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Leaf Maturity and Temperature Affect Removal of Floral Buds from *Camellia* Ethephon

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Abstract. **The influence of temperature and leaf maturity on ethephon-promoted abscission was examined by simultaneously applying either ethylene (10.5 µl·liter^{-1}) or ethephon (0 to 4 ml·liter^{-1}) to potted *Camellia* plants at four constant temperatures (10 to 30C). The abscission rate (time to 50% abscission) and extent of abscission of leaves, and vegetative and floral buds was measured. Increased temperature promoted the rate and extent of ethephon-promoted abscission and increased ethylene-promoted abscission rate of all organs of *Camelliu.* Lower temperatures reduced the abscission rate after ethephon application more than that following ethylene application. Sensitivity to ethephon was greater for leaves on newly extending shoots, although once shoot elongation and leaf expansion had ceased, leaves became less sensitive. Ethephon sensitivity increased progressively with maturation over the following 2 years. Optimal thinning of floral buds . at low temperatures required high ethephon concentrations, while at high temperatures, low ethephon concentrations were optimal. The influence on abscission of the time of year when ethephon was applied, is suggested to be due to tissue maturity, which affects tissue ethylene sensitivity, and temperature, which affects ethylene release from ethephon and tissue response to ethylene. Chemical name used: (2-chloroethyl) phosphoric acid (ethephon).**

Camellia plants are currently exported from New Zealand to the northern hemisphere in late summer and fall. At this time, floral buds must be removed manually, since the presence of floral buds is undesirable for subsequent vegetative budbreak and plant growth. An alternative is chemical thinning, where the aim is to promote target organ abscission with minimal abscission of nontarget organs. Ethephon is an ethylene-releasing compound (ERC), which is widely available and relatively simple to apply in a commercial system. Previous work has demonstrated that ethephon can selectively remove, or thin, floral buds from *Camellia* (Woolf et al., 1992). The efficacy of ethephon application in removing target organs is influenced by a wide range of factors including temperature, concentration, organ type, and organ maturity.

Temperature is the most important environmental factor. Applying ethephon at low temperatures results in significantly lower organ abscission (Jones and Keen, 1985; Klein et al., 1978). Temperature influences ethylene release from ethephon (Klein et al., 1978). The rate of ethylene evolution from ethephon-treated *Prunus* leaves, for example, strongly depends on temperature with an activation energy (E_a) value of 125.6 kJ·mol^{-1} (Olien and Bukovac; 1978). Because high temperature increases the rate of ethylene release from ethephon, the duration of exposure to ethylene will be reduced. Olien and Bukovac (1978) proposed a half-life concept for ethylene release from ethephon, half-life being proportional to the inverse of temperature (5.6 days at 20C and 26.5 h at 30C).

Temperature also influences tissue response to ethylene (Olien and Bukovac, 1978). Abscission at a given ethylene concentration decreases progressively with lower temperatures (Addicott, 1982). For instance, a temperature decrease from 25 to 16C lowers ethylene-promoted leaf abscission of *Fittortia* (9% to 0%) and *Philodendron* (28% to 9%) (Marousky, 1979; Marousky and Harbaugh, 1979).

Much reported research involves application of either a range of ethephon or ethylene concentrations at one temperature or of a single concentration at a range of temperatures (Beaudry and Kays, 1988; Jones and Keen, 1985; Jones et al., 1983; Olien and Bukovac, 1978). However, information on the interaction between temperature and ethephon concentration, required for accurate modelling of ethephon application (Jones and Keen, 1985), is lacking.

Maturity influences the sensitivity of ethylene- and ethephon-promoted abscission of leaves (Morgan, 1969; Weis et al., 1988). Although it is generally accepted that greater leaf maturity increases ethylene sensitivity (Goren et al., 1988), this is not always the case. Abscission responses to ERCS are high for young unexpanded leaves of *Capsicum* and *Gossypium* but decrease as leaves cease expanding (Beaudry and Kays, 1988; Morgan, 1969).

The influence of ethephon concentration, cultivar, and time of year on thinning of floral buds from *Camellia* has been examined, and optimal concentrations have been suggested for selective removal of floral buds, without excessive leaf or vegetative bud abscission (Woolf et al., 1992). Differences in abscission response to ethephon following applications made at different times of the year may have been a result of tissue maturity or environmental factors, particularly temperature. To establish the importance of these factors in ***Camellia,*** the influence of temperature and leaf maturity and their interaction with ethephon concentration were examined.

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Materials and Methods

Plant material. Camellia saluenesis x *C. japonica* 'Anticipation' plants were obtained (Duncan and Davies Nurseries Ltd, New Plymouth, New Zealand) mid-winter 1990 as rooted cuttings with one flush of growth completed. Vegetative budbreak was promoted using simulated summer conditions (15 to 25C and continuous photoperiod obtained using 100-W incandescent light bulbs). Once stem elongation had ceased and matured for 3 weeks, plants were potted into 1.75-liter plastic pots containing a 3 peat: 2 pumice (v/v) growing medium and amendments of dolomite (3 g·liter^{-1}), 3- to 4- and 8- to 9-month Osmocote (0.6 and 3 g·liter^{-1}, respectively; Sierra, N.Z.), and Micromax (0.9 g·liter^{-1}; Sierra). After chilling (3 weeks at 7 ± 2C in darkness), plants were replaced in simulated summer conditions for promotion of a new flush of growth and flower initiation. The resulting plants were about 60 cm high, typically bearing 9 floral buds, 56 leaves, and 16 vegetative buds.

