The effect of host development on the field assessment of disease resistance to *Cercospora* leaf spots in groundnuts (*Arachis hypogaea* L.)

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SUMMARY

In previous studies of the reactions of groundnut varieties to infection with *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton, the existence of disease resistance has been demonstrated. However, these investigations have not resulted in the production of high yielding, disease resistant, varieties and it has been suggested that disease resistance is physiologically linked to low seed yield. In the present study, two aspects of the host–pathogen interaction were investigated: these were varietal response to chemical disease control, and the effect of plant sterility on host and pathogen development. It was found that a general score of resistance to leaf spot did not always relate to the varietal response to disease control and reasons for this were proposed. The prevention of pod production did not affect pathogen development, but vegetative growth of the treated plants was increased. It was concluded that host and pathogen development could be confounded during the assessment of disease resistance. In future varietal screening trials, the use of single branch comparisons should prevent this confusion.

INTRODUCTION

Cercospora arachidicola Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton are important foliar pathogens of groundnuts. In Nigeria, they can cause a 60% reduction in yield of kernels (Fowler, 1970). Owing to their effect on yield, there have been many attempts to assess varietal resistance to these pathogens. Hemingway (1957) and Gibbons (1966) cite reports of disease resistance; and Sulaiman & Agashe (1971), Aulakh, Sandhu & Sunar (1972), Chahal & Sandhu (1972) and Hassan & Beute (1977) have recently conducted field trials in which resistance to one or both of these pathogens has been reported. However, these investigations have not resulted in the development of a high yielding, disease resistant, groundnut variety. Higgins (1956) reported that disease resistant groundnuts were low yielding due to poor setting of the seed. It may be possible to break this undesirable linkage during a breeding programme, but Nwankiti (1976) observed that field-grown groundnuts appeared to become disease resistant if pod formation was prevented. Therefore, there may be a physiological association between low yield and a reduction in pathogen development. This possibility was supported by the work of Kolawole (1976) who observed that sterile triploid progenies from crosses between *Arachis hypogaea* L. and diploid *Arachis* species were disease resistant in the field. Sterile groundnut plants occur in segregating progenies which result from intersubspecific hybridization with *A. hypogaea* and these are also disease resistant (C. Harkness, personal communication).

Two experiments are described here, in which the response of several groundnut varieties to flower removal and disease control was studied. In the first experiment, the response of six varieties to chemical disease control was investigated and the development of the pathogens was assessed by the use of a generalized scoring method. In the second experiment, the interaction between host and pathogens was studied in detail, by the assessment of characters associated with plant and pathogen development.

MATERIALS AND METHODS

Experiment 1

The response of six groundnut varieties (Table 1) to natural infection by the leaf spotting fungi was studied at Samaru (11° N, 8° E), Kaduna State, in the Northern Guinea Savannah zone of Nigeria. A split-plot design with four replicates was used, in

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Table 1. *Details of the six groundnut varieties studied in the field experiments*

Variety	Description
Spanish 205 (SP205)	Subspecies *fastigiata*; a short season Spanish-type cultivar, grown in some areas of Nigeria because of its high oil content
P.I. 262092	Subspecies *fastigiata*; a Valencia-type variety collected in South America and obtained from the North Carolina germplasm collection
Samaru 38 (S38)	Subspecies *hypogaea*; a Virginia bunch groundnut selected from Nigerian farmers' material and widely grown in Nigeria
G153	Morphologically similar to S38, but of Indian origin; recommended for some areas of Northern Nigeria
59-127	Subspecies *hypogaea*; bunch type, selected in Senegal for its drought tolerance
52-14	Subspecies *hypogaea*; bunch type, shows rosette virus resistance and comes from Senegal. It requires a long growing season, greater than 150 days

which a disease control treatment was applied to the main plots and the different varieties were grown in the subplots. Seed was sown on 7 June 1977 and two seeds were planted per hole at 0·23 m intervals on ridges that were 0·91 m apart. Each main plot was 35·5 m long by six ridges wide, and subplots were 5·5 m by six ridges, from which the central four ridges were harvested.

