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Routes of Ethephon Uptake in Pineapple (*Ananas comosus*) and Reasons for Failure of Flower Induction

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Abstract. Ethylene-releasing agents such as ethephon (2-chloroethylphosphonic acid) are used widely to induce flowering in pineapples (*Ananas comosus* (L.) Merrill). However, ethephon treatment is less reliable in summer, particularly if plants are treated on abnormally hot days. [^{14}C]ethephon was used to follow uptake and translocation in leaf tissues. Up to 30% of the ethephon entered the leaf within 4 h, and up to 60% by 24 h. Uptake was dramatically modified by temperature, relative humidity, solution pH, and the surface on which solution droplets were placed. Entry occurred across the leaf cuticle and probably also by way of stomatal pores, and label was recovered at all depths within the leaf. ^{14}C label entered more rapidly through the abaxial epidermis than through the adaxial epidermis. Low-volume spray applications to whole plants resulted in rapidly drying droplets mainly on the adaxial, distal epidermis and were rather ineffective at inducing flowering, possibly because little ethephon or ethylene reaches the shoot apex. High-volume sprays may facilitate ethephon entry because solution accumulates in leaf axils and hence remains in prolonged contact with abaxial epidermis of leaf bases close to the shoot apex. When poured into the center of the plant, 20% of a normal commercial ethephon dose induced full flowering even under adverse temperatures. It is suggested that high-volume evening spraying and avoidance of hot days may reduce the incidence of flowering failure.

Key Words. Pineapple—*Ananas comosus* (L.) Merrill—Flowering—Ethephon (2-chloroethylphosphonic acid)—Ethylene

Abbreviation: RH, relative humidities

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Commercial pineapple production depends heavily on chemicals that induce synchronized flowering, hence promoting good yields and facilitating harvesting. Most commonly, flower induction is caused by application of ethylene (= ethene), generally in the form of ethylene-releasing compounds such as ethephon (2-chloroethylphosphonic acid; Ethrel) (Yang 1969). Other strategies include spraying ethylene-loaded charcoal granules or calcium carbide that releases acetylene (= ethyne), a moderately active analog of ethylene. Auxins such as α-naphthaleneacetic acid are also effective (Gowing 1956, Van Overbeek 1946) and probably operate by stimulating endogenous ethylene production (Burg and Burg 1966, Sakai and Imaseki 1971).

Despite its success and economic advantages on pineapple, ethephon has never been entirely reliable, and partial or total failures of floral induction are often reported. This impinges on continuity of supply of pineapples. Flowering failures not only reduce yields but also affect fruit quality and cause harvesting problems because of slower and more erratic emergence of inflorescences. Natural flowering, which may also be under ethylene control, is unpredictable and commercially undesirable (Min and Bartholomew 1996). However, unsatisfactory responses to ethephon are found only from applications in abnormally hot weather, and frequency of induction failure increases proportionately with temperatures exceeding 28°C (Glennie 1979).

Field experiments have revealed little of the underlying mechanisms. Temperature modifies the rate of ethephon breakdown, which will affect its fate outside and inside the plant. However, influences from ambient humidity, air movement, irradiance, and spray volumes are also likely. Ethephon is stable at low pH (<3.5), but in neutral to alkaline conditions it breaks down rapidly to release ethylene (Biddle et al. 1976, Olien and Bukovac

1978). With many crops, ethephon is sprayed as an acidic solution that does not break down significantly until contacting higher pHs within plant tissues. In recent years, particularly with pineapple, spray solutions have often been modified with phosphate or borate to raise the pH to between 7 and 9. This is likely to alter uptake mechanisms because of rapid breakdown outside the plant and within. Ethylene may be released to the atmosphere and lost by air movement or may enter the plant in solution or in the gas phase. Stomatal aperture will affect gas exchange and permeation of liquids (Beaudry and Kays 1988); pineapple, being a CAM plant, will have maximal stomatal aperture at night.

Temperature may also affect the ability of the plant to respond to ethylene. This might include ethylene receptor stability and inhibition of ethylene metabolizing enzymes or other points in the ethylene signal transduction pathway. In pea seedlings, ethylene binding is reversibly inactivated at temperatures greater than 28°C (Beyer and Blomstrom 1979). The same is possible for pineapple, although a higher temperature threshold might be expected given the species' tropical habitat. Aminocyclopropane carboxylic acid oxidase, a key enzyme in ethylene biosynthesis, also appears to be unstable above that temperature in mung bean and apple (Yu et al. 1980), but in tropical pawpaw fruits it remains active at less than 42°C (Chan 1986).

