Isotria medeoloides, small whorled pogonia and *Isotria verticillata*, large whorled pogonia

Figure 1—Small whorled pogonia. Image courtesy of Robert H. Mohlenbrock @ USDA-NRCS PLANTS Database / USDA NRCS. 1995. Northeast wetland flora: Field office guide to plant species. Northeast National Technical Center, Chester, Pennsylvania.

Figure 2—Large whorled pogonia. Creative Commons image by Judy Gallagher.

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ABSTRACT

This Species Review provides information on the ecology and knowledge gaps of two *Isotria* species: small whorled pogonia (*I. medeoloides*) and large whorled pogonia (*I. verticillata*).

These orchids are native to the eastern United States. Both are rare and have legal protection status in many states. Small whorled pogonia is Federally Threatened. Both species grow in acidic soils that are typically mesic but range from wet to dry. Plant communities with these species include mixed hardwood and coniferous-deciduous woodlands and forests. Red maple is consistently associated with both *Isotria* species across their distributions. Detailed site characteristics and plant community associations are discussed for both species.

The two *Isotria* species show considerable differences in their population structures and reproductive efficiencies. Small whorled pogonia is nonclonal (nonrhizomatous), self-pollinated, and rarely produces flowers while large whorled pogonia is clonal (rhizomatous), insect-pollinated, and produces more flowers than small whorled pogonia. Both species enter a 1- to 4-year period of dormancy, or die, when environmental conditions are unfavorable.

Small and large whorled pogonia are most common in second- or third-growth, midsuccessional forest communities. Openings in the canopy and canopy thinning apparently favor these orchids.

As of 2019, information on the fire ecology and postfire responses of *Isotria* species was lacking in the published literature. Both species grow on sites with accumulated leaf litter, so they may be easily damaged by fire. Because *Isotria* species tend to increase after disturbances that open the canopy, a single fire—or fires at moderate intervals—may increase their abundance, assuming fire does not kill them. Studies are needed on traits that influence the postfire responses of *Isotria* species, including burial depth of perennating organs (root crowns and, for large whorled pogonia, rhizomes), presence/absence of a seed bank, and depth of seed burial. Case studies are needed to document their postfire response. Closely monitoring postfire response, and subsequently modifying burn plans as needed, will increase understanding of the fire ecology of and may promote *Isotria* species.

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INTRODUCTION

TAXONOMY

This Species Review provides information on fiveleaf orchids in the genus *Isotria* Raf. (Orchidaceae). There are two species of *Isotria* [27, 86]:

Isotria medeoloides (Pursh) Raf. [26, 27, 36, 44, 98], small whorled pogonia
Isotria verticillata Raf. [36, 44, 86], large whorled pogonia

These species are not know to hybridize [31, 38].

See table A1 for a complete list of common and scientific names of plant species discussed in this review and links to other FEIS Species Reviews.

Three reviews [31, 58, 91] are cited throughout this Species Review. Within sections, information is arranged first at the genus level (*Isotria*), then for small whorled pogonia, and lastly for large whorled pogonia. The text is bolded at first mention of each taxon.

SYNONYMS

For ***Isotria verticillata*** Raf.:
Isotria verticillata (Willd.) Raf. [69, 78]
Isotria verticillata (Muhl. Ex Willd.) Raf. [15, 62, 98]
Pogonia verticillata (Muhl. Ex Willd.) Nutt. [99]

LIFE FORM

Forb

DISTRIBUTION AND PLANT COMMUNITIES

GENERAL DISTRIBUTION

***Isotria*:** The *Isotria* genus is native to the eastern United States. Historically, it was also distributed a short way into adjacent Canada [31]. *Isotria* spp. occur in parts of the Great Lakes, Northeast, Appalachians, and Southeast [86] (fig. 3).

Small whorled pogonia occurs in scattered populations or colonies from western Maine west to southeastern Missouri and south to northeastern Georgia [65, 73, 86]. It is one of the rarest orchids in North America [31, 53]. In 2014, total population size across its distribution was estimated at <3,000 individuals [58]. Most populations have <25 individuals [16, 88]. For example, in 2003 the Chattahoochee National Forest, Georgia, had 16 known small whorled pogonia sites containing 33 populations. Each population ranged from 1 to 50 individuals [97]. Populations of only one or two stems have been observed in Massachusetts [28] and the Piedmont of Virginia [30].

Although it is nowhere common [25, 40, 62, 73], small whorled pogonia has three main population centers: the Appalachian foothills in New England; the Coastal Plain and Piedmont regions of New Jersey, Delaware, and Virginia; and the Blue Ridge Mountains at the juncture of North and South Carolina, Georgia, and Tennessee [73, 97]. The largest populations are in New England [16, 73, 91]. In descending order of population sizes, these populations are in New Hampshire, Maine, and Virginia [19, 91]. Small whorled pogonia is extirpated and presumed extinct in Ontario, Ohio, West Virginia, and South Carolina [86]. Although historical records exists for Maryland, New Jersey, New York, Missouri, Vermont, and Washington, DC, small whorled pogonia sites have not been relocated in those areas [91]. Stone et al. (2012) suggest that a species-level contraction of small whorled pogonia distribution is occurring in the Southeast [76].

