THE ANALYSIS OF COMPETITION EXPERIMENTS

By E. J. Williams*

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Summary

In experimental studies of the competition between plant species, plants of two species are grown together in the same pot or plot. To compare a number of species, a suitable balanced arrangement is to grow each species in association with each other and on its own (i.e. associated with itself) once in each replication. The interpretation of the results of such experiments is discussed in this paper.

In such balanced designs, species effects are defined in terms of the mean yield, possibly measured on some suitably transformed scale, and associate effects in terms of the mean yields of the associates of a given species. The simplest assumption to make is that species and associate effects are additive; when this assumption is tenable, the "competitive advantage" of any species is independent of the particular associate it has, and may be defined as the reverse of the associate effect.

Where one or more species have a different competitive advantage with different associates, this is indicated in the analysis by a significant interaction of species and associates.

The method of analysis is applied to the results of a competition experiment with seven species of weeds. A logarithmic transformation of the data is found to be effective in making the results comparable and of roughly equal variance. A species showing differential competitive advantage with different associates is isolated, and a simple interpretation given for the remaining species.

I. Introduction

In studying the development of a community of plant species it is important to know how each species is affected by its competition with others for space, light, moisture, nutrients, and other requisites. Such a study is important for an understanding of the development of pastures, the effect of the introduction of beneficial or harmful species, or the use of one species to control others by competition.

To assess these competition effects, experiments in which two or more species are grown together in the same pot or plot are informative. Though they only roughly approximate the more complicated situation in the field, they enable the experimenter to assess some of the effects that are likely to be important.

The effects of competition between different species under different environmental conditions have been studied by many workers (see, for instance, Sakai 1955, and references there given).† The competitive advantage of one species over another depends on a number of factors, including time of germination, rate of growth, and so on; and this advantage may be modified or reversed by changes in conditions, such as fertilizer level, temperature, and rainfall. A considerable amount of study, therefore, is needed in order that the different factors affecting the competitive advantage of a species may be assessed.

* Division of Mathematical Statistics, C.S.I.R.O., Canberra.

† Sakai, K. (1955).—Competition in plants and its relation to selection. *Cold Spr. Harb. Symp. Quant. Biol.* **20**: 137–57.

Again, competitive effects may show up in various ways. Very often, where there is simple competition for space, moisture, light, or nutrients, one species will increase at the expense of the other, so that, although the difference between the yields of the species is enhanced by their being grown together, their average yield, on a suitably measured scale, will be unaffected. This type of effect will be called a main competition effect; more complicated effects, which will be noted in the analysis of experimental data, may also occur; the departure of such effects from the main effects here described will show up in the analysis as interaction effects. As species differences and the effects of treatments are often large, it has been found convenient to transform yield data to logarithms. Therefore main effects and interactions will be defined in terms of these transformed values, rather than the original yields. The merit of such a definition is not so much its theoretical justification as its providing a satisfactory interpretation of the experimental results.

In order to study the effects of competition on the yields of different species, experiments with two or more species grown in the same pot or plot are often carried out. In this paper we discuss the interpretation of the results of experiments designed to estimate these effects, using some pots in which a pair of species is grown together and other pots in which one species is grown on its own. Such experiments are similar in their design to the diallel crosses carried out in genetical studies. Although the analysis of data from such experiments is an application of well-known methods, it presents some points of interest.

II. Notation and Basic Assumptions

We consider an experiment in which p species are being compared in a balanced arrangement. In each replication there are pots containing all the possible pairs of species in competition (C-pots), $\frac{1}{2}p(p-1)$ in number, thus providing $p(p-1)$ yields; and p pots containing single species (S-pots). Thus each replication provides p^2 observations, of each species grown with each other and with itself. The yield of a half pot is taken as the unit of measurement.