Two concurrent experiments involving treatment of plants with either ethephon or ethylene were carried out at the National Climate Laboratory, The Horticulture and Food Research Institute of New Zealand Ltd, Palmerston North, N. Z., in May (late fall). Plants treated with ethephon were placed in controlled-environment rooms (for details refer to Warrington et al., 1978). To avoid the possibility of ethylene contamination, ethylene treatment was carried out simultaneously in smaller growth cabinets (under similar environmental conditions). Ethephon application in controlled-environment rooms was carried out at four constant air temperatures (10, 16.7, 23.3, and 30, all ± 0.5C) with relative humidity (RH) of 70% ± 5% (corresponding to vapor pressure deficits of 0.37,0.57,0.87, and 1.27 kPa, respectively). The light environment consisted of 12 h full light intensity (photosynthetic photon flux intensity of 700*15 µmol·m^{-2}·s^{-1}) and 4h photoperiod extension (10 ± 1 µmol·m^{-2}·s^{-1}). Carbon dioxide concentration varied between 356 and 576 µl·liter^{-1}. Plants were acclimatized in the controlled environment rooms for 10 days before ethephon treatment and watered by microtube irrigation once daily at 10C, twice at 23.3 and 16.7C, and three times at 30C. Due to the possible effect of released ethylene (from ethephon) on plants in close proximity, ethephon treatments were blocked on trolleys and the trolleys randomly relocated twice weekly within each controlled-environment room. Background ethylene was monitored and found to not exceed 0.020 µl·liter^{-1} using a Photovac gas chromatography [photoionization detector, air carrier gas at 45 ml·min^{-1}, fitted with 15 cm precolumn, 1.8 m main column (type XE60), ambient temperature (about 23 C), Alltech Associates NZ Ltd, Auckland, New Zealand].

Ethephon treatment. Ethephon (Ethrel 48, Rhone-Poulenc Ltd, Wellington, N. Z.) was applied as an aqueous foliar spray at six concentrations (0, 0.5, 1, 2, 3, and 4 ml·liter^{-1} a.i.) containing Tween 20 (0.5% v/v) and prepared with distilled reverse osmosis

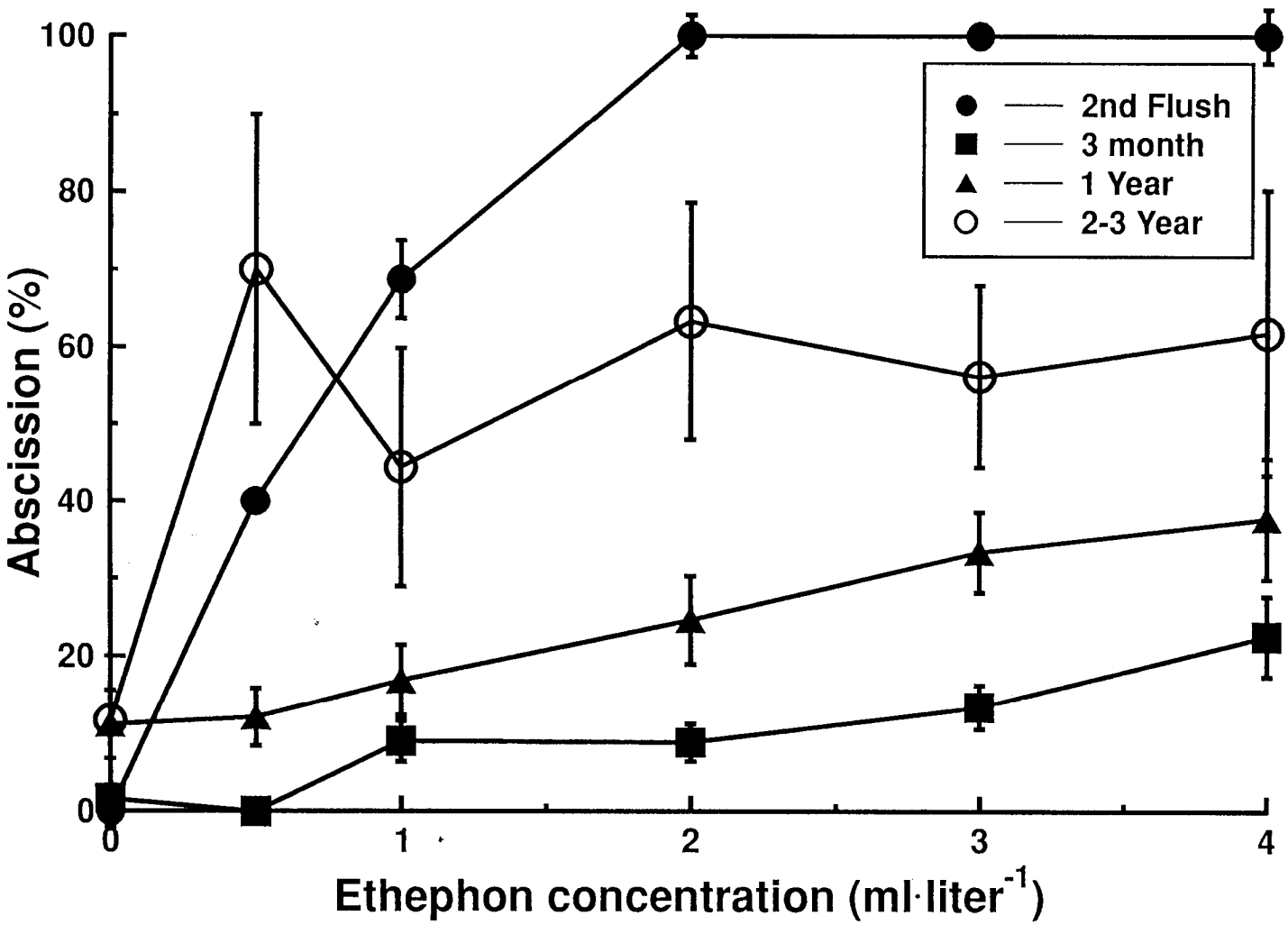

Fig. 1. Effect of ethephon concentration on abscission percent of four leaf maturities of Camellia 'Anticipation' after ethephon application at 16.7C. Vertical bars represent SE of the mean (n = 10).

water. Ethephon was sprayed till incipient runoff (about 20 ml/plaNt) to 10 whole-plant replicates on 7 May 1991 (late fall). Since temperature and RH influence drying time of sprays (Kays and Beaudry, 1987), ethephon was applied outside the facility (12C), and foliage was dried in the laboratory for 45 min. (21C, 60% RH) before plants were placed in the various temperature treatments.

