Growth responses in oilseed rape (*Brassica napus* L.) to combined applications of the triazole chemicals triapenthenol and tebuconazole and interactions with gibberellin

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Abstract

Crop height in the oilseed rape cv. Ariana was reduced more by the triazole retardant triapenthenol at $490 \text{ g ai } \text{ha}^{-1}$, applied as a combined spray with the triazole fungicide tebuconazole at $250 \text{ g ai } \text{ha}^{-1}$, than when triapenthenol was applied alone. The growth responses following combined treatment appeared to be additive of the component effects.

Initial inhibition of stem extension and leaf expansion by tebuconazole was followed by compensatory growth; the pattern of responses was similar to that with triapenthenol applied at approximately one tenth of the rate. However, different mechanisms of effects on growth were indicated by competitive interaction with gibberellic acid.

1. Introduction

The inhibition of stem and leaf growth by plant growth retardants can alter the canopy architecture of oilseed rape and improve production efficiency [2]. The triazole derivative triapenthenol is particularly effective and reduces stem and raceme extension, and leaf expansion, for three to four weeks, resulting in a shorter, erect plant and a more open canopy, with increased light penetration and more even pod distribution.

Triapenthenol consists of a racemic mixture of two enantiomers, both of which show retardant activity in the separated form and fungicidal activity with one form [9]. The mechanism of growth control by triazoles is attributed mainly to inhibition of gibberellin (GA) biosynthesis at the stage of conversion of *ent*-kaurenc and *ent*-kaurenoic acid, which leads to a reduction of active GAs in treated plants [4, 10]. However, the effect of triapenthenol on growth cannot be compensated fully by the addition of gibberellic acid and a further mechanism is assumed to be involved, which has been attributed to reduced stomatal opening and less water consumption [6]. Triapenthenol has been shown to reduce the rate of photosynthesis by decreasing stomatal conductance [1]; although dry matter is consequently reduced, partitioning is not significantly affected [3].

Certain triazole chemicals have fungicidal activity due to their ability to inhibit sterol biosynthesis in fungi. However, distinct changes in sterol content in plants are generally detected only at the high concentrations of applied chemicals used for disease control [5] and they may not significantly influence growth.

Tebuconazole is a racemic mixture of two triazole enantiomers, both of which show strong fungicidal activity. It is a potent fungicide, with a wide spectrum of activity [11], and is used in oilseed rape at the rate of 250 g ai ha⁻¹ at a spray volume of 2501ha⁻¹ to control light leaf spot (*Pyrenopeziza brassicae*), Alternaria leaf and pod spot (*Alternaria brassicae*) and *Phoma* canker (*Phoma lingham*). Slight reductions in the height of crops following treatment with tebuconazole have been reported [13] but the mechanism of this effect is unclear.

During the course of field trials with oilseed rape it was noticed that the growth retarding effect of triapenthenol appeared to be greater when the fungicide tebuconazole was also applied in the spray (T.J. Martin, personal communication). The experiments reported in this paper were designed to investigate the nature and mechanism of the apparent synergistic effect of triapenthenol and tebuconazole on growth in oilseed rape.