Very high leaf temperatures (>48°C) have been recorded in pineapple (Aubert and Bartholomew 1973), resulting from a combination of high air temperature, high irradiance, low surface area/volume ratio, and minimal evaporative cooling because of daytime stomatal closure. Sustained high temperatures, especially at night, reduce carbon assimilation in pineapple (Bartholomew and Kadzimin 1977) and disrupt the normal diurnal cycle of gas exchange (Neales 1973).

Here we have examined whether the characteristics of ethephon uptake into pineapple leaves may explain some of the observed variability in effectiveness of ethephon in flower induction. Most of the experiments have been based on the use of [^{14}C]ethephon applied to leaf tissues under controlled environments.

Materials and Methods

Plant Material

Pineapple plants (*Ananas comosus* (L.) Merrill), cv. Smooth Cayenne clone 13, were grown from crowns in 25-cm pots in glasshouses at Nambour (26°S) and Brisbane (27°S) under natural daylength with day/night temperatures of approximately 30°/20°C. Plants were irrigated and given mineral nutrients as required. Experiments were carried out only on plants of adequate size for flowering (height >60 cm). Leaves were selected by length, the longest on the plant being called the D-leaf. Only the D-leaf and the next oldest and youngest were used.

Chemicals

[2-^{14}C]ethephon (1.7 GBq mmol^{-1}) was synthesized by Amersham UK. Unlabeled ethephon was prepared from dilutions of commercial Ethrel (May and Baker). The pH of ethephon solutions was modified by the addition either of NaOH or sodium tetraborate (borax).

Ethephon Uptake Assay

Leaf disks 18 mm in diameter were cut from green (distal) or white (basal) portions of leaves and placed on wet sponges inside 10-mm lengths of close-fitting 18-mm i.d. polyvinyl chloride tubing to minimize water loss from the cut edges during the experiment. Six disks were placed inside a 250-mL clear polystyrene tissue culture container fitted with an inlet and an outlet tube. This allowed flushing with air, which assisted temperature and humidity control and prevented build-up of released ethylene or other gases around the tissue.

A 20-μL droplet of a solution containing 500 Bq of [^{14}C]ethephon and 500 mg L^{-1} of unlabeled ethephon was placed in the center of each disk. The containers were incubated in a controlled environment cabinet lit by high-pressure mercury and tungsten lamps (PAR approximately 500 μmol m^{-2} s^{-1}). Temperature was either 26° or 32°C. Air flow was 400 mL min^{-1} per container. High relative humidity (>75%) was generated by bubbling air through water and low humidity (<25%) by passing air through a column of dry silica gel. Humidity was measured with a Vaisala probe.

At intervals, disks were removed from the containers and the status of the droplet (wet or dry) noted. Disks were then washed five times with wet cotton swabs to remove ethephon on the leaf surface. Ethephon, and presumably dissolved ethylene gas, were extracted by homogenizing each leaf disk with a Polytron homogenizer in 5 mL of methanol/water/acetic acid (60:39:1 by volume), centrifuging the extract at 1,000 *g* for 5 min to remove insoluble material and rapidly transferring the supernatant to a scintillation vial to which 7.2 mL of scintillation cocktail was added (Beckman Ready Value). ^{14}C content was estimated by counting for 5 min on a Packard Minaxi 4000 scintillation counter using an external standard to calculate counting efficiency.

Cryotome Sectioning

To estimate the depth of [^{14}C]ethephon penetration into the leaf, disks were sectioned parallel to the plane of the leaf surface. The ethephon assay was performed as described previously except that after washing the disks a second smaller disk (d = 8.5 mm) was cut from the center of the larger one exactly over where the droplet of ethephon had been resting. This disk was then immersed in an embedding solution containing gelatin (150 g L^{-1}) and glycerine (10 mL L^{-1}), which was frozen rapidly to −30°C. Sections (50 μm) were cut through the disk starting from the side of application. Individual sections were placed in scintillation vials containing 2.4 mL scintillation cocktail. Vials were sealed, shaken vigorously, then left to settle and counted for 5 min as described previously. In some cases, only every second or third section was analyzed.

