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Seed dormancy and germination of Solanaceae from a phylogenetic and world vegetation perspective

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Abstract

Species of Solanaceae grow in rainforests, grasslands and deserts and especially montane/subalpine habitats of South America. The highest number of genera and species occurs in South America, but centres of species richness also are found in Africa, Australia, China and Mesoamerica. Information on embryo morphology was found for all eight subfamilies of Solanaceae and 236 species in 87 genera. Cestroideae, Pentunioideae, Nicotianoideae and Solanoideae have spatulate and linear-full embryos, while Duckeodendroideae, Goetzeoideae, Schizanthoideae and Schwenckioideae have linear-full embryos. Information on seed dormancy/germination was found for 167 species in 32 genera: 10 tree and 1 vine species in the tropics; 53 and 31 shrubs species in tropical and temperate zones, respectively; and 47 and 25 herb species in tropical and temperate zones, respectively. Physiological dormancy (PD) occurs in 94.5% of the 167 species; the other nine species had nondormant seeds. Regardless of subfamily, embryo morphology and vegetation region, most species have seeds with PD that can be broken during dry storage or cold stratification. Of the six types of nondeep PD, Type 2 occurs in a few temperate species; other types have not been documented. Soil seed banks have been documented in four subfamilies, 12 genera and 39 species, many of which are agricultural weeds. We identified questions that need to be answered about cold and heat tolerance of Solanaceae species, world distribution, especially in northern latitudes with a cold winter, and development of Type 2 nondeep PD as an adaptation of Solanaceae species that enhances survival in cold climates.

Introduction

Dispersal of angiosperm plant families to new parts of the world often is followed by speciation, which leads to the question: are changes in seed dormancy-breaking and germination requirements part of the adaptation of a species to its new habitat? One way to help address this question is to evaluate the dormancy-breaking and germination requirements of plant families that have species growing in a diversity of vegetation regions. This approach has been used to examine seed dormancy/germination in the large families Asteraceae (Baskin and Baskin, 2023), Rubiaceae (Baskin and Baskin, 2024), Myrtaceae (Baskin and Baskin, 2025a) and Malvaceae (Baskin and Baskin, 2025b) from a global perspective. In each of these families, there is a unique combination of ways in which seed dormancy and germination are related to the growth form, habitats and distribution of the species.

The Solanaceae was chosen for study of seed dormancy/germination from a phylogenetic and world vegetation perspective because it (1) has a diversity of embryo morphologies including straight linear to spiralled linear and spatulate (Martin, 1946; Gunn, 1974) and (2) is cosmopolitan but not species rich in northern latitudes with cold winters, e.g. northeastern USA and adjacent Canada (Gleason and Cronquist, 1991). The family is distributed on all continents except Antarctica, and species grow in rainforests, savannas, steppes, deserts and boreal/subalpine forests and meadows. The highest number of genera and species is in tropical/subtropical zones, especially Central and South America (Orejuela et al., 2017; Palchetti et al., 2020b). Sixty-one genera and 1595 species of Solanaceae are native to South America, and species grow from sea level to the subalpine zone on mountains. Peru has 41 genera and 631 species of Solanaceae, of which 295 species are endemic to that country (Palchetti et al., 2020b). Argentina has 315 species (80 endemic) of Solanaceae in 32 genera and Chile has 170 species (89 endemic) in 21 genera (Moreira-Muñoz et al., 2022).

High numbers of genera and species of Solanaceae occur in other South American countries, e.g. Bolivia, Brazil, Columbia and Ecuador (Palchetti et al., 2020b). Other centres of Solanaceae species richness include Africa, 9 genera and 202 species (Jaeger and Hepper, 1986);

Australia, 6 genera and 132 species (Purdie et al., 1982); China, 16 genera and 78 species (Lu, 1986) and Mesoamerica, 27 genera and 282 species (Gentry and D'Arcy, 1986).

In our consideration of the Solanaceae, we present an overview of the family and address various questions. (1) When and where did the family originate? (2) When did diversification and distribution to new habitats occur? (3) What kinds of embryos are found in seeds of Solanaceae? (4) What class(es) of seed dormancy is (are) in the family in various parts of the world? (5) What is the relationship between seed dormancy and embryo morphology? (6) How is seed dormancy distributed in the eight subfamilies of Solanaceae and in the various vegetation regions on earth? (7) What are the dormancy-breaking and germination requirements? (8) Do species of Solanaceae form persistent soil seed banks? (9) Why do so few species of Solanaceae grow in northern latitudes with cold winters?

Overview of Solanaceae

The Solanaceae belongs to the Solanales, which consists of five families in two clades: (1) Hydroleaceae, Montiniaceae and Sphenocleaceae, and (2) Convolvulaceae and Solanaceae (Refulio-Rodríguez and Olmstead, 2014). The Convolvulaceae and Solanaceae differ from the other members of the Solanales in that they have tropane alkaloids instead of iridoid compounds (Wang et al., 2023). The Solanaceae has eight subfamilies (Cestroideae, Duckeodendroideae, Goetzeoideae, Nicotianoideae, Petunioideae, Schizanthoideae, Schwenckioideae and Solanoideae), 18 tribes, 103 genera and 2729 species (POWO, website, 2024). *Solanum* (Solanoideae) is the largest genus with 1237 species (POWO, website, 2024).

The family includes trees, shrubs, lianas/vines, herbaceous perennials, biennials and annuals (Barboza et al., 2016). Trees (e.g. *Duckeodendron*) grow only in wet tropical forests (Fay et al., 1998), while shrubs are found in a diversity of habitats from deserts (*Lycium* and *Solanum*) to wet tropical forests (*Lycianthes* and *Solanum*) (Baskin and Baskin, 2014). Various species of lianas/vines occur in the tropics. In the Neotropics, climbing species of Solanaceae occur in *Capsicum, Cestrum, Dyssochroma, Hawkesiophyton, Juanulloa, Lycianthes, Lycium, Markea, Merinthopodium, Poortmannia, Salpichroa, Schultesianthus, Schwenckia, Solandra, Solandum, Trianaea* and *Witheringia* (Acevedo-Rodríguez, 2020). In wet tropical forest, some species of *Dyssochroma, Hawkesiophyton, Juanulloa, Lycianthes, Markea, Merinthopodium, Poortmannia, Schultesianthus* and *Trianaea* grow as epiphytic shrubs and lianas/vines (Acevedo-Rodríguez, 2020). A new genus (*Doselia*) of Solanaceae with four species of hemiepiphytic lianas has been found in moist premontane forests of the Andes in Colombia and Ecuador (Orejuela et al., 2022). Many species of tribe Juanulloeae (e.g. *Markea*) not only are neotropical epiphytes, but they also are myrmeophilous with swollen leaf bases (Knapp et al., 1997).

Leaves lack stipules and are simple, pinnate or cylindrical and alternate but sometimes opposite or in whorls of three to six. Leaves of some herbaceous plants (*Nolana, Sclerophylax*) are succulent (Barboza et al., 2016). Trichomes are simple, branched or stellate and sometimes glandular. Stems and leaves of many species are smooth, but those of *Solanum* subgenus *Leptostemonum* (350–450 species) have sharp epidermal prickles. Members of this subgenus also have stellate trichomes and tapered anthers with a terminal pore (Wahlert et al., 2014). Vegetative reproduction can occur via formation of stolons (*Nierembergia*), tubers (*Solanum*) and root buds (*Bouchetia, Leptoglossis* and *Solanum*) (Barboza et al., 2016).

Flowers occur in a cyme, lax panicle or a fascicle of two to many flowers, but they can be solitary. The bisexual flowers are actinomorphic, rarely zygomorphic. The five-lobel calyx persists during fruit development. The corolla has 5 [4, 6 or 9] petals that are fused at least at the base, resulting in tubular, rotate or salverform flowers that rarely are bilabiate (*Schizanthus*). The 5 [4 or 8] stamens are adnate to the base of the petals but alternate with corolla lobes. The ovary is superior, and the single pistil is 2-carpellate and usually 2-[3 to 5] loculate. The stigma has two lobes. The ovary has axile placentation, rarely basal, with numerous ovules (Zomlefer, 1994; Hunziker, 2001; Simpson, 2006; Barboza et al., 2016).

Flowers of Solanaceae are visited by various kinds of insects (bees, butterflies and moths), birds (Knapp, 2010) and bats (Sazima et al., 2003). Insect-pollinated flowers have evolved many times; bird-pollinated, ten times; moth-pollinated, eight times; and bat-pollinated, two times (Knapp, 2010). Insects, birds and bats collect nectar and/or pollen (Knapp, 2010). Flowers of the epiphytic shrub *Dyssochroma viridiflorum* in the Atlantic rainforest of southeastern Brazil are visited by bats that collect nectar and fruits (Sazima et al., 2003). Depending on the species, the zygomorphic flowers of the early-diverging *Schizanthus* are pollinated by bees, moths and hummingbirds (Pérez et al., 2006). Species of *Nierembergia* have glands (elaiophores) in the flowers that secrete oil, which is collected by insects (*Tapinotaspis* spp.) to provision their larvae (Cocucci, 1991). Oil flowers do not produce nectar, are zygomorphic and bisexual and have elaiophores located at the base of the filaments (Possobom and Machado, 2017). These authors found that only the Solanaceae and 10 other families (Calceolariaceae, Cucurbitaceae, Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae, Plantaginaceae, Primulaceae, Scrophulriaceae and Stilbaceae) secrete non-volatile oil that serves as a reward for pollinators.

The fruit is a berry, septicidal capsule or rarely a drupe, pyxidium or mericarp (Knapp, 2002). Capsules are plesiomorphic in Solanaceae, and berries have arisen at least three times (Knapp, 2002; Pabón-Mora and Litt, 2011). The endosperm is fleshy with oil and is abundant but scarce in most Juanulloideae. The embryo is straight, curved or coiled and the cotyledons flat or folded (Hunziker, 2001; Barboza et al., 2016). Ovules are unitegmic (Corner, 1976). The seed coat is multiplicative or not, is generally reduced and does not have a palisade layer of Malpighian cells (Souèges, 1907; Corner, 1976; Bhati et al., 2017). According to Bhati et al. (2017), the seed coat of *Atropa, Capsicum, Datura, Solanum* and *Withania* consists of 'the epidermis, hypodermis and parenchymatous layers'.

