Growth and respiratory activity of roots of various Triticineae tolerant or resistant to *Heterodera avenae* Woll., with or without infection by the nematode

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Summary

Morphological changes, elongation, dry matter content and respiratory rate of roots of various lines of Triticineae resistant or tolerant to *Heterodera avenae* were measured during the first eleven days of growth (eight days after infection). In non infected roots, an increase in resistance was associated with a decrease in root elongation and dry matter content, but the respiratory rate barely changed. Uninfected tolerant lines grew longer roots with higher dry matter content and respiratory rate. Root elongation was strongly inhibited in infected resistant lines and the respiratory rate was reduced in proportion with the number of larvae in the root. The respiratory rate was enhanced in infected susceptible lines due to the formation of numerous new rootlets at the infection point. Root growth of tolerant lines was less affected by nematode infection. It is suggested that the variations in respiratory rate during infection are related to changes in the morphology of the root system. The possibility of using such variations in respiratory rate and root growth to assess the level of resistance or tolerance of various lines to *Heterodera avenae* is discussed.

Résumé

Croissance et intensité respiratoire des racines de différentes Triticinées tolérantes ou résistantes à Heterodera avenae *Woll., infestées ou non par le nématode*

Les modifications de la morphologie, de l'élongation, du poids de matière sèche et de l'intensité respiratoire de racines de diverses lignées de Triticinées résistantes ou tolérantes à *Heterodera avenae* ont été mesurées au cours des onze premiers jours de croissance. Chez les plantes non infestées, l'augmentation du niveau de résistance correspond à une diminution de l'élongation et du poids de matière sèche des racines mais leur intensité respiratoire est peu modifiée. L'élongation, le poids de matière sèche et l'intensité respiratoire des racines sont supérieures chez les lignées tolérantes. Après infestation, il y a une forte inhibition de l'élongation des racines et, seule chez les lignées résistantes, une diminution de l'intensité respiratoire est notée. L'importance de cette inhibition est liée au nombre de larves par racine. La production de nouvelles petites racines à partir du point d'infestation entraîne une stimulation de l'intensité respiratoire chez les lignées multiplicatrices. Chez les lignées tolérantes, la morphologie du système racinaire infesté par le nématode est moins modifiée. Le processus d'inhibition ou de stimulation de l'intensité respiratoire après infestation des différentes lignées semble être lié uniquement à la modification de la morphologie du système racinaire. La possibilité d'utiliser de telles observations pour évaluer le niveau de résistance ou de tolérance de différentes lignées vis-à-vis d'*H. avenae* est envisagée.

Heterodera avenae Woll. produces severe stunting of roots of many *Triticineae* (Ritter, 1965) which causes severe crop damages (Ritter, 1982; Meagher, 1982). Resistance in several Triticineae has been investigated in order to incorporate resistance genes into commercial cultivars and then enhance the yields of crops. Tolerance to the parasite has been studied more recently. It is important to introduce tolerance to *H. avenae* in wheat since some susceptible lines sustain more damage from the pathogen in the roots (Fisher, Rathjen & Dube, 1981), and in the other hand loss of yields can be very high even for resistant lines (Doussinault *et al.*, 1986).

The modifications of physiological mechanisms in response to the penetration by nematodes into roots can enhance a hypersensitive reaction (Kaplan & Keen, 1980; Giebel, 1982) and increase respiration in the infected tissues (Zacheo & Bleve-Zacheo, 1987). There are only few results on the effect of *H. avenae* on growth or metabolism (O'Brien & Fisher, 1981), and nothing is known of the nematode effect on root growth or respiratory activity in tolerant plants.

We have shown (Person-Dedryver & Doussinault, 1978) discrepancies in growth and respiratory rate between a susceptible line « Capitole » and a resistant line « Loros » infected by *H. avenae* (Davy de Virville, Chauveau & Person-Dedryver, 1984). There was an increase of the respiratory rate in the susceptible line while a strong decrease occurred in the resistant lines.

In this paper, we report on the modifications of growth and metabolism of the roots of several Triticineae during the first days after germination. The aim of this study was *(i)* to extend previous observations made on « Capitole » and « Loros » to other lines; *(ii)* to determine the nature of the changes in respiratory activity in infected tissues; and *(iii)* to compare changes in tolerant lines to those of other lines. We also attempted to use metabolic changes in infected or non-infected roots, as a quick and easy way to assess the levels of resistance or tolerance of wheat lines to *H. avenae*.