Ethylene Application to Whole Plants

The concentration of gaseous ethylene required to induce flowering was measured by incubating potted plants in an atmosphere containing ethylene. A sealable clear polythene box (2.4 × 2.4 × 1.2 m [high]; total volume 6.9 m^3) was constructed inside a controlled environment glass-

house at Nambour. Twelve plants were placed inside the box, which was flushed with a stream of ethylene (supplied from a gas cylinder fed through a microcontrol valve) in air. Flow rate was adjusted to approx 60 L min^{-1}, which meant the gas inside the box was replaced every 2 h. Two concentration series were used: 0, 10, 20, 30, 40, 50 μL L^{-1} and 0, 1, 3, 6, 35 μL L^{-1}, and these values were verified by gas chromatography calibrated with an ethylene standard. Plants were treated for 48 h at 25°C day/15°C night then transferred to a glasshouse. Plants were bisected 25 days after treatment and percent induction calculated from visible development of inflorescences.

Ethephon Application to Whole Plants

Effects of mode of application and dose on flowering were tested by applying ethephon to plants at a pineapple farm near Nambour (26°S). Flower induction was calculated from percent visible initiation 72 days after treatment. Three treatments were used with 80 plants per treatment:

1. Each plant was sprayed with 12 mg of ethephon in 50-mL solution (40% of normal commercial dose).
2. Each plant was sprayed with 6 mg in 25-mL solution (20% dose).
3. 25 mL of solution containing 6 mg ethephon poured down the heart of each plant (20% dose).
4. Control untreated plants.

Leaf Porometry

Diurnal changes in leaf properties were measured using a Li-Cor LI1600 steady-state porometer. At 2–4 h intervals over a 24-h period, readings were taken of conductance, transpiration, relative humidity, leaf temperature, air temperature, and irradiance.

Results

Influence of Temperature, Humidity, and pH

A standardized assay was developed to enable assessment of effects of varying single factors on ethephon uptake into leaf tissues. The effects of temperature and solution pH on [^{14}C]ethephon uptake through the epidermis of white basal leaf tissue are shown in Fig. 1. In all cases, uptake over the first 3 h was more rapid at 32°C than at 26°C. Penetration of ^{14}C through the abaxial (lower) epidermis was also consistently greater than through the adaxial (upper) epidermis. Overall, uptake was least at pH 8 through the adaxial epidermis and greatest at pH 2 (nearly 30% of applied dose) through the abaxial epidermis. When assays were run under different relative humidities (RH), uptake under low RH was always initially faster than under high RH (Fig. 2*a*). This correlated with observed differences in rates of solution drying on the leaf surface: at the time of sampling (2 h) all droplets under low RH had dried, but all those under high RH were still wet. If all droplets were allowed to dry overnight, there was much less difference in uptake between humidity treatments, but uptake in high humidity was consistently slightly greater (Fig. 2*b*). Maximum

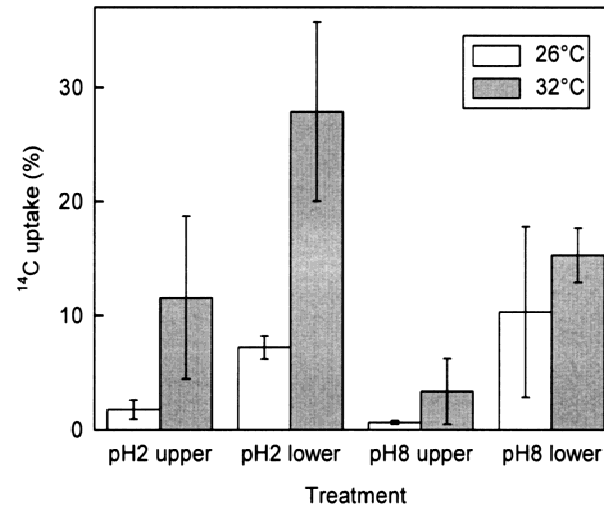

Fig. 1. Effect of temperature and pH on ethephon uptake through adaxial (upper) and abaxial (lower) epidermis of white (basal) leaf tissue of pineapple. Solutions contained 500 mg L^{-1} ethephon and 25 MBq L^{-1} [^{14}C]ethephon. Relative humidity >80%; incubation time 3 h. Data are means of four experiments at each temperature. Bars are ±S.E.

uptake was consistently higher into white leaf tissue (40–50%) than into green leaf (up to 30%). Figs. 3 and 4 confirm the influence of solution drying: here, uptake data have been segregated according to dryness at sampling time and show significantly greater uptake in disks with dried droplets. Generally, at all temperatures and humidities, relatively little uptake appeared to occur until the droplet was nearly or completely dry. This was true for both white basal and fully green tissues. The time taken for drying also varied with air flow and droplet volume (data not shown). No significant difference in patterns of uptake was noted between ethephon applied in the morning or the evening (Fig. 4).