The Solanaceae contains important food plants for humans such as brinjal eggplant (*Solanum melongena*), bush tomato (*S. centrale*), cocona (*S. sessiliflorum*), Gboma eggplant (*S. macrocarpon*), lulo (*S. quitoense*), pepino (*S. muricatum*), peppers (*Capsicum* spp.), potato (*S. tuberosum*), scarlet eggplant (*S. aethiopicum*), tomatillos (*Physalis philadelphica*), tomato (*S. lycopersicum*) and tree tomato (*S. betaceum*) (Hunziker, 2001; Hilgenhof et al., 2023). *Solanum tuberosum* is the third most important food crop in the world, after rice and wheat (Birch et al., 2012), and its production is a vital part of global food security for humans (Devaux et al., 2020). Further, *S. lycopersicum* is one of the world's most important cultivated vegetables (Ramírez-Ojada et al., 2021).

Many kinds of chemical compounds in the Solanaceae, including tropane, pyrrolidine and phyrrolic alkaloids (Hanuš et al., 2005; Shelar et al., 2022), can cause sickness and possibly death if ingested by humans (Dauncey and Larsson, 2018). Thus, species such as *Atropa belladonna, Datura stramonium, Hypscyamus niger,*

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Mandragora officinarum and *Solanum dulcamara* are considered to be poisonous to humans (Hunziker, 2001). Some tropane alkaloids, however, long have been used as medicines (Shah et al., 2013), and research is ongoing to find additional medicinal uses of the diversity of tropane alkaloids, as well as the steroidal lactones, saponins, terpenes, flavonoids and phenolics found in the Solanaceae (Evans, 1986; Parr et al., 1990; Hunziker, 2001; Kohnen-Johannsen and Kayser, 2019; Jan et al., 2024). Many species of Solanaceae such as *Brugmansia, Petunia, Salpiglossis, Schizanthus* and *Solanum* are grown as ornamentals.

Palaeohistory: origin

Various crown ages for Solanaceae have been found/proposed: 30 Ma (Särkinen et al., 2013), 41 Ma (Wikström et al., 2001), 73 Ma (Huang et al., 2023), 81.99 and 109.99 Ma (Zuntini et al., 2024). In a study on the evolution of *Ipomoea aquatica*, Hao et al. (2021) concluded that Convolvulaceae diverged from the Solanaceae 71.7 Ma. However, Carruthers et al. (2020) placed the divergence of Convolvulaceae and Solanaceae at 130–97 Ma and the crown age of Solanaceae at 99–67 Ma.

Fossils of *Physalis infinemunfi* with a highly inflated five-lobed calyx have been collected from Early Eocene (52.2 Ma) deposits in Gondwanan Patagonia (Argentina), leading Wilf et al. (2017) to conclude that the Solanaceae was well diversified long before final breakup of Gondwanan. Also, fossil berries of *Eophysaloides inflata* collected in Columbia from Middle to Late Eocene (47.3–33.9 Ma) and *Lycianthoides calycina* collected in Colorado (USA) from Early Eocene (51.5–49.5 Ma) suggest that the Solanaceae was distributed from South American to North America by the Early Eocene (Deanna et al., 2023). Thus, there is considerable support for the older crown ages of Solanaceae, which occurred after the separation of South America and Africa between 135 and 105 Ma. Huang et al. (2023) stated that 'Solanaceae may have originated in the Late Cretaceous and diversified before the Cretaceous-Paleogene (K-Pg) boundary ….' Särkinen et al. (2013) concluded that Solanaceae originated and subsequently diversified in South America.

A whole-genome duplication (WGD) event is associated with the origin of angiosperms (De Bodt et al., 2005), and Jiao et al. (2011) dated it at 190–130 Ma. A whole-genome triplication (WGT), i.e. two closely occurring WGDs or hexaploidization, known as the gamma event, is associated with the origin of the eudicots (Jiao et al., 2012). In the long history of evolution of the eudicots, many WGD/WGT events have occurred, and the origin of various families is correlated with the time of a polyploidization event (Soltis et al., 2011, 2018; Almeida-Silva and Van de Peer, 2023).

After the divergence of the Solanaceae and Convolvulaceae (see above), a triplication event occurred in the Solanaceae (Bombarely et al., 2016; Wu et al., 2018; Cao et al., 2021a; Zhang et al., 2022). Zhang et al. (2022) concluded that a common Solanaceae hexaploidization occurred 49–43 Ma and was an allohexaploidization event. However, the Tomato Genome Consortium (2012) estimated that the hexaploidization occurred at 71 Ma, and Huang et al. (2023) placed this event at c. 81 Ma, before the Schizanthoideae diverged from the other subfamilies of Solanaceae at c. 73 Ma. On the phylogenetic tree of Solanaceae (minus the branch for *Duckeodentron*), Huang et al. (2023) found seven nodes with high gene duplications bursts (i.e. ≥300 gene duplications), suggesting that WGD/WGT events have occurred at different times.

Many molecular phylogenetic studies have been conducted on the Solanaceae (e.g. Olmstead and Palmer, 1992; Spooner et al., 1993; Santiago-Valentin and Olmstead, 2003; Martins and Barkman, 2005; Olmstead et al., 2008; Särkinen et al., 2013; Huang et al., 2023). The genus *Schizanthus* (Schizanthoideae) is at the base of the phylogeny and is sister to all other Solanaceae (Olmstead et al., 2008). The clade next to *Schizanthus* is the subfamily Goetzeoideae with *Duckeodendron* unplaced (Särkinen et al., 2013; Huang et al., 2023). These authors refer to *Schizanthus* as Clade I and Goetzeoideae as Clade II. Clade III is Schwenckieae plus Cestroideae. Clade IV is Petunieae, Clade V Nicotianoideae and Clade VI Solanoideae. *Duckeodendron* is now placed in the Duckeodrendroideae (Reveal, 2012), but its relationship to other subfamilies has not been resolved (Huang et al., 2023). Divergence of Solanaceae Clade II is 68.9 Ma; Clade III, 64.2 Ma; Clade IV, 63.5; Clade V, 61.3 MA; and Clade VI, 61.3 Ma (Huang et al., 2023). The rapid divergence of Clade VI (Solanoideae) occurred during the Paleocene-Eocene Thermal Maximum and Early Eocene Climate Optimum (Huang et al., 2023).

Palaeohistory: diversification and dispersal

The results of various molecular phylogenetic studies have revealed that diversification occurred in numerous lineages and genera of Solanaceae during the Eocene, Miocene and Pliocene and that often the appearance of new species was accompanied by establishment in new habitats.

Brunfelsia

This genus of mostly medium-size shrubs has a crown age of 18–16 Ma (Miocene), and its ancestral region is in 'eastern Brazil, southeastern South America and the Amazon Basin' (Filipowicz and Renner, 2012). These authors determined that dispersal to Cuba, Hispaniola, Jamaica and Puerto Rico (9–4 Ma) was followed by diversification of new species. In addition to the 23 species of *Brunfelsia* in the Antilles, species of this genus grow in eastern Brazil, southeastern South America and the Amazon Basin; Pacific coastal region of South American; foothills and montane zone of the Andes; and the Guiana Shield (Filipowicz and Renner, 2012).

Capsicum

The genus is endemic to the Americas, and the likely ancestral range is the Andes. Diversification of the nine clades of *Capsicum* began in the mid- to upper Miocene, after which each lineage diversified in a different region of South American in the Pliocene through the Pleistocene. Lineages giving rise to the domesticated species of *Capsicum* grew in the central Andes, i.e. Bolivia (García et al., 2022). Today, species of *Capsicum* are widely cultivated and are used as food in both the New and Old World (Eshbaugh, 2012; García et al., 2022); 22 landraces of *C. annum* have been identified in Mexico (Taitano et al., 2018).

Lycium

This genus of woody plants is found in temperate and dry tropical zones of Africa, Asia, Australia, North America and South America; it is not found in wet tropical habitats. Cao et al. (2021b) determined that the first diverging species in the phylogeny was *L. ruthenicum* in northern Africa. However, these authors were

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not sure if the genus originated in South America and migrated to Africa or if it originated in Africa. Their results indicate that there was migration from northern Africa to Asia where speciation occurred, after which the genus migrated to North America. The Asian and North American species belong to the same clade. Migration from Asia to Australia and from North America to South America may have occurred, but these migrations have not been confirmed. Results from phylogenetic studies involving the 15 species of *Lycium* in China indicated that *Lycium* diverged from its sister genus 17.7 Ma, and speciation in China mostly occurred in the Pliocene (Zhang et al., 2024).

Mandragora

Tribe Mandragoreae is monogeneric with four species: *M. autumnalis*, Mediterranean to W Iran; *M. caulescens*, Nepal to China; *M. officinarum*, N Italy to NW Balkan Peninsula; and *M. turcomanica*, NNE Iran to S Turkmenistan (POWO, website, 2024). The genus originated in the Eocene in the Mediterranean region (Volis et al., 2018). The Mediterranean/Turanian and Tibetan clades diverged c. 20.5 Ma, and the western Mediterranean and near east Turanian clades diverged 11.1 Ma (Volis et al., 2018).

Petunia

The pampas region of Brazil is the ancestral area for *Petunia*, and Reck-Kortmann et al. (2014) concluded that the ancestor may have had bee-pollinated flowers with a short corolla. Two clades developed: Clade I flowers are purple with a short corolla and bee pollinated, and Clade II (three subspecies of *P. axillaris*) flowers are white with a long corolla (except subspecies *occidentalis* with a short corolla) and bee, bird or moth pollinated, depending on the subspecies (Reck-Kortmann et al., 2014). Phylogenetic studies of *Petunia* by Soares et al. (2025) revealed that the two clades of *Petunia* originated c. 2.5 Ma in the early Pleistocene, and divergence in Clades I and II began about 1.0 and 0.8 Ma, respectively.