Different comparisons of the yields will be subject to different experimental errors, the components of which arise from variation between C-pots, within C-pots, and between S-pots. The variances between units will be designated as follows:

C_1	between C-pots
C_2	within C-pots
S	between S-pots

Note that the variances C_1 and C_2 are on a half-pot basis, but that S is the variance of halved whole-pot yields. If plants of different species compete in the same way as plants of the same species, we may expect that

$$C_1 = 2S,$$

since for the S-pots a whole pot is devoted to one species. However, it would be unwise to assume the relation in general, and the possibility of departure from this relation should be tested on the data.

Again, although C_1 will be affected by systematic differences between the pots, which do not affect C_2, it is unlikely that C_1 will exceed C_2; whenever competition effects are appreciable, uncontrolled variation in these effects will contribute to C_2, so that C_2 will often exceed C_1.

TABLE 1

SPECIES AND ASSOCIATE EFFECTS

(a) Yields with their expected values per replication, when general mean is zero

Species \ Associates	1	2	. . .	p	Total*
1	$\mathbf{x}_{11}$ v_1+a_1	x_{12} v_1+a_2	. . .	x_{1p} v_1+a_p	V_1 $(p-1)v_1-a_1$
2	x_{21} v_2+a_1	$\mathbf{x}_{22}$ v_2+a_2	. . .	x_{2p} v_2+a_p	V_2 $(p-1)v_2-a_2$
.	.	.		.	.
.	.	.		.	.
.	.	.		.	.
p	x_{p1} v_p+a_1	x_{p2} v_p+a_2	. . .	$\mathbf{x}_{pp}$ v_p+a_p	V_p $(p-1)v_p-a_p$
Total*	A_1 $-v_1+(p-1)a_1$	A_2 $-v_2+(p-1)a_2$	. . .	A_p $-v_p+(p-1)a_p$	

(b) Sums (above diagonal) and differences (below diagonal) with expected values and variances per replication

1	$\mathbf{x}_{11}$ $2t_1, S$	$x_{12}+x_{21}$ $2(t_1+t_2),\ 2C_1$	. . .	$x_{1p}+x_{p1}$ $2(t_1+t_p),\ 2C_1$	T_1 $2(p-2)t_1,\ 2(p-2)C_1$
2	$x_{12}-x_{21}$ $2(u_1-u_2),\ 2C_2$	$\mathbf{x}_{22}$ $2t_2, S$	. . .	$x_{2p}+x_{p2}$ $2(t_2+t_p),\ 2C_1$	T_2 $2(p-2)t_2,\ 2(p-2)C_1$
.	.	.		.	.
.	.	.		.	.
.	.	.		.	.
p	$x_{1p}-x_{p1}$ $2(u_1-u_p),\ 2C_2$	$x_{2p}-x_{p2}$ $2(u_2-u_p),\ 2C_2$	. . .	$\mathbf{x}_{pp}$ $2t_p, S$	T_p $2(p-2)t_p,\ 2(p-2)C_1$
Total*	U_1 $2pu_1,\ 2pC_2$	U_2 $2pu_2,\ 2pC_2$	. . .	U_p $2pu_p,\ 2pC_2$	

* Excluding diagonal (bold-face) elements.

We shall assume that the estimates of C_1, C_2, and S provided by the data are sufficiently accurate to be treated as constants, so that we need make no allowance for inaccuracies in the weighting of different effects.

We need to consider a suitable way of defining the competitive effect of a species. We may regard the yield of one species grown in association with another as being made up of two components: the average yield of the first species under varying conditions of competition, and the departure from that average due to competition with the second species—called the associate effect of the second species. A species grown on its own may be regarded as competing with itself. The competitive advantage of a species will be measured by the yields of its associates, the greater the average of its associates the less being its competitive advantage.

In defining competition effects, the simplest assumption to make would be that species and associate effects are additive. This would mean that the effect of a given species on the yield of another would be the same, whatever the other species.

