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Seed and Bulb Dormancy Characteristics in New World *Allium* L. (Amaryllidaceae): A Review

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Abstract: Many New World *Allium* L. (Amaryllidaceae) species exhibit seed and bulb dormancy characteristics that are responsive to environmental factors such as temperature, soil moisture and photoperiod. This review is intended to discuss perspectives on the adaptations and mechanisms of dormancy and provide a current summary of research in the area of seed germination, bulb dormancy initiation and bulb dormancy release in *Allium* species found in North America.

Key words: *Allium* L., dormancy characteristics, seed, bulb

INTRODUCTION

Few genera match the species diversity found in *Allium* L. Worldwide, there are estimated to be over 700 known *Allium* species, now classified in the subfamily Alliodeae under the family Amaryllidaceae, part of the order Asparagales (Chase *et al.*, 2009). Some taxonomic uncertainty exists as many botanists still assign the genus *Allium* to the families Liliaceae or Alliaceae (Mc-Neal and Jacobsen, 2002; Kamenetsky and Rabinowitch, 2006). Alliums are characterized by their pungent odor and flavor, umbelliferous inflorescences atop naked spathes and the presence of solitary or clustered subterranean storage bulbs. Many species in this geophytic genus, such as *A. cepa* (onion), *A. sativum* (garlic) and *A. ampeloprasum* (leeks), are regularly cultivated and have economic importance as vegetable crops. Other *Alliums* have gone through selection and breeding for flowering attributes and size and are commonly used as ornamental plants (Hanelt, 2001; Kamenetsky and Rabinowitch, 2006). However, the majority of *Allium* species are not under cultivation remaining in their native habitats.

Allium is widely distributed throughout the Northern hemisphere, with the highest diversity occurring in Iran, Afghanistan and Central Asia where most of the currently cultivated *Allium* crops originated. North America is considered to be a secondary center of diversity and is host to approximately 80 species exhibiting a wide range of distribution and the associated geo-climatic adaptations (Kamenetsky, 1993; Kamenetsky and Rabinowitch, 2006; Hellier, 2000). The generic diversity is demonstrated through the many morphological, physiological, genetic and reproductive adaptations

occurring within and among *Allium* species (McNeal and Ownbey, 1973; Ernst, 1979; Nault and Gagnon, 1988; Kamenetsky, 1996; Specht and Keller, 1997; Kamenetsky and Gutterman, 2000; Kamenetsky and Rabinowitch, 2006; Phillips *et al.*, 2008).

Though the germination and growth characteristics of many *Allium* species have remained relatively unstudied, there is a wealth of current knowledge available to those interested in furthering the understanding of the phenology and life-history attributes of species in this large and widely distributed genus. This review is intended to present a survey of published work examining seed and bulb dormancy in the diverse group of New World *Allium* species.

Adaptation and mechanisms of dormancy: Most New World species of *Allium* exhibit dormancy characteristics related to their seed germination and cessation and resumption of vegetative growth (Hanelt, 1990; Brewster, 1994). Dormancy is an adaptive trait that allows plants to maximize success by increasing the possibility that seed germination and/or vegetative growth occurs in the most advantageous season.

Perennial plants must be able to annually replenish the storage organ/s needed to provide the resources required for vegetative and reproductive growth. Geophytic species such as those in the genus *Allium*, have a unique life-form in which the perennating bud resides in a subterranean storage organ (Dafni *et al.*, 1981). This adaptive feature provides a resource allowing the plant to maintain the capability to persist through seasonally unfavorable climates by entering a dormant phase with storage organ stores reserves allowing for the subsequent seasons growth (Rees, 1972; Dafni *et al.*,

1981). In other species, environmental factors such as temperature and photoperiod have been shown to initiate the onset of dormancy prior to expected seasonal drought or winter conditions (Bradshaw, 1965; Bradshaw and Hardwick, 1989; Vaughton and Ramsey, 2001; Volaire and Norton, 2006). Summer dormancy, common in many New World *Alliums*, is a common adaptation in perennial plants occupying environments where there tend to be predictably long and dry summer periods (Voltaire and Norton, 2006). The induction and release of summer dormancy are thought to be triggered by environmental cues such as temperature and photoperiod (Metzger, 1996; Voltaire and Norton, 2006) and therefore could be habitat correlated.