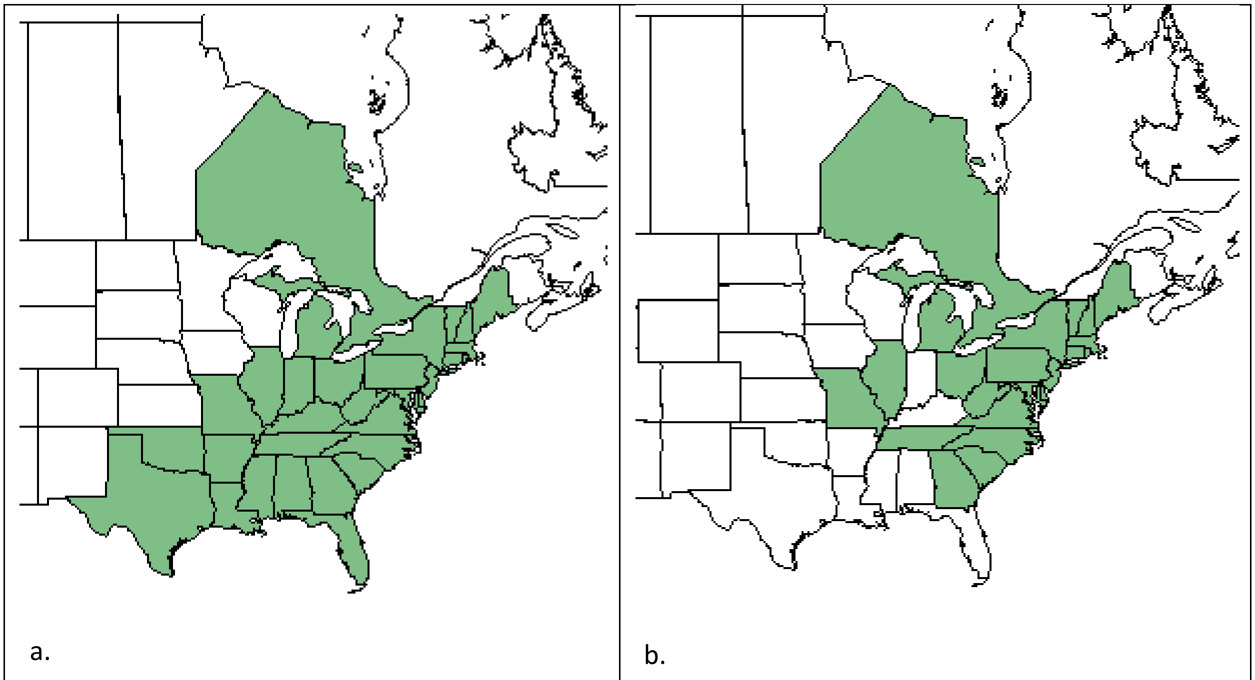

Figure 3—Native ranges of (a) small whorled pogonia and (b) large whorled pogonia. See table 3 for current distributions and protection and conservation status. Maps courtesy of the U.S. Department of Agriculture, Natural Resources Conservation Service [86].

Large whorled pogonia also occurs in scattered populations [31, 62, 86] throughout its range [31], from northern Michigan east to southwestern Maine and south to eastern Texas and the Florida panhandle [86]. It is extirpated and presumed extinct in Ontario [68, 86] and the Upper Peninsula of Michigan [86].

SITE CHARACTERISTICS AND PLANTS COMMUNITIES

Site Characteristics

Isotria species occur from about 30 to 6,500 feet (10-2,000 m) elevation. Given its more restrictive geographic distribution, small whorled pogonia is apparently less tolerant of hot climates than large whorled pogonia [31].

Across its range, sites with **small whorled pogonia** tend to have sparse to moderate ground cover; a relatively open canopy; and proximity to logging roads, streams, or other features that create long, persisting breaks in the forest canopy [10, 73, 91]. In Massachusetts and New Hampshire, for example, populations occur on braided channels of vernal streams and in gullies upslope from streams [73]. Von Oettingen (1992) reports that there are many local and/or regional exceptions and variations to these "common ground" site characteristics [91].

Small whorled pogonia grows at toeslope to midslope positions, generally at inclinations of 0% to 30% [53], but terrain and topographic position often vary across its range. Aspect is often east- [53, 93] or north-facing [30, 73, 93], but small whorled pogonia occasionally occurs on steep slopes and south-facing aspects [73]. It occurs on flat terrain and southerly slopes in West Virginia, and in Pennsylvania it grows above or near intermittent streams and drainages on south- and southeast-facing slopes [73].

Soils on sites with small whorled pogonia are very strongly acidic [28, 48, 53, 73, 79] (pH 4.0-4.9) [53, 79] and nutrient poor [28, 53, 73]. However, small whorled pogonia often grows in decaying organic material such as thick leaf litter, stump, and logs, so nutrient levels in the humus and topsoil likely exceed those in lower soil layers [53]. Soil moisture typically ranges from mesic [31] to dry [73]. On many sites, small whorled pogonia grows above an impermeable (fragipan) soil layer [28, 73].

Although Cook (1983) reported that small whorled pogonia appears to have "very ordinary unspecialized habitats" [16], some combined site characteristics can be used to predict actual or potential small whorled pogonia habitats. Sperduto and Congalton (1996) modeled potential locations of small whorled pogonia in Maine and New Hampshire based on soil, slope, and canopy reflectance data. Field and remotely-sensed data from 26 known small whorled pogonia occurrences showed characteristics of small whorled pogonia habitats included soils with a fragipan layer, slopes from 11% to 17%, and a specific canopy reflectance in near-infrared wavelengths. Using GIS, 90 potential sites with these characteristics were identified. Field surveys found 10 of these sites supported previously unknown small whorled pogonia populations. The model indicated that 94% of the study region was unsuitable small whorled pogonia habitat, although sites classified as suboptimal were not surveyed to verify the model [72].

A habitat suitability study in the southern Appalachian region found mean annual precipitation was the most important environmental factor predicting small whorled pogonia presence ($P < 0.001$), suggesting that adequate moisture is critical for sustaining small whorled pogonia populations. The model indicated that habitat suitability index is highest (>0.6 on a scale from 0 to 1) when mean annual precipitation is around 80 inches (210 cm), mean minimum annual temperature around 44 ^{o}F (7 ^{o}C), aspect close to 50^{o}, and slope from 4% to 7%. Habitat suitability was higher in deciduous (0.60) than coniferous (0.38) forests. Areas of highest habitat suitability were in the southern portion of the Appalachian Mountains where North Carolina, South Carolina, Georgia, and Tennessee meet; and on the Cumberland Plateau. These areas encompassed 2,029 miles^2 of 273,423 miles^2 (5,254 km^2 of 708,163 km^2) that were assessed in the model [53].

Large whorled pogonia is found near roadsides, cliffs, and along streambanks [16, 19, 62]. It typically grows in moist soils [10, 31, 36, 44, 58, 62, 78, 91]. However, soil moisture can range from wet [58] to dry [31, 42, 58, 65, 94, 96]. Large whorled pogonia is considered a facultative upland (FACU) and facultative (FAC) wetland species [86], growing in acidic seeps and sphagnum bogs as well as drier upland forests [31]. In Green Mountain National Forest, Vermont, it often grows on hot, dry sites on south-facing slopes [22].

Soils on sites with large whorled pogonia are extremely to strongly acidic (pH ~4.2-5.2) [35, 79] and usually nutrient-poor below the organic layer [10, 31, 36, 44, 58, 62, 78, 79, 91], particularly in the extreme northern portion of its range [31]. Topsoils are typically, but not always, rich in humus [31]. Thick leaf litter and/or organic surface horizons near vernal streams is apparently preferred habitat [7]. Although it prefers moist substrates, large whorled pogonia may occur on dry but shaded, east- or north-facing slopes when growing in decaying leaf litter. It may also grow in sphagnum [34]. Soils often have a fragipan layer [28, 55, 58].

Large whorled pogonia grows in sands and loams. On Long Island, New York, it grows on rich, loamy soils and dry sands [42]. In Fredericksburg and Spotsylvania National Military Park, Virginia, large whorled pogonia grows in well-drained, acidic, sandy, silty, or gravelly loams with low pH (mean = 4.2) [80]. In Louisiana, it grows in in very acidic sands [31]. On the Kisatchie National Forest, Louisiana, large whorled pogonia grows in well-drained, saturated, strongly acidic loamy fine sands with high organic matter content [55]. It grows in similar soils in forest seeps in East Texas [54]. It grows on sandy and/or loamy bluffs by the Apalachicola River in Florida [15, 65].

Parent soil materials on sites with large whorled pogonia include quartzite [96], schists, granites, sandstones, siltstones, and shales. Depth to bedrock varies from shallow (e.g., under upland heath or pine ridges) to deep (e.g., under bogs on the Coastal Plains) [31]. In Berkshire County, Massachusetts, large whorled pogonia grows in thin, dry, acidic soils derived from quartzite [96]. In southern Illinois, it grows in relatively dry, thinly wooded slopes above sandstone bluffs [65]. In the Ozark region of Missouri, it grows on bottomlands, low slopes, and dry, upland forests in soils derived from chert and sandstone [65].

