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COMPLETE INHIBITION OF SETTING AND GROWTH OF FRUITS OF VICIA FABA L., RESULTING FROM THE DRAINING OF THE PHLOEM SYSTEM BY CUSCUTA SPECIES

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SUMMARY

When luxuriantly growing *Cuscuta* parasitised *Vicia faba* at the time of flowering, fruit setting of the host was generally completely inhibited. When the host was infected in a later stage of development *Cuscuta* seriously interfered with further growth of pods.

The process of translocation of ^{14}C-assimilates from a photosynthesising leaf to other parts of the host and to the parasite was analysed. The process of assimilate withdrawal by *Cuscuta* turned out to be so efficient that usually only negligible amounts of ^{14}C-assimilates – or nothing at all – found its way into pods and seeds of the parasitised host.

1. INTRODUCTION

The stem parasite *Cuscuta* is a holoparasitic flowering plant. Although it is usual to distinguish between hemiparasites and holoparasites, there is no sharp distinction between the two groups. Using $^{14}CO_2$ several authors have demonstrated a considerable transfer of ^{14}C-assimilates from host to hemiparasite and many species of the typical holoparasitic genus *Cuscuta* contain a little chlorophyll, the more so when the plants live more independently. The tips of seedlings are green and also isolated *Cuscuta* filaments or plants growing on an unsuitable host usually become more pronouncedly greenish than luxuriantly growing parasites on a suitable host. In the last years several authors have demonstrated the capacity of *Cuscuta* for photosynthesis, using $^{14}CO_2$ (MACLEOD 1961a and 1961b; CIFERRI & POMA 1963; PATTEE et al. 1965; BACCARINI 1966 and 1967; KERSTETTER & HULL 1970).

The fact that photosynthesis hardly plays a part seems the only reason for the necessity of withdrawal of assimilates from the host. The need for a host is not absolute. When in sterile cultures sugar was added to a mineral nutrient medium it was possible to bring *Cuscuta* into the flowering stage (LOO 1946; ZIETZ 1954; BERTOSSI 1957; BALDEV 1959). In vitro culture of stem apices was used for studying the flowering induction of *Cuscuta reflexa* (BALDEV 1962; JACOB 1966; BARBAT & POP 1970).

Several authors have reported an intensive transfer of ^{14}C-labelled assimilates from host to *Cuscuta* (ALLRED 1966; LITTLEFIELD et al. 1966; JACOB & NEUMANN 1968; SALAGEANU & FABIAN-GALAN 1968; KERSTETTER & HULL 1970).

Frequently, the disturbance of the growth of the host by *Cuscuta* is more

severe under laboratory conditions than under natural conditions where the growing parasite generally can infest many other hosts. In the greenhouse of our laboratory, hosts parasitised by *Cuscuta* usually die within a few weeks after strong infection. When in the growing season of 1970 flowering broad bean plants (grown in the garden) were parasitised by luxuriantly growing *Cuscuta* all flowers dropped and fruit setting was completely inhibited. When the host was infected in a later stage of development the parasite seriously interfered with further growth of fruits.

In the following two summers the process of translocation of ^{14}C-assimilates from a photosynthesising leaf to other parts of the host (with developing fruits) and to the parasite was analysed.

2. MATERIAL AND METHODS

2.1. Cultivation of plants

Seeds of *Vicia faba* L. cv. Witkiem were germinated in the greenhouse and the young plants were transferred to the garden on 27-4-1971 in the first season (experiments shown in *tables 1, 2,* and *3*). In the second season seeds were germinated in the greenhouse on 5-4-1972 and the young plants planted in the garden on 19-4-1972 (experiments shown in *tables 4, 5,* and *7*) and the seeds of the plants of *table 6* were planted in the garden on 27-4-1972. When the lower parts of the broad bean plants were in the flowering stage the stem tips were removed, so resulting in decapitated plants with about 15 leaves.

