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GROWTH, ANATOMY AND CHLOROPHYLL FLUORESCENCE OF CORIANDER PLANTS (*CORIANDRUM SATIVUM* L.) TREATED WITH PROHEXADIONE-CALCIUM AND DAMINOZIDE

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This study evaluates the effects of the two gibberellin inhibitors (daminozide, prohexadione-calcium) on certain growth and anatomical characteristics of coriander (*Coriandrum sativum* L.). Both growth retardants were found effective in reducing stem elongation; that response varied with the concentration used. Prohexadione-Ca at 200 mg l^{-1} reduced height by 38%. Coriander fruits were heavier after the application of prohexadione-Ca, but this did not translate to increased fruit yield or fruit essential oil yield. Prohexadione-Ca induced precocious anthesis (3–5 days earlier). Both prohexadione-Ca and daminozide apparently affected leaf and stem anatomy. Generally, retardant-treated plants possessed thicker leaves, wider stems with more collenchyma tissue, and more vessels in the vascular bundles. Chlorophyll fluorescence measurements disclosed a decrease in the photochemical efficiency of PSII in retardant-treated plants as compared to the controls. The chlorophyll fluorescence parameters F_v/F_m and F_v/F_o can provide a tool for early diagnosis of the use of growth retardant even before any signs of growth retardation are visible in the plants.

Key words: *Coriandrum sativum* L., Coriander, prohexadione-Ca, daminozide, growth, anatomy, chlorophyll fluorescence.

INTRODUCTION

Coriander (*Coriandrum sativum* L.) is an aromatic herb, cultivated as a summer or a winter annual crop, depending on the climatic conditions. The traditional uses of coriander plants, based on the primary products (fruits and the green herb) are twofold: medicinal and culinary. The fruits are considered carminative, diuretic, tonic, stomachic, antibilious, refrigerant and aphrodisiac. They are also used as a condiment in the preparation of sausages, seasonings and cookies, and as a flavoring for alcoholic beverages (Diederichsen, 1996). The essential oils of the fruits are rich in linalool (Smallfield et al., 2001) and possess antibacterial (Lo Cantore et al., 2004) and antioxidant activity (Chericoni et al., 2005). The other primary product, the fresh green herb of coriander, also known as cilantro, has a specific flavor, completely different from that of the fruits. The characteristic smell of the green plant is due to the aldehydic content of the essential oil (Deng et al., 2003). Extracts of the green herb have also been found to exhibit antibacterial (Kubo et al., 2004) and antioxidant activity (Melo et al., 2003).

The use of fertilization and irrigation leads to higher yields of coriander (Tomar et al., 1994). The effects of cutting management and different planting dates on the growth and yield of this crop have been examined (Baboo and Rana, 1995; Kalra et al., 2000). The essential oil composition of coriander is affected by some parameters. It has been shown to vary due to the age of the fruits and the geographic location of cultivation (Carrubba et al., 2002; Pino et al., 1993), fertilization, soil conditions and the level of weediness (Gil et al., 2002).

Worldwide, coriander is cultivated mainly for its ripe fruits. In fruit-producing plants, excessive vegetative growth is a major concern for growers because it competes with fruit growth (Basak and Rademacher, 2000; Costa et al., 2002). Excessive shoot growth may reduce fruit size due to antagonism from leaf-produced assimilates, but also fruit quality and yield (Cowan et al., 2001). Shading has a negative effect on flower bud formation and the

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quality of the return bloom (Greene, 1999), and limits air movement within the canopy, making plants more susceptible to diseases. Apart from the benefit of substantial increases in fruit size and quality, reducing vegetative growth allows producers to seed at higher rates, makes cultivation practices easier, and strengthens stems, preventing lodging. Pruning, girdling, and selection of dwarfing rootstocks are some of the methods used to control shoot growth. These methods are very expensive or difficult, and are only applied to fruit trees. Other methods such as the use of growth retardants (Smit et al., 2005) or photoselective films (Ilias and Rajapakse, 2005) are investigated as ways of efficiently controlling the height of many herbaceous plants.

