



A Simple Screening of Flower Sensitivity to Ethylene in Several Ornamental Asteraceae Species

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Generally, Asteraceae flowers such as chrysanthemums and gerberas, are low ethylene-sensitive and do not exhibit petal wilting and abscission. However, previous research found that the flowers of dahlia, an Asteraceae member belonging to the tribe Coreopsideae, are ethylene-sensitive and show abscission layer development in petal-ovary boundaries. In this study, we investigated the ethylene sensitivity of 17 ornamental Asteraceae species belonging to different tribes by measuring the petal drawing resistance and vase life after 1–3 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene exposure for 20 h. Although more than half of the tested species did not respond to ethylene, several species showed ethylene-sensitive petal wilting and abscission of fresh ray florets. Ethylene-sensitive petal wilting occurred in only two species (*Calendula officinalis* L. and *Osteospermum* L.) of the tribe Calenduleae, while ethylene-sensitive petal abscission occurred mainly in six species (*Bidens ferulifolia* D.C., *Coreopsis lanceolata* L., *Cosmos atrosanguineus* (Hook) Voss., *Cosmos bipinnatus* Cav., *Cosmos sulphureus* Cav. and *Dahlia* Cav.) of tribe Coreopsideae and one species (*Helianthus annuus* L.) of the tribe Heliantheae. In these species, abscission petals maintained their turgidity, and this process could be detected by measuring the petal drawing resistance of the ray florets. The reduction in petal drawing resistance, associated with abscission layer development in the petal-ovary boundaries, was observed only in these ethylene-sensitive species. The results of this study suggest that the ethylene sensitivity and petal senescing patterns in Asteraceae flowers may be associated with the phylogenetic classification at the tribe level.

Key Words: Coreopsideae, floret, petal drawing resistance, tribe, vase life.

Introduction

Asteraceae is one of the largest plant families, followed by Orchidaceae. According to the Angiosperm Phylogeny Group (APG) system, Asterids and Rosids are both the main parts of core eudicots. Among the 11 families of Asterales order in Asterids, Asteraceae is the largest. Asteraceae contains more than 32,000 species of flowering plants, including many cut flower species such as chrysanthemum (*Chrysanthemum morifolium* Ramat.), dahlia (*Dahlia* Cav.), sunflower (*Helianthus annuus* L.) and gerbera (*Gerbera jamesonii* Bol. ex Adlam.), potted plants like marguerite (*Argyranthemum* Schultz-Bip.) and pot marigold (*Calendula officinalis* L.), as well as bedding plants like cosmos (*Cosmos* spp. Cav.) and zinnia (*Zinnia* spp. L.). The tribes in Asteraceae, which remain controversial,

are at least 36 and their phylogeny has recently been rebuilt using molecular markers (Mandel et al., 2019).

The inflorescences of Asteraceae plants are called capitula or “flower heads” and consist of many floret whorls. The inflorescence (flower) longevity of Asteraceae plants varies among species; some, such as chicory (*Cichorium intybus* L.), are ephemeral, while some are long-lasting (more than two weeks), like chrysanthemums. The vase life of cut Asteraceae flowers held in water at room temperature ranged from 3 to 20 days (Clark et al., 2010). This varied longevity may be caused by different senescing mechanisms.

The end of inflorescence life of ornamental plants may be due to petal wilting or abscission, often promoted by ethylene (van Doorn and Woltering, 2008). Asteraceae flowers are generally considered to be ethylene insensitive and exhibit little petal abscission. However, there are two exceptions; dahlias showed ethylene sensitivity (Azuma et al., 2020), and sunflowers showed petal abscission (Tata and Wien, 2014). Abscission involves cell separation in the abscission layer that

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forms at a predetermined site of the organ that is ultimately shed (González-Carranza and Roberts, 2012; Kim, 2014; Nakano and Ito, 2013). Combining anatomical observations with measurements of the force required to remove the organs from the plants could help to quantify the process (Craker and Abeles, 1969). In cut dahlias, there are two types of senescence patterns among the cultivars; petal abscission and petal wilting. Our previous report revealed that abscission layer development in individual florets caused petal senescence, was associated with ethylene and can be easily checked by measuring the drawing resistance in the cultivars exhibiting petal abscission (Yang et al., 2021). Considering the physiology of dahlias, ethylene-sensitive petal abscission should be assessed in other Asteraceae species.