Seeds of *Cuscuta campestris* Yunck., *C. europaea* L., and *C. lupuliformis* Krocker were scarified with concentrated sulphuric acid for 15 minutes, washed in water several times, and germinated on moist filter paper in a petri dish in a growth cabinet with long day conditions and a temperature of about 25 °C. After about a week the *Cuscuta* seedlings were placed in a small tube of glass with tap water near the stem of the host. *Coleus*, grown in the greenhouse, appeared to be a very suitable host for seedlings to attach themselves to (only the seedlings of *C. lupuliformis* are strong enough to attach themselves regularly to broad bean plants grown in the garden). After *Cuscuta* had started luxuriant growth, filaments of the extensively branching parasite were cut off and used for infecting broad bean plants in the garden.

A culture of *Cuscuta reflexa* Roxb. in the vegetative stage was maintained in the greenhouse. On the day of the experiment a broad bean plant with or without *Cuscuta* was dug up carefully at about 10 a.m. and the root system was placed in a jar of water in the laboratory.

2.2. Application of $^{14}CO_2$ to a leaf of Vicia faba

$^{14}CO_2$ was evolved in a small tube of cellulose nitrate sealed with silicone rubber onto the lower side of a leaflet. The tube contained 0.7 ml of a solution of $Na_2{}^{14}CO_3$ with 25 (season 1971) or 10 (season 1972) μCi. The CO_2 was liberated by injection of a few drops of 5N sulphuric acid.

2.3. Analysis of ^{14}C-labelled plants

After the required translocation period (24 hrs. after administration of $^{14}CO_2$ in experiments of *tables 1, 2, 3, 6,* and *7*; the $^{14}CO^2$-source was removed after about 6 hrs. at the end of the afternoon) the plants were divided into various parts, weighed, and stored at −20°C. Plant parts were homogenised with a pestle and mortar or with an Ultra-Turrax mixer in 80% (v/v) ethanol. The mixture of plant debris and ethanol was centrifuged and the supernatant decanted. The extraction procedure was repeated twice with the residue. In some cases the latter was ultimately stored for a ^{14}C-measurement. The combined supernatants were evaporated to dryness in a rotating evaporator. Equal amounts of water and chloroform were added to the residue and the mixture was centrifuged to separate both phases. This procedure was repeated once and the combined water phases were evaporated to dryness. The residue was dissolved in 0.5 or 1.0 ml (depending on the fresh weight of the sample) of demineralised water. From this solution samples of 50 µl were taken with self-filling pipets ("Drummond micro-caps") and added to 15 ml of a counting solution consisting of a mixture of toluene and methanol (3:1 v/v) + "Premix P" (5.3 g/l) and counted in a Packard 3375 Tri-Carb Scintillation Spectrometer. Values in the tables were expressed as cpm/g fresh weight for the experiments of the season 1971, the efficiency of counting for different samples being practically constant. In the experiments of the season 1972 (*tables 4, 5, 6,* and *7*) values were expressed as dpm/g fresh weight.

In many experiments of the season 1971 the amounts of 80% ethanol-insoluble ^{14}C, the chloroform phase, and the amino-acid fraction were measured.

Soluene-100 (Packard) was used as solubilizer of the residue insoluble in 80% ethanol. 1 ml of soluene was added to about 5 mg of the residue in a counting vial and for some days placed at 60°C, with occasional agitation to speed up the dissolution. After this procedure most of the residue had been dissolved. After addition of 15 ml of counting solution the ^{14}C-content of the samples was counted as described above.

To obtain the amino acid fraction the water phase was placed on a 20 × 0.6 cm cation exchange column (Dowex 50W-x8,20–50 mesh, H^+form) before the procedure of evaporating to dryness. After its passage the column was rinsed with 25 ml of demineralised water and then the amino acids were eluated with 50 ml of 2N ammonia. The eluate was collected and evaporated to dryness and the residue counted as described for the water phase.