Ethephon is progressively less stable with increasing pH. However, the influence of pH on ethephon uptake appeared not to be related to rate of ethephon breakdown on the leaf surface. Penetration through the adaxial epidermis was usually more rapid at pH 2 than at pH 8 (Figs. 1 and 2*a*), but the difference was less marked once the droplets had dried (Fig. 2*b*). Uptake through the abaxial epidermis was not markedly affected by pH (Fig. 1).

It was initially assumed that most spray droplets in the field would land on upper rather than lower leaf surfaces. However, with high-volume sprays and given the channel-shaped leaves of pineapple, there is considerable "ponding" of solution into the leaf axils and the heart of the plant. This would result in prolonged contact of active solution with both surfaces of the basal white leaf tissue and might be a significant route of ethephon entry.

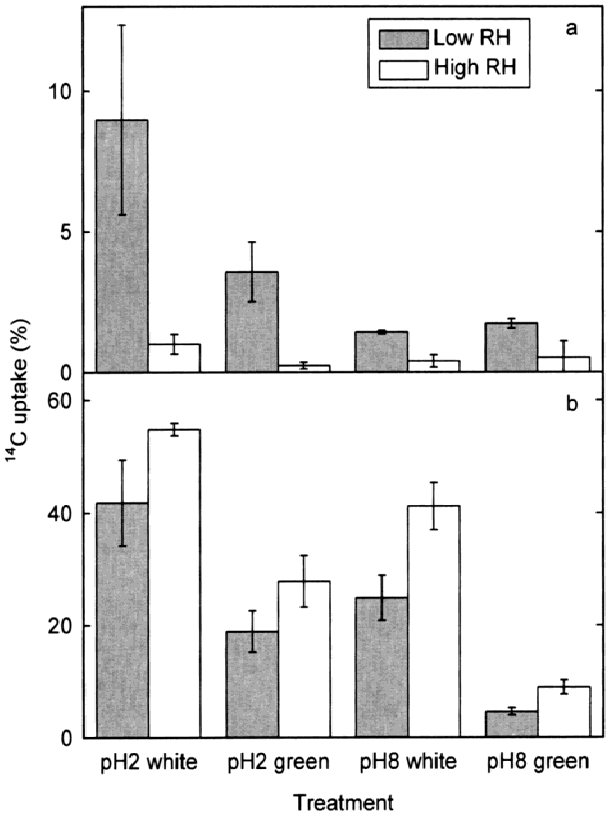

Fig. 2. Effect of relative humidity and solution drying on ethephon uptake through adaxial (upper) epidermis of white and green leaf tissues. Temperature 26°C; RH 20–25% (low) or 80–89% (high). Bars are ±S.E. (*a*) 2 h after ethephon application at which time all droplets under high RH were still wet. (*b*) 22 h after ethephon application at which time all droplets were dry.

Indeed, where conditions were selected to prevent solution drying (high RH and moderate temperature), the abaxial surface was an up to fourfold more efficient route of entry at pH 2 and up to 10-fold at pH 8 (Fig. 1). Under comparable conditions, we consistently noted more rapid disappearance of solution on the abaxial epidermis than on the adaxial surface.

Distribution of Absorbed Ethephon Within Leaf Tissues

To assess label distribution within the different leaf tissues, leaf disks cryosectioned through the thickness of the leaf were analyzed for total ^{14}C content (Fig. 5). Regardless of pH, label entering through the abaxial surface was evenly distributed through the whole depth of the leaf, whereas label entering through the adaxial surface accumulated more in the upper 0.5–1 mm, which corresponds mainly to water storage tissue. Movement of ethephon in 5-cm long white leaf segments was also detected and indicated relatively greater basipetal movement of label entering through the abaxial surface (data not shown).