Thus, considering for simplicity two species with additive species and associate effects, we may write the expected values of log (yield per half pot) as follows:

Species 1 grown alone	v_1+a_1
Species 1 associated with species 2	v_1+a_2
Species 2 associated with species 1	v_2+a_1
Species 2 grown alone	v_2+a_2

If the respective log yields are x_{11}, x_{12}, x_{21}, and x_{22}, a significant departure of $(x_{11}+x_{22})-(x_{12}+x_{21})$ from zero indicates the existence of interactions, or species and associate effects that are not additive.

The object of the analysis will be to assess these associate effects and to test departure of the data from the simple assumption of additivity. Such departure will be detected as a species–associate interaction.

We use the following notation:

r = number of replications,

x_{ij} = total of half-pot yields for the ith species grown in association with the jth species,

x_{ii} = total of yields per half pot for ith species grown alone,

v_i = estimated yield for ith species,

a_i = estimated average yield for ith associate,

$t_i = \frac{1}{2}(v_i+a_i)$,

$u_i = \frac{1}{2}(v_i-a_i)$,

$w = C_1/S$ (the relative weight of estimates from S-pots compared with estimates from C-pots),

$g = w-1$,

$V_i = \sum\limits_j x_{ij}$,

$A_i = \sum\limits_h x_{hi}$,

$T_i = V_i+A_i$,

$U_i = V_i-A_i$,

$T'_i = T_i+2wx_{ii}$.

Throughout the paper we adopt the convention that $j \neq i$ and $h \neq i$, so that in the sums just defined, diagonal terms are omitted.

The total yields, with their estimated values and weights, are set out in Table 1(*a*). The estimates of species and associate effects will be measured from their mean, so that

$$\Sigma v_i = \Sigma a_i = \Sigma t_i = \Sigma u_i = 0.$$

To simplify the normal equations we also assume at this stage that the weighted total of all results is zero, i.e.

$$\Sigma T_i' = 0.$$

Note that necessarily

$$\Sigma U_i = 0.$$

III. Determination of Competition Effects

The estimates of species and associate effects may be determined by the method of least squares. The equations of estimation for v_i and a_i are linear. However, as can be seen from Table 1, these effects depend on comparisons both between C-pots and within C-pots; the totals on which the estimates are based are therefore correlated. On the other hand, the t_i and u_i are estimated from C-pot sums and differences respectively, and so are uncorrelated. It is convenient therefore to determine the t_i and u_i initially and to derive the v_i and a_i from them. The variance of the t_i will depend on C_1, and that of the u_i on C_2.

(*a*) *Between-pot Effects*

It is necessary first to analyse the results for C-pot and S-pot totals separately, in order to obtain estimates of C_1 and S. From these we can determine w, and use it to derive combined estimates of species differences from C-pot and S-pot totals.

In Table 1(*b*) the C-pot totals have been set out above the diagonal and the C-pot differences below the diagonal. The comparisons above the diagonal in Table 1(*b*), and in similar tables for each replication separately, give the effects between C-pots. These effects comprise the T-effects and their interactions. The partition of degrees of freedom is as follows:

Effect		Degrees of Freedom
Replications		$r-1$
Species		
Main effects	$p-1$	
Interactions	$\frac{1}{2}p(p-3)$	
Total		$\frac{1}{2}(p+1)(p-2)$
Error (C_1)		$\frac{1}{2}(r-1)(p+1)(p-2)$
Total		$\frac{1}{2}rp(p-1)-1$