2.4. Numbering of plant parts

Leaves, internodes, and pods were numbered from base to apex; in the tables these numbers are indicated. Leaf 1 and 2 are the very small, reduced leaves at the stem base and leaf 3 is the first normal leaf. Usually the first flowers develop in the axil of leaf 7. The internode number corresponds with that of the leaf above it. Pod 7 means the pod(s) in the axil of leaf 7. The sign (u) after a numbered internode in the tables means the upper half of the internode was sampled and (l) means its lower half was sampled.

Table 1. Translocation of ^{14}C-assimilates from a leaf to growing fruits of *Vicia faba* plants not parasitised by *Cuscuta*.

Exp. A: $^{14}CO_2$ administered to leaf 9 (17-6-1971)			Exp. B: $^{14}CO_2$ administered to leaf 8 (22-6-1971)		
plant part	weight(g)	cpm/g×10^3	plant part	weight(g)	cpm/g×10^3
pod with seeds 11	0.05	2.8			
internode 11	1.37	1.6	pod without seeds 9	0.97	0.55
pod with seeds 10	0.13	20.2	seeds in pod 9	0.10	10.7
internode 10	1.61	9.6	pod without seeds 8	2.04	238.8
pod with seeds 9	0.62	455.0	seeds in pod 8	0.24	798.0
internode 9	2.34	63.0	pod without seeds 7	3.67	40.0
pod with seeds 8	0.52	97.2	seeds in pod 7	0.52	41.0

3. RESULTS

Table 1 shows typical distribution patterns of ^{14}C-assimilates transported from a leaf to growing fruits. Pods and developing seeds were extracted together in experiment A, whereas in experiment B they were extracted separately, since the fresh weight of developing fruits had much increased after five days of growth. The fruits in the axil of the ^{14}C-exporting leaf receive most of the ^{14}C-assimilates. In the stem there is mainly a downward transport. Likewise, pods in the axil of a leaf below the exporting leaf apparently receive considerably more ^{14}C than the pods in the axil of a leaf above the exporting leaf.

Table 2 shows the very deleterious influence of *Cuscuta* attached to the stalk of the pod in the axil of leaf 7. The assimilates, after travelling out of leaf 8 through stem internode 8 into the stalk of pod 7, do not reach the pod and seeds because they are drained by the parasite. The ^{14}C-content of pod 9, the pod above the assimilating leaf 8, is also very low compared with data from *table 1*. There is a striking difference between the values of *Cuscuta* tissue belonging to group a and *Cuscuta* tissue of group b. The first winding of the haustorial coil seems to have withdrawn most of the ^{14}C-assimilates, leaving only a small part for the filaments originating from the second winding.

In a similar experiment *Cuscuta* was attached around a pod by means of a long haustorial coil. ^{14}C-assimilates, having arrived in the pod, did not arrive in the seeds because the pod was drained by the parasite. More data on experiments in which *Cuscuta* was attached to a pod can be found in the *tables 4* and *5*.

Table 3 gives the results of an experiment with a host parasitised for a relatively long period by *C. lupuliformis*. The leaves below leaf 7 had already fallen and some remaining leaves were turning yellow. The parasite, having a total weight of 14.3 g, parasitised the host in several places along the stem. The average ^{14}C-content in the ethanol-soluble substances found for the various *Cuscuta* samples is between 5.10^4 and 10^5 cpm/g fresh weight. In most pods not a trace of ^{14}C could be found. The growth of the fruits had apparently been

Table 2. Translocation of ^{14}C-assimilates from leaf 8 to parts of the host and to *C. europaea* attached to the stalk of pod 7. The haustorial coil of *Cuscuta* goes round twice. The *Cuscuta* filaments, originating from the lower winding round the stalk, are called group *a*. The *Cuscuta* filaments originating from the upper winding round the stalk, are called group *b*. Host flowers in axil of leaf 8 were removed at the time of flowering (24-6-1971).