Flow-through ethylene gas treatment. The effect of temperature on rate of ethylene-promoted abscission was examined by applying ethylene gas in a flow-through system. Ten whole-plant replicates were individually sealed in 15-liter (35-µm) clear polyethylene bags and pure ethylene was mixed with humidified air to attain 10.5 ± 1.4 $\mu l \cdot liter^{-1}$ circulated at a flow rate of 30 $liter \cdot h^{-1}$ for each bag (2 air changes/h). Plants were placed in controlled temperature cabinets to result in air temperatures within bags of 10, 16.7,23.3, and 30 ± 2C with continuous light (720 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Oxygen and CO_2 concentrations were monitored and found to remain at ambient levels in all treatments. Although not measured, RH was maintained at a high level (>90%) by bubbling incoming air through a barostat before mixing with ethylene and passage through the treatment bags. Air temperature and ethylene concentration were monitored inside the bags using a Squirrel data logger (thermistor temperature probes; Grant CM-UU-V5-1) and the Photovac gas chromatography throughout the experiment.

Effect of leaf maturity. In *Camellia*, vegetative budbreak occurs in spring and involves abscission of bud bracts and subsequent shoot elongation. Once elongation has ceased, floral buds are initiated and develop over summer and fall. Apical floral and vegetative buds develop fastest and are, therefore, more mature than axillary buds. In late summer, vigorous apical buds may make a second flush of shoot growth. Flower opening occurs between fall and spring, depending on plant species or cultivar and environmental conditions. Thus, in late summer, shoots and branches bearing leaves of a range of maturities may be present: second flush extending shoots (containing softer, expanding leaves), 3-

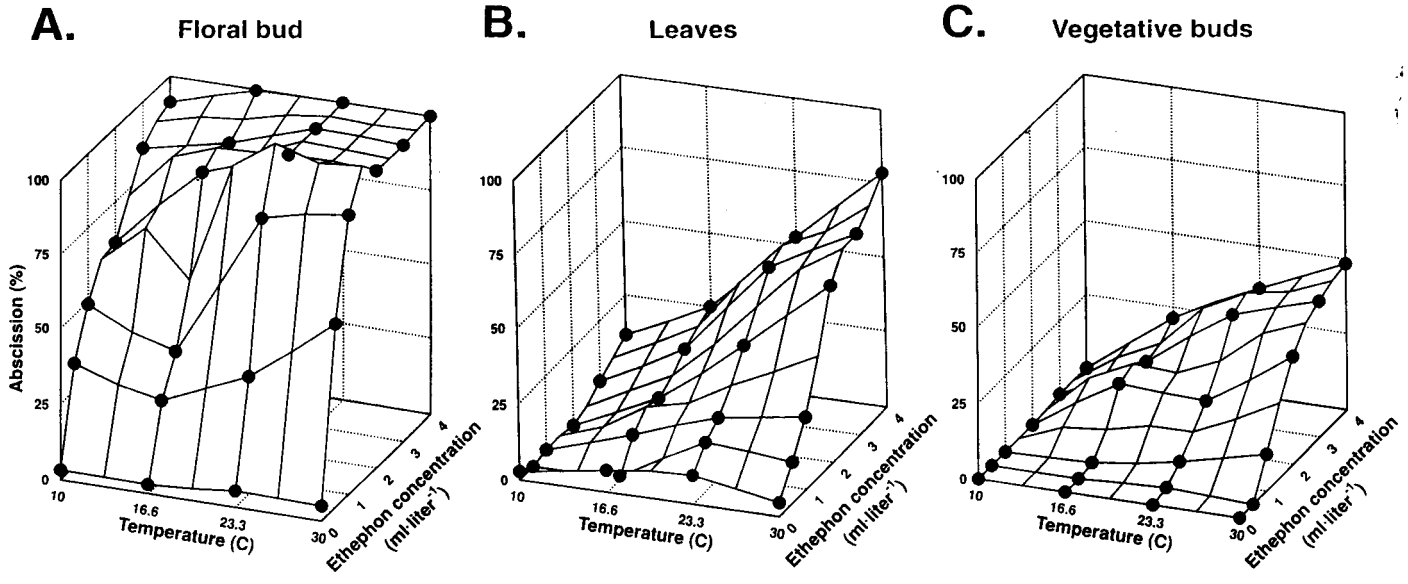

Fig. 2. Effect of temperature and ethephon concentration on abscission percent of floral buds **(A),** leaves **(B),** and vegetative buds **(C)** of *Camellia* 'Anticipation'