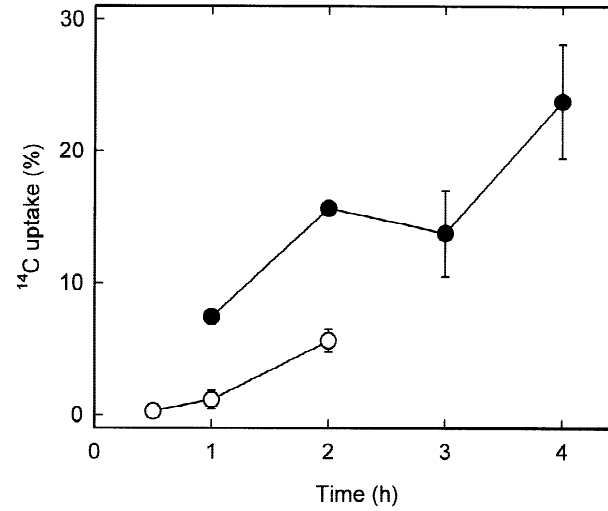

Fig. 3. Influence of solution drying on ethephon uptake through adaxial epidermis of individual white leaf tissue disks. Temperature 26°C, RH 20%, pH 2. ○, disks with wet droplets; ●, dried droplets.

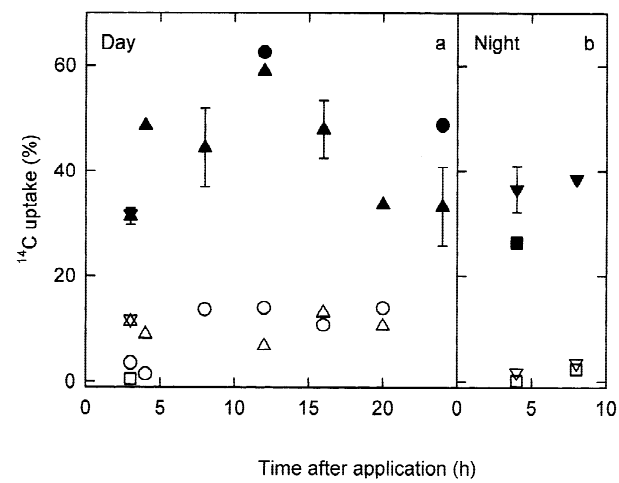

Fig. 4. Influence of solution drying rate and time of day of application on ethephon uptake into white leaf tissue. Open symbols are droplets remaining wet; closed symbols are from dried droplets. ○, ●, pH 2 adaxial epidermis; △, ▲, pH 2 abaxial epidermis; □, ■, pH 8 adaxial epidermis; ▽, ▼, pH 8 abaxial epidermis. RH >80%, temperature 32°C. For clarity, only some error bars are shown ± S.E. (n = 3) leaf disks for each point. (*a*) Daytime application (1030H); (*b*) evening application (1730H).

Route of Ethephon Entry: Influence on Floral Induction

An experiment on whole plants under field conditions tested the influence of different placements of ethephon on the plant. Equivalent amounts of ethephon (20% of

