems to profit in some way from the latter's presence. This is confirmed by numerous experiments, but in others every beneficial effect appears to be absent [1]. The phenomenon may not occur under all circumstances or the beneficial effect may be obscured by opposing factors. Most investigators assume that the stimulating effect on the associated gramineae is caused by excretion or release of nitrogen compounds from the legume roots and nodules into the soil. The increase in nitrogen content of the grass has often been looked upon as a proof of this transfer of nitrogen. However, it is possible that the legume does not compete with non-legumes for soil nitrogen so that this increase in nitrogen content may be due to the lower number of non-legume plants in a mixture compared with a pure stand. Thus a clear proof of transfer is only obtained when the nitrogen yield of grass grown in association with clover is higher than that of a pure grass stand. On the other hand, from the absence of such an increase of nitrogen yield may not be concluded that clover does not excrete or release nitrogen, as this legume may take up some nitrogen from the soil or the grass may utilize the soil nitrogen less effectively. Only few authors mention an increase of nitrogen content and yield of grass grown in association with clover.

Any direct nitrogen effect may be due to nitrogen excretion during the growth of the leguminous plants or nitrogen release as a result of the decomposition of decaying roots and nodules. Some authors agree with the first explanation, some advocate the second, and others support both. Whatever the mechanism, the extent to which grass profits by clover nitrogen depends on the circumstances. Growing conditions resulting in a small C/N quotient should favour nitrogen excretion provided photosynthesis is great enough to ensure sufficient nitrogen fixation.

1 Due to prolonged illness of the first author no proper references to literature could be made, but the literature consulted is listed at the end of the paper.

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FIG. 1

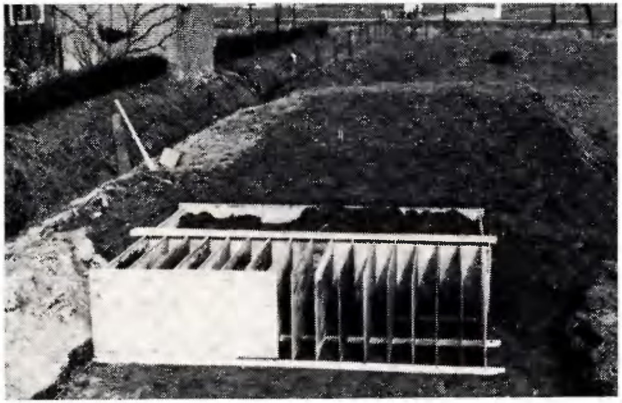


FIG. 2

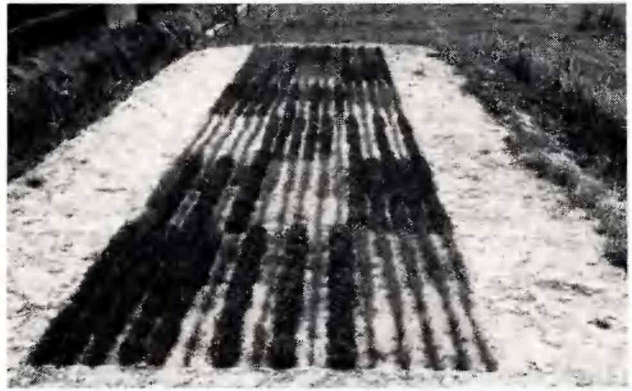


FIG. 3

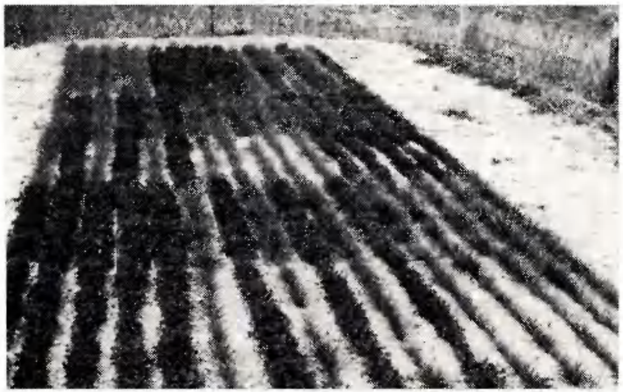


FIG. 4

FIG. 1. The preparation of the experimental site (Feb. '61)

FIG. 2. The experiment some days before the first cut (July '61)

FIG. 3. The difference in growth in compartments without eternite (foreground) and with eternite plates (the next one) (1st cut '61)

FIG. 4. The poor regrowth of the clover after the second cut (Sept. '61) especially of the monoculture clover in the compartments with partitions

FIG. 5a

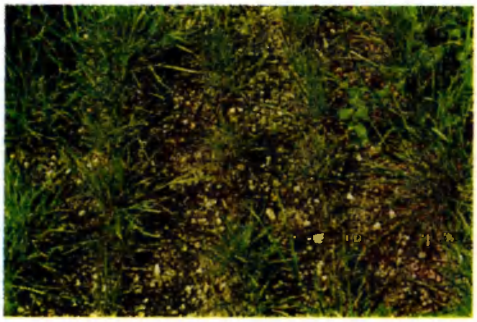


FIG. 5b

FIG. 6a

FIG. 6b

FIG. 5. Difference in growth of perennial ryegrass before the second cut in 1962 (13 July '62);

a. in between perennial ryegrass.

b. in between white clover.

FIG. 6. Difference in growth of cocksfoot before the second cut in 1962 (13 July '62);

a. in between cocksfoot.

b. in between white clover.

As appears from literature, conditions in the Netherlands are very favourable for nitrogen excretion (long days, moderate temperatures and low light intensities) and also for periodical decay of roots and nodules (frequent defoliation, repeated nitrogen fertilization, alternately unclouded and overcast, and a varied water supply).

Under field conditions it is difficult to determine whether nitrogen transfer from clover to grass has taken place. Most investigations on nitrogen transfer from legumes to graminaceous plants were carried out in pots under greenhouse conditions and with seedlings or young plants. RUSSELL reported in 1953 that field experiments on these problems were very scarce. BLACK mentioned in 1957 that "the importance of the transfer of nitrogen from a legume to an associated non-legume crop under field conditions has been shrouded with uncertainty". Evidently, field experiments are needed. There is another reason to investigate this subject: – in many publications much attention has been paid to the beneficial effect of clover on grass through transfer of nitrogen in the soil, while other possible causes have been neglected.

This paper describes a field experiment which gives some results on the above-ground and underground effects of grass and white clover on themselves and on their associates.

2. Material and methods

An experiment with grass and clover rows was set up by the CHAMBLEE method (1958) in which a part of the rows was separated under the ground by eternite plates to a depth of 60 cm. For this purpose the soil was excavated and the eternite plates were held in a vertical position by wooden frames (FIG. 1). After breaking up the clay bottom and refilling as uniformly as possible with a sandy soil, the wooden upper frame was removed. The construction was completed in early March to give the soil chance to settle. FIG. 7 represents a replicate consisting of one compartment with and one without partitions. Each compartment contains 16 rows of grass and clover in various combinations, and each row has a length of 1.25 m and a distance of 15 cm from the adjacent rows. Six replicates were placed next to each other in a north-south direction (FIG. 8). The three northern replicates were sown with *Lolium perenne* and *Trifolium repens*, the three southern ones with *Dactylis glomerata* and *Trifolium repens*. The units of pure grass, pure clover and alternate rows of grass and clover in the east-west direction were randomized within the replicates (FIG. 8). In each of the twelve compartments 565 mg of perennial ryegrass (hay type, late flowering), 375 mg of cocksfoot and 375 mg of white clover per row were sown on 12th May. The ratios of seed quantities of ryegrass, cocksfoot and white clover were obtained from KLAPP (1954).

Soil analyses to a depth of 25 cm in 1961 and 1962 are given in TABLE 1. After the second cuts in August 1961 and July 1962 the soil was uniformly fertilized (kg/ha) as follows: –

	1961	1962
K (KCl)	133	104
P (super phosphate)	—	33
Mg (kieserite)	39	45

After sowing and in June 1961 the field was sprinkled. The soil was weeded and its surface slightly broken up when necessary.

The herbage of each row was separately clipped and oven-dried at 70° C (TABLE 2). The clover was harvested in 1962 and 1963, but not weighed, because formation of runners made it difficult to harvest each row separately. Taking FIG. 7 as an example,

FIG. 7. A replicate consisting of one compartment with and one without partitions