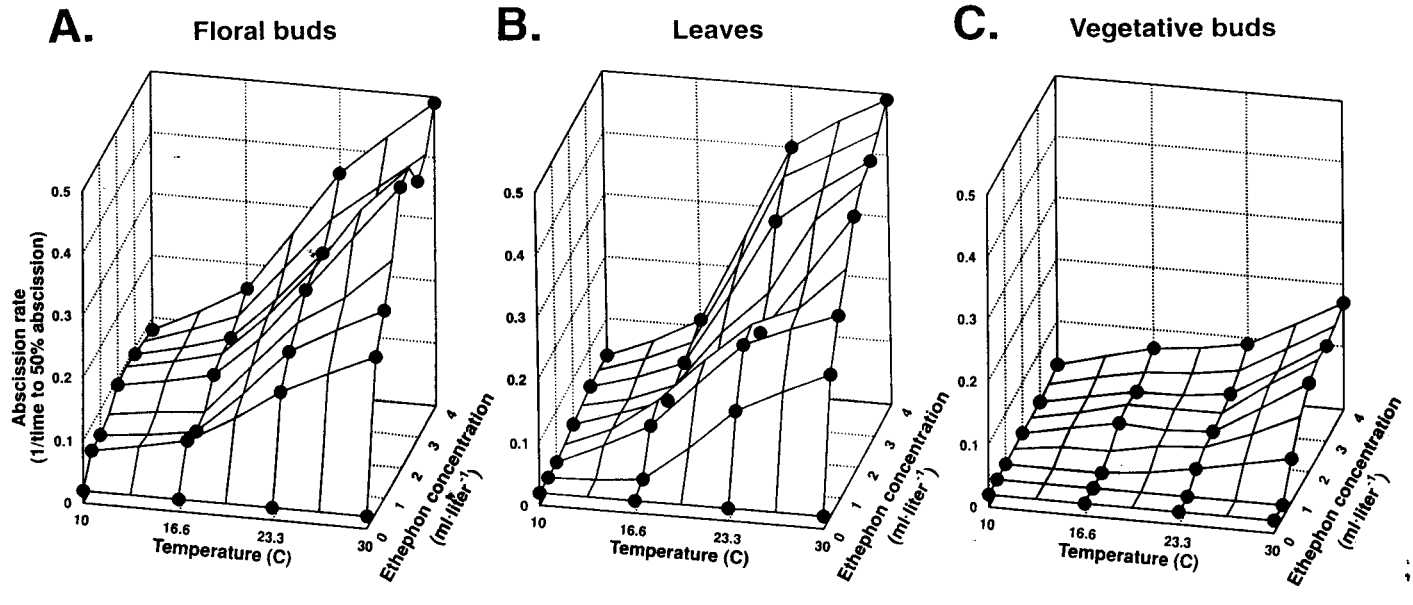

Fig. 3. Effect of temperature and ethephon concentration on abscission rate (1/days to 50% final abscission) of floral buds **(A),** leaves **(B),** and vegetative buds (C)of *Camellia* 'Anticipation'.

month-old (current summer) shoots, 1-year-old shoots, and 2-to 3-year-old shoots. Vegetative buds are present on current-season and previous-season shoots only. Natural abscission occurs at different times for each of the organs of *Camellia:* floral buds after flower opening and subsequent senescence, vegetative bud bracts at budbreak in spring, and leaves after 2 to 3 years with greatest leaf abscission occurring at vegetative budbreak.

At one temperature only (16.7 C), the ethephon sensitivity of within-plant leaf populations was examined by labelling stem maturities (and thus leaves), which were present in later fall in four categories: second flush (extending shoots and shoots that had ceased extending in <2 weeks), 3-month- (current summer shoots bearing floral buds), l-year-, and 2- to 3-year-old leaves. At the time of treatment, plants typically contained four second flush, thirty 3-month, twenty-one 1-year-old, and one 2- to 3-year old leaf.

Measurements. The number of floral and vegetative buds and leaves were counted before applying ethephon and ethylene treatments and at appropriate intervals depending on abscission rate. Each temperature treatment was terminated when abscission rate of treated plants dropped to that of the controls. Vegetative buds damaged or killed following abscission of bud bracts were regarded as abscised for the purposes of this experiment (Woolf et al., 1992).

Except for extending second flush shoots used in the examination of the effect of leaf maturity on ethephon sensitivity (at 16.7C), second flush shoots were tagged and excluded from analysis. This was carried out because abscission characteristics of such shoots differ greatly from those of matured shoots (Woolf, 1993). Low SE values (maximum SE for final abscission of floral and vegetative buds and leaves of 10.1%, 7.7%, and 5.8% respectively) indicated that the presence of extending shoots did not alter abscission of organs on shoots of other maturities.

Statistical analysis. The final level, or extent, of organ abscission was calculated as the percent abscised of the original organ number and is referred to as abscission percent. Analysis of the interaction effects between ethephon concentration and temperature on abscission percent were carried out using SAS (SAS Institute, Cary, N.C.). The percent data were ranked and an analysis of variance carried out for each organ using procedures RANK and ANOVA respectively. This nonparametric analysis is equivalent to the Kruskal-Wallis k sample test.

Abscission rate was calculated as the inverse of days to 50% of the abscission percent. Where no abscission occurred, rate was expressed as the experimental end point. To determine the effect of temperature on abscission rate, the activation energy, or E_a, was calculated. This was carried out by plotting the natural log of l/rate vs. l/K. According to the Arrhenius equation $v = Ae^{Ea/RT}$, where v is the rate of reaction (in this case l/time to 50% abscission), R is the universal gas constant, and T the absolute temperature (K). Thus, activation energy (E_a) and SE could be derived from slope and SE of fitted lines since E_a = slope × –R (Field, 1981).

Results

After ethephon application, leaves that had fully expanded (3 months old) exhibited lowest abscission levels, and older leaf populations (1 year and 2 to 3 years old) were more sensitive (Fig. 1). Leaves on second flush shoots were more sensitive to applied ethephon than leaves on all older shoots, reaching 100% final abscission at 2 ml·liter^{-1} ethephon. Three-month-old and 1-year-old leaves comprised over 98% of the leaves on each plant (excluding second flush leaves) and the abscission percent of these two leaf populations differed by only 10% to 20%. This supports the use of the leaf populations present on these plants to study the response to temperature and ethephon concentrations (Figs. 2–5). Abscission percent of untreated *Camellia* leaves tended to increase with leaf maturity (Fig. 1).