Materials and methods

Plant material

Ten wheat lines (*Triticum aestivum* L.) and one line of *Aegilops ventricosa* Tausch were used : six susceptible lines : « Cappelle », « 8203 » [(Varimek-S × Raven)/111/8/S8)] (Fisher, Rathjen & Dube, 1981), « Lutin », « Capitole », « Fidel » and « Moisson »; two lines with a complete resistance to the four French pathotypes, « Loros » (Aus 11577 × Koga II) and one line of *A. ventricosa* (Vent 11) (Dosba & Rivoal, 1981); two lines with incomplete resistance, « M 36 » issued from *A. ventricosa* (Rivoal *et al.*, 1986) and « 8206 » (Rac-311) (Fisher, Rathjen & Dube, 1981); and « R157 » (H77 RTV Ne 29-4, bulk 24-7-2-5), a resistant line in disjonction for resistance issued from « Loros » (Doussinault *et al.*, 1986).

Estimation of resistance and tolerance levels

Comparison of resistance in all lines was carried out at the INRA experimental station at Rennes by determining the number of gravid females (HA 41 pathotype; Andersen & Andersen, 1982) growing on the roots five weeks after inoculation (Person-Dedryver & Doussinault, 1978). Fresh weight of 70 to 100 roots was also determined. Determination of good tolerance of the « R157 » line and bad tolerance of the « Fidel » line has been made in the fields by Rivoal (pers. comm.). Good tolerance of the « 8203 » and « 8206 » lines has been reported by Fisher, Rathjen and Dube (1981).

Conditions of seedlings growth and infection process

Seedlings were grown and infected in Petri dishes (Person-Dedryver & Doussinault, 1978). Three days after sowing, the caryops were placed on 2 % agar in Petri dishes. The three main roots were inoculated with sixteen juveniles of *H. avenae* (HA41 pathotype; Andersen & Andersen, 1982) on the extremity of each root. For « Vent 11 » line, the number of juveniles were 4, 8, 12 and 16 per root. After 24 h at 20°, the seedlings were transferred to an air-conditionned room (4 000 lux, 15 h/days, 18 ± 1°). The three main roots of each seedling were cut off seven and eleven days after sowing, and the respiratory rate, elongation rate and dry matter content, were measured.

Determination of respiratory rates

The rate of 0_2 consumption by roots or nematodes was assessed with a Clark type oxygen electrode calibrated with $Na_2S_2O_4$ in distilled water. The calibrating solution was replaced with two ml of 20 mM phosphate buffer (pH 7.2) previously stirred vigourously for at least five minutes. As soon as the polarographic recording was stable, roots were introduced in the chamber and O_2 uptake was assessed for three minutes. Dry matter of the roots was measured after desiccation for four days at 90°. Five to seven replicates were used for each line and for each sampling.

For the « Capitole » line only, the respiratory rate was measured on three different parts of the root system. Fragments of roots were cut off and laid down in a Petri dish with a drop of distilled water until enough fragments had been obtained (corresponding to three seedlings). The respiratory rate was then immediately measured. Only fresh weight was determined for this line.

Nematodes were picked off the roots and placed on moist agar until a sufficient number (from 40 to 80) was collected for measurement. The nematodes were then introduced in the vessel chamber. Due to the low respiratory rate of the nematodes, oxygen consumption was measured for up to twenty minutes. Respiration rates were calculated after correction of the residual electrode drift following injection of 0.4 mM potassium cyanide. Five replicates were used for each line.

Results

Study on nematodes

We measured the number of nematodes per root to assess the resistance level, and then the respiratory rate. Due to the large number of seedlings required for these measurements, fresh weight of females was not always taken. The various lines studied could be arranged into susceptible lines, lines with incomplete resistance, and fully resistant lines. The nematodes were always at a high rate (11 to 13) on the roots of susceptible lines. There were no females on the roots of lines with incomplete resistance (« M36 », « 8206 ») except for a few seedlings. No females were observed on the roots of « Vent 11 » and « Loros » which are completely resistant.