2. Materials and methods

2.1 Field experiment with winter oilseed rape

Seed of cv. Ariana was precision-sown with a Stanhay drill, on 3 September, 1988, at a density of 109 seeds m^{-2} , in rows 15 cm apart. Top dressings of a total of 130 kg nitrogen ha⁻¹ were applied in March, 1989. The triapenthenol formulation UK244a (RSW 0411 70 WG), which has been developed for field trials at a rate of 490 g ai ha⁻¹ by Bayer UK, was applied with a Chesterfield Mini-Log Sprayer. The rate of application was 1000 gai ha^{-1} at the beginning of the plot, which reduced to 100 gai ha⁻¹ after 18 m, whilst maintaining a spray volume of 2501 ha⁻¹. The tebuconazole formulation UK200g (HWG 1608 250EC) was applied with an Oxford Precision sprayer at 260 gai ha^{-1} in 2501 water. Each of the triazole treatments was applied alone, or in the combination triapenthenol, followed by tebuconazole on 7 March when the plants were approximately 15 cm tall and had produced 10 leaves, or on 12 April, when stem height was approximately 80 cm, all leaves on the stem had been produced and racemes were beginning to extend. Treatments were applied to 2×24 m plots, which were laid out in a randomised block design including unsprayed control plots, with four complete blocks. Protectant sprays of the fungicide iprodione and the insecticide cypermetherin were applied in March, after the first triazole treatments had been applied. At three metre intervals along the plot the heights of eight labelled plants were measured at weekly intervals until extension growth and flowering had stopped in late May. Variation in the vigour of individual plants in this cultivar was very large and although selected for uniformity before treatment, they subsequently showed large differences in growth. Therefore, the effects of rate of application were difficult to determine and data from within a treatment plot were pooled to show the overall effects of single or combined triazole treatments. At maturity, 10 plants were harvested from control and tebuconazole-treated plots and from areas of maximum and minimum application of triapenthenol (1000 or 100 gai ha⁻¹). Stems and racemes were measured and total plant and seed dry weights were recorded after drying in an oven at 70 °C for 48 h.

2.2 Glasshouse experiments

Selection for uniformity of stem and raceme growth was more reliable with pot-grown plants, under glass, than in the field-drilled crop. Seeds of the spring-sown cultivar Fido were sieved to collect the fraction 1.7-2.0 mm diameter and each seed was sown in a module containing 10 cm^3 compost.

Plants were grown in a glasshouse maintained at a minimum day temperature of 18 °C for 16 h and night-time temperature of 14 °C. High pressure sodium lamps maintained a minimum illumination of 300W m⁻² for 15 h. After ten days, when plants had produced one leaf, they were potted into 700 cm³ compost which contained slowrelease fertiliser granules.

After a further seven days, when the plants had developed three leaves, they were again selected for size-uniformity and treatments were applied with a 'track' sprayer at spray volumes equivalent to the field rate of application $(2501 ha^{-1})$. Triapenthenol, tebuconazole or gibberellic acid ('Berelex') were applied alone, or in combination at rates given later in the text. After spraying, the pots were returned to benches in the glasshouse. The sprayed plants, together with untreated controls, were randomised in eight blocks. The number of plants per block varied with treatment and is indicated in the Results section. One plant from each treatment in each block was harvested at intervals until extension growth had stopped seven to eight weeks later. Stem lengths were measured, individual leaf areas were recorded with a Delta T area meter and plants were dried in an oven at 70 °C for 48 h before being weighed.

2.3 Identification of gibberellins in tissue extracts

Plants were sprayed with triapenthenol or tebuconazole alone or in combination at the one or two leaf stage. GAs in the shoots were determined ten days later according to the method of Hedden *et al.* [7].

3. Results

3.1 Growth of plants in a crop of winter oilseed rape cv. Ariana

Growth continued for eleven weeks after spraying on 7 March and crop height was greatly reduced by triapenthenol applied alone, or in combination with tebuconazole which applied alone did not significantly affect growth (data not presented). Triapenthenol reduced plant heights by 55%, four weeks after treatment (Fig. 1), but by the end of stem extension, after a further six weeks, the difference had declined to approximately 40%. In the combined treatment corresponding values were 63% and 48%, respectively.

Analysis of plant structure at maturity confirmed the overall effects of triapenthenol applied alone, or in combination with tebuconazole, and showed that application of tebuconazole on 12 April did not affect further the response of plants treated with triapenthenol on 7 March. Triapenthenol sprayed alone on 12 April, or in combination with tebuconazole, reduced plant height only by approximately 7% (Table 1). In addition, these records showed that although terminal raceme lengths were unaffected by early treatment with triapenthenol, significant increases were recorded in plants treated only with tebuconazole at this time. The application of triapenthenol on 12 April reduced the length of the terminal raceme and combined treatment with tebuconazole resulted in further shortening. It was observed that in all the treatments applied at early stem extension on 7 March, axillary raceme growth continued after terminal raceme growth had stopped. This tended to compensate for earlier growth retardation and no significant effects of treatments on total raceme growth were recorded at maturity. These changes in structure were accompanied by a reduction in seed weight, from 9.80 to 8.22 g per plant

