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Gaseous ethanol penetration of plant tissues positively effects the growth and commercial quality of miniature roses and dill

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Abstract

The effects of an ethanol based nutrient-supplemented solution on the growth and flowering of potted miniature roses and biomass production of dill sprayed either onto the leaves or applied in gaseous form are reported here. In addition, the uptake of ^{14}C-radiolabelled ethanol by radish was studied. Our findings show that ethanol might partially be taken up through plant stomata, and the radiolabelled carbon was translocated to other parts of the treated plant, especially newly emerging leaves. Translocation appeared to be more rapid during light periods as compared to dark periods. Foliar application of ethanol appeared to induce chlorosis in the dill plants in some cases. In contrast, gaseous ethanol treatments showed no adverse effects, and instead increased the biomass of dill plants and miniature roses. Furthermore, gaseous ethanol improved the commercial quality of miniature roses by increasing the number of flowers per plant and prolonging the flowering time of those flowers. These results further support the practice of spraying ethanol during light periods through high pressure sprayers, which produce a mist of very tiny droplets with high surface area. This method mimics a vapor phase which infiltrates plant tissues without wetting leaf surfaces.

Keywords: Ethanol; Dill; Miniature rose; Radish; Foliar spray

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1. Introduction

Benson (1951) found that green algae can photosynthesize methanol as quickly as carbon dioxide. Later, Cossins (1964) showed that C3-plants also metabolize methanol rapidly. In plants, methanol is first oxidized to formaldehyde and carbon dioxide. The formaldehyde is then converted into sugar phosphates. Nonomura and Benson (1992a) applied methanol and nutrient-supplemented methanol solutions to the foliage of various C3- and C4-plants under arid environments. They found that C3-plants treated with nutrient-supplemented methanol showed yield increases of up to 100%. Repeated methanol application on shaded C3-plants induced toxic symptoms, while C4-plants did not respond to methanol. Nonomura and Benson (1992b) suggested that the growth response of C3-plants to methanol was linked to reduced photorespiration.

Since the paper of Nonomura and Benson (1992a), several research groups have been studying methanol applications on various crops. Positive results have been reported in some studies (Delvin et al., 1994; Valenzuela et al., 1994; Faver and Geric, 1996). However, other studies show no response (Esensee et al., 1995; Feilbert et al., 1995; Mortensen, 1995; Rajala et al., 1998), and even toxic effects have been reported (McGiffen et al., 1995). Because methanol is poisonous to humans, we were interested to see whether ethanol could increase plant biomass, and act as a supplemental carbon source. Previous studies using supplemental ethanol for plant propagation have reported various effects. Rowe et al. (1994) found a positive effect of ethanol spray on the growth of tomato plants, whereas Rajala et al. (1998) did not find any effects of ethanol sprays on cereals. Nevertheless, a number of Finnish greenhouse growers continuously use a commercial ethanol based solution (Carbon Kick, Kekkilä Ltd., Finland) on roses and cucumbers. Perata and Alpi (1991) have shown that carrot (*Daucus carota*) cells growing in cell suspension culture can use ethanol, and convert it to acetaldehyde, which is further assimilated by the plant. Andrés et al. (1990) have shown aliphatic alcohols, including ethanol, improve the association of fructose-1,6-bisphosphate into thylakoids. There are also studies showing positive growth effects of foliar triacontanol (an aliphatic alcohol containing 30 carbon atoms) applications on several plant species (e.g. Shukla et al., 1997). Thus, it is possible that ethanol is simply used by the plant as a carbon source, although other functions cannot be ruled out. In fact, ethanol has been shown to increase the vase-life of carnation flowers (*Dianthus caryophyllus* L.), probably due to the inhibition of ethylene production (Wu et al., 1992).

Here, we studied the effects of ethanol based nutrient-supplemented solution on the growth and flowering of potted miniature roses and on the biomass production of dill. Ethanol was applied either by spraying directly onto the leaves or in a gaseous phase. Rose was selected as a representative of species with a thick cuticle, and dill as a species with a thin cuticle. In addition, a detailed study

of the uptake and translocation of ^{14}C-radiolabelled ethanol was carried out with radish.