Temperature had minimal effect on abscission of *Camellia* organs in the absence of ethephon. Over the 20C increase exam-

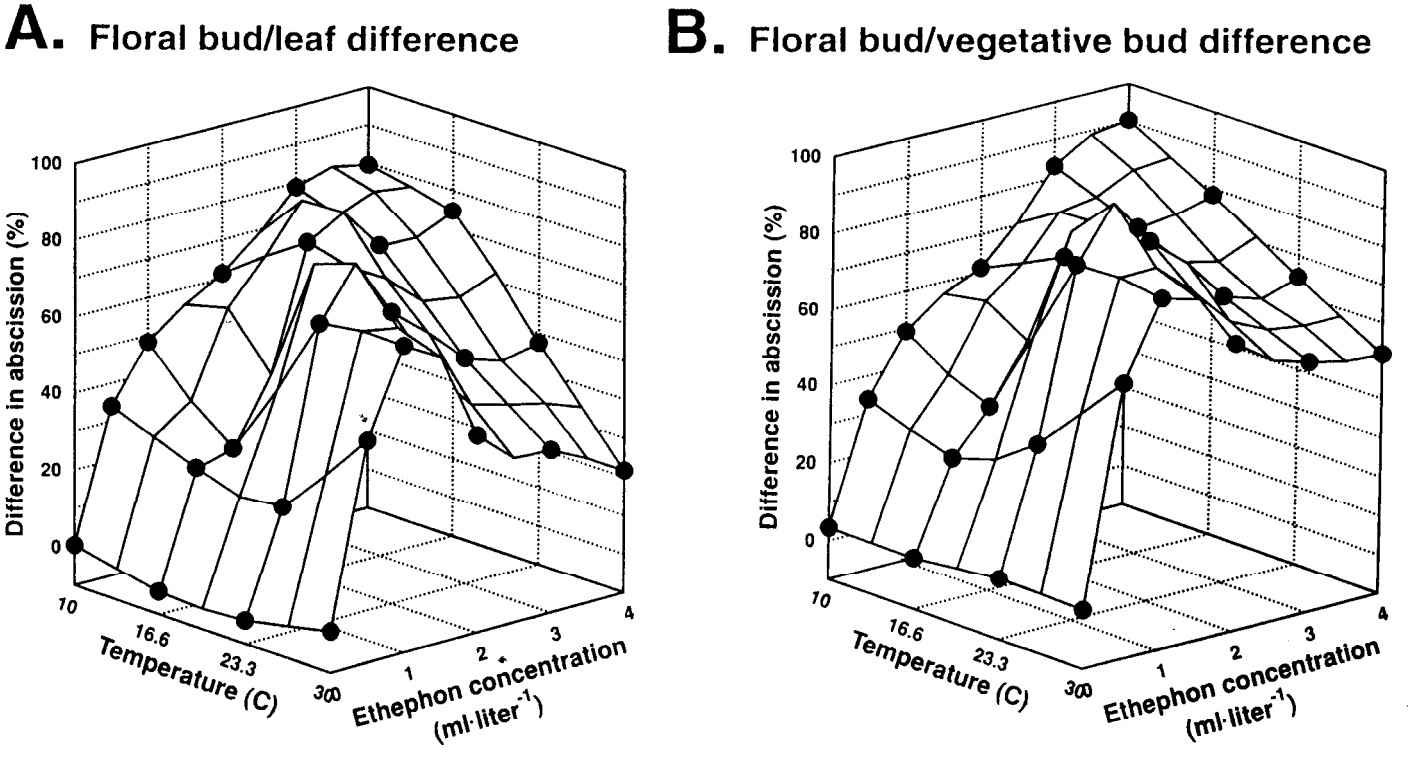

Fig. 4. Effect of temperature and ethephon concentration on difference between abscission percent of floral buds and leaves **(A),** and floral buds and vegetative buds **(B)** of *Camellia* 'Anticipation'.

ined, no abscission occurred in untreated vegetative buds and there was only a marginal increase for floral buds (2%) and leaves (3%). However, increasing temperature and ethephon concentration independently increased abscission percent (Fig. 2) and abscission rate (Fig. 3) of all *Camellia* organs. No interaction was found between temperature and ethephon concentration in any organ.

Analysis of slopes of fitted regression equations for abscission percent indicated a positive response to temperature at all ethephon concentrations (Table 1). Over the 20C increase in temperature, the percentage increase in abscission after application of 1 ml·liter^{-1} ethephon was 55% for floral buds, 25% for leaves, and 13% for vegetative buds (Fig. 2).

Across treatments, more floral buds abscised compared to either leaves or vegetative buds with >90% floral bud abscission in 11 of 24 treatments, while vegetative bud abscission only reached a maximum of 48%. The trend floral buds being the most sensitive and vegetative buds the least sensitive to applied ethephon held at all concentration and temperature combinations for abscission percent (Fig. 4). Abscission rate of floral buds and leaves were both greater than vegetative buds (Fig. 5B), but differed little from each other (Fig. 5A).

Higher temperature increased the abscission percent of all organs, but the magnitude of response was different for each organ. Slope of regression lines fitted to abscission percent data (Table 1) revealed that floral buds were influenced more by temperature than leaves and vegetative buds up to the point where 100% abscission of floral buds occurred (2 to 4 ml·liter^{-1}). Higher temperature increased the abscission percent of leaves more than that of vegetative buds. However, the influence of temperature on abscission rate was different from that of abscission percent. Abscission rate for leaves was increased more by higher temperatures than that for floral buds after ethephon application (E_a values 91.0 to 96.5 cf 52.0 to 67.0 kJ·mol^{-1}, respectively; Table 2), whereas the E_a of floral and vegetative buds were similar (52.0 to 67.0 cf 47.3 to 66.7 kJ·mol^{-1}, respectively). The E_a for each organ showed no consistent trend as ethephon concentration was increased, except for control treatments (0 ml·liter^{-1}) and the 0.5 ml·liter^{-1} treatment of vegetative buds (Table 2).

After application of ethylene gas, leaves and floral buds had a greater abscission rate than vegetative buds at all temperatures. At low temperatures (10C), abscission rate of leaves and floral buds did not differ, but with increased temperature, leaves exhibited a progressively higher abscission rate than floral buds (Fig. 6).

The influence of temperature on abscission rate after application of ethylene gas was different from that of ethephon application. In this case, high temperatures increased leaf abscission by the greatest amount, floral buds were intermediate, and vegetative buds least influenced (E_a values 54.2, 45.1, and 24.1 kJ·mol^{-1}, respectively; Fig. 6, Table 2).