(SED = 0.641; 15df) by early triapenthenol treatments, but an increase in harvest index from 31.21 to 35.72 (SED = 1.035; 15df). Tebuconazole, which alone only affected plant structure marginally, significantly increased seed yield from 7.65 to 9.15 g per plant (SED = 0.641; 15df) and increased harvest index from 31.29 to 33.33 (SED = 0.861; 15df). Combined applications of triapenthenol and tebuconazole had affects on seed yield which were intermediate between those where the compounds were applied separately (data not presented). The effects on yield are consistent with results published previously for triapenthenol [2, 3] and for those with tebuconazole which has known fungicidal effects and which were associated with observations of reduced diseased incidence [13].

These results confirmed the field observations of increased retardation where triapenthenol and tebuconazole had been used together and revealed growth regulatory activity by tebuconazole (Martin, personal communication).

3.2 Responses of pot-grown plants of spring oilseed rape cv. Fido

In the glasshouse, early responses to treatments were greater than those recorded in the field experiment. In plants treated with triapenthenol at the standard field rate of $1.96 \text{ g} \text{ l}^{-1} (= 490 \text{ g} \text{ ai}/250 \text{ l}/1)$ ha), stem extension was 64% less than that in the unsprayed plants three weeks after treatment but, by the end of stem extension, this was only 16% less than the controls. In an experiment where four rates of triapenthenol and two of tebuconazole were applied in combination, there were no significant interactions of the two compounds (data not presented); the growth responses due to the compounds applied separately are shown in Table 2. All concentrations of triapenthenol above 0.2 gl^{-1} and tebuconazole at 1 or 2 gl^{-1} affected growth, and stems were significantly shorter than in unsprayed plants one week after application.

The duration and pattern of response to triapenthenol was similar at all rates of application (Fig. 2). Stem extension rate was reduced for three weeks after treatment and then recovered to the same rate as control after a further four to five weeks. This pattern of response was also similar in plants treated with tebuconazole (Fig. 2).



Fig. 1. Growth of winter oilseed rape plants in a crop of cv. Ariana sprayed with triapenthenol alone (+) or in combination with tebuconazole at 250 g ai ha⁻¹ (\diamondsuit) on 7 March, 1989; unsprayed (\blacksquare). Least significant differences (5%) shown by vertical bars. (Data for triapenthenol are the mean of eight measurements per plot treated with a log sprayer).

Combined applications of the two triazole chemicals resulted in reductions in stem lengths, which were additive of the component effects (Fig. 3a,b). Tebuconazole increased responses by a similar amount at all rates of triapenthenol applied and the effect was greater for tebuconazole at $2 g l^{-1}$ than at $l g l^{-1}$. Up to four weeks after treatment the responses to triapenthenol were well described by parallel exponential curves for the different treatments, with only the intercepts different (Fig. 3a), i.e. $y = A + Be^{-kx}$ where y is the stem length, x the triapenthenol dose and only A differs

Table 1. Modification of responses to triapenthenol by tebuconazole in a crop of winter oilseed rape cv. Ariana. Effects of plant height and raceme growth (cm) at maturity on 7 July, 1989

		Triapenthenol (g ai ha ⁻¹)		Tebuconazole $(250 \text{ g ai } \text{ha}^{-1})$		SED
	Timing		0	7 March	12 April	
Plant	- 0	0	142.3	145.1	144.5	5.73 (21 df)
height	7 March	100	102.2	86.4*	96.0	5.73 (21 df)
	7 March	1000	89.4	74.3*	71.8*	5.73 (21 df)
	12 April	100	127.4	131.4	130.2	5.73 (21 df)
	12 April	1000	124.6	123.4	122.5	5.73 (21 df)
Terminal		0	38.0	44.5*	38.3	1.32 (21 df)
raceme	7 March	100	40.3	42.7*	37.4	1.87 (21 df)
length	7 March	1000	39.3	36.2	32.8**	1.87 (21 df)
	12 April	100	34.6	37.5	31.2	1.87 (21 df)
	12 April	1000	29.7	31.9	25.9*	1.87 (21 df)
Total	_	0	263.1	233.0	261.4	20.90 (21 df)
raceme	7 March	100	271.4	270.7	267.7	29.60 (21 df)
length	7 March	1000	222.9	225.3	199.3	29.60 (21 df)
	12 April	100	222.6	224.5	257.8	29.60 (21 df)
	12 April	1000	209.5	222.4	192.7	29.60 (21 df)

*, ** indicates significant differences at < 0.05, 0.01, respectively, comparing traipenthenol with combined treatments (i.e. across rows).