This study aimed to screen the ethylene sensitivity and senescence patterns in several ornamental Asteraceae species. The occurrences of petal abscission were identified by measuring the petal drawing resistance. In addition, the phylogenetic relationships among these species are discussed.

Materials and Methods

Plant materials

Potted plants of *Bidens ferulifolia* D.C. ‘Golden Emperor’, marguerite (*Argyranthemum* Sch.Bip) ‘Yuuyake Red’ and ‘Morinba Mini-pink’, chocolate cosmos (*Cosmos atrosanguineus* (Hook) Voss.) ‘Chokamocho’, cosmos (*Cosmos bipinnatus* Cav.) ‘Sonata’, yellow cosmos (*Cosmos sulphureus* Cav.) ‘Yellow’, dahlia (*Dahlia* Cav.) ‘Saisetsu’, black eyed Susan (*Rudbeckia hirta* L.) ‘Toto Gold’, *Osteospermum* D.C. ‘Pink Magic’, marigold (*Tagetes* L.), and zinnia (*Zinnia elegans* Jacq.) ‘Profusion Lemon’ were obtained from cutting propagation or purchased from flower shops. These potted plants were grown in the greenhouse at Kyoto University from April to July 2022. The cut inflorescences were harvested from plants when their outermost petals expanded horizontally. Additionally, cut inflorescences of spray chrysanthemum (*Chrysanthemum morifolium* Romat.) ‘Sei Soma’, sunflower (*Helianthus annuus* L.) ‘Sunrich Orange’, *Calendula officinalis* L. ‘Yellow Star’, *Coreopsis lanceolata* L., cornflowers (*Centaurea cyanus* L.) and gerbera (*Gerbera hybrida* hort.) ‘Manga’ were purchased from flower shops. The flowers used in this study are common ornamental species and cultivars which can be bought easily in flower shops.

These inflorescences were recut, leaving 5–25 cm stems (depending on the flower size). All leaves were removed to alleviate transpiration, and the stem bases were placed in deionized water. The postharvest environment was controlled at 25–28°C and 50–60% RH.

Ethylene exposure

On the day of the experiment (day 0), the cut inflo-

rescences were placed in a glass chamber and continuously exposed to exogenous ethylene at 1–3 $\mu\text{L}\cdot\text{L}^{-1}$ for 20 h at room temperature (Fig. 1), then moved to the postharvest environment for the following measurements. Ethylene was permeated through a 0.04 mm thick polyethylene film from a 500 mL erlenmeyer flask containing 100% ethylene, and the concentration was controlled by regulating the air mixing rate.

Vase life

The vase life of the inflorescences was considered terminated when the ray florets in the outermost wholes showed wilting, discoloring, or dropping. Occurrence of fresh petal abscission (separation from the inflorescence) was checked by touching or shaking the inflorescences gently.

Drawing resistance of the petals

The drawing resistance of the petals in the outermost ray florets was measured before ethylene exposure (day 0) and after ethylene exposure (day 1). A device was used to measure the drawing resistance of the petals from an inflorescence, as reported in our previous study (Yang et al., 2021). A clip attached to the petal was connected by a thread to a digital force gauge (FGP-0.5; Nidec Corporation, Tokyo, Japan). The inflorescence was pulled slowly on a smooth plastic plate to measure the peak force when the petal was separated from the receptacle or the ovary. In each species, 10–15 outermost florets in 3–5 inflorescences were randomly chosen to measure their petal drawing resistances.