The plots which received the disease control treatment were sprayed weekly with Bavistin (active ingredient carbendazim) at a rate of 300 g in 400 l water/ha. The aphid *Aphis craccivora* Koch, which is the vector of groundnut rosette virus, was controlled with Pirimor (active ingredient pirimicarb), which was applied at ultra-low volume on 19 and 26 July 1977. Leaf spot severity was estimated on 13 September using a 0–10 scale of measurement to indicate a gradation between no disease and complete defoliation. The disease score for each plot was recorded after observing pathogen development on 10 plants in the two central rows of that plot. The unsprayed plots of the varieties SP205 and P.I. 262092 were harvested on 20 and 26 October respectively, at which time sampled plants were judged to be mature. The rest of the trial was harvested on 11 October 1977. Yields of dry pods and haulm were recorded.

Experiment 2

This experiment was also carried out at Samaru, Nigeria. Two cultivars were studied, namely Spanish 205 (SP205) and Samaru 38 (S38) (see Table 1), and four treatments were applied to each variety. The first (treatment A) comprised a daily removal of all flowers from the beginning of flowering until harvest. Plots receiving this treatment were checked weekly for peg formation, and any developing pods were removed. In the second treatment (B), flowers were removed daily, starting 3 weeks after the commencement of flowering and no peg removal was attempted. The pathogens were

allowed to develop normally on undisturbed groundnuts in plots which received the third treatment (C). The final treatment (D) comprised the application of a fungicidal spray to control disease development. Dithane M45 (active ingredient is a coordination compound of zinc and magnesium) was applied weekly at a rate of 2·2 kg in 400 l water/ha from 19 July until 27 September 1976.

Seed was sown on 19 June 1976 in a randomized complete block design with three replicates. Plots were 6·4 m long by six ridges wide, from which plants on the central four ridges were harvested. Two seeds per hole were sown at 0·23 m intervals on the ridges which were 0·91 m apart, and after germination plants were thinned to give one plant per hole.

Plants were sampled five times, on 9 August, 26 August, 10 September, 29 September and 25 October. Two plants were harvested from each plot. Since processing each of the second, third and fourth samples occupied 3 days, one replicate was studied each day and the date of sampling the second replicate is shown above. The observations were designed so that both host and pathogen development were monitored throughout the growing season. Growth of the plants was described by records of leaf and branch production, and the development of the pathogens was studied by assessing numbers of diseased leaves, numbers of leaves lost, and the mean percentage leaf area covered with disease lesions. This last character was assessed from keys devised by A. M. Fowler and D. McDonald (unpublished research reports, 1974, Institute for Agricultural Research, Samaru). These characters were assessed over all primary, secondary and higher order branches so that the observations were recorded for every leaf on each plant. The two pathogens were not separately identified.

The variety SP205 was harvested on 29 September and the S38 groundnuts were lifted on 29

October, and yields of dry pods and haulm were recorded.

RESULTS

In the first experiment, there was no overall significant effect of disease control on pod yields (Table 2) but there was a highly significant interaction between the effects of the spraying treatments on varieties of the two subspecies (Table 3). Thus the pod yields of genotypes from subspecies *fastigiata* showed a larger response to disease control than did yields of the *hypogaea* varieties. Application of the fungicide gave an increase in yield of haulm for all varieties except P.I. 262092, which showed a statistically insignificant decrease in yield. The disease scores (Table 2) indicated that the variety SP205 was more disease susceptible than the other varieties.

In the second experiment, yields of pods and haulm from the short season variety SP205 were increased by the disease control (treatment D) but there were no significant effects of this treatment

on yields of the cultivar S38 (Table 4). Plants from which all flowers were removed (treatment A) gave a small yield of pods, because some flowers and pegs were missed when they were produced near the centre of the plant at ground level. There was a small increase in haulm yield associated with this treatment, but it was not statistically significant. Partial flower removal (treatment B) did not affect haulm or pod yields. This treatment is not included in the graphs showing results of the samples taken during the growing season (Figs 1–7) because results were never significantly different from those for the untreated plots (treatment C). In the graphs, the standard errors of treatment means are shown as vertical bars and separate errors are included for each variety and each time of sampling.