2. Materials and methods

2.1. Plant material

Miniature roses (*Rosa hybrida* L. cv. Ruby) were grown in a greenhouse (60°23′N, 22°33′E) in a commercial peat–sand mixture (Kekkilä Ltd., Finland) in pots containing four cuttings in the first experiment and three in the second set of experiments. The first experiment was carried out from September 1997 to January 1998, and the second from April 1998 to July 1998. The night temperature during the first experiment was between 20 and 22°C for the first month, and 18–19°C in subsequent months. In the second experiment, the night temperature was between 20 and 22°C throughout the whole experiment. The relative humidity was ≈65–75%, and the CO_2 concentration was kept constant at 400 ppm by supplementation with pure CO_2. Supplemental light (Philips SON-T-PLUS 400 W) was given in the first experiment for 20 h daily, and 14 h daily in the second experiment, when global radiation was lower than 150 W m^{-2}. The photosynthetic photon flux density (PPFD) of the supplemental lights was 140 μmol m^{-2} s^{-1}. Plants were watered regularly with a complete nutrient solution consisting of N 14%, P 5%, K 21% plus micronutrients and calcium nitrate.

The experimental design was a randomized block design with four blocks in the first experiment and seven blocks in the second experiment, with each block containing 10 pots per treatment.

Dill (*Anethum graveolens* L. cv. Bouquet) was grown in a greenhouse using peat pots with ≈49 plants in both the first and second experiment, and 12 plants in the third experiment. The first experiment was carried out during October to November 1997, the second experiment during November 1997 to January 1998 and the third one during February to March 1998. The night temperature in the first and third experiments was in the range of 19–20°C, and 18–19°C during the second experiment. Relative humidity fluctuated between 65 and 70%, while the CO_2 concentration was kept constant at 400 ppm by supplementation with pure CO_2. Supplemental light was provided for 20 h daily, and PPFD was 180 μmol m^{-2} s^{-1}. Plants were watered regularly with a complete nutrient solution consisting of N 14%, P 5%, K 21% plus microelements.

Radish plants (*Raphanus sativus* L. cv. Non-plus ultra) were grown from seeds in a peat–sand medium (1:1 v/v) in the greenhouse. Photoperiod was 17 h, PPFD 300 μmol m^{-2} s^{-1} and day/night temperatures were 20/17°C, respectively. Plants were watered regularly with the complete nutrient solution described

above. Plants used in the experiments had six emerged leaves, and were ≈3 weeks old.

2.2. Ethanol applications in the greenhouse

Rose and dill plants were treated with nutrient-supplemented ethanol sprays (Kekkilä Ltd., Finland) once a week in a greenhouse compartment of 50 m^2. Thus, the roses received 13 ethanol applications in the first experiment and nine in the others, whereas dill received four applications. The spray solutions contained either 20 or 30% ethanol, and a nitrogen supplement of either 0.16 or 0.25% w/v, respectively in the form of glycine and urea. The Fe-supplement in the solutions was 7.3 or 11 mg/l, respectively, in the form of HEDTA-chelate. In addition a 0.02% wetting agent Citowett (BASF, Germany) was added to all spray solutions including a control of water but without added nitrogen or iron. Plants were foliar sprayed to run-off, and all treatments were carried out in the morning between 08:00 and 10:00 h.

In the second rose experiment, and in the third dill experiment, a treatment of gaseous ethanol was included. The plants in this treatment were grown in the same compartment as the 'sprayed plants', but far enough away from them to avoid receiving any liquid ethanol on their foliage when the latter were sprayed manually. The greenhouse vents were closed at the time of spraying and normally remained closed for the next 24 h although in the second rose experiment the vents were opened 5–10% for 2–3.5 h between 3 and 7 h after spraying on six out of the nine spraying occasions. This was done to limit the temperature rise within the greenhouse. The 'gaseous treated' plants were in the same glasshouse compartment as the sprayed plants but were exposed to ethanol only as a gas or as fine droplets of an ethanol–nutrient solution. The control plants were removed from the compartment at the time the ethanol was sprayed, sprayed with 0.02% Citowett in water, and kept in another compartment with identical climatic conditions for 24 h before they were returned.