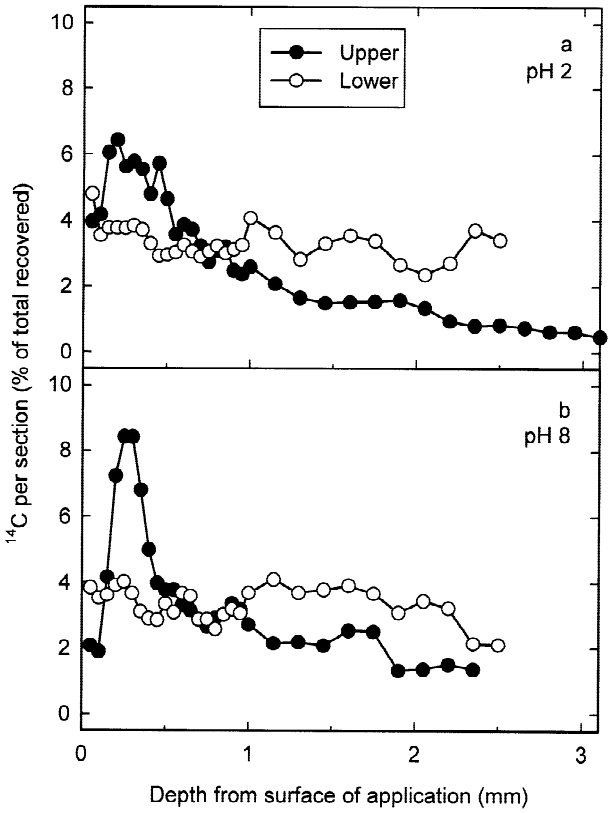

Fig. 5. Tissue distribution of ethephon entering white leaf tissue through adaxial (upper) or abaxial (lower) epidermis, expressed as a percentage of total recovered radioactivity. Background radioactivity has been subtracted from all values. Total radioactivity applied per leaf disk and mean total percent recovered was 670 Bq and 5.3% for pH 2 (*a*) and 450 Bq and 4.1% for pH 8 (*b*) treatments. All droplets had dried at time of sampling. Each curve is mean of two cryosectioned disks. For all plots, zero depth represents the application surface. Incubation time 17 h, RH 50%, temperature 32°C.

the recommended commercial dose) were either sprayed evenly over the whole leaf system or poured into the heart of the plant. The spray treatment resulted in minimal flowering, but the heart-treated plants were 100% induced (Table 1). Even doubling the sprayed dose to 40% of normal was not as effective as direct treatment of the plant heart. In this experiment, plants were sprayed at midday and air temperature was 37°C. Untreated control plants did not flower.

Floral Induction by Ethylene Gas

Experiments were conducted to confirm that ethylene gas was able to induce flowering and to determine the minimum effective concentration of ethylene. Table 2 shows that as little as 1 μL L^{-1} can cause 100% induction. This concentration is equivalent to 60 g of ethephon

Table 1. Influence of ethephon placement on effectiveness of floral induction in field-grown plants. A 240-mg L^{-1} solution of ethephon (pH 9) was applied to each plant as indicated. Plants were treated at midday, and ambient air temperature was 37°C. Flowering was assessed 72 days after treatment ($n = 80$). There was no natural flowering in untreated control plants.

Treatment	Flowering (% of plants)
6 mg sprayed over whole plant	4
12 mg sprayed over whole plant	68
6 mg poured into plant heart	100

(approximately 5% of the usual field dose) being completely broken down, and the resulting ethylene gas spread evenly over 1 ha to a height of 1 m. This result was with plants that appeared to have a propensity for natural flowering, as indicated by the 17% of controls that also flowered. In the second experiment, the minimum dose of 10 μL L^{-1} was also 100% effective, and in this case none of the controls flowered (Table 2).

Leaf Porometry

The diurnal pattern of leaf stomatal behavior was monitored by steady-state porometry, with a particular interest in stomatal apertures through which ethephon solutions or ethylene gas might permeate. The stomata of pineapple are located exclusively on the abaxial surface and, as with normal CAM operation, aperture is greatest during the night (Fig. 6*a*). The minimal conductance measured during the day may be partly cuticular. Transpiration under the cool (May) conditions of the experiment (13–24°C) was relatively constant ranging from 0.85–1.35 mmol m^{-2} s^{-1} throughout the 24-h period. This was presumably due to higher vapor pressure deficit during the day when temperatures were higher and humidity lower (Fig. 6*b*) but compensated by the much lower daytime conductance.

Discussion

This work aimed to provide insight into why ethephon treatments sometimes fail to induce flowering in pineapple by investigating the characteristics of ethephon uptake and translocation. Several factors appear to influence these processes.

The initial premise, based on field observations, was that high temperature was a possible cause of flowering failure. However, comparison of ethephon uptake under hot (32°C) and moderate (26°C) conditions actually showed faster uptake at the higher temperature, regardless of solution pH or site of application (Fig. 1). Some of this increase was probably due to faster solution dry-

Table 2. Dose-response relationship of ethylene gas and floral induction. Ethylene was supplied to plants for 48 h. Temperature was 25°C day and 15°C night. Floral development was assessed from bisected plants 25 days after treatment ($n = 12$).

