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# The Natural History of Aconitum noveboracense Gray (Northern Monkshood), a Federally Threatened Species

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# The Natural History of *Aconitum noveboracense* Gray (Northern Monkshood), a Federally Threatened Species

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*Aconitum noveboracense* Gray (Ranunculaceae), commonly known as northern monkshood, is a federally threatened herbaceous perennial that occurs in disjunct populations in Iowa, Wisconsin, Ohio and New York. It appears to be a glacial relict, existing today only in unique areas with cool, moist microenvironments, such as algific talus slopes. Field studies reveal that *A. noveboracense* has a complex life history. Perennation of individual plants occurs through the annual production of daughter tubers. Vegetative reproduction is commonly observed, and can occur by means of aerial and subterranean bulbils, as well as by development of adventitious root buds. Populations also reproduce sexually and often produce large numbers of seeds and seedlings, though herbivore damage to inflorescences can sometimes significantly reduce seed production. The seeds possess a high degree of viability and germinate readily when exposed to an appropriate stratification regime. Taken together, these life history traits appear to make *A. noveboracense* populations long-lived and quite resilient to environmental perturbations, thus making the species a promising candidate for recovery through habitat protection.

INDEX DESCRIPTORS: *Aconitum noveboracense*, Ranunculaceae, threatened plant, life history, algific talus slopes, glacial relict

A species' rarity is often paralleled by our ignorance of its basic biology. Thus, while federal laws mandate protection and recovery of threatened and endangered species, the information most needed to design sound preservation and management schemes for them is often lacking. Consequently, the first step in any program to protect a rare species must be to describe its life history, to pinpoint what factors are responsible for its current state of rarity, and then to determine which aspects of the life history contribute most to the longevity of populations and which may serve as indicators of a population's decline (Whitson and Massey 1981; Sutter 1986).

*Aconitum noveboracense* Gray (Ranunculaceae), commonly known as northern monkshood (Fig. 1), provides an excellent example to illustrate this point. It is a rare, herbaceous perennial, restricted in range to recently unglaciated areas in Iowa, Wisconsin, Ohio and New York. On April 26, 1978 it was federally classified as a threatened species under the U.S. Endangered Species Act (43 FR 17916). Listing occurred because of plans by the Army Corps of Engineers to inundate the largest populations of the species then known through construction of the LaFarge Reservoir on the Kickapoo River in Wisconsin. Under the provisions of the Endangered Species Act, a recovery plan was approved in September 1983 (Read and Hale 1983). *A. noveboracense* thus became the first plant species to have an approved recovery plan.

In 1983, little was known about the biology of the species or its distribution. Because the future of a large portion of its known habitat was uncertain, the recovery plan mandated a search for undiscovered populations and that life history research be conducted. The goals of the recovery plan were largely oriented toward mitigation of the possible loss of habitat, and therefore, stressed description of population structure and dynamics, the species' growth requirements and mode of reproduction, and development of reliable seed germination and outplanting techniques.

Since the listing of *A. noveboracense* occurred, the LaFarge Reservoir project has been deauthorized (though this action is not necessarily permanent) and the search for new populations has been unexpectedly successful. Currently, there are 119 known localities for *A. noveboracense*. The largest number of plants have been found in Iowa, followed by Wisconsin, New York and Ohio (Fig. 2). Populations range