2.3. Parameters measured from rose and dill plants

The onset of flowering, number of flowers and buds, and the time period to commercial maturity (5 flowers open) were measured on all the rose plants. Half of the rose pots were used for biomass measurements, and half for keeping quality assessments. The biomass measurements included plant height (mean of 3–4 longest shoots per pot), and fresh and dry weight of the above ground phytomass. Also, the number of flowering shoots, total number of shoots and the diameter of the flowers were measured.

Keeping quality was measured under the following conditions: temperature 20–21°C, relative humidity 45%, 12 h duration of 13 μmol m^{-2} s^{-1} PPFD provided

by fluorescent lamps (Philips TL 40 W/32 Deluxe), and mechanical ventilation. The time requirement to reach 50% flowering was recorded as well as the duration for withering of two-thirds of the flowers. The blooming period of a single flower was defined as the period starting when the bud sepals first opened to a fully opened flower stage and ending with the withering of the flower. Fifteen flowers per treatment were monitored for blooming periods.

The dill plants were harvested three times in the first experiment and four times in the two other experiments. Measured and recorded parameters included fresh and dry weight, and mean height of the tallest plant. Other parameters reported included number of leaves, date of root emergence and appearance of damaged and injured leaves.

2.4. Rate of ethanol uptake by radish plants

Four radish plants were placed in 1.5 l glass containers and 10 μl of ^{14}C-labelled ethanol (ethanol-1-^{14}C, Sigma, USA), containing 0.025 μCi of ^{14}C was applied to the adaxial leaf surface of the second growth leaf of each plant. The containers were thereafter tightly sealed and placed in a growth chamber at 20°C, and a PPFD of 159 μmol m^{-2} s^{-1} (Philips SON-T-PLUS 400 W). Leaves of different maturity were collected 1, 2, 3 and 4 h after the treatment. Leaves were thoroughly washed with distilled water, weighed and ashed with 200 mg of paper at 900°C in a Junitek Oxidazer (Junitek Ltd., Finland). Total carbon was then trapped into 8 ml of Lumasorb solution (Lumac LSC B.V, Netherlands), mixed with 8 ml of scintillation liquid Carboluma (Lumac LSC B.V, Netherlands). In order to check the activity of the ethanol solution two standard samples consisting of 200 mg of paper, 10 μl of ^{14}C-ethanol solution, and 800 μl distilled water were ashed between each sample to avoid contaminations. The β-activity of the samples was determined with a scintillation counter (Wallac 1109/14 LSC; Wallac Ltd. Finland). The external standard consisted of 152-Eu. Results are represented as dpm/g freshweight.

2.5. The effect of light on ethanol uptake

Four radish plants were placed in 1.5 l glass containers and ^{14}C-labelled ethanol was applied as outlined above. To examine the effects of light on the absorption of ethanol, two of the containers were covered with aluminum foil and two were exposed to a PPFD of 159 μmol m^{-2} s^{-1} (Philips SON-T-PLUS 400 W). All of the containers were kept at 20°C. After 24 h, the labelled leaf and three other leaves from above the labelled leaf were collected from each plant, washed thoroughly and weighed. Liquid scintillation samples were prepared and measured as described above.

2.6. Ethanol uptake in sealed and open-spaces

Eight radish plants were placed in 1.5 l glass containers, two in each container and 5 ml of ^{14}C-labelled ethanol solution was applied to each plant with a manual sprayer so that every leaf became wet (1.25 μCi/plant). Two containers were sealed and two were left open. After 20 h, four fully expanded leaves were collected and prepared for liquid scintillation as described above.

2.7. Uptake of gaseous ethanol

Four radish plants were placed in 1.5 l containers, one in each container. A 10 μl droplet of radiolabelled ethanol (0.025 μCi/plant) was applied to the second growth leaf of two of the plants. The other two plants were not directly treated with ethanol, but 5 ml of ^{14}C-labelled ethanol solution (0.025 μCi/5 ml) was spread along the inner surface of the container. These plants were not in contact with liquid ethanol at any point. After 20 h, second and third growth leaves were collected from each of the plants and scintillation samples were prepared as described before.

2.8. Statistical analysis

The results of the rose and dill experiments were analyzed using ANOVA and Tukey's HSD tests (SAS statistical package).