It needs to be stressed that summer dormancy does not imply the cessation of all biological activity in the remaining dormant tissue. Kamenetsky (1994) has proposed the term intra-bulb development to better describe summer dormancy in bulbous species. The hypogeous physiological activity that takes place during summer dormancy often includes cell differentiation and floral initiation (Kamenetsky, 1994; Lapointe, 2001; Kamenetsky and Rabinoswitch, 2006). In this review, dormancy is defined as the period between leaf senescence and before the resumption of root and shoot growth.

Furthermore, the seeds generated in the reproductive growth phase must be able to avoid germinating until conditions exist that offer a higher chance of survival in this high-risk life cycle phase (Meyer *et al.*, 1997; Cavieres

and Arroyo, 2000; Phillips *et al.*, 2010). Therefore, centuries of selection pressure for traits allowing for higher survival have resulted in bulb and seed dormancy characteristics specific to the environmental conditions in which the particular *Allium* species or ecotype is found. Seed dormancy is often released upon exposure to prolonged cold temperatures similar to those found during winter in the mother plants natural habitat, although some species require warm temperatures to break dormancy. Just as in bulb summer dormancy, there must be metabolic activity in the dormant tissue for it to respond to the environmental cue. This generally requires imbibition of the seed before the onset of cold or warm temperatures. It should be noted that not all dormancy in seeds responds to temperature. Endogenous dormancy such as physiological and morphophysiological dormancy often require a temperature dependent stratification period, but exogenous dormancy is not affected by temperature (Nikolaeva, 1977; Baskin and Baskin, 1998). For the purposes of this discussion, when I write seed dormancy, I am explicitly referring to endogenous seed dormancy.

Seed dormancy: Seed germination behavior for most New World *Alliums* has not yet been investigated (Hellier, 2000). However, seed dormancy has been a common trait found in many *Alliums* that have undergone formal germination testing. Typically, seed dormancy in New World *Alliums* is habitat correlated, with a significant amount of within-species ecotypic variation (Table 1).

Table 1: A summary of germination experiments conducted on New World *Allium* species with dormancy type, germination treatment with the best results, highest germination percentage from that treatment, seed source and the citation of the original report. Multiple collections were tested in some species

Species	Type	Treatment	%	Source	Citation
<i>A. acuminatum</i> Hooker	PD	CS - 3°C, 8 weeks	77	Utah, USA	Phillips <i>et al.</i> (2010)
	PD	CS - 3°C, 8 weeks	90	Utah, USA	Phillips <i>et al.</i> (2010)
	PD	CS - 3°C, 12 weeks	76	Utah, USA	Phillips <i>et al.</i> (2010)
<i>A. amplexans</i> Torrey	PD	CS - 6.5°C, 2+ weeks	15	California, USA	Hunt <i>et al.</i> (2006)
	PD	CS - 6.5°C, 2+ weeks	46	California, USA	Hunt <i>et al.</i> (2006)
<i>A. brandegei</i> S. Watson	PD	CS - 3°C, 12 weeks	33	Utah, USA	Phillips <i>et al.</i> (2010)
	PD	CS - 3°C, 12 weeks	16	Utah, USA	Phillips <i>et al.</i> (2010)
	PD	CS - 3°C, 16 weeks	5	Utah, USA	Phillips <i>et al.</i> (2010)
<i>A. burdickii</i> (Hanes) A.G. Jones	MPD (Ep)	WS - CS - 25/15°C	ND*		Baskin and Baskin (1988)
<i>A. cernuum</i> Roth	No dormancy	WS - 21/12°C	50-75	Colorado, USA	Butler and Frieswyk (2001)
	PD	CS - outdoors, 5 months	ND	Montana, USA	Luna <i>et al.</i> (2008)
	No Dormancy	WS - 16°C, 120 day	48	Unclear	Specht and Keller (1997)
<i>A. geyeri</i> S. Watson	MPD	ND*	ND*	Western USA and CAN	Bonde (1965)
					Baskin and Baskin (1998)
<i>A. passeyi</i> M. Holmgren and A.H. Holmgren	PD, non-dormant-24%	CS - 3°C, 12 weeks	68	Utah, USA	Phillips <i>et al.</i> (2010)
	PD, non-dormant-19%	CS - 3°C, 12 weeks	54	Utah, USA	Phillips <i>et al.</i> (2010)
	PD, non-dormant-8%	CS - 3°C, 8 weeks	68	Utah, USA	Phillips <i>et al.</i> (2010)
<i>A. tricoccum</i> Aiton	MPD (Ep)	WS - CS, 1+ years	ND*	E. USA and Canada	Nault and Gagnon (1993)
					Baskin and Baskin (1998)
<i>A. drummondii</i> Rgl.	No Dormancy	WS - 26°C, 100 day	80	Unclear	Specht and Keller (1997)
<i>A. kunthii</i> G. Don	Unclear	CS - 11°C, 120 day	6	Unclear	Specht and Keller (1997)

