

## Review Paper

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# Seed dormancy in Asteraceae: a global vegetation zone and taxonomic/phylogenetic assessment

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**Abstract**

The Asteraceae with up to 30,000 species occurs on all continents except Antarctica and in all major vegetation zones on earth. Our primary aim was to consider cypselae dormancy-break and germination of Asteraceae in relation to ecology, vegetation zones and evolution. Cypselae are desiccation-tolerant and in various tribes, genera, species and life forms of Asteraceae are either non-dormant (ND) or have non-deep physiological dormancy (PD) at maturity. All six types of non-deep PD are found among the Asteraceae, and dormancy is broken by cold or warm stratification or by afterripening. Soil cypselae banks may be formed but mostly are short-lived. Much within-species variation in dormancy-break and germination has been found. Using data compiled for 1192 species in 373 genera and 35 tribes of Asteraceae, we considered ND and PD in relation to life form, vegetation zone and tribe. Senecioneae and Astereae had the best representation across the vegetation zones on earth. In evergreen and semi-evergreen rainforests, more species have ND than PD, but in all other vegetation zones, except alpine/high-latitude tundra (where ND and PD are equal), more species have PD than ND. Tribes in the basal and central grades and those in the Heliantheae Alliance have both ND and PD. The high diversity and lability of non-deep PD may have enhanced the rate of species diversification by promoting the survival of new species and/or species in new habitats that became available following globally disruptive events since the origin of the Asteraceae in the Late Cretaceous.

**Introduction**

The Asteraceae is a monophyletic family (Mandel et al., 2019) that has been estimated to have 1100 genera and 20,000 species (Gleason and Cronquist, 1991), 1600–1700 genera and 24,000–30,000 species (Funk et al., 2005), 1600 genera and 23,000 species (Anderberg et al., 2007), 1568 genera and 25,000 species (Mabberley, 2017) and 1700 genera and 25,000–30,000 species (Mandel et al., 2019). Furthermore, the number of subfamilies and tribes varies, with Mabberley (2017) listing 3 subfamilies and 43 tribes. A remarkable feature of the Asteraceae is that it has a global distribution, with species occurring ‘everywhere but Antarctica’ (Funk et al., 2005). However, two species of Asteraceae (four plants of *Nassauvia gellanica* and one plant of *Gamochaeta nivalis*) were observed on Deception Island (West Antarctica) in 2009 (Lewis Smith and Richardson, 2011). Three plants of *N. gellanica* and the plant of *G. nivalis* disappeared due to natural events. The plant of *N. gellanica* was deemed to be an alien and was removed before the species became invasive.

Molecular studies suggest that the family originated in South America (Jansen and Palmer, 1987, 1988; Panero and Funk, 2008) in the Late Cretaceous about 83 Ma (Mandel et al., 2019). Fossil pollen of Asteraceae has been found in the Late Cretaceous (ca. 76–66 Ma) deposits of Antarctica (Barreda et al., 2012, 2015), and fossil flowers of the family have been found in Eocene (47.5 Ma) deposits in Patagonia (Barreda et al., 2010). Some tribes such as the Barnadesieae, which is the basal tribe of the family based on the absence of a 22 kb cpDNA inversion (Bremer and Jansen, 1992), Eupatorieae, Heliantheae, Liabeae and Mutisieae originated in the montane zone of the Andes Mountains in South America (Funk et al., 1995; Mandel et al., 2019). Following its origin in South America, Mandel et al. (2019) proposed that the Asteraceae dispersed to North America and then to Asia and Africa, with rapid radiation of tribes and species occurring in the Eocene and Oligocene.

According to Funk et al. (2005), the Asteraceae ‘is the most diverse of all plant families,’ and Palazzesi et al. (2022) considered it to be ‘a model system for evolutionary studies’. Species of Asteraceae grow in a range of habitats from tropical evergreen rainforest to tundra, and some grow in wetlands, saline habitats and on sand dunes (see tables in chapters 9, 10 and 11 of Baskin and Baskin, 2014). Asteraceae includes trees, shrubs, vines and herbs, and they may be aquatics, succulents or epiphytes (Anderberg et al., 2007; Moreira-Muñoz, 2011). Kress

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(1986) reported 20 species of Asteraceae in 8 genera that are epiphytes. Large caulescent rosettes of some Asteraceae grow at high elevations in the Andes (Fagua and Gonzalez, 2007), the mountains of East and Central Africa (Smith and Young, 1982, 1987; Beck, 1986; Pérez, 1992, 1995) and on the summit of Haleakala (a mountain) on the island of Maui in Hawaii (USA) (Pérez, 2001). On the other hand, cushion plants of at least 50 genera of Asteraceae grow in arctic/subantarctic/alpine regions (Aubert et al., 2014). In the subantarctic islands of New Zealand, mega-herbs of Asteraceae (e.g. *Pleurophyllum* spp.) have a somewhat flat rosette of giant (15–45 × 10–25 cm) corrugated (ribbed) leaves and deeply pigmented flowers (Fraser, 1986). On Campbell Island, leaf and flower temperatures of *P. speciosum* were 8 and 11°C higher than the temperature of the surrounding air, respectively (Little et al., 2016). Among the Asteraceae, there are species that behave as winter annuals, summer annuals, biennials, long-lived monocarpic perennials and polycarpic perennials (e.g. Zedler et al., 1983; de Jong et al., 2000; Law and Salick, 2005; Anderberg et al., 2007; Denisiuk et al., 2009; Baskin and Baskin, 2014; Baskin et al., 2022).

Various kinds of studies have been conducted in an attempt to help explain the diversity of species, habitats, life forms and life cycles of the Asteraceae. The ideas/studies about the reasons for the high diversification rates of Asteraceae include whole-genome duplication (polyploidization) (WGD; Zhang et al., 2021a), genetic diversity (Pascual-Díaz et al., 2021), interaction with insects that serve as pollinators (Panero et al., 2014) and production of secondary metabolites that deter predators especially insects (Seaman, 1982; Vanderplanck et al., 2020). An inflorescence compressed into a head or capitulum is viewed as a pseudanthia or false flower (Zhang and Elomaa, 2021). The capitulum, rather than the flower, is highly variable throughout the family, and it is also considered to be an important characteristic related to the evolutionary success of the Asteraceae (Burt, 1977; Panero and Funk, 2008). It seems that pollen presentation via the capitulum has evolved in response to herbivory, insect-flower interactions and/or seed/fruit dispersal (Leppik, 1977; Panero and Funk, 2008).

Although numerous studies have been conducted on cypsela (diaspore) dormancy-breaking and germination requirements of Asteraceae (see references in Baskin and Baskin, 2014), no attempt has been made to review cypsela dormancy in this huge family in relation to ecology, biogeography and evolution. In this review, we address several general questions. (1) What kind of dormancy is found in cypselae of Asteraceae? (2) What is the distribution of cypsela non-dormancy and dormancy among life forms of Asteraceae and in the various vegetation zones on earth? (3) What is the distribution of cypsela non-dormancy and dormancy in tribes of Asteraceae in relation to life form and vegetation zone?

### The dispersal/germination unit

The dispersal unit of Asteraceae is a single-seeded cypsela (Gleason and Cronquist, 1991), except it is reported to be a drupe in *Chrysanthemoides monilifera* subsp. *monilifera* from South America (Reynolds et al., 2013). However, the dispersal unit of Asteraceae is often referred to as an achene, which is not botanically correct. A cypsela is a dry indehiscent fruit originating from an inferior ovary with two carpels and one locule that produces only one seed. In contrast, an achene is a single-seeded dry indehiscent fruit that originates from a superior ovary (Marzinek et al., 2008). In this paper, we use only 'cypsela'. The

pericarp of Asteraceae cypselae is not adnate to the seed (Frangiote-Pallone and Souza, 2014), and it is water permeable (e.g. Kagaya et al., 2005; Genna and Pérez, 2016; Yuan and Wen, 2018; Sarmiento et al., 2019; Zhang et al., 2019). Furthermore, the large well-developed embryo is spatulate in shape, and endosperm is not present in mature cypselae (Martin, 1946; Lubbock, 1892[1978]). In the Baskin and Baskin (2014) classification scheme for variation in position, size, mass and morphology of plant diaspores on individual plants, most Asteraceae fit under Division I. Monomorphic (but see below). Furthermore, diaspores fit under Group A (diaspores are produced only from chasmogamous flowers) of Supergroup 1 (Monomorphic aerial). However, *Asteriscus pygmaeus* and *Arctotheca populifolia* fit under Supergroup 2 (Monomorphic basal or subterranean). More specifically *A. pygmaeus* fits under Group A (Basicarpy) and *A. populifolia* under Group B (Geocarpy. Subgroup e. Passive geocarpy).

Cypselae of Asteraceae are desiccation-tolerant and thus have orthodox storage behaviour (Dickie and Pritchard, 2002). Hong et al. (1998) list 434 species of Asteraceae: 377 with orthodox cypselae, 55 probable orthodox? and 2 undecided. In their global list of species whose seeds are recalcitrant (desiccation-sensitive), Subbiah et al. (2019) do not list any species of Asteraceae. According to Pence et al. (2022) 'exceptional species' in terms of *ex-situ* seed storage for conservation may have seeds that are desiccation-sensitive, short-lived under conventional seed banking conditions or deeply dormant. However, these authors listed 187 species of Asteraceae as 'non-exceptional' and 151 species of this family as 'probably non-exceptional'. Cypselae of 18 species in 10 genera of Asteraceae stored dry at -18°C for 24–26 years were predicted to have a  $P_{50}$  (number of years before 50% of the cypselae lose viability) of 13 (*Guizotia abyssinica*) to 124 (*Zinnia* sp.) years (Walters et al., 2005).

Venable and Levin (1983) surveyed published floras from Asia, Australia, Africa, North America, Pacific Islands and South America for information on dispersal-related structures on cypselae of Asteraceae. They recorded information for 5893 species, including annuals, biennials, perennials, shrubs and trees, and 71.0, 87.6, 81.2, 86.2 and 83.0%, respectively, had structures on the cypselae that would facilitate dispersal. In all life forms, the rank order of dispersal-facilitating structures was plumes > barb-like > scales, except for annuals in which it was plumes > scales > barb-like structures.

### Capitula and breeding systems

A capitulum may consist of both disc and ray flowers, only disc flowers or only ray flowers. A disc flower has three to five corolla lobes, depending on the species, and is actinomorphic, while the corolla lobes of a ray flower are fused into a single strap-shaped (ligulate) structure that is zygomorphic (Jeffrey, 1977; Leppik, 1977; Bremer, 1994). Various types of capitula (and breeding systems) can be distinguished in Asteraceae (Jeffrey, 2009; Elomaa et al., 2018): (1) both disc and ray flowers are perfect (monocliny), for example, *Cotula* spp. (Lloyd, 1972a); (2) disc perfect and ray pistillate (gynomonoecy), for example, *Aster s.l.* (Bertin and Kerwin, 1998) and *Solidago* (Bertin and Gwisc, 2002); (3) disc staminate and ray pistillate (monoecy), for example, *Lecocarpus pinnatifidus* (Philipp et al., 2004); (4) disc perfect and ray sterile, for example, *Helianthus annuus* (Elomaa et al., 2018) and (5) rarely androdioecy with some perfect flowers and some that are functionally staminate.

Some species of Asteraceae produce two kinds of capitula (Jeffrey, 2009): (1) pistillate and staminate capitula on different plants (dioecy); (2) pistillate and perfect capitula on different plants (gynodioecy), for example, *Bidens sandvicensis* (Schultz and Ganders, 1996) and *Cirsium arvense* (Lloyd and Myall, 1976; Kay, 1985); (3) perfect and staminate capitula on different plants (androdioecy); and (4) pistillate and staminate capitula on the same plant (monoecy). It should be noted that in some sexually dimorphic plant species, the strictness of maleness and/or femaleness in individuals in a population may be constant [invariable (strictly unisexual) sexual expression] or inconstant (continuously variable) sex expression, with inconstant males being more common than inconstant females (Lloyd, 1976; Webb, 1999). Examples of inconstant males and females in sex expression in the Asteraceae include dioecious species of *Cotula* (Lloyd, 1972b, 1975). Also, see Yampolsky and Yampolsky (1922) and Renner (2014) for information on kinds of sexual systems in Asteraceae.

Species of Asteraceae may be self-incompatible (SI) (Hiscock, 2000; Stephens, 2008; Allen et al., 2011), self-compatible (SC) (Carr et al., 1986; Grombone-Guaratini et al., 2004; Picó et al., 2004; Soto-Trejo et al., 2013) or partially self-incompatible (PSI) (Ortiz et al., 2006; Nielsen et al., 2007). Furthermore, populations of some Asteraceae have a mixture of breeding systems (Sun and Ganders, 1988; Arista et al., 2017). In a survey of the breeding system in 571 taxa of Asteraceae, Ferrer and Good-Avila (2007) found that 65, 10 and 25% of the taxa had SI, PSI and SC, respectively. These authors were not able to resolve the ancestral kind of breeding system in Asteraceae, but they did find that SI can be gained and lost. Thus, neither SC nor PSI is a 'terminal state'. Not surprisingly, a relatively higher percentage of SC than of SI has been found for invasive species of Asteraceae, for example, in China (Hao et al., 2011) and for species on islands (Grossenbacher et al., 2017). The latter authors found that 143 of 519 (28.0%) of mainland Asteraceae species had SC, while 162 of 273 (59.3%) of island species had SC.

Some species of Asteraceae produce a low number of cypselae due to a lack of compatible pollen being deposited on the stigma (i.e. pollen limitation); this is especially important for some SI species (Larson and Barrett, 2000). Pollen limitation has been documented in various Asteraceae species (Totland, 1997; Colling et al., 2004; Muñoz and Arroyo, 2006; Campbell and Husband, 2007; Muñoz and Cavieres, 2008; Ferrer et al., 2009; Law et al., 2010; Shabir et al., 2015). In general, pollen limitation decreases cypselae production, and in *Scorzonera humilis*, it reduces the germination percentage of the cypselae that were produced. In the SI species *Achillea ptarmica*, there was a significant relationship between pollen viability and the seed/ovule ratio, but ovule abortion did not result in offspring with increased vigour, suggesting that genetic load results in female sterility (Andersson, 1993). The fruit set ratio (number of cypselae/number of female flowers), a measure of female reproductive success, ranged from 0.242 to 0.630 for monoecious and dioecious species of *Cotula*, respectively (Sutherland, 1986).

It is well documented that the maternal parent has more influence on seed dormancy/germination than the paternal parent, and this is especially true in the F<sub>1</sub> (seed) progeny. However, the father sometimes has an effect on variation in these traits (Baskin and Baskin, 2019). The paternal parent had a positive influence on germination percentage and/or rate for *Aster kantoensis* (Kagaya et al., 2011), *Crepis tectorum* subsp. *pumila* (Andersson, 1990), *Lactuca sativa* (Rideau et al., 1976) and *Solidago altissima* (Schmid and Dolt, 1994).

Breeding between closely related organisms may result in the expression of recessive deleterious genes (if purging has not occurred) that have negative effects on the offspring, that is, inbreeding depression (ID). The negative effects of ID on plants may include seed germination (Baskin and Baskin, 2015). In the Asteraceae, ID for cypselae germination has been found in several species including *Acourtia runcinata* (Cabrera and Dieringer, 1992), *Cotula minor* (Lloyd, 1972b), *Crepis sancta* (Cheptou et al., 2001), *Flourensia cernua* (Ferrer et al., 2009), *Hypochaeris radicata* (Becker et al., 2006), *Leontodon autumnalis* (Picó and Koubek, 2003), *Olearia adenocarpa* (Heenan et al., 2005), *Scorzonera humilis* (Colling et al., 2004), *Scalesia affinis* (Nielsen et al., 2007), *Senecio integrifolius* (Widén, 1993) and *S. pterophorus* (Caño et al., 2008). However, inbreeding and outbreeding did not result in significant differences in germination of *Arnica montana* (Luijten et al., 1996), *Aster amellus* (Raabová et al., 2009), *Carduus pycnocephalus*, *C. defloratus* subsp. *glaucus* (Olivieri et al., 1983), *Crepis sancta* (Cheptou et al., 2000), *Eupatorium resinsum* (Byers, 1998), *Gaillardia pulchella* (Heywood, 1993), *Senecio squalidus* (Brennan et al., 2005), *Tetraneuris herbacea* (Moran-Palma and Snow, 1997) or *Tragopogon pratensis* (Picó et al., 2003). In *Cotula pectinata* (Lloyd, 1972b) and *Eupatorium perfoliatum* (Byers, 1998), outbreeding led to a decrease in germination. Although *Helianthus verticillatus* is a rare diploid SI perennial known from only four locations in southeastern USA, Ellis and McCauley (2009) did not find any evidence for outbreeding depression for germination percentages of F<sub>1</sub> or F<sub>2</sub> cypselae from interpopulation crosses.