Abscission layer development in the florets

The cut inflorescences of the spray chrysanthemum ‘Sei Soma’, *Bidens* ‘Golden Emperor’, yellow cosmos ‘Yellow’, dahlia ‘Saisetsu’, and sunflower ‘Sunrich Orange’ were treated with or without ethylene, and the outermost florets were dissected from the inflorescences before and after ethylene exposure (on day 0 and day 1, respectively). Samples containing the petal-ovary boundaries were trimmed to approximately 3 mm and then fixed using FAA (ethanol: water: formaldehyde: acetic acid = 12:6:1:1). Next, the samples were dehydrated using an ethanol series at 30%, 50%, 70%, 80%, 90%, 95%, 99.9%, and 100%. The prepared samples

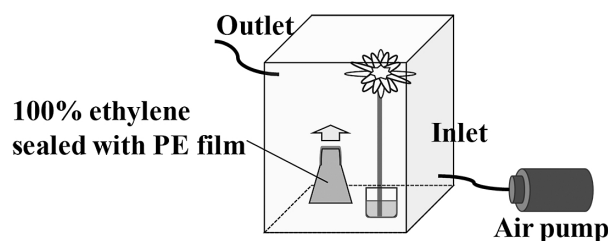


Fig. 1. Equipment designed for ethylene exposure. Ethylene concentrations in the chamber were maintained at 1–3 $\mu\text{L}\cdot\text{L}^{-1}$ by regulating the flow rate of the air pump.

were embedded in resin (Technovit 7100 kit; Kulzer, Germany) and 5- μ m thick sections were cut using a rotary microtome (RM2155; Leica, Germany). The sections were stained using Delafield's hematoxylin for 30 min and then observed under a microscope (BX-53; Olympus Corporation, Tokyo, Japan). Photographs were taken using a digital camera (DP74; Olympus Corporation).

Results

Vase life

In the untreated cut inflorescences, the vase lives ranged from one to more than 20 days among species. The longest vase life was measured in *Chrysanthemum* (> 20 days), followed by *Bidens* (11 days) and then by two *Argyranthemum* cultivars, *Helianthus*, *Rudbeckia*, *Zinnia* and *Tagetes* (7–9 days). *Coreopsis*, three *Cosmos* species, *Dahlia*, *Centaurea* and *Gerbera* had an intermediate life (3–7 days). *Calendula* and *Osteospermum* had a relatively short life (< 3 days). Fresh petal abscission (separated from the ovaries), which was checked by touching or shaking, was only found in the Coreopsideae species and *Helianthus*, and others showed wilting petals attached to inflorescences (Table 1). Interestingly, natural petal dropping was only observed in *Helianthus*, and the detached petals of Coreopsideae species were still held in the bracts and rarely dropped without being touched.

In the ethylene-treated cut inflorescences, the vase life and outlook on day 1 was unchanged in two *Argyranthemum*s, *Chrysanthemum*, *Rudbeckia*, *Zinnia*, *Tagetes*, *Centaurea*, and *Gerbera* (Table 1; Fig. S1A, B, C, M, N, O, P, Q). In *Calendula* and *Osteospermum*, which belong to the tribe Calenduleae, the petals showed wilting, and the vase life ended immediately after ethylene exposure (Table 1; Fig. S1D, E). In all six species of the Coreopsideae tribe, although ethylene exposure significantly shortened the vase lives, petals did not wilt immediately after ethylene exposure (Table 1; Fig. S1F, G, H, I, J, K). Instead, fresh petal detachment from the ovaries was accelerated by ethylene and these detached petals wilted without dropping a few days later. In *Helianthus*, for which the vase life ended by fresh petals dropping without touching, ethylene accelerated the petal dropping, but did not cause immediate wilting (Table 1; Fig. S1L).

Drawing resistance of petals

The petals of the outermost whorls were pulled individually to record the force when the petals or florets were separated from the inflorescences. In two *Argyranthemum*s, *Chrysanthemum*, *Rudbeckia*, *Zinnia*, *Tagetes*, *Centaurea*, and *Gerbera*, the petal drawing resistance after ethylene treatment was almost the same as the untreated ones (Fig. 2A, B, C, M, N, O, P, Q). In two Calenduleae species (*Calendula officinalis* L. and *Osteospermum* D.C.), six Coreopsideae species

(*Bidens ferulifolia* D.C., *Coreopsis lanceolata* L., *Cosmos atrosanguineus* (Hook) Voss., *C. bipinnatus* Cav., *C. sulphureus* Cav. and *Dahlia* Cav.) and one Heliantheae species (*Helianthus annuus* L.), petal drawing resistance declined significantly after ethylene exposure (Fig. 2D, E, F, G, H, I, J, K, L).