plant part	weight(g)	cpm/g $\times 10^3$
Parasite:		
group a:		
Apical part of 10 cm of main filaments and side branches of 3 filaments	0.60	260
Middle region, below apex, 15 cm long	0.96	340
Parts near haustorial coil, 5–20 cm long	1.24	133
group b:		
Apical parts of 10 cm (cf. group a)	1.09	55
Middle region, 15 cm long	2.26	35
Parts near haustorial coil, 10–25 cm long	3.04	17.7
Flower clusters along the filaments	0.37	72
Haustorial coil (both windings)	0.16	57
2 flower clusters attached to haustorial coil	0.45	121
Host:		
pod + seeds 11	0.31	0.30
pod 9	10.21	0.02
seeds in pod 9	1.32	0.11
internode 9	3.41	0.09
internode 8	4.71	3.10
pod 7	8.81	0.06
seeds in pod 7	1.71	0.12

stopped completely by the process of assimilate withdrawal by *Cuscuta*. The very low fresh weight of the fruits indicates that growth had already stopped before the day of the experiment.

In another experiment (24-6-1971) similar results were obtained. *C. lupuliformis*, attached to int. 10 and having a weight of almost 10 g, received almost all ^{14}C-assimilates exported by leaf 9. Parts of a filament originating from a haustorial coil around int. 10 after 24 hrs. had received between 10^5 and 2.10^5 cpm/g whereas a filament originating from 1 haustorial coil around the base of int. 11 contained 15.10^3 cpm/g. The seeds in pod 9 (weighing 0.31 g, in pod of 2.88 g) had received only 25.10^2 cpm/g. This experiment showed a strong change in the direction of movement of assimilates. Normally, assimilates in our fruiting broad bean plants moved mainly towards the pods in the axil of the exporting leaf and also downwards through the stem but in the host parasitised above the ^{14}C-exporting leaf almost all assimilates moved upward through the stem to the parasite.

In all experiments of the season 1971 the ^{14}C-content of ethanol-soluble substances was measured, expressed as cpm/g fresh weight. In most experiments also the ^{14}C-content of the residue of *Cuscuta* tissue or pods and seeds of broad

Table 3. Translocation of ^{14}C-assimilates from leaf 9 to parts of the host and to the parasite *C. lupuliformis* (28–6–1971).

plant part	weight(g)	cpm/g	plant part	weight(g)	cpm/g $\times 10^3$
Host:			int. 12	1.14	0.05
pod + seeds 11	0.13	+	int. 9	2.22	9.7
pod + seeds 10	0.06	0	int. 8(u)	1.88	6.9
pod + seeds 9	0.32	0	int. 8(l)	2.30	3.7
pod + seeds 8	0.42	0	int. 7(u)	2.10	2.0
Parasite:					
filament originating at top of internode 8				0.21	157
filament originating below top of internode 8				0.90	121
Further data: see also the comment on pages 51 and 52.					

bean insoluble in 80% ethanol was determined. Results corresponded very well with those found for the ethanol-soluble substances. In most experiments, in which samples were taken 24 hrs. after administering $^{14}CO_2$ to a leaf, the ^{14}C-content of the residue was quantitatively comparable to the values found for the ethanol-soluble fraction. This applies to the parasite and to pods and seeds of broad bean as well, but with the exception of the tissues of haustorial coils, which showed to have a much lower ^{14}C-content in the residue than in the ethanol-soluble fraction. The chloroform phase in most samples contained a few % of the values found for the water phase. In the amino acid fraction of the water phase mostly about 10% of the total activity of the water phase could be found in pods and seeds of broad bean and in dodder tissue as well.

Tables 4 and *5* show experiments carried out in July 1972, in which different *Cuscuta* species parasitised a pod in the axil of the ^{14}C-exporting leaf. These experiments lasted less than 12 hrs.