As an extension of the concern about effects of ID on germination of cypselae, attention has been given to germination of cypselae produced by Asteraceae species growing in small versus large populations. That is, do small populations have ID that could decrease germination? Germination percentages were significantly lower for cypselae produced in small than in large populations of *Arnica montana* in Germany (Kahmen and Poschlod, 2000), *Cheirolophus uliginosus* (Vitales et al., 2013), *Centaurea jacea*, *Cirsium dissectum*, *Hypochaeris radicata* (Soons and Heil, 2002), *Lamyropsis microcephala* (Mattana et al., 2012), *Senecio paludosus* (Winter et al., 2008) and *Solidago albopilosa* (Albrecht et al., 2020). On the other hand, the size of population was not significantly related to germination percentages for cypselae of *Arnica montana* in The Netherlands (Luijten et al., 2000), *Carduus defloratus* (Vaupel and Matthies, 2012), *Cirsium dissectum* (de Vere et al., 2009), *Leucochrysum albicans* var. *tricolor* (Costin et al., 2001), *Rutidosia leptorrhynchoides* (Morgan, 1999) and *Tragopogon pratensis* (Mölken et al., 2005). However, in a later paper, Morgan et al. (2013) concluded that there was a significant positive relationship between population size and mean percentage of cypselae germination for *R. leptorrhynchoides*.

## Kinds of dormancy in Asteraceae

### Non-dormancy

We found that when freshly matured cypselae of *Amphiachyris dracunculoides*, *Arctium minus*, *Coreopsis tinctoria*, *Erigeron philadelphicus*, *Helenium amarum*, *Pseudognaphalium obtusifolium* and *Senecio sylvaticus* were tested over a range of temperatures, 95–100% of them germinated in light with relatively low germination percentages in darkness. Treatments such as cold stratification, however, did not increase germination in darkness in *H. amarum* (e.g. Baskin and Baskin, 1973). Thus, we concluded

that cypselae of these Asteraceae are not dormant. As discussed below, non-dormancy has been found in the cypselae of many species of Asteraceae.

Two suggestions have been made as to how timing of germination is controlled in species whose freshly matured cypselae are non-dormant (ND) (Baskin and Baskin, 1998). (1) Environmental conditions are not favourable for germination (e.g. too cold) when cypselae mature, which delays germination until temperatures increase. (2) Cypselae mature at the time when conditions are favourable for germination and seedling establishment. In Asteraceae, we find species with ND cypselae that fit both suggestions, for example, *Helenium amarum*. This temperate zone species has a long season of cypselae maturation and dispersal, and in Tennessee (USA) cypselae are dispersed from July to late November. Cypselae dispersed from July to early November germinate immediately (if the soil is moist), and the resulting plants behave as winter annuals. However, cypselae dispersed in late November do not germinate because the temperatures in the habitat are below those required for germination. The cypselae overwinter on/in the soil and germinate in spring, with the resulting plants behaving as summer annuals (Baskin and Baskin, 1973). In some Asteraceae with ND cypselae, for example, *Ageratina havanensis* (Baskin et al., 1998), *Brickellia dentata* (Baskin et al., 1998), *Erigeron strigosus* (Baskin and Baskin, 1988), *Gymnosperma glutinosum* (Baskin et al., 1998) and *Heterotheca villosa* (Baskin and Baskin, 1998), cypselae mature when temperature and soil moisture conditions are favourable for germination and seedling establishment.

#### Pre-dispersal germination of non-dormant cypselae

One consequence of cypselae being ND at maturity is that they might germinate on the mother plant prior to dispersal, if moisture levels in the capitulum are high. Pre-dispersal germination of cypselae has been reported in *Abrotanella linearis* var. *apiculata* (Simpson, 1979), *Ageratina adenophora* (Karmakar and Hazra, 2016), *Bidens pilosa* (Karmakar et al., 2019), *Grindelia squarrosa* (Pliszko and Górecki, 2021), *Pachystegias insignis* var. *minor* (Simpson, 1979), *Saussurea lappa* (Chauhan et al., 2018) and *Tagetes erecta* (Anand and Mathur, 2012). Germination of cypselae of *A. linearis* var. *apiculata* and *P. insignis* var. *minor* while still in the capitulum on the mother plant was attributed to 'lack of dormancy' by Simpson (1979). Interestingly, other authors (e.g. Farnsworth, 2000; Leck and Outred, 2008) cite Simpson's paper as an example of viviparous germination in the Asteraceae (but see below). For the other five species listed above, except *A. adenophora*, which was reported to have pseudo-viviparous germination, the authors said that the species had viviparous germination. Pseudo-vivipary means asexually produced propagules such as bulbils, which replace sexual reproduction in whole or in part, are formed on the shoot of the plant (e.g. Lee and Harmer, 1980; Lo Medico et al., 2018). However, Karmakar and Hazra (2016) stated that cypselae germinated while still attached to the mother plant, indicating that they are not talking about asexual propagules.

However, these seven Asteraceae taxa reported to have pre-dispersal germination do not have sexually based true vivipary or cryptovivipary as shown by mangroves, which are the model for these kinds of germination. Seeds of mangroves are desiccation-intolerant (recalcitrant), and the embryo grows continuously after fertilization of the egg, with no rest period prior to germination and seedling establishment (Goebel, 1905;

Guppy, 1906, 1912; Tomlinson, 1986; Elmqvist and Cox, 1996). In contrast to mangroves, cypselae of Asteraceae are desiccation-tolerant (orthodox), thus ND cypselae could dry to a low moisture content and survive. For example, both fresh and dried ND cypselae of *Saussurea lappa* germinated to 65–70% (Chauhan et al., 2018). If ND cypselae are exposed to high moisture conditions before they are dispersed, it is expected that they would germinate on the mother plant, somewhat similar to pre-harvest sprouting (PHS) in cereal crops (e.g. Singh et al., 2021; Sohn et al., 2021). Tuttle et al. (2015) define PHS as '... as the germination of mature seeds on the mother plant when rain occurs prior to harvest'. For the seven species of Asteraceae listed above with pre-dispersal germination, the authors mention a prolonged period of rainfall, heavy monsoon or high humidity when discussing their observations of seedlings with a radicle and cotyledons attached to the mother plants. On the other hand, if ND cypselae are dispersed before onset of the wet season, they would germinate on the soil when the rains begin, that is, germination is regulated by timing of dispersal and beginning of the rainy season and not by dormancy.

#### Physiological dormancy

Freshly matured cypselae of many species of Asteraceae exhibit little or no germination at any test condition, or they germinate to relatively high or high percentages only over a limited range of conditions, for example, either high (25/15, 30/15, 35/20°C) or low (15/6, 20/10°C) temperature regimes, but not at both. Since cypselae of Asteraceae are water-permeable, the lack of germination is not due to physical or combinational dormancy. Furthermore, since cypselae have a fully developed spatulate embryo lack of germination is not due to morphological or morphophysiological dormancy, in which a small, underdeveloped embryo needs to grow inside the seed prior to radicle emergence. Failure of Asteraceae cypselae to germinate means the embryo has a germination-inhibiting mechanism, that is, physiological dormancy (PD) (Nikolaeva, 1969). The embryo does not have enough growth potential to overcome the mechanical restriction of the pericarp, which in some species of Asteraceae can be strong and thick (e.g. Sun et al., 2009; Lu et al., 2020). Consequently, mechanical or acid scarification, which removes the mechanical restraint of the pericarp on the Asteraceae embryo, may promote germination (e.g. Rout et al., 2009; Aguado et al., 2011; Gandy et al., 2015). Also, treatment with GA<sub>3</sub> may promote germination by increasing the growth potential of the embryo (Afolayan et al., 1997; Dissanayake et al., 2010; Duarte et al., 2012; Aiello et al., 2017; Guo et al., 2021). Scarification followed by treatment with GA<sub>3</sub> of the perennials *Helianthus angustifolia*, *H. glaucophyllus* and *H. pumilus* promoted cypselae germination (Castillo-Lorenzo et al., 2019).

Cypselae of Asteraceae have regular PD as opposed to epicotyl PD. In regular PD, the shoot emerges within a few days after the radicle emerges, but in epicotyl PD emergence of the shoot is delayed 1–3 mo or longer after radicle emergence (Baskin and Baskin, 2021). The three levels of regular PD (hereafter PD) are non-deep, intermediate and deep, and they are distinguished based on temperature requirements for dormancy break, response to the plant growth regulators gibberellins and ability (or not) of excised embryos to develop into normal plants (Nikolaeva, 1969).

Dormancy in seeds with non-deep PD is broken by moist-warm ( $\geq 15^{\circ}\text{C}$ ) or moist-cold (ca. 0–10°C) stratification, depending on the species (Baskin and Baskin, 2022a). Also, dormancy-break can

occur during dry storage, especially at room temperatures, that is, afterripening (Baskin and Baskin, 2020), and germination is promoted by gibberellins. Furthermore, embryos excised from seeds give rise to normal plants (Nikolaeva, 1969). PD is the most common kind of seed dormancy on earth, and most seeds with PD have non-deep PD (Baskin and Baskin, 2014). The characteristics of seeds with non-deep PD fit those of dormant cypselae of Asteraceae very well (see breaking dormancy in cypselae of Asteraceae, below).

Seeds with intermediate PD require an extended period of cold stratification (12–16 weeks) for dormancy break to occur; however, a period of warm stratification prior to cold stratification will decrease the length of the cold stratification period required to break dormancy. Gibberellins may, or may not, promote germination, depending on the species, and excised embryos grow into normal plants. Only about 20 species in 13 angiosperm families are known to have intermediate PD, but none of them belongs to the Asteraceae (Nikolaeva, 1969; Baskin and Baskin, 2014). However, see trimorphic cypselae of Asteraceae below.

Seeds with deep PD in the temperate zone require 12–24 weeks of cold stratification for dormancy break. About 20 species in the Balsaminaceae, Celastraceae, Rosaceae and Sapindaceae have this level of PD. Seeds with deep PD do not germinate when treated with gibberellins, and excised embryos either do not germinate or give rise to abnormal plants (Nikolaeva, 1969; Baskin and Baskin, 2014, 2021). It should be noted that seeds of the tropical montane shrub *Leptecophylla tameiamiae* (Ericaceae) have deep PD. Seeds of this species required 4–16 (or more) months of warm stratification for dormancy-break and germination and did not respond to gibberellins, and excised embryos did not grow (Baskin et al., 2005). We are not aware of any species of Asteraceae whose cypselae have deep PD.

## Breaking dormancy in cypselae of Asteraceae

### Cold stratification

A cold stratification requirement for dormancy-break occurs only in species of Asteraceae growing in habitats with a cold winter. However, in many temperate/arctic-zone plant communities, species of Asteraceae whose cypselae require cold stratification grow next to those whose dormant cypselae require exposure to warm temperatures (afterripening) during summer for dormancy break. The length of the cold stratification period required to break PD varies with the species and ranges from 30 d in *Coreopsis tripteris* (Diboll, 2004) to 120 d in *Rudbeckia subtomentosa* (Greene and Curtis, 1950). Species whose cypselae become ND via cold stratification can germinate as soon as temperatures increase in spring (Mattana et al., 2012), and this includes Asteraceae species that behave as summer annuals as well as many short-lived monocarpic perennials and polycarpic perennials (Baskin and Baskin, 1979a,b, 2022b; Baskin et al., 2022).

After PD has been broken by cold stratification, germination may not occur at the beginning of the growing season if light-requiring cypselae are buried and thus in darkness. For example, if buried cypselae of the summer annual Asteraceae *Ambrosia artemisiifolia* are exposed to natural temperate-zone seasonal temperature changes, most of them fail to germinate in spring (Baskin and Baskin, 1980). The increase in habitat temperatures in late spring induces the buried cypselae into secondary dormancy, and PD is broken again by cold stratification the following winter. Dormancy-break in winter and dormancy induction in

late spring result in an annual dormancy/non-dormancy cycle of temperate-zone Asteraceae such as *A. artemisiifolia* (Baskin and Baskin, 1980), *Bidens cernua* (Brändel, 2004b) and *Bidens polylepis* (Baskin et al., 1995a). In the case of *A. artemisiifolia*, buried cypselae have the potential to persist in the soil for at least 40 years (see Baskin and Baskin, 1977). Cypselae of *Senecio aquaticus*, *S. jacobaea* and *S. erucifolius* germinated to ca. 75, 95 and 45%, respectively after 3 months of cold stratification at 4°C, but dry storage for 5 months after cold stratification decreased germination to ca. 35, 30 and 25%, respectively (Otzen and Doornbos, 1980).

Freshly matured cypselae of *Erechtites hieraciifolius* germinated to 51% in light at 35/20°C in autumn (September) but to 0–15% in light at 15/6, 20/10, 25/15 and 30/15°C; only 1% of the cypselae germinated in darkness (at 35/20°C) (Baskin and Baskin, 1996). When cypselae were buried in soil and exposed to natural seasonal temperatures in Kentucky (USA), they became ND. In spring (April), they germinated to 98–100% in light and in darkness at the five temperature regimes. These increases in germination in spring indicate that the freshly matured cypselae were conditionally dormancy (i.e. germinated at some of the test conditions but not at all conditions possible after dormancy was broken). However, during summer cypselae lost their ability to germinate to high percentages in light at 15/6, 20/10 and 25/15°C but not at 30/15 and 35/20°C, and by October they germinated to 0, 23, 91, 100 and 100%, respectively, in light and to 0, 0, 6, 27 and 26%, respectively in the dark. Thus, the cypselae had entered conditional PD, that is, they could germinate at some temperatures but not at all of them. When tested in October of eight consecutive years, cypselae were in conditional dormancy. It is assumed that during winter of each year cypselae became ND and that in summer they entered conditional dormancy, that is, cypselae of this species have an annual conditional dormancy/non-dormancy cycle (Baskin and Baskin, 1996). An annual conditional dormancy/non-dormancy cycle has been reported in cypselae of the summer annuals *Bidens tripartita* (Brändel, 2004b) and *Coreopsis tinctoria* (Baskin and Baskin, 2014) and the polycarpic perennials *Eupatorium cannabinum* (Brändel and Jensen, 2005), *Solidago altissima*, *S. nemoralis* and *S. shortii* (Walck et al., 1997b).

### Warm stratification and/or afterripening

In tropical and subtropical regions on earth and for various species in temperate regions, the breaking of PD occurs during exposure to high summer temperatures. The high-temperature dormancy-breaking treatment may be warm (moist) stratification or dry afterripening, and in various habitats that receive intermittent rainfall during the dormancy-breaking period both warm stratification and afterripening occur. Warm stratification is a more effective dormancy-breaking treatment than dry afterripening for some species of Asteraceae, while dry afterripening is more effective than warm stratification for other species of Asteraceae (Karlsson et al., 2008). The cypselae of *Senecio morisii* collected in 2007 and stored for 10 years –25°C germinated to higher percentages over a range of temperatures than fresh cypselae collected and tested in 2017 (Cuena-Lombraña et al., 2020). Thus, it appears that cypselae underwent considerable afterripening at –25°C, assuming that fresh cypselae collected in 2007 would have germinated to similar percentages as those collected in 2017.

In tropical rainforests of Malaysia, seeds of forest trees (no Asteraceae included) incubated on moist soil at natural

temperatures required from about 12 to 22–36 weeks to begin germinating, showing that dormancy-break via warm stratification may require 12 or more weeks (Kiew, 1982; Ng, 1991, 1992). On the other hand, the cypselae of the winter annual Asteraceae *Gaillardia pulchella*, *Krigia cespitosa*, *Pyrrhoppappus pauciflorus* and *Tetranneuris linearifolia* from Texas (USA) exposed to simulated Texas summer temperatures and a wet (1 d)/dry (14 d) cycle for 0–4 months were ND after 4 months (i.e. in October). ND cypselae of the four species germinated to 86–99% at the Texas simulated October temperature (28/15°C) (Baskin et al., 1992b). Thus, the time required for dormancy break via mostly dry afterripening may be about the same as that required for dormancy break via warm stratification.

Afterripening in dry storage is an effective dormancy-breaking treatment for various species of Asteraceae, for example *Ambrosia trifida* (Ruziev et al., 2020), *Anthemis cotula* (Rashid et al., 2007), *Artemisia* spp. (Ali and Hamed, 2012; Lombardi et al., 2019), *Coreopsis lanceolata* (Banovetz and Scheiner, 1994), *Hyoseris scabra* (Gresta et al., 2010), *Lychnophora ericoides* (Melo et al., 2007), *Scorzoneroides* spp. (Cruz-Mazo et al., 2010) and *Silybum marianum* (Monemizadeh et al., 2021).