Plant Communities

Isotria species grow in similar habitats, and they sometimes cooccur [13, 91]. Indian cucumber, which resembles *Isotria* spp., may also cooccur. American beech, red maple, scarlet oak, American witchhazel, partridgeberry, liverleaf wintergreen, Christmas fern, and New York fern are common associates across both species' distributions [1, 48], particularly red maple and scarlet oak [48].

Small whorled pogonia grows in mixed-deciduous [48, 61, 80, 98], mixed deciduous-coniferous [44, 48, 91, 94, 98], and coniferous [44, 91, 94, 98] woodlands and forests. In approximate order of frequency, overstory species frequently associated with small whorled pogonia include red maple, scarlet oak, American beech, white oak, eastern white pine, black oak, eastern hemlock, tuliptree, and paper birch [48]. The only known small whorled pogonia population in Michigan grows in a red maple forest [91]. Paper birch stands on slopes with a dense herbaceous layer of ferns are considered an indicator of small whorled pogonia habitat. A study of 11 extant populations across small whorled pogonia's historical range found that in its northern distribution, small whorled pogonia was consistently associated with red maple, scarlet oak, American witchhazel, Canada mayflower, and Indian cucumber and in its southern distribution, with white oak, chestnut and/or swamp chestnut oak, eastern white pine, flame azalea, flowering dogwood, Indian cucumber, Christmas fern, and New York fern [48].

Understory vegetation associated with small whorled pogonia varies from virtually none in eastern hemlock and American beech groves with a dense overstory to a dense layer of ferns including eastern hayscented fern, New York fern, and osmunda [58]. Understories with small whorled pogonia tend to be sparse unless ferns are present [91], although clubmosses and evergreen shrubs, including eastern teaberry and partridgeberry, may be present to abundant [37, 58]. Understory species frequently associated with small whorled pogonia include lowbush blueberry, northern spicebush, partridgeberry, Indian cucumber, wild sarsaparilla, and white snakeroot [73]. Graminoids tend to be sparse or absent on sites with small whorled pogonia [58]. It is frequently associated with other orchids including brown widelip orchid, downy rattlesnake plantain, green adder's-mouth orchid, and moccasin flower [37, 58].

Small whorled pogonia is mentioned in these plant community classifications for the Southeast:

- Fredericksburg and Spotsylvania National Military Park, Virginia: Small whorled pogonia is considered a characteristic species in dry white oak-scarlet oak-black oak/black huckleberry forests. Small whorled pogonia also grows in American beech-white oak-northern red oak/American holly/Christmas fern forests on gentle gradients and adjacent to small streams [80].

- Southern Blue Ridge Mountains and the Upper Piedmont of Virginia and Georgia: It occurs in tuliptree-sweet birch-eastern hemlock/great laurel forests [56, 57]. In the Southern Blue Ridge Mountains, small whorled pogonia grows in eastern hemlock-sweetgum/great laurel/heartleaf foamflower cove forests at midelevations (1,300-3,500 feet (400-1,000 m)). On the Upper Piedmont, it grows in coves and on sheltered slopes at lower elevations. Associated understory species include partridgeberry, downy rattlesnake plantain, and Christmas fern [4].

Large whorled pogonia grows in mixed conifer-deciduous and deciduous woodlands and swamps [44, 61]. Throughout its distribution, red maple is a common overstory dominant [31, 35], and laurel and eastern teaberry are common understory associates [78, 91].

Large whorled pogonia occurs with oaks, pines, and maples in its northern distribution. In northern New England and historically in Ontario, it grows in sphagnum bogs and oak-pine forests. Red maple, scarlet oak, black oak, eastern white pine, and pitch pine are typical overstory dominants [31]. American hazelnut, American witchhazel, and common serviceberry are common mid- or understory associates in the northern part of its range [91]. On Long Island, large whorled pogonia grows in mixed-deciduous woodlands and in pitch pine barrens [42]. In Berkshire County, Massachusetts, it is uncommon in dry, acidic white oak-black oak-pitch pine forests [96]. In Vermont, a population of >1,000 stems grew with "apparent vigor" in a red maple-northern red oak-white oak/striped maple-hophornbeam/Canada mayflower-Indian cucumber forest [24]. In Michigan, large whorled pogonia grows in sphagnum bogs [13, 31] and upland, mesic-dry deciduous forests [13, 31], red maple- sassafras swamps, and red maple-tamarack-black spruce/sheep laurel-highbush blueberry/sphagnum forests [31]. In the Midwest (Illinois and Indiana), it grows in mixed hardwood forests, often dominated by red maple, sugar maple, American beech, and/or hickories [31]. In Missouri and Oklahoma, large whorled pogonia grows in American beech-sweetgum-tuliptree/common winterberry/Lescur's sphagnum forests adjacent to streams and on uplands [31].

In the southern portion of its range, large whorled pogonia is most common in mature beech-oak and red maple forests [31]. It also grows in oak-hickory and oak-pine forests dominated by scarlet oak, white oak, and other oaks; and/or shortleaf pine, pitch pine, and Virginia pine [31]. Flame azalea, flowering dogwood, and sourwood are common mid- or understory associates [91]. Herb associates may be few due to dense, but Christmas fern and western brackenfern sometimes grow in association with large whorled pogonia [31].

Figure 4a—Small whorled pogonia growing with ferns in litter on the Pisgah National Forest, North Carolina. Image by James Henderson, Golden Delight Honey, Bugwood.org.

Figure 4b—Large whorled pogonia growing in litter on Lookout Mountain, Georgia. Image courtesy of Alan Cressler, Lady Bird Johnson Wildflower Center.

Many plant community classifications include large whorled pogonia in their descriptions:

- Great Falls National Park, Virginia: Large whorled pogonia occurs in white oak-scarlet oak-shagbark hickory-mockernut hickory/flowering dogwood-mountain laurel forests [29].
- Appomattox Court House National Historical Park, Virginia: It is considered a characteristic groundlayer species in oak-pine forests dominated by chestnut and/or swamp chestnut oak, scarlet oak, white oak; and/or eastern white pine, pitch pine, shortleaf pine, and Virginia pine. Black huckleberry, Blue Ridge blueberry, and/or deerberry dominate the understories [60].
- North Carolina: Large whorled pogonia grows in acidic to neutral soils in unevenaged, rich cove tuliptree-American basswood-sugar maple forests and mesic American beech-scarlet oak-tuliptree-red maple forests [67].
- Black and Craggy mountains, North Carolina: It is considered a characteristic species in scarlet oak-red maple forests on open, southerly aspects [15].
- Louisiana: Large whorled pogonia grows sweetbay-blackgum forest seeps within an oak-pine matrix [31, 43].
- Kisatchie National Forest, Louisiana: Large whorled pogonia and ferns codominate the ground layer of sweetbay-red maple/southern bayberry/netted chainfern forests. Dominant ferns include cinnamon fern, royal fern, and sensitive fern. These forests occur in saturated soils associated with springs and seeps near flat stream bottoms [55].