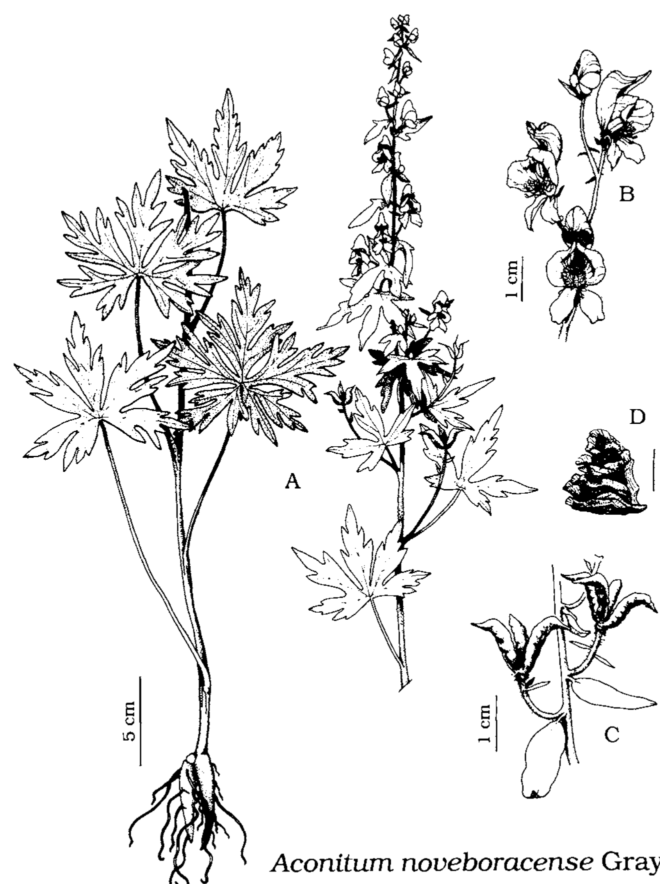


Fig. 1. *Aconitum noveboracense* Gray (Ranunculaceae). This illustration is a composite of several plants. It shows typical leaf form and inflorescence structure (A), as well as flower (B), fruit (C) and seed morphology (D). (Drawing by Kandis Elliot.)

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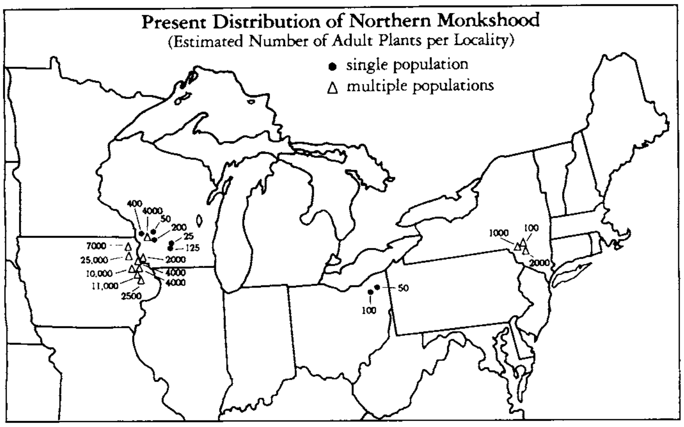


**Fig. 2. The distribution of *Aconitum noveboracense*. The species is confined to recently unglaciated areas. Note that the largest concentration of populations is in the "Driftless Area" of Iowa and Wisconsin. Other populations are found in northeastern Ohio and in the Catskill Mountains of New York.**

in size from as few as eight to as many as 10,000-20,000 adult plants. Approximately one-third of the known populations are currently protected by a federal, state or county agency, or by The Nature Conservancy (unpubl. U.S. Fish and Wildlife Service records).

## ORIGIN AND DISTRIBUTION

Today, *Aconitum noveboracense* is found only in disjunct populations in the northeastern and midwestern United States (Fig. 2). However, during or at the end of the Pleistocene, the progenitor of *A. noveboracense* was probably common along the glacial margin (Brink 1982; Dixon and May 1990; Frest 1986b; Iltis 1965; Iltis et al. unpublished data). As the glaciers retreated *A. noveboracense* was left in the only suitable habitat remaining: unique areas with cool, moist microenvironments, places that are ecologically equivalent to the montane and periglacial environments occupied by other *Aconitum* species (Epling and Lewis 1952; Kadota 1987). This distribution pattern is shared by numerous species in the northeastern United States (Iltis 1965).

In Iowa and Wisconsin, the species is found exclusively on karst topographic features known as algific (cold-producing) talus slopes and maderate cliffs, as described by Frest (1981; 1986b). Frest (1986b) believes that both types of features originated near the end of the Pleistocene during the Wisconsinan glacial maximum (late Woodfordian, ca. 14,500 y.b.p.). He hypothesizes that the close approach of the Des Moines lobe to the Paleozoic Plateau ("Driftless Area") interacted with the presence of a particular lithologic sequence to induce the development of these unique features. Similar processes have been described in current periglacial environments (Black 1965; Palmquist 1965). The bedrock units in which these features developed share common characteristics: a thick-bedded carbonate unit is underlain by a series of thinner carbonates interbedded with other thin, partly impervious layers of shale, bentonite or chert. The whole structure is underlain by a much thicker and more impervious shale unit that cuts the system off from deep groundwater circulation (Fig. 3). Here, the periglacial environment produced mechanical karst features in the bedrock, forming sinks and vertical fissures in the thick carbonate layer and horizontal fissures in the thinly bedded layers. Stream erosion exposed the areas of decomposed bedrock which slumped to form the talus slopes. During the late winter ice forms in the fissures and talus, and is responsible for maintaining the flow of cold air that characterizes these slopes during most of the growing season. Though formed through similar processes, maderate cliffs are steeper than algific slopes. They lack the talus and extensive formations of ice found on algific slopes, but because cold water drips out