3. Results

3.1. Miniature roses

There was a clear tendency for foliar ethanol spraying to increase both the fresh and dry weights of the second topping phytomass of miniature roses, i.e. the phytomass harvested at the stage of visible buds 5 cm above the ground (Table 1). However, statistically only the treatment with 30% ethanol in the second experiment was significant. It also appears that foliar ethanol spraying increased the number of flowers and buds in the first experiment when a 30% ethanol solution was used. This treatment also accelerated the development to commercial maturity by 3 days, and extended the flowering time of a single flower by almost 2 days, compared to the control plants (Table 1).

Although foliar spraying showed some beneficial effects, gaseous ethanol clearly showed stronger effects on rose growth and development. The plants that received ethanol in gaseous form had more flowering shoots, more flowers and buds and higher fresh and dry weights than control plants (Table 1).

Table 1
Effects of foliar ethanol sprays and ethanol in gaseous form on fresh and dry weight of miniature roses in their second topping (phytomass harvested 5 cm above the ground at the stage of visible buds) and effects at the stage of sale[a]

Stage of development	Measurements	Experiment 1				Experiment 2				
		Treatment				Treatment				
		Ethanol 20%	Ethanol 30%	Control	*p*-Value	Ethanol 20%	Ethanol 30%	Gaseous ethanol	Control	*p*-Value
2nd topping	Fresh weight, g	15.1	13.7	12.3	0.127	9.6 ab	10.2 a	9.9ab	8.6 b	0.054
	Dry weight, g	3.1	2.8	2.4	0.059	2.0	2.1	2.1	1.9	0.101
Saleable	No. of flowering shoots	15.7	15.2	14.2	0.222	17.3 ab	17.9 ab	18.1a	16.0 b	0.046
	No. of flowers and buds	34.8 ab	37.9 a	32.0 b	0.045	34.4 ab	36.4 ab	39.3a	31.6 b	0.003
	Fresh weight, g	33.2	33.4	33.6	0.514	48.3 ab	49.4 ab	51.5a	44.9 b	0.029
	Dry weight, g	56.6	58.6	57.0	0.156	9.8 ab	10.1 ab	10.7a	9.2 b	0.014
	Opening of a single flower, days	3.6 b	3.6 b	4.7 a	0.008	–	–	–	–	–
	Time from a bud to a withered flower, days	15.2 ab	16.0 a	14.2 b	0.007	17.8	17.7	17.7	15.7	0.070
	Saleable plant, developing time in days	113.5 ab	112.2 b	115.5 a	0.019	104.3	104.5	104.8	105.1	0.182

[a] Results from two different experiments are shown. Values accompanied by different letters differ significantly from each other.

In contrast, none of the ethanol regimes used showed significant effects on plant mean height, total number of shoots, time period for 50% opening of flowers, and withering time of flowering plants (data not shown).

Interestingly, but possibly not surprisingly ethanol application, clearly decreased the occurrence of rose powdery mildew (*Sphaerotecha pannosa* (Wallr., Fr.) Lev.) infections of rose leaves. Both gaseous and foliar applications had similar effects, and although, this observation is outside the original objectives of this study, it may be an additional advantage for growers.

3.2. Dill

There was a tendency or foliar ethanol applications to affect the third harvest height and dry weight of dill plants in the first two experiments (Fig. 1). In the two first harvests there was no significant difference between treated and control plants in any of the experiments (Fig. 2). In the third and fourth harvest, plants treated with gaseous ethanol showed the most significant differences as compared to control plants (Fig. 2).

None of the ethanol treatments affected the time to maturity of the plants, nor the number of leaves in any of the harvests (results not shown). Foliar sprayed ethanol caused color changes in the leaves after two or three sprayings. Chlorosis was observed in the top of some leaves, otherwise leaves appeared dark green.