The total species sum of squares is

$$\{\Sigma(x_{ij}+x_{ji})^2-(\Sigma T_i)^2/2p(p-1)\}/2r.$$

TABLE 2

EXPERIMENTAL VALUES OF LOG {(WEIGHT IN GRAMS)+1} FOR THE TWO REPLICATES

Species \ Associates	1	2	3	4	5	6	7	V_i
1	**1·48** **1·51**	2·03 1·76	1·68 1·76	1·68 1·66	1·79 1·65	1·77 1·82	1·76 1·61	10·71 10·26
2	1·60 1·69	**1·78** **1·80**	1·98 1·82	1·88 1·89	1·97 1·96	2·01 2·01	1·81 1·73	11·25 11·10
3	0·74 0·58	0·97 1·16	**0·96** **1·05**	0·82 0·91	1·23 1·14	1·29 1·23	0·97 0·69	6·02 5·71
4	0·79 0·74	1·25 1·18	1·11 1·06	**1·07** **1·06**	1·35 1·16	1·23 1·21	1·09 1·05	6·82 6·40
5	0·37 0·21	0·39 0·77	0·74 0·97	0·59 0·59	**1·00** **1·02**	1·12 1·03	0·38 0·29	3·59 3·86
6	0·14 0·23	0·42 0·47	0·37 0·58	0·38 0·35	0·77 0·93	**0·93** **0·57**	0·20 0·18	2·28 2·74
7	1·00 1·03	1·41 1·53	1·62 1·56	1·39 1·41	1·55 1·59	1·65 1·59	**1·43** **1·40**	8·62 8·71
A_i	4·64 4·48	6·47 6·87	7·50 7·75	6·74 6·81	8·66 8·43	9·07 8·89	6·21 5·55	49·29 48·78
							Σx_{ii} =	**8·65** **8·41**

The main effects are given by comparisons among the totals T_i; the sum of squares is

$$\{\Sigma T_i^2-(\Sigma T_i)^2/p\}/\{2r(p-2)\}.$$

It may be verified that the divisor $(p-2)$ rather than $(p-1)$ is needed because the different T_i have elements in common and so are correlated. The interaction sum of squares is found by subtraction.

For the S-pots the analysis is even simpler, the comparisons being

Effect	Degrees of Freedom
Replications	$r-1$
Species	$p-1$
Error (S)	$(r-1)(p-1)$
Total	$rp-1$

On theoretical grounds (provided plants compete with members of their own species in the same manner as with members of other species) it may be expected that $C_1 = 2S$. If the estimates of C_1 and $2S$ (denoted by c_1 and $2s$ respectively) do not differ significantly, it would therefore be reasonable to determine a combined estimate of C_1:

$$\frac{\frac{1}{2}(p+1)(p-2)c_1+2(p-1)s}{\frac{1}{2}(p^2+p-4)}.$$

Accordingly, we should have $w = 2$. If, however, c_1 and $2s$ do differ significantly, w needs to be taken as the ratio c_1/s.

With w taken as known, the normal equation for t_i is

$$r[\{2(p-2)/C_1\}+4/S]t_i = (T_i/C_1)+(2x_{ii}/S),$$

which reduces to

$$2r(p+2w-2)t_i = T_i+2wx_{ii}$$

$$= T'_i,$$

or

$$2r(p+2g)t_i = T'_i.$$

The estimates t_i just given are satisfactory for comparative purposes, but for presentation it is convenient to give estimates whose average is the general (weighted) mean of all the data. Based on actual totals rather than deviations, the weighted mean is

$$m = \Sigma T'_i/2rp(p+g).$$

TABLE 3

SUMS (UPPER) AND DIFFERENCES (LOWER) OF TRANSFORMED VALUES FOR THE TWO REPLICATES

Species \ Associates	1	2	3	4	5	6	7	V_i
1	**2·99**	3·79	3·44	3·34	3·44	3·59	3·37	20·97
	—0·03	0·27	—0·08	0·02	0·14	—0·05	0·15	0·45
2	3·29	**3·58**	3·80	3·77	3·93	4·02	3·54	22·35
	—0·09	**—0·02**	0·16	—0·01	0·01	0·00	0·08	0·15
3	1·32	2·13	**2·01**	1·73	2·37	2·52	1·66	11·73
	0·16	—0·19	**—0·09**	—0·09	0·09	0·06	0·28	0·31
4	1·53	2·43	2·17	**2·13**	2·51	2·44	2·14	13·22
	0·05	0·07	0·05	**0·01**	0·19	0·02	0·04	0·42
5	0·58	1·16	1·71	1·18	**2·02**	2·15	0·67	7·45
	0·16	—0·38	—0·23	0·00	**—0·02**	0·09	0·09	—0·27
6	0·37	0·89	0·95	0·73	1·70	**1·50**	0·38	5·02
	—0·09	—0·05	—0·21	0·03	—0·16	**0·36**	0·02	—0·46
7	2·03	2·94	3·18	2·80	3·14	3·24	**2·83**	17·33
	—0·03	—0·12	0·06	—0·02	—0·04	0·06	**0·03**	—0·09
A_i	9·12	13·34	15·25	13·55	17·09	17·96	11·76	98·07
	0·16	—0·40	—0·25	—0·07	0·23	0·18	0·66	0·51