- West Gulf Coastal Plain of East Texas: It codominates the ground layer and is considered characteristic in sweetbay-red maple/southern bayberry/fern forests. These forests are associated with springs and seeps near flat stream bottoms. Dominant ferns include cinnamon fern, royal fern, and sensitive fern [54].
- Florida: Large whorled pogonia is rare on Appalachia River bluffs in American beech/alternateleaf dogwood-mountain laurel forests [31].

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

GENERAL BOTANICAL CHARACTERISTICS

Botanical Description

This description covers characteristics that may be relevant to fire ecology and is not meant for identification. Identification keys are available (e.g., [15, 26, 27, 44, 62, 69, 98]).

The ***Isotria*** genus is noted for its single, terminal whorl of smooth, flat leaves [31]. At the stem apex, *Isotria* plants support five or six leaves growing from a single node. Stems are hollow [31, 69] and lack extrafloral nectaries [33, 51]. The leaves are arranged in a circle (whorl) at the apex of the stem. Rarely, a single plant produces two stems [31]. The leaves are deciduous [58]. Flowers in this genus are not showy or fragrant [20, 33] and lack nectar [27, 33, 59]. Flowers are generally solitary, growing terminally just above the leaves; rarely, there are two flowers [31, 33, 44, 62, 69, 78, 91]. Three sepals spread outward and are about equal in length (fig. 4b); the attributes for which *Isotria* derives its name (*isos*, equal; *treir*, three) [91]. The fruit is a capsule [62, 65] containing thousands of tiny seeds [91]. In general, orchid seeds are among the smallest produced by flowering plants [77]. Slender, fibrous roots descend from the stem's root crown [91]. Burial depths of perennating organs (i.e., the root crown and, for large whorled pogonia, the rhizomes) were not provided in the literature. Roots of this genus are fibrous and somewhat fleshy [27, 44, 62, 65, 93]. Root hairs are normally lacking. Instead, the hyphae of mycorrhizal fungi serve to uptake water and nutrients [31]. Mycorrhizae associated with *Isotria* are discussed in Value for Restoration.

It is usually possible to distinguish between the two species in the field. Small whorled pogonia has a greenish-white stem and a yellow-green flower with a greenish-white tip, while large whorled pogonia has a purple-green stem and flower. The two species are also distinguished by relative length of the sepals, petals, and length of the seed capsule stem (peduncle) relative to length of the actual seed capsule [1, 13, 91]. Von Oettingen (1992) provides a table contrasting morphological characteristics of the two *Isotria* species [91]. Indian cucumber, a lily, has similar botanical characteristics and can be misidentified as *Isotria* orchids [1]. Distinguishing between small whorled pogonia and large whorled pogonia is not always possible based on morphology, especially when plants are vegetative. In one case, plants growing at Fort A.P. Hill, Virginia, were positively identified as small whorled pogonia only after DNA analysis [47].

The stem of **small whorled pogonia** is short, with a maximum height of about 10 inches (25 cm). The stem and leaves are a glaucous gray-green [1]. Flowers are described as "relatively drab" and "diminutive" [33]. They lack pollination guides and odor [51]. Small whorled pogonia is relatively long-lived [58]. Estimated average lifespan of individuals in a large New Hampshire population is 13.2 years [2].

Small whorled pogonia has a nonclonal growth pattern. Population structure is usually that of few, scattered single plants [31, 37]. All individuals in a Michigan population growing in an old orchard succeeding to a mixed-deciduous forest had single stems, with plants separated by "several yards" [13].

Large whorled pogonia ranges from about 2 to 16 inches (4-40 cm) in height [26]. The leaves are green to dark green and about 3.5 inches long and 2 inches wide (9 cm and 5 cm) [35]. Although the flower produces no nectar [31, 51], it is fragrant and has pollination guides [31, 35, 51]. The purplish sepals are narrow, spreading, and longer than the yellowish-green petals [7, 35]. Capsules are 1.0 to 1.4 inches (2.5-3.5 cm) long [65].

Large whorled pogonia has a clonal growth pattern. Structurally, large whorled pogonia populations form colonies that range from a few to hundreds of stems [31]. Clonal growth is due to short rhizomes that extend from the root crown [31, 44, 62, 69, 78]. House (1906) reported that in central New York, plants growing in sphagnum had longer rhizomes than plants growing in other substrates [34]. Longevity of large whorled pogonia is unknown [38].

Raunkiaer Life Form
Small whorled pogonia:
Chamaephyte

Large whorled pogonia:
Chamaephyte
Geophyte [63]

SEASONAL DEVELOPMENT
In ***Isotria***, buds that form next year's stems overwinter on the root crown [91]. Within *Isotria* populations, individual plants commonly go dormant for 1 to several years [31, 35, 89]. Orchid seeds mature and are dispersed in fall (late September-October) [77]. After seed dispersal, empty *Isotria* capsules usually persist [31, 62] until the next growing season [31].

Within populations, **small whorled pogonia** has staggered phenology. Flowering plants usually emerge before vegetative plants [73]. On average, plants with viable flower buds emerge first, followed by plants with abortive flower buds, and lastly, by vegetative plants [91]. Plants that are large one year are most likely to flower the next. Small plants are most likely to go dormant or die the next year [48, 49, 90]. Without digging it up, it is impossible to tell if a small plant is young, or a mature plant that flowered the previous year [91]. Individual plants may emerge but remain vegetative for up to 8 years between flowering [1]. All or nearly all individuals within a population may fail to flower in some years [93].

In the northern part of small whorled pogonia's range, flowering plants emerge from leaf litter in May and flower in June. In the southern part, flowering plants emerge in April and flower from late April to mid-May. Individual plants may stay in flower from 4 days [51, 73] to almost 2 weeks [19, 51, 73, 91]. Within populations, the flowering period lasts about 2.5 weeks [93]. A second wave emergence, of nonflowering plants, may occur in midsummer. Small whorled pogonia leaves droop downward until flowering time, when they begin uplifting. By fruiting time, they are held horizontally [7]. The seed capsule ripens in fall [73, 91]. Many plants produce an overwintering vegetative bud on the root crown in August or September [73, 91]. Seeds disperse in fall, usually after a frost [11]. Phenology of small whorled pogonia by geographic location is shown in table 1.

Table 1—Phenology of small whorled pogonia by state or region.

Area	Event and timing
Atlantic states, mid- and southern	Flowers May-June [33, 95]
Blue Ridge Mountains	Flowers May-June [98]
Carolinas	Flowers May-June [62]
Midwest	Flowers May-June [65]
Missouri, Ozark Plateau	Flowers May [65]
New England	Flowers mid-June–early July [69]
New Hampshire	Emerges late May–early June [9], flowers June [7, 9], new vegetative buds form July-September [11], capsules ripen July-August [9], onset of dormancy September, seeds disperse October [11]
New York	Flowers May–mid-June [1]
Northeast	Emerges in May [73], flowers May-June [36, 73]
Southeast (Carolinas, Virginia, and Georgia)	Flowers May-June [94]
Virginia	Emerges March–mid-May [73, 93], flowers late April–mid-May, capsules ripen and dehisce in fall [93]
West Virginia	Emerges in May, flowers June–early July [73]

Where small whorled pogonia and large whorled pogonia grow together, small whorled pogonia usually flowers 1 to 2 weeks later than large whorled pogonia [32, 51].

