

## Influence of Four Nematodes on Root and Shoot Growth Parameters in Grape<sup>1</sup>

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**Abstract:** Two grape cultivars, susceptible French Colombard and tolerant Rubired, and four nematodes, *Meloidogyne incognita*, *Pratylenchus vulnus*, *Tylenchulus semipenetrans*, and *Xiphinema index*, were used to quantify the equilibrium between root (R) and shoot (S) growth. Root and shoot growth of French Colombard was retarded by *M. incognita*, *P. vulnus*, and *X. index* but not by *T. semipenetrans*. Although the root growth of Rubired was limited by all the nematodes, the shoot growth was limited only by *X. index*. The R:S ratios of Rubired were higher than those of French Colombard. The reduced R:S ratios of Rubired were primarily an expression of reduction in root systems without an equal reduction in shoot growth, whereas in French Colombard the reduced R:S ratios were due to a reduction in both shoot growth and root growth and to a greater reduction in root growth than shoot growth. All nematodes reproduced equally well on both cultivars. Both foliage and root growth of French Colombard were significantly reduced by *M. incognita* and *P. vulnus*. Nematodes reduced the shoot length by reducing the internode length. Accumulative R:S ratios in inoculated plants were significantly smaller than those in controls in all nematode treatments but not at individual harvest dates. Bud break was delayed by *X. index* and was initiated earlier by *P. vulnus* and *M. incognita*. All buds in nematode treatments were less vigorous than in controls.

**Key words:** French Colombard grape, *Meloidogyne incognita*, *Pratylenchus vulnus*, Rubired grape, *Tylenchulus semipenetrans*, *Vitis vinifera*, *Xiphinema index*.

Several plant-parasitic nematode genera are commonly found associated with grapes in California. Four of the most important are *Meloidogyne*, *Pratylenchus*, *Tylenchulus*, and *Xiphinema* (10,16,17). *Meloidogyne incognita* (Kofoid and White) Chitwood and *Pratylenchus vulnus* Allen and Jensen are associated with premature decline of vineyards and subsequent replant problems in the field (5,10,14,20). *Xiphinema index* Thorne and Allen, in addition to serving as a virus vector (4) in some growing areas, produces pronounced symptoms of malformation and necrosis of root tips (3,7,12,15). *Tylenchulus semipenetrans* Cobb is found in California vineyards, although little is known about its effect on fruit production (17).

Frequently, evidence of pathogenicity has been based upon the association of high numbers of nematodes with declining

plants, reduction in root and top weights, root symptoms caused by the nematodes, and yield increase after chemical treatment of nematode-infested soils (12,13,16). Good quantitative growth data characterizing the effects of nematode stress on the root-shoot equilibrium is lacking.

The purpose of this study was to compare the effects of feeding by nematodes that invade grape root-tip cortical and vascular tissues on the different plant growth parameters often used to characterize the root-shoot equilibrium.

### MATERIALS AND METHODS

Two commercial grape cultivars were chosen on the basis of their field stress response to *Meloidogyne* infection. Rubired is more tolerant in the field than French Colombard (McKenry, pers. comm.). Single bud cuttings of grapes (*Vitis vinifera* Linnaeus cv. French Colombard and cv. Rubired) were obtained from virus-free plants. They were rooted in steam-sterilized sand in plastic tubes (2.5 cm d × 7.5 cm long) embedded in a moist sand bed. After 2 months, 50 French Colombard and 35 Rubired plants were selected on the basis of top and root uniformity and transferred to 15-cm-d clay pots containing 2,000 cm<sup>3</sup> steam-sterilized loamy sand (85.6% sand,

Received for publication 22 January 1988.

<sup>1</sup> This paper represents a portion of the dissertation submitted by the first author in partial fulfillment of the requirement for the Ph.D. degree at the University of California at Riverside.

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The authors thank Leann Gudmundson, Marc Monson, and Betty Pennington for help in collecting data and preparing it for publication.

13.5% silt, 0.9% clay). The plants were grown in a greenhouse and were fertilized twice (18.5 g/pot each time) with a slow release fertilizer (N 18%, P 6%, K 12%).

