Neth. J. Plant Path. 71 (1965): 167–175

STUDIES ON *BOTRYTIS CINEREA* IN TOMATOES

MYCELIAL DEVELOPMENT IN PLANTS GROWING IN SOIL WITH VARIOUS NUTRIENT LEVELS, AS WELL AS IN INTERNODES OF DIFFERENT AGE [1]

Botrytis cinerea *in tomaten*

De ontwikkeling van mycelium, zowel in planten groeiend in grond met verschillende bemestingsniveaus als in internodiën van verschillende leeftijd

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Stems and petioles of tomatoes growing in soils with different amounts of N, P, K, Mg and $CaCO_3$, were wound-inoculated. Only N consistently affected lesion development. Increasing the amounts of N progressively decreased the rates at which lesions developed linearly, the effects being relatively larger on the development of stem lesions than on that of petiole lesions. In pot experiments with three levels of nitrogen and three of potassium, a higher nitrogen level also resulted in a slower mycelial extension in stems of plants growing in this soil. With a certain N level, a higher K level decreased the rates at which lesions developed, this N/K interaction being significant in two series. By inoculating stems at many sites, lesions were found to develop more rapidly in young tissues, near main-stem apices, than in old tissues at the base of stems.

INTRODUCTION

Hobbs & Waters (1964) found that increasing the nitrogen supply to chrysanthemums increased attack by *Botrytis cinerea* Pers. ex Fr., whereas Glasscock *et al.* (1944) showed that phosphate deficient beans were more liable to invasion by this pathogen than were beans with an adequate phosphate supply. Because of this evidence showing that the incidence of *B. cinerea* is affected by the nutrition of some hosts, experiments were done to test the effects of differences in tomato nutrition.

MATERIALS AND METHODS

Cultures of *B. cinerea*, seven to ten days old, were used as inoculum, when incubated at 23 °C on modified Richard's agar, containing per 1000 ml distilled water: 10 g KNO_3, 0.25 g $MgSO_4$, 5 g KH_2PO_4, 50 g sucrose, a trace $FeCl_3$ and 20 g agar. Plants of the variety 'Moneymaker' were wound-inoculated. Pieces of mycelial agar culture measuring circa 16 mm^2 were bound with Sellotape to the exposed surfaces of wounds, approximately 6 × 5 mm, made in the cortex parenchyma of petioles or stems. After three days incubation the Sellotape was removed and subsequently lesion lengths were measured daily. From the data obtained regression coefficients (a), giving the rate at which lesion size increased linearly per 24 hours, were calculated as follows:

$$a = \frac{\Sigma xy - \dfrac{\Sigma x . \Sigma y}{n}}{x^2 - \dfrac{(\Sigma x)^2}{n}}$$

[1] Accepted for publication 30 August, 1965.

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where x is the number of days after inoculation, y the increase in length of the lesion and n the number of observations.

The first experimental series was done at the Glasshouse Crops Research Institute (G.C.R.I.), Littlehampton, England, with tomato plants growing in whalehide[3] pots filled with soil from a longterm manurial trial. The following nutrient treatments, arrranged factorially, had been applied in six consecutive seasons: three levels of nitrogen, three levels of potassium, two levels of phosphate, two levels of magnesium and two levels of calcium carbonate. The mean pH's and soil nitrogen concentrations found in these plots are given in Table 1.

TABLE 1. Nitrogen content and pH of the soil in the different plots from the manurial trial. *Stikstofgehalte en pH van de grond in de verschillende objecten uit het bemestingsproefveld.*

	Levels of nitrogen and calciumcarbonate *Stikstof- en calciumcarbonaattrappen*					
	N_1Ca_1	N_1Ca_2	N_2Ca_1	N_2Ca_2	N_3Ca_1	N_3Ca_2
Total nitrogen[1], in ppm *Totaal stikstof*	22.0	26.3	46.0	49.8	167.9	184.8
pH[2]	6.55	7.79	5.72	7.65	5.03	7.40

[1] As found at the beginning of the experiments. / *Bepaald aan het begin van de proef.*
[2] After six weeks of growth of the plants in the soil. / *Na zes weken groei der planten in de grond.*

Plants, propagated in sterilised compost, were planted into pots with experimental soil about 20 cm high. They were usually wound-inoculated six weeks later. Instead of the usual single stem inoculations, some plants were inoculated at three different sites.