In Figs 1–4, results for the main stem are shown and the conclusions from these results were supported by the assessments of the other branches. The removal of flowers (treatment A) did not significantly affect any character associated with

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Table 2. *The effect of disease control on the yields of pods and haulm for six groundnut varieties*

Variety	Disease score	Pod yield			Haulm yield		
		No spray (t/ha)	Spray (t/ha)	Ratio of no spray to spray	No spray (t/ha)	Spray (t/ha)	Ratio of no spray to spray
SP205	7·50	1·45	2·38	0·61	3·26	4·84	0·67
P.I. 262092	5·75	1·54	2·31	0·67	6·00	5·00	1·20
S38	6·00	1·77	2·20	0·80	4·82	7·87	0·61
G153	5·75	1·97	2·15	0·92	5·43	6·88	0·79
59-127	5·50	2·10	2·06	1·02	4·50	7·15	0·63
52-14	5·25	1·02	1·27	0·80	5·88	8·85	0·66
Means	5·95	1·64	2·06	0·80	4·98	6·77	0·74
S.E. of a variety mean (30 D.F.)	0·172	0·233			0·452		

Table 3. *Summary of analysis of variance (mean squares) for the effect of disease control on yield of six groundnut varieties*

Source of variation	D.F.	Pod yield	Haulm yield
Blocks	3	0·760	0·719
Spray	1	0·549	10·490
Error A	3	0·714	1·806
Variety	5	1·512	9·257
Between subspecies	1	0·286	27·517
Within *fastigiata*	1	0·001	8·080
Within *hypogaea*	3	2·426	3·562
Spray × variety	5	0·549	4·461
Spray × (between subspecies)	1	2·163	12·312
Spray × (within *fastigiata*)	1	0·035	6·331
Spray × (within *hypogaea*)	3	0·180	1·217
Error B	30	0·217	0·817

Table 4. *The effect of flower removal and disease control on haulm and pod yields of two groundnut varieties*

	Haulm yield (t/ha)		Pod yield (t/ha)	
Treatment	S38	SP205	S38	SP205
Total flower removal (A)	3·10	2·41	0·090 ± 0·0173	0·060 ± 0·0081
Partial flower removal (B)	2·41	2·04	0·601 ± 0·0178	0·68 ± 0·177
Untreated (C)	2·89	2·12	1·03 ± 0·132	1·04 ± 0·241
Fungicidal spray (D)	2·61	5·78	1·27 ± 0·032	1·56 ± 0·472
Means	2·75	3·09	0·748	0·835
s.e. of a treatment mean	0·453		Not applicable	

pathogen development (shown in Figs 1–3). However, for the variety SP205 at the end of the growing season, there was a small reduction in the percentage diseased leaf area on plants receiving treatment A. This was probably caused by the continued growth of individual branches (Fig. 4) in response to flower removal. The extended period of leaf production gave a greater percentage of younger leaves on branches of these plants. These leaves had been exposed to the pathogens for a shorter period of time than older leaves and therefore showed reduced disease development and thus caused a reduction in mean percentage leaf area showing leaf spot lesions. The flower removal increased leaf production when assessed on a whole plant basis (Fig. 5). This effect was associated with an increase in numbers of vegetative branches

(Fig. 6) as well as increased leaf production on individual branches (Fig. 4). It was found that the variety SP205 from subspecies *fastigiata* produced tertiary branches only when flowers were removed.

When the effect of fungicide application (treatment D) is compared with the natural development of the epidemic (treatment C), it is noted that, during the early part of the growing season, variables associated with pathogen development (Figs 1, 2 and 3) were reduced by the chemical disease control. During the later part of the growing season, the comparison between these treatments becomes more complex. Thus, when there was normal development of the pathogens (treatment C), defoliation increased rapidly (Fig. 1) which caused a reduction in the number of diseased leaflets (Fig. 2). The fungicide application (treatment D)
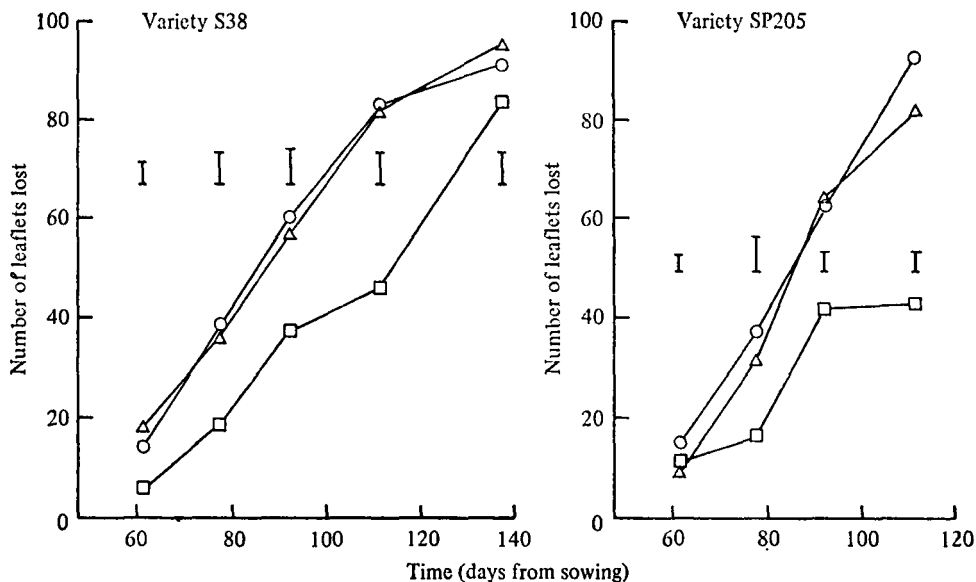