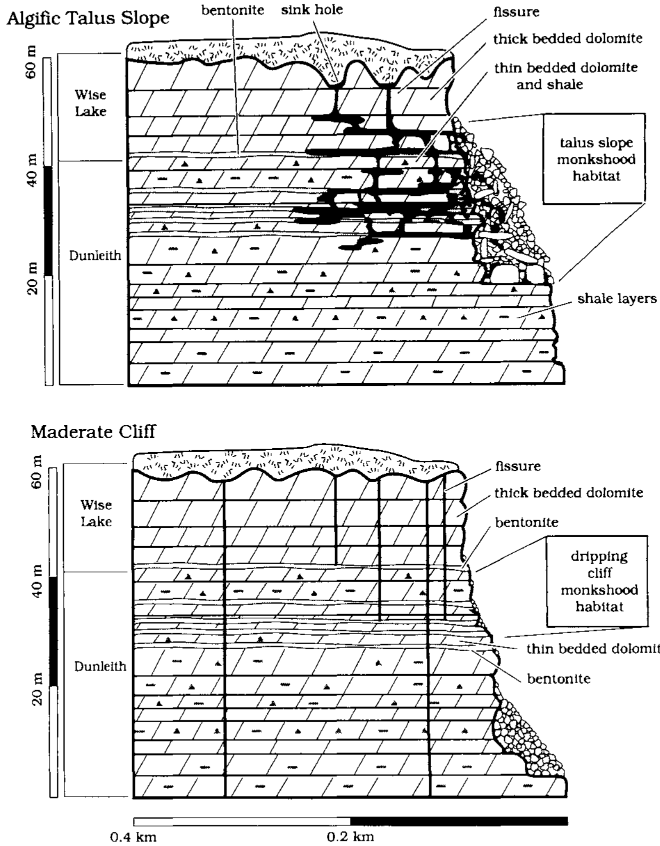


**Fig.3. Cross-sections of an algific talus slope (upper) and a maderate cliff (lower). Note thick layers of calcareous rocks overlying thinner layers that are interbedded with shales and bentonites, all underlain by impervious shale layers. The system includes sinkholes on the uplands and vertical and horizontal fissures along joints and bedding planes. Talus and accumulated soil covers the face of the algific talus slope. Ice forms in the talus, and in the horizontal fissures behind it, and provides refrigerated air flow out of the slope face during the growing season. Maderate cliffs are steeper and lack the talus and extensive ice formation of algific slopes. Instead, cold water seeps out of the cliff face at the contacts of the calcareous units and the shales or bentonites. (Adapted from Frest 1986b.)**

of the face of the cliff at the contacts between the thin carbonates and shale or bentonite layers, they maintain a similar microenvironment. Because the formation of algific talus slopes and maderate cliffs required a unique combination of climatological and geologic conditions, they represent a very rare habitat type.

*A. noveboracense* populations in Ohio occur on sandstone cliffs that are similar to those in Wisconsin (Read and Hale 1983; and unpubl. revision 1988). In contrast, the majority of populations in New York are found on gravel beds, cobble point-bars, and moss covered rocks along creeks that have their headwaters on Double Top Mountain in the Catskill Mountains. However, several additional populations in New York are found on sandstone cliffs (Dixon and May 1990).

*A. noveboracense* shares its unique habitat with many other state and federally protected species; some of which are federally listed or are candidates for listing. These include the plants *Sullivantia sullivantii* (T. & G.) Britton and *Chrysosplenium iowense* Ryberg, and numerous snails, such as *Discus macclintocki* Baker, *Vertigo spp.*, *Succinea chittenangoensis* Pilsbury and *Catinella gelida* Baker, some of which were known previously only from the fossil record (Frest 1986a; 1987).