In Kentucky (USA), buried cypselae of the winter annual *Krigia cespitosa* exposed to natural summer temperatures and simulated rainfall regimes from May to October were ND in October (Baskin et al., 1991). Dormancy-break during the hot dry weather of summer means that cypselae can germinate when soil moisture becomes non-limiting in autumn, at which time temperatures are decreasing. In the Chihuahuan Desert of North America, germination of annual species occurs only after an about 10-mm rainfall event (Freas and Kemp, 1983). In the case of *K. cespitosa*, light is required for germination in autumn, and if cypselae are buried they cannot germinate. During winter, the buried cypselae of *K. cespitosa* were induced into secondary dormancy, which was broken the following summer. Dormancy-break in summer and dormancy induction in winter result in an annual dormancy/non-dormancy cycle of the buried cypselae (Baskin et al., 1991). Based on results from only one test temperature, cypselae of *Carthamus lanatus* (Grace et al., 2002) appear to have an annual dormancy/non-dormancy cycle and those of *Centaurea solstitialis* (Joley et al., 2003) an annual conditional dormancy/non-dormancy cycle. Cypselae of *Coreopsis lanceolata* stored dry at room temperature were ND after 6–8 months (Banovetz and Scheiner, 1994). When ND cypselae of this species were incubated on a moist substrate at 5°C, they entered secondary dormancy. It is not known if cypselae of *C. lanceolata* undergo an annual dormancy cycle.

### Types of non-deep physiological dormancy in Asteraceae

Six types of non-deep PD have been distinguished based on temperature requirements for seed germination as dormancy-break occurs (Baskin and Baskin, 2014, 2021; Nur et al., 2014; see Figure 3 in Soltani et al., 2017). In Types 1, 2 and 3, the temperature range over which seeds will germinate widens during dormancy-break. In Type 1, the maximum temperature at which seeds can germinate increases, and in Type 2, the minimum temperature at which seeds can germinate decreases. In Type 3, the maximum temperature for germination increases and the minimum temperature decreases. In Types 4, 5 and 6, the temperature range for germination does not widen during dormancy-break. Seeds with Type 4 gain the ability to germinate only at high temperatures, and those with Type 5 gain the ability

to germinate only at low temperatures. Seeds with Type 6 germinate to low percentages over a range of low to high temperatures in the early stages of dormancy-break, and the germination percentage increases at all temperatures as dormancy-break progresses. In addition to changes in the temperature range for germination during dormancy-break of seeds, particularly those with Types 1 and 2 non-deep PD, there is a gradual increase in germination rate (speed) and synchrony and in sensitivity to germination-promoting factors such as GA and light. Furthermore, like temperatures, sensitivity to these factors decreases as ND seeds are induced into secondary dormancy [see Table 4.3 in Baskin and Baskin (2014) and Maleki et al. (2022)].

Information about the type of non-deep PD in cypselae of Asteraceae is available for 103 species in 75 genera and 18 tribes (Table 1). Types 1, 2, 3, 4, 5 and 6 occur in 10, 13, 7, 3, 3 and 7 tribes of Asteraceae, respectively. The Heliantheae has the most types (1, 2, 3, 4 and 6). Five genera (one genus in each of five tribes) have species with two or three types, and *Silybum marianum* has two types (1 and 6) (Monemizadeh et al., 2021). The information for types of non-deep PD in tribes of Asteraceae was plotted on the tribe-level phylogeny of Mandel et al. (2019) (supplementary Fig. S1). No clear pattern about relationships between types and tribes was revealed, except that the occurrence of Types 1 and 2 or of Types 1, 2 and 3 in a tribe is fairly common. When plotted on the figure showing the proposed evolutionary history of Asteraceae by Huang et al. (2016), types of non-deep PD occurred from the Mutisieae to the Heliantheae Alliance (supplementary Fig. S2). Although information about the types of non-deep PD in Asteraceae is rather limited in terms of the number of species studied in detail, the results provide some insight into the great flexibility of cypselae dormancy and germination in the Asteraceae in relation to plant life cycle and environmental conditions in the habitat.

In temperate regions with generally hot and relatively dry summers and cold moist winters, Type 1 is found in cypselae of winter annual (Baskin et al., 1995b; Schütz et al., 2002) and some perennial (Baskin et al., 1994) species of Asteraceae. High temperatures during summer promote dormancy-break, and by the time the soil is moist in autumn the maximum temperature at which cypselae can germinate overlaps with temperatures in the habitat. Type 2 occurs in summer annual and many perennial species of Asteraceae (Baskin and Baskin, 1988; Baskin et al., 1993, 1995a, 1998). Low temperatures and moist soil during winter promote dormancy-break, that is, lowering the minimum temperature at which cypselae can germinate, and germination usually occurs in early to mid-spring. Type 3 occurs in species of Asteraceae that behave as winter annuals (Baskin et al., 1991, 1992b) and as perennials (Baskin and Baskin, 1988; Baskin et al., 1993, 1994, 1998) with dormancy being broken in summer and winter, respectively.

Little is known about Type 4 non-deep PD, except that both dormancy-break and germination occur at relatively high temperatures. The four species of Asteraceae known to have Type 4 (Table 1) occur in hot deserts (two species of *Pectis*) or in relatively mesic tropical/subtropical areas (*Tridax procumbens* and *Synedrella nodifolia*). In a habitat that is warm all year, it is assumed that timing of onset of the wet season is a major factor in determining the timing of germination. However, much additional research is needed on the environmental conditions required for dormancy-break and germination of species of Asteraceae (and other families) growing in tropical/subtropical regions.

**Table 1.** Types (1–6) of non-deep physiological dormancy in Asteraceae species

| Species                          | Tribe        | Type(s) | References  |
|----------------------------------|--------------|---------|---|
| <i>Actinobole uliginosum</i>     | Gnaphalieae  | 1       | Hoyle et al. (2008a,b)                            |
| <i>Ageratina altissima</i>       | Eupatorieae  | 2       | Baskin and Baskin (1988)                          |
| <i>Ageratina luciae-brauniae</i> | Eupatorieae  | 2       | Walck et al. (1997a)                              |
| <i>Ambrosia artemisiifolia</i>   | Heliantheae  | 2       | Baskin and Baskin (1980)                          |
| <i>Ambrosia trifida</i>          | Heliantheae  | 2       | Davis (1930)                                      |
| <i>Arctotheca calendula</i>      | Arctotideae  | 2       | Chaharsoghi and Jacobs (1998)                     |
| <i>Arnoglossum plantagineum</i>  | Senecioneae  | 1       | Baskin and Baskin (unpubl.)                       |
| <i>Bidens cernua</i>             | Coreopsideae | 2       | Baskin and Baskin (unpubl.)                       |
| <i>Bidens laevis</i>             | Coreopsideae | 2       | Leck et al. (1994)                                |
| <i>Bidens pilosa</i>             | Coreopsideae | 2       | Karlsson et al. (2008)                            |
| <i>Bidens polylepis</i>          | Coreopsideae | 2       | Baskin et al. (1995a)                             |
| <i>Boltonia decurrens</i>        | Astereae     | 6       | Baskin and Baskin (1988, 2002)                    |
| <i>Boltonia diffusa</i>          | Astereae     | 6       | Baskin and Baskin (unpubl.)                       |
| <i>Brickellia eupatorioides</i>  | Eupatorieae  | 2       | Baskin et al. (1993) and Baskin and Baskin (1998) |
| <i>Centaurea solstitialis</i>    | Cynareae     | 1       | Joley et al. (2003)                               |
| <i>Centaurea stoebe</i>          | Cynareae     | 2       | Eddleman and Romo (1988)                          |
| <i>Chaptalia nutans</i>          | Mutisieae    | 3       | Baskin et al. (1994)                              |
| <i>Coespeletia timotensis</i>    | Millerieae   | 5?      | Guariguata and Azocar (1988)                      |
| <i>Coreopsis nuecensis</i>       | Coreopsideae | 2       | Baskin and Baskin (unpubl.)                       |
| <i>Cirsium dissectum</i>         | Cynareae     | 2       | de Vere (2007)                                    |
| <i>Cirsium vulgare</i>           | Cynareae     | 2       | Michaux (1989)                                    |
| <i>Coreopsis leavenworthii</i>   | Coreopsideae | 6       | Kabat et al. (2007)                               |
| <i>Craspedia</i> sp.             | Gnaphalieae  | 1?      | Plummer and Bell (1995)                           |
| <i>Dimorphotheca pluvialis</i>   | Calenduleae  | 3?      | de Villiers et al. (2002a,b)                      |
| <i>Echinacea angustifolia</i>    | Heliantheae  | 3       | Baskin et al. (1992a)                             |
| <i>Echinacea pallida</i>         | Heliantheae  | 3       | Baskin and Baskin (unpubl.)                       |
| <i>Echinacea simulata</i>        | Heliantheae  | 3       | Baskin et al. (1993)                              |
| <i>Echinacea tennesseensis</i>   | Heliantheae  | 3       | Baskin et al. (1993)                              |
| <i>Echinops gmelinii</i>         | Cynareae     | 6       | Nur et al. (2014)                                 |
| <i>Eclipta prostrata</i>         | Heliantheae  | 2       | Baskin and Baskin (unpubl.)                       |
| <i>Elephantopus</i> sp.          | Vernonieae   | 2       | Baskin and Baskin (unpubl.)                       |
| <i>Epilasia acrolasia</i>        | Cichorieae   | 6       | Nur et al. (2014)                                 |
| <i>Erechtites hieracifolia</i>   | Senecioneae  | 2       | Baskin and Baskin (1996)                          |
| <i>Ericameria nauseosa</i>       | Astereae     | 2       | Meyer et al. (1989)                               |
| <i>Erigeron modestus</i>         | Astereae     | 1       | Baskin et al. (1994)                              |
| <i>Eupatorium cannabinum</i>     | Eupatorieae  | 2       | Schütz (1999)                                     |
| <i>Eurybia divaricata</i>        | Astereae     | 3       | Baskin et al. (1993)                              |
| <i>Eutrochium fistulosum</i>     | Eupatorieae  | 2       | Baskin et al. (1993)                              |
| <i>Gaillardia pulchella</i>      | Helenieae    | 1       | Baskin et al. (1994)                              |
| <i>Gaillardia suavis</i>         | Helenieae    | 1       | Baskin et al. (1992b)                             |
| <i>Galinsoga ciliata</i>         | Millerieae   | 2       | Baskin and Baskin (1981)                          |
| <i>Galinsoga parviflora</i>      | Millerieae   | 2       | Baskin and Baskin (1981)                          |
| <i>Garhadiolus papposus</i>      | Cichorieae   | 1       | Sun et al. (2009)                                 |

(Continued)

Table 1. (Continued.)

| Species                                      | Tribe       | Type(s) | References                      |
|--|-------------|---------|---------------------------------|
| <i>Gazania leiopoda</i>                      | Arctotideae | 1?      | de Villiers et al. (2002a,b)    |
| <i>Glebionis coronaria</i>                   | Anthemideae | 6       | Puglia et al. (2015)            |
| <i>Grindelia lanceolata</i>                  | Astereae    | 2       | Baskin and Baskin (1979a, 1988) |
| <i>Guizotia scabra</i>                       | Millerieae  | 2       | Karlsson et al. (2008)          |
| <i>Helenium autumnale</i>                    | Helenieae   | 2       | Baskin et al. (1993)            |
| <i>Helianthus annuus</i>                     | Heliantheae | 2       | Baskin and Baskin (1988)        |
| <i>Helianthus atrorubens</i>                 | Heliantheae | 2       | Baskin and Baskin (unpubl.)     |
| <i>Helianthus maximilliani</i>               | Heliantheae | 2       | Baskin et al. (1998)            |
| <i>Heterotheca subaxillaris</i>              | Astereae    | 2       | Baskin and Baskin (1976, 1988)  |
| <i>Hieracium caespitosum</i>                 | Cichorieae  | 2       | Panebianco and Willemsen (1976) |
| <i>Hymenopappus scabiosaeus</i>              | Bahieae     | 1       | Baskin et al. (1992b)           |
| <i>Hymenoxys scaposa</i>                     | Helenieae   | 1       | Baskin et al. (1992b)           |
| <i>Hyoseris scabra</i>                       | Cichorieae  | 3?      | Gresta et al. (2010)            |
| <i>Iva annua</i>                             | Heliantheae | 3       | Baskin and Baskin (unpubl.)     |
| <i>Jacobaea erucifolia</i>                   | Senecioneae | 2       | Otzen and Doornbos (1980)       |
| <i>Jamesianthus alabamensis</i>              | Tageteae    | 2       | Baskin and Baskin (unpubl.)     |
| <i>Koelpinia linearis</i>                    | Cichorieae  | 6       | Nur et al. (2014)               |
| <i>Krigia cespitosa</i> var. <i>gracilis</i> | Cichorieae  | 1       | Baskin et al. (1994)            |
| <i>Krigia oppositifolia</i>                  | Cichorieae  | 2       | Baskin et al. (1991)            |
| <i>Lactuca canadensis</i>                    | Cichorieae  | 2       | Baskin and Baskin (unpubl.)     |
| <i>Lactuca floridana</i>                     | Cichorieae  | 2       | Baskin and Baskin (1988)        |
| <i>Liatris squarrosa</i>                     | Eupatorieae | 2       | Baskin and Baskin (1988, 1989)  |
| <i>Logfia filaginoides</i>                   | Inuleae     | 5?      | Juhren et al. (1956)            |
| <i>Marshallia mohrii</i>                     | Helenieae   | 6?      | Dell et al. (2019)              |
| <i>Mikania scandens</i>                      | Eupatorieae | 2       | Baskin et al. (1993)            |
| <i>Millotia myosotidifolia</i>               | Gnaphalieae | 1       | Schütz et al. (2002)            |
| <i>Palafoxia callosa</i>                     | Bahieae     | 2       | Baskin et al. (1999)            |
| <i>Pectis angustifolia</i>                   | Tageteae    | 4?      | Freas and Kemp (1983)           |
| <i>Pectis papposa</i>                        | Tageteae    | 4?      | Juhren et al. (1956)            |
| <i>Pinaropappus roseus</i>                   | Cichorieae  | 1       | Baskin et al. (1992b)           |
| <i>Podotrochea chrysantha</i>                | Gnaphalieae | 1       | Schütz et al. (2002)            |
| <i>Podotrochea gnaphalioides</i>             | Gnaphalieae | 1       | Schütz et al. (2002)            |
| <i>Polymnia canadensis</i>                   | Heliantheae | 6       | Bender et al. (2003)            |
| <i>Pseudognaphalium obtusifolium</i>         | Gnaphalieae | 1       | Baskin and Baskin (unpubl.)     |
| <i>Pyrrhopappus pauciflorus</i>              | Cichorieae  | 1       | Baskin et al. (1994)            |
| <i>Ratibida pinnata</i>                      | Heliantheae | 2       | Baskin et al. (1993)            |
| <i>Reichardia tingitana</i>                  | Cichorieae  | 1       | Schütz (1999)                   |
| <i>Schoenia cassiniana</i>                   | Gnaphalieae | 5?      | Plummer and Bell (1995)         |
| <i>Senecio aquaticus</i>                     | Senecioneae | 2       | Otzen and Doornbos (1980)       |
| <i>Senecio arenarius</i>                     | Senecioneae | 1?      | de Villiers et al. (2002a,b)    |
| <i>Senecio jacobaea</i>                      | Senecioneae | 3       | Otzen and Doornbos (1980)       |
| <i>Senecio vulgaris</i>                      | Senecioneae | 3       | Popay and Roberts (1970a,b)     |
| <i>Silybum mariarum</i>                      | Cynareae    | 1, 2    | Monemizadeh et al. (2021)       |

(Continued)



Table 1. (Continued.)

| Species                          | Tribe       | Type(s)        | References                                     |
|----------------------------------|-------------|----------------|--|
| <i>Solidago albopilosa</i>       | Astereae    | 2 <sup>a</sup> | Albrecht et al. (2020)                         |
| <i>Solidago altissima</i>        | Astereae    | 2              | Baskin et al. (1993) and Walck et al. (1997b)  |
| <i>Solidago nemoralis</i>        | Astereae    | 2              | Walck et al. (1997b)                           |
| <i>Solidago ptarmicoides</i>     | Astereae    | 3              | Baskin and Baskin (1988)                       |
| <i>Solidago shortii</i>          | Astereae    | 2              | Buchele et al. (1991) and Walck et al. (1997b) |
| <i>Symphytotrichum pilosa</i>    | Astereae    | 2              | Baskin and Baskin (1979b, 1988)                |
| <i>Synedrella nodiflora</i>      | Heliantheae | 4              | Chauhan and Johnson (2009)                     |
| <i>Tetranneuris linearifolia</i> | Helenieae   | 3              | Baskin et al. (1994)                           |
| <i>Tithonia rotundifolia</i>     | Heliantheae | 2              | Upfold and Van Staden (1990)                   |
| <i>Tragopogon pratensis</i>      | Cichorieae  | 2              | Qi and Upadhyaya (1993)                        |
| <i>Tridax procumbens</i>         | Millerieae  | 4              | Chauhan and Johnson (2008)                     |
| <i>Ursinia anthemoides</i>       | Anthemideae | 1              | Schütz et al. (2002)                           |
| <i>Verbesina alternifolia</i>    | Heliantheae | 2              | Baskin et al. (1993)                           |
| <i>Verbesina encelioides</i>     | Heliantheae | 1              | Karlsson et al. (2008)                         |
| <i>Verbesina helianthoides</i>   | Heliantheae | 2              | Baskin and Baskin (1988)                       |
| <i>Verbesina virginica</i>       | Heliantheae | 2              | Baskin et al. (1998)                           |
| <i>Viguiera dentata</i>          | Heliantheae | 2              | Baskin et al. (1998)                           |
| <i>Xanthium strumarium</i>       | Heliantheae | 2              | Norsworthy and Oliveira (2007)                 |

<sup>a</sup>Arguably, this could be Type 6 because fresh cypselae germinated over the entire range of test temperatures, although to a very low percentage at 15/5°C (the lowest test temperature regime).