Fig. 1. Cumulative defoliation from the main stems of plants of varieties S38 and SP205. Treatments A (○), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.
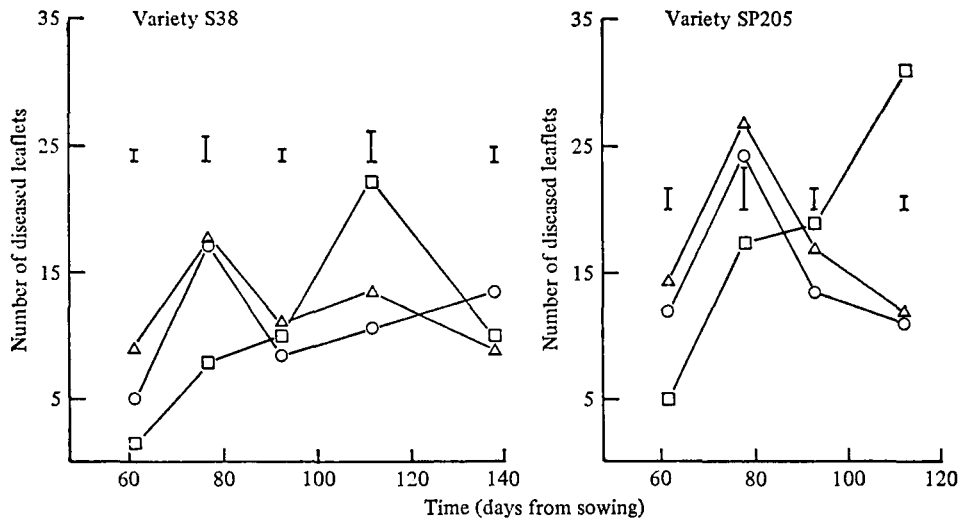
Fig. 2. The variation during the growing season of the numbers of diseased leaflets on the main stems of varieties S38 and SP205. Treatments A (O), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.
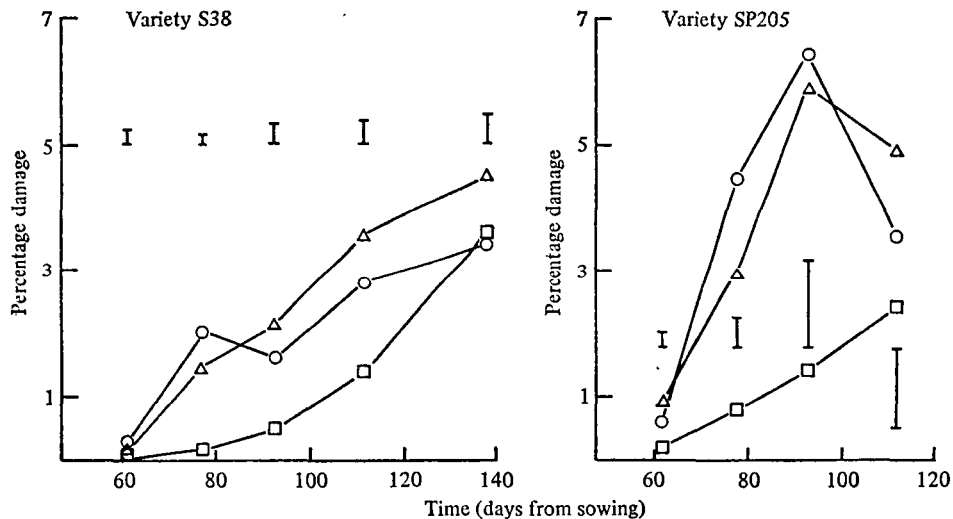

Fig. 3. The variation during the growing season of the mean percentage leaf area damaged by lesions of the leaf spotting fungi. Results are for leaves on the main stems of varieties S38 and SP205. Treatments A (O), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.

prevented the loss of leaflets (Fig. 1) and therefore there was a continuing increase in numbers of diseased leaflets (Fig. 2) until disease control ceased. For the variety S38, application of the fungicide did not continue until harvest, and therefore there were no significant differences between treatments C and D at the end of the growing season. Disease

control did not significantly affect any of the plant growth characters which are depicted in Figs 4, 5 and 6.