The mean number of nematodes decreased as the level of resistance increased, but the size of the adult females became more heterogeneous. Some very small females had a rather fragile cuticle. For example, we were able to pick off all the nematodes from the roots of « Capitole » or « Lutin » whereas 20 % of the females

Table 1

Influence of the resistance level of various Triticineae on the number, fresh weight and respiratory rate of adult females of *Heterodera avenae* (Ha 41) after five weeks of development into roots. (T) : tolerant lines; (I) : intolerant lines.

Lines	*Females per seedling*	*Fresh weight (mg female^{-1})*	*Respiratory rate*	
			$QO_2^{(c)}$	*QO_2 $FW^{(d)}$*
SUSCEPTIBLE				
« Cappelle »	9.4 (3-13) (b)	—	0.068	—
« 8203 » (T)	8.5 (3-11)	—	0.044	—
« Lutin »	7.1 (3-12)	0.046	0.090	1 957
« Capitole »	6.3 (2-11)	0.032	0.090	2 750
« Fidel » (I)	6.4 (4-11)	—	0.069	—
« Moisson »	5.9 (1-13)	0.042	0.055	1 310
INCOMPLETE RESISTANCE				
« M36 »	2.7 (0-7)	0.038	0.060	1 580
« 8206 » (T)	2.0 (0-3)	—	—	—
COMPLETE RESISTANCE				
« R157 » (T) (a)	0.5 (0-2)	—	—	—
« Vent 11 »	0	—	—	—
« Loros »	0	—	—	—

(a) Segregated line
(b) mean and range
(c) µl O_2 h^{-1} female^{-1}
(d) µl O_2 h^{-1} g FW^{-1}
(70 to 100 replicates for the fresh weight; five replicates for the respiratory rate.)

were destroyed for « Moisson », and the percentage increased to 30 or 40 % for « M36 ». By contrast, the nematodes could be collected easily from the susceptible and tolerant line « 8203 », although they were as heterogeneous as on the more resistant lines.

The decrease in size of the nematodes was associated with a significant decrease ($P = 0.05$) of the fresh weight except for « Capitole » (Tab. 1). The respiratory rate of females was variable, and in some cases the difference in respiratory rate coincide with a decrease in the size of the nematode (« 8203 », « Moisson » and « M36 »). With « Moisson » and « M36 », we could only measure the respiratory rate of the biggest females due to the brittleness of the cuticule. Thus the mean respiratory rate was probably an overestimate. This explains why the respiratory rate of the females was higher for « Moisson » and « M36 » than for the susceptible line « 8203 » where all the nematodes (even the little ones) were collected. Finally, the respiratory rate expressed on a fresh weight basis was significantly decreased for nematodes originating from « Moisson » and « M36 » lines.

ROOT GROWTH AND RESPIRATORY ACTIVITY IN NON-INFECTED ROOTS

Root of the two most susceptible lines « Cappelle » and « 8203 » were longer after the first eleven days of growth (Tab. 2). The intolerant line « Fidel » had the shortest roots compared to other susceptible lines. Root length was generally decreased as the resistance level increased, and the shortest roots were observed on the two most resistant lines « Vent 11 » and « Loros ». Dry matter increased between the 7th and the 11th day, and there were no strong discrepancies between the lines.

Table 2

Influence of the resistance level on length, dry matter and respiratory rate of roots of various Triticineae susceptible or resistant to *Heterodera avenae* after 7 and 11 days of development.

Lines	*Time (d)*	*Root length (cm)*	*Dry matter (mg)*	*Respiratory rate*	
				$QO_2^{(b)}$	*QO_2 $DM^{(c)}$*
SUSCEPTIBLE					
« Cappelle »	7	7.5	6.1	20.3	3 327
	11	14.3	7.4	23.8	3 216
« 8203 » (T)	7	9.7	6.2	26.0	4 193
	11	16.9	8.3	25.7	3 096
« Capitole »	7	8.6	4.2	15.8	3 750
	11	13.2	7.6	21.7	2 855
« Fidel » (I)	7	8.8	5.3	24.3	4 493
	11	12.7	9.6	22.4	3 163
INCOMPLETE RESISTANCE					
« 8206 » (T)	7	7.3	5.6	20.2	3 607
	11	11.2	7.3	21.7	2 993
COMPLETE RESISTANCE					
« R157 » (T) (a)	7	8.2	6.0	24.2	4 640
	11	12.3	6.9	21.0	3 093
« Vent 11 »	7	3.6	1.6	7.2	4 497
	11	6.3	2.5	10.7	4 367
« Loros »	7	8.4	4.5	17.5	3 708
	11	11.0	5.1	20.5	3 500

(a) Segregated line
(b) µl O_2 h^{-1} per three seminal roots
(c) µl O_2 h^{-1} g DM^{-1}
(Five to seven replicates. Standard mean deviations were about 5 % for root elongation and 10 % for the other parameters.)