The effect of temperature on ethylene-promoted abscission could be separated from its influence on ethephon-promoted abscission by comparison of E_a (slope of fitted regression lines to Arrhenius plots of abscission rate). For each organ, the E_a of ethylene treatment was less than that of all ethephon concentrations (excluding 0 values; Table 2). The proportion of temperature effect on ethephon-promoted abscission due to its influence on ethylene-promoted abscission was 75%, 58%, and 41% for floral buds, leaves, and vegetative buds, respectively (Table 3).

The thinning potential of each concentration and temperature treatment was highlighted by subtraction of abscission percent of leaves from floral buds and vegetative buds from floral buds (Fig. 4 A and B, respectively). Temperature markedly affected the ethephon concentration, which brought about the maximum abscission percent difference. Greatest difference was found at the lowest temperature (10C) and highest ethephon concentration (4 ml·liter^{-1}) for floral bud–leaf and floral bud–vegetative bud comparisons. The ethephon concentration resulting in the greatest thinning potential decreased as temperature increased from 10 to

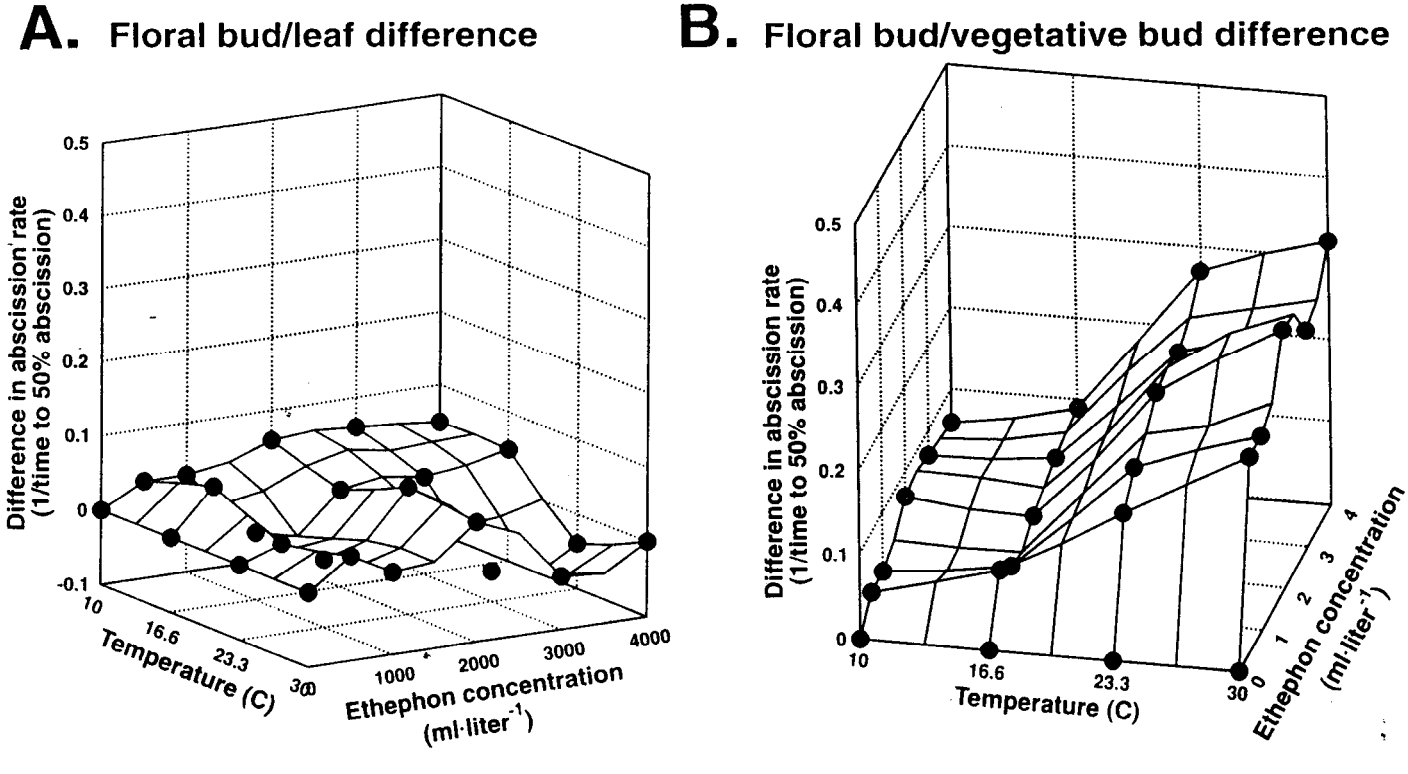

Fig. 5. Effect of temperature and ethephon concentration on difference between abscission rate (l/days to 50% final abscission) of floral buds and leaves **(A)** and floral buds and vegetative buds **(B)** of Camellia 'Anticipation'.

Table 1. Effect of temperature (10 to 30C) on linear regressions produced line slope, correlation coefficient (r^2), and slope SE and effect of abscission percent of three *Camellia* organs-floral buds, leaves, and vegetative buds—treated with ethephon (0 to 4 ml·liter^{-1}).

		Ethephon concn (ml·liter^{-1})					
Organ type		0	0.5	1	2	3	4
Floral buds	Slope	0.11	1.40	2.72	0.88	0.86	0.41
	r^2	0.65	0.66	0.72	0.79	0.86	0.63
	SE	0.05	0.71	1.20	0.69	0.23	0.20
Leaves	Slope	0.11	0.84	1.18	2.95	3.25	3.42
	r^2	0.10	0.74	0.98	0.98	0.98	0.98
	SE	0.23	0.35	0.13	0.28	0.36	0.30
Vegetative buds	Slope	0.00	0.02	0.62	1.58	2.26	2.36
	r^2	1.00	0.06	0.91	0.88	0.98	0.99
	SE	0.00	0.05	0.14	0.41	0.22	0.20

Table 2. Activation energy (E_a; kJ mol^{-1}) derived from abscission rate (Mime to 50% final abscission) after ethephon (0 to 4 ml·liter^{-1}) and ethylene (10.5 µl·liter^{-1}) treatment at temperatures of 10 to 30C of three *Camellia* organs—floral buds, leaves, and vegetative buds. Abscission rate data was graphed as Arrhenius plots and linear regressions used to calculate E_a, (line slope), correlation coefficient (r^2), and slope SE of the fitted regression line and, therefore, of the E_a.