Fig. 2. Growth rate (mm/day) as % of unsprayed (\blacksquare) in pot-grown plants of spring oilseed rape cv. Fido treated with triapenthenol at 0.08 (+), 0.84 (\diamondsuit), 1.96 gl⁻¹ (\triangle), or tebuconazole at 1.0 g ai (×) or 2.0 g ai l⁻¹ (\bigtriangledown). Least significant differences (5%) between any two treatments shown as vertical bars.

between different tebuconazole levels. However, by seven weeks these responses had become close to linear (Fig. 3b).

Significant reductions in individual leaf areas were recorded within one week of treatments with triapenthenol at 1.96 gl^{-1} , or tebuconazole at

 1 gl^{-1} , applied alone or in combination (Fig. 4). Leaves present at nodes one and two at the time of spraying, failed to expand further in all treatments and abscinded by the time data were collected seven weeks after spraying. In plants sprayed with triapenthenol alone or in combina-

Table 2. Stem lengths (cm) of spring oilseed rape cv. Fido sprayed with triapenthenol or tebuconazole at the beginning of stem extension (3 leaf stage) in the glasshouse

Rate of application	Weeks after spraying								
(g1 ⁻)	1	2	3	4	5	6	7		
Triapenthenol							······		
0	3.1	7.6	21.3	67.2	104.4	125.7	143.4		
0.08	2.9	7.0*	19.7	62.9	102.5	124.8	143.4		
0.20	2.9	6.9*	20.6	62.2	102.0	124.0	141.9		
0.28	2.7***	6.2***	16.9***	56.9**	101.5	125.3	145.6		
0.84	2.3***	4.9***	12.5***	45.2***	90.9***	113.4***	132.2**		
1.96	2.1***	3.8***	7.8***	31.2***	75.4***	99.2***	117.0***		
SED (153 df)	0.10	0.30	1.26	3.26	2.35	2.51	3.01		
Tebuconazole									
0	2.8	6.7	18.7	58.9	99.4	121.4	139.3		
1.0	2.6**	6.1**	16.4*	54.2*	95.3*	118.2	137.2		
2.0	2.5***	5.5***	14.3***	49.7***	93.6***	116.7**	135.2		
SED (153 df)	0.07	0.21	0.89	2.31	1.66	1.78	2.13		

*, **, or *** indicates significant difference from control (unsprayed) at p < 0.05, 0.01 or 0.001, respectively.



Fig. 3. Modification of the effects on stem length (mm) of triapenthenol applied at different rates (\blacksquare) by tebuconazole at 1.0 g ai 1^{-1} (+) or 2.0 g ai 1^{-1} (\diamondsuit), four weeks (a) or seven weeks (b) after spraying pot-grown plants of spring oilseed rape cv. Fido.

tion with tebuconazole, leaf area was reduced at nodes three to six and compensatory increases in area took place in leaves that were produced subsequently.

The net effects of changes in individual leaf size was, for triapenthenol applications, a significant reduction in total leaf area compared with untreated plants, until four weeks after treatment (Table 3). The compensatory growth in leaves above node seven (Fig. 4) increased total leaf area significantly by the end of stem extension, six weeks after treatment (Table 3). Combined treatment effects on total leaf area were similar to those when triapenthenol was applied alone. The



Fig. 4. Effects of triapenthenol at 1.96 g ai 1^{-1} (+), tebuconazole at 1.0 g ai 1^{-1} (\diamond) or combined treatment (\triangle) compared with unsprayed control (\blacksquare), on individual leaf areas one week (inset) or seven weeks (main graph) after treatment, in spring oilseed rape cv. Fido. Least significant differences (5%) between any two treatments shown by vertical lines for specified leaves, numbered from the base of the stems.

