

Cardamine maxima

Large Toothwort

Brassicaceae



Cardamine maxima by Tomás Curtis, 2020

***Cardamine maxima* Rare Plant Profile**

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
State Forest Fire Service & Forestry
Office of Natural Lands Management
New Jersey Natural Heritage Program

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Life History

Large Toothwort (*Cardamine maxima*) is a perennial member of the Brassicaceae (Mustard family). It is rhizomatous, with cylindrical rhizomes 3–6 mm in diameter. Each rhizome is “jointed”, having conspicuous constrictions at intervals along its length. The stems are unbranched and erect, growing 9–30 or 40 cm in height. There are usually three (rarely two) alternate petiolate stem leaves and each of these is divided into three leaflets. Leaf margins are coarsely toothed or with minute hairs that are 0.2–0.3 mm long and spreading. Basal leaves are similar (Al-Shehbaz et al. 2023; Britton and Brown 1913; Gleason and Cronquist 1963; MNAP 2021; Native Plant Trust 2023; WIDNR 2022).

The flowers of Large Toothwort are four-parted, bell-shaped, thin and delicate, and short-racemose. White, pink or pale purple in color, they are about 10–17 x 3–6 mm wide and much longer than the sepals (Al-Shehbaz et al. 2023; Britton and Brown 1913; MNAP 2021, WIDNR 2022). In New Jersey the flowers bloom in late April or early May (Snyder 1994); however, elsewhere in its range it may bloom through early June (Al-Shehbaz et al. 2023; WIDNR 2022). Seeds are produced in dried capsules (siliques) 2–4 cm long with an elongated beak of 6–8 mm (Gleason and Cronquist 1963).

The closely related *C. diphylla* has white flowers with two opposite, three-parted leaves whose margins are glabrous/scabrous, and the rhizome is not constricted into joints (Newcomb 1977; WIDNR 2022). *C. concatenata* has heavily dissected leaves that appear in a whorl; the rhizomes are narrowly jointed (linked together like a string of beads) and readily break apart (Wisconsin Horticulture Division of Extension 2023). The upper stem is usually downy (vs. *C. maxima* where the stem is glabrous) (Al-Shehbaz et al. 2023; Native Plant Trust 2023).



Left: Britton and Brown, 1913, courtesy USDA NRCS 2022a. Center: Ross D. Dickson, 2017. Right: Jeff Poloni, 2018.

It is unclear whether Large Toothwort produces viable seed or whether it only spreads vegetatively through rhizomal growth. In some areas it is considered a fertile hybrid, though the

resulting fruits/seeds are sometimes sterile (MNAP 2021). According to Al-Shehbaz et al. (2023), because mature fruit or seeds from *Cardamine maxima* have not been observed, many taxonomists believe it is a sterile hybrid between *C. concatenata* and *C. diphylla*. However, Sweeney and Price (2000, 2001) found that *C. maxima* differs molecularly and morphologically from those two species; for these reasons, and due to its wide distribution, the Flora of North America currently recognizes *C. maxima* as a distinct species.

Pollinator Dynamics

There is no information in the literature about pollination in Large Toothwort. Related species such as *C. bulbosa* (Bulbous Bittercress) and *C. douglassii* (Limestone Bittercress) are visited by an array of insect pollinators. Visiting insects include long-tongued bees (e.g., Apidae, Anthophoridae and Megachilidae) and short-tongued bees (e.g., Halictidae, Colletidae, and Andrenidae). Also visiting are flies (e.g., Stratiomyidae, Syrphidae, Empididae, Bombyliidae, Conopidae, Calliphoridae and Fanniidae) and butterflies and skippers (e.g., Nymphalidae, Lycaenidae, Pieridae and Hesperidae) (Hilty 2020). There is also a specialist bee (*Andrena arabis*) that will visit most *Cardamine* in the region, including *C. maxima* (Fowler 2016). The West Virginia White butterfly (*Pieris virgeniensis*) also relies on *Cardamine* with *C. diphylla* as the primary larval host plant, although *C. concatenata* is occasionally used as is *C. multifida* (Schweitzer et al. 2011). There was one report of *C. maxima* possibly serving as a host plant for the larvae of this declining butterfly species at Howard Falls George, Pennsylvania (Howard 2021). (Larval host plant or not, the adult butterflies may also visit *C. maxima* for nectar.) Although *Cardamine maxima* is considered predominantly sterile, pollen is produced and would be transferred from plant to plant by visiting pollinators but ensuing pollination would not necessarily contribute to viable seed production. See Seed Dispersal for further discussion.