$\Sigma x_{ii} =$ **17·06** **0·24**

In order that the average of the t_i be equal to m, we need to take

$$t_i = (T'_i + 2rgm)/2r(p+2g).$$

The variance of the t_i is $C_1/2r(p+2g)$.

(b) Combined Analysis for C-pot and S-pot Totals

In combining the results for C-pots and S-pots we weight the results inversely as their variances, so that the basic variance for the combined analysis is C_1.

The sum of squares for main effects (T-effects) is

$$(\Sigma T'_i)^2/2r(p+2g) \tag{1}$$

with $p-1$ degrees of freedom, which may be tested against C_1. The interaction sum of squares may be found by deducting this sum of squares from the weighted total of the species sums of squares for C-pots and S-pots separately. Alternatively, it may be found directly from analysis of the quantities

$$H_i = T_i - (p-2)x_{ii}.$$

It is readily verified that the H_i are uncorrelated with the T'_i, and so represent interaction effects, the differences between species effects from C-pots and S-pots.

The interaction sum of squares is

$$\frac{w\{\Sigma H_i^2 - (\Sigma H_i)^2/p\}}{r(p-2)(p+2g)}. \tag{2}$$

This interaction sum of squares, together with the interaction sum of squares from the C-pot analysis, provides evidence of the departure of the competition effects from the simple additive model. We then have the analysis

Effect	Degrees of Freedom
Main T-effect	$p-1$
Interactions	
From C-pots	$\frac{1}{2}p(p-3)$
H-effects	$p-1$
Total of species effects	$\frac{1}{2}(p^2+p-4)$

As a check, the total for this analysis will equal the total species sum of squares from the C-pots plus w times the species sum of squares from the S-pots.

There is one additional comparison between C-pot and S-pot totals, which it is convenient to mention here. This is the comparison between the mean for all C-pots and that for all S-pots. Such a comparison would indicate whether species grown alone do better or worse on the average than species grown in competition, regardless of any enhancement or reduction of species differences. It is not likely to

TABLE 4

POT TOTALS AND DIFFERENCES

Totals / Differences	1	2	3	4	5	6	7	T_i	$w = 2$: T'_i	$w = 2$: H_i
1	**2·99**	7·08	4·76	4·87	4·02	3·96	5·40	30·09	42·05	15·14
	—0·03	0·18	0·08	0·07	0·30	—0·14	0·12	0·61		
2	0·50	**3·58**	5·93	6·20	5·09	4·91	6·48	35·69	50·01	17·79
	0·36	**—0·02**	—0·03	0·06	—0·37	—0·05	—0·04	—0·25		
3	2·12	1·67	**2·01**	3·90	4·08	3·47	4·84	26·98	35·02	16·93
	—0·24	0·35	**—0·09**	—0·04	—0·14	—0·15	0·34	0·06		
4	1·81	1·34	—0·44	**2·13**	3·69	3·17	4·94	26·77	35·29	16·12
	—0·03	—0·08	—0·14	**0·01**	0·19	0·05	0·02	0·35		
5	2·86	2·77	0·66	1·33	**2·02**	3·85	3·81	24·54	32·62	14·44
	—0·02	0·39	0·32	0·19	**—0·02**	—0·07	0·05	—0·04		
6	3·22	3·13	1·57	1·71	0·45	**1·50**	3·62	22·98	28·98	15·48
	0·04	0·05	0·27	—0·01	0·25	**0·36**	0·08	—0·28		
7	1·34	0·60	—1·52	—0·66	—2·47	—2·86	**2·83**	29·09	40·41	14·94
	0·18	0·20	0·22	0·06	0·13	—0·04	**0·03**	0·57		
U_i	11·85	9·01	—3·52	—0·33	—9·64	—12·94	5·57	196·14	264·38	110·84
	0·29	0·55	0·56	0·49	—0·50	—0·64	—0·75	1·02		