*ND = No data, or incomplete data. PD: Physiological dormancy; MPD: Morphophysiological dormancy; (Ep): Epicotyl; CS: Cold moist stratification; WS: Warm moist stratification

This disparity creates difficulty in discerning precise germination requirements for a species and often requires the investigation of multiple ecotypes to achieve a clear picture of the germination behavior of a single species. This becomes evident when reading seemingly conflicting results such as in the germination of *A. cernuum* where published reports assert varying levels of dormancy including the complete lack of dormancy. In a multi-species germination study conducted by Specht and Keller (1997), germination percentages of *A. cernuum* did not vary considerably when exposed to a range of temperatures from 5-26°C. Nonetheless, maximum germination was achieved sooner when seeds were exposed to the highest temperature in their experiment (26°C) implying that cold moist stratification was not required. Butler and Frieswyk (2001) also recommended germinating *A. cernuum* seeds collected in Colorado, USA by exposing them to a diurnal temperature fluctuation of 21°C during the day and 12°C at night. Conversely, other published results showed the existence of physiological seed dormancy with cold moist stratification needed in order for germination to occur (Baskin and Baskin, 1988; Luna *et al.*, 2008). Apparent in these studies is the natural adaptive nature of within-species seed dormancy characteristics and the need to account for this fact in germination testing, particularly widely distributed species such as *A. cernuum*. One such seed germination experiment examined seed dormancy characteristics in three North American *Allium* species, *A. acuminatum*, *A. brandegei* and *A. passeyi*, across altitudinal gradients to search for patterns that might be helpful to propagators (Phillips *et al.*, 2010). All three species were found to have dormant seeds that germinated after cold moist stratification. The specific duration of chilling required for maximal germination in each species was related to the altitudinal variation in the seed collection sites. Seeds from higher elevations required longer periods of stratification in comparison to conspecific seed lots collected from lower elevations and in one species, *A. passeyi*, a fraction of the seeds collected from the lowest elevation site were non-dormant. The species occupying the highest elevation sites in these tests (*A. brandegei*) expressed the highest level of dormancy with low germination rates of viable seeds after six months of stratification. Other species collected from high elevation sites have likewise produced low germination percentages in formal tests (Hunt *et al.*, 2006). It is possible that seeds from these high elevation populations would require even longer chilling periods coinciding with the natural winter conditions existing at their collection site.