In another series of experiments, seedlings were planted into soils with different nitrogen and potassium levels (Table 2) at a much earlier stage of development *viz.* the second leaf stage. When the most rapidly growing plants were about 25–30 cm high, stems of all plants were similarly inoculated, mostly in the internode between the second and third leaves. These experiments were duplicated, being done in England between April and October 1964 and at the Glasshouse Crops Research and Experiment Station, Naaldwijk, the Netherlands, between November 1964 and March 1965. At Naaldwijk, the mixture of loam, peat and grit (Table 2) was replaced by peat and sand, using ground leather instead of hoof and horn.

The effect of age of stem tissue on the spread of *B. cinerea* was tested on plants growing in whalehide pots, when about 110 cm high. They were inoculated simultaneously in five different internodes.

RESULTS

Plants growing in soil from the G.C.R.I. manurial trial differed in height and leaf colour when inoculated. Those in soil with a low nitrogen level were circa

[3] In Dutch „tompot".

TABLE 2. Soil mixtures with different nitrogen and potassium levels. Fertilizers were added to a mixture of loam, peat and grit, 7,3 and 2 parts by volume, respectively.
Grondmengsels met verschillende hoeveelheden stikstof en kalium. De meststoffen werden toegevoegd aan een mengsel van leemgrond, turfmolm en zeer grof zand, gemengd in de volumeverhouding 7:3:2.

Mixture *Mengsel*	Fertilizers added, in ounces per bushel *Toegevoegde meststoffen*[1]			
	Hoof and horn *Organische stikstof*	Superphosphate *Superfosfaat*	Potassiumsulphate *Kaliumsulfaat*	Calcium carbonate *Calciumcarbonaat*
N_1K_1	–	4	–	2
N_2K_1	3	4	–	3
N_1K_2	–	4	1,5	2,5
N_2K_2	3	4	1,5	3,5
N_2K_3	3	4	3	4
N_3K_2	6	4	1,5	4,5
N_3K_3	6	4	3	5
N_1K_3	–	4	3	3
N_3K_1	6	4	–	4

[1] *De hoeveelheden zijn weergegeven in* ounces per bushel, *1* ounce per bushel *is ongeveer 780 mg per liter.*

59 cm high and had light green foliage; those growing in soils with intermediate and high amounts of nitrogen were about 69 and 80 cm high and had green and dark green leaves respectively.

In six experiments, where petioles of leaves 7, 8 and 9 were inoculated, lesion elongation was influenced only by nitrogen. The data in Table 3 show that with increasing nitrogen level of the soil the spread of *B.cinerea* lesions decreased from 9.2 to 7.0 mm per day.

Nitrogen nutrition affected the development of stem lesions relatively more than those in petioles. In the experiments summarized in Table 4, lesion development in plants growing in soil with a low nitrogen level was twice that in plants growing with a high nitrogen level. The mean rate of increase in stem lesion size was greater in series 1 (Table 4) wihen the day temperature in the glasshouse was approximately 21 °C than in series 2, when the day temperature

TABLE 3. Mycelial extension of *B.cinerea* in petioles of plants, growing in soil at three nitrogen levels.
Mycelium-uitbreiding van B.cinerea *in bladstelen van planten, groeiend in grond met drie verschillende stikstofniveaus.*

Nitrogen level *Stikstofniveau*	Regression coefficient *Regressiecoëfficient*[1]			
	Series 1	Series 2	Series 3	Means *Gemiddelden*
Low/*Laag*	10.5	8.9	8.1	9.2
Intermediate/*Middelmatig*	9.2	8.2	6.4	7.9
High/*Hoog*	8.7	6.4	5.8	7.0

[1] Aangevende de uitbreiding der lesies in mm per etmaal.