Large whorled pogonia plants frequently go dormant [7, 35] for several years [35]. However, Case (1964) documented a population in Michigan that produced stems annually for at least 13 years [12].

The leaves of large whorled pogonia point upward until flowering, when they drop to horizontal [7]. Flowers remain open for 4 [31] to 7 [1, 31] days. Total length of flowering time for a North Carolina population was 2 weeks [51]. Flowers produce a vanilla scent during early anthesis [51]. The flower parts abscise and the capsule develops quickly if the flower is fertilized [31]. Capsules ripen in late summer to mid-fall (15 September-15 October) in most of large whorled pogonia's range [31]. The seed capsule splits and releases seeds when it dries in fall [91]. Phenology of large whorled pogonia by geographic location is shown in table 2.

Table 2—Phenology of large whorled pogonia by state, province, or region.

Area	Event and timing
Atlantic states, mid- and southern	Flowers April-July [95]
Blue Ridge Mountains	Flowers April-July [98]
Carolinas	Flowers April-May [51, 62, 94]
Florida	Flowers in spring [65]
bluffs above the Apalachicola River	Flowers April [15]
Georgia	Flowers April-May [94]
Indiana	Flowers early May–mid-June [31]
Louisiana	Flowers early spring [31]
Midwest	Flowers mid-April–late May [31]
Missouri	Flowers April–mid-June [31, 65]
Ozark Plateau	Flowers May [65]
New England	Flowers mid-May–mid-June [69]
New Hampshire	Flowers mid-May–mid-June [7]
New York	Flowers May–mid-June [1]
Long Island	Flowers May-June [42]
Northeast	Flowers May-June [36, 44]
Oklahoma	Capsules 1st ripen mid-August [31]
Texas	Flowers early spring, sometimes as early as late March [31]
West Virginia	Flowers May-June [23213]
Ontario	Emerges mid-May [74], flowers late May [35, 38, 74]–early June [35, 38]

REGENERATION PROCESSES

The two ***Isotria*** species show considerable differences in their population structures and reproductive efficiencies. Small whorled pogonia is nonclonal (nonrhizomatous), self-pollinated, and rarely produces flowers while large whorled pogonia is clonal (rhizomatous), insect-pollinated, and produces more flowers than small whorled pogonia [50, 51]. Attempts to transplant *Isotria* have not been successful (see Value for Restoration).

Both species are totally reliant on mycorrhizal symbionts for nutrients and water as long as they remain dormant [31]. Due to dormancy, it is difficult to assess *Isotria* population sizes and densities [31, 35]. The Fish and Wildlife Service, U.S. Department of the Interior (1992), defines small whorled pogonia sites and colonies (i.e., populations) as follows [91]:

> "**A site** is considered to be the proximal area where one isolated small whorled pogonia colony or a cluster of colonies occurs. All the colonies comprising a site are usually **within** the same watershed and are usually separated from one another by no more than a quarter of a mile to one half of a mile. **A colony** is a single natural grouping of plants in a particular locality. There may be gaps between clusters of stems **within** the colony, but there should be no large disjunctions and no major habitat discontinuities" [91].

Pollination and Breeding System

Small whorled pogonia is self-fertile [19, 33, 59, 65, 73, 90, 91] (i.e., autogamous [14, 50, 51]), and it does not require insects for pollination [33, 59, 90]. In a North Carolina study, 83% of small whorled pogonia flowers were successfully pollinated through natural selfing [51].

Selfing is most common in orchids with small, fragmented populations such as small whorled pogonia. The trade-off for an autogamous mating system is a tendency toward inbreeding depression [8, 33]. Given small whorled pogonia's federal legal status and small populations, sample sizes for genetic studies are necessarily small. Limited data show genetic diversity tends to be higher in small whorled pogonia populations in the northeastern and mid-Atlantic states than those in the southeastern states [17, 47, 76]. Decreases in genetic fitness have been suggested as a factor in decline of small whorled pogonia populations in the Southeast [33, 76]. Populations in Virginia and Georgia in particular have "extremely low" genetic diversity, indicating a high incidence of inbreeding [17]. Studies of populations in Prince William Forest Park, Virginia, and Fort A.P. Hill, North Carolina, found genetic diversity was high among populations, with each population being "genetically unique". Genetic diversity was low within populations because "nearly all seed produced is likely accomplished by self fertilization". There was an "almost complete lack of heterozygotes" in 12 of 13 populations [47].

Studies of small whorled pogonia populations in Maine, New Hampshire, Virginia, and Georgia found overall genetic diversity was low within populations (i.e., populations were inbred), and populations were highly differentiated genetically. The authors suggest that "gene flow between populations is practically nonexistent, with populations continuing to diverge following initial establishment". Genetic diversity decreased, and genetic differentiation increased, with decreasing population size. Genetic diversity was higher in the Northeast than in the South ($P = 0.006$). Estimated immigration rate between populations was <1 individual per 10 generations [76].

Large whorled pogonia is cross-pollinating (xenogamous) [14, 31, 50, 51]. Its flower contains a shield-like organ (the rostrellum) that prevents self-pollination. Large whorled pogonia is pollinated by small, solitary bees [31, 51, 65] (Andrenidae, Anthophoridae, and Halictidae families) [31, 51]. Although nectarless, it produces a nectarlike substance that attracts nectar-seeking insects to the flowers [51, 59]. Plants do not produce capsules unless animal pollinators are present and active [31]. In North Carolina, only 21% of flowers were successfully pollinated, and only 6% of flowers produced mature capsules [51]. Even so, Hill (2017) reports that capsule production "is not rare in this species" [31]. Vitt and Campbell (1997) speculate that small whorled pogonia reproduction is limited by resources rather than by pollination failure [90], although they do not speculate on which resources may be limiting. Isolated large whorled pogonia populations are subject to inbreeding, and cross-pollination within sibling groups may be common [31]. Hill (2017) reports that among-population pollen exchange and seed migration are unlikely for large whorled pogonia due to isolated populations and erratic flowering [31].

Flower and Seed Production

Age at first flowering was unknown for ***Isotria*** species as of 2019. Hill (2017) suggested that like the orchid genus *Cypripedium*, *Isotria* may require 10 to 16 years for plants to mature and flower [31]. Mehrhoff (1983) considers seed production in *Isotria* low to moderate compared to other orchid genera [51].