## LIFE HISTORY OF *ACONITUM NOVEBORACENSE*

Much study of the life history and population dynamics of *A. noveboracense* has occurred since its listing in 1978 (Cervelli 1986; Dixon and Cook 1990; Kuchenreuther et al. 1986; Kuchenreuther 1991; Whitson et al. 1986). The findings of these studies are summarized below, with special reference to populations in Iowa and Wisconsin.

### Habitat Requirements

As described above, *A. noveboracense* inhabits a narrow range of habitats that are geologically unique. What precisely it is about this habitat that is critical for the maintenance of these populations in not clearly understood.

From continuous recordings of air temperatures at the Kickapoo River populations in Wisconsin, we established that daily maximum temperatures in July and August were significantly lower at the study sites (23.0 - 25.5° C) than at the two nearest NOAA reporting stations (28.5° C) (Kuchenreuther et al. 1986). Conversely, daily minimum temperatures were significantly higher on these sites (17.5° C) than at the weather reporting stations (15.5° C). Similarly, the recordings established that air temperatures directly adjacent to plants averaged 1.4 - 2.5° C below those measured away from the microsite. Therefore, it appears that cliff-dwelling *A. noveboracense* populations experience cooler than average temperature in the summer, as well as smaller than average fluctuations in daily temperature range.

Relative humidity readings made concurrently with the temperature measurements revealed that humidity levels rarely dipped below 50% and were usually higher than 80%.

Soil temperatures in the Kickapoo populations were equal to or only slightly below those on the adjacent floodplain. However, soil temperatures in algific slope populations can be as much as 15° C below temperatures off-slope (Kuchenreuther 1991).

Dixon and Cook (1990) measured the physical environment of *A. noveboracense* along streams in New York state. They found considerable variation among sites, though all were characterized as moderately acid with generally low nutrient availability. They also found that all sites remained moist throughout the growing season but this was not significantly different from the conditions measured in the adjacent forest. They did not measure soil or air temperatures.

Temperature and moisture probably interact to produce a favorable microclimate for *A. noveboracense* establishment and survivorship. Laboratory experiments have demonstrated that seedlings are very sensitive to desiccation (Kuchenreuther et al. 1986). Unless the substrate in which they were grown remained continuously moist, mortality was high. This observation was made in an experiment designed to investigate the influence of cool soil temperatures on plant growth. Plants growing at the highest soil temperature (24° C versus 13° C and 17° C) had significantly greater root and shoot biomass at the end of the experiment than those in the cool treatments, but survivorship was poor. We attributed this high mortality to the difficulties encountered in keeping the soil moist in the warmest treatment. This observation suggests that it is not cold substrate temperature, *per se*, that controls where seedlings can establish, but that cold temperatures act to produce the high soil and atmospheric moisture conditions that are critical for *A. noveboracense* establishment.

Adult plants seem to be somewhat less sensitive to environmental conditions and can be grown in garden situations, though they have never successfully reproduced there (R. Read, T. Kessenich, WI DNR, pers. comm.). Plants can also be grown in a greenhouse, but often develop unusual morphologies, such as stunned growth and abnormal leaf shape (pers. obs.). Outplanting to cliff sites that did not have existing populations has been attempted and was not considered a success (WI DNR, pers. comm.).

### Plant Morphology

*A. noveboracense* plants can be readily classified into three stage categories based upon stature and leaf morphology. Seedlings are first-year plants bearing cotyledons. They rarely produce true leaves in their first year and the cotyledons persist through the end of the growing season. Juveniles are non-reproductive plants of indefinite age and are characterized by thin, lax stems, and small to medium-sized leaves with round or pointed lobes. Adults are potentially reproductive plants generally having robust, erect stems, and large leaves with pointed lobes.

### Perennation and Vegetative Reproduction

Brink (1975) made detailed morphological and anatomical observations of the means by which California populations of the closely related *Aconitum columbianum* Nutt. in T. & G. perennate and vegetatively reproduce. His descriptions, for the most part, also accurately describe *A. noveboracense* (Cervelli 1986).