Plant growth retardants are commonly used to suppress growth in many plants. Daminozide has been in use for many years. It reduces excessive vegetative growth in many trees and ornamental plants. Due to toxicological concerns, its use is controversial nowadays and has been significantly restricted (Rademacher, 2000). In recent years, prohexadione-Ca has been used as an alternative to daminozide. It is considered safe because of its negligible toxicological effects on mammals and its low potential for bioaccumulation in the environment. Its mode of action is similar to that of daminozide, as they both inhibit the late stages of gibberellin metabolism (Brown et al., 1997). They interfere with 3-β-hydroxylation of GA_{20} to GA_1. The net effect is a reduction of immobile, biologically active GA_1 and an increase in the levels of mobile but inactive GA_{20} (Rademacher, 2000). Prohexadione-Ca is currently used for suppressing vegetative growth in pome trees (Basak and Rademacher, 2000) and also to control plant height in other fruit trees (Lo Giudice et al., 2003; Elfving et al., 2003), vegetables (Hamano et al., 2002), and grain crops (Lee et al., 1998).

This study evaluates the use of these two gibberellin inhibitors on certain growth and anatomical characteristics of coriander. Chlorophyll fluorescence was employed in order to examine (i) possible changes in PSII activity after the application of these growth retardants, and (ii) whether it can provide a tool for early detection of the use of growth retardants even before any suppression of growth is visible.

MATERIALS AND METHODS

PLANT MATERIAL AND CULTURE

The experiment was conducted from December 2004 to June 2005 at the Technological Educational Institute of Thessaloniki, Greece. The site is located at 22°55'N, 40°38'E. Coriander seeds (*Coriandrum sativum* L.) were sown individually and randomly inside a greenhouse in fifteen experimental plots. The experiment was established on sandy loam soil [silt 18%, clay 5.6%, sand 70.4%, organic matter 0.88%, $CaCO_3$ 0.9%, Ec 1.5 μS/cm, pH (1:2 H_2O) 7.4]. After germination the plants were acclimatized for 4 weeks in the greenhouse before treatment. Each plant was watered as required and fertilized weekly with 300 ml of nutrient solution containing 60 mg N, 26.2 mg P, and 49.8 mg K (water-soluble fertilizer, 20–20–20 F-TOP Ledra Ltd, Thessaloniki) during the experiment. The plants were maintained in the greenhouse under natural sunlight, relative humidity 70–80%, photosynthetically active radiation 500–700μmol m^2 s^{-1}; average temperatures were 24±2°C/17±2°C (day/night). The experiment was terminated when all plants possessed ripe fruits.

DOSE RESPONSE TO PROHEXADIONE-CA AND DAMINOZIDE

Prohexadione-calcium (BAS 125 10W, BASF Corp., Research Triangle Park) at 100, or 200 mg l^{-1} and daminozide (Alar) at 500, or 1000 mg l^{-1} were evaluated. Each solution contained 0.1% Agral 90 as surfactant (Syngent Ltd, UK). A set of 21 plants from each plot was foliar-sprayed (to runoff) with a low-pressure hand-wand sprayer three times at 10-day intervals with the above prohexadione-Ca or daminozide solutions. The first application of prohexadione-Ca or daminozide was made 4 weeks after germination. Control plants were treated with water and surfactant. The growth retardant concentrations and application frequencies were selected based on preliminary results.

EXPERIMENTAL DESIGN, DATA COLLECTION AND ANALYSIS

Fifteen experimental plots (three replications for each treatment) were set up randomly inside the greenhouse using a randomized complete block design. Each plot contained 21 single plants in 3 rows with 7 plants per row spaced 50 cm apart within each row. Distance between rows was 50 cm, and between plots 100 cm.

Plant height, number of branches, number of inflorescences (umbels), herb and fruit yields and weight of 1000 fruits were recorded at the end of the experiment. Days to anthesis were counted from germination.