Table 3. Total leaf area (cm^2) produced by pot-grown plants of cv. Fido treated with triapenthenol at 1.96 gl^{-1} or tebuconazole at 1 gl^{-1} alone, or in combination at three-leaf stage

	Weeks after treatment						
	1	3	4	5	6		
Unsprayed	62.6	345.9	392.3	399.8	409.8		
Triapenthenol	42.8***	278.1***	342.2*	401.2	471.0*		
Tebuconazole	48.1**	348.9	394.4	448.3*	382.0		
Triapenthenol+ tebuconazole	37.1***	260.1***	322.6**	423.8	484.0*		
SED (21df)	4.90	10.38	19.33	18.03	28.90		

*, **, or *** indicates significant difference from control at p < 0.05, 0.01 or 0.001, respectively.

reductions in individual leaf areas recorded one week after treatment with tebuconazole alone resulted in significant reductions in total leaf area, but subsequent increases in later-formed leaves were sufficient to increase total leaf areas five weeks after application.

Total plant dry weight was significantly reduced by triapenthenol throughout the growing period (Table 4). This was influenced primarily by the consistent, large reductions in stem weight, but was counteracted during the later stages of stem extension by significant increases in leaf weight, which corresponded with the increases in individual leaf areas described above. The smaller but significant increases in leaf area caused by tebuconazole apparently resulted in corresponding small increases in dry weight, which were significantly greater than those in unsprayed control plants five weeks after treatment. Tebuconazole also reduced stem dry weight for up to four weeks after treatment. Combined applications appeared to reduce component and total dry weights more than individual triazole treatments and an additive effect was indicated.

Competitive interactions of retardants with applied growth-promoting hormones have been used to investigate the endogenous mechanisms involved in the inhibition of stem extension [8]. In this present work, rates of each triazole which inhibited stem extension by similar amounts were determined in preliminary experiments. Interactions with GA indicated that different mechanisms, resulting in growth inhibition were involved for each triazole chemical (Fig. 5). Combined treatment of GA ('Benelex') at rates between 10- 300 mg l^{-1} with tebuconazole gave a growth response equal to that when GA was applied alone. Combined treatment of GA with triapenthenol, only partially restored growth to that of plants treated with GA alone, indicating that inhibition by retardant was likely to involve another mechan-

		Weeks after treatment				
		3	4	5	6	
Stem	Unsprayed	0.33	0.96	2.17	3.57	
	Triapenthenol	0.13***	0.33***	0.75***	1.55***	
	Tebuconazole	0.24*	0.83*	1.90	3.38	
	Triapenthenol + tebuconazole	0.11***	0.18***	0.74***	1.79***	
	SED (21df)	0.034	0.061	0.138	0.180	
Leaves	Unsprayed	1.45	1.71	1.66	1.64	
	Triapenthenol	1.25*	1.78	2.17***	2.21**	
	Tebuconazole	1.46	1.73	2.07***	1.60*	
	Triapenthenol + tebuconazole	1.15**	1.63	2.11***	1.94*	
	SED (21df)	0.082	0.156	0.096	0.158	
Total	Unsprayed	1.78	2.66	3.83	5.21	
	Triapenthenol	1.38***	2.11**	2.91***	3.77***	
	Tebuconazole	1.70	2.56	3.98	4.98	
	Triapenthenol + tebuconazole	1.27***	1.82***	2.85***	3.73***	
	SED (21df)	0.097	0.173	0.119	0.201	

Table 4. Effects of triapenthenol at 490 g ai/250 l/ha or tebuconazole at 250 g ai/250 l/ha applied alone or in combination at the three-leaf stage on dry weight (g/plant) accumulation and distribution in oilseed rape cv. Fido

*, **, or *** indicates significant difference from control at p < 0.05, 0.01 or 0.001, respectively.

ism in addition to effects on gibberellin biosynthesis. Combined treatment of GA with triapenthenol/tebuconazole gave a growth response similar to that of the GA controls one week of treatment (Fig. 5a), but by three weeks after treatment the response of the combined triazole and GA application was similar to that of triapenthenol alone (Fig. 5b).