Flowering **small whorled pogonia** populations can produce large amounts of seed, but flowering and seed production are inconsistent among and within populations [23, 89]. In some years, an entire population may fail to flower and/or set seed [89]. In the laboratory, Mehrhoff (1983) observed that contents of small whorled pogonia capsules ranged from 0 to 38,000 seeds, averaging 9,653 seeds/capsule (SE 1,781) [51]. He considered this a "moderate" rate compared to other orchid species [48]. However, in a study of two populations in North Carolina and Georgia, Mehrhoff (1980) found flowering rate was "extremely small", averaging 1.2 flowers/population [50]. Only 21% of naturally pollinated small whorled pogonia flowers matured into capsules; most were either aborted or destroyed by seed predators [48]. In studies in Prince William Forest Park and Fort A.P. Hill, very few small whorled pogonia individuals successfully produced capsules over 4 years. Capsule set (flowers that developed into capsules) averaged 38%, with no plants flowering in the 2 smallest populations (*n* = 13 populations) [47]. In a 4-year study of 13 populations in Virginia and North Carolina, researchers determined that the "regenerative potential of *I. medeoloides* populations in our study region…appears to be very low" [47]. In a 4-year study of an Illinois population, abortion of seed capsules and seed mortality due to environmental stresses (soil temperature and moisture and vapor pressure deficit) reduced small whorled pogonia's seed output. Low soil moisture and dry weather resulted in aborted small whorled pogonia capsules and seed death (abstract [32]). Cairns (2005, unpublished data cited in [87]) reports that some populations with ≤20 individuals produce flowers and capsules over long time periods, with the populations persisting indefinitely.

Open sites apparently promote small whorled pogonia flower and seed production, while closed canopies inhibit them [9, 23, 31] (see Other Management Considerations). In a population in a mid-Atlantic site, plants that flowered received more light than vegetative plants ($P = 0.001$) [8]. Stuckey (1967) reported that in Rhode Island, shaded plants were about one-fourth the size of plants in full sun, and heavily shaded plants were nonreproductive [79]. Brackley (1985) noted a large increase in population size and number of flowers after the canopy of a New Hampshire population was defoliated by gypsy moths [7]. A 1989 study of 11 extant populations across small whorled pogonia's historical range (Ontario and Michigan to Georgia) found populations with flowering plants had less vegetative cover and more available light than populations without flowering plants, and flowering was positively associated with open canopies ($P = 0.1$). Historical sites in Maine, New York, and Georgia where small whorled pogonia has become extinct had highest vegetative cover and lowest available light. Survivorship and flowering were positively associated with available light ($P < 0.05$) [48].

Plant size is a good predictor of potential reproductive success. In a 10-year study, Vitt and Campbell (1991, 1997) found that seed production was greater in large than in small plants ($P < 0.001$) [89, 90]. In a long-term study of five populations across the mid-Atlantic states, mean stem length of vegetative plants was less than that of flowering plants (2.8 vs. 5.5 inches (7.2 vs. 13.9 cm), $P = 0.001$), and plants with double flowers had longer stems than those with single flowers (4.6 vs. 6.1 inches (11.8 cm vs. 15.6 cm), $P = 0.02$). "Many fewer" flowering stems than vegetative stems emerged. One population had ≤25 plants emerge annually, and four had <10 plants emerge annually. In 2015, a total of 58 plants emerged, 34 flowered, and 17 (50%) of the flowering plants produced seed capsules. In 2016, 44 plants flowered, but only 10 (23%) produced seed capsules.[33].

Like small whorled pogonia, **large whorled pogonia** does not consistently flower and set seed, but unlike small whorled pogonia, "it has no known reproductive problems" [31] associated with very low long-term rates of flowering or pollination. Flowering is reportedly "sporadic" in large whorled pogonia [7, 31] but does not appear to be limiting. In contrast to near-zero flowering rates in two North Carolina small whorled pogonia populations [50, 51], a large whorled pogonia population produced "dozens of flowers" [50]. Most plants in a large whorled pogonia population do not flower in a given year, and not all flowers are pollinated. Sometimes most or all of an entire colony remains vegetative [31]. However, numerous seeds can result from pollination of a single flower [31], and mature capsules are observed in the wild "occasionally" [31]. In the laboratory, Mehrhoff (1983) observed that two immature large whorled pogonia capsules contained 40,783 and 46,820 ovules. In the field, he reported seed output averaged 12,638 seeds/capsule in North Carolina (ranged from 0-24,700 seeds/capsule). An average of 10% of naturally pollinated flowers matured into capsules. The "vast majority" of initiated capsules [51] (85%) [50] were either aborted or consumed by seed predators [50, 51].

Seed Dispersal

***Isotria*:** Being very tiny, orchid seeds are generally dispersed by wind and gravity [31, 77, 100], although dispersal has not been described for the *Isotria* genus [19, 38]. *Isotria* seeds float, so water dispersal may also occur [53]. Dispersal may happen incrementally, as wind shakes the splitting, upright capsule and seeds fall out [31, 77].

Stone et al. (2012) speculate that new **small whorled pogonia** populations originate from rare long-distance seed dispersal [76]. New **large whorled pogonia** populations have not been observed [31], suggesting that long-distance dispersal is rare for both *Isotria* species.

Seed Banking

The presence and longevity of ***Isotria*** seed banks had not been documented as of 2019. Preliminary field and laboratory studies of small whorled pogonia seed collected in New Hampshire suggests that seeds remain viable in the soil for at least 4 years [47].

Germination

Fresh ***Isotria*** seeds are apparently dormant, and conditions needed to break dormancy are unknown [77]. Germination times are generally slow for orchids [77]. Bromback (2017, personal observation cited in [2]) noted no small whorled pogonia seedling emergence for 5 years after initiation of a seed burial experiment. As of 2013, attempts to germinate small whorled pogonia seed had not been successful in either the laboratory or the field [40].

Seedling Establishment, Dormancy, Plant Growth, and Mortality

Seedlings of ***Isotria*** and other orchids grow very slowly compared to associated plant species [77]. The embryos contain very little or no food reserves, and the seeds cannot germinate and establish unless they fall on a substrate with suitable mycorrhizae [77, 91]. Orchids generally require 1 to several years of underground development before seedlings emerge above ground [77]. While below ground, the young, nonphotosynthetic orchids receive all water and nutrients from the mycorrhizae, but the mycorrhizae do not receive carbohydrates from the orchids until the orchids emerge and develop photosynthetic tissues [91]. Studies to identify *Isotria* mycorrhizae are ongoing (see Value for Restoration).

Estimating *Isotria* colony size is difficult because plants can remain dormant for several years, so stem counts can fluctuate widely across years [58, 87, 91, 97]. It is also difficult to distinguish *Isotria* seedlings from long-dormant, small plants, so it is difficult to assess rates of seedling establishment [47, 93]. After at least 3 years of monitoring in a given area, National Park Service, U.S. Department of Interior staff tally any newly-emerging small whorled pogonia plants as seedlings [47].

Dormancy likely slows *Isotria* growth and lengthens the time to reproductive age. Unfavorable environmental conditions apparently trigger *Isotria* dormancy [77] and re-emergence, although these conditions were not well identified as of 2019. Drought stress may induce plant dormancy [58].