3.3. The rate of foliarly applied ethanol uptake

Application of radiolabelled ethanol to radish leaves led to an increase in β-activity, on a fresh weight basis, in sampled leaves during the 4 h period directly after ^{14}C-ethanol application (Fig. 3). As β-activity increased in treated leaves

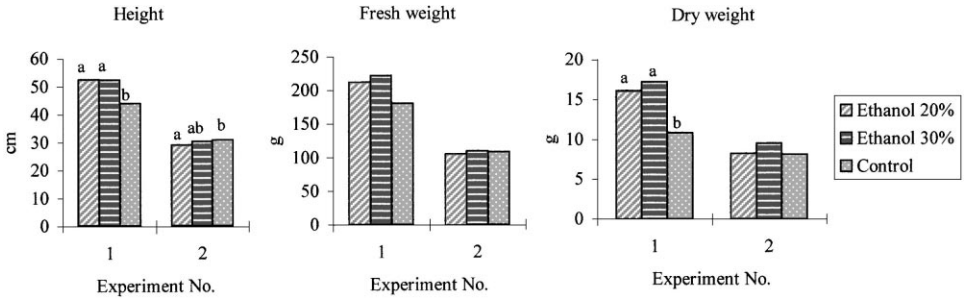

Fig. 1. Effects of foliar ethanol sprays on dill height (cm), and fresh and dry weights (g) from the third harvest of two experiments. Values accompanied by different letters differ significantly from each other.

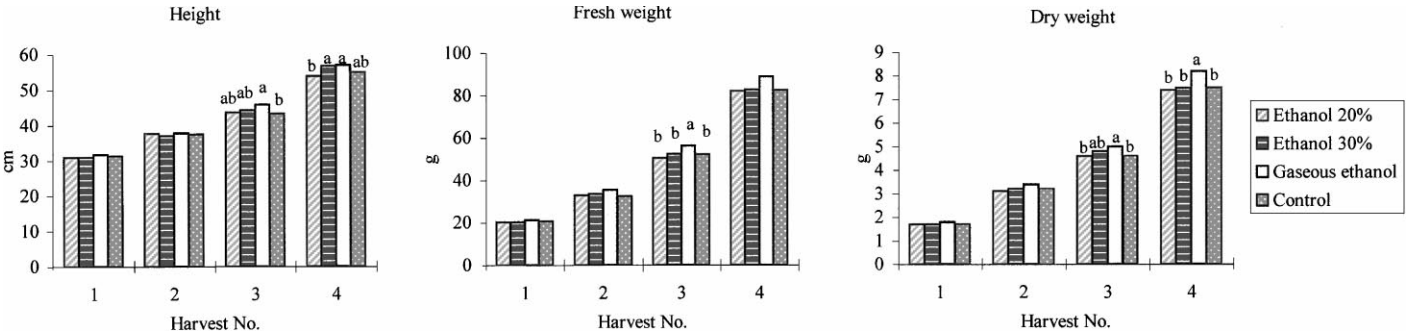

Fig. 2. Effects of foliar ethanol sprays and ethanol in gaseous form on dill height (cm), and fresh and dry weights (g) in the third experiment. Results are from four harvests and values accompanied by different letters differ significantly from each other at $p<0.05$.

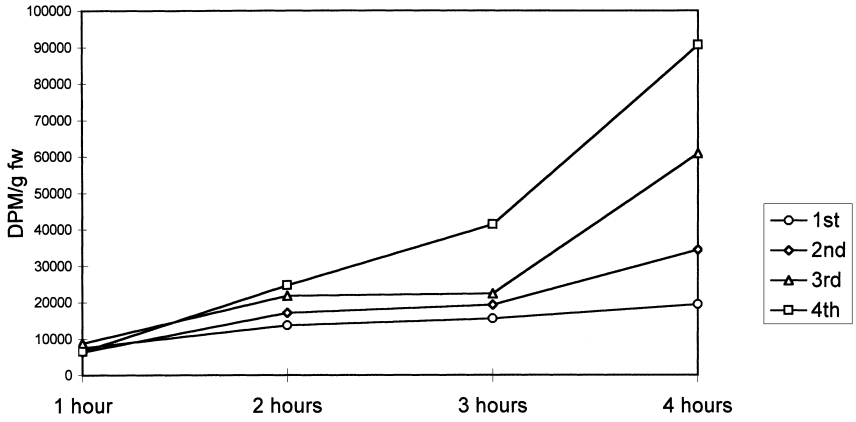

Fig. 3. Uptake of radiolabelled ethanol as a function of time after application. A 10 μl droplet containing 0.025 μCi of ^{14}C was applied to the adaxial surface of a second emerged leaf of radish plants. 1st, 2nd, 3rd and 4th represent leaf numbers beginning from the youngest one.

during this 4 h period, it seems that a longer period than 4 h is required for complete uptake of the droplet. The highest levels of β-activity were found in younger leaves, that were not directly exposed to the label. This suggest that ethanol derived carbon compounds were transported from older to younger leaves.