Varietal differences in pathogen development were evident in the middle of the growing season. The short-season variety SP205 gave the larger maxima in the graphs of numbers of diseased
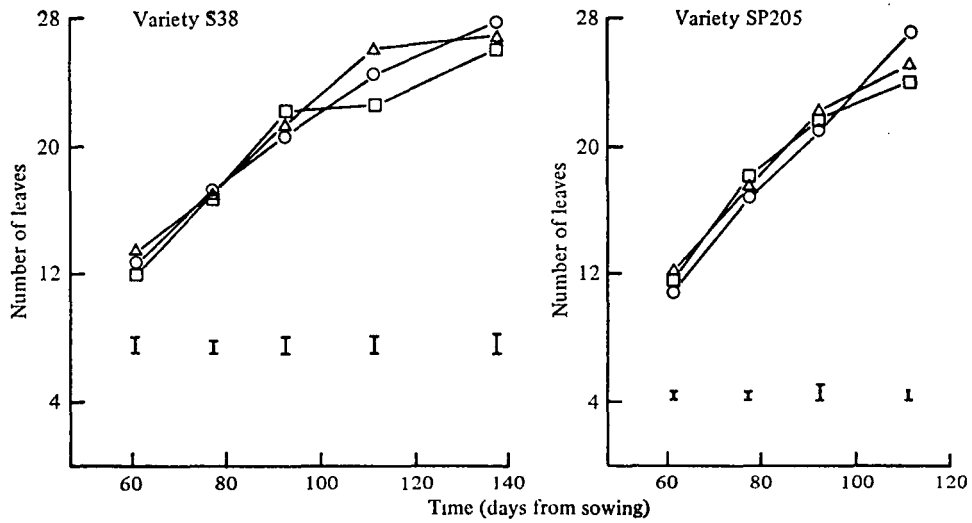
Fig. 4. Cumulative leaf production on the main stems of varieties S38 and SP205. Treatments A (O), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.
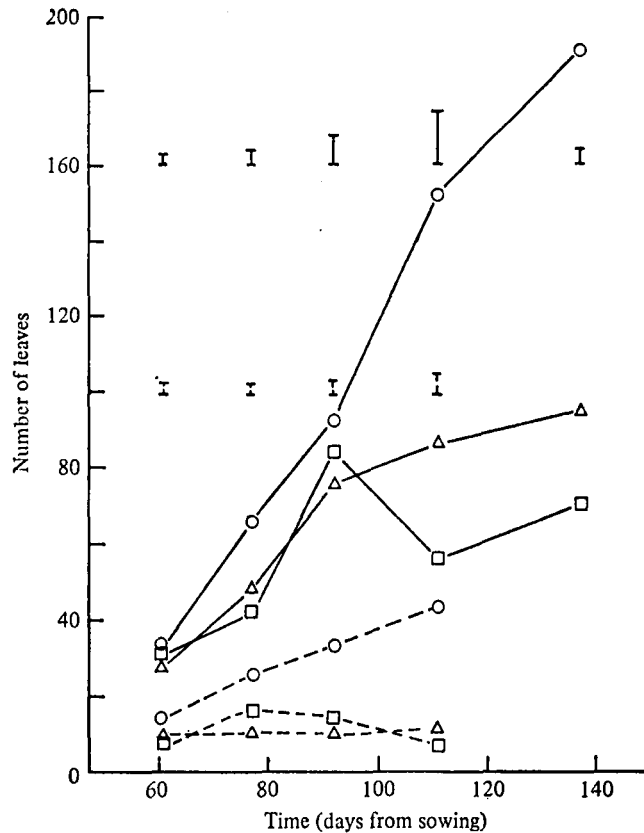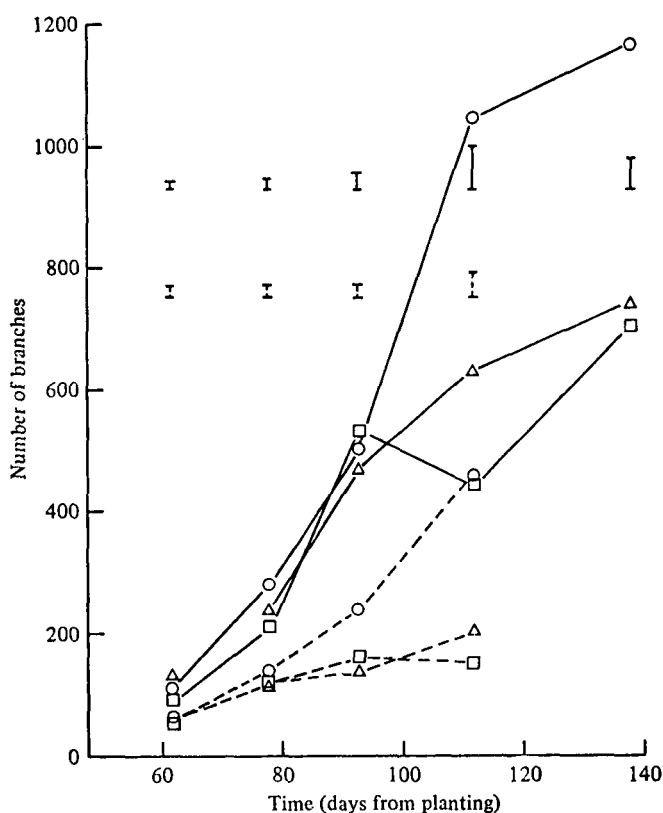