Seed Dispersal

Typically, in *Cardamine*, once the seed capsules (siliques) dry out, they split open to release the seeds. However, some *Cardamine* species are considered sterile. Montgomery (1955) found that although pollen in *D. diphylla* (= *Cardamine diphylla*), *D. laciniata* (= *C. concatenata*), and *D. maxima* (= *C. maxima*) did mature, the siliques did not fully mature to produce viable seeds and instead contained aborted ovules. Even with careful hand pollination of those species, viable seeds were not produced in the studies he conducted. However, more recent observation and research has found that *C. diphylla* and *C. concatenata* do produce seedlings and that sexual reproduction may still occur in those species (Sweeney and Price 2001 and references therein).

Although *Cardamine maxima* does produce seed pods, the seeds have not been found to be viable and it does not appear to set seed in nature. Considered “largely or entirely” sterile, instead, it reproduces vegetatively through rapid rhizomal growth in early spring and at flowering time (Al-Shehbaz et al. 2023; Gleason and Cronquist 1963; Montgomery 1955; Sweeney and Price 2001). In part for this reason, there is little to no information about seed dispersal or viability in the literature for *C. maxima*, although the seeds of the closely related *C. concatenata* and *C. diphylla* are reported to lose viability rapidly when stored (North Carolina

Cooperative Extension 2023). While *Cardamine maxima* does spread by rhizomal growth, it does not produce bulbils or bulblets (Native Plant Trust 2023). Some members of the Brassicaceae family (e.g., Lake Cress [*Neobeckia aquatica*]) are known to readily disperse via rhizome fragments in their aquatic habitat (Les et al. 1995); however, it is not known whether *C. maxima* or other closely related *Cardamine* can disperse longer distances in wetter sites in this manner.

Habitat

There is only one extant population of *Cardamine maxima* in New Jersey (NJNHP 2022). It is found in a deep ravine along the banks and on the narrow floodplain of a small flowing stream. As reported by Snyder (1994), the plants were growing in a mixed deciduous forest with a canopy of Sugar Maple (*Acer saccharum*), American Sycamore (*Platanus occidentalis*), and Eastern Hemlock (*Tsuga canadensis*). Other native herbaceous species at the site included Jack-in-the-Pulpit (*Arisaema triphyllum*), Skunk-Cabbage (*Symplocarpus foetidus*), False Solomon's Seal (*Maianthemum racemosum*), American Trout Lily (*Erythronium americanum*), Crinkleroot (*Cardamine diphylla*), and Perfoliate Bellwort (*Uvularia perfoliata*).

Range wide, Large Toothwort is found in rich soil of riparian and mesic upland forests, along wooded streams, in ravines, or on calcareous wooded slopes (hardwood to mixed forest), in shade to part shade (MNAP 2021; Native Plant Trust 2023; PNHP 2012; WIDNR 2022). New Hampshire populations have been found on rocky ridges and cliff and talus slopes (NHWAP 2015). Bouchard et al. (1983, cited in Higman and Penskar 1999) reported the plant from “wet maple stands”. *Cardamine maxima* is considered a Rich Mesic Forest indicator species in western Massachusetts and is reported to have a “near exclusive association with primary forest” in part due to its limited ability to recolonize secondary forests (Bellemare et al. 2002).

Many of the Brassicaceae are not considered to have mycorrhizal associations and of the nine *Cardamine* species that were reviewed by Wang and Qiu (2006) only three species (*C. bulbifera*, *C. flexuosa*, and *C. hirsuta*) were considered facultatively mycorrhizal, exhibiting an association with arbuscular mycorrhizal only in some habitats. The remainder, including the closely related *Cardamine concatenata* were nonmycorrhizal. Although *Cardamine maxima* was not included, it is unlikely that the species has any strong mycorrhizal relationships that would have implications for conservation, restoration, or management.

Wetland Indicator Status

Cardamine maxima is a facultative upland species, meaning that it usually occurs in nonwetlands but may occur in wetlands (USACE 2020).

USDA Plants Code (USDA, NRCS 2022b)

CAMA36

Coefficient of Conservatism (Walz et al. 2018)

CoC = 9. Criteria for a value of 9 to 10: Native with a narrow range of ecological tolerances, high fidelity to specific habitat conditions, and sensitive to anthropogenic disturbance (Faber-Langendoen 2018).

Distribution and Range

The global range of *Cardamine maxima* is restricted to the eastern United States and Canada. The map in Figure 1 depicts the extent of Large Toothwort in North America.