Abscission layer development in the florets

In spray chrysanthemums, the petals remained attached to the ovaries, and the cell size in the petal-ovary boundaries remain unchanged after ethylene treatment (Fig. 3A, F, K). In *Bidens*, yellow cosmoses and dahlias, the cells in the petal-ovary boundaries at harvest seemed to be smaller and more flattened than the petal cells (Fig. 3B, C, D). These cell layers did not increase and develop further in the control florets (Fig. 3G, H, J). After ethylene treatment, the cell layers broke down resulting in petal separation from the ovaries (Fig. 3L, M, N). In sunflowers, compared with the petal cells, smaller and flattened cells were also found in the petal-ovary boundaries of the florets in the untreated cut flowers (Fig. 3E, J). In the ethylene-treated sunflower inflorescences, the cells in the petal-ovary boundaries seemed to be more flattened and the separation layers became more obvious compared with those in the untreated ones. However, these cell layers did not break down after ethylene treatment like those of Coreopsideae species, and the petals were still attached to the ovaries on day 1 (Fig. 2O).

Discussion

Flower life cessation symptoms can be largely divided into petal wilting and petal abscission. The latter is characterized by fresh and turgid petal separation from ovaries or receptacles. The categories of senescence symptoms and flower ethylene sensitivity appeared consistent within families (van Doorn, 2001, 2002; Woltering and van Doorn, 1988). Among these 17 Asteraceae species, which had varying vase lives from one to over 20 days (Table 1), both petal wilting and petal abscission were observed.

In two *Argyranthemum*s, *Chrysanthemum*, *Rudbeckia*, *Zinnia*, *Tagetes*, *Centaurea*, and *Gerbera*, the petals were attached to the inflorescences even after they wilted. In *Calendula* and *Osteospermum*, which rapidly senesced within 1–2 days, obvious petal abscission was not observed at the end of vase life. In *Helianthus annuus* L. (sunflowers) and the six Coreopsideae species, including three *Cosmos* species, the petals firstly separated from the ovaries and then wilted. However, in the Coreopsideae species, the detached fresh petals rarely dropped without being touched or shaken. This may explain why petal abscission in Asteraceae flowers was rarely detected and has rarely been reported. On the other hand, fresh petals dropped from the capitula more easily in *Helianthus*. These differences may be caused by the long flaky

Table 1. Effects of ethylene exposure on the vase life and petal abscission in Asteraceae flowers.