The tolerant line « 8203 » had the highest respiratory rate. The other susceptible lines had identical but lower respiratory rates (about 22 to 24 µl O_2 per hour and per seedling). Respiratory rates of resistant lines were higher for tolerant lines « 8206 » and « R157 », but lower for « Loros » and « Vent 11 ». It is interesting to compare « R157 » and « Loros » in the resistant group, since

« R157 » was obtained by selection from « Loros ». The good tolerance of « R157 » line was indeed correlated with a better elongation and higher respiratory rate. There were no significant differences on a dry matter basis between the lines except for « Vent 11 ». Due to the increase of dry matter after the 11th day, the respiratory rate was often lower after this period.

To better assess the differences between lines, daily elongation, dry matter increase and mean respiratory rates were determined (Tab. 3). Regression analysis of the parameters measured and the number of females per roots were determined. The results showed a good correlation between the elongation rates or dry matter increments and the number of females per plant (level of resistance) with the lowest for the most resistant lines (« R157 », « Loros » and « Vent 11 »). On the other hand, there was no correlation between the number of females and the respiratory rate, expressed by root or dry weight basis.

Table 3

Elongation rate, dry matter rate and mean respiratory rate between the 7th and the 11th day of root development of various Triticineae susceptible or resistant to *Heterodera avenae.*

Lines	*Growth rate* $(cm\ d^{-1})$	*Dry matter* $(mg\ d^{-1})$	*Respiratory rate between days 7 and 11*	
			QO_2[b]	QO_2 DM[c]
SUSCEPTIBLE				
« Cappelle »	1.7	0.33	22	3 300
« 8203 » (T)	1.8	0.53	26	3 600
« Capitole »	1.3	0.46	19	3 200
« Fidel » (I)	0.98	0.58	24	3 800
INCOMPLETE RESISTANCE				
« 8206 » (T)	0.98	0.41	21	3 300
COMPLETE RESISTANCE				
« R157 » (T) (a)	1.04	0.25	23	3 900
« Loros »	0.76	0.24	19	3 600
« Vent 11 » 0.68	0.21	9	5 200	
(r^2) (d)	(0.88)	(0.70)	(0.56)	(0.52)

(a) Segregated line
(b) $\mu l\ O_2\ h^{-1}$ per three seminal roots
(c) $\mu l\ O_2\ h^{-1}\ g\ DM^{-1}$
(d) correlation coefficient of the number of females per plant and the parameters analyzed.
Values were calculated from results of Table 2. (T) : tolerant lines; (I) : intolerant lines.

ROOT GROWTH AND RESPIRATORY ACTIVITY IN INFECTED ROOTS

Root growth was strongly inhibited after the first days of infection in all lines tested. The upper part of the roots became thicker and curved and developped numerous root hairs. Root growth of all lines started between three and eight days after inoculation with the formation of many new rootlets at the apex (infection point) (Fig. 1). However, the inhibition of elongation was lower in most resistant lines (Tab. 4), and new rootlets appeared about eight days after infection compared to four days in susceptible lines. Consequently, the root system was less branched in the resistant lines at the beginning of infection (up to fifteen days) than in the susceptible lines. For the two tolerant lines « 8203 » and « 8206 », independently of their resistance level, root growth resumed after the 4th day of infection by elongation of the main root rather than by the formation of new rootlets (Fig. 1). In the tolerant but resistant line « R157 », this type of growth was rarely observed.

Modifications of the length, dry matter and respiratory rate of the roots during the first eight days of infection are shown in Table 4. Root length of all lines was severely decreased. There was also an inhibition of the dry matter content always less than for root length. The respiratory rate of infected roots of resistant lines was significantly decreased ($P = 0.05$). For the susceptible lines, a strong and significant stimulation ($P = 0.05$) of the respiratory rate (expressed on a dry matter basis) was observed.