Mortality rates are "extremely high" for orchid seedlings, and few survive long enough to flower [77]. Fungal infection may account for substantial seedling losses [31]. The specific fungi responsible for seedling mortality had not been identified as of 2019. Many orchid species require several years of vegetative growth before flowering [77]. Mortality and population stability is correlated with size of individual plants. In a 6-year study across small whorled pogonia's historical distribution, large plants were most likely to re-emerge from dormancy, while small plants were more likely to go dormant and then die. Stable populations had larger plants and more flowering plants than declining populations ($P < 0.05$) [49].

Von Oettingen (1992) noted that for **small whorled pogonia**, populations with high percentage of vegetative plants could be either a new colony or an established colony in decline, and it is "virtually impossible" to tell the difference. Conversely, a colony with a high percentage of flowering plants and few to no vegetative plants may be on a site that can no longer support small whorled pogonia germination and/or seedling establishment [91].

Studies show re-emergence of small whorled pogonia after 1 to 2 years [11, 93], 2 to 3 years [11, 23, 48, 49], and 4 years [10, 11] of dormancy, with likelihood of reemergence lessening over time [32, 47, 89]. After 4 years with no re-emergence, it is likely that the plant is dead [10]. Claims of dormancy for 10 to 20 years have not been substantiated [7, 91]. Plants that were heavily grazed may not emerge the following year, or may emerge as small plants [11, 73]. In Maine, length of dormancy varied by site and year. Most plants were dormant for only 1 year before re-emerging, but some were dormant for up to 4 years. Among five populations monitored for 4 to 7 years in Virginia, 14 plants were dormant for 1 year, and 2 plants for 2 years [91]. In a long-term monitoring study in New England, Cairns (2001, cited in [47]) found 87% of dormancies lasted 1 to 2 years. After 3 years of dormancy, the chances of re-emergence were only about 8%. The status of two plants was undetermined: they either re-emerged after 9 years of dormancy or were seedlings. Studies in Virginia and North Carolina found that over 4 years, 15 of 93 plants (16%) were dormant for 1 year, 1 of 93 plants re-emerged after 2 years of dormancy, and 0 plants re-emerged after 3 years. Previously undetected plants emerged each year [47]. Small plants are more likely to go dormant than large plants [11, 47]. For example, studies in Virginia and North Carolina showed that almost half of small whorled pogonia seedlings (44%) went dormant the year after emergence [47]. In studies of two small whorled pogonia populations in Virginia and one in New Hampshire, abundance of Russulaceae ecotomychorrizal hyphae in the soil and on small whorled pogonia root tips was positively associated with emergence of previously dormant small whorled pogonia plants. For each increase in the number of adjacent root tips colonized by Russulaceae, the odds of small whorled pogonia emergence increased by a factor of 2.32 ($P = 0.011$) [64].

Based on 20 years of data for a large New Hampshire population, Alahuhta et al. (2017) developed models to predict chances of re-emergence of dormant small whorled pogonia plants and their potential reproductive state in the year of re-emergence (i.e., vegetative, flowering, or flowering and fruiting). For example, plants that went dormant while in the small, vegetative stage had an estimated 28% chance of re-emerging and flowering, while plants that went dormant after fruiting had an estimated 77% chance of re-emerging and flowering [2].

Open sites apparently promote small whorled pogonia growth, while closed canopies inhibit it [9] (see Other Management Considerations). On five sites in Rhode Island, small whorled pogonia plants growing in near-full sunlight were four times the size of small whorled pogonia plants growing on a shaded site [79]. Based on studies of 11 populations from Ontario to Georgia, Mehrhoff (1989) stated that growth and reproductive performance "in one year is probably closely tied to resource accumulation in the previous season, when [vegetative] shoot buds are formed" [49]. Nutrient-rich decaying organic matter, including litter and rotting wood, is likely important in promoting small whorled pogonia growth [53, 91].

Little information was available on seedling establishment, dormancy, and growth of **large whorled pogonia**. In Prince William Forest Park and Fort A.P. Hill, McCormick et al. (2011) report that large whorled pogonia populations are "very small and very dynamic". Over 4 years, "large numbers" of individuals were dormant each year, and individuals not previously found emerged [47]. Large whorled pogonia plants may go dormant [7, 35, 47] for several years [35]. However, Case (1964) documented a population in Michigan that produced plants annually for at least 13 years [12].

Vegetative Regeneration

Small whorled pogonia occasionally produces two or more stems from a single root crown [10, 91], but it does not form clonal colonies or otherwise reproduce vegetatively [19, 47, 51, 87].

Large whorled pogonia sprouts from rhizomes [31, 34, 35, 58]. Sprouting is its main method of regeneration [35, 38]. Each rhizome can send up multiple aerial stems [58], and a single plant may eventually produce up to 300 shoots [51]. A 1906 publication reported that all young, excavated plants near Washington, DC, were connected to parent plants via rhizomes, but the rhizomatous connection no longer existed for some large (presumably older) excavated plants. Rhizomes on old plants were "very brittle". Intact rhizomes had sprouting vegetative buds [34]. Not all rhizomes produce sprouts in any given year, and in some years, no new stems may emerge for entire populations [31].

SUCCESSIONAL STATUS

Small whorled pogonia usually grows under open, second- or third-growth [9, 10, 48, 53, 89, 93] canopies. Although it prefers open areas and declines as the canopy closes [16, 48, 73], it may tolerate a broad range of light intensities. It has been found in young [58], mature [91], and old-growth [58] stands. It has been observed in 30-year-old eastern white pine stands in South Carolina and 60- to 80-year old mixed-deciduous stands in Virginia [91].

Small whorled pogonia population declines across the eastern United States may be caused, at least in part, by decreased light availability resulting from forest maturation [23, 48, 49]. Cook (1983) reports that the "healthiest occurrences" of small whorled pogonia are in areas that have succeeded to forest following a heavy or stand-replacing disturbance [16]. A study in the Southern Appalachian region found small whorled pogonia was most common in midsuccession, when the canopy was dominated by shade-intolerant species such scarlet oak and eastern white pine, but the subcanopy was dominated by shade-tolerant species such as red maple and eastern hemlock . Midstory snag density was positively associated with small whorled pogonia density ($P = 0.03$), and overstory snag density was higher in large small whorled pogonia populations (>9 individuals/location) than in small populations ($P = 0.01$) [53]. Defoliation of the canopy by gypsy moths may increase small whorled pogonia population sizes [16].

A 1989 study of 11 extant populations across small whorled pogonia's historical range (from Ontario and Michigan to Georgia) found small whorled pogonia was most common in relatively open, second-growth forests with thin to thick leaf litter, a low- to moderate-density shrub layer, and an open herbaceous layer. Overstory density ranged from 300 to 1,180 stems/acre (750-2,925/ha), basal area from 55.1 to 185.1 ft^2/acre (12.8-42.5 m^2/ha), shrub cover from 1% to 200%, and ground cover from 0% to 60%. Sites had a history of disturbance, although not recent disturbance. These sites included old fields, windthrow areas, and cutover forests; and populations were often noted near canopy breaks such as logging or other roads and streambanks [48]. Fire histories of these sites were not noted.

Historical agricultural use may have favored small whorled pogonia [48, 73]. Small whorled pogonia grows in old fields on sites from New Hampshire to Georgia. A large colony in Virginia grows on a site that may have once been used as a hog farm [91].