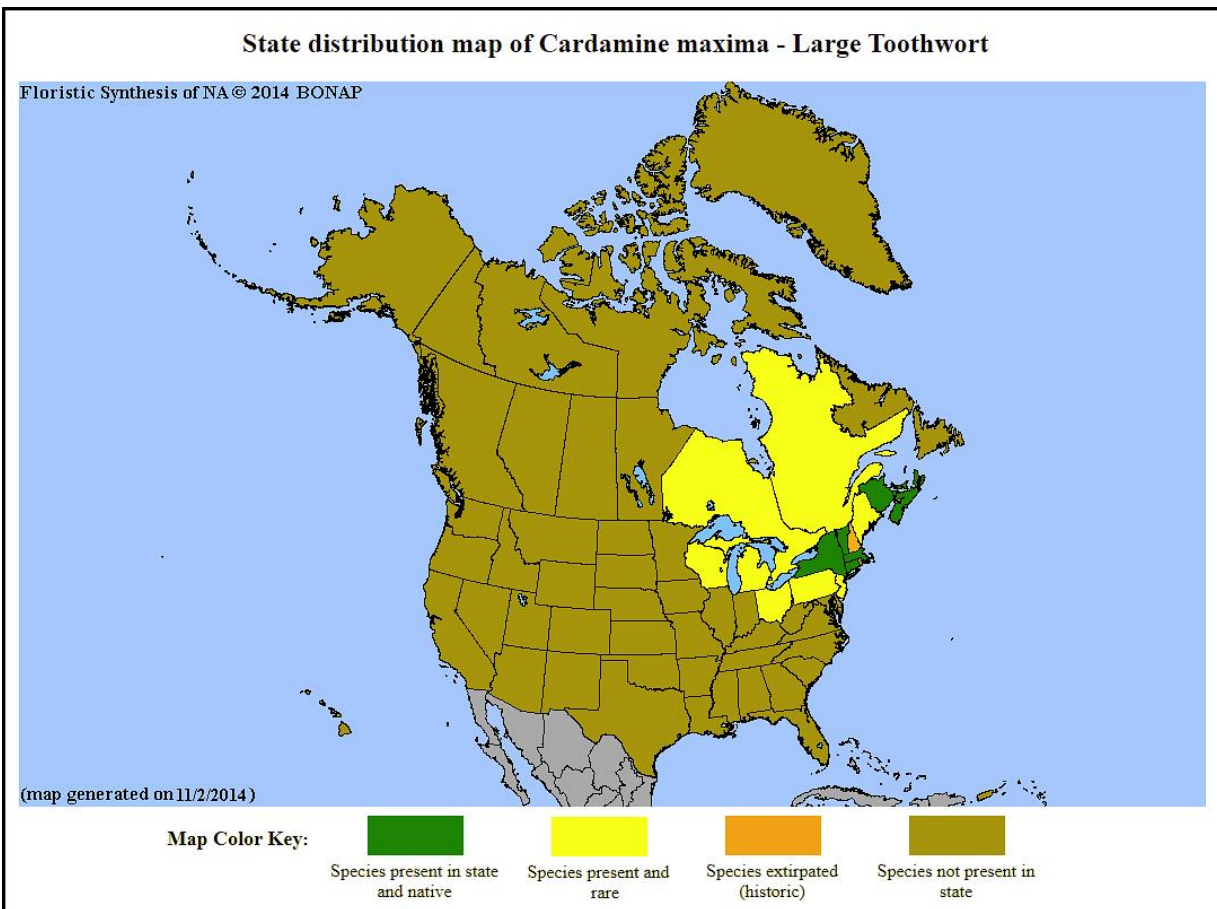


Figure 1. Distribution of *C. maxima* in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2022b) shows records of *Cardamine maxima* in four New Jersey counties: Hunterdon, Mercer, Somerset, and Sussex (Figure 2 below). However, no documented records of the species' occurrence outside of Sussex County were found, and only one population has been confirmed in the state (NJNHP 2022).