The effects of treatments with triapenthenol applied alone at 175 g ai/250 l/ha, or in combination with tebuconazole at 250 g ai/250 l/ha, on the concentration of endogenous GAs were determined in plants sprayed at the one-two leaf stage. Whole shoots were harvested for GA analysis ten days after treatment. Reductions in the amounts of all the GAs determined, including GA₁ which is known to be the main biologically active GA, relative to the unsprayed controls were recorded for each treatment (Table 5), with triapenthenol having a greater effect than tebuconazole. The combined triapenthenol/tebuconazole treatment resulted in GA concentrations similar to those obtained in plants treated with triapenthenol alone.

4. Discussion

Although no overall effects of tebuconazole on crop height of oilseed rape were recorded in the field experiment, significant increases in the length

of the terminal raceme were shown in maturity. This suggested compensatory growth as a response to earlier retardation which was supported by the effects on stem extension and leaf expansion recorded in the experiments with potgrown plants. Although the magnitude of the initial response was less, the pattern and changes in growth rate were similar to those shown by plants treated with triapenthenol. The effects of plant morphology were indicative of underlying effects on the hormonal complement of the plants, which were confirmed by the reduction in GAs (particularly GA_1 and GA_3) ten days after treatment with each triazole. The growth reduction caused by tebuconazole was completely overcome by the addition of GA, but such an effect was not shown when triapenthenol, a more potent growth retardant, was applied suggesting that inhibition of endogenous gibberellin was not the sole mechanism by which the latter triazole affected growth.

The early reduction in stem dry weight induced by tebuconazole (Table 4) could have been influenced by changes in endogenous GAs which are known to be associated with changes in photosynthetic rate. A close correlation has been found by Stoddart [12] between the level of residual endogenous GAs and the activity of the CO₂fixing enzyme ribulose bisphosphate carboxylase/ oxygenase (RUBISCO) which was depressed in



Fig. 5. Effects of interaction of gibberellic acid (\blacksquare) with triapenthenol at 0.20 gai l^{-1} (+), tebuconazole at 1.0 gai l^{-1} (\diamondsuit) or combined treatments (\triangle) on stem length (mm) in pot-grown plants of spring oilseed rape cv. Fido one week (a) or three weeks (b) after treatment. Least significant difference between any two treatments shown as vertical bars.

dwarf beans by the growth retardant AMO 1618. However, early reductions in dry weight by tebuconazole could involve another mechanism related to effects on stomatal resistance, which has previously been shown to increase in oilseed rape plants treated with triapenthenol [1].

The growth responses following combined treat-

ment with the triazoles appeared to be additive of the component effects. Competitive interaction with GA resulted in complete reversal of the effects on stem extension one week after treatment, soon after which endogenous GA levels were shown, in a separate experiment, to be reduced.

Three weeks after application, GA failed to

Table 5. Effects of triapenthenol (175 gai/250 l/ha) alone or in combination with tebuconazole (250 gai/250 l/ha) applied at the one-two leaf stage on gibberellin concentration (ng/g fresh weight) in the shoots 10 days after spraying

	GA ₈	GA ₁	GA ₃	GA ₂₀	GA29
Untreated	0.21	0.13	0.18	0.45	0.08
Tebuconazole	0.12	0.08	0.07	0.32	0.04
Triapenthenol	0.07	0.06	0.04	0.10	0.04
Triapenthenol+ tebuconazole	0.10	0.06	0.03	0.08	0.06

reverse the effects of triapenthenol, and another growth-inhibiting mechanism related to changes in the rate of photosynthesis and resulting in reduced dry weights, may be involved at this later stage. Other triazoles have been shown to affect abscisic acid (ABA) levels, for example the triazole retardant BAS111..W increased this hormone in oilseed rape seedlings, in which transpiration rate was also reduced [6].

The effects of tebuconazole on crop growth are unlikely to be of practical significance because the magnitude of response is small and the overall effect, after compensatory extension takes place, appears to be difficult to measure. From a practical point of view, the implication of the enhanced response to the combined application of the two triazoles are important to determine, and data indicate that triapenthenol could be used at reduced rates. Changes in canopy structure, due to reduced stem or raceme extension and affects on leaf expansion, would appear to be similar to those caused by triapenthenol alone, which have already been described [2].

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