First trial		Second trial	
Ethylene (μL L^{-1})	Flowering (%)	Ethylene (μL L^{-1})	Flowering (%)
0	17	0	0
1	100	10	100
3	100	20	100
6	100	30	100
35	100	40	100
		50	75

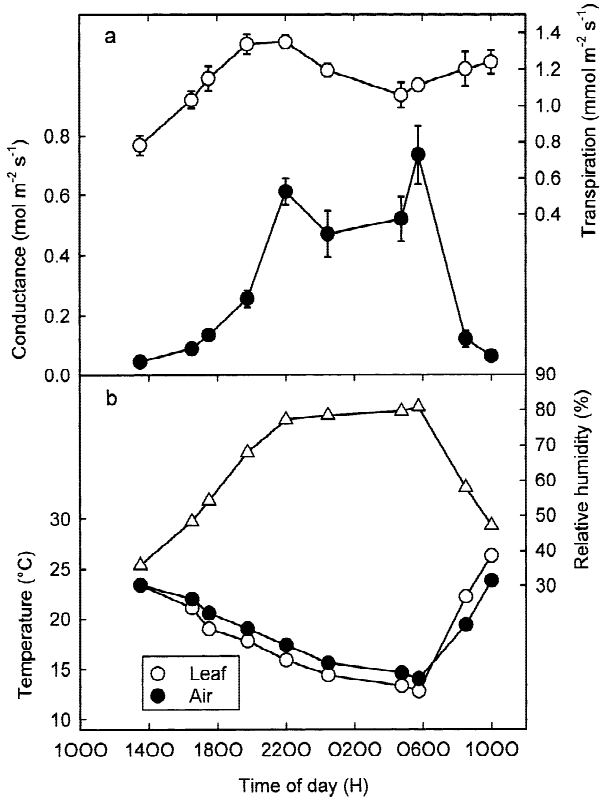

Fig. 6. Diurnal pattern of leaf conductance and transpiration (*a*) under shown temperature and humidity conditions (*b*). Potted plants in open air were monitored in Brisbane on May 1 1992. Bars are ± S.E. ($n = 3$).

ing. In fact, drying always enhanced uptake (Figs. 3 and 4), and a large proportion may enter the leaf just before complete evaporation of the liquid when the ethephon exists in a highly concentrated solution. This pattern of rapid ethephon uptake into olive fruits was noted by Epstein et al. (1977) and similar conclusions were reached for gibberellic acid in citrus tissues (Greenberg and Goldschmidt 1990). Variability between individual leaf disks was high where some replicates had dried droplets and some remained wet (e.g., some large error bars in Figs. 1 and 2*a*) compared with much less variation where replicates were either all dry or all wet (e.g., Figs. 2*b* and 4).

However, under field conditions dried spray droplets may not contribute much to the active dose. Three components of the results support this notion. First, uptake through the adaxial epidermis of green leaf tissue (i.e., most of the upward-facing plant surfaces) is limited particularly with high pH formulations such as currently used commercially (Figs. 1 and 2*b*). In fact, uptake at pH 8 was rarely faster than at pH 2 and was often slower. A similar dependence on pH has been found for gibberellin uptake (Greenberg and Goldschmidt 1989).

Second, the green leaf tissue is distant from the shoot apex where the flowering stimulus must ultimately be perceived. Relatively limited translocation was detected away from adaxially applied label and may also be inferred from label accumulating in the water storage tissue (Fig. 5) and hence away from the more metabolically active photosynthetic layers and the vascular system. Nir and Lavee (1980) similarly found slow but significant basipetal translocation of [^{14}C]ethephon applied to grapevine leaves. In barley, ethephon was transported from leaves to inflorescence more than to the plant base (Foster et al. 1992).

Third, a dose of ethephon poured into the heart of the plant was more effective at inducing flowering than the same quantity sprayed and allowed to dry on the exposed leaf surfaces (Table 1).

It is possible that ethylene released inside the leaf activates production of a second messenger signal that is transmitted to the apex. For example, Lavee and Martin (1975) presented data on ethephon binding to sugars, which might subsequently be transported in the phloem. There is no direct evidence for this in pineapple, but ethephon applied to the heart of the plant and low concentrations of ethylene gas are both highly effective (Tables 1 and 2). These two observations indicate that ethylene may be able to act directly on the apex.