Solanum

This genus has a crown and stem age estimated at 53.2 and 44.98 Ma, respectively, (early Eocene) with 'most clades diverging between 35 and 27 Ma' (Messeder et al., 2024). The centre of diversity of *Solanum* is the Andes Mountains in South America with small centres of diversity in the Atlantic rainforest of Brazil, Amazon Basin and mountains of Central America (Echeverría-Londoño et al., 2020; Tovar et al., 2021). Divergence of extant species of *Solanum* begins in the middle Eocene. Clades I and II diverged at 42.49 Ma, and the Petota (potato and close relatives) and Tomato clades split c. 16.85 Ma (Messeder et al., 2024). According to Echeverría-Londoño et al. (2020), dispersal of *Solanum* from the Neotropics to the Old World was followed by diversification. The spiny clade of *Solanum* has had its highest rate of diversification in the Old World, i.e. 0.68 lineages Myr^{-1}. The global mean rate of *Solanum* speciation is estimated to be 0.25 lineages Myr^{-1} (Echeverría-Londoño et al., 2020).

The six most evolutionary labile traits (>100 transitions) of *Solanum* are as follows: (1) growth form (herb, shrub, tree, herbaceous vine, woody vine and epiphyte), (2) type of glandular trichomes (absent, simple, glandular and stellate), (3) sympodial unit structure (plurifoliate, trifoliate, defoliate non-geminate, defoliate geminate and unifoliate), (4) corolla shape (deeply stellate, broadly stellate and rotate), (5) corolla colour (white, green, purple and yellow) and (6) fruit colour (green, white, purple, yellow, orange and red) (Hilgenhof et al., 2023). On the other hand, conserved traits (<10 to 10 to 49 transitions) of *Solanum* with high taxonomic value are as follows: (1) pseudostipules (absent, present-single and present-pair), (2) corolla bilateral symmetry (present and absent), (3) anther shape (cylindrical, tapered and cordate), (4) pedicel insertion (flat and cup-shaped), (5) pedicel articulation (basal, near-basal, basal ¼ to ½, distal ½ and absent) and (6) stone cells (absent and present).

Due to the critical role that *Solanum tuberosum* plays in the food supply for humans, much research has been conducted on its origin and evolutionary history (e.g. Spooner et al., 2005, 2007, 2014; Sotomayor et al., 2023; Zhang et al., 2025). The cultivated potato and its wild relatives belong to section Petota of *Solanum*, and this is a monophyletic lineage in the genus *Solanum* derived from a hybridization event c. 8.6 Ma (Zhang et al., 2025). Phylogenetic studies by Zhang et al. (2025) reveal that the hybridization occurred between a diploid species of section Tomato and a diploid species of section Etuberosum (of *Solanum*), which have underground re-sprouting organs. These authors estimate that in the six species of Petota that they analysed c. 60 and 40% of the ancestry were from Etuberosum and Tomato, respectively. All Petota species produce tubers, which are thought to be a major innovation resulting from the hybridization.

After the hybrid with tubers was formed, rapid speciation occurred, especially in cool and relatively dry habitats (Zhang et al., 2025). Today, there are four cultivated species of potato (*Solanum ajanhuiri, S. curtilobium, S. juzepczukii* and *S. tuberosum*) (Spooner et al., 2007) and 107 wild tuber-producing *Solanum* species (Spooner et al., 2014). Depending on the species, wild potato relatives grow in Argentina, Bolivia, Chile, Columbia, Ecuador, Guatemala, Honduras, Mexico, Peru and Venezuela; Peru also has the highest number of species (51) of wild potatoes (Spooner et al., 2014). Further, in addition to the cultivated tomato (*S. lycopersicum*), there are 12 wild tomato species in western South America ranging from central Ecuador to northern Chile with two species in the Galápagos Islands (Peralta et al., 2005; Ramírez-Ojada et al., 2021).

In summary, a major point about the palaeohistory of the Solanaceae is that there has been much dispersal and diversification, resulting in species that currently grow on all continents except Antarctic and in all major vegetation regions excluding alpine/tundra. Moving forward in this review, we will see that much diversification also has occurred with respect to embryo morphology but not in class of seed dormancy. That is, in this family, species growing in the same vegetation region may have seeds with physiological dormancy (PD), but the seeds vary with regard to embryo morphology.

Embryo morphology

In our consideration of the embryos in Solanales and Solanaceae, we find linear, spatulate and folded embryos (sensu Martin, 1946), all of which are fully developed at seed maturity and do not grow inside the seed prior to radicle emergence (Baskin and Baskin, 2014, 2021). Linear embryos are longer than wide, and the cotyledons are the same width as the hypocotyl/radicle (stalk). Spatulate embryos have cotyledons that are noticeably wider than the stalk, and the full length of the stalk is visible below the cotyledons. In folded embryos, the cotyledons are wider than the stalk and are

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folded/twisted together, and the full length of the stalk is visible, i.e. not covered by the cotyledons.

On Martin's (1946) family tree of seed phylogeny, families with a linear embryo are above the base of the tree, and they are at the junction of the two branches of the tree. One branch goes from seeds with a linear embryo to dwarf seeds and then to micro seeds. The second branch goes in sequence from seeds with linear embryos to those with spatulate, bent, folded and investing embryos, i.e. investing embryos are at the top of the tree. At the linear embryo position on Martin's tree, there are two kinds of linear embryos. One, the linear embryo is underdeveloped (small with organs) and must grow inside the seeds before germination (radicle emergence) occurs. Two, the linear embryo is fully developed and does not grow inside the seed prior to germination. These two kinds of linear embryos are grouped together at the same location on Martin's tree. That is, his families with linear embryos include the Apiaceae with underdeveloped linear embryos and Solanaceae and Linaceae with fully developed linear embryos. Hereafter, linear fully developed embryos are referred to as linear-full, sensu Baskin and Baskin (2007).

In the Solanales, one clade consists of Montiniaceae with spatulate embryos (Takhtajan, 2000; Kirkbride et al., 2006) that is sister to Sphenocleaceae with linear-full embryos (Martin, 1946; Monod, 1980) and Hydroleaceae with linear-full embryos (Martin, 1946; Goldberg, 1986; Watson and Dallwitz, 1992 onward). The second clade in the Solanales consists of Convolvulaceae with linear-full and folded embryos (Martin, 1946; Hutchinson, 1959; Kirkbride et al., 2006) and Solanaceae with linear-full and spatulate embryos (Martin, 1946; Hunziker, 2001).

Literature searches resulted in us finding drawings/photographs/descriptions of the embryo morphology for 236 species in 87 genera of Solanaceae. Some information on embryo morphology has been found for the eight subfamilies of Solanaceae (Table S1): Cestroideae, 9 genera, 20 species; Duckeodendroideae, 1, 1; Goetzeioideae, 2, 2; Nicotianoideae, 7, 17; Petunioideae, 8, 15; Schizanthoideae, 1, 5; Schwenckioideae, 4, 5; and Solanoideae, 58, 169. There are six general types of embryo morphology in seeds of the Solanaceae (Fig. 1): spatulate (Fig. 1A) and five variations of linear-full, i.e. straight, slightly curved, curved, strongly curved and spiralled (Fig. 1B–F).

For 232 of the 236 species, we examined drawings or photographs of the embryo, but in four species the authors wrote that the embryo was linear but did not describe it in detail. Thirty-one species had a spatulate embryo, and this kind of embryo was in the Cestroideae, Petunioideae, Nicotianoideae and Solanoideae (Table 1). Curved linear embryos are in all subfamilies except Goetzeioideae, which has a straight linear embryo. Straight linear embryos also occur in the Schizanthoideae, Schwenckioideae and Nicotianoideae. On Martin's (1946) family tree of seed phylogeny, the linear embryo is placed below the spatulate embryo. When we consider the stem ages of the subfamilies, it seems that the spatulate embryo may have appeared in the Solanaceae after the linear embryo, but more studies are needed on embryos of the early diverging subfamilies.

Seed dormancy and germination

In addition to information on seed dormancy and germination of Solanaceae species, we collected from the literature, beginning in about 1988, a web-based search that included the name of each genus and subfamily of Solanaceae and the words seed dormancy, seed germination, semillas, sementes, germinación and germinação was conducted in May–June 2025. The database includes the life form of each species and the vegetation region where it grows. The temperature regime(s) at which the highest percentages of germination was (were) obtained and the most favourable light/dark conditions for germination were recorded. Information was found for 167 species in 32 genera: Cestroideae, 2 genera, 5 species; Duckeodendroideae, 1, 1; Goetzeoideae, 1, 2; Nicotianoideae, 5, 9; Petunioideae, 4, 7; Schizanthoideae, 1, 5; Schwenckioideae, 1, 1; and Solanoideae, 17, 136 (Table S2).

Seeds of Solanaceae readily imbibe water. For example, intact mericarps/seeds of *Nolana divaricata, N. jaffuelii, N. linerifolia* and *N. sedifolia* were fully imbibed after 48 hours (Hepp et al., 2021) and intact seeds of *Datura ferox* after 24 hours (Soriano et al., 1964), *Solanum lycocarpum* in c. 10–12 hours, *S. aphydendron* in 15 hours (Zuloaga-Aguilar et al., 2010) and eight species of *Solanum* in Australia in 24–48 hours (Commander et al., 2008). Thus, if freshly matured seeds of Solanaceae species take longer than about 4 weeks to germinate, we conclude that they have PD (Baskin and Baskin, 2014). That is, the embryo in seeds with PD has a germination-inhibiting mechanism or low growth potential. After seeds imbibe water, the embryo does not exert enough force to break the seed coat or any other embryo-covering structures such as endosperm (Nikolaeva, 1969; Baskin and Baskin, 2014).

The 167 species of Solanaceae grow in seven tropical and seven temperature vegetation regions with eight subfamilies in the tropics and five subfamilies in the temperate zone (Table 2). Trees (10 species) are found only in the tropics, while 53 and 31 species of shrubs grow in tropical and temperate zones, respectively. In tropical and temperate zones, there are 47 and 25 species of herbs, respectively. Trees, shrubs, vines and herbs are in four, five, one and six subfamilies, respectively (Table 3). PD occurs in 94.5% of the 167 species of Solanaceae. Nondormant (ND) seeds, which germinate quickly after maturation, were recorded in one species of Cestroideae and eight species of Solanoideae (Table S2). Thus, seeds of most Solanaceae have PD, regardless of life form, subfamily, embryo morphology and vegetation region in which the species grows.