*A. noveboracense* plants overwinter as tubers. In the spring, a bud at the apex of the tuber breaks dormancy and rapidly produces a tight cluster of leaves. Dissection of laboratory-grown plants revealed that these leaves are preformed in the bud, making rapid expansion possible (Dixon and Cook 1990). In early summer, the internodes elongate and produce a single stem. By this time each parent tuber has also begun production of at least one daughter (collateral) tuber. By mid-season, the parent tuber begins senescence and an abscission zone develops between the stem and the tuber. New collateral tubers remain dormant during their first summer, then overwinter and produce the next year's shoot (Fig. 4).

Vegetative reproduction in *A. noveboracense* occurs through development of subterranean bulbils and aerial bulbils on the stem, and by adventitious root buds. Bulbils form as bipolar axillary buds that can produce both root and shoot meristems.

Non-destructive excavation of several plants in the Kickapoo Valley (Cervelli 1986; Kuchenreuther et al. 1986) revealed that tubers are often set several centimeters beneath the soil surface. Because the first few internodes of the stem are relatively short, at least the first node of the stem is buried and often produces a subterranean bulbil. Excavations in Wisconsin populations revealed as many as four below-ground nodes with bulbils. These subterranean bulbils usually produce large tubers and a shoot apex with a white, waxy appearance. In the fall, with senescence of the parent stem, the tubers produced in this manner lose their connections with each other and become independent stems (Fig. 4). Development of large numbers of subterranean bulbils would explain the clustering of stems observed in some populations (Kuchenreuther 1991).

The production of aerial bulbils was observed, to greater or lesser degree, in nearly all the *A. noveboracense* populations examined in Iowa and Wisconsin, but was not mentioned by Dixon and Cook (1990) in their discussion of New York populations. Bulbils are borne in leaf axils on the lower to middle above-ground nodes of the plant and seem to be produced in greatest abundance after the middle of the growing season (pers. obs.). They can be distinguished from ordinary axillary buds by their white, waxy appearance. Unlike bulbils observed in California populations of *A. columbianum* (Brink 1975), they do not appear to be deciduous, and seem to be capable of forming independent plantlets only after they make soil contact. In this way, they resemble the bulbils of *Aconitum uncinatum* L. (Brink 1982).

Brink (1975) used the presence or absence of bulbifery to separate California populations of *A. columbianum* into two subspecies. In the Midwest, the degree of bulbil production showed more of a continuum, and seemed to be correlated with differences in environmental conditions among populations. Bulbils were found more often in populations with the lowest substrate temperatures (Kuchenreuther 1991), and in riverside populations that are most susceptible to inundation by flood waters (Kuchenreuther et al. 1986). Whether the observed variation is genetically based, or is a plastic response to the plants' environment, is unknown.

In both the field and the laboratory there have been instances where a plant bearing a single true leaf has appeared at some distance

(5 to 25 cm) from other plants. This phenomenon was first noticed on a plant growing in a growth chamber (Kuchenreuther et al. 1986). An individual plant growing in sterile soil mix in a plastic pot had been placed on a bed of vermiculite and allowed to grow for several months. A single true leaf appeared in the vermiculite about 17 cm from the pot. The plant in the pot had not flowered, nor had any other plants in the chamber. Careful excavation revealed that this single leaf had its own tuber and was unconnected to its suspected parent, though the larger plant had numerous roots that had grown out of the bottom of the pot and into the vermiculite. During exploratory soil excavations by Cervelli (1986) at the Weister Creek site in the Kickapoo Valley, two distinct root swellings were found on long lateral roots growing from a large tuber. The internal anatomy of the swellings showed the development of supernumerary cambia, a precursor of endogenous root development (Esau 1977). If these adventitious root buds give rise to new tubers, the lateral connection to the parent must senesce quickly. Excavation of small single or collateral tubers bearing single true leaves has never shown them to be connected to other plants. However, the small tubers often showed scars or what appeared to be roots with senescent ends. These may have been the remnants of an earlier connection with a parent plant.

During the course of demographic studies in Wisconsin, plants that were neither marked nor mapped in the previous year sometimes appeared in the permanent quadrats (Kuchenreuther et al. 1986). These plants were usually small juveniles, bearing one to several true leaves, but no cotyledons, implying that they must have arisen through vegetative reproduction, either from rooting of aerial bulbils or from adventitious root buds. The appearance of these plants has also been noted in Iowa (Kuchenreuther 1991) and New York (Dixon and Cook 1990).