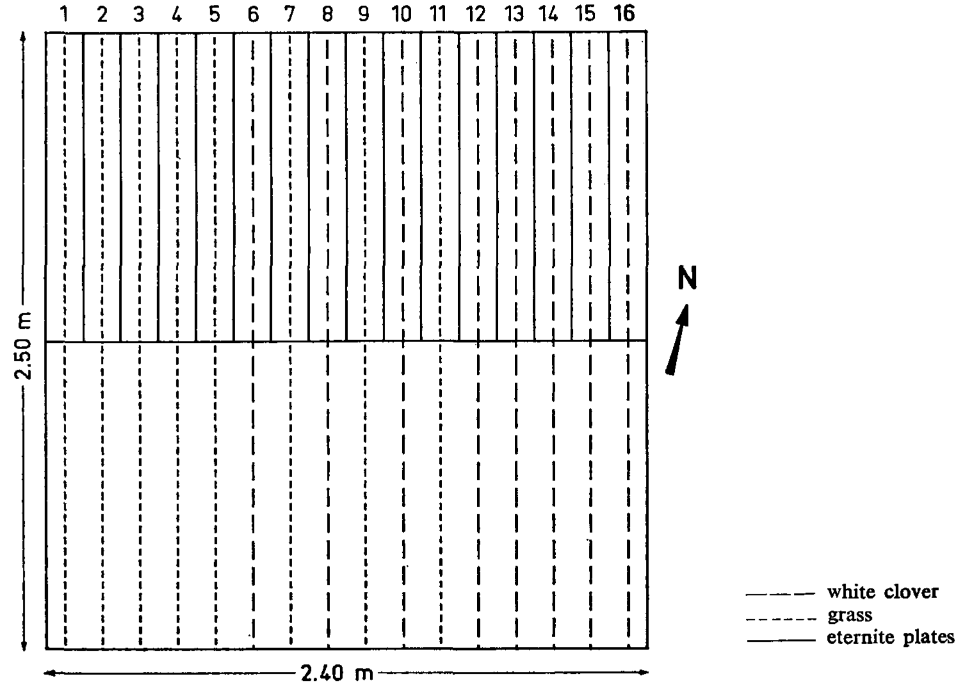


FIG. 8. Lay-out of the experimental field

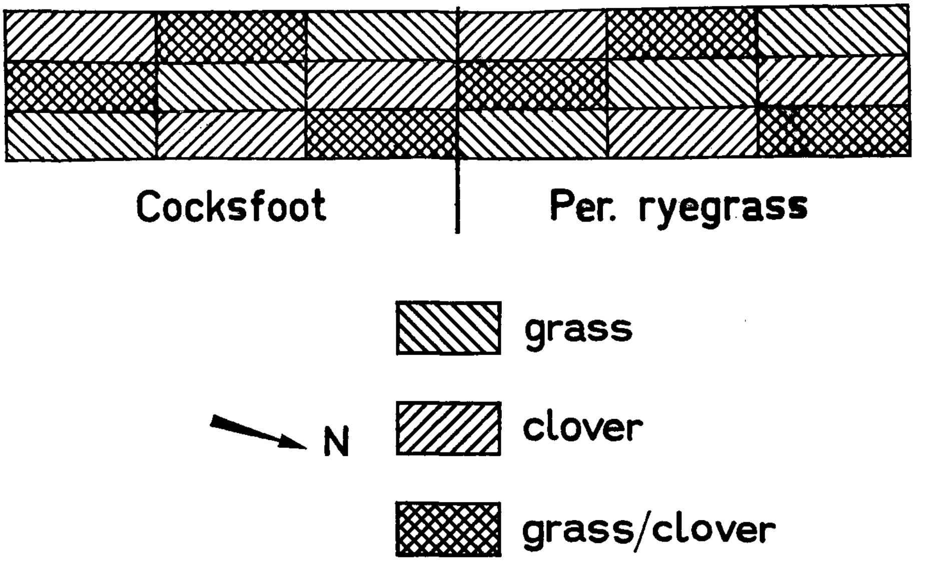


TABLE 1. Analyses of the soil

	1961	1962
pH-KCl	6.5	6.1
Humus (G) %	2.0	2.0
$CaCO_3$ %	0.1	0.1
Clay %	7	—
Sand % coarse	64	—
total	91	—
P-AL	77	75
K $^1/_{1000}$ %	9	11
MgO $^1/_{10000}$ %	27	30
N (total) %	—	0.05
N (water) %	1	0

TABLE 2. Dates of harvesting

	1961	1962	1963
1st cut	July 13th	June 6th	May 24th
2nd „	August 8th	July 19th	
3rd „	September 12th	September 19th	
4th „	October 26th		

the grass rows 2, 3, 4 and 7, 9, 11, and the clover rows 6, 8, 10 and 13, 14, 15 represent plots with grass only, grass in association with clover, clover in association with grass and clover only respectively. No two rows are identical when we take into account the species of the two rows on either side. However, a careful examination of the yields over the two years showed that there was no relation between the yield and the location of the rows in the experiment. Grass row 5 and clover row 12 in FIG. 7 are only adjacent to one row of their own species. Figures relating to these rows have been disregarded because of the unreliability of a single observation.
In the TABLES 3 and 4 the average yield of crude protein and dry matter is presented as a mean of 9 rows. For grass in association with clover and clover with grass only 8 rows were available.
In the analysis of variance the unknown value was calculated by: –

$$x = \frac{3\,R + 2\,Tr - T}{14}$$

R = sum of the 5 experimental values in the concerning replicate.

Tr = sum of the 8 experimental values in the concerning treatment.

T = total sum of the 17 experimental values.

In addition, the results of this experiment were treated according to the competition theory of DE WIT (1960). In this theory the results of competition between two plant species are treated quantitatively and a mathematical approach is applied to the development of the competitive struggle in supersession series. It gives us a few formulae for the relation between seed frequency and seed yield of plant species in a mixed culture. These are for grass and clover: –

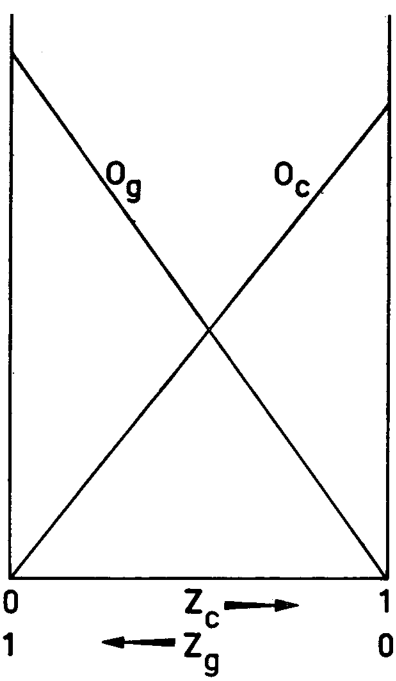
$$O_g = \frac{K_{gc}\, z_g}{K_{gc}\, z_g + z_c}\, M_g \text{ and}$$
$$O_c = \frac{K_{cg}\, z_c}{K_{cg}\, z_c + z_g}\, M_c \qquad (1)$$

in which O_g and O_c represent the yield of grass and clover, z_g and z_c the relative seed frequencies of the components in the seed mixture, M_g and M_c the yield of pure stands of similar seed density; K_{gc} and K_{cg}, being constants, are measures of the competitive power of each species in the mixture. K_{gc} is called the relative crowding coefficient of grass compared with clover. The space occupied by a grass plant surrounded by clover plants is K_{gc} $\times$ the space of a clover plant between grass plants. In this experiment the seed frequencies can be given by the relative number of rows and the production of each component by dry-matter or crude-protein yields.

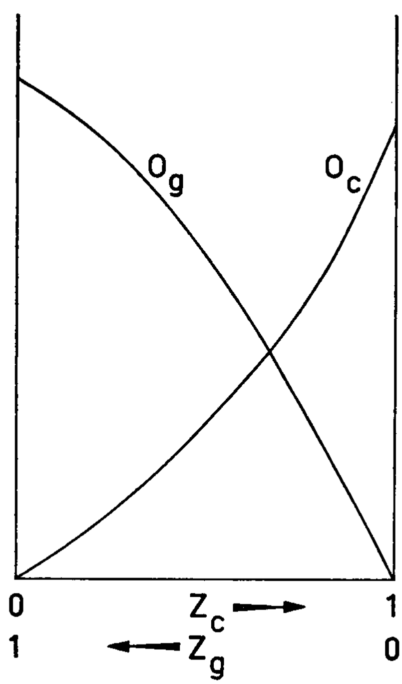
From DE WIT's theory different MODELS of competition can be derived. The MODELS applicable to the results of our experiment are treated on the next pages. The diagrams show the relation between the relative seed frequency (z_g of grass and z_c of clover along the x-axis) and the yield of the components (O_g and O_c along the y-axis). In MODEL I and II the plant species having the same growing period are crowding for the same "space". The term "space" may also comprehend "growth factors" like light, water and mineral supply *etc.*, homogeneously distributed over the field.

The yield of one component in MODEL I is proportional to the quantity of seeds sown in the mixed stand.

MODEL I: $K_{gc} \times K_{cg} = 1$



MODEL II: $K_{gc} \times K_{cg} = 1$



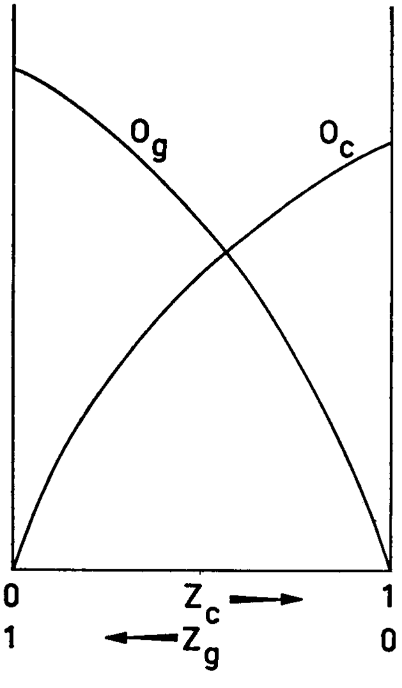
In MODEL II the yield of one component is not proportional to the quantity of seeds sown, but the sum of the yields in a mixed culture expressed as fractions of the yields in monoculture is 1.

In MODEL III the sum of the yields in a mixed culture expressed as fractions of the yields in monoculture is larger than 1. The species are crowding for space, which is not completely the same.

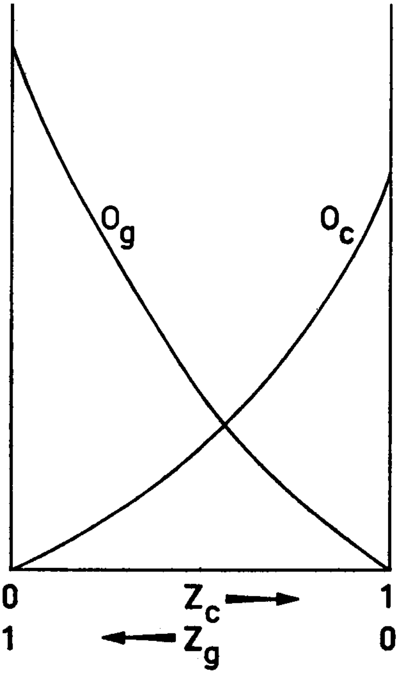
a. the explored spaces are partly separated by time (different growth periods);
b. the explored spaces are partly separated by place (different rooting depth, nitrogen fixation *etc.*). This model should be distinguished from MODEL V.