Fig. 5. Cumulative leaf production for entire plants of varieties S38 (———) and SP205 (– – –). Treatments A (O), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.

Fig. 6. Cumulative production of vegetative branches for varieties S38 (———) and SP205 (– – –). Treatments A (○), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.

leaflets (Fig. 1), and this genotype also demonstrated a greater leaf area showing leaf spot lesions (Fig. 3) than did S38. There were, however, no differences between the varieties in the numbers of leaves lost (Fig. 2).

DISCUSSION

In both these experiments, pod yields of varieties from subspecies *fastigiata* were increased to a greater extent by disease control than were pod yields of the varieties from subspecies *hypogaea*. This agrees with the conclusions of Hemingway (1957) and Smartt (1976). In the second experiment, a reduced varietal response to disease control was associated with a reduction in pathogen development. Thus the cultivar SP205 showed a greater increase in pod yield and also showed more rapid pathogen development in unsprayed plots, compared with the variety S38. However, in the second experiment, pod yield of the variety P.I. 262092 from subspecies *fastigiata* was significantly increased by chemical disease control, although its disease score was similar to those of the subspecies *hypogaea* cultivars. Pod yields of these latter varieties were not significantly increased by the fungicidal spraying treatment.

There are several possible explanations for this discrepancy. First, the varietal differences in pathogen development may not have affected pod yields, but the yields may have been influenced by morphological variation between the two subspecies of *A. hypogaea*. Elston, Harkness & McDonald (1976) suggested that different responses to disease control were caused by the different branching patterns of varieties from the two subspecies. The alternately branched varieties, which are from subspecies *hypogaea*, have a greater capacity for leaf and stem production than the sequentially branched genotypes. The extra photosynthates which are available when disease is controlled may then be used by the subspecies
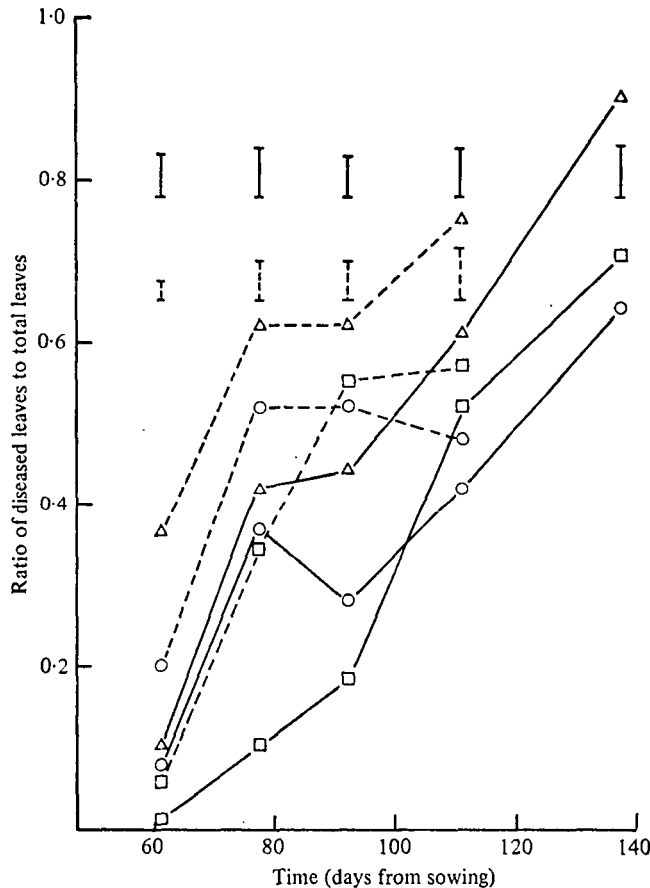
Fig. 7. The variation during the growing season of the ratio of numbers of diseased leaves to total numbers of leaves for the varieties S38 (———) and SP205 (— — —). Treatments A (O), C (△) and D (□) are described in the text and standard errors of means are shown as vertical bars.