### Sexual Reproduction

Pollination — Whitson et al. (1986) studied the pollination biology of *A. noveboracense,* extending the work of Leppik (1964), Macior (1974) and Pyke (1974, 1978a, 1978b), all of whom worked on *A. columbianum*. Bumblebees (*Bombus* spp.) are the most important pollinators. They are attracted by the large, blue, zygomorphic flowers, comprised of petals that are modified to form nectaries and concealed inside a hood formed by modified sepals (Fig. 1). Though visitations by hummingbirds and hawkmoths have been observed, their role as pollinators has not been verified. Whitson et al. (1986) recorded detailed phenological observations and manipulated flowers to describe the breeding system of *A. noveboracense.*

Mature plants commonly develop a single, terminal raceme or panicle, however, large plants may also produce secondary racemes from the upper nodes of the stem. Inflorescenses are indeterminate and flowers mature acropetally. Because of this developmental pattern, large plants may bear many flowers and bloom for over 60 days. Nectar production begins at anthesis. Flowers are protandrous, with stamens maturing centripetally before the emergence and split of the pistil apex to expose receptive stigmatic lobes. The acropetal foraging pattern of *Bombus* spp. promotes outcrossing as the bees visit the lower, functionally female flowers of an individual first, then move upward to the functionally male flowers, before flying to another plant. The data of Whitson et al. (1986) suggest that apomixis is not common in *A. noveboracense*, though it has been observed in *A. columbianum* (Pyke 1974). In 1988, I manipulated flowers in four populations in Iowa by bagging them with nylon mesh before anthesis and found that no viable seeds were set.

Because the seeds lack adaptations for effective long-distance dispersal (see below), pollen flow is the most likely mechanism of genetic exchange among adjacent populations, at least in the Midwest.

Flower and Fruit Production — Most of the Midwestern populations sampled produced large numbers of flowers. The flowers and fruits of most plants were three-carpellate (though one-, two- and

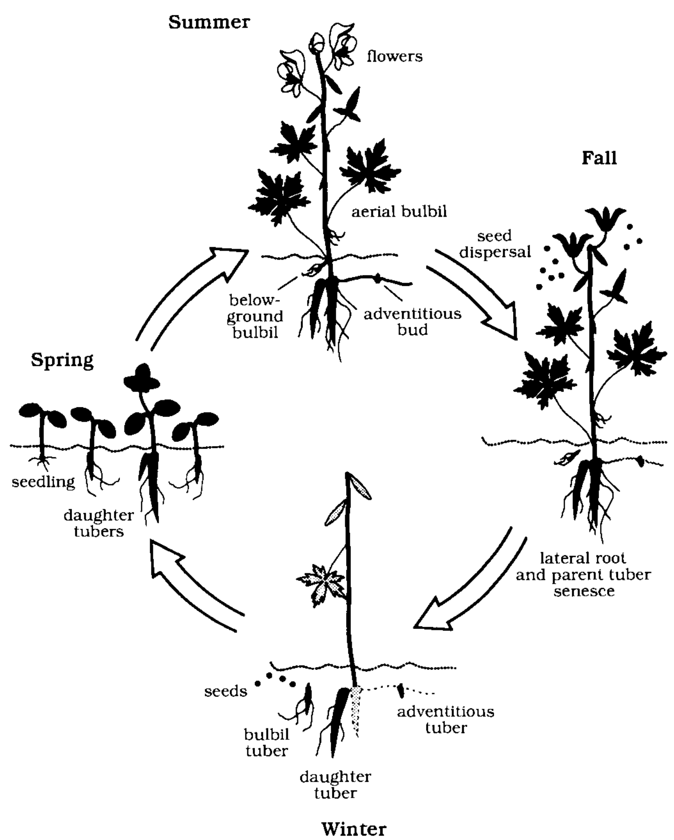


Fig. 4. Diagrammatic outline of the life history of *Aconitum noveboracense. A. noveboracense* perennates from a tuber. In early spring, a cluster of leaves, separated by very short internodes, emerges from each tuber. In early summer, the internodes elongate and produce a single stem. By this time each parent tuber has also begun production of at least one daughter tuber. Daughter tubers remain dormant during their first summer, then overwinter and produce the next year's shoot.