Empirical flowering data from field applications of ethephon suggested that high-volume spraying was sometimes more effective (E. R. Sinclair unpublished). It was observed that the excess liquid runs down the channel-shaped leaves and accumulates in “ponds” in the leaf axils and around the apex. This solution would have a much slower drying rate than droplets on the distal adaxial leaf surfaces because of lower solution surface area/volume ratios and some degree of protection from sunlight and air movement. In addition, these ponds would also contact the abaxial leaf epidermis of the white leaf bases. Ethephon uptake characteristics under these circumstances were completely different. Penetration through the abaxial epidermis of the leaf base was

rapid (up to 40% within 3 h) without the need for droplet drying, particularly in the first few hours after applications, but was not greatly affected by pH (Fig. 1). Label was recovered at all depths within the leaf. It was not possible to distinguish [^{14}C]ethephon from released [^{14}C]ethylene, but the rapid cryosectioning method may also have trapped some of the [^{14}C]ethylene released within the leaf tissues, and this would contribute to the total ^{14}C signal. Other reports of [^{14}C]ethephon localization and transport have involved alternative methods in which ethylene, either in solution or in the gas phase, would probably not be retained (Denney and Martin 1994, Nir and Lavee 1980).

There was also evidence that solution disappeared more rapidly from abaxial than from adaxial surfaces, suggesting permeation of liquid through the stomata. Beaudry and Kays (1988), working with non-CAM plants, found little uptake of ethephon through astomatous epidermis or through epidermis with closed stomata. In this study, uptake through the astomatous adaxial epidermis was clearly occurring. Although Wassman (1989) found more efficient induction from evening ethephon applications, no differences in uptake rates were seen between day and night experiments (Fig. 4) when there should have been markedly different stomatal apertures (Fig. 6). This was unexpected given the consistently more rapid uptake of solution and of label by the abaxial epidermis. It is possible that the cutting of leaf disks disrupted stomatal behavior compared with intact plants. However, label entering through the abaxial epidermis was always found distributed evenly through the whole thickness of the leaf. Taking all these characteristics together, it is likely that solution in contact with the abaxial epidermis of the leaf bases and the shoot apex could contribute much of the ethephon required for flower induction.

In experiments in which flower induction was monitored (Table 1), it was shown that as little as 20% of the normal commercial ethephon dose caused full flowering but only when applied to the plant heart (i.e., in contact with the younger leaf axils and possibly the apex itself). This amount when sprayed onto the whole plant induced minimal flowering and even increasing the spray dose to 40% of normal was not as effective as the 20% heart treatment. This experiment was deliberately conducted on a very hot day (37°C) with plants sprayed at midday, giving rapid spray drying and conditions likely to result in flowering failure. Placement of the ethephon solution has a major influence on effectiveness of induction, but it is not clear whether ethylene released into the atmosphere from distal leaf surfaces would diffuse sufficiently to the shoot apex. However, direct treatment with ethylene gas was an efficient method of flower induction, with concentrations as low as 1 μL L^{-1} sustained for 48 h being fully effective. That concentration of gas would be released from complete breakdown of 5% of a normal ethephon dose if the ethylene was restricted to 1 m above ground. This may be a further indication that only a small amount of ethylene is needed for induction. However, such comparisons are not very meaningful partly because gas dissipation characteristics would be vastly different between field and closed growth chamber conditions.

Conclusions

It appears that (1) conditions that increase chances of flowering failure do not necessarily reduce ethephon uptake, (2) the abaxial leaf surface is possibly a more efficient route of ethephon entry into the plant, and (3) the minimum dose required for full floral induction depends on placement of the ethephon.

Failure to flower may be related to more than one factor. The detrimental effect of high temperature probably operates partly through causing very rapid spray drying on the distal adaxial leaf surfaces, little of which will run down the leaf channels or be translocated within the leaf, and a consequent lack of ethephon contact with proximal and abaxial surfaces and/or directly with the shoot apex. Flore and Bukovac (1982) also found that uptake of ethephon into cherry leaves was temperature-dependent and required placement of the solution on the abaxial (stomatous) epidermis. In addition, although not directly investigated here, high temperature may render plants physiologically less receptive to floral induction. Indeed, natural flowering is partially inhibited by high temperatures, especially at night (Friend 1981).

High-volume spraying (increased time before droplets dry and increased ponding in leaf axils), avoidance of spraying on hot days (reduced rate of spray drying and reduced risk of plant being unreceptive to inductive treatments), and evening spraying (reduced temperatures and hence lower spray drying rates and coinciding with nocturnal stomatal opening facilitating liquid and/or gas penetration) may diminish the frequency of flowering failures and are therefore worth exploring further under field conditions.

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