In MODEL IV the sum of the yields in a mixed culture expressed as fractions of the yields in a monoculture is smaller than 1. This may occur when a species is poisonous to the other.

MODEL III: $K_{gc} \times K_{cg} > 1$



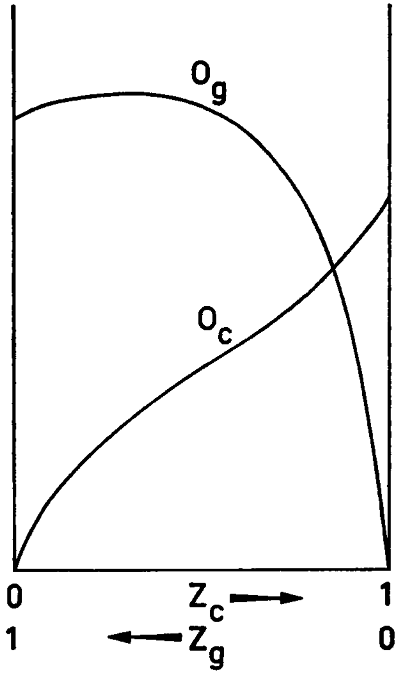
MODEL IV: $K_{gc} \times K_{gc} < 1$



DE WIT did not properly distinguish the case in which a species profits from the presence of another of MODEL III. Then it is possible that in the mixed culture one species yields more per unit of soil surface than in the monoculture. This may occur for instance when grass associated with clover grows and competes better because of the uptake of nitrogen produced by the clover. Now DE WIT's treated this case as follows. In MODEL V the equation

$$O_c = \frac{(K_{cg})_z \times z_c}{(K_{cg})_z \times z_c \times z_g} M_c \qquad (2)$$

is true for any seed frequency.



MODEL V

See text

But here $(K_{cg})_z$ is a decreasing function of the seed frequency of clover, because with decreasing clover content less clover nitrogen is transferred to the grass and the grass becomes less competitive. This function can be calculated from the yield curve of clover by equation (2). For instance, in MODEL V the yield of clover with z_c equal to 1.00, 0.50 and 0.20 is 20, 10.6 and 6.0 respectively, so that $(K_{cg})_{0.5}$ and $(K_{cg})_{0.2}$ are equal to 1.13 and 1.71. The solid line in FIG. 9 gives the relation between K_{cg} and z_c calculated from the clover yields in MODEL V.

Now in addition, it is either possible that clover and grass crowd for the same space (as in MODEL II) or partly for different spaces. In the first case $(K_{gc})_z = 1/(K_{cg})_z$ and the second case $(K_{gc})_z = c/(K_{cg})_z$ in which c is greater than unity and is constant in the first instance. The dashed line in FIG. 9 presents $(K_{gc})_z$ calculated on the assumption that c is equal to 3.

The yield of grass in the mixed stands can be represented by:

$$O_g = \frac{(K_{gc})_z \times z_g}{(K_{gc})_z \times z_g + z_c} (M_g)_z \qquad (3)$$

in which $(M_g)_z$ is again a function of z. It represents the yield of a monoculture of grass at a nutrient level similar to that created by clover. The relation between $(M_g)_z$ and z_c calculated from the yield curve of grass in model V and the K_{gc}-curve in FIG. 9 is shown as a dotted line in FIG. 10.

3. Results

The grass and clover established themselves very well (FIG. 2), although the stand of

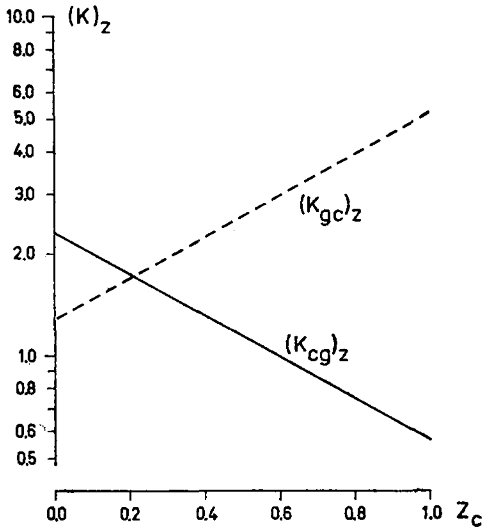


FIG. 9
Model V. A relation between the relative crowding coefficients and the seed frequency

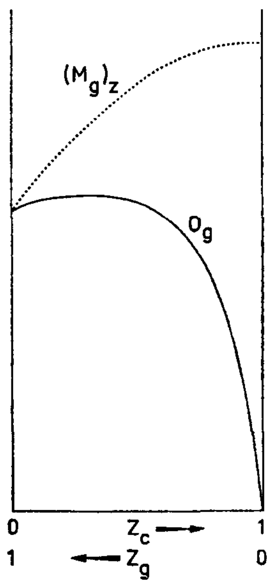


FIG. 10
Model V. The relation between M_g and Z_c (dotted line) calculated from the yield curve of grass (solid line)

cocksfoot was rather thin at the beginning. The late frost in the latter part of the winter of 1961—1962 did not affect the grass and clover unfavourably.

TABLES 3 and 4 give the average yields of crude protein and dry matter per row of grass only, grass in association with clover, clover only and clover in association with grass, and the coefficients of variance of the individual yield values with and without partitions. The differences between yields of rows in pure and mixed stands within each compartment (the sign indicates whether the difference is in favour of the mixed stand) are also given in these tables.

We have tried to eliminate the difference in yield with and without partitions by

TABLE 3. Average crude-protein yields of grass and clover rows in pure and mixed stands, with separated and unseparated root systems

Treatment	Cuts in 1961							
	July 13th		August 8th		September 12th		October 26th	
	partitions		partitions		partitions		partitions	
	with	without	with	without	with	without	with	without
Perennial ryegrass								
In between per. ryegrass	3.388	1.561	2.323	1.102	2.484	1.387	3.027	1.803
w. clover	3.059	1.484	2.222	1.603	3.459	3.121	4.808	4.193
Coeff. of var. %	12.0	12.7	11.9	13.8	15.0	22.8	11.9	23.9
Difference	—0.329*	—0.077NS	—0.101NS	+0.501****	+0.975****	+1.734****	+1.781****	+2.390****
Per cent diff.	+4.8NS		+49.8****		+85.7****		+73.8***	
Cocksfoot								
In between cocksfoot	1.506	0.857	1.288	0.733	1.461	1.114	1.871	1.640
w. clover	1.231	0.629	1.215	0.713	1.409	1.688	2.280	3.041
Coeff. of var. %	26.4	20.9	13.9	22.9	17.3	21.2	13.1	25.4
Difference	—0.274NS	—0.227***	—0.072NS	—0.020NS	—0.052NS	+0.575***	+0.409***	+1.401****
Per cent diff.	—8.3NS		+2.8NS		+55.1***		+63.6***	
White clover								
In between w. clover	8.056	5.355	10.695	9.555	—	—	3.844	7.203
per. ryegrass	7.651	6.116	11.512	11.547	—	—	4.980	6.105
Coeff. of var. %	9.27	15.4	8.47	10.9	—	—	28.3	16.3
Difference	—0.405NS	+0.761*	+0.817*	+1.983***	—	—	+1.137*	—1.098*
Per cent diff.	+19.1**		+13.1*		—		—44.8**	
White clover								
In between w. clover	8.227	5.591	10.928	11.037	—	—	4.249	5.004
cocksfoot	8.993	8.794	13.108	13.245	—	—	5.366	5.385
Coeff. of var. %	5.93	9.09	7.09	9.30	—	—	16.9	18.4
Difference	+0.767***	+3.203****	+2.180****	+2.207***	—	—	+1.117**	+0.381NS
Per cent diff.	+48.0****		+0.05NS		—		—18.7NS	

	Cuts in 1962						Cut in 1963	
	June 6th		July 19th		September 19th		May 24th	
Perennial ryegrass								
In between per. ryegrass	1.336	1.166	2.826	1.453	2.292	1.801	2.784	1.862
w. clover	2.607	2.781	5.010	3.770	5.635	5.650	4.960	6.052
Coeff. of var. %	29.7	31.1	20.3	22.2	22.8	18.8	31.9	25.1
Difference	+1.271****	+1.615****	+2.184****	+2.317****	+3.343****	+3.849****	+2.176***	+4.190****
Per cent diff.	+43.4 NS		+82.2***		+67.9**		+146.8****	
Cocksfoot								
In between cocksfoot	1.482	1.280	1.239	1.083	1.392	1.497	1.651	1.588
w. clover	1.901	2.257	1.687	2.524	3.179	5.107	4.698	7.300
Coeff. of var. %	21.0	32.8	13.6	33.0	17.6	43.9	31.1	49.8
Difference	+0.420**	+0.978***	+0.448****	+1.442****	+1.787****	+3.611****	+3.047****	+5.712****
Per cent diff.	+48.0*		+97.0***		+112.9**		+175.3**	

NS not significant.
* significant at the 10 % level.
** „ „ „ 5 % „
*** „ „ „ 1 % „
**** „ „ „ 0.1 % „

TABLE 4. Average dry-matter yields of grass and clover rows in pure and mixed stands, with separated and unseparated root systems