*Pratylenchus vulnus* from walnut (*Juglans* spp.) was increased on French Colombar plants in a greenhouse. Virus-free *X. index* was maintained on fig (*Ficus carica* Linn) for 4 years in a greenhouse. *Meloidogyne incognita* was reared on tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) roots in a greenhouse. Eggs of *M. incognita* were recovered by the NaOCl method (6). *Tylenchulus semipenetrans* juveniles were collected from roots of field grown citrus trees. The soil was infested by pipetting the suspension of adults, juveniles, and eggs into two holes in each pot. The holes were then filled with sterile loamy sand.

The experiment consisted of five treatments with 10 replications for French Colombar and 7 for Rubired. Treatments were 1) check, no nematodes; 2) *P. vulnus*, Pi = 1,000/pot; 3) *M. incognita*, Pi = 1,000/pot; 4) *T. semipenetrans*, Pi = 10,000/pot; and 5) *X. index*, Pi = 500/pot. The pots were completely randomized on a greenhouse bench at a temperature of  $24 \pm 5$  C.

Plants were inoculated on 15 October, grown for 75 days, cut back to two buds, and allowed to go into dormancy for 2 months in an outdoor lathhouse with a temperature range of 6.5 to 18.4 C. Vines were placed back in a greenhouse on 1 March and allowed to grow for 125 days. The tops were harvested above the second internode and another bud allowed to grow another 100 days until the experiment was terminated 360 days from planting.

Leaf area was determined with an area meter (LI-3100, Li-Cor, Lincoln, NE) at harvest. Fresh shoot weight was recorded immediately after harvest and dry weights after drying for 96 hours at 55 C. Stem diameters of the second stem internode from the bottom, the middle internode, and the second internode from the shoot tip were measured with a caliper at final harvest. The time required for buds to break and initiate growth was used to mea-

sure the effectiveness of the individual treatments. The terminal node in each plant was used to compare the number of days to bud break, since this node broke in nearly all plants.

All root parameters were determined at final harvest. Roots were washed free of sand particles, and each root system was divided into four equal parts. One part was oven dried at 55 C and weighed, and the other three parts were used to determine root length, root absorbent area, and number of endoparasitic nematodes. Root length was measured by a combination of two methods (19,21). The roots were spread in a thin layer of water in a clear plastic dish (37 × 30 × 2 cm) and superimposed on 2-cm grid squares. The roots traversing the horizontal and vertical lines were counted systematically; scores of one were given to a root crossing a line, a root-end touching a line, or a curved portion touching a line. A score of two was given to portions lying on or immediately alongside a line. Scores were converted to length by the modified formula of Marsh (9). The root absorbent (dead + living) and active living areas were measured by the methylene blue method (8).

Except for *X. index*, nematode densities in soil were obtained after mixing the soil from each pot by placing two 50-cm<sup>3</sup> subsamples on Baermann funnels for 72 hours. In the *X. index* treatments, 250 cm<sup>3</sup> mixed soil was processed by the Cobb wet seiving technique using 250- $\mu$ m-pore (60-mesh) and 74- $\mu$ m-pore (200-mesh) sieves. Total number of nematodes per pot was estimated based on soil volume. One-fourth of the root system was chopped finely in a blender, and a 5-g subsample was extracted in a mist chamber for 7 days. Nematode counts were made every 3 days, and total numbers of endoparasitic nematodes in root were calculated.

## RESULTS

*French Colombar vegetative growth:* Plant-parasitic nematodes did not cause reductions in vegetative growth during the first 75 days. Following dormancy significant top

TABLE 1. Shoot length, leaf area, and shoot dry weight of French Colombard (FC) and Rubired (RR) grapes inoculated with four species of nematodes.