CHLOROPHYLL CONTENT MEASUREMENTS

Chlorophyll content (Chl *a*+*b*) was determined according to Wintermans and Demots (1965) at the end of the experiment. Samples (five discs each) were taken from fully expanded leaves of each treatment and were extracted with 95% ethanol in a water bath at 80°C. Full extraction of chlorophyll was achieved

TABLE 1. Effects of daminozide and prohexadione-Ca on plant height, number of branches, number of umbels and days to anthesis

Treatment	($mg\ l^{-1}$)	Plant height (cm)	Number of branches ($plant^{-1}$)	Number of umbels ($plant^{-1}$)	Days to anthesis
Control		116 c	9.4 b	43 a	83 b
Daminozide	500	90 b	9.4 b	39 a	83 b
	1000	87 b	9.5 b	38 a	83 b
Prohexadione-Ca	100	86 b	8.1 a	35 a	78 a
	200	72 a	9.1 b	38 a	80 ab

N = 50. Means with the same letter in the same column do not significantly differ at p = 0.05.

when the sample was discolored. The absorption of the extracts was measured at 665 and 649 nm with an LKB Ultraspec II spectrophotometer.

CHLOROPHYLL FLUORESCENCE MEASUREMENTS

Chlorophyll fluorescence recordings, using a Hansatech Plant Efficiency Analyser (Hansatech Instruments Ltd), were obtained twice, at 10 days (10DAA) and 30 days (30DAA) after the last growth retardant application. Fully expanded leaves were dark-adapted for 30 min. Special clips were placed on the leaves ~3 cm from their base, with the clip slide opened to reveal a 4 mm diameter aperture for illumination of the leaf with the instrument's light sensor unit. This was set at 1500–2000 pmol photons m^{-2} s^{-1} saturating light intensity, and the leaves were exposed to light for 5 sec. The fluorescence values F_o, F_v, F_m, F_v/F_m, F_v/F_o, T_m (F_o – initial fluorescence, F_v – variable fluorescence, F_m – maximal fluorescence, T_m – Time of F_m, Area – area over the fluorescence curve between F_o and F_m) and area of fast induction kinetics were calculated.

ESSENTIAL OIL ISOLATION

Samples for essential oil isolation were taken at the end of the experiment. Mature coriander fruits were air-dried at room temperature for 20 days and then stored at room temperature and ambient humidity for 6 months. As the oil receptacles are inside the fruits, they were crushed slightly immediately before distillation. The essential oils were isolated by hydrodistillation for 2 h, using a Clevenger apparatus. The essential oil content is expressed in ml 100 g^{-1} dry weight.

ANATOMY

Samples for anatomical observations and measurements were taken at the end of the experiment. Small pieces of fully expanded leaves and their neighboring stems were initially fixed in situ for 3 h with 5% glutaraldehyde in 0.05 M phosphate buffer at pH 7.2. After washing in buffer, the specimens were postfixed for 4 h with 2% osmium tetroxide, similarly buffered. The temperature of all solutions was kept at 0°C to avoid leaching of the phenols during fixation. The samples were then dehydrated in an alcohol series followed by propylene oxide. For light microscopy (LM), after dehydration the tissue was embedded in Spurr's (1969) resin. Semithin sections for LM were cut with a Reichert Om U_2 ultramicrotome, stained with toluidine blue O and photographed in a Zeiss III photomicroscope.

STATISTICS

The data were subjected to ANOVA using the SPSS statistical package. For comparisons of the means, the Duncan's multiple range test was employed.