be important for these experiments, but is mentioned here for completeness. The relevant comparison is

$$\Sigma T_i - 2(p-1)\Sigma x_{ii}$$

whose variance is

$$4rp(p-1)\{C_1+(p-1)S\} = 4rp(p-1)(p+g)C_1/w.$$

The sum of squares for testing this comparison against C_1 is accordingly

$$w(\Sigma T_i - 2(p-1)\Sigma x_{ii})^2/\{4rp(p-1)(p+g)\}. \tag{3}$$

(c) *Within-pot Effects*

The comparisons within C-pots are provided by the results below the diagonal in Table 1(*b*), and in similar tables for each replication separately. The degrees of freedom for the different effects are:

Effect		Degrees of Freedom
Species		
Main effects	$p-1$	
Interactions	$\frac{1}{2}(p-1)(p-2)$	
Total		$\frac{1}{2}p(p-1)$
Error (C_2)		$\frac{1}{2}(r-1)p(p-1)$
Total		$\frac{1}{2}rp(p-1)$

The total species sum of squares is

$$\Sigma(x_{ij}-x_{ji})^2/2r,$$

and that for main effects is

$$\Sigma U_i^2/2rp.$$

The interaction sum of squares is found as the difference of these.

The within-pot estimate for the ith species is given as

$$u_i = U_i/2rp,$$

with variance $C_2/2rp$.

(d) *Standard Errors of Species and Associate Effects*

The variances of the t_i and u_i are determined from the between-pot and within-pot analyses respectively. Since the species and associate effects are simply sums and differences of the t_i and u_i, their variances are readily found. We have

$$v_i = t_i + u_i,$$

and

$$a_i = t_i - u_i,$$

and the variance of v_i or a_i is

$$\{C_1/2r(p+2g)\}+C_2/2rp. \tag{4}$$

The variance of a difference between any two a_i is simply twice the quantity (4).

The variance of any other linear compound of t_i and u_i may be found in a similar manner.

Table 5

ANALYSES OF VARIANCE OF C-POT TOTALS, S-POT TOTALS, AND C-POT DIFFERENCES

Analysis of:	Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
C-pot totals	Replications	1	0·003 096	
	Species			
	Main effects	6	5·220 740	
	Interactions	14	0·519 760	0·037 126**
	Total	20	5·740 500	
	Error (C_1)	20	0·128 229	0·006 411
S-pot totals	Replications	1	0·004 114	
	Species	6	1·547 571	
	Error (S)	6	0·066 086	0·011 014
C-pot differences	Species			
	Main effects	6	18·767 857	
	Interactions	15	0·180 768	0·012 051†
	Total	21	18·948 625	
	Error (C_2)	21	0·227 525	0·010 835

** Significant at the 1% level. † Not significant.

IV. Numerical Example

To illustrate the method of analysis we present some data from an experiment of R. M. Moore and J. D. Williams, Division of Plant Industry, C.S.I.R.O. In this experiment, seven species were grown in pots, both on their own and in pairs. There were two replications. One species showed competition effects differing markedly from those for the other species; a further analysis is therefore given with this species omitted, to show how a simple interpretation may be made for species with similar competition effects.

The variate recorded was dry weight of tops, in grams, per half pot. This variate was transformed, the analysis being carried out on log {(weight in grams)+1}.

Since the experiment has only two replications, the sums of corresponding values for the two replications will give estimates of the species effects and their interactions, and the differences will give the estimates of error. For this reason it was convenient to present the results for the two replications together in Table 2. The sums and differences of values from the two replications are set out in Table 3.