Carol and Jerry Baskin have contributed greatly to the knowledge base of seed ecology in North American temperate species, including the seed dormancy characterization of some *Alliums* (Baskin and Baskin, 1998). Besides the aforementioned *A. cernuum*, in their multi-species evaluation (1988) they also reported on *A. geyeri* (physiological dormancy) and *A. burdickii* (morphophysiological dormancy). They have also described *A. tricoccum* germination experiments in which radicle emergence did not occur until the second autumn after sowing and only after radical elongation did shoot growth occur (Baskin and Baskin, 1998). These results were similar to those obtained by Nault and Gagnon (1993) in their multi-year *A. tricoccum* germination trials. These results suggest deep simple epicotyl morphophysiological dormancy (Baskin and Baskin, 1998). Morphophysiological dormancy may be an under-diagnosed mechanism in *Allium*. Many of the germination experiments that have been conducted have resulted in unexplained low germination percentages in some *Allium* species despite seemingly viable or full seeds such as *A. kunthii* (Specht and Keller, 1997) and *A. brandegei* (Phillips *et al.*, 2010). It is recommended that warm moist stratification preceding cold moist stratification be employed to test for morphophysiological dormancy in the larger fraction of seeds (Baskin and Baskin, 1998).

With most New World *Alliums* existing in temperate zones with distinct seasonal differences in temperature and precipitation, it is intuitive that seed dormancy release would be triggered by a period of cold moist chilling. This would mimic the natural environment that the seed is exposed to in the winter period prior to germination when conditions are more favorable in the spring. However, testing germination response to warm moist stratification in the seeds of *Allium* species occupying mild winter habitats should not be ignored. Although not commonly reported, at least one species, *A. drummondii* has achieved higher germination percentages and rates when stratified at 26°C compared to 16°C. Furthermore, only a tiny fraction of seeds germinated when stratified at 5°C and none at 11°C (Specht and Keller, 1997).

Further complicating the description of germination behavior is the variation from year to year in germination characteristics, including germination percentages and even the required duration of cold chilling to achieve maximal germination (Baskin and Baskin, 1988). Source-specific seed propagation protocols must account for the effects of environmental conditions present during the seed development and maturation in the collection site. Germination behavior will likely be more consistent in habitats less prone to yearly climatic fluctuations.

Table 2: A summary of formal bulb dormancy experiments conducted on New World *Allium* species including a brief habitat description, the most effective treatment for breaking bulb dormancy, bulb source location and citation of original report

Species	Habitat	Dormancy release	Source	Citation
<i>A. schoenoprasum</i> L.	Wet meadows and riparian areas	Heat treatment (water or air)	Grolau cultivar	Folster and Krug (1977)
<i>A. acuminatum</i> Hooker	Dry slopes and plains	12-16°C, 16 weeks	Utah, USA	Phillips <i>et al.</i> (2010)
<i>A. brandegei</i> S. Watson	Alpine meadows	12°C, 12 weeks	Utah, USA	Phillips <i>et al.</i> (2010)
<i>A. passeyi</i> M. Holmgren and A.H. Holmgren	Dry limestone outcroppings	16°C, 6 weeks	Utah, USA	Phillips <i>et al.</i> (2010)
<i>A. vineale</i> L.*	Disturbed moist soils	22°C, 2 months	Eastern USA	Krochmal (1960)

*Non-native, but naturalized throughout North America

Allium bulb dormancy: Bulb dormancy in New World *Allium* species has rarely been examined by formal experimentation. The bulk of the current information is gleaned from botanical field reports and notes. However, there are a few examples of direct examination regarding environmental and physiological effects on the onset and release of bulb dormancy in multiple New World *Alliums* (Table 2).

Bulb dormancy initiation: Most New World *Alliums* spend a portion of their annual life cycle in a dormant state (Kamenetsky and Rabinowitch, 2006). The mechanisms inducing dormancy are not well understood and there is considerable variation among and within *Allium* species in regards to the timing of leaf senescence and the ensuing dormant period. It is thought that environmental factors such as air and soil temperature, decreasing soil moisture and photoperiod serve key roles in the initiation of both summer and winter bulb dormancy (Dafni *et al.*, 1981; Kamenetsky and Rabinowitch, 2006).