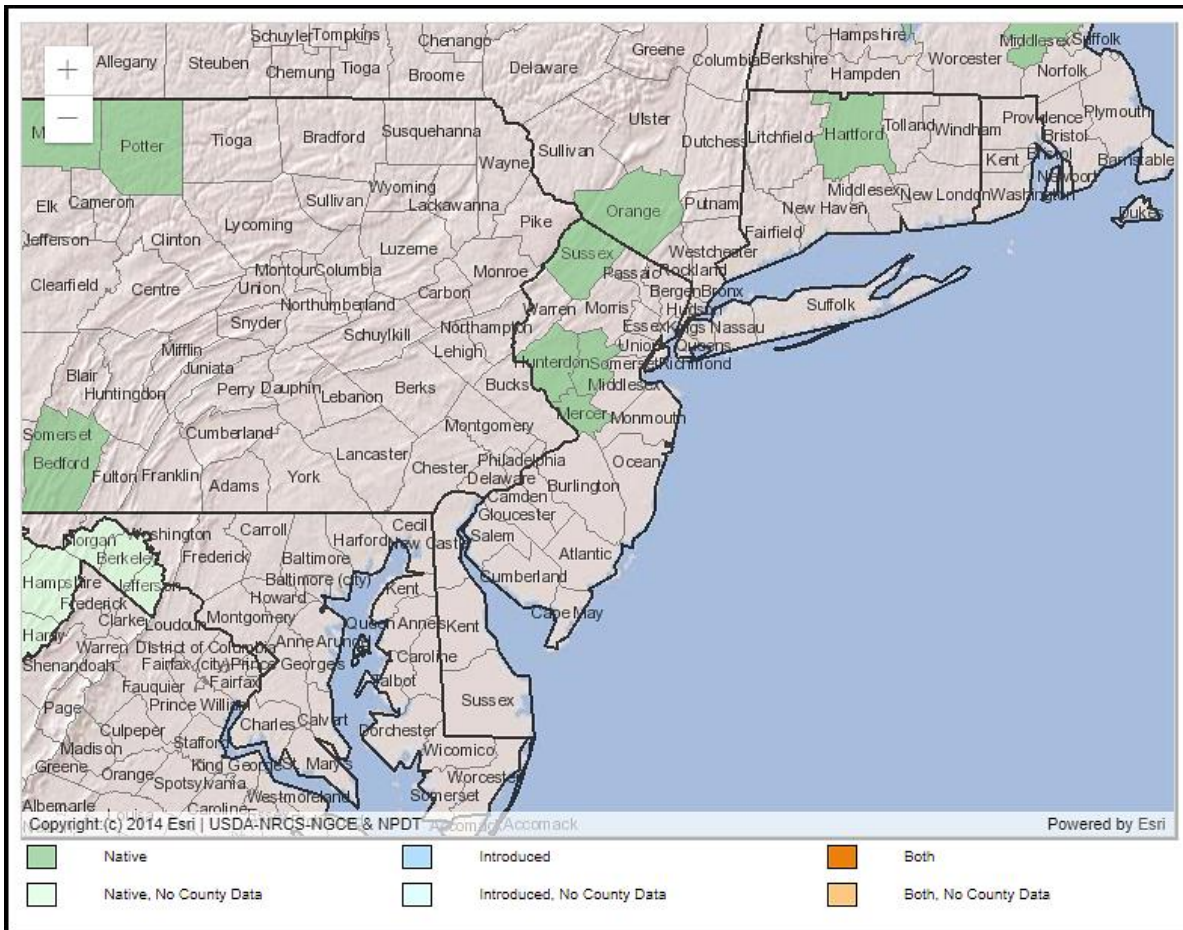


Figure 2. County records of *C. maxima* in New Jersey and vicinity (USDA NRCS 2022b).

Conservation Status

Cardamine maxima is considered globally secure. The G5 rank means the species has a very low risk of extinction or collapse due to a very extensive range, abundant populations or occurrences, and little to no concern from declines or threats (NatureServe 2022). The map below (Figure 3) illustrates the conservation status of *C. maxima* throughout its range. Large Toothwort is not considered secure anywhere in Canada, and the species has been ranked as apparently secure in only one state (New York), although it is unranked in two other states where it occurs.

Cardamine maxima is critically imperiled (very high risk of extinction) in three states and one province, imperiled (high risk of extinction) in four states and one province, and vulnerable (moderate risk of extinction) in one state and three provinces. Imperiled or critically imperiled populations, including those in New Jersey, are located at the western, southern, or easternmost edges of its range. According to Montgomery (1955) *Dentaria maxima* (= *C. maxima*) is entirely found within the range of the Wisconsin glaciation—centered in New York State and north into Ontario and Quebec.