These sums and differences are each treated separately after the manner of Table 1(*b*), and the results shown in Table 4; pot totals (of replicate sums and differences) are set out above the diagonal, and pot differences (of replicate sums and differences) below the diagonal. The totals T_i are found from terms above the main diagonal in the ith row or column. Their total is therefore equal to twice the total of off-diagonal elements given in Table 3 (73·53). The totals U_i are found from the sum of terms below the diagonal in the ith column, less the terms in the ith row, and their sum is zero.

TABLE 6

INTERACTION EFFECTS FROM POT TOTALS

Interaction calculated from expression $30(x_{ij}+x_{ji})-6(T_i+T_j)+\Sigma T_i$

Species \ Associates	2	3	4	5	6	7
1	13·86	−3·48	1·08	−11·04	−3·48	3·06
2		−1·98	7·38	−12·54	−8·58	1·86
3			−9·36	9·42	0·48	4·92
4				−1·02	−7·26	9·18
5					26·52	−11·34
6						−7·68

This compact method of setting out the analysis can be used for any number of replications, except that, with more than two replications, individual replications need to be tabulated where replication sums and differences have been tabulated here.

The analyses between C-pots, between S-pots, and within C-pots are set out in Table 5. These analyses give estimates of the different error variances, and also enable interactions among the species to be tested. Table 5(*a*) shows significant interactions between the species. The between-pot interaction effects, set out in Table 6, show that species 5, in association with species 1, 2, or 7, gives results lower than expected, and with species 6 gives results higher than expected. The other interaction effects, apart from the isolated interaction of species 1 and 2, are relatively small.

Since the existence of interactions is already established, so that the simple model of competition effects is not tenable, no further analysis of between-pot effects is needed. However, to illustrate the method that would be used if interactions did not exist, we combine the results from C-pots and S-pots. Table 5 shows that the estimates of C_1 and $2S$ differ significantly only at the 5% level. We assume that a combined estimate of variance is sufficiently accurate, take $w = 2$, and determine a combined estimate of C_1:

$$(0\cdot128\,229+2\times0\cdot066\,086)/26 = 0\cdot010\,015.$$

Values of T_i' corresponding to $w = 2$ are given in Table 4.

The combined analysis is given in Table 7. The species main effect is determined from the T_i', according to (1), with $g = 1$. The interactions have three components : the interaction from the C-pots, already given in Table 5, the difference between effects for C-pots and S-pots (H-effects), and the mean difference between C-pots and S-pots. The divisor for the sum of squares of the H_i, according to (2), is 45, and the divisor for the difference between the total of the x_{ij} values and six times the total of the x_{ii} values is 336, by (3).

Table 7

ANALYSIS OF C-POT AND S-POT TOTALS

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Main effects	6	8·127 919	
Interactions			
C-pots	14	0·519 760	0·037 126
H-effects	6	0·187 964	0·031 327
C-pots v. S-pots	1	0·054 774	0·054 774
Total	21	0·762 498	0·036 309**
Total of species effects	27	8·890 417	
Combined error	26		0·010 015

** Significant at the 1% level.

Table 8

TOTALS FROM TABLE 4, WITH SPECIES 5 OMITTED

Species (i)	U_i	x_{ii}	T_i	$T_i' = T_i+0\cdot6x_{ii}$	$H_i = T_i-4x_{ii}$
1	8·99	2·99	26·07	27·864	14·11
2	6·24	3·58	30·60	32·748	16·28
3	−4·18	2·01	22·90	24·106	14·86
4	−1·66	2·13	23·08	24·358	14·56
6	−12·49	1·50	19·13	20·030	13·13
7	3·10	2·83	25·28	26·978	13·96
Total	0·00	15·04	147·06	156·084	86·90
Divisor for sum of squares	24	2	16	18·4	36·8/0·3

V. Analysis for Six Species showing Similar Competition Effects

In order to show more fully the analysis when there are no major interactions among the species, we now consider the data with species 5 omitted. The relevant totals U_i, T_i, T_i', and H_i, adjusted for this omission, are given in Table 8. Table 9 gives the analyses between C-pots, between S-pots, and within C-pots, similar to those of Table 5. From these analyses it appears that the estimates c_1 and $2s$ differ significantly, since $2s/c_1 = 6\cdot70$. Accordingly we take $w = c_1/s = 0\cdot3$, and $g = -0\cdot7$. Although these estimated weights will have large sampling error, we shall treat them as constants and ignore any disturbance due to inaccuracies in weighting.