RESPIRATORY RATE IN SUSCEPTIBLE LINES

In order to understand the significance of the stimulation of respiration, the respiratory rate of the upper and lower parts of the roots of the susceptible line « Capitole » infected or not by *H. avenae* was measured (Tab. 5). This line was selected because numerous rootlets were formed after infection (Davy de Virville, Chauveau & Person-Dedryver, 1984), and there was an important stimulation (30 %) of respiration. In non-infected roots, the respiration of the lower part of the root (last third) increased relatively to the upper part. This was attributed to meristematic activity. In infected roots, an increase of respiration was observed in the lower part of the root with new rootlets, and the increase was correlated to the number of rootlets. Respiration in the rest of the root (including the infected portion) was slightly decreased relatively to the same area in non infected roots. However the respiration of tissues at the infected point was not modified (data not shown).

RESPIRATORY RATE IN RESISTANT LINES

The decrease of respiratory rate in infected roots of resistant lines could be due to the high number (16) of juveniles per root. We therefore measured length, dry

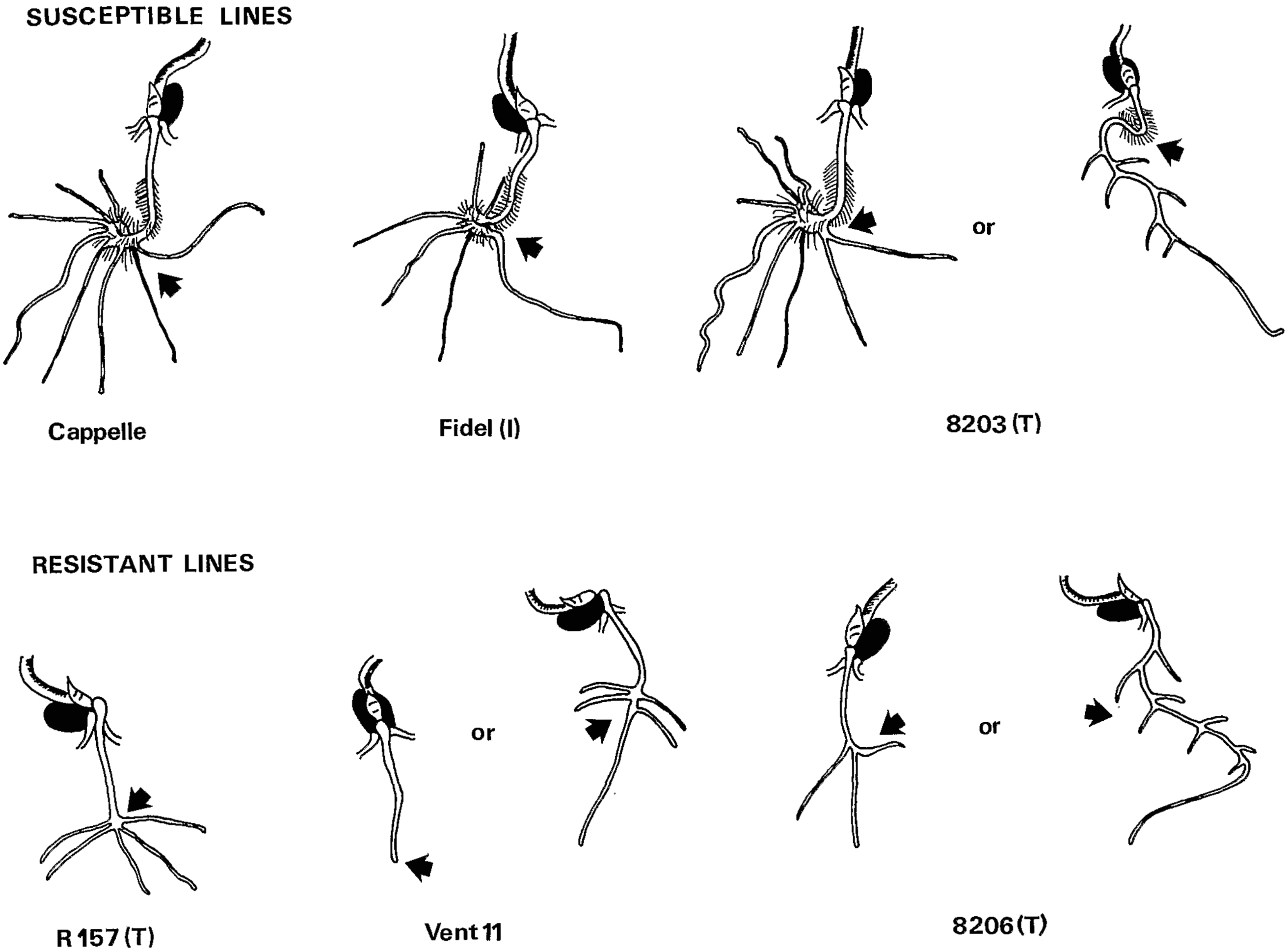

Fig. 1. Morphology of the root system of susceptible and resistant lines eight days after infection by *Heterodera avenae.* Arrows indicate the penetration point.

matter and respiratory rate of " Vent 11 " roots eight days after infection for various number of invading juveniles (Fig. 2). This line was selected due to its very strong decrease of elongation relatively to other resistant lines (cf. Tab. 4). Root elongation, dry matter content and respiratory rate were always decreased, even with only four juveniles per root and the decrease was correlated to the number of invading larvae in the tissues, but was mainly obtained with eight juveniles per root.

Discussion

Oxygen measurement