The parasite withdraws almost all assimilates from the host, as shown in *table 4*. Only the parasitised pod 8 contains a considerable quantity of ^{14}C – although almost negligible in comparison with the parasite – which probably originates from remnants of haustoria and from assimilates in the phloem system of the pod moving in the direction of the parasite; seeds in the parasitised pod contain only a trace of ^{14}C.

The parasite almost completely withdrew the assimilates exported by leaf 9 of the host as shown in *table 5*. In the seeds of the large pod in the axil of leaf 9 no ^{14}C could be found. In this experiment, which lasted only 6½ hrs., the highest value for ^{14}C/g fresh weight was found in the tissue of the haustorial coil.

In the season 1972 experiments were carried out in which in a series of subsequent stages of development of parasitised broad bean plants the distribution pattern of ^{14}C-assimilates was compared with the normal pattern within unparasitised plants of the same age. None of the parasitised hosts showed a sign of damage by the parasite in the form of retarded growth because the parasite had just started luxuriant growth. Some results of these experiments are shown

Table 4. Translocation of ^{14}C-assimilates from leaf 8 to other parts of the host and to *C. europaea*, attached mainly to the pod in axil of leaf 8. Pod 8A stands for a pod in axil of leaf 8, not parasitised by *Cuscuta*, and pod 8B stands for a pod in axil of leaf 8, parasitised by *Cuscuta*. Plant sampled 10 hrs. after administration of $^{14}CO_2$. A filament of *Cuscuta* growing from another host was laid around the stem on 14-6-1972. On 4-7-1972 several filaments originating from the haustorial coil around pod 8B, had a length of 10–15 cm whereas on 7–7–1972 the length was 30–40 cm. (7-7-1972).

plant part	weight(g)	dpm/g
Host:		
seeds in pod 9	3.72	53
internode 9	3.29	+
pod 8A (not parasitised)	6.68	54
seeds in pod 8A	0.98	0
lower part of pod 8B (parasitised by *Cuscuta*)	5.95	3660
upper part of pod 8B (parasitised by *Cuscuta*)	5.28	1375
seeds in lower part of pod 8B	0.80	0
seeds in upper part of pod 8B	1.01	306
internode 8	2.94	523
seeds in pod 7	0.78	170
Parasite:		
filaments attached to base of stalk of pod 10	4.83	4219
filaments attached to lower part of pod 8B	1.93	17088
haustorial coil around upper part of pod 8B	0.33	26630
basal parts of filaments attached to upper part of pod 8B	4.44	14176
apical parts of filaments attached to upper part of pod 8B	2.11	104775
filaments attached to internode 5	3.56	+

Table 5. Translocation of ^{14}C-assimilates from leaf 9 to other parts of the host and to *C. lupuliformis*, attached to pod 9. Plant sampled 6½ hrs. after administration of $^{14}CO_2$. A filament winding around another plant was replaced on 3-7-1972 to make a winding around pod 9 of the new host. On the day of the experiment the haustorial coil around pod 9 (having a length of 17 cm) was attached from 4 cm above the base to 1 cm below the apex of the pod (13-7-1972).

plant part	weight(g)	dpm/g
Host:		
pod 10	6.15	108
seeds in pod 10	0.97	340
pod 9	17.68	1384
seeds in pod 9	3.98	0
Parasite:		
haustorial coil around pod 9	1.17	21023
tip (12 cm) of main filament + side branches	3.03	17772
75 cm of main filament, below tip	5.69	10895
basal part of main filament, near haustorial coil	4.18	8313
side branch of 50 cm, originating from basal end of haustorial coil	2.71	3658
side branch of 70 cm originating from apical end of haustorial coil	1.97	18061
15 cm of filament below haustorial coil	0.75	9452
C. europaea attached to internode 3 and 5	1.05	187

Table 6. Translocation of ^{14}C-assimilates from leaf 4 of a stem developed from an axillary bud (main stem removed before experiment) to parts of broad bean and dodder. The latter attached to internodes 4, 5 and 9 (6-7-1972).