RESULTS AND DISCUSSION

The application of daminozide and prohexadione-Ca to *Coriandrum sativum* plants resulted in characteristic alterations of their external morphology and growth parameters. Both growth retardants induced reduction of stem internode length, leading to shorter plants (Tab. 1). Coriander plants treated with daminozide were up to 25% shorter than the controls. There was no significant difference between 500 and 1000 mg l^{-1} daminozide treatments. Prohexadione-Ca affected plant height even more strikingly. This decrease in plant height was dose-dependent; plants were 26% shorter in the 100 mg l^{-1} treatment and 38% shorter in the 200 mg l^{-1} treatment (Tab. 1). Similar reductions of vegetative growth due to growth retardant use have been observed in fruit trees (Rademacher et al., 2004; Elfving et al., 2003), grain crops (Lee et al., 1998) and ornamentals (Pinto et al., 2005; Lewis et al., 2004). Despite this sharp decrease of height in the retardant-treated coriander plants, the number of branches per plant and umbels per plant did not dif-

TABLE 2. Effects of daminozide and prohexadione-Ca on herb yield, fruit yield, fruit essential oil yield and weight of 1000 fruits

Treatment	(mg l^{-1})	Herb yield (g $plant^{-1}$)	Fruit yield (g $plant^{-1}$)	Fruit essential oil yield (%)	Weight of 1000 fruits (g)
Control		41.6 b	17.1 c	1.67 c	0.86 b
Daminozide	500	45.7 b	6.1 a	1.10 a	0.78 a
	1000	47.5 b	12.9 b	1.30 b	0.91 b
Prohexadione-Ca	100	27.9 a	7.0 a	1.13 a	0.97 c
	200	33.3 a	11.1 b	1.15 a	0.92 b

N = 50 (for columns 5 and 6, n = 3). Means with the same letter in the same column do not significantly differ at p = 0.05.

fer between the retardant-treated and control plants (Tab. 1), except for the 100 mg l^{-1} prohexadione-Ca-treated plants, which had fewer branches than the plants of all other treatments.

The time to anthesis of coriander plants was not affected after daminozide treatment (Tab. 1). Daminozide has also been found to have no effect on time to anthesis in poinsettia, pansy (Lewis et al., 2004) and chrysanthemum (Schuch, 1994). Prohexadione-Ca dosing promoted precocious (3–5 days earlier) flowering of coriander plants (Tab. 1). Promotion of flowering after the application of prohexadione-Ca has been reported for *Matthiola incana* grown in plastic-film greenhouse conditions (Hisamatsu et al., 1999), but it has been found to delay anthesis in petunia; the delay increased with an increase of the dose from 0 to 200 mg l^{-1} (Ilias and Rajapakse, 2005; Cerny-Koenig et al., 2005).

Daminozide and prohexadione-Ca affected the herb yield and fruit yield of coriander, expressed as fresh weight per plant (Tab. 2). The herb yield decreased significantly only after the application of prohexadione-Ca, but fruit yield was reduced by both growth retardants. The lowest concentrations (100 mg l^{-1} prohexadione-Ca and 500 mg l^{-1} daminozide) led to significant decreases of fruit yield versus the controls, but higher concentrations resulted in slight decreases of fruit yield. Essential oil yield from fruits also declined (Tab. 2).

The weight of the coriander fruits differed after the application of the growth retardants (Tab. 2). Daminozide treatment at 500 mg l^{-1} resulted in lighter fruits, but the higher dose (1000 mg l^{-1}) did not lead to significant differences from the controls. Prohexadione-Ca had a greater effect on fruit weight. Both concentrations of prohexadione-Ca resulted in heavier and more voluminous fruits, but only the lower dose (100 mg l^{-1}) gave a significant result for this parameter.

The effects of growth retardants on growth parameters of coriander showed some similarities with those for fruit trees, but also differences. The higher prohexadione-Ca concentration was more effective in reducing shoot growth, enhancing fruit weight and controlling fire blight incidence and severity in pear trees (Costa et al., 2001). In this case, four sprays of 100 mg l^{-1} prohexadione-Ca were applied to trees in the orchard at two-week intervals starting at petal fall. Sugar et al. (2004) found that the fruit weight of two pear cultivars was not affected by prohexadione-Ca treatments at any location in either year, but the weight of the fruit of another cultivar was decreased in all prohexadione-Ca treatments. In apple trees, fruit yield was not affected except in cv. Royal Gala, which had increased crop-load and decreased fruit size (Medjdoub et al., 2005). In that study, however, the plants were first sprayed at ~200 mg l^{-1} from full bloom up to 12 days after full bloom. In another study, Rademacher et al. (2004) found that fruit yields in apple and pear trees generally were slightly increased after the application of prohexadione-Ca. In grapevines, to retard shoot growth, prohexadione-Ca had to be applied prior to bloom; however, prebloom application had the potential to severely reduce crop yield (Lo Giudice et al., 2003).