TABLE 4. Mycelial extension of *B.cinerea* in stems of tomato plants growing in soil from the manurial trial.
Mycelium-uitbreiding van B.cinerea *in stengels van tomateplanten, groeiend in grond uit het bemestingsproefveld.*

Regression coefficients / *Regressie-coëfficiënten*	Nutrient levels of *Bemestingstrappen van*											
	N			K			P		Mg		$CaCO_3$	
	1	2	3	1	2	3	1	2	1	2	1	2
Series 1	9.8	7.9	4.5	7.6	7.5	7.7	7.4	7.7	8.8	6.4	7.9	7.3
Series 2	5.2	4.6	2.4	4.3	4.7	3.2	3.2	5.1	4.0	4.2	4.0	4.2

was about 28 °C. The differences between lesion extension in plants growing in soil with low and intermediate nitrogen levels and in plants growing with the high nitrogen level are significant in series 1 ($P < 0.01$) and in series 2 ($P = 0.02$).

Although nitrogen supply affects stem lesion development, other experiments have shown that the size of the effects differs at different sites of inoculation (Table 5). Whereas increasing nitrogen level significantly ($P = 0.04$) decreased lesion extension from 9.3 to 5.6 mm per day when inoculation wounds were made near stem apices, development near ground level remained unaffected, 1.6 to 1.7 mm per day.

At the inoculation, there were distinct growth differences among plants growing in soil differing only in amounts of nitrogen and potassium. Growth data are given in Table 6, together with the regression coefficients, representing the rate of lesion extension. As before, nitrogen nutrition influenced these significantly in series 1 and 2 ($P < 0.01$). In series 2, adding of potassium decreased the lesion extension significantly ($P < 0.01$), whereas in series 4, adding of potassium increased this significantly ($P < 0.01$) at the second nitrogen level. At the high nitrogen level adding of potassium to the second level gave an increase in lesion extension, but decreased this at the highest potassium level, the N/K interaction being significant ($P < 0.01$).

TABLE 5. The influence of the nitrogen level of the soil on mycelial extension of *B.cinerea* in stems of tomato plants growing in soil from the manurial trial. Stems inoculated at three different sites.
De invloed van het stikstofniveau op de myceliumuitbreiding van B.cinerea *in stengels van tomateplanten, groeiend in grond afkomstig uit het bemestingsproefveld. De stengels zijn op drie verschillende plaatsen geïnoculeerd.*

	Site of inoculation *Inoculatieplaats*		
	10 cm from top of stem *10 cm van de stengeltop*	1st internode above truss 1 *1ste internodium boven tros 1*	10 cm above soil level *10 cm boven de grond*
Nitrogen level *stikstofniveau*	Regression coefficient *Regressiecoëfficient*		
Low/*Laag*	9.3	5.2	1.7
Intermediate/*Middelmatig*	8.0	4.6	2.5
High/*Hoog*	5.6	2.4	1.6

TABLE 6. Plant development in soil at three nitrogen and three potassium levels, and extension of lesions caused by *B.cinerea* in the stems of these plants. Experiments done at the G.C.R.I.
Vegetatieve ontwikkeling der planten, groeiend in grond met drie stikstof- en drie kaliumtrappen en de uitbreiding van B.cinerea *in de stengels van deze planten. Proeven genomen op het G.C.R.I.*

N and K levels / N- en K-trappen	Plant height in cm / *Hoogte van de plant in cm*	Length of leaf 3 in cm / *Lengte van blad 3 in cm*	Area of leaf 3 in cm^2 / *Oppervlakte van blad 3 in cm^2*	Regression coefficient / *Regressiecoëfficiënt* — Series 1	2	3	4
N_1K_1	13.0	12.5	10.6	11.1	12.3	5.0[1]	4.1[1]
N_1K_2	14.0	13.5	11.0	–	–	4.0[1]	4.9[1]
N_1K_3	13.5	14.0	57.5	8.9	8.9	4.3[1]	5.9[1]
N_2K_1	14.5	15.5	14.5	–	–	5.2	5.3
N_2K_2	25.0	24.0	90.0	–	–	6.4	9.5
N_2K_3	21.0	20.5	87.0	–	–	4.1	9.1
N_3K_1	10.0	14.0	33.5	4.9	7.4	3.8	5.0
N_3K_2	18.0	20.0	95.0	–	–	5.1	8.3
N_3K_3	24.0	22.5	112.0	3.3	5.2	4.4	4.5

[1] See discussion.