Type 5 non-deep PD has been reported in cypselae of *Coespeletia timothensis*, *Filago californica* and *Schoenia cassiniana* (Table 1). The thing that these species have in common is that their cypselae germinate only at low temperatures. At high elevations in the Andes Mountains, it is reasonable that cypselae of *C. timothensis* would gain the ability to germinate only at low temperatures. However, for *F. californica* and *S. cassiniana* that grow in habitats with a Mediterranean-type climate, a low temperature requirement for germination would delay germination until late in autumn when the soil is likely to be moist. That is, a delay of germination until temperatures are low helps ensure that there is enough soil moisture for seedling establishment and growth.

Nine species of Asteraceae are listed in Table 1 as having Type 6 non-deep PD, and they can be divided into two general categories depending on their habitat: (1) cold desert and (2) relatively moist temperate. In the cold desert, timing of rainfall is highly unpredictable. Thus, ability of cypselae to germinate over a wide range of temperatures as dormancy-break is occurring would allow at least some cypselae of the cold desert winter annuals *Echinops gmelinii*, *Epilasia acrolasia* and *Koelipia linearis* to germinate at any time during the growing season in response to a rainfall event or snowmelt in late winter/early spring (Nur et al., 2014). In the case of *Glebionis coronata* in the Mediterranean region, Type 6 would allow cypselae to germinate regardless of whether the onset of the wet season began early or late in the autumn. The other five species with Type 6 grow in the regions of the deciduous forest in eastern North America, where there is no definite dry season. Presumably Type 6 would allow cypselae to germinate at any time during the growing season, but this has not been tested. However, cypselae of *Boltonia decurrens* (Baskin and Baskin, 1988) and *Polymnia canadensis*

(Bender et al., 2003) exposed to natural temperature regimes germinate in both spring and autumn.

### Intraspecific variation in dormancy

Not only is there species-to-species variation in dormancy in the Asteraceae due to different types of non-deep PD, but there may be variation in dormancy between the cypselae produced by the same species. For example, cypselae of various species of Asteraceae differed in their germination characteristic when collected in different populations (Schütz and Urbanska, 1984; Meyer et al., 1989, 1990; Ren and Abbott, 1991; Maluf, 1993; Martin et al., 1995; Keller and Kollmann, 1999; Qaderi and Cavers, 2000a; Giménez-Benavides et al., 2005; Bischoff et al., 2006; Jorritsma-Wienk et al., 2007; Li and Feng, 2009; Bischoff and Muller-Schärer, 2010; Bartle et al., 2013; Torres-Martínez et al., 2017; de Pedro et al., 2021). However, the reason (genetic and/or maternal environmental effects) for population differences in dormancy was not determined in these studies.

Cypselae of the invasive *Senecio madagascariensis* from populations at the edge of its range in eastern Australia germinated to significantly higher percentages than those from populations in the established part of its range in eastern Australia (Bartle et al., 2013). Simulation studies of cypselae germination and seedling survival of *Artemisia tridentata* under climate change conditions across its western North American range suggest that regeneration from cypselae will be higher at the leading (relatively moist) than at the trailing (relatively dry) edge of the range of distribution shift (Schlaepfer et al., 2015).

Cypselae dormancy in Asteraceae has a genetic component, for example, *Helianthus bolanderi* (Olivieri and Jain, 1978), *Lactuca*

*sativa* (Eenink, 1981) and *Senecio vulgaris* (Kadereit, 1984). In particular, the genetics of cypselae dormancy have been investigated in detail for *Helianthus annuus* (Snow et al., 1998; Weiss et al., 2013; Layat et al., 2014; Lachabrouilli et al., 2021; Hernández et al., 2022) and *L. sativa* (Argyris et al., 2011; Huo et al., 2016). Inbred dormant and non-dormant lines of *H. annuus* exhibit differences in pericarp anatomy and hormone profiles (Andrade et al., 2015). Also, the dormancy/germination characteristics of the mature cypselae can vary depending on the environmental conditions under which the maternal plant was growing during cypselae development, including day length (Guterman et al., 1975), mineral nutrition (Thompson, 1937; Allison, 2002), soil moisture (Qaderi and Cavers, 2000b) and temperature (Nosova, 1981; Zhang et al., 2012; Bodrone et al., 2017). Furthermore, the maternal environment and genetics of the embryo can interact to influence cypselae dormancy (Weiss et al., 2013), and there could be epigenetic (i.e. non-genetic trans-generational inheritance, e.g. Robertson and Richards, 2015; Skinner and Nilsson, 2021) control of dormancy via maternal inheritance, as in *Arabidopsis thaliana* (Iwasaki et al., 2019).

In the case of *Silybum marianum*, populations vary with regard to the type of non-deep PD in the mature cypselae (Monemizadeh et al., 2021). Cypselae from plants of *S. marianum* growing at three population sites in northern Iran were allowed to afterripen in dry storage. Cypselae from two populations first gained the ability to germinate over a range of temperatures, indicating Type 6 non-deep PD. However, cypselae from the third population first germinated only at low temperatures but as afterripening continued the maximum temperature at which they germinated increased, indicating Type 1 non-deep PD. The cypselae with Type 6 developed under relatively dry, warm conditions and those with Type 1 developed during relatively wet, cool conditions. These results suggest that the maternal environment affected the type of non-deep PD that developed in the cypselae, but the effects of genetics and environment  $\times$  genetics on the type of non-deep PD that developed in the cypselae in different populations have not been investigated.

### Heteromorphic cypselae

According to Scholl et al. (2020), heteromorphic diaspores differ in morphology and ecology, and the variation can be discrete or continuous, and if continuous the extreme diaspores differ greatly. In the classification scheme for variation in diaspore size/mass and morphology of Baskin and Baskin (2014, p. 341), Asteraceae species mentioned in this section fit into Subgroup a (Heterocarpy) of Group A (Heterodiaspory) of Division II (Heteromorphic). Diaspore heteromorphism occurs primarily in annual plants, and it is viewed as an adaptation (via a bet-hedging strategy) to unpredictable or disturbed environments (Mandák, 1997; Imbert, 2002; Cruz-Mazo et al., 2009, 2010). The majority (ca. 80%) of heterodiasporous species occurs in three eudicot families: Asteraceae > Amaranthaceae > Brassicaceae (Mandák, 1997). The number of diaspore heteromorphic species of Asteraceae worldwide has not been determined, but in southwestern North America it is the family with the most diaspore heteromorphic species, that is, 64 species in 38 genera. The Boraginaceae is the second most important family with heteromorphic diaspores in this region with 23 species in 5 genera (Scholl et al., 2020).

Cypselae produced in the same capitulum of many species of Asteraceae vary in size, mass, colour, shape, ornamentation, presence/absence of pappus, thickness of pericarp, dispersal ability,

presence/absence of dormancy and degree of non-deep PD (Baskin et al., 2013; Baskin and Baskin, 2014). Various dimorphic, and a few trimorphic, species of Asteraceae have been studied in detail. In general, peripheral cypselae are more dormant (higher degree of non-deep PD) than central cypselae, which are ND in some species; however, central cypselae can be more dormant than peripheral cypselae (Table 2). Cypselae that differ in degree of dormancy also can be produced by species with only ligulate (El-Keblawy, 2003) or only ray (Olivieri et al., 1983) flowers. Both the peripheral and central cypselae of *Crepis sancta* (Imbert et al., 1996) and *Synedrella nodiflora* (Souza Filho and Takaki, 2011) have been reported to be ND.

Germination of trimorphic cypselae of Asteraceae has been studied in some detail for *Calendula arvensis* (Ruiz de Clavijo, 2005), *Garhadiolus papposus* (Sun et al., 2009), *Heteracia szovitsii* (Cheng and Tan, 2009; Lu et al., 2020) and *Heterosperma pinnatum* (Venable et al., 1987). Trimorphic cypselae have been reported for *Xanthocephalum* spp. (Lane, 1983) and *Chaptalia hieracioides* (Xu et al., 2018), but their dormancy has not been studied. We note that some species of *Chaptalia* in Brazil (Pasini et al., 2014) and Mexico (Redonda-Martínez, 2018) have trimorphic florets and presumably trimorphic cypselae. In *G. papposus* (Sun et al., 2009), *H. szovitsii* (Lu et al., 2020) and *H. pinnatum* (Venable et al., 1987), the central cypselae are the least dormant and the peripheral cypselae the most dormant. Central, intermediate and peripheral cypselae of the cold desert annual *H. szovitsii* allowed to afterripen for 48 months germinated to 85% (30/15°C), 30.5% (5/2°C) and 10.5% (15/2°C), respectively. However, when the pericarp was removed from intermediate and peripheral cypselae they germinated to 100 and 69.3%, respectively (Lu et al., 2020). Since seedlings derived from excised embryos of intermediate and peripheral cypselae produced normal plants and since afterripening, scarification/pericarp removal and GA<sub>3</sub> promoted germination of both kinds of cypselae (but more germination of intermediate than peripheral cypselae), it was concluded that intermediate and peripheral cypselae have intermediate PD. When central, intermediate and peripheral cypselae were sown outdoors in spring 2016, germination of central cypselae occurred in autumn 2016 and spring 2017; intermediate in spring and autumn 2017, 2018 and 2019; and peripheral in spring and autumn 2017, 2018, 2019 and spring 2020, showing that intermediate and peripheral cypselae can form a persistent soil cypselae bank.

Cypselae heteromorphism translates into differences not only in degree of dormancy but also differences in dispersal and timing of germination (Baskin and Baskin, 2014). Generally, in Asteraceae, the central cypselae have low dormancy and high dispersal, and peripheral cypselae have high dormancy and low dispersal (Venable and Lawlor, 1980; see Baskin et al., 2013). This combination of traits for cypselae from the same plant allows seedlings to escape an unfavourable environment for establishment and growth in both time and space. Variability in degree of dormancy spreads the risk over time, and variability in dispersal ability spreads the risk over space. Cypselae with low dormancy and high dispersal may be dispersed to a new site where they may germinate immediately. Most cypselae with high dormancy and low dispersal remain near the mother plant and germinate after some period of time during which the mother plant may have died, creating a favourable site for establishment of a seedling of the same species.

In studies on dormancy and dispersal of the trimorphic cypselae of *Heterosperma pinnatum*, Venable et al. (1987) concluded that the low dormancy-high dispersal of the central cypselae was a high-risk strategy, and the high dormancy-low dispersal of the peripheral cypselae was a low-risk strategy, with the intermediate cypselae

**Table 2.** Comparison of dormancy in examples of Asteraceae species with heteromorphic (dimorphic) cypselae

| Species   | Comparison of dormancy | References   |
|---|------------------------|--|
| <i>Anacyclus radiatus</i>                               | PA (ND) = CA (ND)      | Bastida and Menéndez (2004) and Bastida et al. (2010)          |
| <i>Anthemis chrysantha</i>                              | PA > CA                | Aguado et al. (2011)   |
| <i>Bidens bipinnata</i>                                 | PA > CA                | Dakshini and Aggarwal (1974)                                   |
| <i>Bidens frondosa</i>                                  | CA > PA                | Brändel (2004a)  |
| <i>Bidens pilosa</i>                                    | PA > CA                | Forsyth and Brown (1982), Rocha (1996) and Zhang et al. (2019) |
| <i>Blepharizonia plumosa</i>                            | CA > PA                | Gregory et al. (2001)  |
| <i>Carduus pycnocephalus</i>                            | PA > CA (ND)           | Olivieri et al. (1983)   |
| <i>Carduus tenuiflorus</i>                              | PA > CA (ND)           | Olivieri et al. (1983)   |
| <i>Centaurea solstitialis</i>                           | PA = CA                | Young et al. (2005)  |
| <i>Crepis aspera</i>                                    | PA > CA                | El-Keblawy (2003)  |
| <i>Crepis sancta</i>                                    | PA (ND) = CA (ND)      | Imbert et al. (1996)   |
| <i>Deinandra increscens</i>                             | PA > CA                | Tanowitz et al. (1987)   |
| <i>Dimorphotheca sinuata</i>                            | PA > CA                | Beneke et al. (1993)   |
| <i>Galinsoga quadriradiata</i>                          | PA > CA                | Kucewicz et al. (2011)   |
| <i>Glebionis coronaria</i>                              | PA > CA (ND)           | Bastida and Menéndez (2004) and Bastida et al. (2010)          |
| <i>Grindelia lanceolata</i>                             | PA > CA                | Baskin and Baskin (1979a)                                      |
| <i>Grindelia squarrosa</i>                              | PA > CA                | McDonough (1975)   |
| <i>Hedypnois rhagadioloides</i>                         | PA > CA                | Kigel (1992)   |
| <i>Heterotheca grandiflora</i>                          | PA > CA                | Flint and Palmblad (1978)                                      |
| <i>Heterotheca subaxillaris</i>                         | PA > CA (ND)           | Awang and Monaco (1978)  |
| <i>Heterotheca subaxillaris</i> subsp. <i>latifolia</i> | PA > CA                | Venable and Levin (1985a)                                      |
| <i>Jacobaea vulgaris</i>                                | PA > CA                | McEvoy (1984)  |
| <i>Leontodon saxatilis</i>                              | PA > CA                | Brändel (2007)   |
| <i>Leontodon saxatilis</i> subsp. <i>rothii</i>         | PA > CA                | Ruiz de Clavijo (2001)   |
| <i>Oedera genistaefolia</i>                             | CA > PA                | Levyns (1935)  |
| <i>Packera tomentosa</i>                                | PA > CA                | Leverett and Jolls (2014)                                      |
| <i>Synedrella nodiflora</i>                             | PA (ND) = CA (ND)      | Souza Filho and Takaki (2011)                                  |

CA, central cypselae; ND, non-dormant; PA, peripheral cypselae.

having a strategy between the two extremes. The proportion of heteromorphic cypselae (morphs) in *H. pinnatum* varied genetically between populations and between individuals (Venable and Búrquez, 1989). Furthermore, the percentage of central cypselae with awns increased from dry open to mesic closed habitats and with an increase in annual precipitation (Venable et al., 1995).

Fenesi et al. (2019) found evidence that cypselae heteromorphism is related to naturalization success of Asteraceae, but a short life cycle (annual or biennial) and relatively tall height of mature plants also contribute to the naturalization success of the heteromorphic species. Thus, the authors concluded that cypselae heteromorphism may be a part of the combination of traits that leads to naturalization success.

### Amphicarp

In the Baskin and Baskin (2014, p. 341) classification scheme, the two Asteraceae species mentioned in this section belong to Subgroup b sensu lato of Group B (Amphicarp) of Division II (Heteromorphic). In the two known amphicarpic species of

Asteraceae, *Gymnarrhena micrantha* and *Catananche lutea*, plants produce subterranean and aerial cypselae (Zhang et al., 2020). The subterranean and aerial cypselae of the winter annual *G. micrantha* are ND and germinate to higher percentages in light than in dark with the optimum temperature for germination being 15°C (Koller and Roth, 1964). The aerial cypselae are smaller than the subterranean cypselae and may not be formed in years with low soil moisture; however, the plants always produce subterranean cypselae. The aerial cypselae potentially distribute the species to new suitable habitats, while the subterranean cypselae maintain the species in a habitat that has already proven to be suitable for production of offspring.

Individual plants of the annual *C. lutea* can produce five morphs: two kinds of subterranean cypselae (amphi-I that are non-dormant and amphi-II that have non-deep PD) and three kinds of aerial cypselae (central intermediate and peripheral) that are mostly ND but require light and relatively low (12, 19°C) temperatures for high germination percentages (Ruiz de Clavijo, 1995). The aerial central cypselae have a more highly developed pappus than the intermediate cypselae, which in turn

have more pappus than the peripheral cypselae. Thus, central, intermediate and peripheral acenes have high, intermediate and low dispersal, respectively. Overall, the subterranean cypselae ensure that the species is distributed in time, and the aerial cypselae ensure dispersal in both time and space. That is, the aerial peripheral and the aerial central cypselae of *C. lutea* ensure dispersal in time and space, respectively. We are not aware of any species of Asteraceae with amphi-basicarpy (Zhang et al., 2020).