The three levels of PD are nondeep, intermediate and deep, and nondeep is the most common, occurring in all vegetation zones on earth and in numerous plant families including the Solanaceae (Baskin and Baskin, 2014). Nondeep PD can be broken by relatively short periods (8–12 weeks) of moist cold (ca. 0–10°C) or warm (≥15°C) stratification. In temperate regions, intermediate and deep PD are broken by 13–16 weeks and 13–24 weeks of cold stratification, respectively (Baskin and Baskin, 2022). However, if seeds with intermediate PD are given c. 4 weeks of warm stratification at summer temperatures, the cold stratification period required to break PD is decreased to about 8–10 weeks (Baskin and Baskin, 1995). The amount of cold stratification required to break PD varies with the species: *Physalis longifolia*, 12 weeks (Bandara et al., 2019), *Schizanthus* spp., 8 and 13 weeks (Moreno et al., 2024), *Solanum americanum*, 3 weeks (Zhou et al., 2005b), *S. nigrum*, 6 weeks (Wagenvoort and van Opstal, 1979; Bithell et al., 2002) and *S. sarrachoides*, 12 weeks (Zhou et al., 2005a).

Dry storage of seeds with nondeep PD frequently results in dormancy-break, i.e. after-ripening (Baskin and Baskin, 2022). During dry storage, dormancy was broken in seeds of *Datura ferox* (Soriano et al., 1964), *Schizanthus* spp. (Moreno et al., 2024), *Physalis angulata* (Ozaslan et al., 2017), *P. peruviana* (Gaier et al., 2019), *P. philadelphica* var. *immaculata* (Ozaslan et al., 2017), *Solanum americanum* (Ladeira, 1997), *S. incanum* (Joshua, 1978),

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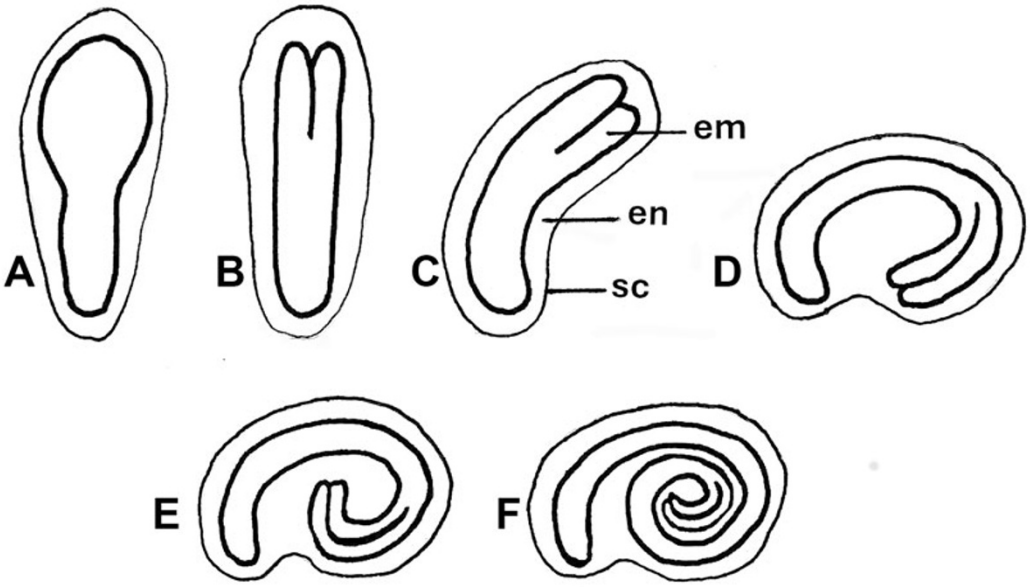

Figure 1. Illustrations of the diversity of embryo morphology in Solanaceae seeds. Spatulate embryo (A) and linear-full embryos (B–F): B, straight; C, slightly curved; D, curved; E, strongly curved; and F, spiralled. Em, embryo; en, endosperm, sc, seed coat.

Table 1. Kind/shape of embryo in 232 of 236 species of Solanaceae[a]

			Linear-full embryos				
Subfamily	Stem age (Ma)[b]	Spatulate	STR	SLCU	CU	STCU	SP
Schizanthoideae (*Schizanthus*)	73.3	-	+	+	+	-	-
Goetzeioideae	68.9	-	+	-	-	-	-
Duckeodendroideae	-[c]	-	-	-	-	+	-
Schwenckioideae	64.2	-	+	+	+	-	-
Cestroideae	64.2	+	-	+	+	+	+
Petunioideae	63.5	+	-	+	+	-	-
Nicotianoideae	61.3	+	+	+	+	+	-
Solanoideae	61.3	+	-	+	+	+	+
Total number of species		31	8	59	28	85	21

Linear-full embryos: STR, straight; SLCU, slightly cured; CU, curved; STCU, strongly curved; SP, spiralled; -, not found.
[a]Four species with linear-full embryos were not identified to general shape of embryo.
[b]Stem age of subfamily according to Huang et al. (2023).
[c]Not placed by Huang et al. (2023).

S. melongena (Yogeesha et al., 2006), *S. sarrachoides* (Zhou et al., 2005a), *S. stramonifolium, S. torvum* (Hayati et al., 2005) and *S. viarum* (Vicente, 1972). After cold stratification for 1, 2 and 9 months, seeds of *Nicandra physalodes* germinated to only 3.9, 7.2 and 0%, respectively (Watanabe et al., 2002), and cold stratification (1 week) decreased germination of *Withania somnifera* seeds (Kambizi et al., 2006). Perhaps, after-ripening would be a good dormancy-breaking treatment to try on seeds of these two species.

Seeds of *Solanum* species can after-ripen enough to begin to germinate within 1–2 months. Seeds of *S. viarum* were stored dry in flasks at room temperatures in São Paulo, Brazil, and tested at monthly intervals at 25/18°C (Vicente, 1972). At 2 months, seeds germinated to c. 65 and 20% in light and dark, respectively, and at 5 months they germinated to 95 and 80%, respectively, after which germination began to decline. At 25 months, no seeds germinated; however, the authors did not determine if the seeds had lost viability or entered secondary dormancy. Diploid seeds of potato (*S. tuberosum*) incubated in water and GA_3 1 week after extraction from the fruits germinated to 18.3 and 53.9%, respectively, but after 1 month of dry storage (at room temperatures?) they germinated to 35.6 and 61.7%, respectively (Balderrama et al., 2025).

We have found that a period of drying promotes seed germination of *Solanum incompletum* from Hawai'i. Seeds incubated on moist sand in Petri dishes at daily alternating temperatures regimes of 15/6, 20/10 and 25/15°C germinated to 53, 17 and 9%, respectively, after 12 weeks and to 57, 31 and 42% after 60 weeks. After 60 weeks, seeds at 15/6 and 20/10°C were allowed to dry at room temperatures for 12 weeks and then returned to 15/6 and 20/10°C, respectively. After an additional 12 weeks at 15/6°C germination had increased from 57 to 90%, and at 20/10°C germinated had

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Table 2. Number of species of Solanaceae of each growth form in each vegetation region for which seed dormancy/germination data were found (see Table S2)

Vegetation region	Trees	Shrubs	Vines	Herbs	Total
Tropical					
Rainforest (RF)	5	3	-	-	8
Montane	2	7	-	21	30
Alpine	-	1	-	-	1
Semi-evergreen RF	2	16	1	1	20
Dry tropical forest	-	5	-	3	8
Savanna	1	14	-	3	18
Desert	-	7	-	19	26
Temperate					
Matorral	-	19	-	4	23
Broad-leaved evergreen	-	3	-	3	6
Deciduous	-	-	-	6	6
Steppe	-	5	-	8	13
Desert	-	3	-	1	4
Woodland zone	-	1	-	1	2
Subalpine/boreal	-	-	-	2	2
Total	10	84	1	72	167

-, no information available.

Table 3. Presence of various growth forms in subfamilies of Solanaceae in tropical and temperate zones of the world

Growth form	Subfamilies	Tropical	Temperate
Trees	Duckeodendroideae	x	-
	Goetzeoideae	x	-
	Nicotianoideae	x	
	Solanoideae	x	-
Shrubs	Cestroideae	x	-
	Goetzeoideae	x	
	Nicotianoideae	x	x
	Petunioideae	x	x
	Solanoideae	x	x
Vines	Solanoideae	x	-
Herbs	Cestroideae	-	x
	Nicotianoideae	x	x
	Petunioideae	-	x
	Schizanthoideae	x	x
	Schwenckioideae	x	-
	Solanoideae	x	x

x, yes; -, no.

increased from 31 to 80%. The wet seeds at 25/15°C remained wet (control) with no increase in germination, i.e. still 42% after a total of 84 weeks (Baskin and Baskin, unpublished).

Nondeep PD also is broken in many species by treatment with gibberellin (GA), whereas GA may or may not promote germination of seeds with intermediate PD. GA has no effect on germination of seeds with deep PD (Baskin and Baskin, 2022). Treatment with GA_3 promoted seed germination in various species of Solanaceae, including *Capsicum annuum* (Hernandez-Verdugo et al., 2001), *Datura ferox* (Soriano et al., 1964), *Datura stramonium* (Popay, 1974), *Hyoscyamus niger* (Verma et al., 2014), *Jaltomata procumbens* (Saldívar-Iglesias et al., 2010), *Nicandra physalodes* (Lovey et al., 2007), *Physalis helicacabum* (Nosratti et al., 2016), *Salpiglossis sinuata* (Rivas et al., 2021), *Schizanthus* spp. (Moreno et al., 2024), *Solanum acaule* (Bamberg, 1999), *S. betaceum* (Neto et al., 2015; Torres-González, 2019), *S. quiroense* (Torres-González, 2019), *S. scuticum* (Araújo et al., 2025), *S. sessiliflorum* (Silva et al., 2024), *S. torvum* (Cutti and Kulckzynski, 2016; Jena et al., 2024; Wu et al., 2024; Priya et al., 2025), *S. trilobatum* (Sundaralingam et al., 2025) and *Withania somnifera* (Khanna et al., 2013; Malavika et al., 2020). Seeds of some species of Solanaceae also are stimulated to germinate when treated with KNO_3, e.g. *Alkekengi officinarum* (Aghilian et al., 2014), *Capsicum annuum* (Flores-Sánchez et al., 2022), *Iochroma arborescens* (Brito et al., 2016), *Solanum betaceum* (Torres-González, 2019), *S. crinitum* (Dias-Filho, 1998), *S. physalifolium* (Bithell et al., 2002) and *S. torvum* (Cutti and Kulckzynski, 2016; Jena et al., 2024).