Subfamilies, tribes, species and cultivars ^z	Ethylene treatment	Vase life (days) ^y	Fresh petal abscission
Asteroidae, Anthemideae			
<i>Argyranthemum</i> Sch. Bip. ‘Yuuyake Red’	No	8.4±0.4 NS ^x	No
	Yes	7.2±0.2	No
<i>Argyranthemum</i> Sch. Bip. ‘Morinba Mini-pink’	No	7.3±0.4 NS	No
	Yes	7.5±0.5	No
<i>Chrysanthemum morifolium</i> Ramat ‘Sei Soma’	No	>20.0 NS	No
	Yes	>20.0	No
Asteroidae, Calenduleae			
<i>Calendula officinalis</i> L. ‘Yellow Star’	No	2.0±0.3 *	No
	Yes	1.0±0.0	No
<i>Osteospermum</i> D.C. ‘Pink Magic’	No	2.1±0.2 **	No
	Yes	1.2±0.1	No
Asteroidae, Coreopsidae			
<i>Bidens ferulifolia</i> D.C. ‘Golden Emperor’	No	11.6±0.7 ***	Yes
	Yes	2.0±0.0	Yes
<i>Coreopsis lanceolata</i> L.	No	6.0±0.3 **	Yes
	Yes	4.0±0.5	Yes
<i>Cosmos atrosanguineus</i> (Hook) Voss. ‘Chokamocha’	No	6.7±0.3 **	Yes
	Yes	3.3±0.3	Yes
<i>Cosmos bipinnotus</i> Cav. ‘Sonata’	No	6.0±0.0 **	Yes
	Yes	3.3±0.3	Yes
<i>Cosmos sulphureus</i> Cav. ‘Yellow’	No	3.6±0.2 ***	Yes
	Yes	2.1±0.2	Yes
<i>Dahlia</i> Cav. ‘Saisetsu’	No	4.2±0.2 *	Yes
	Yes	2.8±0.2	Yes
Asteroidae, Heliantheae			
<i>Helianthus annuus</i> L. ‘Sunrich Orange’	No	7.1±0.4 *	Yes
	Yes	5.0±0.9	Yes
<i>Rudbeckia hirta</i> L. ‘Toto Gold’	No	8.1±0.3 NS	No
	Yes	8.3±0.2	No
<i>Zinnia elegans</i> Jacq. ‘Profusion Lemon’	No	8.0±1.0 NS	No
	Yes	7.0±0.5	No
Asteroidae, Tageteae			
<i>Tagetes</i> L.	No	8.4±0.4 NS	No
	Yes	8.2±0.3	No
Carduoideae, Cardueae			
<i>Centaurea cyanus</i> L.	No	3.0±0.4 NS	No
	Yes	2.5±0.3	No
Mutisioideae, Mutisieae			
<i>Gerbera hybrida</i> hort. ‘Manga’	No	4.7±0.3 NS	No
	Yes	4.0±0.6	No

^z This taxonomy is followed by Fu et al. (2016) and Mandel et al. (2019).

^y Means±SE (n=3–8).

^x NS, *, **, *** indicate non-significant or significant at $P \leq 0.05$, 0.01 and 0.001, respectively by *t*-test.

bracts, which held the petals of ray florets tightly, in the Coreopsidae species. Overall, fresh petal abscission caused petal senescence in six Coreopsidae species, and the vase lives of these species were also shortened by ethylene exposure (Table 1).

The abscission of flower organs is often accelerated by ethylene (Ichimura et al., 2009; van Doorn, 2001). During organ abscission, the third stage characterized

by decreasing organ breaking strength results from cell wall loosening and degradation in the abscission layers (Bleecker and Patterson, 1997; Estornell et al., 2013; Kim, 2014; Roberts et al., 2002; Taylor and Whitelaw, 2001). In this study, we checked abscission layer development in the petal-ovary boundaries by measuring the petal drawing resistance of ethylene-treated or untreated inflorescences. From the data in Figure 2 and Figure S1,