Treatment	Cuts in 1961							
	July 13th		August 8th		September 12th		October 26th	
	partitions		partitions		partitions		partitions	
	with	without	with	without	with	without	with	without
Perennial ryegrass								
In between per. ryegrass	22.54	13.14	23.48	11.00	21.07	11.69	20.98	13.51
w. clover	20.35	11.91	19.90	13.04	26.53	22.63	30.65	28.70
Coeff. of var. %	13.4	13.1	9.8	15.3	14.1	20.7	11.0	21.7
Difference	—2.19NS	—1.23NS	—3.58***	+2.04**	+5.47***	+10.94****	+9.67****	+15.19****
Per cent diff.	+0.3NS		+33.8***		+67.6****		+66.3****	
Cocksfoot								
In between cocksfoot	8.56	5.88	9.73	5.96	10.24	7.84	11.78	9.87
w. clover	6.75	4.75	8.11	4.73	9.04	9.66	13.12	17.87
Coeff. of var. %	30.1	25.3	15.3	16.5	17.5	17.5	10.1	22.6
Difference	—1.81NS	—1.13*	—1.63**	—1.23**	—1.20NS	+1.82**	+1.34**	+8.00****
Per cent diff.	+1.9NS		—3.9NS		+34.9***		+69.7****	
White clover								
In between w. clover	34.96	26.16	41.09	35.49	6.39	17.21	15.59	31.89
per. ryegrass	34.49	29.59	45.36	44.18	14.58	19.11	20.73	27.58
Coeff. of var. %	10.1	10.4	9.0	11.6	28.9	21.7	28.9	20.0
Difference	—0.47NS	+3.44**	+4.27**	+8.70***	+8.19****	+1.90NS	+5.14*	—4.31NS
Per cent diff.	+14.5*		+14.1*		—117.2****		—46.5**	
White clover								
In between w. clover	36.71	27.34	41.03	40.37	8.99	15.51	16.03	19.23
cocksfoot	40.40	39.46	49.62	49.46	18.43	18.91	20.61	20.78
Coeff. of var. %	6.2	7.4	6.7	9.3	24.7	17.7	17.9	19.0
Difference	+3.69***	+12.12****	+8.59****	+9.09****	+9.45****	+3.40**	+4.58**	+1.55NS
Per cent diff	+34.3****		+1.6NS		—83.2****		—20.5NS	

	Cuts in 1962						Cut in 1963	
	June 6th		July 19th		September 19th		May 24th	
Perennial ryegrass								
In between per. ryegrass	16.83	16.11	27.40	16.19	25.37	19.47	33.58	22.91
w. clover	34.81	36.25	39.97	37.25	46.46	45.73	49.58	61.13
Coeff. of var. %	35.6	29.5	12.5	21.1	22.3	17.7	27.3	26.0
Difference	+17.98***	+20.14****	+12.57****	+21.06****	+21.10****	+26.27****	+16.00**	+38.22****
Per cent diff.	+18.2NS		+84.3****		+51.8**		+119.2****	
Cocksfoot								
In between cocksfoot	19.10	16.64	13.74	11.81	14.84	16.36	20.82	19.14
w. clover	23.45	26.83	16.44	24.32	29.66	49.11	48.49	75.57
Coeff. of var. %	23.7	34.3	15.8	31.4	18.8	45.8	31.3	39.5
Difference	+4.35*	+10.18**	+2.70**	+12.51****	+14.82****	+32.76****	+27.7****	+56.4****
Per cent diff.	+38.4NS		+84.2***		+100.5**		+162.0***	

NS not significant.
* significant at the 10 % level.
** „ „ „ 5 % „
*** „ „ „ 1 % „
**** „ „ „ 0.1 % „

expressing the yields per row in the mixed cultures as a percentage of the yields in the pure stands. These percentages were subtracted and the differences are given in TABLES 3 and 4 as "per cent differences".

The question arises why the yield values with and without partitions were not compared directly. From the first cut in 1961 onwards there was a great discrepancy in yield of grass and clover between compartments with and without partitions, which cannot be explained by the separation of the root systems only (FIG. 3). During the experiment this discrepancy gradually decreased in clover more rapidly than in grass. It is unlikely that the eternite partitions left any nutritive element in the soil because before starting the experiment the plates were left in the open for two years to give them a chance to leach. Probably these plates kept the soil in a favourable structure, although this was not revealed by physical measurements during the first year. At the end of the experiment in 1963 the roots were dug up. It was observed that relatively more roots were growing close to the plates. Since we also found more active nodules at a greater depth on the clover roots growing close to the plates, we conclude that this "plate factor" was due to a better aeration of the soil near the partitions. The effect of this superior aeration may depend on the kind of soil in the compartments; a similar experiment which was started with another soil in the next year (1962) did not show this phenomenon. In CHAMBLEE's (1958) experiment this complication did not occur either.

FIG. 11 and 12 represent the per cent differences more distinctly. Because we may assume that, firstly, on this very sandy and nitrogen-deficient soil (see TABLE 1) nitrogen limits growth and, secondly, that the relation between nitrogen supply and nitrogen uptake by the grass can be represented by a straight line, these per cent differences in nitrogen (or protein) yield are an estimation of the underground nitrogen

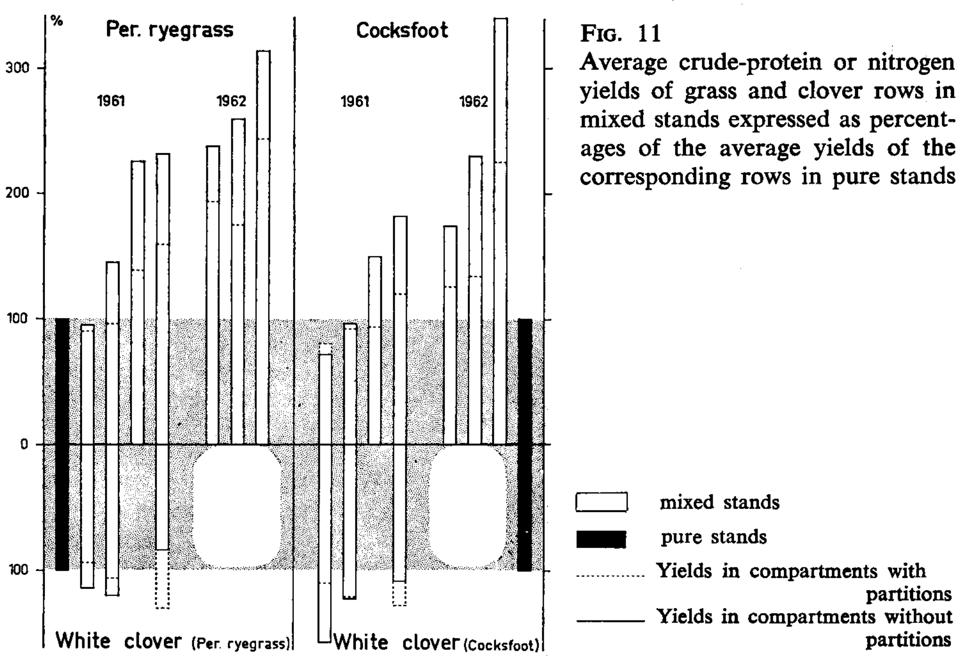


FIG. 11
Average crude-protein or nitrogen yields of grass and clover rows in mixed stands expressed as percentages of the average yields of the corresponding rows in pure stands

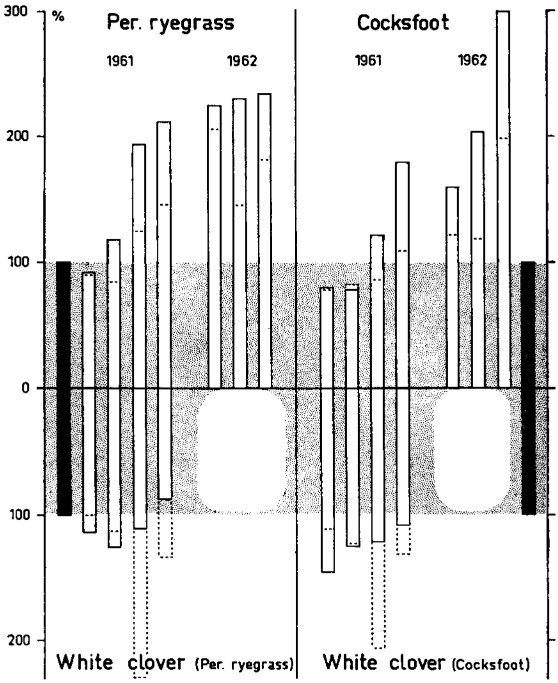


FIG. 12
Average dry-matter yields of grass and clover rows in mixed stands expressed as percentages of the average yields of the corresponding rows in pure stands

effects. In the first instance we cannot assume any linear relation between dry-matter production and nitrogen supply because with increasing nitrogen supply the dry-matter production reaches its maximum earlier than the nitrogen uptake. Secondly, the higher nitrogen content of grass in association with clover as compared with that of grass only (TABLE 8) prevents us from assuming a linear relation.

4. Discussion of results

4.1. Crude protein

4.1.1. *Differences between pure and mixed stands*

In FIG. 11 the dashed lines represent the crude-protein yield of the mixed stands in the compartments with partitions, the solid lines those in the compartments without partitions, both expressed as percentages of the pure stands.

As time went on grass in association with clover yielded considerably more than grass only (FIG. 5a and b, 6a and b). The representation in FIG. 11 suggests that this was due to certain favourable above-ground and underground influences of clover on grass in comparison with grass only, but it may be that onfavourable underground and above-ground effects of grass on grass suppressed the yield as compared with grass in association with clover. And perhaps it may be a combination of unfavourable influences of grass on grass and favourable influences of clover on grass.