plant part	Exp. A: Non-parasitised plant			Exp. B: Parasitised by *C. lupuliformis*		
	weight(g)	dpm/g	% of total ^{14}C	weight(g)	dpm/g	% of total ^{14}C
apical part of host	8.10	35	0.1	7.92	125	0.1
pods of apical part	4.19	282	0.6	0.43	2727	0.1
pod 7	1.85	384	0.3	0.29	626	<0.05
int. 7	3.13	554	0.8	2.59	338	0.1
pod 6	0.86	299	0.1	0.65	555	<0.05
int. 6	3.63	813	1.4	3.44	667	0.2
pod 5	1.37	5657	3.8	0.78	920	0.1
int. 5	5.33	1880	4.8	4.08	750	0.2
pod 4	1.32	94430	60.3	1.04	24464	2.0
int. 4	6.09	3566	10.5	4.31	5392	1.9
int. 3	8.10	1224	4.8	7.48	110	0.1
int. 1+2	17.08	761	6.2	7.80	95	0.1
Parasite:						
haustorial coil				2.51	45661	8.8
filaments originating from haustorial coil				14.37	44905	51.4
apical parts (7 cm) of the filaments				3.61	115718	33.3

in *tables 6* and *7*. In the last column the amounts of ^{14}C found in the different plant parts are expressed as % of the total amount of ^{14}C exported by the leaf (including ^{14}C found in the other leaves of broad bean, which have a very low ^{14}C-content which is not presented in the tables).

In experiment B shown in *table 6*, 93.5% of exported ^{14}C was translocated to the parasite. In the parasitised host, pod 4 received a small quantity of ^{14}C compared with the corresponding pod of the non-parasitised plant. In the parasitised broad bean the ^{14}C-content of stem parts below int. 4 decreased sharply whereas in the control this occurred gradually.

Pod 8 of the control plant represented a very strong sink, accumulating 93.4% of the exported ^{14}C-assimilates, as shown in *table 7*. In the parasitised plant only a trace of ^{14}C could be found in pod 8 and 87.8% was found in the parasite. A strongly stimulated translocation to more basal parts of the host stem was caused by the parasite attached to stem parts below the ^{14}C-exporting leaf.

In another experiment with younger plants (8-6-1972), $^{14}CO_2$ was administered to leaf 8 of broad bean plants in which the flowers in the axil of the leaves 7, 8 and 9 had finished flowering but flowers above that part of the stem were still present. In the non-parasitised plant the highest value of dpm/g was found for the very small developing fruits in the axil of leaf 8, indicating a strong sink

Table 7. Translocation of ^{14}C-assimilates from leaf 8 to parts of broad bean and dodder, the latter attached to int. 6 and 7 and to the inflorescence axis in the axil of leaf 7. *: sampling differs from the usual procedure; only the inflorescence axis was sampled from which the flowers had dropped (29-6-1972).

	Exp. A: Non-parasitised plant			Exp. B: Parasitised by *C. reflexa*		
plant part	weight(g)	dpm/g	% of total ^{14}C	weight(g)	dpm/g	% of total ^{14}C
apical part of host	30.20	14	0.1	10.13	34	0.1
pods of apical part	4.79	0	0	3.12	30	<0.05
pod 11	1.09	150	<0.05	2.81	89	0.1
int. 11	3.97	548	0.4	2.81	96	0.1
pod 10	13.74	43	0.1	3.89	64	0.1
int. 10	4.08	37	<0.05	3.19	146	0.1
pod 9	4.50	37	<0.05	4.20	0	0
int. 9	5.72	286	0.3	2.85	585	0.4
pod 8	7.64	61200	93.4	5.09	298	0.4
int. 8	4.81	3632	3.5	4.47	2608	3.1
pod 7	7.68	17	<0.05	2.63*	864*	0.6*
int. 7	6.27	76	0.1	6.28	1264	2.1
int. 4+5+6	10.40	11	<0.05	14.33	530	2.0
Parasite:						
haustorial coil				2.51	4953	3.3
filaments originating from haustorial coil				22.56	11860	69.9
apical parts (7 cm) of the filaments				1.68	33265	14.6

activity and representing about 2% of total exported ^{14}C. In the parasitised plant no ^{14}C could be found in the fruits whereas almost 65% of total exported ^{14}C was found in the parasite. The parasite apparently interferes completely with translocation to the young fruits.