In experiments done during November and December 1964 at the Naaldwijk Station, differences in plant development attributable to different amounts of nitrogen and potassium, were small. Foliage of plants given large amounts of nitrogen was darker green than with small amounts. Also, plants growing in soil with a low concentration of potassium developed slight symptoms of potassium deficiency. Lesions extend linearly by 8.5, 5.4 and 6.0 mm per 24 hours on plants growing in soils with 20, 190 and 305 ppm nitrogen respectively. Because of the variation within treatments, the differences in lesion extension are not significant.

In other experiments at Naaldwijk, done during January and February 1965, growth and disease differences, attributable to the different nutrients, were greater than during November and December. Growth data together with the regression coefficients are given in Table 7.

Here again, increasing the nitrogen level of the soil decreases significantly ($P < 0.01$) the lesion extension on plants growing in this soil. At the low and intermediate nitrogen level adding of potassium has hardly any effect on the spread of the lesions, but at the high nitrogen level adding of potassium to the second level increases the lesion extension, but decreases this at the third level, the N/K interaction being significant ($P = 0.05$).

As already indicated (Table 5), the rate of lesion development was greater in young stem tissues than in old. This result was confirmed in a series of five experiments where lesions usually developed five times more rapidly when the site of inoculation was moved from 10 to 100 cm above ground level on stems measuring 110 cm (Table 8). The differences between "a" and the other treatments and those between "b" and "d" and between "b" and "c" are significant ($P < 0.01$).

TABLE 7. Plant development in soils at three nitrogen and three potassium levels and extension of lesions caused by *B.cinerea* in the stems of these plants. Experiments done at Naaldwijk.
Vegetatieve ontwikkeling der planten groeiend in grond met drie stikstof- en drie kaliumtrappen en de uitbreiding van B.cinerea *in de stengels van deze planten. Proeven genomen te Naaldwijk.*

N and K levels *N en K trappen*	Plant height in cm *Hoogte van de plant in cm*	Length of leaf 3 in cm *Lengte van blad 3 in cm*	Regression coefficient *Regressiecoëfficient*
N_1K_1	11.6	12.6	10.9
N_1K_2	12.8	14.3	8.4
N_1K_3	9.8	12.6	10.9
N_2K_1	11.0	14.2	6.2
N_2K_2	21.0	20.2	4.8
N_2K_3	23.3	24.6	7.3
N_3K_1	11.0	14.0	3.8
N_3K_2	25.6	22.5	4.9
N_3K_3	24.2	23.3	2.4

TABLE 8. Lesion extension of *B.cinerea* in different internodes of a tomato plant. Each figure of the five series represents the average of a minimum of eight observations. At the inoculation time the plants were about 110 cm high.
Mycelium-uitbreiding van B.cinerea *in verschillende internodiën van een tomateplant. Elk cijfer van de vijf series is het gemiddelde van minstens acht waarnemingen. Op het moment van de inoculatie waren de planten ongeveer 110 cm lang.*

Site of inoculation *Plaats van inoculeren*	Regression coefficient *Regressiecoëfficiënt*					Means *Gemiddelden*
	1	2	3	4	5	
a About 10 cm from the top of the stem *Ongeveer 10 cm onder de stengeltop*	18.8	14.9	7.6	7.0	15.0	12.7
b 1st Internode above truss 3 *1ste Internodium boven tros 3*	14.2	10.5	5.2	4.4	11.3	9.1
c 1st Internode above truss 2 *1ste Internodium boven tros 2*	11.5	8.7	3.4	2.7	9.6	7.0
d 1st Internode above truss 1 *1ste Internodium boven tros 1*	9.8	2.1	2.4	2.3	6.0	4.5
e About 10 cm above soil level *Ongeveer 10 cm boven het grondoppervlak*	5.8	1.2	1.8	1.7	2.6	2.6