3.4. The effect of light on ethanol uptake

β-activity was detected in all sampled leaves, but activity on a fresh weight basis, was several times greater in the leaves collected from plants exposed to label under light conditions compared to plants exposed in dark conditions (Fig. 4). Again, the activity was highest in youngest leaves in both light and dark conditions. This indicates that the metabolism and transport of foliar applied ethanol is not totally prevented by the lack of light.

3.5. Ethanol uptake in closed and open systems and in liquid and gaseous forms

The β-activity, on a fresh weight basis, of leaves collected from plants kept in closed glass containers was about twice as high as the activity measured in leaves from plants in open containers (Fig. 5). This difference is most likely due to the decrease in available ethanol vapor for plants in the open system compared to plants in closed system (i.e. evaporated ethanol can freely diffuse away from plants in the open system decreasing overall effects, while in the closed system, ethanol vapor pressure is held constant and higher). In addition, β-activity was

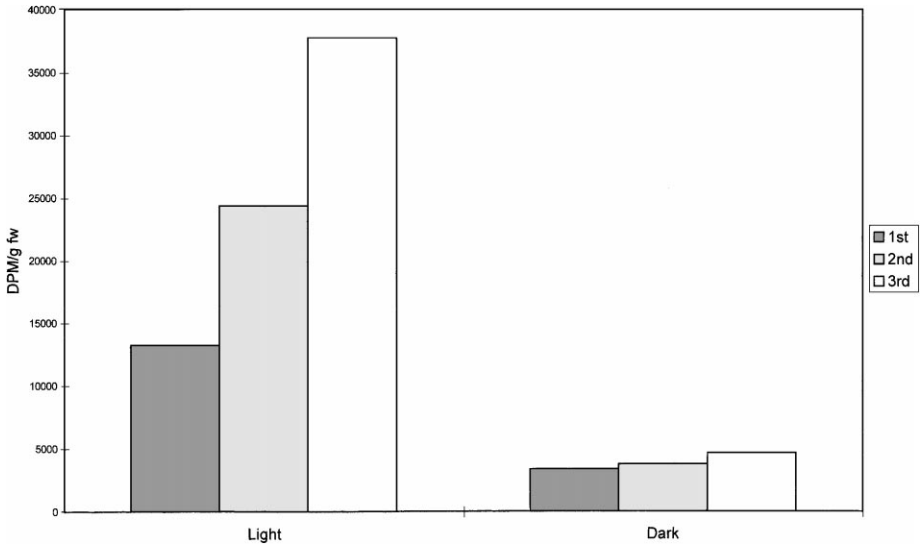

Fig. 4. Uptake of radiolabelled ethanol in the light (159 μmol m^{-2} s^{-1}) and in the dark. A 10 μl droplet containing 0.025 μCi of ^{14}C was applied to the surface of the second emerged leaf of radish plants. β-activity was measured 24 h after the application. The results are the means of eight leaves. 1st, 2nd and 3rd represent leaf numbers beginning from the youngest one.

observed in radish plants placed in closed glass containers, which had radiolabelled ethanol sprayed on the inside surface of the container (data not shown). This strongly suggest that radish plants are also able to take up ethanol in a gaseous form.