4. DISCUSSION

The experiments with ^{14}C-assimilates illustrate the deleterious influence of *Cuscuta* on the development of broad bean plants. In some experiments the parasitised host clearly exhibited signs of damage in the form of retarded growth (*table 3*), but in most experiments growth of the host seemed comparable to that of non-parasitised plants on the day of the experiment. In most cases, however, pods and seeds appeared to be already completely cut off from the supply of ^{14}C-assimilates when *Cuscuta* had started luxuriant growth.

Our results show that *Cuscuta* can reach an efficiency of practically 100% in absorbing ^{14}C-assimilates exported by an assimilating leaf of a fruiting host. The most complete absorption within a small area was found in the experiment shown in *table 2*. All ^{14}C-assimilates, moving from leaf 8 in the direction of pod 7, are drained from the stalk by the parasite. A large number of haustoria had

intruded a small part of the length of the stalk of the pod the phloem system of which is very well developed for translocating assimilates to the pod (cf. OTHLINGHAUS et al. 1968). Usually, a considerable quantity of ^{14}C-assimilates is found below or above stem parts to which *Cuscuta* is attached, indicating a situation not optimal for complete absorption as in the stalk of pod 7 of *table 2*.

JACOB & NEUMANN (1968) have carried out experiments on the absorption of ^{14}C-sucrose (applied as solution to surface of host leaf) by *C. reflexa* from broad bean in experiments of 1 to 72 hrs. duration. They found no noticeable relation between the ratio of the fresh weights of host and parasite and the distribution of the sugar: by cutting off important parts of the host the portion in the parasite could not be increased and the sugar absorption of *Cuscuta* was not reduced by removing its growing tip and buds. On the basis of data of DÖRR (1967) and their own results the authors have stressed not to share the opinion of BALDEV (1962) that "the haustoria provide a natural graft between the host and the parasite."

Jacob & Neumann used young greenhouse-grown broad bean plants with four leaves as hosts to be infected by *Cuscuta*. In the experiments presented in this paper fruiting broad bean plants were used. Fruits are known to be very strong sinks as is also shown in our experiments with non-parasitised plants. Fruiting *Vicia faba* could be a host system from which the parasite cannot withdraw assimilates as easily as from young vegetative plants. However, the sink activity of developing fruits can disappear completely or almost completely in a parasitised host (*tables 2, 3, 4, 5, 6* and *7*). As to several aspects a parallel can be found between *Cuscuta* and fruits, both being strong sinks and having a mineral composition characterised by a very high K/Ca ratio, caused by a preponderant phloem-feeding (cf. ANSIAUX 1958). Their behaviour as sink for assimilates exported by the source leaf turns out to be very different when they are present together and compete for assimilates. Fruits get the worst of it and *Cuscuta* is the victor. A parallel can be found between the inhibition of fruit setting by *Cuscuta* and the inhibition caused by the presence of pods already developing on the plant (e.g. BLACKWALL 1969).

One could wonder why the normally very strong sink activity of developing fruits can be reduced to a very low level after strong infection by *Cuscuta*. It is not known whether fruits of broad beans do not receive assimilates only because *Cuscuta* is an exceptionally strong sink draining all assimilates or whether broad bean fruits become weakened as sink after dodder infection. One could imagine that the level of growth substances in the sink becomes lower in fruits with a reduced growth resulting from dodder infection and that the activity of the sink, assumed to be dependent on its level of growth substances, becomes reduced which ultimately would result in a complete disappearance of the rôle as sink of the flowers.