DISCUSSION

Applying nitrogen fertilizers increases the damage done in many host-parasite complexes, but the experiments described in this paper show that the reverse is true for tomatoes – *B. cinerea*. Adding nitrogen to tomatoes decreases the rate of lesion development and also probably the mycelial growth of *B. cinerea*. There are other examples of a similar effect. COLE (1964) when comparing two levels of nitrogen in water culture experiments found less powdery mildew on leaves of tobacco plants growing with the larger amount of nitrogen. THOMAS (1948) and BARRATT & RICHARDS (1944) found that the incidence of *Alternaria solani* (Ell. & G. Martin) Sor. on tomatoes was inversely related to amounts of nitrogen. Similar effects of nitrogenous fertilizers were found by COOPER (1956), working with *Senecio cruentus* D.C. and *Alternaria senecionis* Neerg., and by RILEY (1949) with *A. longipes* (Ell. & Ev.) Mason on tobacco leaves.

GRAINGER (1962) suggested that *B. cinerea* needs, when parasitizing its host, large amounts of carbohydrate. As NIGHTINGALE *et al.* (1928) showed that the total concentration of carbohydrate is reduced by increasing amounts of soil nitrogen, the effects of nitrogen supply on *B. cinerea* may be attributable to differences in carbohydrate.

Potassium deficiency also induces a higher concentration of plant carbohydrates (WALL, 1940), but in the present experiments differences of potassium rarely affected disease development significantly. Only in the experiments recorded in Table 6 series 1 and 2 adding potassium decreased lesion extension, whereas in some experiments (Table 6, series 4; Table 7) higher levels of potassium affected disease development at the high nitrogen level. In the G.C.R.I. manurial trial, however, many plants died prematurely in 1963, death often being associated with invasion by *B. cinerea*. Most of the dead plants occurred in plots with low concentrations of soil nitrogen and potassium *viz.* 346 against 127 and 119 respectively in the plots with high levels of both nutrients. The main effects of these nutrients upon numbers of plants killed were significant ($P < 0.01$). Here again, adding of potassium strongly decreased the numbers of dead plants at the higher nitrogen levels, this N/K interaction being significant ($P < 0.01$).

When different internodes on the same plant were inoculated it was evident that the age of tomato stem-tissue played an important role in determining damage done by *B. cinerea*. Circumstantial evidence again suggests an inverse relation with carbohydrates because sucrose, glucose and fructose are less concentrated in old than in young stem-tissues (VAN DIE, 1962). On the other hand, there is a greater development of xylem in old stems which are harder than young stems. Consequently there may be an inverse relation between lesion size and the host's dry matter content.

WILSON (1963) found that lesions developed very slowly in the basal internodes of tomato plants when fresh leaf scars were inoculated with spores of *B. cinerea*. There was a difference of about seven weeks between the development of lesions in young stems and those in old stems. The mycelium of *B. cinerea* spreads less rapidly in excised lengths of stem from the plant base than in sections taken from nearer the main stem apex.

In my experiments the effects of tissue age were greater than those of nitrogen fertilizers (Table 5). Increasing nitrogen from low to high affected lesion development at 10 cm from the stem apex and in the first internode above truss 1 more or less equally, but there was no influence of the nitrogen level upon the lesion development in the basal internodes, in hard stem-tissue.

In the experiments mentioned in Table 8, hardness of stems greatly influenced lesion extension. In experiments 3 and 4 in Table 6, plants in the low nitrogen treatments had very hard stems, possibly because of high light intensities and high temperatures in the glasshouse. This hardness of stems resulted in slower lesion extension, as might be expected. In comparing the hardness of stems of these plants with that of those in the same treatment in earlier experiments (Table 6, 1 and 2) and with that of different internodes of one plant (Table 8), lesion extension had to be greater.

In the experiments carried out in November and December 1964 at the Naaldwijk Station, the nitrogen level of the soil did not affect lesion development significantly, but the results tend to confirm those of the other experiments. In the experiments done in January and February 1965, plant development was better, resulting in significant differences between the lesion development on the plants of the three groups (Tabel 7).

In the experiments described in this paper, nitrogen fertilizers have been shown to influence damage done by *B. cinerea* after inoculation, but this is only one aspect of the host-parasite complex. At the end of this discussion it is worth mentioning that the benificial effect of large quantities of nitrogen may be offset by the disease promoting influence of a high relative humidity resulting from a more luxurious development of the hostplants.