Nematode	256 DAI†		360 DAI		Total	
	FC	RR	FC	RR	FC	RR
	Shoot length (cm)					
None	105 a	127 a	156 a	139 a	285 a	294 a
<i>M. incognita</i>	85 b	97 b	84 b	128 ab	191 b	257 ab
<i>X. index</i>	79 bc	92 b	79 b	109 b	180 b	218 b
<i>P. vulnus</i>	65 c	69 c	97 b	130 ab	182 b	232 b
<i>T. semipenetrans</i>	95 ab	104 b	152 a	148 a	275 a	279 a
	Leaf area (cm <sup>2</sup> )					
None	2,425 a	3,301 a	3,046 a	3,376 ab	6,077 a	7,517 a
<i>M. incognita</i>	2,171 ab	2,395 bc	1,907 b	3,015 ab	4,592 b	6,374 bc
<i>X. index</i>	1,777 b	2,299 bc	1,913 b	2,720 c	4,207 b	5,508 c
<i>P. vulnus</i>	1,326 c	1,675 c	2,228 b	3,020 bc	3,943 b	5,495 c
<i>T. semipenetrans</i>	2,103 ab	2,489 b	3,105 a	3,635 a	5,798 a	6,865 ab
	Shoot dry weight					
None	20.0 a	26.9 a	29.3 a	25.6 a	53.7 a	56.1 a
<i>M. incognita</i>	13.9 b	17.2 b	10.9 c	18.6 ab	27.6 b	39.9 b
<i>X. index</i>	11.3 bc	15.3 bc	10.0 c	14.7 b	24.1 b	32.6 b
<i>P. vulnus</i>	9.2 c	10.6 c	16.2 b	19.6 ab	27.6 b	34.2 b
<i>T. semipenetrans</i>	18.8 a	20.7 ab	28.1 a	27.8 a	50.4 a	51.9 a

Figures followed by the same letter within a column are not significantly different ( $P = 0.05$ ) according to Duncan's multiple-range test.

Number of replications: French Colombard = 10; Rubired = 7.

† Days after inoculation.

growth reduction occurred during the second regrowth period (256 days after inoculation). *Meloidogyne incognita*, *P. vulnus*, and *X. index* significantly reduced shoot length (Table 1). Reductions in shoot length by *Meloidogyne incognita*, *P. vulnus*, and *X. index* were not significantly different during this regrowth cycle. *Pratylenchus vulnus* and *X. index* significantly reduced the leaf area, whereas *M. incognita* and *T. semipenetrans* did not. *Pratylenchus vulnus* suppressed leaf area more than did *X. index* (Table 1). *Meloidogyne incognita*, *P. vulnus*, and *X. index* significantly lowered shoot dry weight. *Pratylenchus vulnus* reduced shoot dry weight by 50%. The reduction in shoot dry weight by *X. index* was intermediate between *P. vulnus* and *M. incognita*, but they were not significantly different (Table 1).

After the third regrowth cycle (360 days), *M. incognita*, *P. vulnus*, and *X. index* had significantly lower shoot length, leaf area, and shoot dry weight than the check (Table 1). *Tylenchulus semipenetrans* did not affect any growth parameters during the third regrowth cycle. Circumference of the sec-

ond internode from the stem bottom was significantly smaller at final harvest of plants inoculated with *M. incognita*, *P. vulnus*, and *X. index* (Table 2). *Tylenchulus semipenetrans* did not reduce the circumference of this internode. The middle internode was reduced by *P. vulnus* and *X. index*, and the upper internode by *X. index* only (Table 2).

The number of days to bud break after dormancy was variable and not affected by the nematodes in the second growth cycle; however, in the third growth cycle, *X. index* delayed bud break by 3 days, compared with the control plants. Bud break on plants inoculated with *M. incognita* and *P. vulnus* occurred 3 or 4 days earlier than in the control plants.

*Rubired vegetative growth:* There was no significant effect of nematodes on plant top growth during the first 75 days of growth. Shoot length and leaf area were substantially reduced by all nematode treatments during the second regrowth cycle (Table 1). *Tylenchulus semipenetrans*-infected plants did not have lower shoot dry weight (Table

TABLE 2. Stem circumference of French Colombard (FC) and Rubired (RR) grapes 360 days after inoculation with four species of nematodes.

Nematode	Bottom		Middle		Top	
	FC	RR	FC	RR	FC	RR
	Stem circumference					
None	2.18 a	2.02 a	1.77 a	1.54 a	0.81 a	0.81 a
<i>M. incognita</i>	1.60 b	1.81 ab	1.60 ab	1.36 ab	0.68 ab	0.69 a
<i>X. index</i>	1.70 b	1.63 b	1.31 c	1.18 b	0.62 b	0.78 a
<i>P. vulnus</i>	1.73 b	1.55 b	1.43 bc	1.34 ab	0.66 ab	0.72 a
<i>T. semipenetrans</i>	2.06 a	2.07 a	1.76 a	1.46 a	0.77 ab	0.65 a

Figures followed by the same letter within a column are not significantly different ( $P = 0.05$ ) according to Duncan's multiple-range test.