		Ethephon concn (ml·liter^{-1})						Ethylene
Organ type		0	0.5	1	2	3	4	10.5 µl·liter^{-1})
Floral buds	E_a	0.00	52.0	62.4	60.2	56.9	67.0	45.1
	r^2	1.00	0.98	0.94	0.97	0.98	0.98	0.93
	SE	0.00	5.1	11.0	7.9	6.2	7.4	8.5
Leaves	E_a	0.00	94.1	96.5	91.0	91.1	94.6	54.2
	r^2	1.00	0.93	0.92	1.00	0.96	0.94	0.91
	SE	0.00	18.6	20.2	8.0	18.0	16.2	12.3
Vegetative buds	E_a	0.00	0.00	47.3	62.5	66.7	58.5	24.1
	r^2	1.00	1.00	0.89	0.90	0.95	0.97	0.78
	SE	0.00	0.00	12.0	14.9	11.0	7.8	8.9

30C. The ethephon concentrations which brought about maximal difference between abscission percent of floral buds and leaves and vegetative buds were 1 ml·liter^{-1} at 30C, 1 to 2 ml·liter^{-1} at 23.3C, 2 to 4 ml·liter^{-1} at 16.7C, and 3 to 4 ml·liter^{-1} at 10C.

Discussion

The chief aim of thinning is the promotion of target organ abscission with minimal abscission of nontarget organs. This work with *Camellia* demonstrated the potential for high ethephon concentrations applied at low temperatures, and *vice versa*, to selectively remove floral buds (the target organ), while resulting in low abscission levels of nontarget organs (leaves and vegetative buds). Ethephon at 4 ml·liter^{-1} at 10C achieved maximum thinning efficiencies of 90% for the floral bud–vegetative bud and 80% for the floral bud–leaf differences.

Ethephon-promoted *Camellia* abscission was highly temperature dependent with comparable results to other genera. As measured using abscission percent, the temperature response in *Malus* flowers is greater than that of *Camellia* with a 71% increase from 12 to 24C after application of 0.4 ml·liter^{-1} ethephon (Jones and Keen, 1985). Regression analysis produced a slope of 5.93 for *Malus*, which is also larger than the maximum for *Camellia (2.72* at 1 ml·liter^{-1}; Table 1). After application of an ERC silane (CGA-15281), abscission rate of *Prunus persica* leaves increased from 2 to 4 days at 16C to <2 days at 27C (Porpiglia and Barden, 1980), which was similar to *Camellia* leaves.

Ethylene-promoted abscission rate of all *Camellia* organs increased with higher temperatures in a similar manner to that of *Capsicum*, where a temperature increase from 18 to 32C increased leaf abscission 375% and floral bud abscission 40% (Beaudry and Kays, 1988). In contrast, the temperature effect on ethylene-promoted abscission in *Prunus* is very low (Olien and Bukovac, 1982).

Ethylene gas application allowed separation of the influence of temperature on ethylene release from ethephon from the effect of temperature on the ethylene-promoted abscission response. Although increased ethephon concentration resulted in faster abscission, the influence of temperature on ethephon-promoted abscission was similar at all ethephon concentrations. That is, E_a values showed no consistent trend with changing ethephon concentration, while E_a values of ethylene treated organs were lower than those of all ethephon-treated tissue (Table 3). This clearly demonstrated that, in all organs of *Camellia*, temperature influenced ethylene-promoted abscission less than ethephon-promoted abscission.

The influence of temperature on ethephon-promoted abscission was not an artifact of drying time, since all plants were dried at the same temperature. Moreover, the possibility that RH may have influenced the response obtained was discounted because, in field trials, only extremes of RH have been shown to influence ethephon-promoted abscission (Klein et al., 1978). The greater effect of temperature on ethephon-promoted, compared to ethylene-promoted, abscission, was most likely due to increased ethephon absorption (Flore and Bukovac, 1982), greater ethylene release from ethephon, or both (Olien and Bukovac, 1978).

Abscission rate and abscission percent showed similar trends in organ sensitivity. However, there were two cases in which there was a lack of correspondence between these two abscission param-