The relatively higher yields of grass in association with clover occur in compartments with and without partitions, although in the latter case the increase occurred somewhat earlier and reached a higher level. In other words, the effect on the grass did

not depend on the presence or absence of the partitions, but on the species of the adjacent rows.
An interpretation of the clover yields appears to be more complicated. The clover in a mixed culture yielded more than that in a pure stand, but after the second cut the regrowth of clover in all replicates was poor and irregular in both mixed and pure stands. However, the plots of pure clover were exceptionally poor in all compartments with partitions (FIG. 4). We will discuss this in chapter 4.2. The yields of the third cut are not recorded in TABLE 3 and FIG. 11 because the nitrogen content was not determined.
We may conclude that the protein yield of clover does not diverge so much as that of grass, but in general clover rows produced more protein in mixed stands. This was also observed by other investigators.

4.1.2. *Above-ground influences*

It can be seen from TABLE 3 and FIG. 11 that, when compared with the effects of grass on grass and expressed in terms of crude protein or nitrogen, the above-ground effects of clover on grass become highly significant, starting from the third cut of ryegrass and the fourth cut of cocksfoot, both in 1961. In spite of an abundant clover vegetation in 1962 (see FIG. 5b and 6b) grass yields per row in the mixed stands were 105,3 % and 64,5 % higher than in the pure stands of ryegrass and cocksfoot respectively.
Ryegrass benefited by the poor condition of the clover in the third cut in 1961, but for cocksfoot it did not make much difference whether it stood between poor clover or in a pure stand, its growth at first being not so vigorous as the growth of ryegrass. From FIG. 11 it can be seen that only in the third cut of 1962 cocksfoot profited to about the same degree as ryegrass. This is in agreement with the opinion that cocksfoot is clover-tolerant in its youth, but gradually becomes more and more competitive to clover so that at last it may surpass ryegrass in this respect. This point was reached at the end of 1962, both in compartments with and without partitions.
In the second cut of ryegrass and in the first and second cuts of cocksfoot, clover profited by above-ground factors to about the same degree when growing in association with grass as grass profited when growing in a pure stand. The complication attached to the clover after the second cut prevented us from drawing any conclusion, but it seems that in this case the clover is not so much influenced by above-ground factors as grass.
In the older sward the above-ground influences, especially when compared with the grass yields, played a more important role. These differences between grass in mixed and in pure stands may be due to: –

a. roots growing under the partitions,
b. above-ground effects.

The first possibility is ruled out because there were hardly any roots below a level of 60 cm (see TABLE 5) and these few roots did not grow under the plates into the clover soil. The clover roots even did not reach as far. The above-ground effects are the result of leaching of nitrogen by decaying clover leaves and petioles into the grass soil. This is illustrated by FIG. 13 and 14 in which the accumulation curves of nitrogen in grass were constructed for grass in association with clover and for grass only. This means that for compartments with partitions the yields given represent

TABLE 5. Crop and root weights in g dry matter of ¾ row of grass in pure and mixed stands with partitions at different depths in the summer of 1963

Root weights at a depth of	Per. ryegrass in between		Cocksfoot in between	
	per. ryegrass	w. clover	cocksfoot	w. clover
crop yield :	21.14	28.04	41.38	45.89
0—10 cm	25.64	29.73	18.39	24.98
10—28 „	6.44	8.90	4.79	4.16
28—60 „	4.06	4.62	4.85	4.61
60 „	0.76	0.38	0.24	0.56

the quantity of nitrogen harvested in a grass row and taken up from the same quantity of soil, *viz.* 112.5 litres.

From the lines in FIG. 13 and 14 for compartments with partitions it is clear that in 1961 ryegrass and cocksfoot of mixed stands took up more nitrogen per row after the second and the third cuts from the same quantity of soil than ryegrass and cocksfoot in pure stands. It is even safe to say that the quantity was so great that in 1962 ryegrass in association with clover took up about twice as much nitrogen as ryegrass in pure stands.

We may also observe that ryegrass took up nitrogen far more effectively than cocksfoot.

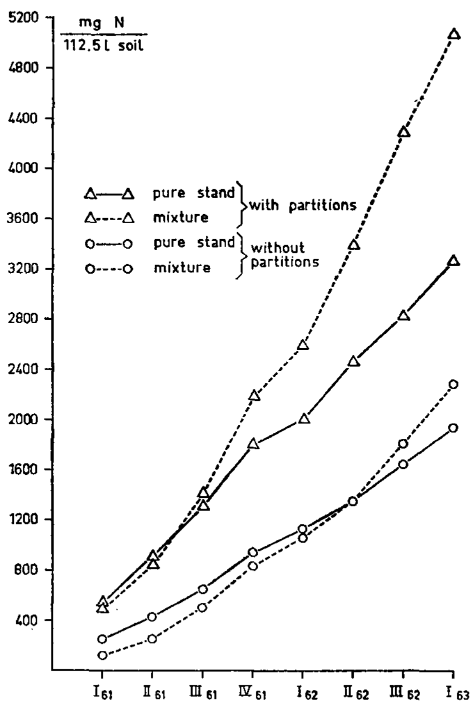


FIG. 13
Accumulation of nitrogen in perennial ryegrass (mg) on 112.5 litres of soil

4.1.3. *Underground influences*

As we discussed in chapter 3, the "per cent difference" is an estimate of the under-

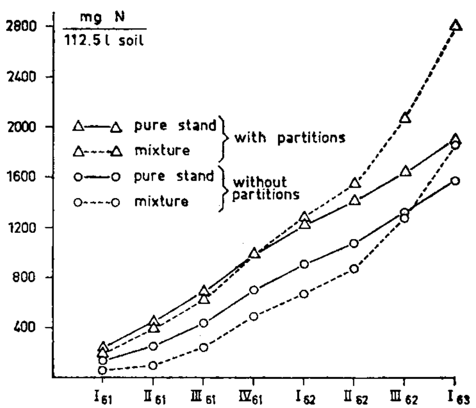


FIG. 14
Accumulation of nitrogen in cocksfoot (mg) on 112.5 litres of soil

ground nitrogen effect on the yields of mixed stands expressed as percentages of the nitrogen yields of pure stands. In FIG. 11 ryegrass and cocksfoot after the first and second cuts in 1961 show a beneficial and significant above-ground nitrogen effect of the associated growth of clover, increasing with time to 66—70 % at the end of 1961 and to 68 % (ryegrass) and 113 % (cocksfoot) at the end of 1962. At the same time in the compartments without partitions, the first two cuts of clover in mixed stands yielded significantly more nitrogen, and in three out of four cases this was due to the significant underground influence of the associated grass. Because of lack of further data we cannot conclude more about clover. To find out whether the beneficial underground influence of clover rows on grass rows is a consequence of clover nitrogen in FIG. 13 and 14 the nitrogen uptake by grass per unit of soil has been taken as representative of the nitrogen level of the soil.

We have already discussed the lines in the case of compartments with partitions in chapter 4.1.2. from which appears that the nitrogen accumulation in grass per unit of soil with partitions is considerably higher than without partitions.

This discrepancy in the monocultures may be totally due to the "plate factor" (see chapter 3), but in the mixed cultures this may also be ascribed to a less efficient utilization of the soil by the grass roots under grass and clover in compartments without partitions as compared with roots in the space restricted within plates.

In the compartments without partitions grass in mixed stands is more backward than grass in pure stands when only half the quantity of seed per unit of soil is sown. This is clearly demonstrated in FIG. 13 and 14 by the nitrogen yields of the first cut in 1961. Already after the second cut the lines of the mixed and the pure stands run parallel, which means that despite a start with different seed quantities, the uptake of nitrogen by the grass became equal in both the mixed and pure stands, probably through uptake of nitrogen from under the clover.

There are two factors which may have determined the further slope of the grass lines in the mixed cultures without partitions. First, the utilization of space under mixed stands by grass roots may be considered less efficient than in pure stands, which leads to a decrease of the slope of the line. Secondly, the utilization of clover nitrogen by grass in mixed stands leads to a further increase. Such a parallelism of the grass lines of the mixed and pure stands may be concluded from the equilibrium between these effects. But after the second cut in 1961 the positive effect of clover nitrogen seemed to dominate. The negative effect of a less efficient utilization of the rooting space by grass in mixed stands makes it impossible to compare the differences in nitrogen uptake per unit of soil in compartments with and without partitions, and thus to get an idea of the quantity of clover nitrogen by which grass profited when no partitions were present. To estimate these profits more exactly a similar experiment was set up in 1962 in which grass and clover were included at different spacings. DE WIT's interpretation of the results gives a better approximation of the nitrogen profits of grass caused by clover, as described in the next chapter.

4.1.4. *The crude-protein results worked out by the competition theory*

The results of the three years are represented in the competition diagrams of crude protein and relative seed frequency in FIG. 15. The yields of the seed frequencies 1.0, 0.67, 0.50 and 0.33 are given as averages of 9, 4, 8 and 2 replicates respectively. Hence, in the following treatment the greatest importance is attached to the data for the relative seed frequencies of 1.0 and 0.5.

The value of the relative crowding coefficients was estimated in all diagrams where the yield curves are increasing functions of the relative seed frequencies. These values are given in TABLE 6 and the corresponding yield curves calculated according to equation (1) are shown in FIG. 15. From the K_{gc} - values of TABLE 6 and from the crude-protein diagrams of FIG. 15 we may conclude that in the compartments with and without partitions the competitive power of the grass (ryegrass as well as cocksfoot) increases with time, whereas cocksfoot shows this increment a little later than ryegrass. This is in agreement with the statement in chapter 4.1.2. that cocksfoot is probably clover-tolerant in its youth, but gradually becomes more competitive to clover. Besides this, the curves and also the K_{gc} - values indicate that in unseparated root systems the competitive power of the grass was considerably higher than in separated root systems.