Depending upon locality, flowering can begin as early as June or as late as the end of July or early August. The inflorescence is an indeterminate raceme or panicle of protandrous flowers. After flowering, seeds are gravity dispersed from ripe follicles.

*A. noveboracense* can also reproduce vegetatively, by the production of bulbils and adventitious root buds. Plants often produce bulbils in the axils of lower leaves or at nodes located below ground. Bulbils are axillary buds that bear both shoot and root apical meristems. Above-ground bulbils are stimulated to produce tubers when they come in contact with the soil. Below-ground bulbils have been observed to produce large tubers. Adventitious buds on lateral roots have also been observed to initiate tubers.

Late in the season, parent tubers, roots and all above ground plant parts begin senescence, leaving only the daughter tuber and tubers produced by bulbils or adventitious buds to overwinter. All tissue connections between tubers and the parent plant are lost. In the spring each independent tuber forms leaves and begins to produce its own daughter tuber. Concurrently, seeds germinate, often giving rise to large numbers of seedlings.

four-carpellate fruits have also been observed; with carpel number often decreasing acropetally). At maturity, the fruits (follicles) dehisce at the apex, and as time passes, along the margins as well. Except under stressful environmental conditions (Kuchenreuther 1991), each carpel produces from 10-15 seeds.

Seed Biology — Examination of *A. noveboracense* seeds has shown no obvious adaptation for dispersal. The seeds are light (0.6-0.7 g.) and bear membranous outgrowths of the seeds coat (Fig. 1). Capelletti and Poldini (1984) noted that in European aconites these outgrowths improve floating ability and suggested that they may imbibe water to provide optimum moisture conditions for seed germination. In some populations plants grow where their stems hang directly over water (pers. obs.) so there is no doubt that the potential for dispersal by water exists. This may be a factor in establishment of plants along streams in New York habitats (Dixon and Cook 1990). However, because cliff ledges and algific slopes are commonly perched some distance above water level, water borne seeds must rarely reach "safe sites" to colonize new cliff ledges or algific slopes, except perhaps during extreme high water periods. Consequently, in some populations, a large portion of the seed crop is lost because seeds fall into unfavorable habitats.

Production of large numbers of seeds and seedlings was observed annually in many of the populations that have been studied, although the New York populations studied by Dixon and Cook (1990) and some Iowa populations (Kuchenreuther 1991) were observed to produce few seedlings. Laboratory and field germination trials have shown generally high seed viability. In two out of three years, laboratory germination trials produced in excess of 80% germination by seeds that had received nine to twelve weeks of warm, moist stratification (17° C), followed by six weeks of cold stratification (-5° C) (Cervelli et al. 1986). Dissections of stratified and unstratified seeds revealed that embryos were not fully developed at the time of dispersal, but matured during the warm stratification period (pers. obs.). This germination syndrome is common in the Ranunculaceae (Grushvitzky 1967; Martin 1946) and has been classified as deep, simple morphophysiological dormancy (Baskin and Baskin 1989).

Field germination trials, in which seeds were sown into apparently favorable, but unpopulated, locations adjacent to populations in the Kickapoo valley, produced results that parallel the laboratory trials (Kuchenreuther et al. 1986). Of 200 seeds sown in September 1984, 125 germinated the following spring. However, only 18 of 800 seeds planted in 1985 germinated in the spring of 1986. This was the same crop of seeds that produced poor germination results in the laboratory, suggesting that drought stress (observed in summer 1985), might have adversely affected the viability of seeds in that year.

*A. noveboracense* populations probably possess little or no seed bank. The high germination rate of seeds in the laboratory supports this contention, as does extended observation of the field germination trials. After the first spring, only one new seedling was found in the experimental gardens, though 75 seeds presumably remained after the original flush of seedlings. Observations by Dixon and Cook (1990) in both the field and in greenhouse seed bank experiments, further support this assessment.

### Herbivory

*A. noveboracense* plants are routinely attacked by herbivores, resulting in removal of leaf area, and/or removal of all or part of the terminal inflorescence of adult plants. In some populations the damage was extreme, with up to 70% of plants suffering removal of over half of their leaf area. Herbivore damage often reduced or completely eliminated seed production by mature plants (Kuchenreuther 1991).