This study confirms that it is possible to measure root respiration accurately by the use of a Clark type oxygen electrode. Measurements taken for two lines, " Cappelle " and " 8203 " with a manometric technique, were similar to those obtained with the oxygen electrode. The same technique was used for the measurement of nematode respiration. Therefore, it is possible to measure, simultaneously and with good accuracy, the respiration of roots and that of nematodes just picked off the roots.

Development of nematodes in resistant lines

The results show that resistance leads both to a significant decrease of the number of adult females, and to a poor development (low respiratory rate, small size and brittleness) of the few nematodes which are able to grow on the roots. Results show that resistance leads to the destruction of juveniles. Moreover, a poor development of the syncytium in the tissues, as shown for *H. avenae* (Lavail, pers. comm.) or for other nematodes (Giebel, 1982), leads to poor growth conditions for the females.

Table 4

Elongation, dry matter content and respiratory rate of roots of susceptible and resistant lines to *Heterodera avenae*. Numbers between brackets indicate the time after infection.

Lines	*Time (d)*	*Stimulation [+] or inhibition [—] (%)*			
		Root length	*Dry matter*	*Respiratory rate*	
				Root	*Dry matter*
SUSCEPTIBLE					
« Cappelle »	7 (4)	— 27	— 13	+ 3	+ 19
	11 (8)		+ 15	— 4	+ 13
« 8203 » (T)	7 (4)	— 22	— 10	— 8	+ 2
	11 (8)		— 30	— 2	+ 40
« Fidel » (I)	7 (4)	— 50	0	— 14	— 3
	11 (8)		— 20	+ 23	+ 33
INCOMPLETE RESISTANCE					
« 8206 » (T)	7 (4)	— 32	— 7	— 1	+ 7
	11 (8)		— 14	— 19	— 9
COMPLETE RESISTANCE					
« R157 » (T) (a)	7 (4)	— 38	— 23	— 17	— 10
	11 (8)		— 20	— 14	— 5
« Vent 11 »	7 (4)	— 64	— 40	— 29	— 10
	11 (8)		— 9	— 14	— 5

(a) segregated line
(five to seven replicates). Root length was not measured after rootlets development (11th day). Computed from the data of table 2.

Table 5

Respiratory rate of different parts of uninfected and infected roots of the susceptible line « Capitole » fifteen days after infection.

Conditions	*Respiratory rate (a)*	
	Upper part of the root	*Lower part of the root*
Control (uninfected roots)	130	160
Infected root with 12 rootlets	120	250
Infected root with 18 rootlets	110	350

(a) $\mu l\ O_2\ h^{-1}\ g\ FW^{-1}$
(five replicates). Standard mean deviation was about 10 %.