### Bet-hedging

When viewed from an evolutionary perspective, the production of cypselae with different strategies by the same plant is an adaptive bet-hedging strategy. That is, the production of two or more kinds of cypselae with different dormancy, dispersal and germination characteristics can increase the geometric mean and reduce variance in fitness. A commonly held idea is that, on average (i.e. arithmetic mean) the most-fit individuals leave the most offspring. However, this is not true in an environment that fluctuates stochastically, thus causing the number of offspring (fitness, e.g.  $R_0$ ) to vary among the years. In this case, geometric mean is the best measure of fitness, and it is maximized across generations (years) by bet-hedging.

Geometric mean is the product of the number of values being considered raised to the  $1/n$  power, for example,  $(4 \times 12 \times 20)^{1/3} = (960)^{1/3} = 9.86$ , which is lower than the arithmetic mean (i.e. 12). Thus, with a decrease in variance ( $\sigma^2$ ) or an increase in arithmetic mean ( $\mu_A$ ), geometric mean ( $\mu_G$ ) increases, and this relationship is expressed as  $\mu_G = \mu_A - (\sigma^2/2)$  when fitness is  $>0$  (Gillespie, 1977; Crean and Marshall, 2009; Simons, 2011). According to Seger and Brockmann (1987), 'The geometric mean is the natural measure of long-term fitness under temporal variation because, like population growth itself, it is inherently multiplicative rather than additive'. Thus, the production of heterodiaspores is a way to decrease variance in the number of offspring produced per year and thus increase the geometric mean of the number of offspring across generations, that is, by bet-hedging.

A bet-hedging strategy is adaptive in temporally varying environments that result in both good and poor years for seedling establishment and survival (Venable 1985a,b; Venable and Levin, 1985a,b; Philippi and Seger, 1989; Philippi, 1993; Simons, 2011; Gremer et al., 2012; Starrfelt and Kokko, 2012; Gianella et al., 2021). The production of two kinds of offspring as in diaspore heteromorphic Asteraceae is a diversified bet-hedging strategy (Rajon et al., 2009; Crowley et al., 2016; Haaland et al., 2018). The cypselae with a low-risk strategy germinate immediately, but those with a high-risk strategy delay germinating, thereby providing a reserve of cypselae for the future regardless of whether a good or poor year follows the year of cypselae production. Based on a demographic–life-history study of disc *versus* ray cypselae, Venable (1985a,b) and Venable and Levin (1985a,b) present a strong case for bet-hedging in the heterocarpic (dimorphic) species *Heterotheca subaxillaris* var. *latifolia*. This is an annual species that grows in disturbed and open sites in which the disc and ray cypselae and the plants that originate from them have a high-risk–low-risk strategy, that is, high risk for disc cypselae and low risk for ray cypselae. The disc cypselae increase the  $\mu_G$  by increasing  $\mu_A$ , and the ray cypselae increase  $\mu_G$  by decreasing  $\sigma^2$ .

In addition to cypselae differences in dispersal ability and degree of dormancy, bet-hedging has been attributed to other differences between disc and ray cypselae, including pre-dispersal insect predation, persistence in the seed bank and thickness of

the pericarp (Evans et al., 2007; Kistenmacher and Gibson, 2016). Also, genetic diversity between ray and disc cypselae has been considered. The observed heterozygosity across all populations of *Grindelia ciliata* was significantly higher in the disc pool than the ray cypselae pool, but the mean outcrossing percentage did not differ between ray and disc cypselae (Gibson, 2001). In *Heterotheca subaxillaris*, the level of genetic diversity did not differ significantly between ray and disc cypselae, and there was a mixed mating system with some inbreeding in most populations, which may result in founder effects (Gibson and Tomlinson, 2002). However, the authors concluded that differences in size and dispersal ability between ray and disc cypselae helped reduce the effects of inbreeding depression on the populations.

### Local adaptation

Ecotypes/local adaptations not involving cypselae dormancy/germination have been documented in various species of Asteraceae (Wacquand and Picard, 1992; Andersson and Shaw, 1994; Imbert et al., 1999; Scherber et al., 2003; Becker et al., 2006; Sambatti and Rice, 2006; Ramsey et al., 2008; Raabová et al., 2011; Wang et al., 2012; Imani et al., 2014; Moore et al., 2014; Pánková et al., 2014; Müller et al., 2017; Molina-Montenegro et al., 2018; Sakaguchi et al., 2018; van Boheemen et al., 2019; Ollivier et al., 2020; Challagundla and Wallace, 2021; de Pedro et al., 2021; Lin et al., 2021). However, *Carlina vulgaris* (Jakobsson and Dinnetz, 2005) and *Centaurea hyssopifolia* (Sánchez et al., 2017) did not exhibit local adaptation, except the survival of juveniles of *C. hyssopifolia* was higher in native than in non-native sites. Thus, there is evidence that some, but not all, species of Asteraceae can adapt to the local habitat conditions.

Some invasive species of Asteraceae, for example, *Ambrosia artemisiifolia* (van Boheemen et al., 2019), *Arctotheca populifolia* (Brandenburger et al., 2019), *Helianthus annuus* (Hernández et al., 2019), *Sonchus oleraceus* (Ollivier et al., 2020) and *Taraxacum campyloides* (Molina-Montenegro et al., 2018) not only have developed local adaptations in new (invaded) sites but have done so rapidly. These results lend support to the conclusion of Oduor et al. (2016) that invasive species develop local adaptations as frequently as native species. Rapid local adaptation of Asteraceae to new habitats, no doubt, has contributed not only to the great diversification of species in this family but also to its occurrence in all major vegetation zones on earth.

### Species diversification

According to Tank et al. (2015), '... we still do not have a clear idea of the drivers of differential diversification among plant species'. Zhang et al. (2021b) proposed that phylogenomic, morphological, ecological and model-based approaches need to be integrated into studies of diversification. Magallón et al. (2019) identified a species diversification rate shift in Asteraceae at a mean time of 76.79 Ma, as one of 30 exceptional changes in species diversification rates of angiosperms.

An outstanding example of species diversification in Asteraceae is the 28 species of *Argroxiphium*, *Dubautia* and *Wilkesia* that evolved in the Hawaiian Islands (USA) from a single dispersal event of a tarweed (*Madia/Raillardropsis* group) from California to Hawaii. Among the three genera, the diversity of life forms in the Hawaiian Islands includes trees, shrubs, cushion plants, vines and long-lived monocarpic and polycarpic rosette plants that

grow in a range of habitats from dry woodland/scrublands to bogs (Robichaux et al., 1990; Baldwin and Sanderson, 1998). Other examples of species diversification in the Asteraceae include: (1) *Bidens*, Hawaiian Islands, 19 species (Knape et al., 2012), (2) *Brachyglottis*, New Zealand, 30 species (Wagstaff and Breitwieser, 2004), (3) *Cheirolophus*, Macaronesia, 20 species (Vitales et al., 2014), (4) *Dendroseris*, Juan Fernández Islands, Chile, 11 species (Cho et al., 2020), (5) *Encelia*, deserts of the Americas, 15 species and 5 subspecies (Singhal et al., 2021), (6) *Espeletia* complex, tropical Andes, 140 species (Pouchon et al., 2018), (7) *Hypochaeris apargioides* complex, central-south Chile and adjacent Argentina, 4 species (López-Sepúlveda et al., 2013), (8) *Ligularia-Chremanthodium-Parasenecio* complex, Qinghai-Tibetan Plateau, 11 species (Liu et al., 2006), (9) *Psiadia*, Madagascar and surrounding islands in western Indian Ocean, about 60 species (Strijk et al., 2012), (10) *Saussurea*, high mountains of temperate Asia including the Qinghai-Tibetan Plateau, about 100 species (Zhang et al., 2021b), (11) woody *Sonchus* alliance, Canary Islands, 19 species (Kim et al., 1999) and (12) *Senecio*, high equatorial Andes, 29 species (Dušková et al., 2017).

### Hybridization

Hybridization in plants, and Asteraceae in particular, can be between biotypes or subspecies of the same species or between species. Cypselae from crosses between wild and domesticated plants of *Helianthus annuus* had increased germination (Snow et al., 1998; Mercer et al., 2006; Presotto et al., 2014). Cypselae from hybrids between *Artemisia tridentata* subsp. *tridentata* and *A. tridentata* subsp. *vaseyana* germinated to higher percentages than those from *A. t.* subsp. *tridentata* but to lower percentages than those from *A. t.* subsp. *vaseyana* (Graham et al., 1995; Wang et al., 1997). Cypselae from crosses between *Solidago canadensis* and *S. virgaurea* germinated to higher percentages than those from *S. canadensis* but to lower percentages than those from *S. virgaurea* (Pliszko and Kostrakiewicz-Gierałt, 2017). However, cypselae from the hybrid germinated faster than those from either parent (Pliszko and Kostrakiewicz-Gierałt, 2018).

Hybridization can lead to offspring having more than two sets of chromosomes, and in some cases, a new polyploid species is formed (e.g. Abbott and Lowe, 2004). In general, there are two main kinds of polyploids: autopolyploids and allopolyploids. Autopolyploidy results from crosses within the same species or from WGD, while allopolyploidy results from crosses between species (see Parisod et al., 2010). Both kinds of polyploids are found in the Asteraceae.

### Polyploidization and its consequences

WGD occurred in the early evolution of angiosperms (Masterson, 1994; Simillion et al., 2002; Otto, 2007; Soltis and Burleigh, 2009; Van de Peer et al., 2009; Schranz et al., 2012; Ren et al., 2018). Tank et al. (2015) noted that increases in rates of angiosperm diversification tend to occur after WGD (palaeopolyploidization). Barker et al. (2008) concluded that three WGDs occurred in the early history of the Asteraceae, prior to rapid radiation of its tribes in the Oligocene. Barker et al. (2016) concluded that the Asteraceae share a paleotetraploid ancestor with the Calyceraceae (sister to Asteraceae) and that most Asteraceae 'are descendants of a paleo-hexaploid'. Huang et al. (2016) suggested that WGDs have been an important driving force in the evolution of Asteraceae and that they may have occurred during times of global catastrophe

and dramatic changes in the environment, leading to stressful conditions for plant growth. These authors found WGDs in the core Asteraceae and at the separation of Asteraceae and Calyceraceae, crown node of Heliantheae alliance and clades Tussilaginatae and Tragopogon-Scorzonerina. In addition, a WGD was found within Gnaphalieae. It should be noted that Zenil-Ferguson et al. (2019) concluded that lineage diversification in the Solanaceae was better explained by breeding system than by polyploidy.

In a consideration of polyploids in angiosperms, Barker et al. (2015) found diploids, autopolyploids and allopolyploids in various genera of Asteraceae including *Artemisia*, *Carthamus*, *Centaurea*, *Helianthus*, *Melampodium* and *Senecio* but only diploids and allopolyploids in *Stephanomeria*. Although studies comparing seed germination of diploids and polyploids have been conducted for species in various plant families including Amaryllidaceae (Fialová et al., 2014), Asteraceae (Thomas et al., 1994), Brassicaceae (Neuffer and Eschner, 1995), Cactaceae (Cohen et al., 2013), Cyperaceae (Escudero et al., 2016), Fabaceae (Eliášová et al., 2014), Onagraceae (Smith-Huerta, 1984), Plantaginaceae (Puech et al., 1998) and Poaceae (Hacker, 1988), relatively few species have been investigated in most families including the Asteraceae.

Among the Asteraceae that have been studied, diploid and tetraploid cypselae of *Centaurea stoebe* had similar germination percentages and rates when sown in a greenhouse (Hahn et al., 2013). Diploid and tetraploid cypselae of *Matricaria perforata* had similar responses to temperature with the optimum for germination being 30/10°C. However, at suboptimal temperatures (5–15°C), tetraploid cypselae of *M. perforata* germinated to higher percentages than diploid cypselae. Cypselae of the polyploids *Taraxacum venustum* and *T. albidum* had higher germination percentages at the optimum temperature (19°C) than those of the diploid *T. platycarpum*. However, at a low temperature (4°C), *T. platycarpum* cypselae germinated to a higher percentage than those of *T. venustum* but about the same as *T. albidum* (Hoya et al., 2007). Furthermore, cypselae mass of polyploids may be greater than that of diploids (Hoya et al., 2007; Hahn et al., 2013), which could have effects on germination, establishment and growth of the seedlings. The more or less lack of differences in germination of diploids and polyploids at least seems to suggest that ancient polyploidization had little, or no, effect on germination of cypselae in the Asteraceae.

In general, polyploidization may lead to changes/increases in breeding systems (Soltis et al., 2003; Hojsgaard and Hörandl, 2019), adaptability to new ecological niches (Levin, 1983; Fawcett and Van de Peer, 2010; Ramsey, 2011), invasiveness (te Beest et al., 2012; Hahn et al., 2013), plant morphology (Zhang et al., 2021a), seed size (Thompson, 1990), speciation/diversification (Comai, 2005; Tank et al., 2015; Parisod and Broennimann, 2016; Stuessy and Weiss-Schneeweiss, 2019), tolerance to stress (Godfree et al., 2017; Van de Peer et al., 2017) and mediators of gene flow (Peskoller et al., 2021). That is, polyploidy is not an 'evolutionary dead-end' (Soltis et al., 2014a,b). Many of these changes in polyploids could have helped ameliorate the risk of extinction during times of catastrophic environmental (mass extinction) events (McElwain and Punyasena, 2007; Fawcett et al., 2009; Soltis and Burleigh, 2009; Vanneste et al., 2014).

### Apomixis

Another consequence of polyploidization could be the loss of sexual reproduction due to the failure of gamete production (Tucker

and Koltunow, 2009; te Beest et al., 2012; Hojsgaard and Hörandl, 2019), which is a first step in the development of non-sexual formation of seeds (i.e. apomixis). The Asteraceae is an important family in terms of the number of species that can produce seeds asexually. The non-sexual formation of embryos and seeds is called agamospermy, but it usually is referred to as apomixis. However, apomixis *s.l.* includes agamospermy and reproduction only by vegetative means (de Meeüs et al., 2007; Noyes, 2007, 2022; Hojsgaard et al., 2014; Majesky et al., 2017). In gametophytic apomixis, the embryo sac is diploid, and the egg develops parthenogenetically and includes apospory and diplospory (Richards, 2003). In apospory, the embryo sac forms from a diploid somatic cell, and in diplospory an embryo sac forms from a megaspore mother cell that fails to undergo meiosis. In sporophytic or adventitious embryony, the embryo forms from somatic tissue, that is, usually from the nucellus or the integument, and is related to the production of multiple embryos in a seed (polyembryony) (Whitten et al., 2008; Hand and Koltunow, 2014; Cardoso et al., 2018). Carman (1997) listed 10 genera of Asteraceae in which polyembryony has been reported. It should be noted that Carman (1997) did not include sporophytic embryony in his definition of apomixis. In diplospory, the endosperm must be fertilized or seeds will not form (Hojsgaard and Hörandl, 2019). However, in autonomous diplospory, which occurs predominantly in Asteraceae, both the embryo and endosperm develop without fertilization (Vinkenoog and Scott, 2001).

Although asexual progeny of apomictic plants are genetically identical to the mother plant (Koltunow, 1993; Koltunow and Grossniklaus, 2003), they may vary epigenetically. Thus, for common dandelion (*Taraxacum officinale*, Asteraceae) genetically identical apomictic plants exposed to various stress treatments exhibited epigenetic variation that was heritable (Verhoeven et al., 2010). That is, the stress-induced DNA methylation changes in the F<sub>0</sub> generation (maternal stress exposure) were faithfully transmitted to the F<sub>1</sub> (progeny) generation.

Sexuality and apomixis could/can occur in the same species (i.e. facultative apomixis), and a seed lot collected from a population site of a species might be a mixture of sexually and asexually produced seeds (Koltunow, 1993; Hand et al., 2015). Hojsgaard et al. (2014) found apomictic seed production in 32 orders, 78 families and 293 genera of plants, and Asteraceae, Poaceae and Rosaceae had the majority of apomictic genera. In general, apomictic species are polyploids (Thompson and Ritland, 2006; Mráz and Zdvůrák, 2019), and they occur mostly in tropical and temperate regions, with few species occurring in boreal and Arctic zones (Hojsgaard et al., 2014). In the Asteraceae, apomictic species occur in 47 genera (e.g. *Antennaria*, *Crepis*, *Erigeron*, *Hieracium*, *Taraxacum*) in four subfamilies (Asteroideae, 34; Cichorioideae, 9; Carduoideae, 2 and Mutisioideae, 2), accounting for 13.9% of the genera in these subfamilies (Hojsgaard et al., 2014).

It is not clear how apomixis develops in a natural population of a plant species (Hojsgaard and Hörandl, 2019). Hybridization long has been regarded as an important reason for the origin of apomictic taxa (Carman, 1997; Bicknell and Koltunow, 2004). Although some apomictic species are diploid hybrids (Beck, 1986), many apomictic species are polyploids (Carman, 1997). Thus, hybridization, but not polyploidy *per se*, seems to be a requirement for development of apomictic reproduction (Koltunow and Grossniklaus, 2003). Genetic studies have revealed that apomixis is an inherited trait, for example, *Erigeron* (Noyes, 2000, 2022; Noyes and Rieseberg, 2000), *Hieracium* (Bicknell

et al., 2001) and *Taraxacum* (Van Dijk et al., 1999), which helps explain why apomixis may appear in hybrids.