Leaf senescence and flowering dates in several North American *Allium* species showed variation between and among species (Phillips, 2007). Differences in the timing of the onset of dormancy within these species was habitat-correlated and likely tied to differences in temperature, photoperiod, and/or soil moisture. Within the two widely distributed species, *A. acuminatum* and *A. brandegei*, the onset of dormancy occurred later with increasing elevation. The dormancy timing for all three species corresponded with a sharp increase in soil temperature. This correlation between habitat and the bulb dormancy initiation is apparent in many North American *Allium* species adapted to regions with distinct dry seasons followed by cold winter months. Species occupying riparian areas or other moist habitats such as *A. geyeri* and *A. glandulosum*, are more likely to persist through the summer months and enter their dormant phase as winter approaches (Jacobsen, 1979; Bonde, 1965; Traub, 1968; McNeal and Ownbey, 1973).

Allium seedlings may not be as responsive to external cues. Growth chamber experiments with *A. acuminatum*, *A. brandegei* and *A. passeyi* seedlings suggest that dormancy initiation is obligate regardless of temperature, soil moisture and photoperiod (Phillips, 2007). Seedlings of all three species grown at either a

constant 12 or 16°C entered a state of dormancy despite continued soil moisture and a constant 12:12 h photoperiod. One explanation for this phenomenon may be related to proteins accumulated in the seedling leaf tissue. Studies with *Dactylis glomerata* and *Poa bulbosa* have shown an accumulation of dehydrin proteins in dormant tissue under well watered conditions (Volaire and Lelievre, 2001; Volaire, 2002). Dehydrins are known to exist in the seeds of *Allium sativa* L. and the presence of dehydrins in seedling tissues is not necessarily related to environmental stressors as usually is the case in more mature plants (Close *et al.*, 1993). This may imply a stage-specific phenomenon related to an accumulation of dehydrins in seedling leaf tissue. Whatever the case, it seems evident that in at least some *Allium* species, the initiation of bulb dormancy in seedlings may not be under the same influences as the onset of dormancy in mature bulbs.

Bulb dormancy release: McNeal and Ownbey (1973) reported that botanical specimens of *A. acuminatum* and other related *Allium* species, collected and pressed while flowering in the spring, sprouted in the herbarium the following spring as long as the bulb coat resistant layers were not compromised. They also reported that bulbs of multiple species remained dormant even when watered throughout the summer. These bulbs did not break dormancy until November when the fall rains began. Moreover, they demonstrated that bulbs subjected to cold temperatures (4°C) and regular irrigation for eight weeks before being placed in a greenhouse resumed vegetative growth two weeks earlier in comparison to dormant bulbs in the greenhouse that were watered later in the Fall. These findings suggest an obligate dormant period is internally enforced throughout the summer months and that colder temperatures combined with moisture promotes root and shoot growth in late fall. However, as the sprouting herbarium specimens demonstrate, these *Allium* bulbs will sprout at a much later date in the absence of cold temperatures and moisture (McNeal and Ownbey, 1973). This would indicate that stored water in the dormant bulb is sufficient to initiate the processes necessary for breaking dormancy, but that these processes are quickened in colder temperatures.

Other western North American *Alliums* share bulb dormancy traits similar to those described by McNeal and Ownbey (1973). Three species native to the intermountain west region of North America, *Allium acuminatum*, *A. brandegei* and *A. passeyi*, undergo a period of summer dormancy before re-sprouting in late autumn in advance of rapid spring growth (Phillips, 2007). It was likewise observed with *A. passeyi* that dormant bulbs collected in the summer would sprout in storage at ambient laboratory temperatures months later. Experiments showed that dormant first-year bulbs produced from these three species seedlings re-sprouted following re-hydration in cool temperature conditions. Bulbs from each species in this experiment were exposed to either a 2, 4, or 8 week dry period after going dormant. They were subsequently placed in growth chambers at either 12 or 16°C where they received regular watering. Each of the species was unique in regards to the duration of exposure to cool moist conditions required to break dormancy, with a range between 2 and 10 weeks. Responses to the differing temperatures appeared to be habitat-correlated, with *A. passeyi*, a lower elevation species, sprouting sooner in the 16°C environment and the higher elevation *A. brandegei* sprouting sooner in the 12°C environment. The duration of the preceding dry dormant period had little effect on sprouting times. This appears to indicate that the intra-bulb development phase described by Kamenetsky (1997) does not solely occur during the dry summer dormant period in bulbs such as *A. passeyi*. However, it is unknown whether intra-bulb floral initiation occurred prior to sprouting in the *A. passeyi* bulbs that were forced early. A shortening of the dormant period in response to cold temperatures was also found in the aerial bulblets of *A. canadense*. This species typically is dormant from July to November, but when exposed to dry air temperatures of 0.5 to 4°C, sprouting began two months earlier. Conversely, sprouting in bulblets in 22°C temperatures occurred two months later than observed in the wild (Krochmal, 1960).