Smoke water prepared by bubbling smoke from burning pine-oak forest litter in Mexico increased germination of *S. aphydodendron* seeds from c. 50 to 60%, while ash increased germination from c. 50 to 78% However, seeds given a dry-heat treatment at 60°C for 5 min plus smoke water germinated to 90% (Zuloaga-Aguilar et al., 2011). In additional experiments, heat treatments were very effective in promoting germination of *S. aphydodendron* seeds. About 100% of the seeds germinated after dry heat at 60, 80 and 120°C for 5 min and after dry heat at 60 and 80°C for 60 min. Wet heat at 60 and 80°C for 5 min and wet heat at 60°C for 60 min also resulted in c. 100% germination. Seeds were killed by dry heat at 120°C for 60 min, wet heat at 80°C for 60 and wet and dry heat at 100 and 120°C for 5 and 60 min (Zuloaga-Aguilar et al., 2010).

Aerial smoke had no effect on germination of *S. aculeastrum* seeds (Koduru et al., 2006). Soaking seeds of *Solanum tomentosum* in a 1/10 concentration of smoke water promoted germination (82%), while a diluted 1/100 concentration of smoke water had little effect on germination (6.7%) (Aliero and Afolayan, 2010). The effects of smoke water and karrikinolide isolated from smoke were tested on seed germination of eight species of *Solanum* in Australia (Commander et al., 2008). At 26/13 and 33/18°C, smoke water and karrikinolide significantly increased germination percentages of *S. centrale, S. diocicum* and *S. orbiculatum*. At 26/13°C, smoke water and karrikinolide significantly increased germination of *S. cunninghamiii* seeds, and at 33/18°C karrikinolide significantly increased germination of *S. phlomoides* seeds. Seeds of *S. chippendalei, S. diversiflorum* and *S. sturtianum* showed no response to either smoke water or karrikinolide, but GA_3 promoted some germination at both temperature regimes. In additional experiments, seeds of *S. centrale* and *S. orbiculatum* treated with smoke water and karrikinolide were incubated at constant temperatures of 10, 15, 20, 25 and 30°C. Seeds of *S. centrale* treated with smoke water germinated to ≥10% at 15 and 20°C, and those treated with karrikinolide germinated to ≥10% at 10, 15 and 20°C; maximum germination (c. 35%) was for karrikinolide-treated seeds at 20°C. In contrast, seeds of *S. orbiculatum* treated with smoke water germinated to c. 50, 45, 75, 85 and 70% at 10, 15, 20, 25 and 30°C, respectively,

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and those treated with karrikinolide germinated to 95–100% at all temperatures.

Commercially available aqueous smoke extract used to flavour food promoted germination of *Nicotiana attenuata* seeds (Cao et al., 2021a). Fractionation of this aqueous smoke and subsequent use of the fractions to test germination of *N. attenuata* seeds revealed that syringaldehyde was the germination-promoting compound.

When PD is broken in response to warm (≥15°C) and/or cold (c. 0–10°C) moist stratification, dry after-ripening or treatment with GA_3 or KNO_3, the embryo gains enough 'push power' to emerge from the structures that cover it. Thus, if seeds with PD are scarified, they may germinate because the mechanical resistance of the seed coat has been removed/reduced. Both mechanical scarification with a blade, pin or sand paper (Rick, 1956; Sousa-Silva et al., 2001; Gupta, 2003; Lovey et al., 2007; Gonzaga et al., 2009; Suthar et al., 2009; Oyelana, 2011; Cabrera et al., 2015; Hepp et al., 2021) and chemical scarification with conc. H_2SO_4 (Wei et al., 2009, 2010; Ramamoorthy et al., 2010; Palchetti et al., 2020a) have been shown to promote germination of various species of Solanaceae. Further, if the embryo is removed from seeds with nondeep PD, it will grow into a normal seedling. However, the embryo removed from seeds with intermediate or deep PD may, or may not, grow, or it could give rise to an abnormal/stunted plant. Embryos from mature seeds of *Datura ferox* (Soriano et al., 1964) and *Mandragon autumnalis* (Al-Ahmad, 2020) and immature seeds of *Capsicum annuum* (Manzur et al., 2014) produced healthy plants.

Dormancy cycling also is a characteristic of seeds of many species with nondeep PD (Baskin and Baskin, 2014), and it has been documented in seeds of *Datura ferox* (Reisman-Berman et al., 1991), *D. stramonium* (Stoller and Wax, 1974), *Physalis physalifolium* (Taab and Andersson, 2009), *Solanum nigrum* (Roberts and Lockett, 1978; Taab and Andersson, 2009) and *S. sarrachoides* (Roberts and Boddrell, 1983). In these studies, dormancy was broken during winter when environmental conditions were suitable for cold stratification, and seeds germinated in spring. However, if seeds fail to germinate in spring they were re-induced into dormancy (secondary dormancy) during summer with dormancy-break occurring the following winter.

Changes in the temperature requirements for germination as seeds undergo dormancy-break are characteristic of many seeds with nondeep PD. However, only a few Solanaceae species have been studied in enough detail to determine if seeds exhibit changes in their temperature requirements for germination during dormancy-break. In several species, however, there was a decrease in the minimum temperature at which seeds could germinate, which is Type 2 nondeep PD (Soltani et al., 2017). Seeds of *Datura stramonium* exhibited a decrease in the minimum temperature for germination from 30/15°C for freshly matured to 15/6°C for seeds buried 3 months in moist soil at natural temperature regimes in Kentucky (USA) from mid-October to mid-January (Baskin and Baskin, 1988; unpublished). Fresh seeds of *Solanum dulcamara* germinated to 3% at 25°C and to 0% at 10, 15 and 20°C (Roberts and Lockett, 1977). After 1 month of cold stratification at 4°C, seeds of *S. dulcamara* germinated to c. 80% at 25 and 30°C and to c. 28, 20 and 15% at 20, 15 and 10°C, respectively. After 3 months of cold stratification, seeds of this species germinated to 40–85% at all temperatures. As dormancy was broken during dry storage at 4°C, seeds of *S. rostratum* exhibited a decrease in the minimum temperature at which seeds would germinate. In light, the minimum temperature for germination decreased from 30/15 to 20/10°C and in darkness from 30/15 to 5/2°C (Shalimu et al., 2012). As dormancy-break occurred in *S. sarrachoides* seeds buried in soil in England, they first gained the ability to germinate at 30, 25 and 20°C, then at 15°C and finally at 10°C (Roberts and Boddrell, 1983). We conclude that seeds of *S. dulcamara, S. rostratum* and *S. sarrachoides* have Type 2 nondeep PD.

We have presented various kinds of evidence that seeds of Solanaceae have nondeep PD. However, for each category of evidence, e.g. dormancy cycling, only a few examples of species have been presented because only a small number of species of Solanaceae have been investigated. One possible reason for the small number of detailed studies on dormancy-break could be related to the rapid loss of dormancy when seeds of Solanaceae are stored for several weeks or months before the first germination test. These high germination percentages have, no doubt, removed the incentive for many researchers to conduct detailed studies on dormancy-break, e.g. changes in temperature requirements for germination during the dormancy-breaking process.

Temperature and light requirements for germination

For the 167 species of Solanaceae listed in Table S2, the mean temperature at which seeds germinated to a high percentage is 22.6 ± 0.4°C. In some species of Solanaceae, seeds incubated at an alternating temperature regime germinate to a higher percentage than those incubated at a constant temperature. Seeds of *Solanum dennekense, S. incanum, S. luteum* and *S. nigrum* germinated to a higher percentage at 27/13 than at 20°C (Teketay, 1998); *S. dulcamara*, higher at 30/20 than at 30 or 20°C (Roberts and Lockett, 1977); *S. elaeagnifolium*, higher at 25/15 than at 20 or 30°C (Stanton et al., 2012); *S. lycocarpon*, higher at 30/20 than at 30 or 20°C (Pinto et al., 2007); and *S. physalifolium*, higher at 25/15 than at 25°C (Del Monte and Tarquis, 1997). Seeds of *S. carolinense* germinated to c. 85 and 97% at 30/20 and 35/20°C, respectively, and to 0 and c. 3% at 15 and 20°C, respectively (Brown and Porter, 1942).

Information on germination in light (L) vs. dark (D) was found for 44 species (Table S2): light (L) required, 7 species; germination higher in light than in dark (L > D), 18; germination equal in light and dark (L = D), 7; and germination higher in dark than in light (D > L), 5. In seven additional species, more than one response was found, e.g. *Solanum americanum*, L > D, L = D; *S. betaceum*, L > D, L = D; *S. mauritianum*, L > D, L = D; *S. villosum*, L, D>L; *Physalis angulata*, L = D, L > D; *Withania somnifera*, L, L > D (Table S2). Seeds of *S. americanum* incubated in light at 30 and 35/20°C germinated to 92 and 90%, respectively, but in darkness to 82 and 92%, respectively (Zhou et al., 2005b). Seeds of *S. nigrum* incubated in light germinated equally well at 21 and 25/19°C (97 and 96%, respectively), but in darkness they germinated to 89 and 96%, respectively (Wagenvoort and van Opstal, 1979). Seeds of *Physalis philadelphica* incubated in light at 30 and 30/25°C germinated to c. 95%, but in darkness they germinated to 20 and 45%, respectively (Madrid et al., 1989).