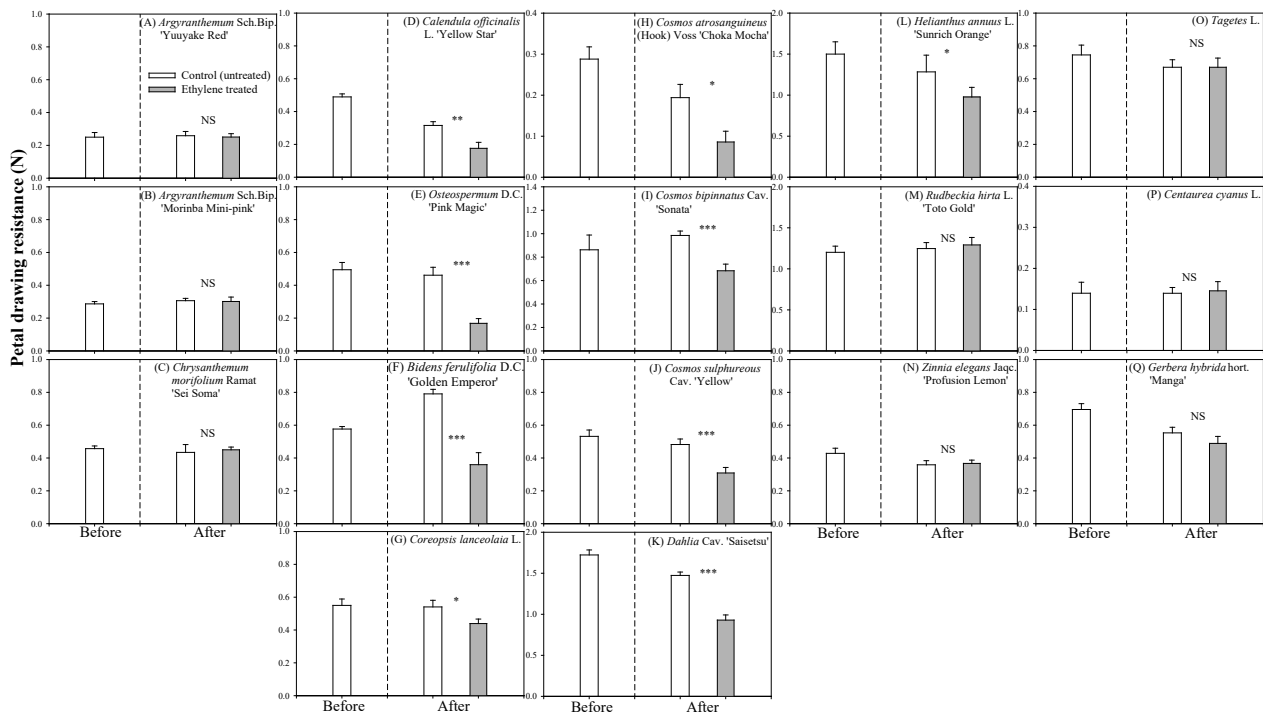


Fig. 2. Effects of ethylene on petal drawing resistance. Bars indicates SEs ($n = 10-15$). NS, *, **, and *** indicate non-significant or significant at $P \leq 0.05$, 0.01 and 0.001, respectively by t -test. The petal drawing resistance was measured before (day 0) and after ethylene exposure (day 1), respectively.