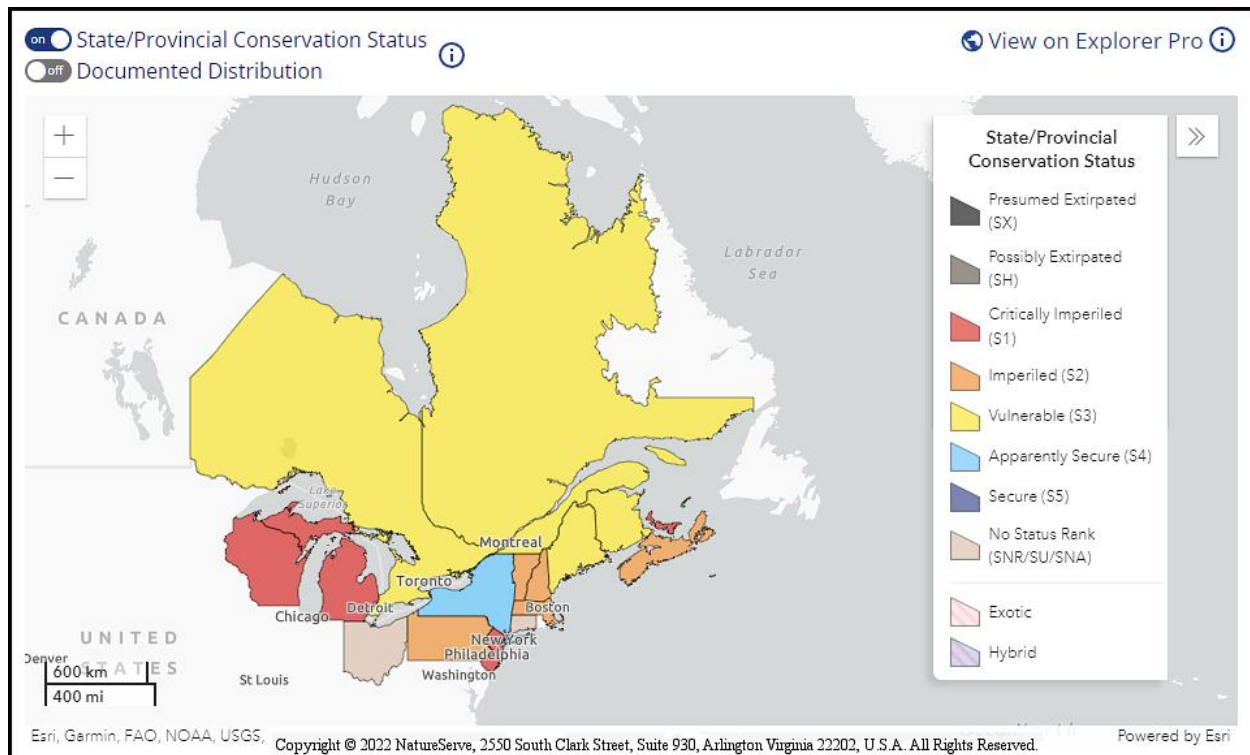


Figure 3. Conservation status of *C. maxima* in North America (NatureServe 2022).

Cardamine maxima is ranked S1.1 in New Jersey (NJNHP 2022), meaning that it is critically imperiled due to extreme rarity. A species with an S1.1 rank has only ever been documented at a single location in the state. *C. maxima* is also listed as an endangered species (E) in New Jersey, meaning that without intervention it has a high likelihood of extinction in the state. Although the presence of endangered flora may restrict development in certain communities such as wetlands or coastal habitats, being listed does not currently provide broad statewide protection for the plants. Additional regional status codes assigned to *C. maxima* signify that the species is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Threats

In New Jersey, invasive species were the only threat noted. Snyder (1994) specifically mentions Garlic Mustard (*Alliaria petiolata*) as being “ubiquitous” at the site and a 2008 site visit record (NJNHP 2022) mentions that invasive species had moved into the *Cardamine* population at that time. Although notes from the most recent site visit in 2013 indicated that there appeared to be fewer *Cardamine maxima* individuals than in past years, there was no specific threat (e.g., herbivory, disease) associated with this perceived decline (NJNHP 2022).

It is not known what factors led to the past decline of this species in New Jersey. According to Gustafsson (1947, cited in Montgomery 1955), the combination of hybridization and polyploidy as is found in the genus *Dentaria* (= *Cardamine*) may contribute to an increase in sterility factors present in certain species, such as *C. maxima*. Eventually, such species would persist solely by

vegetative reproduction (Stebbins 1941). While hybridization and polymorphism may have allowed these populations to adapt quite well to the specific environment in which they developed, the lack of sexual reproduction reduces their ability to adapt to changing conditions over time and eventually populations (and perhaps the entire species) will die out (Stebbins 1941). Despite the Large Toothwort's ability to reproduce vegetatively by rhizomal growth, its apparent inability to produce viable seeds may threaten the long-term persistence of this species in New Jersey, especially given the fragmented nature of the landscape.