Effects of animals on seeds

Dispersal

Seeds of Solanaceae may be dispersed when animals eat fleshy fruits and subsequently discard the seeds. Animals that have been documented to disperse seeds of Solanaceae include bats (Sazima et al., 2003; Albuquerque et al., 2006; Mello et al., 2008; Caves, 2010; Rossaneis et al., 2015), birds (Barnea et al., 1990; Nogales et al., 1998; Burrows, 1999; Albuquerque et al., 2006; Vasconcellos-Neto

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Table 4. Examples of Solanaceae in which seed germination percentage was increased after seeds passed through the digestive system of an animal

Species of Solanaceae	Kind of animal	References
Lycium intricatum	Bird	Nogales et al., 1998
Solanum americanum	Bat	Rossaneis et al., 2015
Solanum granulosoleprosum	Bats, birds, caviomorph rodents, marsupials, murid rodents	Cáceres and Moura, 2003
Solanum mauritianum	Bat	Rossaneis et al., 2015
Solanum mauritianum	Bird[a]	Jordaan et al., 2011
Solanum nigrum	Bird	Barnea et al., 1990; Clergeau, 1992
Solanum pimpinellifolium	Giant tortoise	Rick and Bowman, 1961
Solanum thomasiifolium	Lizard	Vasconcellos-Neto et al., 2009
Solanum villosum	Bird	Barnea et al., 1990

[a]Seeds that passed through the digestive system of dark-capped bulbuls germinated to the same final percentage as those removed from fruits by hand (c. 73%), but germination of ingested seeds began sooner than that of seeds removed from fruits by hand.

et al., 2009; Jordaan et al., 2011), fox (Canidae) (Bueno and Motta-Junior, 2004), lizards (Nogales et al., 1998), tortoises (Rick and Bowman, 1961) and maned wolf (Canidae) (Lombardi and Motta-Junior, 1993; Bueno and Motta-Junior, 2024). Rodents also disperse seeds of *Solanum lycocarpum*, but in doing so they predate/destroy some of the seeds (Briani and Guimerães, 2007). Seeds of *S. rostratum* are dispersed when the berry enclosed by the spiny calyx becomes attached to animal fur and wool of sheep; fruits with the attached calyx also float in water in irrigation canals (Eminniyaz et al., 2013).

Germination

Seeds of some species of Solanaceae collected after they passed through the digestive system of animals and tested for germination have germinated to higher percentages than de-fruited (non-eaten) control seeds (Table 4). In some studies, however, the ingested seeds germinate to the same percentage as control seeds, i.e. fruit removed by hand (Lombardi and Motta-Junior, 1993; Vasconcellos-Neto et al., 2009). However, seeds of *Solanum thomasiifolium* ingested by a fox germinated to a lower percentage than the control (Vasconcellos-Neto et al., 2009). Seeds of S. *nigrum* in the droppings of the great bustard (bird) in Spain had a lower percentage of germination and lower percentage of viable seeds than the control, but they germinated faster than the control seeds (Bravo et al., 2014). Seeds of *S. nigrum* defecated and regurgitated by blackbirds and starlings in France germinated to a higher percentage than those in the control, and germination percentage of regurgitated seeds was significantly higher than that of defecated seeds (Clergeau, 1992).

Germination mechanism: the endosperm cap and radicle emergence

After dormancy is broken in seeds of Solanaceae, the radicle emerges from the seed, first by penetration of the endosperm located in the micropylar region of the seed (endosperm cap) and second by penetration of the seed coat. Breakdown/softening of the endosperm cap precedes radicle emergence, but various studies on different species of Solanaceae indicate that this is a complicated (and still not completely understood) process. Softening involves exposure to red light, production of GA by the embryo, increased activity of hydrolysing enzymes such as endo-β-mannanase and expansin, decrease in level of ABA and a decrease in the puncture force required to break the endosperm cap (Soriano et al., 1964; Groot and Karssen, 1987, 1992; Groot et al., 1988; Sánchez and de Miguel, 1997; Chen and Bradford, 2000; Nonogaki et al., 2000; Pinto et al., 2007; Lee et al., 2012; Martínez-Andújar et al., 2012; Steinbrecher and Leubner-Metzger, 2017; Shi et al., 2022; Chen et al., 2024). Basically, exposure of ND imbibed seeds to red light leads to formation of Pfr, followed by GA production by the embryo, which promotes activity of enzymes. These enzymes hydrolyse cell wall components of the cells in the endosperm cap. In particular, endo-β-mannanase and the genes involved in its activity and how they relate to hormonal regulation have received considerable research attention (Nonogaki et al., 2000; Martínez-Andújar et al., 2012; Steinbrecher and Leubner-Metzger, 2017). The puncture force required to break the endosperm cap has been measured after various dormancy-breaking treatments in seeds of *Capsicum, Datura, Nicotiana, Petunia* and *Solanum* (see Steinbrecher and Leubner-Metzger, 2017).

The force required to break the endosperm cap in seeds of *Solanum lycocarpum* imbibed in water decreased in two major phases: (1) days 1–10, a decrease from 2.12 to 1.82 N, and (2) days 25–30, a decrease of 1.73 to 1.20 N. After 30 days, the radicle emerged (Pinto et al., 2007). However, for seeds imbibed in 100 μM ABA, there was only one major period of decrease in puncture force, and it was between days 15 and 20; puncture force at days 1 and 40 was 2.33 and 1.84 N, respectively. After 40 days of imbibition in water and ABA, endo-β-mannanase activity was 120 and 90 pmol min^{-1} cap^{-1} ec^{-1}, respectively. ABA decreased activity of endo-β-mannanase and thus softening of the endosperm cap, and it decreased the amount of water imbibed and ability of seeds to germinate.

Persistent soil seed banks

In a persistent soil seed bank, seeds remain viable and can germinate in the second or some later germination season (Walck et al., 2005). A persistence soil seed bank not only helps to ensure long-term persistence of a species at a site, but it could increase the ability of a species to become naturalized in new habitats (Gioria et al., 2020, 2021).

In our search for information about soil seed banks of Solanaceae, we identified 193 published research articles in which the methods were such that presence of a persistent seed bank could be detected. That is, soil samples were collected after the germination season but before dispersal of newly produced seeds. Thirty-two of the 193 papers included species of Solanaceae. We found soil seed bank information for four of the eight subfamilies (Cestroideae, Petunioideae, Schwencioideae and Solanoideae), 12 genera and 39 species of Solanaceae (Table 5). *Atropa, Cestrum,*

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Table 5. Persistent soil seed banks for species of Solanaceae

Species	Subfamily	Habitat, country	Density (m^{-2})	References
**Atrope belladona*	Solanoideae	Deciduous forest, Iran	34.4	Asadi et al., 2012
Cestrum schlechtendalii	Cestroideae	Secondary tropical montane forest, Brazil	1.8	Baider et al., 2001
Datura metel	Solanoideae	Semi-arid woodland, South Africa	0.4	Mndela et al., 2019
Discopodium penninervium	Solanoideae	Dry Afromontane forest, Ethiopia	2.17	Birhanu et al., 2022
Fabiana imbricata	Petunioideae	Steppe, Argentina	0.1	Ghermandi et al., 2013
Nolana gayana	Solanoideae	Coastal dunes, Peru	115	Ohga, 1992
Nolana humifusa	Solanoideae	Coastal dunes, Peru	646	Ohga, 1992
Petunia × hybrid	Petunioideae	Urban domestic gardens, England	3.5	Thompson et al., 2005
**Physalis angulata*	Solanoideae	Tropical agricultural soil, Belize	26	Kellman, 1974
**Physalis angulata*	Solanoideae	Weedy pasture, Brazil	1	Calegari et al., 2013
**Physalis angulata*	Solanoideae	Alluvial palm forest, Brazil	1	Ribeiro Mesquita et al., 2014
**Physalis angulata*	Solanoideae	Cleared secondary rainforest, Brazil	6	Ribeiro Mesquita et al., 2016
**Physalis peruviana*	Solanoideae	Dry Afromontane forest, Ethiopia	6	Teketay and Granström, 1993
**Physalis pubescens*	Solanoideae	Secondary tropical forest, Mexico	+	Guevara and Gómez-Pompa, 1972
**Physalis pubescens*	Solanoideae	Disturbed tropical seasonal forest, Brazil	4.7	Martins and Engel, 2007
Quincula lobata	Solanoideae	Semiarid grassland, Texas (USA)	28	Kinucan and Smeins, 1992
**Schwenkia americana*	Schwenckioideae	Moist tropical forests, Republic of Congo	2.2, 3.3	Douh et al., 2018
**Schwenkia americana*	Schwenckioideae	Shrub savannas, Republic of Congo	8.33	Douh et al., 2023
**Schwenkia americana*	Schwenckioideae	Tropical savannah, Brazil	<1	Andrade and Miranda, 2014
**Solanum aculeatissimum*	Solanoideae	Disturbed tropical seasonal forest, Brazil	7.8	Martins and Engel, 2007
Solanum americanum	Solanoideae	Disturbed tropical seasonal forest, Brazil	12.8	Martins and Engel, 2007
Solanum americanum	Solanoideae	Restoration sites of tropical semi-evergreen forests, Brazil	2, 3, 4, 8, 18	Moressi et al., 2014
Solanum americanum	Solanoideae	40-year-old restored savanna, Brazil	476	Neto et al., 2014
Solanum americanum	Solanoideae	Secondary semideciduous seasonal forest, Brazil	15	Braga et al., 2016
Solanum anguivi	Solanoideae	Dry Afromontane forest, Ethiopia	106.5	Birhanu et al., 2022
**Solanum carolinense*	Solanoideae	Old agricultural fields undergoing succession, USA	+	Leck and Leck, 1998
Solanum cernuum	Solanoideae	40-year-old restored savanna, Brazil	62	Neto et al., 2014
Solanum cernuum	Solanoideae	Secondary semideciduous seasonal forest, Brazil	3	Braga et al., 2016
Solanum erianthum	Solanoideae	Rainforest, New Guinea	1	Enright, 1985
Solanum erianthum	Solanoideae	Secondary semideciduous seasonal forest, Brazil	2	Braga et al., 2016
Solanum erianthum	Solanoideae	Secondary tropical montane forests, Brazil	1.8, 5.6, 10.7	Baider et al., 2001
Solanum grandiflorum	Solanoideae	Seasonal rainforest, Brazil	0.8	Neto et al., 2007
Solanum granuloso-leprosum	Solanoideae	Gallery forests, Brazil	1.5, 9.2	Grombone-Guaratini et al., 2004
Solanum granuloso-leprosum	Solanoideae	Seasonal rainforest, Brazil	1.9	Neto et al., 2007