hypogaea varieties to produce vegetative growth rather than an increased yield of pods. However, in the second experiment described, there was no evidence for the production of extra leaves and branches as a result of disease control by the fungicide treatment. Therefore the hypothesis of Elston *et al.* (1976) was not confirmed. Another difference in growth may, however, have affected the response to disease control. It has been shown that the alternately branched cultivar S38 produced more leaves than SP205 (Fig. 4) and it is possible that, because of the higher canopy density in plots where disease was controlled there were more leaves than were photosynthetically useful. The loss of some of these leaves would affect pod yield.

Secondly, the variety P.I. 262092 is poorly adapted to agricultural production. It is a primitive variety that shows an extended period of flower production and this yields pods which are variable

in maturity at harvest. The disease control may improve pod maturity by delaying whole plant senescence.

Finally, the validity of the visual estimations of disease reactions which were recorded during the second experiment must be examined, and in this respect the present study can be compared with previous investigations. In Fig. 7, it is shown that the flower removal (treatment A) can cause a reduction in a measure of pathogen development if that measure is confounded with host development. Thus the ordinate of this graph, the ratio of numbers of diseased leaves to total numbers of leaves on the plants, confounds a characteristic of pathogen development (numbers of diseased leaves) with a characteristic of plant growth (total leaves). The apparent reduction in pathogen development is therefore due to the increase in plant growth. It is likely that previous field studies of disease resistance

have resulted in false conclusions because of this confusion. Thus Nwankiti (1976), who reported the resistance of sterile groundnut plants, took random samples of leaves from plots receiving the flower-removal treatments. Therefore he would have recorded this spurious reduction in pathogen development. The other reports of the association between plant sterility and disease reduction can be explained in a similar manner.

This confusion between host and pathogen development has probably led to erroneous reports of disease resistance from previous varietal screening trials. A number of generalizations have been deduced from such work: resistant genotypes are alternately branched (Gibbons, 1966); they are long season varieties (Gibbons, 1966; Sowell, Smith & Hammons, 1976) and they are low yielding (Higgins, 1956). All these characteristics indicate that the supposedly resistant genotypes are vegetatively active and possess a dense canopy due to plant effects that are independent of pathogen development. In confirmation of this viewpoint it has been reported (Williams, Wilson & Bate, 1975), from detailed studies of plant growth, that one groundnut variety which had been observed to be resistant to the leaf spot pathogens in the field continued to produce leaves for a longer period than varieties which had been described as disease susceptible. Also, Hammons (1973) observed that if varieties were compared at the same relative stage in their life cycles, then no variation in disease reaction could be detected. Therefore the reliability of previous varietal screening experiments must be doubted.

In the present study, by the use of detailed comparisons, varietal differences in pathogen development were demonstrated. Variation was also demonstrated by means of a general disease scoring technique and by assessing the response of the cultivars to disease control. However, the relationship between these characters was not elucidated. Since the aim of varietal screening trials is to select genotypes that will be useful in the breeding of agronomically acceptable, disease-resistant varieties, then in further studies, the difficulty of interpreting indirect measures of disease reaction must be considered. Records of pathogen development on single branches made at several times during the growing season should exclude the effect of host development from the assessment of disease resistance.

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