In Maine (MNAP 2021), possible threats mentioned include habitat loss, the species' location at its edge of its range, and possible negative impacts of forest management practices. Given its lack of seed production and dispersal mechanisms, it would be difficult for Large Toothwort to recolonize secondary forest after disturbances such as logging (Bellemare et al. 2002). In the Ottawa National Forest in Michigan, listed threats to *Cardamine maxima* populations included loss of habitat, competition with exotic species, and herbivory (Trull and Shackleford 2018). At three Erie County, Pennsylvania Natural Heritage Areas, reported threats to *Cardamine maxima* populations were similar, mainly non-native invasive species (e.g., *Alliaria petiolata*, *Rosa multiflora* [Multiflora Rose]) and herbivory by White-tailed Deer (*Odocoileus virginianus*) (PNHP 2012). In addition to deer over-browsing and non-native species, the Pennsylvania Natural Heritage Program (PNHP) (2022) noted that heavy recreational use (e.g., hiking, ATV's) in some areas may damage plants.

Climate change is an ongoing widespread threat, with varying implications depending on population location and the species' life history traits. Cao et al. (2016) found that simulated warming temperatures altered the flowering period and seed production of the related *Cardamine hirsuta*, although the effects depended in part on plant density. However, since *C. maxima* reproduces vegetatively, similar effects of climate change on sexual reproduction may not be a main concern. In Pennsylvania, *Cardamine maxima* is considered "highly vulnerable" to climate change, with significant reductions in the species' range predicted by 2050. Reasons for its vulnerability include its limited dispersal capability, the fact that it may only reproduce vegetatively, and its sensitivity to changes in precipitation patterns (PNHP 2022). In New Jersey, the climate is predicted to become warmer and wetter, with altered precipitation patterns such that hotter drier summers and periods of summer drought may become more common (NJDEP 2020). It is unclear whether the current streamside location in northern New Jersey will remain suitable over time or whether *C. maxima* will be able to find and/or migrate and colonize new habitat rapidly enough through only vegetative reproduction.

Management Summary and Recommendations

New Jersey's single remaining population of Large Toothwort should be regularly monitored and protected from any threats if possible. Specifically, invasive species removal should be implemented with care not to harm the rare plants and to minimize soil disturbance. Regular monitoring could also help with the early detection of other potential threats, such as herbivory or the presence of disease pathogens at this isolated population. It would also be helpful to determine what forest/overstory management activities, if any, are occurring at the site, whether streamside flooding is a threat, or if there are potential management issues.

The Wisconsin Department of Natural Resources (WIDNR) (2022) provides a list of recommended precautions for management when working in habitat supporting *Cardamine maxima*. Those include cautions against the broadcast spraying of herbicides, limiting forest operations that would damage soil to the winter months when ground is frozen or during the late fall when soils are dry, and avoiding any site preparation that heavily disturbs the herbaceous layer and soil. Minimizing disturbance to the local hydrology (including soil disturbance from rutting) and avoiding drastic reductions in canopy cover in wet areas are also suggested.

Because so little is known about seed viability in this species and there are differing opinions about the extent of sterility in *C. maxima*, a more definitive study of sterility in populations of *C. maxima* would be warranted. Is it fully sterile throughout its range? Or are there still some populations that do produce viable seeds and seedlings? Does it always co-occur with *C. diphylla* and *C. concatenata*? Is *C. maxima* able to disperse more widely via rhizome fragments in wetter sites? A closer look at the genetic makeup of the New Jersey population would also be informative as the remaining New Jersey population has been isolated for so long.

Synonyms

The accepted botanical name of the species is *Cardamine maxima* (Nutt.) Alph. Wood. Orthographic variants, synonyms, and common names are listed below (ITIS 2022, POWO 2022, USDA NRCS 2022b, WIDNR 2022).

Botanical Synonyms

Cardamine X anomala (Eames) K. Schum.
Cardamine X maxima A. Wood
Dentaria anomala Eames
Dentaria maxima Nutt.
Dentaria maxima f. *albiflora* Louis-Marie
Dentaria maxima f. *aphylla* Louis-Marie

Common Names

Large Toothwort

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