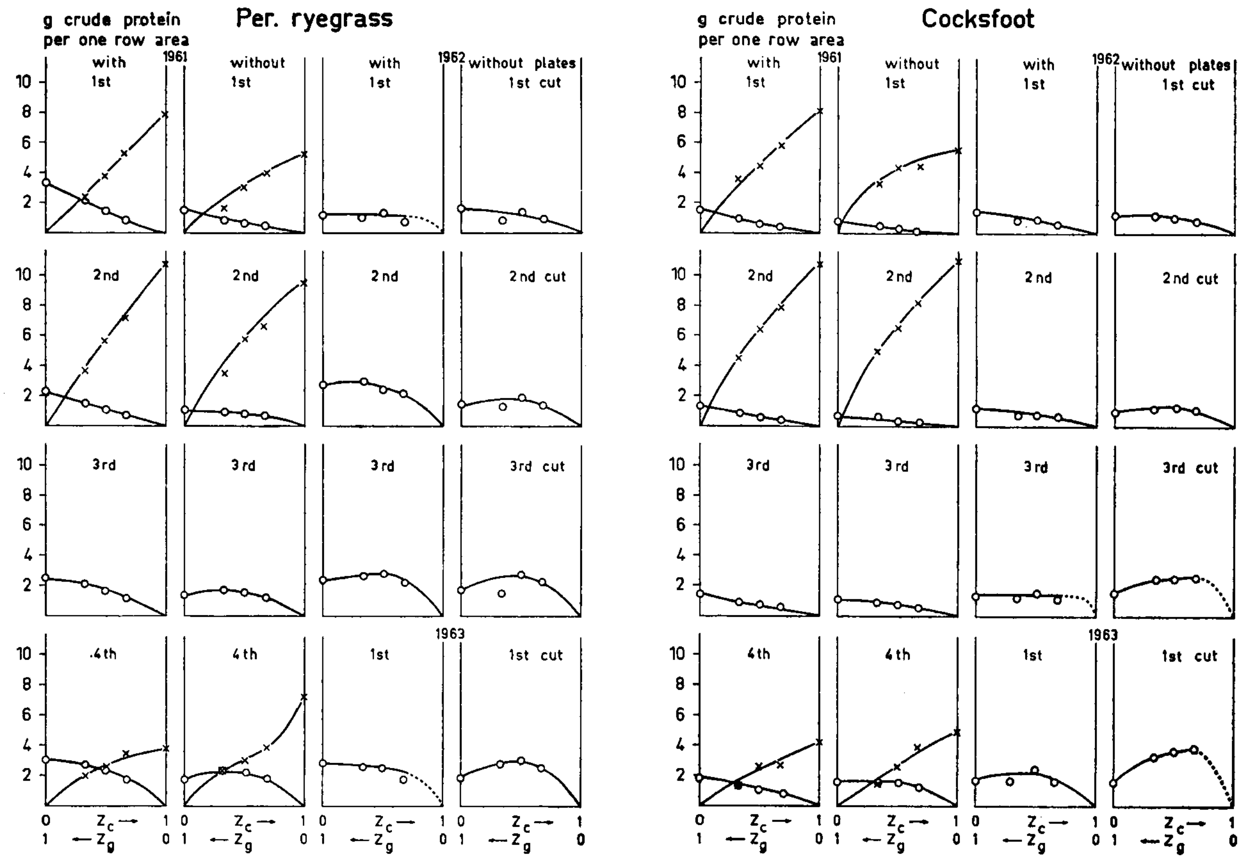
The diagrams of the first two cuts in 1961 of the compartments with partitions give a normal picture of two plant species competing for the same "space" and not af-

TABLE 6. The values of the relative crowding coefficients of the crude-protein yields of grass and clover and their products

	Perennial ryegrass			Cocksfoot		
	K_{gc}	K_{cg}	$K_{gc} \times K_{cg}$	K_{gc}	K_{cg}	$K_{gc} \times K_{cg}$
With partitions						
1961 1st cut	0.89	0.92	0.82	0.77	1.22	0.94
2nd „	1.00	1.11	1.11	1.00	1.44	1.44
3rd „	2.40	—	—	0.92	—	—
4th „	3.88	2.30	8.92	1.48	1.40	2.07
1962 1st „	13.9	—	—	1.40	—	—
2nd „	—	—	—	1.50	—	—
Without partitions						
1961 1st cut	0.85	1.38	1.17	0.62	3.02	1.87
2nd „	2.66	1.39	3.70	1.30	1.50	1.95
3rd „	—	—	—	3.80	—	—
4th „	—	—[1]	—	14.00	1.10[1]	15.4
1962 1st „	4.97	—	—	—	—	—

[1] Calculated from the yields at the seed frequencies 0.33 and 0.66.

FIG. 15. Diagrams of relative seed frequencies of grass and clover and the crude-protein yields for compartments with and without partitions in 1961, 1962 and 1963



fecting each other in any other way so that $K_{gc} \times K_{cg} = 1$ (MODELS I and II, chapter 2). In unseparated root systems the product of $K_{gc} \times K_{cg}$ in the first and second cut is mostly larger than 1 (MODELS III and V), which indicates that some extra space must have been occupied. The difference in competition between compartments with and without partitions may be explained as follows: – With or without partitions, clover has a supply of extra nitrogen from its rhizobial nitrogen fixation as follows from the high protein yield of monoculture clover compared with monoculture grass.

During the growth of the first two cuts in compartments with partitions the grass neither profited from N in the soil below the clover nor from N fixed by the clover. In the compartments without partitions, where $K_{gc} \times K_{cg}$ exceeds 1 in three out of four cases, not only clover attained its own nitrogen space, but at the same time grass took up some soil nitrogen from under the clover. This was prevented by the plates of the compartments with partitions.

The crude-protein figures of clover of the third cut are not available. The diagrams of the fourth cut with partitions correspond with MODEL III, which is due to rhizobial nitrogen fixation. The diagram of ryegrass in the compartments without partitions corresponds with MODEL V, which is due to clover nitrogen taken up by the grass.

From the grass lines it is concluded that also in 1962 grass profited from clover nitrogen either from excretion of nitrogen by the clover roots into the soil or from nitrogen of decaying leaves, petioles, roots and nodules.

To decide to what extent clover fixes nitrogen in association with grass, we calculated the gain of nitrogen in the mixed stands compared with that of the pure grass stands in the same compartments without partitions (TABLE 7). To account for the amount of nitrogen in the roots, we multiplied the nitrogen content of the cut parts

TABLE 7. Nitrogen fixation and benefit of grass by clover in an association of alternate grass and clover rows at distances of 15 cm, expressed as kg N per ha

	Fixation on a field with alternate rows of clover and perennial ryegrass or cocksfoot	
	per. ryegrass	cocksfoot
1961 1st cut	23.8	41.6
2nd „	60.9	68.6
3rd „	28.9	22.7
4th „	37.8	28.3
Total 1961	151.4	161.2

of grass by 3/2, and that of clover by 5/4, which ratios were obtained from literature. The ultimate figure is still rather low, because the fixed nitrogen leached from the soil and taken up by micro-organisms or left in the soil was not taken into account.

The crude-protein content of clover of the 3rd cut was not determined, but estimated at about 25 % (TABLE 8). The uptake of nitrogen by clover in 1962 could not be estimated because neither yields nor N-contents were known.

An estimate of the amount by which grass profited from clover can be obtained by calculations based on the competition theory appllied to MODEL V. The nitrogen yields of the last cut of clover and perennial ryegrass in 1961 on the plots without partitions have also been shown in FIG. 16a. A comparison with the dry-matter yields of

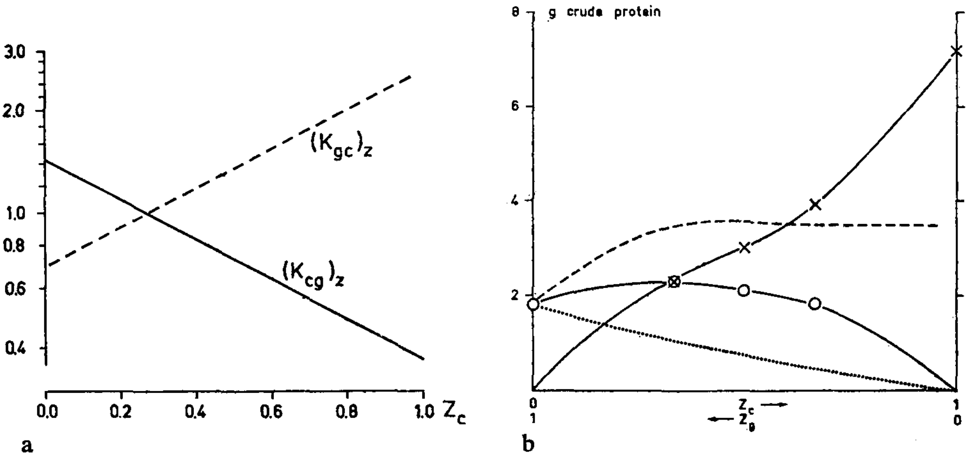
TABLE 8. Crude-protein contents in dry matter of grass and clover rows in mono- and mixed cultures, and in compartments with and without partitions