(*Continued*)

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Table 5. (*Continued.*)

Species	Subfamily	Habitat, country	Density (m^{-2})	References
Solanum hayesii	Solanoideae	Seasonally moist tropical forest, Panama	4.4	Dalling et al., 1997
**Solanum jamaicense*	Solanoideae	3.3-year-old secondary tropical premontane wet forest, Costa Rica	426	Young et al., 1987
Solanum leucodendron	Solanoideae	Secondary semideciduous seasonal forest, Brazil	1	Braga et al., 2016
Solanum mauense	Solanoideae	Dry Afromontane forest, Ethiopia	22	Teketay and Granström, 1993
**Solanum mauritianum*	Solanoideae	Disturbed tropical seasonal forest, Brazil	32.8	Martins and Engel, 2007
**Solanum mauritianum*	Solanoideae	Restoration site of tropical semi-evergreen forests, Brazil	2	Moressi et al., 2014
**Solanum mauritianum*	Solanoideae	40-year-old restored savanna, Brazil	20	Neto et al., 2014
Solanum montanum	Solanoideae	Coastal dunes, Peru	44, 2178	Ohga, 1992
Solanum multifidum	Solanoideae	Coastal dunes, Peru	646	Ohga, 1992
Solanum nigrescens	Solanoideae	3.3-year-old secondary tropical premontane wet forest, Costa Rica	235	Young et al., 1987
**Solanum nigrum*	Solanoideae	Secondary tropical forest, Mexico	+	Guevara and Gómez-Pompa, 1972
**Solanum nigrum*	Solanoideae	Fields abandoned for 1, 7 and 15 years, Mediterranean region of France	18, 1, 3	Lavorel et al., 1993
Solanum nigrum	Solanoideae	12-year-old rehabilitated *Banksia* woodland, Australia	1.25	Grant and Koch, 1997
**Solanum nigrum*	Solanoideae	Dry Afromontane forest, Ethiopia	22	Teketay and Granström, 1993
**Solanum nigrum*	Solanoideae	Irregularly flooded arable fields, Germany	31	Bissels et al., 2005
**Solanum nigrum*	Solanoideae	Riparian woodland, Botswana	1, 2	Mmusi et al., 2021
**Solanum nigrum*	Solanoideae	Dry Afromontane forest, Ethiopia	43.5	Birhanu et al., 2022
**Solanum paniculatum*	Solanoideae	Restoration sites of tropical semi-evergreen forests, Brazil	1, 5, 34	Moressi et al., 2014
**Solanum paniculatum*	Solanoideae	40-year-old restored savanna, Brazil	61	Neto et al., 2014
**Solanum paniculatum*	Solanoideae	Secondary semideciduous seasonal forest, Brazil	2	Braga et al., 2016
Solanum pseudoquina	Solanoideae	Secondary tropical montane forests, Brazil	3.6, 7.1, 8.9	Baider et al., 2001
Solanum pubigerum	Solanoideae	Secondary tropical forest, Mexico	+	Guevara and Gómez-Pompa, 1972
Solanum schlechten-dalianum	Solanoideae	3.3-year-old secondary tropical premontane wet forest, Costa Rica	15	Young et al., 1987
**Solanum sisymbriifolium*	Solanoideae	Disturbed tropical seasonal forest, Brazil	0.8	Martins and Engel, 2007
**Solanum sisymbriifolium*	Solanoideae	40-year-old restored savanna, Brazil	1	Neto et al., 2014
**Solanum torvum*	Solanoideae	Secondary tropical forests, Mexico	+	Guevara and Gómez-Pompa, 1972
**Solanum torvum*	Solanoideae	Tropical agricultural soil, Belize	4	Kellman, 1974
Solanum umbellatum	Solanoideae	Tropical wet forests, Costa Rica	272, 60	Young, 1985
Solanum umbellatum	Solanoideae	3.3-year-old secondary tropical premontane wet forest, Costa Rica	809	Young et al., 1987
**Solanum villosum*	Solanoideae	Dry Afromontane forest, Ethiopia	24	Teketay and Granström, 1993
Vassobia breviflora	Solanoideae	Secondary semideciduous seasonal forest, Brazil	6	Braga et al., 2016

+, species present, but no information was provided about seed density; *, listed as a weed by Holm et al. (1979).

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Datura, Discopodium, Fabiana, Petunia, Quincula, Schwenkia and *Vassobia* were represented by only one species; *Nolana* by two species; *Physalis* by three species; and *Solanum* by 25 species. Thirteen species were found in two or more locations, and seeds of *S. nigrum* were found in seven locations, including Australia, Botswana, Ethiopia, France and Germany. Seeds of Solanaceae have been found in soils of forests, coastal dunes, deserts and savannas, and they often are found in disturbed soils, e.g. agricultural soils, gardens, pastures and secondary forests.

Only a relatively few studies in which seeds were buried in the soil and seed longevity monitored for 1 or more years have been conducted for species of Solanaceae. The longest such experiment (1902–1941) that included Solanaceae is the Duvel buried seed experiment conducted in Rosslyn, Virginia (USA). The experiment included *Datura stramonium, Nicotiana tabacum* and *Solanum nigrum*. After 39 years of burial, seeds of each species from burial depths of 55 and 105 cm germinated: *D. stramonium*, 91 and 88%, respectively; *N. tabacum*, 22 and 17%, respectively; and *S. nigrum*, 83 and 70%, respectively (Toole and Brown, 1946).

In a 6-year study of buried seeds in England, Roberts and Dawkins (1967) disturbed (dug to a depth of 22.5 cm) 540 × 300 cm plots in March and September (first year) and other plots in March, June, September and December in each year of the study. Seeds of *Solanum nigrum* germinated in each of the 6 years. Since no seed set was allowed to occur in the plots, we can assume that seeds of *S. nigrum* can live in the soil for at least 6 years.

Four studies have been done in which seeds of Solanaceae have been placed in mesh bags and buried in soil in the field. *Solanum elaeagnifolium* seeds were buried in a weedy pasture in Australia, and after 36 months seed viability at 10 cm was 59% but only 18–25% viability at 0, 2.5 and 5 cm (Stanton et al., 2012). Viability of *S. hayseii* seeds buried in a seasonal rainforest in Panama for 18 months was 45% (Dalling et al., 1997), and viability of *S. mauritianum* seeds buried for 2 years in a rainforest in Australia was c. 75% (Hopkins and Graham, 1987). However, viability of *S. mauritianum* seeds buried in a grassland in South Africa for 13 months was 15–35% (Witkowski and Garner, 2008).

Freshly matured seeds of *Solanum carolinense and S. elaeagnifolium* were mixed with soil and placed in vials with perforated caps that in turn were placed in soil in jars with perforated lids; the jars then were buried in a field in Iowa (USA) (Brown and Porter, 1942). Each species was buried at soil depths of 10–15 cm and 40–45 cm. After 3 years of burial at 10–15 and 40–45 cm, exhumed seeds of *S. carolinense* germinated to 98 and 0.5%, respectively, and those of *S. elaeagnifolim* to 50 and 66%, respectively.

Seeds of *Hyoscyamus niger* germinated in soil samples removed from two archaeologically dated sites in Denmark (Sjørrind and Hirsholm) abandoned in 1300 and 1871, respectively, and one site Sweden (Tommarp) abandoned in 1300 (Ødum, 1965). However, the presence of viable/germinable seeds of *H. niger* in these long-abandoned sites does not prove that seeds have lived in the soil since 1300. Unknown soil disturbances may have resulted in seed burial. For example, seeds may have been buried due to the activities/feeding of earth worms (McTavish and Murphy, 2021). In the future, genomic sequencing of presumably long-buried and recently produced seeds of *H. niger* (and other species found in archaeological sites) might provide more information on how long seeds have lived in the soil (see Pérez-Escobar et al., 2022).

Many questions remain about Solanaceae

Distribution in temperate zone

In terms of number of species in each of the vegetation regions on earth, the Solanaceae is not evenly distributed. The centres of distribution for this family are in South America, Mesoamerica, China, Africa and Australia (see Introduction). With an increase in distance from the equator in the Northern Hemisphere, there is a decrease in the number of species of Solanaceae. For example, Mexico has 381 species in 34 genera (Martínez et al., 2017); northeastern USA and adjacent Canada, 29 species in 10 genera (Gleason and Cronquist, 1991); and Canada, 8 species in 1 genus (*Solanum*) with only one native species (*S. carolinense*) (https://thecanadianencyclopedia.ca/en/article/nightshade). Alaska has one species, the weedy *S. nigrum* (Hultén, 1968). If numerous species of Solanaceae, in particular species of *Solanum*, live at high elevations in the Andes, why do so few species grow in the temperate latitudes, e.g. central and northern USA and southern Canada?

Heat and cold tolerance of Solanaceae species

Does the ability of Solanaceae plants to tolerate heat and cold play a role in determining global distribution? The search for genes to help improve growth and production of potatoes and tomatoes has resulted in various tests of the response of wild species of *Solanum* to heat and cold stress.

Tolerance of 16 species of wild potatoes collected between 450 and 4200 m a.s.l. in Bolivia and Pera and one species from 2500 m a.s.l. in Mexico were tested for both heat and cold tolerance (Smillie et al., 1983). Newly expanded (dark-adapted) leaves of each species were cold- and heat-stressed at 0 and 41°C, respectively, then assayed for changes in chlorophyll fluorescence. Cold-stressed leaves were placed at 0°C and assayed at hourly intervals until fluorescence decreased by 50%. For the heat-stressed leaves, fluorescence was measured first at 0°C, after which leaves were warmed to 22°C and then exposed to 41°C for 10 min. After the heat treatment, fluorescence was measured again at 0°C. In general, with an increase in elevation where the species grew cold tolerance increased and heat tolerance decreased.

Nine diploid wild potato species from South American and one from Mexico were tested for production of microtubers in culture media in a cool (1°C) and warm (25°C) environment (Guedes et al., 2019). Microtuber production was similar at 19 and 25°C for four species, greater at 19 than at 25°C for six species and greater at 25 than at 19°C for one species. Overall, *S. kurtzianum* (from Argentina) and *S. sogarandinum* (from Peru) were the most heat tolerant. In another study, *S. chacoese* (accession BGB444 from South America) produced significantly more tubers at 24–34°C than at 14–27°C (Bashir et al., 2020).