DEVELOPMENT AND RESPIRATORY RATE OF ROOT SYSTEM IN RESISTANT LINES

In non-infected roots, resistance was associated with a low growth rate and dry matter content of the roots. The respiratory rate was similar for all lines except for « Vent 11 », a consequence of the very low content of dry matter in the roots of this line. After infection, and perhaps linked to this low growth rate, there was a strong inhibition of root elongation as generally observed for wheat (Brown, 1974; Meagher, 1982) or oat and barley (Price, Clarkson & Hague, 1983). The results show that the inhibition was higher for the resistant lines than for the susceptible lines, up to the 7th day of infection. The respiratory rate of roots always decreased in resistant lines, but less than root growth at least during the first four days of infection. The decrease in elongation rate of the infected roots was not directly associated during this period with a concomitant decrease in tissue metabolic activity. As a consequence, the roots became thicker and more rigid. These modifications of metabolism in infected roots may be linked to the formation of a syncytium (Kaplan & Keen, 1980; Giebel, 1982). Such an effect on root growth has been artificially induced by antibiotics (Signol, 1963).

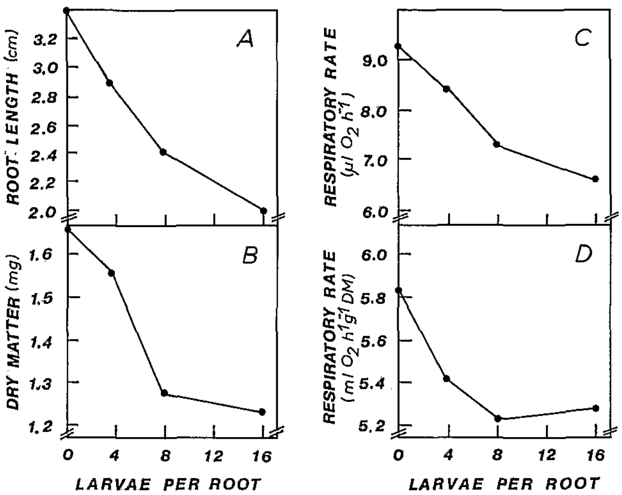

Fig. 2. Length, dry matter and respiratory rate of roots of « Vent 11 line » eight days after infection by *Heterodera avenae* and number of larvae per root (five replicates). A : mean length of one seminal root; B and C : dry matter and respiratory rate of three seminal roots; D : respiratory rate of 1 g of root dry matter.

The decrease in metabolic activity, directly linked to the induction of a resistance process, could result in a development of the syncytium less important than in the susceptible line « Capitole », as was shown for « Loros » (Lavail, pers. comm.) after fifteen days of infection. It must be stressed that the importance of this inhibition occurring during the first days of infection is correlated to the presence and number of the invading juveniles (results obtained with *A. ventricosa* 11). There may be a relationship between the low rate of growth in non-infected plants of resistant lines and the poor formation of a syncytium in the infected tissues, but this needs to be confirmed. In all cases, and according to previous reports (Davy de Virville, Chauveau & Person-Dedryver, 1984), the low growth rate of resistant lines seems to be characteristic of resistance during the first days of growth. Besides, the damage is higher when infection occurs at the beginning of seed germination (O'Brien & Fisher, 1981; Meagher, 1982). Moreover, in resistant lines, the inhibitions of growth and respiratory rates are clearly the first reaction of the plant to the development of the nematodes in the roots tissues.

DEVELOPMENT AND RESPIRATORY RATE OF ROOT SYSTEM IN SUSCEPTIBLE LINES

Root growth starts again several days after infection (about four days for the susceptible lines and eight days for the resistant lines), but with different aspects depending on the resistance level. In the susceptible lines, numerous rootlets appear. The root system is much shorter and divided by comparison with the non-infected plants. An increase in root respiratory rate is observed, which corresponds to the development of new rootlets (results obtained with « Capitole »). Results of cell division and elongation in the apex result in higher respiration and the root dry matter is not much modified by the very small weight of the new rootlets. That is why this stimulation of respiration is mostly measured only when the respiratory rate is expressed on a dry matter basis. For the resistant lines, this root formation is also observed, but only later, between the 8th and the 15th day of infection and, as a consequence, the inhibition of the respiratory rate is released (Davy de Virville, Chauveau & Person-Dedryver, 1984). Therefore, the increase of respiration seems highly characteristic of susceptibility, and the degree of stimulation is probably related to the number of rootlets appearing on the main root. This could explain why the stimulation observed after infection of susceptible lines is quite variable. There is no stimulation of respiration linked to the enhancement of a hypersensitive mechanism like that which occurs in the roots of the resistant tomato cultivar « Rossol » infected by *Meloidogyne incognita* (Zacheo & Bleve-Zacheo, 1987; Zacheo & Molinari, 1987).