Anatomical examination of coriander leaves and stems gave some interesting results. Normal leaves exhibited the typical anatomical pattern for dicots (Fig. 1). Between the upper and lower epidermises lies the mesophyll, which is composed of two parts, the palisade parenchyma being in contact with the upper epidermis and the spongy parenchyma with the lower one. The spongy parenchyma contains large intercellular spaces and variously sized vascular bundles adjacent to the essential oil-secreting tubes. Comparative leaf cross sections of controls, prohexadione-Ca-treated and daminozide-treated plants revealed differences in the thickness of the leaf lamina and the contained tissues (Tab. 3). The leaf lamina of the plants treated with prohexadione-Ca (Fig. 1b) and daminozide (Tab. 3) were significantly thicker than those of control plants (Fig. 1a). This increase was due mainly to the larger volume of the palisade parenchyma tissue. Leaf thickness increased by 17–37% after daminozide application on *Epidendrum radicans* (Pateli et al., 2004); in that work, similar increases in leaf thickness were

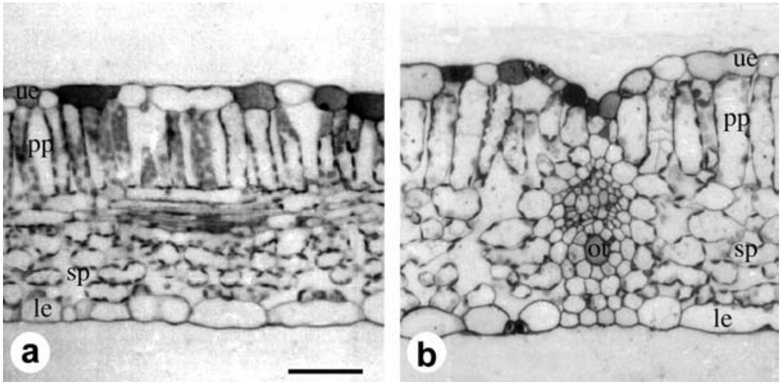

Fig. 1. Leaf cross sections from control (**a**) and prohexadione-Ca-treated (**b**) coriander plants. ue – upper epidermis; pp – palisade parenchyma; sp – spongy parenchyma; le – lower epidermis; ot – essential oil-secreting tube. Bar = 50 μm.