Li (1977) tested plants of 60 tuber-producing species of *Solanum* at temperatures ranging from −2.5 to −6.5°C (at 0.5°C intervals). The temperature that killed the leaves ranged from −2.5 to −6.5, depending on the species and accession. Leaves of eight species were killed at −2.5°C, while those of *S. acuale* were killed at −4.5 to −6.5°C, depending on the accession of this species. In another study, natural frosts (two nights of c. −2°C) on plants of 101 species of *Solanum* from the U.S. Potato Collection growing in field plots in Wisconsin (USA) killed all the leaves on 59 species but had little or no effect on leaves of seven species (Vega and Bamberg, 1995).

Hijmans et al. (2003) evaluated frost tolerance in 87 wild potato species in South America. The species with high frost tolerance

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grew in regions in which the mean minimum yearly temperature was below 3°C, i.e. in 'central and southern Peruvian Andes, the lowlands of Argentina and adjacent areas and a small area in the central Chilian Andes'. In the plains of north central India, a 3-day period of day temperatures of 19.5–20.5°C and night temperatures of 1–3°C killed 90% of the leaves of one or more accessions of *Solanum alandiae, S. arnexii, S. berthaultii, S. boliviense, S. cardiophyllum, S. microdontum* and *S. sparipilum* (Luthra et al., 2007).

Phylogenetic analyses revealed that *Solanum pimpinellifolium* originated in Ecuador and subsequently diverged southward along the western side of the Andes into Peru (Lin et al., 2020). The range of the species now spans from wet tropical rainforest in Ecuador to deserts in Peru. The authors asked why *S. pimpinellifolium* did not expand northward but did not answer this question. We think the authors have asked an important question about heat-tolerant Solanaceae lineages, and answers to this question could provide insight on the low number of Solanaceae species in cool temperate climates, especially in North America.

Was the northward migration of heat-tolerant Solanaceae from South to North America blocked? For example, did the separation of South and North America during the Miocene when much speciation and dispersal were occurring in Solanaceae prevent northward dispersal? Was migration of Solanaceae to North America, especially to Mexico, promoted when the Isthmus of Panama formed in the Pliocene, c. 2.8 Ma (O'Dea et al., 2016)? On the other hand, was northward migration of cold-tolerant lineages in the Andes blocked by the high temperatures of the rainforests of northern South America and of Central America? Are the native species of Solanaceae in eastern USA derived from heat-tolerant lineages from South America?

Molecular phylogenetic studies of the Carolinense Clade in *Solanum* subgenus *Leptostemonum* (the spiny solanums) identified four North American (*S. carolinense, S. dimidiatum, S. perplexum* and *S. pumilum*) and five South American (*S. aridum, S. comptum, S. juvenale, S. moxosense* and *S. reineckii*) species (Wahlert et al., 2014, 2015). Since the North American species 'are nested among a large clade of mostly Neotropical species in the overall phylogeny', Wahlert et al. (2014) hypothesized that there was a single dispersal event of a South America *Solanum* to North America. Further, they suggested that diversification of the South American progenitor explains the present-day occurrence of four species in the Carolinense Clade in North America. Three of the four *Solanum* species in the South American and North American parts of the Carolinense Clade are weedy and grow in disturbed habitats (Wahlert et al., 2015); however, the fourth species *S. pumilum* is an endemic on outcroppings of Ketona dolomite and amphibolite in Alabama (USA) (Allison and Stevens, 2001).

PD, timing of germination and life cycle

Does Type 2 nondeep PD promote growth of Solanaceae species in habitats with cold winters and warm summers?

Since dormancy-break in seeds with Type 2 nondeep PD results in a decrease in the minimum temperature at which seeds can germinate, they do so at low temperatures in the habitat in early spring. Thus, seeds with Type 2 could germinate in tropical mountains and in temperate regions at the end of the cold season, and young plants have the full length of the warm season for growth. The number of studies on type of nondeep PD in seeds of Solanaceae species is limited; however, seeds of some species have been shown to have Type 2 (e.g. Roberts and Lockett, 1977; Roberts and Boddrell, 1983; Baskin and Baskin, 1988; Shalimu et al., 2012). More studies in which seeds of Solanaceae are tested over a range of temperatures at various times during the dormancy-breaking are needed before we have a good understanding of the importance of the various types of nondeep PD in the adaptation of Solanaceae species to different kinds of habitats.

Cold-sensitive plant species can grow in winter-cold habitats if they are dormant during winter, i.e. species behave as herbaceous perennials with dormant buds in winter or as summer annuals present as seeds during winter. Species of Solanaceae in temperate regions behave as herbaceous perennials or summer annuals. For example, in northeastern USA and adjacent Canada, Gleason and Cronquist (1991) list 29 species of Solanaceae in 10 genera, and 14 and 15 of the species are perennials and annuals, respectively. All the annuals behave as summer annuals with flowering and fruiting occurring in summer to autumn. Do seeds of these 29 species have Type 2 nondeep PD?

In Canada, shoots of the perennial *Solanum carolinense* emerge from the soil by mid-May but die after the first frost in autumn (Bassett and Munro, 1986). Do seeds of *S. carolinense* have Type 2, which would promote seed germination in spring? Chandler and Travers (2024) found that vegetative and reproductive traits of *S. carolinense* from a northern population (Minnesota, USA) were more heat tolerant than those of plants from a southern population (Texas, USA). However, plants from the southern population were more cold tolerant than those from the northern population. Do seeds from the northern and southern populations have the same dormancy-breaking and germination requirements?

Type 2 nondeep PD has been found in two summer annual Solanaceae species living in the temperate zone. The weedy summer annual *Solanum rostratum* is native to central America, Mexico and the Great Plains of the USA and has been introduced into northeastern USA and southwestern Ontario (Canada). It also has become established in Australia, China, Europe, the Middle East and South Africa (POWO, website, 2024). In Ontario, seeds of *S. rostratum* germinate in spring. Plants flower in late June to early July, and fruits are mature by early September (Bassett and Munro, 1986). Seeds of this species have Type 2 nondeep PD (Shalimu et al., 2012). The weedy summer annual *S. sarrachoides* is native to South America (Argentina, Bolivia, Brazil, Paraguay and Uruguay), but it now has been introduced into Australia, Europe, South Africa and the USA (POWO, website, 2024). Its seeds not only have Type 2 nondeep PD but dormancy can be broken during dry storage or cold (moist) stratification (Roberts and Boddrell, 1983). It seems reasonable that seeds of many other summer annual species of Solanaceae have Type 2 nondeep PD.

In winter-cold habitats in South America, e.g. upper slopes of the Andes, germination at the beginning of the summer warm season would be adaptive. Seedling establishment at the beginning of the growing season means that plants would have the whole warm season for growth. Thus, do high elevation species of Solanaceae in the Andes produce seeds that have Type 2 nondeep PD?

Many species of Solanaceae, however, grow in climates that are warm throughout the year; some areas are wet and others have an annual wet/dry cycle. The ability of seeds to after-ripen in dry warm conditions and to germinate at high temperatures with the onset of the wet season means that germination occurs after conditions are favourable for seedling establishment and growth. Did Type 2 nondeep PD develop when migrating lineages of Solanaceae came in contact with winter-cold climates or when lineages growing outside the tropical zone in the Eocene began to experience cold

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winters in the late Eocene and Oligocene (Zachos et al., 2001; Westerhold et al., 2020)?

Concluding thoughts/questions

We found seed dormancy/germination information for only 167 of the 2729 (6.1%) species of Solanaceae; thus, much additional research is needed on members of this family. Most (94.5%) of the 167 species had seeds with PD, and this class of dormancy was found in all subfamilies, vegetation regions and growth forms of Solanaceae. However, spatulate and five kinds of linear-full embryos are found among the species of Solanaceae, but seeds have only PD. Why is there more diversity in embryo morphology than in class of seed dormancy in the Solanaceae? Clearly, there is more to be learned about the evolution of Solanaceae. In general, nondeep PD is easily broken, often by dry after-ripening, and seeds germinate to a high percentage at relatively high temperatures (mean = 22.6°C). Thus, from a seed dormancy-breaking and germination perspective, species of Solanaceae are well suited for living in either wet or seasonally wet/dry tropical and subtropical zones.

The heat and cold tolerances of Solanaceae, especially *Solanum*, have received much recent attention by scientists involved in crop development, e.g. potatoes. One hypothesis for the lack of high numbers of Solanaceae in northern cold winter climates is that the lineage(s) that migrated north, e.g. to North America, was (were) heat tolerant but not cold tolerant. The heat-tolerant lineage of the Carolinense Clade of *Solanum* that migrated from South America to North America presumably had PD that was broken by high temperatures with the ND seeds germinating at high temperatures. A lowering of the minimum temperature at which seeds could germinate (i.e. Type 2 nondeep PD) would facilitate survival and speciation of members of the clade in the temperate zone. That is, the ability of seeds to germinate in spring at the beginning of the warm season enhances adaptation to winter-cold, summer-warm habitats.

This scenario for development of temperate species in the Carolinenese Clade of *Solanum* fits the model for the origin and evolutionary relationships of the various levels and types of PD proposed by Baskin and Baskin (Baskin and Baskin, 2014, see their Fig. 12.21) with regard to origin of Type 2 nondeep PD. In this model, after dormancy is broken seeds with Type 4 nondeep PD germinate only at high temperatures and those with Type 2 nondeep PD germinate at both high and low temperatures. Type 4 in seeds of species growing in tropical seasonally wet/dry habitats is broken by warm dry conditions, and seeds germinate during the warm wet season. With climate cooling or dispersal of lineages to seasonally cool climates, the favourable season for germination and subsequent plant growth and establishment has low (spring) temperatures. Thus, the model proposes that Type 4 gave rise to Type 2 via a lowering of the minimum temperature at which seeds can germinate, i.e. the ability to germinate at low temperatures has been 'added' to ability to germinate at high temperatures. Thus, seeds germinate in spring at the beginning of the warm wet season.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0960258526100142.

Competing interests. The authors have no conflict to declare.

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