Five-month-old dry stored (i.e. probably afterripened) cypselae from autonomously apomictic biotypes of *Taraxacum officinale* differed in mass and germination percentages (Tweney and Mogie, 1999). Cypselae that weighed >0.8 mg germinated to 87.3% in moist soil (compost) in a greenhouse. On the other hand, cypselae that weighed 0.7–0.79 mg germinated to 52.4% but those weighing <0.3 mg germinated to only 0.28%. In another study of the germination of apomictic cypselae, Sailer et al. (2021) used a common garden experiment to determine if plants from asexual cypselae of the facultative apomictic species *Pilosella officinarum* competed better than plants from sexual cypselae. They found that germination proportion of offspring (cypselae) of sexual plants was higher than that of apomictic plants.

### Soil cypselae banks

Cypselae of Asteraceae have been found in soil samples collected in a wide diversity of habitats. In the results from 185 soil seed bank studies (see Tables 7.2, 7.4 and 7.5 in Baskin and Baskin, 2014 for references) that were conducted in such a way that it is highly probable that persistent seeds were present (i.e. samples collected after germination but before input of new seeds), we found species belonging to 155 families, including Asteraceae. In the Asteraceae, there were 131 species in 73 genera. However, the presence of cypselae in the soil tells us very little about how long they can live after burial. Studies of individual species of Asteraceae that involved collecting soil samples at population sites and counting the number of viable cypselae in the sample or the number of seedlings that emerged from them have been conducted for various species, for example, *Ageratina adenophora* (Shen et al., 2006), *Artemisia quettensis* (Ahmad et al., 2007), *Brachyscome muelleri* (Jusaitis et al., 2003), *Centaurea solstitialis* (Joley et al., 2003), *Chromolaena odorata* (Epp, 1987; Witkowski and Wilson, 2001), *Pilosella aurantiaca*, *P. piloselloides* subsp. *praealta* (Bear et al., 2012), *Polyminia canadensis* (Bender et al., 2003) and *Symphyotrichum laurentianum* (Kemp and Lacroix, 2004). Unfortunately, even with these individualized studies, the longevity of cypselae in the soil is not known.

To determine their longevity, cypselae of various species of Asteraceae have been placed in mesh bags/containers and buried in the soil (Table 3). The period of burial ranged from a few months to 40 years, and viability at the end of burial varied from 0 to 97%, with a mean ( $\pm$ SE) survival of 25.6 $\pm$ 3.7%. These burial studies included 39 species in 10 tribes, which is a very low representation of the species and tribes in Asteraceae. Furthermore, only in the study of *Galinsoga parviflora* was the survival of ray and disk cypselae (which are dimorphic) compared with 21.3 and 0% of the cypselae, respectively, viable after 2.1 years (Espinosa-Garcia et al., 2003). Overall, it does not appear that long-lived persistent cypselae banks are very common for species of Asteraceae.

Also, if cypselae are dispersed/sown onto the soil surface, they generally germinate in the first year, but some may delay germination until the second or a later year. We sowed freshly matured cypselae of 52 species of Asteraceae (78 datasets because cypselae of some species were collected and sown in more than one year) on soil and exposed them to natural seasonal temperature cycles (see temperature data in Baskin et al., 2019) and semi-natural watering regimes in a non-heated glasshouse in Lexington, Kentucky (USA). Germination was monitored weekly for 1 year

**Table 3.** Survival of cypselae of Asteraceae species placed in bags or other containers and buried in soil in the field for 0.25 to 40 years, depending on species

| Species   | Tribe       | Years of burial | % viable cypselae at the end of burial | References                    |
|---|-------------|-----------------|--|-------------------------------|
| <i>Achillea erba-rotta</i> subsp. <i>moschata</i> | Anthemideae | 5               | 0.7                                    | Schwiebacher et al. (2010)    |
| <i>Ambrosia artemisiifolia</i>                    | Heliantheae | 40 <sup>a</sup> | 4                                      | Telewski and Zeevaart (2002)  |
| <i>Ambrosia trifida</i>                           | Heliantheae | 4               | 19                                     | Harrison et al. (2007)        |
| <i>Anthemis cotula</i>                            | Anthemideae | 15              | 10                                     | Telewski and Zeevaart (2002)  |
| <i>Artemisia genipi</i>                           | Anthemideae | 5               | 0.2                                    | Schwiebacher et al. (2010)    |
| <i>Artemisia tridentata</i>                       | Anthemideae | 2               | 30–40                                  | Wijayratne and Pyke (2012)    |
| <i>Aster amellus</i>                              | Astereae    | 3               | 21.7                                   | Mašková and Poschlod (2022)   |
| <i>Bidens gardneri</i>                            | Coreoideae  | 1               | 0                                      | Sasaki et al. (1999)          |
| <i>Bidens pilosa</i>                              | Coreoideae  | 1               | 20–36                                  | Sahoo and Jha (1997)          |
| <i>Brachyscome lineariloba</i>                    | Astereae    | 2               | 72                                     | Facelli et al. (2005)         |
| <i>Brachyscome muelleri</i>                       | Astereae    | 2               | 8                                      | Jusaitis et al. (2003)        |
| <i>Carlina acaulis</i>                            | Cynareae    | 3               | 28.3                                   | Mašková and Poschlod (2022)   |
| <i>Carlina vulgaris</i>                           | Cynareae    | 3               | 36.7                                   | Mašková and Poschlod (2022)   |
| <i>Carthamus lanata</i>                           | Cynareae    | 2               | 20–75                                  | Grace et al. (2002)           |
| <i>Centaurea stoebe</i>                           | Cynareae    | 5 <sup>b</sup>  | 54                                     | Davis et al. (1993)           |
| <i>Centaurea stoebe</i>                           | Cynareae    | 8 <sup>b</sup>  | 29                                     | Davis et al. (1993)           |
| <i>Chaetanthera</i><br>12 annual species          | Mutisieae   | 1.3–1.75        | 0.7–30                                 | Arroyo et al. (2006)          |
| <i>Chaetanthera</i><br>5 perennial species        | Mutisieae   | 1.3–1.75        | 0–13.3                                 | Arroyo et al. (2006)          |
| <i>Chrysocephalum apiculatum</i>                  | Gnaphalieae | 1               | 61                                     | Lunt (1995)                   |
| <i>Chrysolaena herbacea</i>                       | Vernonieae  | 0.25            | 0                                      | Sasaki et al. (1999)          |
| <i>Cirsium acuale</i>                             | Cynareae    | 3               | 11.6                                   | Mašková and Poschlod (2022)   |
| <i>Cirsium vulgare</i>                            | Cynareae    | 2.5             | ca. 10 at 3 cm; 73 at 15 cm            | Doucet and Cavers (1996)      |
| <i>Craspedia variabilis</i>                       | Gnaphalieae | 1               | 8                                      | Lunt (1995)                   |
| <i>Crepis paludosa</i>                            | Gnaphalieae | 2               | <1                                     | Bekker et al. (1998)          |
| <i>Edmondia sesamoides</i>                        | Gnaphalieae | 3               | 80                                     | Holmes and Newton (2004)      |
| <i>Eremanthus elaeagnus</i>                       | Vernonieae  | 0.25            | 0                                      | Velten and Garcia (2007)      |
| <i>Eremanthus glomerulatus</i>                    | Vernonieae  | 0.25            | 0                                      | Velten and Garcia (2007)      |
| <i>Eremanthus incanus</i>                         | Vernonieae  | 1.5             | 30                                     | Velten and Garcia (2007)      |
| <i>Espeletia timotensis</i>                       | Millerieae  | 1               | 55                                     | Guariguata and Azocar (1988)  |
| <i>Galinsoga parviflora</i> ray                   | Millerieae  | 2.1             | 21                                     | Espinosa-Garcia et al. (2003) |
| <i>Galinsoga parviflora</i> disk                  | Millerieae  | 2.1             | 0                                      | Espinosa-Garcia et al. (2003) |
| <i>Gymnocoronis spilanthoides</i>                 | Eupatorieae | 3               | 6.8–61                                 | Panetta (2009)                |
| <i>Helianthus annuus</i>                          | Heliantheae | 4               | 47                                     | Alexander and Schrag (2003)   |
| <i>Jacobaea aquatica</i>                          | Senecioneae | 2               | 30                                     | Bekker et al. (1998)          |
| <i>Latua serriola</i>                             | Cichorieae  | 3               | 96.7                                   | Mašková and Poschlod (2022)   |
| <i>Leontodon hispidus</i>                         | Cichorieae  | 3               | 33.3                                   | Mašková and Poschlod (2022)   |
| <i>Leptorhynchus squamatus</i>                    | Gnaphalieae | 1               | 36                                     | Lunt (1995)                   |
| <i>Metalasia muricata</i>                         | Gnaphalieae | 3               | 19                                     | Holmes and Newton (2004)      |
| <i>Onopordum acanthium</i>                        | Cynareae    | 3               | 1–36                                   | Qaderi et al. (2002)          |
| <i>Parthenium hysterophorus</i>                   | Heliantheae | 2               | 74                                     | Navie et al. (1998)           |
| <i>Parthenium hysterophorus</i>                   | Heliantheae | 2.2             | 50                                     | Tamado et al. (2002)          |

(Continued)

**Table 3.** (Continued.)

| Species                            | Tribe       | Years of burial | % viable cypselae at the end of burial | References                  |
|------------------------------------|-------------|-----------------|--|-----------------------------|
| <i>Rutidosia leptorrhynchoides</i> | Gnaphalieae | 0.31            | 0                                      | Morgan (1995)               |
| <i>Senecio magellanicus</i>        | Senecioneae | 0.92            | 54                                     | Arroyo et al. (2004)        |
| <i>Syncarpha speciosissima</i>     | Gnaphalieae | 3               | 44                                     | Holmes and Newton (2004)    |
| <i>Syncarpha vestita</i>           | Gnaphalieae | 3               | 39                                     | Holmes and Newton (2004)    |
| <i>Tephrosia longifolia</i>        | Senecioneae | 5               | 12                                     | Janišová and Škodová (2016) |
| <i>Vittadinia cuneata</i>          | Astereae    | 2               | 72                                     | Facelli et al. (2005)       |

<sup>a</sup>Cypselae placed in a soil-filled bottle that was inverted and buried in the soil.

<sup>b</sup>Cypselae placed in short cylinders (7.6 wide × 2.5 cm deep) cut from polyvinylchloride pipe with nylon mesh on each end.

after the last cypselae of a species/sowing germinated (Baskin et al., 2022). For one group of species, including *Echinacea tennesseensis*, *Helianthus atrorubens*, *Liatris squarrosa*, *Solidago altissima* and *Symphotrichum pilosum*, cypselae sown in autumn germinated only the following (first) spring. In another group of species, including *Boltonia decurrens*, *Echinacea simulata*, *Eupatorium altissimum*, *Helenium amarum* and *Rudbeckia triloba*, many cypselae sown in autumn germinated in the first spring, but in the second, and sometimes the third, spring a few additional cypselae germinated (Baskin et al., 2022). For short-lived monocarpic perennial (MP), polycarpic perennial (PP) summer annuals (SA) and winter annual (WA) Asteraceae, the mean ( $\pm$ SE) number of years for germination was  $1.70 \pm 0.20$ ,  $1.69 \pm 0.25$ ,  $1.56 \pm 0.22$  and  $1.81 \pm 0.28$ , respectively (Table 4). Species whose cypselae germinated in 3 or more years include *Polymnia canadensis* (MP, 3 years), *Achillea millefolium* (PP, 7), *Ambrosia artemisiifolia* (SA, 4), *A. trifida* (SA, 3), *Crepis pulchra* (WA, 3) *Helenium amarum* (WA, 5) *Krigia virginica* (WA, 3) and *Lactuca serriola* (WA, 3).

The germination responses of *Lactuca floridana* cypselae that we buried in soil in the non-heated glasshouse help explain why a species has only one germination season. At maturity in autumn, cypselae of this species germinated to 9, 9, 66, 99 and 93% when incubated in light at 15/6, 20/10, 25/15, 30/15 and 35/20°C, respectively, with no germination at any temperature regime in darkness. During exposure to low temperatures during burial in winter, cypselae gained the ability to germinate to 98–100% in both light and dark at the five temperature regimes. When bags of buried cypselae were exhumed in spring (1 March), 50% of the cypselae had already germinated, and when bags were exhumed on 1 April, 1 May and 1 June, only 29, 21 and 0%, respectively, of the cypselae remained non-germinated. That is, during cold stratification, cypselae gained the ability to germinate in darkness and thus germinated as soon as temperatures increased in spring (Baskin and Baskin, unpublished).

### Life form, vegetation zone and phylogeny (tribes) of cypselae dormancy in Asteraceae

Information on cypselae dormancy and life form of Asteraceae species previously was compiled for 755 species growing in the various vegetation zones on earth (Baskin and Baskin, 2014). Since 2014, we have continued to collect information on cypselae dormancy in Asteraceae. In addition to regularly checking new issues of plant-related journals for dormancy/germination information, we conducted many web searches using a variety of

search terms in various combinations: Asteraceae, Compositae, names of tribes and genera of Asteraceae, names of countries in South America, Asia and Africa, achene, cypselae, germination, germinación, semillas and sementes.

In the papers found in the literature, if fresh cypselae germinated to a relatively high percentage over a range of temperatures and dormancy-breaking treatments such as afterripening, cold stratification, warm stratification, scarification and gibberellin did not increase germination, the species was listed as having ND cypselae. However, if any dormancy-breaking treatment increased the percentage and/or rate of germination, the species was listed as having PD. In the case of heteromorphic species, if one cypselae morph was ND and another had PD, the species was listed as PD. If a species was listed in Baskin and Baskin (2014) as ND/PD or PD/ND, it was counted as PD in this review. In comparing ND and PD of tropical and temperate regions, the data for Asteraceae species from special habitats were included under the temperate region.

We found information for 450 additional species, bringing the total to 1205 species entries in supplementary Table S1. All species of Asteraceae were recorded according to life form and vegetation zone/special habitats (supplementary Table S1). However, 12 species of weeds (*Ageratum conyzoides*, *Bidens pilosa*, *Chromolaena odorata*, *Cirsium arvense*, *Emilia sonchifolia*, *Galinsoga parviflora*, *Synedrella nodiflora*, *Tithonia diversifolia*, *T. rotundifolia*, *Tridax procumbens*, *Senecio vulgaris* and *Tanacetum vulgare*) are common in more than one vegetation zone in supplementary Table S1, which reduces the total number of species to 1182. The 1182 species occur in 373 genera and 35 tribes of Asteraceae. In working with the results of our compilation, the multiple listings of the 12 weeds were counted as separate species based on research done in different vegetation zones.