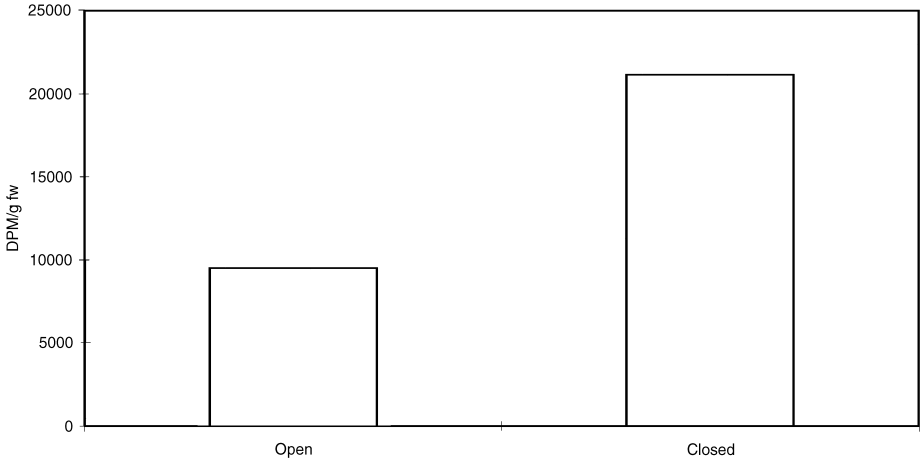

Fig. 5. Uptake of radiolabelled ethanol in an open container and in a closed container. A 10 μl droplet containing 0.025 μCi of ^{14}C was applied to the second emerged leaf of radish plants. β-activity was measured 20 h after the application. The results are the means of 16 leaves.

4. Discussion

Since Nonomura and Benson (1992a) published their work, research efforts have mainly concentrated on foliar applications of methanol (e.g. Delvin et al., 1994; Valenzuela et al., 1994; Feilbert et al., 1995; McGiffen et al., 1995). In contrast, Rowe et al. (1994) reported that foliar applications of ethanol increased the growth of tomato plants, although they also showed that methanol had a stronger growth stimulating effect. Our results confirm that foliar applications of nutrient supplemented ethanol increase the yield and improve the quality of miniature roses and dill. According to Nonomura and Benson (1992b) the positive effects of methanol are based on diminished photorespiration, which then increases photosynthate allocation. Whether ethanol has a similar mode of action is not known. Other reports (Wu et al., 1992) show that ethanol can inhibit ethylene production, which is correlated with longer vase-life of flowering plants. Our results support this finding, as we also observed an increase in the duration of miniature rose flowering following ethanol applications.

Our results also show that ethanol is taken up by plants in gaseous form. This is in agreement with a recent study by Loreto et al. (1999). It has been observed in some studies that methanol application induces chlorotic symptoms on leaves (McGiffen et al., 1995). Similarly, we observed that foliar spray applications of nutrient supplemented ethanol on dill plants can cause chlorosis, whereas gaseous ethanol treatment did not have any observable adverse effects. The adverse effects of foliar ethanol spraying may be explained by the build up of toxic ethanol concentrations in plant tissues. This seems to be the case, especially in species having a thin cuticle, such as radish and dill. But for plants with a relatively thick cuticle, such as roses, chlorotic symptoms were only observed with ethanol solutions of 40% (results not shown). Gaseous ethanol treatment clearly showed stronger positive effect on the growth of the rose plants as compared to the foliar treatment.

β-activity was about ten times higher in plants that were treated under light as compared to plants treated in the dark. This indicates that the plants exposed to light exhibited faster uptake of ethanol. Nonomura and Benson (1992b) postulated that the need of high light for positive effects of methanol is due to its effect via reduced photorespiration. Our results suggest that in the case of ethanol application the increased effectiveness of treatment during light periods maybe partly due to carbon transport. This could also give a possible explanation for the results reported in the literature, which show a lack of alcohol related effects on growth when foliar spaying was done under dim light (e.g. Rajala et al., 1998).

It can be concluded from our study, that nutrient supplemented methanol application can be replaced by nutrient supplemented ethanol, even though the positive effects found were weaker than those reported by Nonomura and Benson

(1992a, b). According to our results, ethanol application was most effective when it was conducted in the light and in gaseous form, as compared to direct foliar application of liquid ethanol. This supports the practice of using high pressure sprayers in the greenhouse, which produce tiny droplets, thus facilitating better ethanol penetration into the plant tissues in gaseous form. Furthermore, our radiolabelled ethanol droplet results suggest that more than 4 h is required for the ethanol to completely penetrate the leaf. Therefore, it would be reasonable to suggest that vents should remain closed during the application and for several hours after.

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