Several organisms were probably responsible for the damage observed. Snails and slugs were common in the moist substrate at the base of plants and probably accounted for some damage, especially to the leaves of small plants. Grasshoppers were also present at several sites, especially during the drought year 1988, and may have also inflicted damage. Herbivory by deer may have occurred also. It is common for populations on algific slopes to be bisected by deer trails, however, casual observation did not suggest a greater incidence of herbivory near these trails. In fact, damage to leaves and inflorescences of apparently similar type has been observed among plants on cliff ledges that would be inaccessible to deer. Whether the alkaloids present in *A. noveboracense* (Read and Hale 1983) make the plant unpalatable to deer is unknown.

The organism most likely to have been responsible for the majority of damage to both the leaves and inflorescences of *A. noveboracense* is the larva of the noctuid moth, *Platypolia anceps.* Larvae were found occasionally on damaged plants and, more commonly, in the litter at the base of plants. One of the larvae was captured and reared in the laboratory on a diet of *A. noveboracense* leaves (Kuchenreuther et al. 1986). The adult was identified by R.W. Poole of the Smithsonian Institution (pers. comm.). During the course of rearing the larva it was observed to feed only at night, and could completely devour several large leaves during each feeding session. This observation supports the conclusion that *Platypolia* is probably responsible for much of the damage observed. Its secretive behavior may explain why Dixon and Cook (1990) did not mention it, invoking instead the impact of deer .

## CONCLUSIONS

Approval of the federal recovery plan for *Aconitum noveboracense* provided the impetus for life history studies of this rare and previously poorly known species. In the last decade, through the efforts of many researchers, much has been learned about its distribution, the characteristics of its unique habitat, its autecology, and strategies to promote its protection.

*A. noveboracense* is a species that is rare, but often locally abundant. Its populations appear to be relicts from the Pleistocene, when its progenitor species may have been widespread in the periglacial environment. As the glaciers retreated, populations persisted in disjunct localities where the microenvironment remained favorable for it. In the Midwest, these localities are rare geologic features known as algific talus slopes and maderate cliffs which are thought to have also originated during the late Pleistocene. Thus, the number of sites that can now support *A. noveboracense* is finite. Suitable habitat can be expected to decline over time due to continuing (though slow) erosion of these features, and through anthropogenic disturbance of the habitat by activities such as grazing, logging, powerline maintenance and highway construction. Simple acquisition of populations or negotiation of conservation agreements with landowners can do much to remove this second class of threats to the species.

The life history of *A. noveboracense* has proven to be complex. Plants reproduce both from seed, and vegetatively by the production of subterranean and aerial bulbils, and root sprouts. The degree to which each mode of reproduction is important in a given population may be genetically determined or may depend on the local environment in a complex and, as yet, not completely understood way.

Given our current understanding, the prospects for long-term conservation of the species are encouraging. A large number of new populations of *A. noveboracense* have been discovered, and the Driftless Area National Wildlife Refuge system has been established to protect it and the other rare species with which it occurs.

Most *A. noveboracense* populations (at least those in the Midwest) produce large numbers of seeds. In the event that the augmentation of existing populations or the establishment of new populations becomes necessary, transferring seeds would be a simple, and potentially effective method that would have a negligible effect on the donor population(s). Anthropogenically degraded talus slopes (of which there are many) might be restored using this method, though several attempts might be necessary before establishment of a new population was achieved, since we still lack complete understanding of the environmental requirements of the species. Refinement of a seed germination protocol further enhances the recovery potential of the species by making it possible to produce large numbers of seedlings for experimental studies, outplanting, or *ex situ* conservation efforts.

*A. noveboracense's* perennial habit, and its considerable potential for vegetative reproduction, make it resilient (*sensu* Brussard 1985) to environmental perturbations, and are perhaps the key factors that promote its persistence. Since observation of these populations began, this capacity has been expressed frequently. When drought made the growing season stressful, plants became dormant until the following year (Kuchenreuther 1991). When herbivores reduced the capacity to reproduce sexually, vegetative reproduction continued. When flood waters knocked plants over and covered them with silt, bulbils rooted and formed new stems (Kuchenreuther et al. 1986). Because of this resilience, environmental stochasticity might be expected to temporarily reduce population size or reproductive output, but would be unlikely to lead to population extinction, except in the very smallest populations. Thus, given adequate protection from human disturbance, *Aconitum noveboracense* appears to be a promising candidate for successful recovery.

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