As mentioned in the introduction, young broad bean plants growing in the greenhouse usually die within a few weeks after strong infection by *Cuscuta*. An important factor in the parasitic relationship could be the exhaustion of the

root. Heavily parasitised hosts start to turn yellow, followed by abscission of the lower leaflets, but a very marked point in the development of the relationship is often the sudden wilting of the host. According to WHITNEY (1972) carbohydrate depletion of bean roots by *Orobanche* is sufficient for reducing their ability to extract water from dry soil, causing death of the bean shoots by desiccation. In our experiments, however, hosts grown on a nutrient solution also died by wilting.

One could wonder if the draining action of *Cuscuta*, causing the death of the host in many cases, does not lead to self-destruction. It should be stressed in this context that the parasite accumulates an abundance of nutrients and metabolites in its long filaments, collected during the very intensive absorption from the host and forming a stock for the future development of fruits. The long dodder filaments can contain reserves sufficient for the development of seeds. *C. lupuliformis*, a species in the Netherlands specially growing on blackberry bushes (see also ZILLIG 1942), shows this phenomenon very clearly. When the flower buds develop, the leaves of the strongly parasitised blackberry plants usually already lose their green colour. In this stage the parasite has formed an enormous mass of "cables" filled with reserve substances and later in the season the seeds will grow while the filaments shrivel. Since the epidermis of *Cuscuta* is a strong barrier to evaporation, also a water reserve can be contained by the filaments.

SINGH et al. (1968), analysing three species of *Cuscuta* for starch, found a maximum of about 10% of dry weight (see also MISRA et al. 1970). According to SINGH et al. (1970) the filament can functionally be separated into a proximal and a distal region. The proximal region has an enzyme make-up preferentially directed to synthesis of starch; the distal region is more suited for the catabolism of carbohydrate. Another distinctive feature of *Cuscuta* and other parasites seems to be the accumulation of phytic acid – also found in seeds of many plants – forming a reservoir of phosphate (SINGH et al. 1963, BEG et al. 1968, MISRA et al. 1970). One may conclude that the parasite very efficiently accumulates nutrients and metabolites and so becomes almost independent from the host in the last stages of development, including the production of viable seeds.

Since the transfer of assimilates between host and parasite is almost complete, the haustorial organ must be very well suited for the task of withdrawing assimilates from the host. An important feature seems to be the enlargement of the surface area in the haustorial tissues, occuring on three levels. As can easily be seen with a microscope, the haustorium of *Cuscuta* stops its intrusive growth at a certain depth and then its superficial cells, especially those near the apex, start developing into separate filaments ("hyphae") in various directions, thus representing the first enlargements of surface area. Secondly, attaching itself to the sieve element of the host, the apical region of a "searching hypha" forms a special contact cell resembling a hand which with many fingers grasps around the sieve tubes of the host (SCHUMACHER 1934). Thirdly, in the parts of the wall adjacent to the sieve element, the parasitic cell develops a conspicuous wall

labyrinth, thus enlarging the absorbing surface many (6–20) times (DÖRR 1967, 1968a, b and 1972; KOLLMANN & DÖRR 1969) and showing "transfer cell" characteristics (GUNNING & PATE 1969; PATE & GUNNING 1972).

Looking at the enlargement of the surface area for absorption of metabolites, a strong parallel can be found between the absorptive parts of the haustorium of *Cuscuta* and the absorptive epithelium of the small intestine of animals the surface of which is covered by the so-called brush border consisting of microvilli. In both situations of a very efficient absorption of sugars and other metabolites from the space surrounding the absorptive cells, three levels of enlargement of surface area can be discerned.

In a subsequent paper evidence will be given that in addition to a very efficient absorption by the parasite, as suggested by the anatomical details, also an enhanced unloading rate of the host phloem seems to be essential for the transfer of metabolites from host to parasite.

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