Bottom measurements were taken on the second internode from the ground, middle from the middle, and top from the second internode from the growing top.

1). *Pratylenchus vulnus* reduced the leaf area more than did *T. semipenetrans* but not more than *M. incognita* and *X. index* (Table 1). *Pratylenchus vulnus*, *X. index*, and *M. incognita* caused lower shoot dry weights (Table 1). During the third regrowth cycle, the shoot length, leaf area, and dry weight were significantly reduced by *X. index* only (Table 1). *X. index* significantly reduced the stem circumference at the bottom and middle internodes; however, the differences were not significantly greater than with *M. incognita* and *P. vulnus* (Table 2). *Pratylenchus vulnus* significantly reduced the circumference of the bottom internode only. The circumference of the upper internode was not affected by any nematode treatment.

The number of days to bud break after dormancy was variable and not significantly different among treatments in Rubired on the second growth cycle. Bud appearance on *P. vulnus*-inoculated Rubired plants was about 4 days earlier than on

control during the third growth cycle (Table 3). Other nematode treatments were not different from the control.

*French Colombard root growth:* Root dry weight and total root absorbent and active areas were significantly reduced by *M. incognita*, *P. vulnus*, and *X. index* but not by *T. semipenetrans* (Table 4). Roots of plants inoculated with *M. incognita* were significantly heavier than those of plants inoculated with *P. vulnus* and *X. index*. None of the nematode treatments were significantly different from each other in absorbent and active root areas. Root length was significantly reduced by all the nematodes. Plants inoculated with *M. incognita* and *P. vulnus* had lower root lengths than those infected with *T. semipenetrans*.

*Rubired root growth:* Root dry weight and total length were significantly reduced by all the nematode treatments, but differences among nematode treatments were not significant (Table 4). Total absorbent and active root areas were not significantly

TABLE 3. Number of days to bud break of French Colombard and Rubired grapes inoculated with four species of nematodes.

Treatments	French Colombard		Rubired	
	2nd growth cycle	3rd growth cycle	2nd growth cycle	3rd growth cycle
Check	18.60 a	15.70 b	12.14 a	15.28 a
<i>M. incognita</i>	9.90 a	12.50 c	7.75 a	16.25 a
<i>X. index</i>	14.60 a	18.60 a	12.43 a	16.00 a
<i>P. vulnus</i>	11.20 a	11.80 c	4.71 a	12.00 b
<i>T. semipenetrans</i>	15.60 a	16.40 ab	9.00 a	16.14 ab

Figures followed by the same letter within a column are not significantly different ( $P = 0.05$ ) according to Duncan's multiple-range test.

TABLE 4. Root growth of French Colombard (FC) and Rubired (RR) grapes 360 days after inoculation with four species of nematodes.

Treatments	Dry weight (g)		Length (cm)		Absorbent area† (m <sup>2</sup> )		Active area‡ (m <sup>2</sup> )	
	FC	RR	FC	RR	FC	RR	FC	RR
None	46.7 a	58.3 a	15,428 a	26,430 c	210 a	292 a	105 a	136 a
<i>M. incognita</i>	31.6 b	37.4 b	5,990 c	17,203 b	139 a	264 a	68 b	106 ab
<i>X. index</i>	18.9 c	29.4 b	8,237 bc	14,879 b	135 b	193 b	58 b	83 bc
<i>P. vulnus</i>	18.8 c	28.2 b	5,983 c	17,603 b	128 b	187 b	58 b	58 c
<i>T. semipenetrans</i>	45.9 a	38.5 b	10,088 b	16,778 b	171 ab	155 b	79 ab	65 c

Figures followed by the same letter within a column are not significantly different ( $P = 0.05$ ) according to Duncan's multiple-range test.

† Dead and living area as measured by staining with methylene blue.

‡ Living area only.

reduced by *M. incognita*, but *P. vulnus*, *T. semipenetrans*, and *Xiphinema index* greatly reduced the total absorbent and active areas compared with the control. Differences were not significant among these three nematode treatments.