Other New World species reported to exhibit summer dormancy prior to re-sprouting in the cool wet fall season include *A. aaseae* (Prentice, 1988) and *A. tricoccum* (Nault and Gagnon, 1988). Similar fall re-growth patterns are common in Old World species such as Mediterranean *Alliums* in the section *Molium* and *Alliums* in the subgenus *Melanocrommyum* found in the Oriental-Turanic region (Kamenetsky, 1994; Kamenetsky and Rabinoswitch, 2006). It is difficult to ascertain the prevalence of fall-sprouting New World *Alliums* due to the lack of published information. Based on the available literature and the similar geo-climatic habitats occupied by Old World *Alliums* that sprout in the fall, I hypothesize

that this particular annual life cycle is the predominate mode of plant regeneration among *Alliums* found in North America.

Cool temperatures are not always optimal in breaking bulb dormancy in *Alliums*. *Allium schoenoprasum* is unique among North American *Alliums* in that it is native to both the Old World and the New World (Mc-Neal and Jacobsen, 2002). Folster and Krug (1977) demonstrated that a hot treatment of water beginning at 40°C and gradually dropping to 25°C over the course of 16 h stimulated re-growth to occur on dormant *A. schoenoprasum* bulbs. Bulbs exposed to hot humid air between 22 and 36°C for two days similarly produced new vegetative growth in the dormant *A. schoenoprasum* bulbs. The plants used in Fölster and Krugs experiments were from a commercial chive cultivar Grolau and it remains to be seen whether native ecotypes would respond similarly, or even whether Old World and New World *A. schoenoprasum* plants would vary in their dormancy breaking characteristics. However, these results do suggest that dormant plants of this particular species may remain dormant in their natural habitats until warmer spring weather initiates the resumption of vegetative growth.

This discussion would not be complete without examining bulb dormancy characteristics in *A. vineale*. This is likely the most well known wild *Allium* in North America due to its broad distribution and invasive nature. However, *A. vineale* is a non-native naturalized Old World *Allium* species introduced to North America. It is characterized by its prolific production of aerial bulblets which have helped it become a noxious weed that is difficult to control. Krochmal (1960) performed a series of experiments investigating the behavior of bulblets collected in the eastern USA and evaluated their re-growth response to temperature. The bulblets did not sprout when exposed to low temperatures (0.5 and 4°C), but achieved maximum sprouting after two months in a 22°C environment. This behavior can be explained as an adaptive mechanism which favors new plant establishment in early fall giving the plant a higher possibility of survival through the winter months. The growth attained in the fall gives the plant an advantage over other spring species due to its readiness to photosynthesize immediately upon the arrival of favorable temperatures (Duchoslav, 2009).

CONCLUSIONS

What remains clear is that when discussing seed and bulb dormancy in New World *Alliums*, there is more unknown than known. The works summarized in this

review provide some background upon which future New World *Allium* dormancy studies can build. Likewise, there are a number of similar types of experiments that have been conducted on Old World *Alliums* with similar life cycles and existing in similar habitats that can provide useful information for those interested in designing an experiment to examine dormancy characteristics in New World *Allium* species (Kamenetsky, 1994; Gutterman *et al.*, 1995; Kamenetsky and Gutterman, 2000; Zammouri *et al.*, 2008). In designing such a study, I would recommend to take into account the probability of within-species variation in germination and growth characteristics. Through careful examination of the patterns of variability that are likely related to geo-climatic differences between collection sites, we will arrive closer at understanding the underlying mechanisms controlling seed and bulb dormancy in New World *Allium* species.

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