ACKNOWLEDGEMENTS

Most of the experiments reported were done during a stay at the Glasshouse Crops Research Institute (G.C.R.I.) Littlehampton, England. The author is very much indebted to the director and the staff of this Institute, especially to Dr. F. T. LAST, Dr. G. W. WINSOR and Mr. P. ADAMS. He is also much indebted to Dr. J. G. TEN HOUTEN, director of the I.P.O., Wageningen, for allocation of funds derived from a grant by Shell Research Ltd., and to Dr. A. R. WILSON (S.H.R.I., Invergowrie, Scotland), and Ir. J. H. VAM EMDEN (I.P.O., Wageningen) for criticism and advice.

SAMENVATTING

Tomateplanten, groeiend in grond met verschillende hoeveelheden meststoffen, werden in bladstelen en stengels geïnoculeerd met een zeven tot tien dagen oude cultuur van *B. cinerea*, groeiend op gewijzigde Richard's agar bij 23 °C. Een stukje agar met mycelium, ca. 16 mm^2 groot, werd met behulp van Sellotape in kleine wonden in het schorsparenchym gebracht; na drie dagen werd het Sellotape verwijderd en daarna werd de uitbreiding van de lesie dagelijks gemeten. De uitkomsten werden omgewerkt tot regressiecoëfficiënten; de regressiecoëfficiënt komt overeen met de uitbreiding der lesies per etmaal.

De eerste proeven werden in het voorjaar en in de zomer van 1964 tijdens een verblijf van zes maanden op het Glasshouse Crops Research Institute, Littlehampton, Engeland, genomen. Aanvankelijk werden inoculaties uitgevoerd met planten, groeiend in grond afkomstig uit het bemestingswarenhuis (tabel 1), naderhand met planten groeiend in grond met verschillende stikstof- en kaliumniveaus (tabel 2).

De inoculatieproeven met bladstelen wijzen op een negatieve correlatie tussen het stikstofgehalte van de grond en de uitbreiding der lesies (tabel 3). In proeven met stengelinoculaties, uitgevoerd in het internodium boven de eerste bloemtros, bleken deze correlaties zeer betrouwbaar te zijn (tabel 4). In jonge internodiën van deze planten waren deze verschillen in lesie-uitbreiding geringer, maar toch betrouwbaar; in oude internodiën was de invloed van de stikstofbemesting op de uitbreiding der lesies in de stengel niet merkbaar (tabel 5).

Ook de inoculatieproeven in stengels van planten, groeiend in grond met verschillende stikstof- en kaliumniveaus, gaven duidelijk de invloed van de stik-

stofbemesting aan (tabel 6). In twee proefseries had een hogere kaliumbemesting een remmende invloed op de uitbreiding der lesies in de planten (tabel 6, 1 en 2), in serie 4 was dit alleen het geval bij het hoge stikstofniveau.

In de periode van november 1964 tot maart 1965 werden dergelijke proeven genomen op het Proefstation te Naaldwijk. De inoculatieproeven, uitgevoerd in december, wijzen eveneens op de mindere uitbreiding der lesies in planten groeiend in grond met een hoog stikstofniveau, maar de verschillen zijn niet betrouwbaar. Als gevolg van de voor tomateplanten slechte uitwendige omstandigheden in deze periode, was er ook weinig verschil in ontwikkeling van de planten, ondanks de verschillen in bemesting. In de proeven, genomen in februari, was het effect van de stikstofbemesting op de uitbreiding der lesies wel betrouwbaar. De verschillen in vegetatieve ontwikkeling der planten door de diverse bemestingsniveaus traden toen ook duidelijker naar voren (tabel 7).

Uit de inoculatieproeven, waarbij verschillende internodiën van één plant op hetzelfde tijdstip werden geïnoculeerd, blijkt dat de leeftijd van het internodium grote invloed heeft op de uitbreiding der lesies (tabel 8). Zoals blijkt uit de resultaten, weergegeven in tabel 5, is de invloed van de leeftijd van het stengelweefsel op de uitbreiding der lesies groter dan die van de stikstofbemesting. Een en ander staat misschien in verband met de beschikbare suikers en met het drogestofgehalte van het stengelweefsel.

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