*Root: shoot ratio:* The root length to third growth cycle leaf area ratio was significantly reduced by all nematodes on French Colombard and Rubired plants (Table 5). The root length to total leaf area ratio was reduced by *M. incognita*, *P. vulnus*, and *T. semipenetrans* on French Colombard and by *T. semipenetrans* on Rubired plants (Table 5).

*Nematode population:* The Pf of *M. incognita* and *P. vulnus* was 312 and 128 times greater than the Pi on French Colombard and 326 and 72 times greater than the Pi on Rubired. There were more individuals

of *M. incognita* and *P. vulnus* in soil of Rubired than that of French Colombard. A 1-cm piece of French Colombard root produced about four and nine times more *M. incognita* (second-stage juveniles) and *P. vulnus* (all stages), respectively, than on Rubired. *Xiphinema index* reproduced equally well on both cultivars. The Pf of juveniles of *T. semipenetrans* per centimeter of root of Rubired was about 1.5 times more than on French Colombard (Table 6).

## DISCUSSION

Roots and shoots are mutually dependent upon each other for exchanging nutrients, carbohydrates, and growth substances and are physiologically in equilibrium (22). Presumably, any stress factor(s) affecting one organ will affect the growth of the other to bring the plant back into equilibrium. If the stress of either becomes too severe or too prolonged, the normal root: shoot balance will be altered and the plant will become physiologically unbalanced (1) and may exhibit severe plant stress and yield reductions. Root-feeding nematodes provide a biological model system for testing these physiological concepts as well as for obtaining more information on the dynamics of host-parasite relations. Studies such as this have not been attempted previously because of the difficulty in measuring all of the growth parameters.

This model system employed two varieties of grape with different field reactions to nematode stress and four nematodes—a root tip feeder, a vascular feeder, and

TABLE 5. Root: shoot (R:S) ratios of Rubired and French Colombard grapes 360 days after inoculation with four species of nematodes.

Nematode	R:S for Rubired		R:S for French Colombard	
	Third growth cycle†	Total‡	Third growth cycle†	Total‡
None	7.8 a	3.5 a	5.1 a	2.5 a
<i>M. incognita</i>	5.7 b	2.7 a	3.2 b	1.3 b
<i>X. index</i>	5.4 b	2.7 a	3.2 b	1.9 ab
<i>P. vulnus</i>	5.8 b	3.2 a	2.7 b	1.5 b
<i>T. semipenetrans</i>	5.7 b	2.4 b	3.1 b	1.7 b

Figures followed by the same letter within a column are not significantly different ( $P = 0.05$ ) according to Duncan's multiple-range test.

† Root length/leaf area of third growth cycle.

‡ Root length/total leaf area.

TABLE 6. Nematode population levels on Rubired and French Colombard grapes 360 days after inoculation.

Treatment	Final population		Root fresh weight (g)	Nematodes/g root	Nematodes/cm root	Nematodes/50 cm <sup>3</sup> soil
	Root	Soil				
Rubired (7 replications)						
<i>M. incognita</i>	109,807	216,320	187.5	586	6	5,408
<i>X. index</i>		2,234	151.7			56
<i>P. vulnus</i>	47,950	24,800	135.1	355	3	620
<i>T. semipenetrans</i>	44,126	27,314	148.7	297	3	683
French Colombard (10 replications)						
<i>M. incognita</i>	140,515	172,480	140.6	1,000	23	4,312
<i>X. index</i>		2,913	148.4			55
<i>P. vulnus</i>	114,026	14,560	82.6	1,381	19	364
<i>T. semipenetrans</i>	19,074	31,520	113.0	169	2	788

two cortical feeders. During the initial 75 days of growth, the nematodes did not stress the top growth of either cultivar. After the top was pruned and the root went through a period of dormancy, all of the nematodes exerted sufficient stress to reduce growth of the root system and the top. The reduced rate of top growth after a second pruning suggests that the combined stresses greatly inhibited growth. French Colombard was stressed more than Rubired, which agrees with previous field observations (McKenry, pers. comm.). *Tylenchulus semipenetrans*, a cortical feeder and normally a pest of citrus, did not sufficiently stress French Colombard or Rubired grapes to significantly reduce the top growth of either, even though it significantly reduced root growth in both.