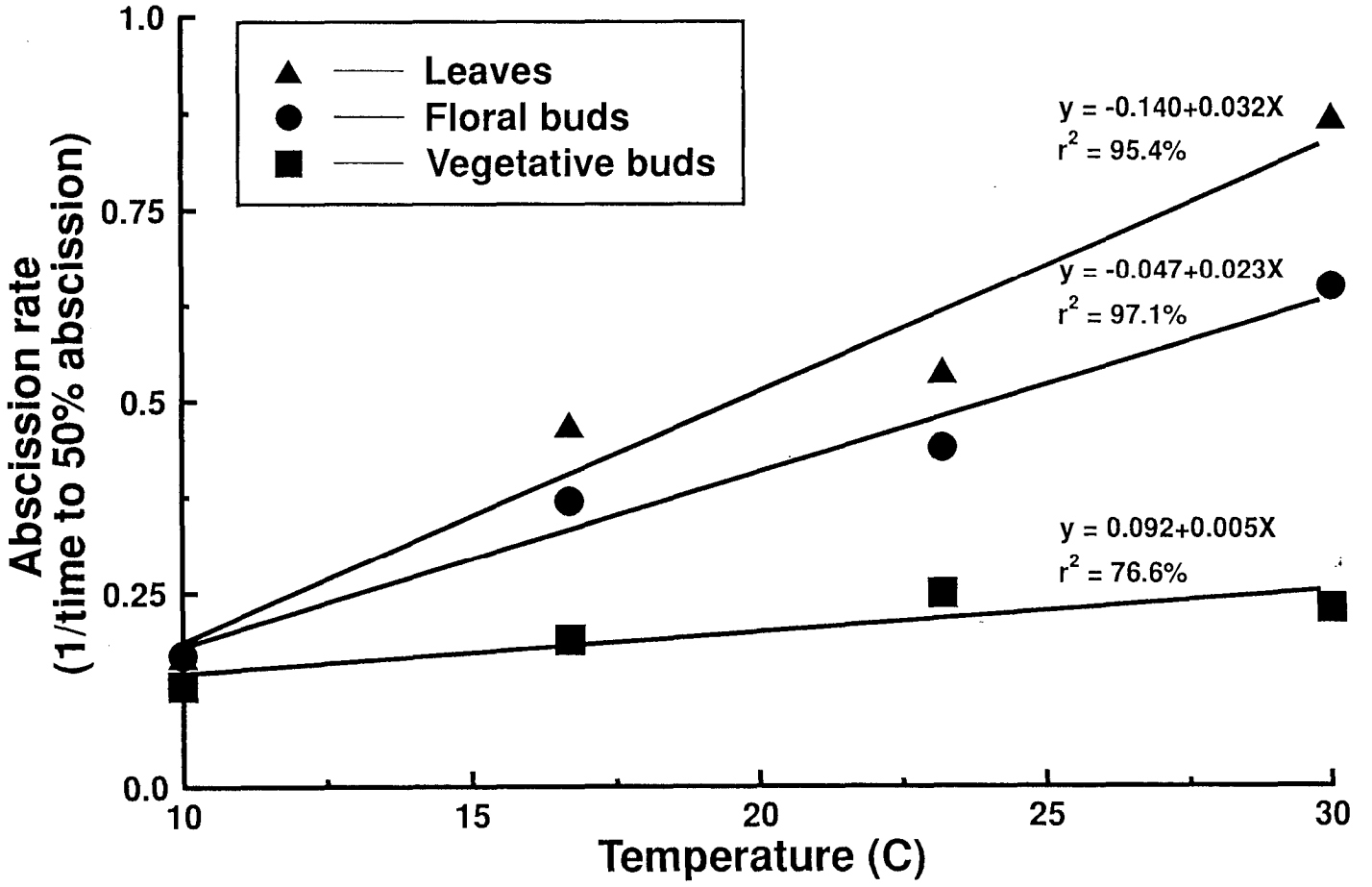

Fig. 6. Effect of temperature on abscission rate (mean 1/days to 50% final abscission of 10 plants) of 3 organs (floral buds, vegetative buds, and leaves) of *Camellia* 'Anticipation' after ethylene application (10.5 µl·liter^{-1}) on 7 May 1991. Equations and correlation coefficient *(r^2)* determined by linear regression.

eters. Although abscission percent of floral buds was greater than that of leaves (Fig. 4A), abscission rate revealed no consistent trend (Fig. 5A). Secondly, at 10C, abscission rate of floral buds and leaves plateaued above 2 ml·liter^{-1} ethephon (Fig. 2 A and B, respectively), yet abscission percentage continued to increase markedly with increasing ethephon concentration (Fig. 3 A and B, respectively). Thus, ethephon sensitivity trends as measured by abscission percent cannot accurately be predicted from abscission rate, abscission percent being the most useful parameter from a commercial perspective.

Floral buds were the most sensitive organ to ethephon, a result which is consistent with a range of genera including *Malus* (Irving et al., 1989) and *Cupsicum* (Tripp and Wien, 1989). In contrast, after ethylene application, leaf abscission rate was greater than that of floral buds. Differences in the ranking of organ sensitivities to ethylene and ethephon were also obtained for *Olea* and may result from either differences in sensitivity or the amount of ethylene in the abscission zone (Weis et al., 1988). As it is difficult to measure ethylene within specific cell layers, it is generally assumed that no differences exist between the ethylene concentration within different organs (Lang and Martin, 1989; Weis et al., 1988). Differences in tissue response maybe due to the interaction of tissue sensitivities and the concentration and duration of ethylene present at the abscission zone (Lang and Martin, 1989). It is suggested that the greater ethephon sensitivity of floral buds than leaves was due to floral buds being more sensitive to low ethylene concentrations than leaves, while leaves abscise more rapidly at high ethylene concentrations (Woolf, 1993).

Table *3.* Proportion (%) of temperature effect on ethephon-promoted abscission rate due to influence of temperature on ethylene-promoted abscission rate of three *Camellia* organs-floral buds, leaves, and vegetative buds. Mean activation energy (E_a; KJ·mol^{-1}) calculated from Table 2 (zero values excluded).

Organ type	Ethephon (E_a)	Ethylene (E_a)	Ethylene/ethephon × 100 (%)
Floral buds	59.9	45.1	75
Leaves	93.9	54.2	58
Vegetative buds	58.8	24.1	41

Greater ethephon sensitivity of young (expanding) leaves has also been found for ethephon-promoted abscission in *Gossypium* (Morgan, 1969) and silane (CGA-15281)-promoted abscission of *Capsicum* (Beaudry and Kays, 1988). The increase in ethephon sensitivity with leaf maturity of *Camellia* was similar to that found in *Olea* (Weis et al., 1988) and *Gossypium* (Morgan, 1969), where ethephon sensitivity increases with leaf age once leaf expansion has ceased. Endogenous auxin levels decrease as leaves senesce naturally (Sexton et al., 1985). Thus, the increasing sensitivity with maturity after expansion of *Camellia* leaves most likely reflects increased senescence with concomitant reduction in auxin concentrations distal to the abscission zone, thereby rendering leaves. more sensitive to released ethylene (Osborne 1989).

These results support the hypothesis. (Woolf et al., 1992) that the time of the year of ethephon application influences the response of *Camellia* by its effects on tissue maturity and temperature, the

former affecting tissue ethylene sensitivity, and the latter influencing ethylene release from ethephon and tissue response to ethylene. Thus, when applying ethephon in the field, careful attention must be paid to environmental conditions, particularly temperature, and to tissue maturity so that the optimal ethephon concentration can be chosen to efficiently and selectively remove floral buds from *Camellia*.

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