	Perennial ryegrass				Cocksfoot			
	with partitions		without partitions		with partitions		without partitions	
	in between		in between		in between		in between	
	per. ryegrass	w. clover	per. ryegrass	w. clover	cocksfoot	w. clover	cocksfoot	w. clover
1961 1st cut	14.77 [1]	16.06 [1]	10.90 [1]	12.62 [1]	17.62	19.48	14.72	14.54
2nd „	9.87	11.29	10.33	12.19	13.15 [1]	15.60 [1]	13.52 [1]	16.38 [1]
3rd „	11.81	13.04	12.07	13.85	14.40	15.50	14.32	17.38
4th „	14.39	15.70	13.33	14.60	15.90	17.25	15.88	17.04
1962 1st „	8.51	7.64	7.43	7.61	7.78	8.14	7.69	8.60
2nd „	10.23	12.45	9.01	10.08	9.03	10.33	9.20	10.49
3rd „	9.04	12.15	9.20	12.36	9.37	10.84	9.13	10.61
	White clover							
	with partitions		without partitions		with partitions		without partitions	
	in between		in between		in between		in between	
	w. clover	per. ryegrass	w. clover	per. ryegrass	w. clover	cocksfoot	w. clover	cocksfoot
1961 1st cut	22.63 [1]	22.13 [1]	18.63 [1]	19.78 [1]	22.28	22.29	20.31	22.28
2nd „	26.03	25.43	27.00	26.13	26.72	26.36	27.39	26.75
3rd „	—	—	—	—	—	—	—	—
4th „	24.93	24.09	22.74	22.29	26.52	26.21	26.67	26.11

[1] Averages of 2 replicates instead of 3.

the third cut shows that the S-shape of the clover curve is genuine, so that the data are in agreement with MODEL V. By means of equation (2) it is now possible to calculate the relation between the relative seed frequency of clover and the relative crowding coefficient of clover as compared with grass (K_{cg}). This relation is shown in FIG. 16b. During the first harvests MODEL II appeared to be applicable, which indicates that as long as nitrogen fixation does not interfere with the product of the

FIG. 16a. Replacement diagram for the fourth cut in 1961 of clover and perennial ryegrass in the compartments without partitions
b. Relation between the relative seed frequency of clover and the relative crowding coefficients used for the calculations



----- Yield of monoculture grass calculated assuming that the nutrition level is the same as in the mixture.

.... Yield of grass in the mixture, calculated assuming that the grass does not profit from the clover.

relative crowding coefficient of grass (with respect to clover) and of clover (with respect to grass) which is 1. Hence, we may accept that the value of $c = (K_{cg})_z \times (K_{gc})_z$ equals 1, so that the dashed line which is a representation of the solid line in FIG. 16b represents the value of K_{gc} at different seed frequencies. By means of this curve it is possible to calculate two important yield relations. By applying equation (3) for instance it is possible to calculate the yield of a pure stand of grass at a same nutrient level as that of grass in association with clover. The result is shown by the dashed line. The yield does not increase after a relative seed frequency of clover of 0.3 onwards. As the percentage of crude protein of the grass is only 15 % this indicates that the grass does not fully benefit from its association with clover. This may be due to the arrangement of clover and grass in rows.

The relative crowding coefficient of grass as compared with clover at a clover frequency of zero is about 0.7 (FIG. 16b). This relative crowding coefficient would have occurred throughout the whole frequency range if the grass did not profit at all from the clover. Hence, under such conditions the protein yield of grass in association with clover can be calculated by substituting 0.7 for K and 1.8 g N for M (the

yield of the monoculture) in equation 1. The result is shown by the dotted line in FIG. 16a. The difference between this curve and the original curve of grass gives the amounts by which grass profited from clover at all seed frequencies.
The higher nitrogen yields of grass rows in mixed stands as compared with grass rows in pure stands may be caused by either a higher dry-matter yield or a higher protein content or by both. TABLE 8 shows that there is a considerable difference in nitrogen content in favour of the grass in mixed stands in compartments with and without partitions. This is a consequence of nitrogen depletion in the grass of pure stands. At the same time we may observe from TABLE 8 that in the second and fourth cuts the crude-protein content of clover in association with grass is always slightly lower than that of clover only.

4.2. Dry matter

The yields and competitive power in TABLE 4 and FIG. 12 are shown in the same way as in TABLE 3 and FIG 11, except that TABLE 4 and FIG. 12 refer to dry matter and not to crude protein. The differences between the dry-matter yields in FIG. 12 and the crude-protein yields in FIG. 11 are not essential at all. Only the level of the relative protein yields of grass in mixed stands is higher than that of dry matter. There is hardly any difference between the competition diagrams in FIG. 15 and 17. Any slight difference in protein content of the grass in mixed and pure stands usually causes the relative crowding coefficient K_{gc} to be lower for dry matter than for protein (TABLE 9).

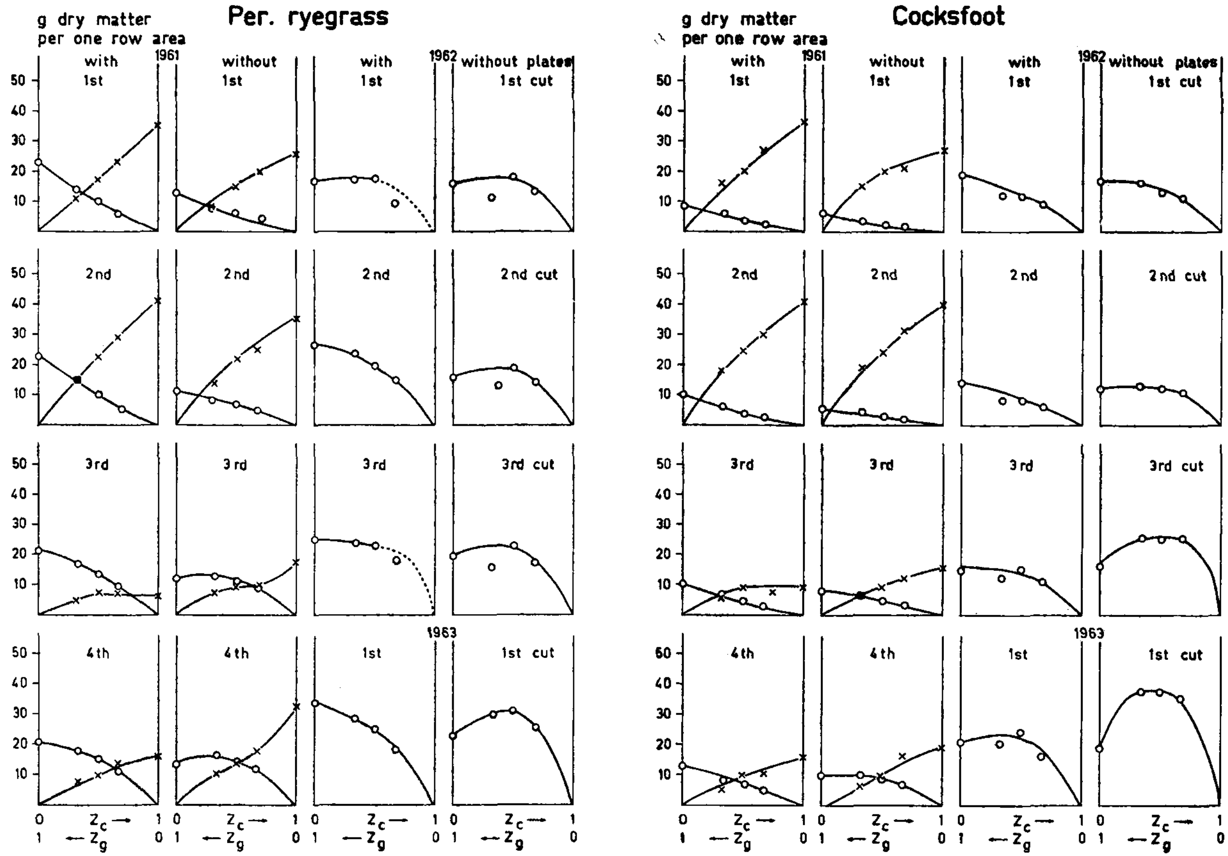
TABLE 9. The values of the relative crowding coefficients of grass compared with clover (K_{gc}) and of clover compared with grass (K_{cg}) and their products for the dry matter in the cuts in 1961 and 1962

	Perennial ryegrass			Cocksfoot		
	K_{gc}	K_{cg}	$K_{gc} \times K_{cg}$	K_{gc}	K_{cg}	$K_{gc} \times K_{cg}$
With partitions						
1961 1st cut	0.85	0.97	0.82	0.76	1.26	0.96
2nd „	0.79	1.23	0.97	0.75	1.48	1.11
3rd „	1.74	—	—	0.85	—	—
4th „	2.80	2.50	7.00	1.20	1.50	1.80
1962 1st „	—	—	—	1.40	—	—
2nd „	2.74	—	—	1.33	—	—
3rd „	±10.75	—	—	8.64	—	—
Without partitions						
1961 1st cut	0.73	1.40	1.02	0.67	2.32	1.55
2nd „	1.43	1.49	2.13	0.75	1.52	1.14
3rd „	—	1.44—0.62 [1]	—	1.80	1.65	2.97
4th „	—	0.94—0.61 [1]	—	—	1.1 [1]	—
1962 1st „	—	—	—	—	—	—

1 Calculated from the yields at the seed frequencies 0.33 and 0.66.

For the third cut in 1961 in the compartments with partitions (FIG. 17) we see a deviating clover line with relatively low yield values at z_c 0.67 and 1.00. There are two ways to account for it: – first, we may consider this as a coincidence for which no explanation can be given; secondly, we may consider this phenomenon as a consequence of certain regularities. The first solution has little to recommend it, because

FIG. 17. Diagrams of relative seed frequencies of grass and clover and the dry-matter yields for compartments with and without partitions in 1961, 1962 and 1963



ryegrass and cocksfoot showed this phenomenon in every replicate as appears from TABLE 10. Moreover ENNIK (1960) found the same in his pots under a low light intensity. This confirms our observations that it is not a question of extra high yields at z_c equal to 0.5, but of extra low yields at z_c equal to 1.0.