A comparison of reduction in accumulated shoot dry weight, shoot length, leaf area, root dry weight, root length, root surface area, and root active area by *M. incognita*, *P. vulnus*, and *X. index* indicates the nematode stress applied was the same from vascular, cortical, and root tip feeders. The reduction in all growth parameters was greater in French Colombard than in Rubired. The top growth parameters, leaf area, height, and dry weight were equally indicative of growth reduction. The same was true for the root growth parameters, root length, root weight, and root surface area (total or active).

Richard and Rowe (18) suggested that root length and leaf area were better for

characterizing plant health than dry weights because both represent the site of physiological activities. A measure of the resultant pattern of differential growth of two organs, expressed as the R:S ratio, can provide an index for the performance of each organ and the state of the physiological equilibrium of the plant (1). Root length and leaf area were used for computing R:S ratio. At the termination of the experiment, the R:S ratio of the nematode-inoculated plants of both French Colombard and Rubired was less than the controls (Table 5). All treatments on Rubired had higher R:S ratios than the same treatments on French Colombard, suggesting that Rubired has a much stronger root system even in the presence of equal numbers of nematodes (Table 6). The reduced R:S ratios of Rubired were primarily an expression of a reduction in root system without an equal reduction in the top growth. The reduced R:S ratios of French Colombard were due to reductions in both top growth and root growth but greater reduction in root growth than top growth (Table 7). This type of response was accentuated in *T. semipenetrans* treatments where root growth parameters were reduced by about the same percentages as the other three nematodes, but the reduction was not translated into a similar reduction in top growth. If R:S ratios of the total accumulated leaf area and root lengths are compared with R:S ratios of the plants at harvest, the results are similar except that all the ratios are

TABLE 7. Reduction (%) in accumulated top growth and root growth of French Colombard and Rubired grapes by four nematodes.

Treatments	Leaf area	Plant height	Shoot weight	Root length	Root weight	Root area	
						Total	Active
French Colombard (10 replications)							
<i>M. incognita</i>	24	33	49	61	32	36	37
<i>X. index</i>	31	37	55	47	59	36	45
<i>P. vulnus</i>	35	36	48	61	60	39	44
<i>T. semipenetrans</i>	4	4	6	35	2	19	25
Rubired (7 replications)							
<i>M. incognita</i>	15	13	29	35	36	10	22
<i>X. index</i>	27	25	42	44	49	34	39
<i>P. vulnus</i>	27	21	39	33	51	36	57
<i>T. semipenetrans</i>	9	5	7	36	34	47	52

numerically lower in value. These data suggest that continued parasitism and (or) feeding of nematodes on plant roots cause a significant shift in the R:S equilibrium. It would appear that this shift in R:S ratios is more physiological than mechanical in nature.

Since the top growth appears to be uncoupled from root growth in tolerant Rubired cultivar and in the *T. semipenetrans* treatments of both cultivars, the exchange of growth substances may be more important than water, nutrients, and carbohydrates. Kirkpatrick et al. (7) also suggested that *X. index* altered the auxin relationship within the Carignane cultivar. Observations on bud regrowth, which is regulated by the hormones (23), would support this observation. The uncoupling of the R:S balance may also be directly related to carbohydrate partitioning (2). In nematode-infected plants, carbohydrates produced by the leaves apparently are not fully utilized or stored by the reduced root system, and any excess continues to be recycled into top growth shifting the R:S balance in favor of the shoot and starvation of the root system. Although no data were obtained on fruit production, it seems reasonable to extrapolate that an added stress from fruit production could not be compensated for by foliar production alone; this may explain why nematode damage is usually more severe in the field than in the greenhouse.

Grape plants clearly could lose some roots without showing a significant reduction in

top growth, as was shown for corn (20) and sugarbeets (11). This was particularly true for *T. semipenetrans* on both cultivars. Compared with *P. vulnus*, another cortical feeder, *T. semipenetrans* had less effect on top growth. The difference in nematodes may have been reflected as a quality factor rather than a quantity factor. *Pratylenchus vulnus*, because of its migratory nature, is known to destroy numerous cortical cells and produce necrosis in roots, whereas *T. semipenetrans* produces discrete feeding sites with less necrosis in the cortex.

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