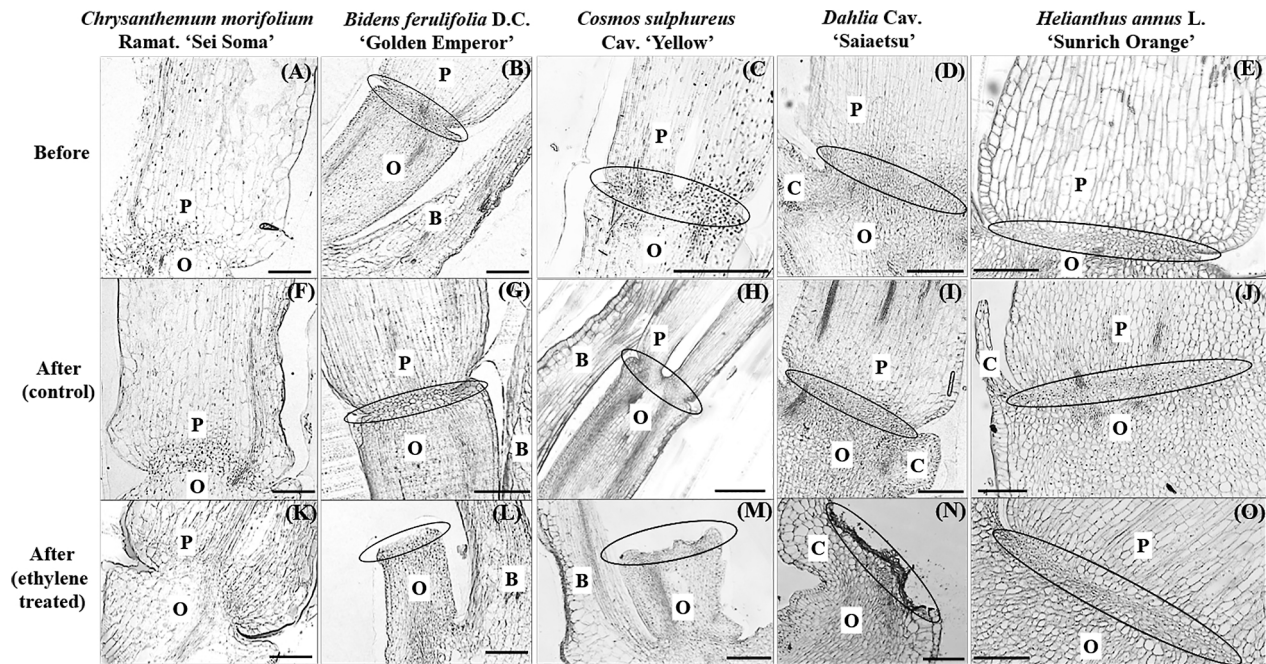


Fig. 3. Micro-observation of the petal-ovary boundaries of inflorescences before treatment (A, B, C, D, E), the untreated ones (F, G, H, I, J), and the ethylene treated ones (K, L, M, N, O) in spray chrysanthemum, *Bidens*, yellow cosmos, dahlia and sunflower. B: bracts. C: calyx. O: ovaries. P: petals. Bar = 200 μm . Notice that the petals had separated from the ovaries in the ethylene treated *Bidens*, yellow cosmos and dahlia (L, M, N). These florets were sampled before (day 0) and after ethylene exposure (day 1), respectively.

three types of responses to ethylene were observed; 1) no wilting and no decrease in petal drawing resistance (two *Argyranthemum* cultivars, *Chrysanthemum*, *Rudbeckia*, *Zinnia*, *Tagetes*, *Centaurea*, and *Gerbera*),

2) immediate petal wilting and a decrease in petal drawing resistance (*Calendula officinalis* L. and *Osteospermum* L.) and 3) no immediate petal wilting, but a decrease in petal drawing resistance (six

Coreopsidae species and *Helianthus annuus* L.). The species with fresh petal abscission also showed decreased petal drawing resistance and a shortened vase life after ethylene exposure (Table 1; Fig. 2).

The cells in the petal abscission zone are usually smaller than the surrounding cells (Patterson, 2001; Patterson and Bleecker, 2004; van Doorn and Stead, 1997). Microscopical observations of longitudinal sections of the petal-ovary boundaries of the outermost florets in five species showed consistent results with petal drawing resistance. In cut chrysanthemums, which showed unchanged petal drawing resistance and vase life, there were no marked differences in the cells in the petal-ovary boundaries between the control and ethylene-treated florets (Fig. 3A, F, K). In *Bidens*, yellow cosmoses and dahlias, which had decreased petal drawing resistance and a shortened vase life after ethylene exposure, the petals separated from the ovaries in ethylene treated inflorescences, but did not in controls (Fig. 3L, M, N). In *Helianthus annuus* L., ethylene exposure caused decreased petal drawing resistance as in Coreopsidae species, but did not cause an immediate end to vase life. Compared with the abscission cell layers in the untreated cut flowers, these cell layers became more flattened, but had not broken down on day 1 in the ethylene treated flowers (Fig. 3E, J, O). These results reveal that Coreopsidae species have higher ethylene sensitivity and a faster rate of abscission layer development than *Helianthus annuus* L.

Based on the results of this study, the decreased petal drawing resistance, which indicates abscission layer development, is an easy indicator of the ethylene sensitivity of Asteraceae flowers with petal abscission. Our results also indicate that the responses to ethylene seem to vary among tribes. The Calenduleae species responded to ethylene and subsequent petal wilting and abscission may have occurred simultaneously. Coreopsidae species and *Helianthus annuus* L. (Heliantheae) responded to ethylene with no immediately wilting, but displayed accelerated petal separation from ovaries. The other tribes tested exhibited no response to ethylene. The senescing symptoms of all Coreopsidae species and one Heliantheae species (*Helianthus annuus* L.), all of which are interestingly native to central and south America (Funk, 1991; Mandel et al., 2019; Ryding and Bremer, 1991), are characterized by abscission of fresh petals, indicating that their senescence type is “ethylene-sensitive petal abscission”. In Asteraceae flowers, ethylene sensitivity appeared to be closely associated with tribes.

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