TABLE 10. Average dry-matter yields in g of clover rows in pure and mixed stands in the third cut of 1961 in the compartments with and without partitions

	Perennial ryegrass			Cocksfoot		
Replicate:	I	II	III	I	II	III
Pure stand						
with partitions	5.8	9.4	3.9	11.4	4.7	10.9
without partitions	16.1	20.4	15.1	19.5	10.4	16.6
Mixed stand						
with partitions	17.5	13.8	13.1	21.5	10.8	21.1

The question arises why the yield depression did not occur in the compartments without partitions. We have not yet been able to explain this phenomenon, but in the future we hope to give a reasonable interpretation after having carried out pot experiments under controlled conditions.

It is important to know whether a mixed grass/clover stand yields more or less than: –

a. a pure stand of either grass or clover on the same area;
b. the average yield of the pure stands of grass and clover.

a. The average dry-matter yields of mixed stands and of clover only are compared with the corresponding stands of grass only in FIG. 18. In this soil, which is also deficient in nitrogen, the clover yields exceed the grass yields by far, in particular those of cocksfoot. The mixed stands yielded more than the pure stands of grass, but less than the pure stands of clover.

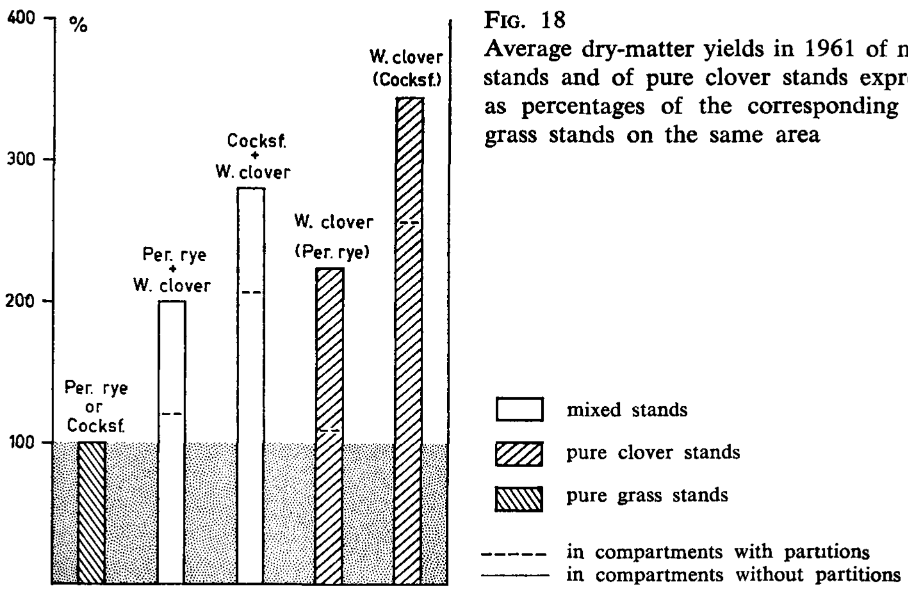


FIG. 18
Average dry-matter yields in 1961 of mixed stands and of pure clover stands expressed as percentages of the corresponding pure grass stands on the same area

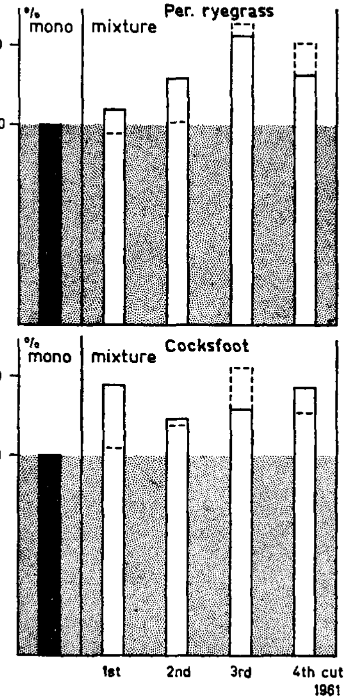


FIG. 19
Average dry-matter yields of one row of clover + one row of grass in mixed stands expressed as percentages of the corresponding sum of yields in pure stands

mixed stands
pure stands

----- in compartments with partitions
——— in compartments without partitions

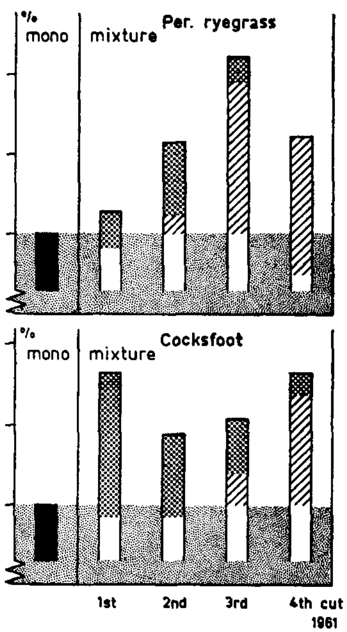


FIG. 20
Extra yields of FIG. 19

white clover
grass

b. In FIG. 19 the average dry-matter yields of one row of clover and one row of grass in mixed stands are compared with those in pure stands for each cut in 1961. In all cuts, even in the first, the yields of the mixed stands in the compartments without partitions expressed as percentages of the pure stands were the highest. Considering the four cuts in 1961, it can be seen that the extra yield approximated to 24 % ; in the last cuts this was largely due to above-ground influences.

In FIG. 20 is indicated to what degree these extra yields obtained by cultivating grass and clover together, were induced by a better growth of each of the associates. Initially these extra yields were mainly due to an increased clover growth, but in the third and fourth cuts of ryegrass and in the fourth cut of cocksfoot the extra yields were mainly due to an increase in grass yields. This figure also demonstrates that ryegrass becomes competitive to clover at an earlier stage than cocksfoot.

5. Conclusions

The above description of a two-year field experiment with pure grass, pure clover, alternate grass and clover rows and separated and unseparated root systems on a nitrogen-deficient soil, leads us to draw the following conclusions: –

The general picture of the dry-matter yields of grass in association with clover in comparison with grass only (FIG. 12) was practically true for both the compartments with and without partitions, only the yields of compartments without partitions being higher than those with partitions. This means that the development based on the relative yields of the grass depended upon underground as well as on above-ground influences. The general pattern of the crude-protein yields of grass in association with clover as compared with those of grass only (FIG. 11) was nearly the same as that of the dry-matter yields.

The crude-protein contents in the dry matter of grass in mixed stands were higher than those of grass in pure stands as the figures in TABLE 8 demonstrate.

In the mixed stands of grass and white clover especially the grass component had undergone above-ground and underground influences from the clover as compared with pure stands.

We had to account for considerable above-ground influences: – in the first two cuts of 1961 of ryegrass and in the first three cuts of cocksfoot, grass only yielded more than grass in association with clover. In the next cuts the grass benefited increasingly and significantly from the clover. For 1962 this amounted to 46 % (cocksfoot) and 74 % (ryegrass) of the dry-matter yield of pure grass and 65 % (cocksfoot) and 105 % (ryegrass) of the crude-protein yield of pure grass. The above-ground influences of clover on grass which may be seen as a result of nitrogen leached by decaying clover leaves and petioles, resulted in a higher nitrogen uptake by grass rows in mixed stands on the same quantity of soil. Cocksfoot took up this nitrogen far less effectively than ryegrass (FIG. 13 and 14).

Ryegrass after the first cut and cocksfoot after the second cut in 1961 showed a beneficial and significant underground nitrogen effect by the associated growth of clover, increasing with time to 64—74 % at the end of 1961 and to 68 % (ryegrass) and 113 % (cocksfoot) of the nitrogen yield in pure grass at the end of 1962. At the same time clover was not so much influenced by the adjacent vegetation as grass. The few clover data do not give sufficient information, but in general clover in association with grass yielded slightly more than clover only.

The crude-protein contents of the dry matter of clover in mixed stands were mostly slightly lower than those of clover in pure stands (TABLE 8).
We have to reckon with a particular influence of the partitions on plant growth when we carry out experiments like these. This influence may cause grass in pure stands to take up considerably more nitrogen per unit of soil than in compartments without partitions (FIG. 13 and 14). The influence may depend on the kind of soil.
Mixed stands of grass and clover in 1961 yielded considerably more than pure grass stands on the same area, but less than pure stands of clover (FIG. 18).
In all 1961 cuts the yields of the mixed stands in the compartments without partitions were higher than the average of the pure stands of grass and clover (FIG. 19). Initially these extra yields of the mixed stands have been mainly obtained by increased clover growth. In the third and fourth cut of ryegrass and in the fourth cut of cocksfoot the extra yields were mainly due to increased grass growth (FIG. 20).
From DE WIT's competition theory we may conclude that the competitive power of the grass, increasing with time, ultimately gave better results in unseparated than in separated root systems (FIG. 15 and 17). From the values of the relative crowding coefficients (TABLES 6 and 9) and from the competition diagrams (FIG. 15 and 17) we may conclude that in compartments with and without partitions ryegrass is initially more competitive to clover than cocksfoot, but at the end of 1962 this difference in competitive behaviour had fully disappeared. This experiment led to the development of a new model of competition diagram in the case where grass in association with clover competes better because of uptake of nitrogen produced by the clover (MODEL V). In the year of establishment the quantity of nitrogen fixed by clover at a seed frequency of 0.50 in above-ground and underground parts of the plants amounted to about 150—160 kg N/ha (TABLE 7).
With the data available we cannot determine the origin of the clover nitrogen; perhaps it comes from excretion by clover roots and nodules, perhaps from decaying roots and nodules, petioles and leaves.

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