### Life forms and dormancy

Among the 1205 entries in the database, there were 14 (1.2%), 180 (14.9%), 8 (0.7%) and 1003 (83.2%) trees, shrubs, vines (including woody and herbaceous climbers) and herbs, respectively (Table 5). Overall, 22.2% of the species had ND cypselae, and 50.0, 20.6, 25.0 and 22.0% of the tree, shrub, vine and herb species, respectively, had ND cypselae; thus, 50.0, 79.4, 75.0 and 78.0%, respectively, had PD. We found germination data for 14 species of Asteraceae that are trees, and 13 of them occur in tropical vegetation zones and one in the warm moist temperature woodlands (i.e. the broad-leaved evergreen forest). Trees occur in various tribes of Asteraceae, including Astereae, Bahieae,



**Table 4.** Number of years cypselae of Asteraceae germinated in the non-heated glasshouse in Lexington, Kentucky (USA)

| Species                            | Date sown  | Year(s) cypselae germinated |
|------------------------------------|------------|-----------------------------|
| <b>Monocarpic Perennials</b>       |            |                             |
| <i>Carduus nutans</i>              | 6/19/1970  | 1                           |
| <i>Cirsium discolor</i>            | 11/1/1970  | 1                           |
| <i>Grindelia lanceolata</i> (ray)  | 11/1/1970  | 2                           |
| <i>Grindelia lanceolata</i> (disc) | 11/1/1970  | 2                           |
| <i>Lactuca floridana</i>           | 9/25/1985  | 2                           |
| <i>Lactuca floridana</i>           | 10/25/1994 | 2                           |
| <i>Polymnia canadensis</i>         | 8/30/1982  | 1                           |
| <i>Polymnia canadensis</i>         | 10/24/1982 | 2                           |
| <i>Polymnia canadensis</i>         | 11/16/1985 | 3                           |
| <i>Tragopogon pratensis</i>        | 5/30/1970  | 1                           |
| <b>Polycarpic perennials</b>       |            |                             |
| <i>Achillea millefolium</i>        | 9/15/1972  | 7                           |
| <i>Arnoglossum plantagineum</i>    | 6/28/1971  | 1                           |
| <i>Boltonia decurrens</i>          | 10/2/1985  | 2                           |
| <i>Brickellia eupatorioides</i>    | 10/18/1969 | 1                           |
| <i>Leucanthemum vulgare</i>        | 6/19/1970  | 1                           |
| <i>Echinacea pallida</i>           | 8/10/1972  | 3                           |
| <i>Echinacea pallida</i>           | 11/8/1988  | 1                           |
| <i>Echinacea simulata</i>          | 9/22/1991  | 2                           |
| <i>Echinacea tenneeseensis</i>     | 10/15/1969 | 1                           |
| <i>Echinacea tenneeseensis</i>     | 10/5/1987  | 2                           |
| <i>Eupatorium altissimum</i>       | 10/18/1969 | 2                           |
| <i>Eupatorium altissimum</i>       | 11/1/1970  | 1                           |
| <i>Eupatorium fistulosum</i>       | 10/6/1987  | 1                           |
| <i>Eurybia divaricata</i>          | 12/2/1988  | 1                           |
| <i>Helenium autumnale</i>          | 10/18/1969 | 1                           |
| <i>Helenium autumnale</i>          | 11/8/1987  | 2                           |
| <i>Helianthus atrorubens</i>       | 10/22/1990 | 1                           |
| <i>Helianthus divaricatus</i>      | 10/11/1969 | 2                           |
| <i>Heterotheca villosa</i>         | 10/18/1969 | 1                           |
| <i>Liatris squarrosa</i>           | 10/5/1979  | 1                           |
| <i>Pilosella caespitosa</i>        | 6/26/1988  | 1                           |
| <i>Prenanthes barbata</i>          | 10/28/1990 | 1                           |
| <i>Ratibida pinnata</i>            | 9/30/1970  | 2                           |
| <i>Rudbeckia hirta</i>             | 11/1/1970  | 1                           |
| <i>Rudbeckia triloba</i>           | 9/27/1969  | 3                           |
| <i>Packera anonyma</i>             | 6/11/1970  | 1                           |
| <i>Smallanthus uvedalia</i>        | 9/17/1987  | 8 <sup>a</sup>              |
| <i>Solidago altissima</i>          | 11/1/1970  | 1                           |
| <i>Solidago altissima</i>          | 11/15/1988 | 1                           |
| <i>Solidago nemoralis</i>          | 11/15/1988 | 1                           |

(Continued)

Table 4. (Continued.)

| Species                               | Date sown  | Year(s) cypselae germinated |
|---------------------------------------|------------|-----------------------------|
| <i>Solidago ptarmicoides</i>          | 10/29/1979 | 1                           |
| <i>Symphyotrichum patens</i>          | 11/12/1970 | 1                           |
| <i>Symphyotrichum pilosum</i>         | 10/27/1981 | 1                           |
| <i>Symphyotrichum pilosum</i>         | 11/19/1975 | 1                           |
| <i>Symphyotrichum pilosum</i>         | 11/1/1970  | 1                           |
| <i>Vernonia gigantea</i>              | 11/1/1970  | 2                           |
| Summer annuals                        |            |                             |
| <i>Ambrosia artemisiifolia</i>        | 10/18/1969 | 1                           |
| <i>Ambrosia artemisiifolia</i>        | 11/10/1975 | 4                           |
| <i>Ambrosia artemisiifolia</i>        | 10/22/1977 | 1                           |
| <i>Ambrosia artemisiifolia</i>        | 10/18/1981 | 1                           |
| <i>Ambrosia artemisiifolia</i>        | 11/23/1981 | 1                           |
| <i>Ambrosia trifida</i>               | 10/23/1978 | 3                           |
| <i>Ambrosia trifida</i>               | 10/19/1984 | 2                           |
| <i>Artemisia annua</i>                | 11/19/1971 | 1                           |
| <i>Bidens bipinnata</i>               | 10/10/1970 | 2                           |
| <i>Coreopsis tinctoria</i>            | 11/1/1988  | 1                           |
| <i>Coreopsis tinctoria</i>            | 9/14/1990  | 1                           |
| <i>Erechtites hieracifolia</i>        | 9/25/1987  | 2                           |
| <i>Galinsoga quadriradiata</i>        | 10/10/1978 | 1                           |
| <i>Galinsoga parviflora</i>           | 10/4/1978  | 1                           |
| <i>Helianthus annuus</i>              | 10/19/1984 | 1                           |
| <i>Xanthium strumarium</i>            | 10/20/2000 | 2                           |
| Winter annuals                        |            |                             |
| <i>Amphiachyris dracunculoides</i>    | 10/18/1969 | 1                           |
| <i>Amphiachyris dracunculoides</i>    | 11/23/1971 | 2                           |
| <i>Amphiachyris dracunculoides</i>    | 11/1/1978  | 1                           |
| <i>Crepis pulchra</i>                 | 6/11/1970  | 3                           |
| <i>Crepis pulchra</i>                 | 6/14/1971  | 2                           |
| <i>Erigeron strigosus</i>             | 7/16/1970  | 1                           |
| <i>Helenium amarum</i>                | 10/19/1969 | 1                           |
| <i>Helenium amarum</i>                | 8/6/1970   | 1                           |
| <i>Helenium amarum</i>                | 11/9/1971  | 5                           |
| <i>Heterotheca subaxilaris</i> (disk) | 9/18/1971  | 1                           |
| <i>Heterotheca subaxilaris</i> (ray)  | 9/18/1971  | 1                           |
| <i>Krigia virginica</i>               | 5/30/1970  | 3                           |
| <i>Krigia virginica</i>               | 5/31/1971  | 2                           |
| <i>Krigia virginica</i>               | 9/12/1988  | 1                           |
| <i>Lactuca serriola</i>               | 7/16/1970  | 3                           |
| <i>Lactuca serriola</i>               | 8/8/1971   | 1                           |

<sup>a</sup>Cypselae may have intermediate physiological dormancy, but this has not been confirmed by laboratory experiments.

**Table 5.** Number of species of trees, shrubs, vines and herbs of Asteraceae in different vegetation zones/special habitats with non-dormant (ND) and physiologically dormant (PD) cypselae

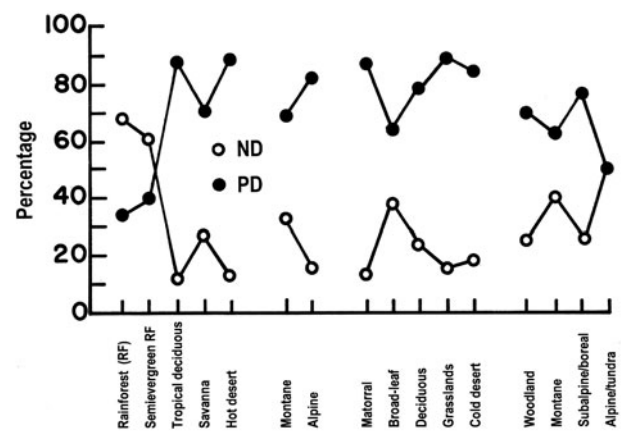
| Vegetation zones/special habitats                         | Trees |    | Shrubs |     | Vines |    | Herbs |     | Total |
|---|-------|----|--------|-----|-------|----|-------|-----|-------|
|   | ND    | PD | ND     | PD  | ND    | PD | ND    | PD  |       |
| <b>Tropical</b>   |       |    |        |     |       |    |       |     |       |
| Evergreen rainforest                                      |       |    | 1      |     | 1     |    | 8     | 5   | 15    |
| Montane   | 2     |    | 2      | 12  |       | 1  | 8     | 12  | 37    |
| Alpine  |       |    | 3      | 13  |       |    | 1     | 4   | 21    |
| Semi-evergreen rainforest                                 | 3     | 3  | 3      | 1   | 1     | 1  | 12    | 7   | 31    |
| Tropical deciduous  |       | 1  | 1      | 5   |       |    | 3     | 21  | 31    |
| Savannas  | 1     | 3  | 5      | 4   |       |    | 10    | 38  | 61    |
| Hot deserts   |       |    | 5      | 35  |       |    | 9     | 61  | 110   |
| <b>Temperate</b>  |       |    |        |     |       |    |       |     |       |
| Matorral  |       |    | 5      | 47  |       | 1  | 25    | 171 | 249   |
| Warm moist temperature woodlands (Broad-leaved evergreen) | 1     |    | 1      |     |       | 1  | 2     | 6   | 11    |
| Deciduous-temperate                                       |       |    |        |     |       | 2  | 36    | 113 | 151   |
| Grasslands  |       |    | 8      | 8   |       |    | 11    | 119 | 146   |
| Cold deserts  |       |    |        | 7   |       |    | 7     | 30  | 44    |
| Subalpine/boreal  |       |    |        | 2   |       |    | 35    | 111 | 148   |
| Alpine/high-latitude tundra                               |       |    |        | 1   |       |    | 46    | 51  | 98    |
| Montane   |       |    |        | 1   |       |    | 2     | 5   | 8     |
| Woodland  |       |    | 2      | 1   |       |    |       | 2   | 5     |
| <b>Special habitats</b>                                   |       |    |        |     |       |    |       |     |       |
| Aquatics  |       |    |        |     |       |    | 2     | 11  | 13    |
| Salt marsh/desert   |       |    |        | 3   |       |    | 2     | 10  | 15    |
| Psammophytes  |       |    | 1      | 3   |       |    | 2     | 5   | 11    |
| Totals  | 7     | 7  | 37     | 143 | 2     | 6  | 221   | 782 | 1205  |

Coreopsideae, Eupatorieae, Gochnatieae, Heliantheae, Inuleae, Liabeae, Millerieae Neurolaeneae, Senecioneae and Vernoniaeae (Ricker et al., 2013; Beech et al., 2017; Redonda-Martínez et al., 2021). Thus, clearly cypselae dormancy has been studied in only a small fraction of the tree species of Asteraceae.

The lack of research is even more apparent for Asteraceae vines than for trees. Only eight species of vines were recorded – two with ND and six with PD. Gentry (1991) says there are 470 species and 23 genera of climbing Asteraceae in the New World, but he does not show Asteraceae in bar diagrams depicting the most important plant families of vines in the Amazon rainforest of Brazil or in Africa or Borneo. However, he does show vines of Asteraceae for upper Andean sites in Bolivia, Ecuador and Columbia and for a lowland dry forest in Ecuador. Gentry (1991) gives the number of vine species of Asteraceae in temperate North America and Europe as one to three but does not provide their names. Vines occur in tribes Astereae, Barnadesiaeae, Coreopsideae, Eupatorieae, Gnaphalieae, Heliantheae, Mutisieae, Senecioneae and Vernoniaeae of Asteraceae (Morellato and Leitão-Filho, 1996; Cai et al., 2009; Schnitzer et al., 2012; Seger and Hartz, 2014; Sánchez-Chávez et al., 2019).

Of the 180 species of shrubs, germination of 90 each has been studied in the tropical and temperate regions; four of the

temperate region shrubs are psammophytes (i.e. in a special habitat). However, for the 1003 herbs, 199, 772 and 32 species are from the tropics, temperate region and special habitats,

**Fig. 1.** Proportion of Asteraceae species with non-dormant (ND) and physiologically dormant (PD) cypselae in each tropical and temperate vegetation zone.

**Table 6.** Number of species of trees, shrubs, vines and herbs with non-dormant (ND) and physiologically dormant (PD) cypselae in tribes of Asteraceae in tropical and temperate regions

| Tribe         | B/C/HA | Tropical/Subtropical |    |        |    |       |    |       |    | Temperate/Arctic |    |        |    |       |    |       |     | Total species |
|---------------|--------|----------------------|----|--------|----|-------|----|-------|----|------------------|----|--------|----|-------|----|-------|-----|---------------|
|               |        | Trees                |    | Shrubs |    | Vines |    | Herbs |    | Trees            |    | Shrubs |    | Vines |    | Herbs |     |               |
|               |        | ND                   | PD | ND     | PD | ND    | PD | ND    | PD | ND               | PD | ND     | PD | ND    | PD | ND    | PD  |               |
| Anthemideae   | C      |                      |    | 2      | 6  |       |    |       | 6  |                  |    | 6      | 19 |       |    | 34    | 68  | 141           |
| Arctotideae   | C      |                      |    |        | 1  |       |    |       | 5  |                  |    |        |    |       |    |       | 10  | 16            |
| Astereae      | C      |                      |    | 5      | 14 |       | 1  | 11    | 18 |                  |    | 6      | 12 |       | 1  | 36    | 103 | 202           |
| Athroismeae   | C      |                      |    |        |    |       |    |       | 1  |                  |    |        |    |       |    |       |     | 1             |
| Bahieae       | HA     |                      |    |        |    |       |    |       | 3  |                  |    |        |    |       |    |       | 1   | 4             |
| Barnadesieae  | B      |                      |    |        |    |       |    |       |    |                  |    |        |    |       |    | 1     |     | 1             |
| Calenduleae   | C      |                      |    |        | 3  |       |    |       | 4  |                  |    |        | 1  |       |    | 2     | 10  | 20            |
| Chaenactideae | HA     |                      |    |        |    |       |    |       |    |                  |    |        |    |       |    |       | 1   | 1             |
| Cichorieae    | C      |                      |    |        |    |       |    |       | 6  |                  |    | 1      | 2  |       |    | 19    | 75  | 103           |
| Coreopsideae  | HA     |                      |    |        | 1  | 1     |    | 4     | 8  |                  |    |        |    |       |    | 4     | 23  | 41            |
| Corymbieae    | C      |                      |    |        |    |       |    |       |    |                  |    |        |    |       |    |       | 1   | 1             |
| Cynareae      | C      |                      |    |        |    |       |    |       | 3  |                  |    |        | 2  |       |    | 19    | 78  | 102           |
| Dicomeae      | C      |                      |    |        |    |       |    |       | 1  |                  |    |        |    |       |    |       | 1   | 2             |
| Eupatorieae   | HA     |                      |    | 1      | 3  | 1     |    | 8     | 14 |                  |    |        |    |       | 1  | 3     | 24  | 55            |
| Gnaphalieae   | C      |                      |    |        | 1  |       |    |       | 20 |                  |    |        | 22 |       |    | 17    | 64  | 124           |
| Gochnatieae   | B      | 2                    |    | 1      | 2  |       |    |       |    |                  |    |        |    |       |    |       |     | 5             |
| Gymnarrheneae | C      |                      |    |        |    |       |    | 1     |    |                  |    |        |    |       |    |       |     | 1             |
| Helenieae     | HA     |                      |    | 1      |    |       |    |       | 8  |                  |    |        |    |       |    | 3     | 7   | 19            |
| Heliantheae   | HA     | 1                    |    |        | 13 |       |    | 7     | 22 |                  |    |        | 1  |       |    | 3     | 60  | 107           |
| Hyalideae     | B      |                      |    |        | 1  |       |    |       |    |                  |    |        | 1  |       |    |       |     | 2             |
| Inuleae       | C      |                      |    |        | 2  |       |    | 1     | 1  |                  |    |        | 1  |       |    | 7     | 15  | 27            |
| Liabeae       | C      | 1                    |    | 1      |    |       |    |       |    |                  |    |        |    |       |    |       |     | 2             |
| Madieae       | HA     |                      |    |        | 4  |       |    |       | 3  |                  |    |        |    |       | 1  |       | 16  | 24            |
| Millerieae    | HA     |                      |    | 1      | 7  |       |    | 4     | 5  |                  |    |        |    |       |    | 1     | 3   | 21            |
| Mutisieae     | B      |                      |    | 1      | 1  |       | 1  | 1     | 1  |                  |    |        | 1  |       | 1  | 5     | 5   | 17            |
| Nassauvieae   | B      |                      |    |        |    |       |    |       |    |                  |    |        |    |       |    | 1     |     | 1             |
| Perityleae    | HA     |                      |    |        |    |       |    | 1     |    |                  |    |        |    |       |    |       |     | 1             |
| Pertyeae      | B      |                      |    |        |    |       |    |       |    |                  |    |        |    |       |    |       | 1   | 1             |
| Plucheeae     | C      |                      |    |        |    |       |    | 1     | 4  |                  |    |        |    |       |    |       | 1   | 6             |

|                |    |   |   |    |    |   |   |    |    |    |    |     |   |   |   |    |    |  |   |   |    |
|----------------|----|---|---|----|----|---|---|----|----|----|----|-----|---|---|---|----|----|--|---|---|----|
| Polymnieae     | HA |   |   |    |    |   |   |    |    |    |    |     |   |   |   |    |    |  | 1 | 1 | 1  |
| Senecioneae    | C  | 2 | 7 | 3  | 7  | 2 | 7 | 2  | 7  | 11 | 62 | 101 |   |   |   |    |    |  |   |   |    |
| Stiffieae      | B  | 1 |   |    |    |   |   |    |    |    |    |     |   |   |   |    |    |  |   |   | 1  |
| Tageteae       | HA |   | 1 | 3  | 5  |   |   |    |    | 3  | 2  | 14  |   |   |   |    |    |  |   |   |    |
| Tarhongantheae | C  | 2 |   |    |    |   |   |    |    |    |    |     |   |   |   |    |    |  |   |   | 2  |
| Vernonieae     | C  | 4 | 4 | 3  | 4  | 6 | 6 | 1  |    |    |    |     |   |   |   |    |    |  |   |   | 38 |
| Total tribes   |    | 4 | 2 | 11 | 17 | 2 | 2 | 13 | 22 | 1  | 0  | 6   | 9 | 0 | 4 | 17 | 25 |  |   |   |    |

B, basal grade; C, central grade; HA, Heliantheae Alliance of Asteraceae. Tribes of Asteraceae are sensu Susanna et al. (2020).  
 \*No information was found for species in tribes Eremothamneae, Famatinantheae, Feddeae, Hecastocleideae, Moquiniae, Neurolaeneae, Oldenburgeae, Onoserideae, Platycarpheae or Wunderlichieae.

respectively, with 74.4, 78.8 and 81.3% of them having cypselae with PD, respectively.