DEVELOPMENT AND RESPIRATORY RATE OF ROOT SYSTEM IN TOLERANT LINES

At the beginning of growth and up to the 7th day after sowing, there are usually three main roots appearing per seedling. In the tolerant lines « 8203 » and « 8206 » five to seven roots can develop, as was sometimes the case for « R157 ». These data can be related to other observations showing that tolerance is higher in barley than in wheat or especially in oat, and its depends on the number of seminal roots (Fisher, 1982). Tolerance decreased with number of seminal roots for a mutant barley variety (Rawsthorne & Hague, 1985).

For lines « 8203 » « 8206 » and « R157 », independently of their resistance level, tolerance like susceptibility leads to a higher capacity for growth and metabolic activity. This particularly high activity, and the development of the root system agrees with previous observations by Fisher, Rathjen and Dube (1981) who showed a good correlation between early growth and tolerance. However, roots in soil may be more susceptible at the beginning of their growth than later on. This remark holds true since hatching and germination take place at about the same time [for the pathotype used in this study (HA41) (Rivoal, 1982) or for the Australian pathotype (Brown, 1984)]. Thus, the number of seminal roots and a higher capacity of growth, particularly at the beginning of germination, could be important factors allowing the roots to grow better in spite of the presence of the nematodes, and could contribute to the tolerance of the plant to *H. avenae.*

After infection, there is no modification of the root respiratory rate in tolerant lines relatively to other resistant or susceptible lines, although the growth of the new roots in the « 8203 » and « 8206 » tolerant lines after infection is quite particular. Root growth resumes by elongation of the main root rather than by the appearance of new rootlets, so the morphology of the root system after infection is much less modified. The particular growth of non infected roots in these two lines may be a consequence of the already high metabolic activity and growth rate. In any case, the increase in tolerance for some lines is clearly linked to a special type of root system development after infection.

Rawsthorne and Hague (1985) showed that in barley growth of infected roots was less reduced, at least at the beginning of the infection. The tolerant line « Bomi » showed a higher growth rate of roots in the non-infected tissue. These observations and our results suggest that root system morphology may be a major factor for tolerance. Rawsthorne and Hague (1985) also suggest counts of nematodes per root cm to assess the real effect of infection.

ASSOCIATION OF TOLERANCE AND RESISTANCE

Contrary to tolerance, the more resistant the wheat lines the less active the roots during the first few days of growth. The existence of the resistant and tolerant line « R157 » shows that it is possible to combine good levels of resistance and tolerance in the same plant. Root growth and respiratory rate in « R157 », although higher than those of « Loros » from which this line is derived, are always lower than those of susceptible lines. It seems that tolerance leads only to a partial recovery of root development but perhaps sufficient to allow a full development of the plant. The fact that this type of growth after infection was rarely observed with the « R157 » tolerant line might be correlated with the high level of resistance originating from « Loros » (Doussinault *et al.*, 1986), where infection inhibited growth.

Conclusion

These results show that, independently of the nematode *H. avenae*, and in addition to classical mechanisms of induced resistance, plants *per se* have growth characteristics promoting resistance or tolerance, and the first days of root growth seem to be critical to further development of the plants. Resistant lines but not susceptible ones are characterized by a poor development of the root system leading to a strong inhibition of the respiratory rate after infection. Tolerant lines had numerous seminal roots with high elongation and repiratory rates. After infection the root system of these lines was longer and less divided than of other lines, but their respiratory rate varied like that of other resistant or susceptible lines. All the measurements reported in this paper (root morphology, growth, dry matter content, and respiratory rate), were taken during the first fifteenth days of growth of the plants. These measurements were very easy to carry out and did not require expensive equipment. Such measurements could be done routinely to assess the levels of resistance or tolerance of various wheat lines susceptible to *H. avenae*. This could be of greatest interest for selection in plant breeding programs.

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