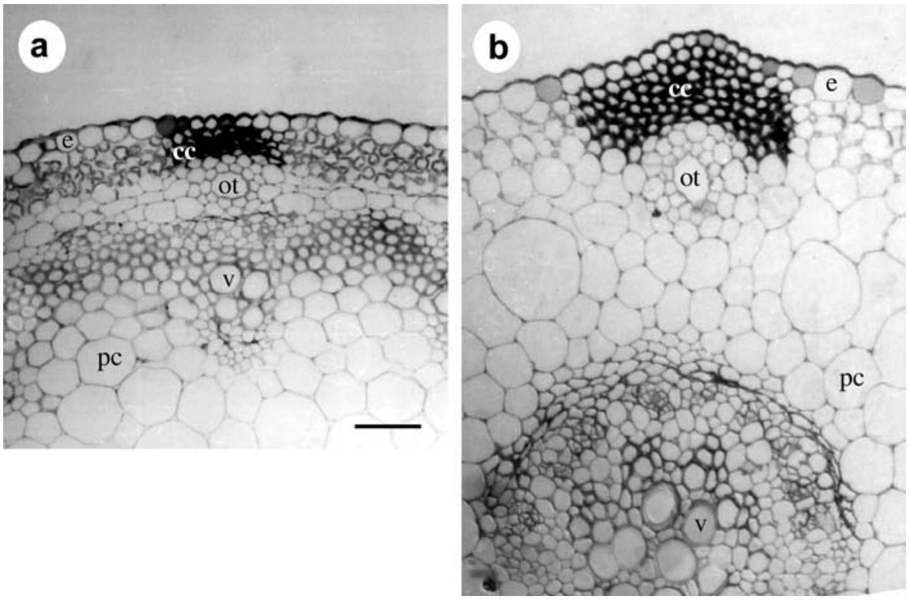

Fig. 2. Stem cross sections from control (**a**) and daminozide-treated (**b**) coriander plants. e – epidermis; cc – collenchyma cells; pc – parenchyma cells; v = vessel; ot – essential oil-secreting tube. Bar = 50 μm.

noted after application of other growth retardants such as paclobutrazol, triapenthenol and chlormequat chloride. In chrysanthemum and helianthus plants, leaf anatomy of plants treated with plant growth retardants resembled that of sun-grown plants: thicker, more compact leaves (Crittendon, 1966; Starman et al., 1990); untreated plants possessed leaves of shade-type anatomy, mainly due to shading in the canopy and reflection of light from neighboring plants.

Coriander stems also presented the characteristic pattern of dicots (Fig. 2). Externally the stem is bounded by the epidermis, which consists of small, closely arranged cells. In the hypodermal area, collenchyma cells are developed in the form of separate poles. In the cortex, apart from the collenchyma, several layers of chlorenchyma cells (giving green coloration to the stem) and other parenchyma cells also occur. Internal to the cortex is the conductive tissue, present in the form of vascular bundles arranged in one ring. Adjacent to the vascular bundles are essential oil-producing tubes. In the center of the stem axis, enclosed by vascular tissues, is the pith, composed of large parenchyma cells. Stems of plants treated with prohexadione-Ca and daminozide had greater diameter than the controls (Tab. 3), and were more compact and stronger due to the increased volume of the collenchyma tissue and the increased number of vessels in the vascular bundles (Fig. 2). In another study, the application of 2500 mg l^{-1} daminozide spray on tomato was also found to increase stem strength relative to controls (Latimer, 1992). Application of prohexadione-Ca has also been found to lead to stem stabilization in cereal crops,

TABLE 3. Effects of daminozide and prohexadione-Ca on leaf thickness, stem diameter and total chlorophyll content

Treatment	(mg l⁻¹)	Leaf thickness (μm)	Stem diameter (mm)	Chl $a+b$ (mg g^{-1} f.w.)
Control		164.8 a	2.24 a	2.28 b
Daminozide	500	176.0 b	3.08 c	2.64 c
	1000	182.4 bc	3.20 c	1.98 a
Prohexadione-Ca	100	174.5 b	2.61 b	2.21 b
	200	184.4 c	2.80 b	2.17 b

N = 5. Means with the same letter in the same column do not significantly differ at p = 0.05.

TABLE 4. Effects of daminozide and prohexadione-Ca on F_v/F_m, F_v/F_o and the area above the fluorescence induction curve at 10 days after the last growth retardant application (10 DAA) and 30 days after the last growth retardant application (30 DAA)

Treatment	(mg l^{-1})	F_v/F_m		F_v/F_o		Area	
		10 DAA	30 DAA	10 DAA	30 DAA	10 DAA	30 DAA
Control		0.813 a	0.818 a	4.45 a	4.39 a	50225 a	52425 a
Daminozide	500	0.793 b	0.793 b	3.86 b	3.89 b	47225 a	45100 a
	1000	0.776 c	0.763 c	3.47 c	3.25 c	48675 a	28025 b
Prohexadione-Ca	100	0.780 c	0.746 d	3.48 c	2.96 d	56700 a	46933 a
	200	0.758 d	0.695 e	3.19 d	2.15 e	45000 a	32625 b

N = 8. Means with the same letter in the same column do not significantly differ at p = 0.05.

rice and oilseed rape (Rademacher, 2000). The parenchyma cells of coriander also seem larger in the stems of daminozide-treated plants than in the stems of the control plants (Fig. 2). As a result of this effect, plants treated with growth retardants are generally broader than the controls. In paclobutrazol-treated tomato plants stem diameter increased by ~58% due to induction of thicker cortex, larger vascular bundles, and wider pith diameter associated with larger pith cells (Tsegaw et al., 2005).