Table 9 shows that interactions (T-effects) are significant at the 5% level, but as these effects are not large we shall not take them into account here.

TABLE 9

ANALYSES OF VARIANCE OF C-POT TOTALS, S-POT TOTALS, AND C-POT DIFFERENCES WITH SPECIES 5 OMITTED

Analysis of:	Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
C-pot totals	Replications	1	0·005 042	
	Species			
	Main effects	5	4·606 000	
	Interactions	9	0·102 810	0·011 423*
	Total	14	4·708 810	
	Error	14	0·053 783	0·003 842
S-pot totals	Replications	1	0·005 633	
	Species	5	1·446 067	
	Error	5	0·064 367	0·012 873
C-pot differences	Species			
	Main effects	5	12·733 158	
	Interactions	10	0·125 367	0·012 537†
	Total	15	12·858 525	
	Error	15	0·134 925	0·008 995

* Significant at the 5% level. † Not significant.

The combined between-pot analysis is shown in Table 10. This analysis reveals no new significant interaction effects. Using the results of the between-pot and within-pot analyses we may now set out the estimates of species and associate effects. The estimates t_i and u_i are determined from the pot totals and differences respectively, and the v_i and a_i deduced from them. The calculations and final results are set out in Table 11. The estimated have been adjusted so that their mean equals the weighted mean of all results. The weighted mean of the transformed yields is

$$m = \Sigma T'_i/2rp(p+g) \quad = 156\cdot084/127\cdot2 = 1\cdot2271,$$

so

$$t_i = (T'_i - 2\cdot8m)/18\cdot4 = (T'_i - 3\cdot436)/18\cdot4.$$

Also

$$u_i = U_i/24,$$
$$v_i = t_i + u_i,$$

and

$$a_i = t_i - u_i.$$

TABLE 10

ANALYSIS OF C-POT AND S-POT TOTALS WITH SPECIES 5 OMITTED

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square
Main effects	5	4·994 000	
Interactions			
C-pots	9	0·102 810	0·011 423*
H-effects	5	0·045 820	0·009 164†
C-pots v. S-pots	1	0·002 631	0·002 631†
Total	15	0·151 261	
Total of species effects	20	5·145 261	
Error variance (C_1)	14		0·003 842

* Significant at the 5% level. † Not significant.

The variance of the t_i is $0 \cdot 003\,842/18 \cdot 4 = 0 \cdot 000\,209$ and that of the u_i is $0 \cdot 008\,995/24 = 0 \cdot 000\,375$. Hence, the variance of the v_i and the a_i is $(0 \cdot 000\,209 + 0 \cdot 000\,375) = 0 \cdot 000\,584$. The standard errors of the estimates are given at the foot of Table 11.

TABLE 11

ESTIMATES OF SPECIES AND ASSOCIATE EFFECTS WITH $w = 0 \cdot 3$

i	t_i	u_i	v_i	a_i
1	1·328	0·375	1·703	0·953
2	1·593	0·260	1·853	1·333
3	1·123	−0·174	0·949	1·297
4	1·137	−0·069	1·068	1·206
6	0·902	−0·520	0·382	1·422
7	1·279	0·129	1·408	1·150
Standard error of estimate	0·014	0·019	0·024	0·024

The a_i column in Table 11 shows that there are considerable differences in competitive ability of the six species, which is usually but not always in the same order as their actual yields; species 1 shows a competitive advantage over all the others, while species 6 appears to be dominated by all the others.

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