### Vegetation zone and dormancy

The proportion of species with ND and PD cypselae for each vegetation zone is shown in Fig. 1. In evergreen and semi-evergreen rain forests, more species have ND than PD cypselae. However, in all other vegetation zones, except the (temperate) alpine/high-latitude tundra, where the number of species with ND and PD is the same, more species have cypselae with PD than ND.

### Tribes, life forms, vegetation zones and dormancy

In the tropical region (all tropical vegetation zones combined), the number of tribes of tree species with ND and PD was 4 and 2, respectively; shrubs 11 and 17, respectively; vines 2 and 2, respectively; and herbs 13 and 22, respectively (Table 6). In the temperate region, the number of tribes of tree species with ND and PD was 0 and 1, respectively; shrubs 6 and 9, respectively; vines 0 and 4, respectively; and herbs 17 and 25, respectively. Thus, in the tropical region, more tribes are represented by shrubs and herbs than by vines or trees, and more shrubs and herbs have PD than ND. In the temperate region, more tribes are represented by herbs than by trees, shrubs and vines, and more herbs have PD than ND.

Across the tropical and temperate zones and all life forms, the tribes with  $\geq 10\%$  of the 1205 species were Anthemideae (11.7%), Astereae (16.7%) and Gnaphalieae (10.3%). The tribes Antroismeae, Barnadesieae, Chaenactideae, Corymbieae, Gymnarrheneae, Nassauvieae, Perityleae, Pertyeae, Polymnieae and Stiffieae are represented by only one species (0.08%) each (Table 6). Among the 35 tribes, 19 had both ND and PD, 7 only ND and 9 only PD. In the basal grade (B), central grade (C) and Heliantheae Alliance (HA) of Asteraceae (sensu Susanna et al., 2020), if a tribe was represented by two or more species, both ND and PD were found among them, except for Bahieae, Liabeae and Tarhongantheae. Bahieae (HA) was represented by four PD species, Liabeae (HA) by two ND species and Tarhongantheae (C) by two ND species. We note that tribes Eremothamneae, Famatinantheae and Feddeae are monospecific. Information about the occurrence of ND and PD is plotted on the Asteraceae tribe-level chronogram of Mandel et al. (2019) shows that both ND and PD are widely distributed throughout the family (supplementary Fig. S1).

Tropical trees occurred in 1, 2 and 1 tribe(s) in B, C and HA, respectively, but temperate trees were in only one C tribe (Table 6). Except for one tropical C tribe (Vernonieae) with both ND and PD, all tribes of trees had only ND cypselae. Tropical shrubs were in 3, 10 and 7 tribes of B, C and HA, respectively, and temperate shrubs in 2, 8 and 1 tribe(s), respectively. With the exception of species in 1 C and 2 HA tribes in the tropical zone and 1 B and 1 C tribes in the temperate zone with ND cypselae, all tribes had either both ND and PD or only PD. Tropical vines were in 1, 1 and 2 tribes of B, C and HA, respectively, and temperate vines in 1, 1 and 2, respectively. With the exception of species in 2 HA tribes in the tropical zone with ND cypselae, all tribes had cypselae with PD. Tropical herbs were in 1, 14 and 9 tribes of B, C and HA, respectively, and with the exception of species in 1 C tribe with ND cypselae all tribes had either both ND and PD or only PD. Temperate herbs were in 2, 14 and 10 tribes, respectively, and with the

**Table 7.** Tribes of Asteraceae in different vegetation zones represented by one or more species with non-dormant (N) or physiologically dormant (P) cypselae

| Tribe         | Rainf |   | Mont |   | Alpine |   | Semie |   | Dry |   | Sav |   | H-D |   | Mator |   | Br |   | Decid |   | Grassl |   | C-D |   | Boreal |   | Alpine |   | Mont |   | Woodl |   |  |
|---------------|-------|---|------|---|--------|---|-------|---|-----|---|-----|---|-----|---|-------|---|----|---|-------|---|--------|---|-----|---|--------|---|--------|---|------|---|-------|---|--|
|               | N     | P | N    | P | N      | P | N     | P | N   | P | N   | P | N   | P | N     | P | N  | P | N     | P | N      | P | N   | P | N      | P | N      | P | N    | P |       |   |  |
| Anthemideae   |       |   |      |   | x      |   |       |   |     |   |     |   | x   | x | x     | x | x  |   | x     | x | x      | x | x   | x | x      | x | x      |   |      |   | x     | x |  |
| Arctotideae   |       |   |      |   |        |   |       |   |     |   |     | x |     |   | x     | x | x  |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Astereae      |       |   | x    | x | x      | x | x     | x |     |   | x   | x | x   | x | x     | x | x  | x | x     | x | x      | x | x   | x | x      | x | x      | x | x    | x | x     | x |  |
| Athroismeae   |       |   |      |   |        |   |       |   | x   |   |     |   |     |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Bahieae       |       |   |      |   |        |   |       |   | x   |   |     |   | x   |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Barnadesieae  |       |   |      |   |        |   |       |   |     |   |     |   |     |   |       |   |    |   |       |   |        | x |     |   |        |   |        |   |      |   |       |   |  |
| Calenduleae   |       |   |      |   |        |   |       |   |     |   |     |   | x   | x | x     |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Chaenactideae |       |   |      |   |        |   |       |   |     |   |     |   |     |   |       |   |    |   |       |   |        |   |     | x |        |   |        |   |      |   |       |   |  |
| Cichorieae    |       |   |      |   |        |   |       |   | x   |   |     |   | x   | x | x     |   |    |   | x     | x | x      | x | x   | x | x      | x | x      | x |      |   |       |   |  |
| Coreopsideae  |       |   | x    | x |        |   | x     |   |     | x |     | x |     |   |       |   |    |   | x     | x |        | x |     |   |        |   |        |   |      |   |       | x |  |
| Corymbieae    |       |   |      |   |        |   |       |   |     |   |     |   |     |   | x     |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Cynareae      |       |   |      |   |        |   |       |   |     |   | x   |   | x   | x | x     |   | x  | x | x     | x | x      | x | x   |   | x      | x | x      | x |      | x |       | x |  |
| Dicomeae      |       |   |      |   |        |   |       |   |     |   |     |   |     |   | x     |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Eupatorieae   | x     | x | x    | x | x      | x | x     |   | x   |   | x   | x | x   |   |       |   | x  |   | x     | x | x      | x |     |   |        | x |        |   |      |   | x     | x |  |
| Gnaphalieae   |       |   |      | x |        |   |       | x |     |   | x   |   | x   | x | x     |   |    |   | x     | x |        | x |     |   |        | x | x      | x | x    | x |       |   |  |
| Gochnatieae   |       |   |      |   |        |   |       |   | x   | x | x   |   | x   |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Gymnarrheneae |       |   |      |   |        |   |       |   |     |   |     |   | x   |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Helenieae     |       |   |      |   |        |   |       |   |     |   |     |   | x   | x | x     |   |    |   | x     | x |        | x |     |   |        |   | x      | x |      |   |       |   |  |
| Heliantheae   | x     | x | x    | x |        |   | x     | x | x   | x | x   | x |     | x |       | x |    |   |       | x |        | x | x   | x | x      | x |        |   |      |   |       | x |  |
| Hyalideae     |       |   |      |   |        |   |       |   |     |   |     |   | x   |   |       |   |    |   |       |   |        | x |     |   |        |   |        |   |      |   |       |   |  |
| Inuleae       |       |   |      | x |        |   |       | x |     |   | x   | x | x   | x | x     |   |    |   | x     | x |        |   | x   |   | x      |   | x      |   |      |   |       | x |  |
| Liabeae       |       | x | x    |   |        |   |       |   |     |   |     |   |     |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Madieae       |       |   |      | x |        | x |       |   |     |   |     |   | x   |   | x     |   |    |   |       |   |        | x |     | x |        |   |        | x |      |   |       |   |  |
| Millerieae    | x     |   |      | x | x      | x |       | x |     | x | x   |   |     |   |       |   |    |   | x     | x |        |   |     |   |        | x |        |   |      |   |       |   |  |
| Mutisieae     |       |   |      |   |        |   | x     | x |     |   |     |   | x   | x | x     | x |    | x |       |   |        | x |     |   | x      | x | x      |   |      |   |       |   |  |
| Nassauvieae   |       |   |      |   |        |   |       |   |     |   |     |   |     |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   | x     |   |  |
| Perityleae    |       |   |      |   |        |   |       |   |     |   |     |   | x   |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Pertyeae      |       |   |      |   |        |   |       |   |     |   |     |   |     |   |       |   |    | x |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Plucheeae     |       |   |      |   |        |   |       | x |     |   |     |   |     |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Polymnieae    |       |   |      |   |        |   |       |   |     |   |     |   |     |   |       |   |    |   |       |   |        |   |     |   |        |   |        |   |      |   |       |   |  |
| Senecioneae   | x     |   |      | x | x      | x |       | x |     | x | x   | x |     | x | x     | x | x  |   | x     | x | x      | x | x   | x | x      | x | x      | x |      |   |       | x |  |

|                |  |  |  |  |   |   |   |  |   |  |   |  |  |  |  |  |  |  |  |  |
|----------------|--|--|--|--|---|---|---|--|---|--|---|--|--|--|--|--|--|--|--|--|
| Stiffeae       |  |  |  |  |   |   |   |  | x |  |   |  |  |  |  |  |  |  |  |  |
| Tageteae       |  |  |  |  | x |   |   |  |   |  |   |  |  |  |  |  |  |  |  |  |
| Tarhoniantheae |  |  |  |  |   | x |   |  |   |  |   |  |  |  |  |  |  |  |  |  |
| Vernonieae     |  |  |  |  |   |   | x |  |   |  |   |  |  |  |  |  |  |  |  |  |
|                |  |  |  |  |   |   |   |  |   |  | x |  |  |  |  |  |  |  |  |  |

Tropical: Rainf; rainforest; Mont, montane zone on mountains; Alpine, alpine zone on mountains; Semi, semi-evergreen rainforests; Dry, dry deciduous forests; Sav, savanna; H-D, hot deserts. Temperate/arctic: Mator, matorral/sclerophyllous woodlands; Br, broad-leaved evergreen or moist-warm temperature woodlands; Decid, deciduous (nemoral) forests; Grass, grasslands; C-D, cold deserts; Boreal, subalpine/high-latitude boreal; Alpine, alpine/high-latitude tundra; Mont, montane zone on mountains; Woodl, woodland zone on mountains.

exception of species in 2 B tribes with ND cypselae, all tribes had either both ND and PD or only PD.

The tribes with the best representation across the different vegetation zones are: Senecioneae (in all zones except temperate montane) and Astereae (not in rainforest or hot desert) (Table 7). The second most geographically widely distributed tribes are the Eupatorieae and Heliantheae, but each is missing from four vegetation zones. Eupatorieae was not recorded in temperate montane, temperate alpine, matorral or cold desert and Heliantheae was not in tropical alpine, temperate alpine, temperate montane or broad-leaved evergreen.

The number of tribes represented by one or more species (with ND or PD) in each vegetation zone ranges from 3 to 20 (Table 7). The low number (3) is for tribes in the temperate montane zone, where data were found for only five species of Asteraceae, while the high number (20) is for hot deserts, where data are available for 108 species (Table 5). Of the six tribes found in the rainforest, 5 and 3 of them had species with ND and PD, respectively. However, for all vegetation zones, except the rainforest and the tropical alpine (5 and 5 with ND and PD, respectively), the tribes were represented by more species with PD than ND. Tribes represented by either ND or PD (but not by both) in only one vegetation zone are Antroisemeae, Barnadesieae, Chaenactideae, Corymbieae, Dicomeae, Gymnarrheneae, Nassaurieae, Perityleae, Petryeae, Plucheeae and Polymnieae. Clearly, more data are needed for Asteraceae in many of the vegetation zones, especially for the poorly represented tribes.

### Dormancy/germination flexibility and adaptability

ND and PD are found in cypselae of Asteraceae in various tribes, genera and species; life forms and life cycles; and in all vegetation zones on earth. Except for one of the three morphs of the cypselatrimorphic species *Heteracia szovitsii* (Lu et al., 2020) with intermediate PD, the level of PD in the Asteraceae is non-deep. Furthermore, six types of non-deep PD have been identified, and all of them are known to occur in the Asteraceae. The types of non-deep PD are broken by exposure of cypselae to environmental conditions that are not favourable for seedling establishment and growth. Since dormancy-break occurs during the non-favourable season for growth, cypselae are ND and can germinate at the beginning of the favourable season for growth, giving the seedling the full length of the favourable season to become established. Variation in the types of non-deep PD allows for fine-tuning of germination, which is part of the suite of adaptations of Asteraceae species to many of the vast diversity of habitats on earth. In general, we can conclude that cypselae dormancy in Asteraceae is not complicated but that it is very flexible.

According to the evolutionary transition analysis between seed dormancy states, morphophysiological dormancy (MPD) is probably the ancestral dormancy state, and there have been three major shifts from MPD to PD (Willis et al., 2014). PD has been an evolutionary hub and has given rise to seeds that are ND and to those with MPD, morphological dormancy (MD), physical dormancy (PY) and combinational dormancy (PY + PD). However, there have been transitions from ND, MPD, PY, PY + PD and MD back to PD. Thus, the close association between ND and PD throughout the Asteraceae is no doubt related to the transitions between PD and ND (i.e. PD ↔ ND). Willis et al. (2014) described ND as ‘either a recent evolutionary development or an ephemeral state’. However, in an investigation of the evolutionary transitions between seed dormancy and ND,

Zhang et al. (2022) found no evidence that ND is an evolutionary end point or that species with ND seeds have a higher extinction rate than those with dormant seeds. Further ND 'has adaptive evolutionary significance' (Zhang et al., 2022).

Clearly, PD is an adaptive strategy for the persistence of Asteraceae species growing in habitats with annually fluctuating favourability/unfavourability of conditions for germination and seedling survival. On the other hand, the lack of dormancy in cypselae of an Asteraceae species would seem to indicate that cypselae mature and are dispersed at a time of high predictability that environmental conditions are favourable for seedling establishment. That is, there is no benefit in germination being delayed via PD. However, as described for *Helenium amarum* (Baskin and Baskin, 1973), cypselae dispersed late in a so-called favourable season for seedling establishment may not germinate due to environmental temperatures being below those required for germination. In which case, germination can be delayed until the temperatures increase again. Would this scenario lead to selection for Type 2 non-deep PD?

In response to the selective pressure due to changes in seasonal patterns of temperature and precipitation and/or dispersal of seeds/cypselae to new habitats, six types of non-deep PD have evolved. The evolutionary pathways proposed for type of non-deep PD are Type 4 → Type 2 → Type 3 and Type 5 → Type 1 → Type 3 (see Fig. 12.21 in Baskin and Baskin, 2014). Type 6 was not known at the time these pathways were proposed. However, the occurrence of Types 1 and 6 in cypselae of *Silybum marianum* (Monemizadeh et al., 2021) from different populations suggests a close relationship between Types 1 and 6. Type 6 in which seeds/cypselae germinate over a wide range of temperatures without going through conditional dormancy may represent a response to unpredictable timing of rainfall during the growing season.

## Conclusions

ND and the six types of non-deep PD in Asteraceae enhance the flexibility of the dormancy-break/germination and seedling establishment stages of the life cycle. Thus, germination is closely linked to the time/season when the probability of successful seedling establishment is high. In addition to the various reasons that have been proposed (see Introduction) to help explain high species diversification in Asteraceae, we suggest that dormancy-break and germination need to be considered. The great flexibility/adaptability in terms of control of timing of dormancy-break and germination of Asteraceae helped ensure the survival of new species as they evolved, and it promoted successful establishment when cypselae were dispersed to new habitats. Furthermore, the occurrence of ND and PD in the basal tribes of Asteraceae suggests that flexibility of dormancy/germination has long been a part of the ability of species in this family to adapt to new habitats.

**Supplementary material.** To view supplementary material for this article, please visit: <https://doi.org/10.1017/S0960258523000107>.

**Conflicts of interest.** The authors declare that they have no competing interests.

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