In light of the mentioned differences in leaf anatomy, we measured leaf chlorophyll content (Tab. 3). The results showed no significant differences between prohexadione-Ca-treated leaves and control leaves. The plants treated with 500 mg l^{-1} daminozide had dark green leaves with 16% more chlorophyll than the control leaves, and those treated with 1000 mg l^{-1} daminozide had leaves with 13% less chlorophyll than the controls. Sabatini et al. (2003) reported that prohexadione-Ca positively affected the leaf chlorophyll content of apple and pear trees; in that research, net photosynthesis was often increased and had a positive influence on fruit weight and yield. In our work, no increases in chlorophyll content and significantly lower F_v/F_m values indicated a possible decrease of photosynthesis in prohexadione-Ca-treated coriander leaves (Tab. 4). This might be why the prohexadione-Ca treatments were not followed by an increase in coriander fruit yield.

In our experiment, chlorophyll fluorescence measurements were recorded twice after the last application of the growth retardants (Tab. 4). At 10 DAA, before any visible signs of growth or development of the plants were noted, significant changes were observed in F_v/F_m, implying that the maximum quantum yield of PSII photochemistry was significantly influenced by the growth retardant treatments. As the concentration of growth retardants increased, F_v/F_m values decreased. Prohexadione-Ca was more effective than daminozide in decreasing these ratios. The F_v/F_m values were lowest when plants were treated with 200 mg l^{-1} prohexadione-Ca. In another study, cucumber plants grown on medium with higher concentrations of growth regulators had also lower photochemical efficiency of PSII (Burza et al., 1994). These large decreases in F_v/F_m in the growth retardant-treated coriander plants were accompanied by corresponding decreases in F_v/F_o, indicating possible structural damage to the thylakoid membranes of the chloroplasts (Pereira et al., 2000). No significant differences between treatments were found in the area above the chlorophyll fluorescence induction curve at 10 DAA.

Later on, at 30 DAA, when plants exhibited some signs of growth retardation, another series of measurements was made. In these measurements the decreases in F_v/F_m and F_v/F_o ratios were sharper. There were also differences in area values between the growth retardant treatments and the controls. This parameter was found to decrease as the growth retardant concentration of increased, but the differences were significant only at the higher doses of daminozide (1000 mg l^{-1}) and prohexadione-Ca (200 mg l^{-1}).

We conclude that the chlorophyll fluorescence ratios F_v/F_m and F_v/F_o were strongly influenced by the growth retardant concentration, even when, at 10 DAA, no signs of growth or development changes were observed in the coriander plants. Thus these ratios are good chlorophyll fluorescence parameters for detection of differential responses between growth retardant-treated plants and controls. Korres et al. (2003) found that F_v/F_m and the area above the fluorescence induction curve can be used for detection of differential responses to herbicides between wheat cultivars. In our experiment the area values were affected only by the higher doses of growth retardants, and only when visible signs of stem shortening were already observed.

Both daminozide and prohexadione-Ca were effective in reducing stem elongation in coriander plants, and the response varied with the concentration. A concentration of 200 mg l^{-1} prohexadione-Ca can be used to achieve 38% height reduction. Precocious anthesis of to 5 days was noted after the application of prohexadione-Ca, and coriander fruits were heavier after its application. However, this did not translate to an increase in fruit yield or fruit essential oil yield. Further trials are needed to optimize these parameters. There were also differences in leaf and stem anatomy and in chlorophyll fluorescence values between the retardant-treated plants and the controls. The reduction of the chlorophyll fluorescence parameters F_v/F_m and F_v/F_o may be used as a tool for detecting the use of growth retardant even before the plants show any signs of growth retardation.

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