Small whorled pogonia populations apparently increase after small-scale disturbances that create canopy gaps [2, 9, 48, 49]. Small whorled pogonia grows on sites with persistent breaks in the tree canopy [91]. Brumback (1985, New England Wild Flower Society, personal communication cited in [58]) noted that small whorled pogonia plants in a clearcut were “exceptionally vigorous”, while plants away from the clearcut were smaller and less vigorous. Brumback (2018, cited in [70]) observed that small whorled pogonia density increased after a utility company trimmed trees on a site in New Hampshire. He postulated that the increased sunlight promoted growth of small whorled pogonia and its associated mycorrhizae [70]. Small whorled pogonia is found along road and wood edges in South Carolina, and higher light intensity at those sites may promote small whorled pogonia growth [58].

Small whorled pogonia grows in forests with sparse to dense understories [58]. Although it is most common on sites with open ground layers [16, 48], it apparently tolerates crowding in the understory, and it is unclear how *s*mall whorled pogonia may respond to thinning of the shrub and groundlayer species. Mehrhoff (1980) suggests that declines in its populations "are probably related to an increase of vegetative cover at the sites" [50], and Sheffan (2004) suggests that ferns may replace small whorled pogonia successionally, especially in areas with large white-tailed deer populations [73] (see Other Management Considerations). However, other studies report that density of associated understory vegetation has minimal impacts on the size of small whorled pogonia populations. NatureServe (2019) reports that in New Hampshire, small whorled pogonia is most common growing in dense fern cover [58]. Brumback and Fyler (1983, unpublished report cited in [58]) suggested that high cover of other herbs did not limit small whorled pogonia flowering in New Hampshire. They stated that while “it may be true that dense herbaceous cover could certainly limit the size of *I. medeoloides*, in our study several blooming plants appeared in over 60% herbaceous cover”.

Large whorled pogonia occurs in both relatively open and closed forests. Large whorled pogonia has been noted in mature upland forests of New Jersey [21], and it persists in areas with relatively dense shrubs (Ware 1987, cited in [31]). Hill (2007) reports that large whorled pogonia “is not known to grow successfully in completely open sites, especially in the southern portions of its range—instead, it is generally found in rather mature forests of beech and oak” [31]. These forests often contain red maple [31], a shade-tolerant, mid- to late-seral species [18, 92]. However, other authors report large whorled pogonia on open sites. In Colonial National Historic Park, Virginia, large whorled pogonia is considered a characteristic groundlayer species in very open to closed black oak-white oak/black huckleberry forests with sometimes dense shrub understories [61]. In the Appomattox Court House National Historical Park, it grows in the ground layer of very open to closed oak-pine forests. The shrub layer is often dense [60].

Several authors report that large whorled pogonia is most frequent in open, second- [48, 58, 91] and third-growth [91] hardwood and pine-hardwood stands with open to dense understories. It apparently prefers light shade [31, 35] and may benefit from disturbances that either create openings in or thin the canopy and/or understory. Managers on the Shawnee National Forest, U.S. Department of Agriculture (2005) report that large whorled pogonia habitats in seep springs are succeeding to trees and nonnative Nepalese browntop. A report states that open, “sunny seep springs benefit *Isotria verticillata* and cannot be achieved without prescribed fire and selective tree and shrub removal”, and that “vegetation treatments, fire management, and integrated pest management are expected to have positive direct and indirect short-term and long-term effects” to large whorled pogonia [82].

FIRE EFFECTS AND MANAGEMENT

FIRE EFFECTS

Immediate Fire Effects on Plant

***Isotria*:** Information on the immediate effect of fire on *Isotria* species was lacking as of 2019. Both species grow on sites with accumulated leaf litter [31, 53], so they may be easily damaged or killed by surface or ground fire. This is speculative, however: information on how deeply small whorled pogonia and large whorled pogonia perennating organs are buried in (and protected by) soil was lacking. Because it is rhizomatous, large whorled pogonia may be only top-killed by fire, but information on how deeply its rhizomes are buried was lacking.

Possible Postfire Regeneration Strategies

Small whorled pogonia:
Herbaceous root crown

Large whorled pogonia:
Herbaceous root crown
Rhizomatous herb
Geophyte [75]

FIRE ADAPTATIONS AND PLANT RESPONSE TO FIRE

Fire Adaptations

***Isotria*:** Literature on the possible fire adaptations of small whorled pogonia and large whorled pogonia was lacking as of 2019. Rhizomes buried in soil may help large whorled pogonia survive fire.

Plant Response to Fire

Because ***Isotria*** species tend to increase after disturbances that thin or create openings in the canopy (see Successional Status), a single fire—or fires at moderate intervals—may increase their abundance, assuming fire does not kill them. Since these species are most common in second- and third-growth forests in midsuccession, their abundance may decrease with stand-replacing fire [31]; however, data on this are lacking. *Isotria* and their mycorrhizae grow in habitats that sometimes have deep litter and humus. Effects to *Isotria* and their associated mycorrhizae due to burning of leaf litter are unknown [31].

Small whorled pogonia: Although there is generally more ecology literature on small whorled pogonia than on large whorled pogonia, fire ecology literature on small whorled pogonia was lacking as of 2019.

Observations and unpublished reports [31, 38, 45] suggest that **large whorled pogonia** benefits from low-severity fire that opens the canopy [31], and fire may promote flowering [38]. Anecdotally, the number of flowering individuals in a large whorled pogonia population has been observed to increase the year after fire [31, 71, 81]. In a mixed oak-pine forest in Virginia that had burned "within the past few months", large whorled pogonia density averaged 84.5 plants/5 m^2, with "many of the plants in prime flower" in early May [5]. Hill (2017) suggests that the postfire influx of nutrients may stimulate postfire flowering, especially if the first postfire growing season is relatively wet. Phosphorus in particular is known to promote flowering of large whorled pogonia. However, it is possible that large whorled pogonia flowers just as well on unburned as burned sites, but flowers are more conspicuous on burns [31].

In an oak forest on the Green Mountain National Forest near Pownal, Vermont, large whorled pogonia was more abundant in burned than in unburned areas following a low-severity, April prescribed fire, even though most of the population occurred outside the burned area [45, 46, 71]. Managers on the

Forest report that “large populations” of large whorled pogonia once occurred on south-facing, convex slopes that were burned in the early 1900s to promote berry production, although these populations were apparently declining in the 2010s [71]. Three months after the spring prescribed fire, density of large whorled pogonia averaged about 60 vegetative stems in a ~30 × 40-foot area [45]. Most of these were large plants (4-7 inches (11-18 cm) tall): no seedlings were present [45, 46]. Marcus (2019) reports that many of the plants “are growing right out of burnt soil, right against charred branches and logs”, with the previous year’s stems sometimes visible as charred stalks (fig. 5). Outside the burn, large whorled pogonia was “very rare and difficult to find above ground” [45].

Figure 5—Large whorled pogonia plants emerging after a prescribed April fire near Pownal, Vermont. U.S. Department of Agriculture, Forest Service image by Aaron Marcus.

In the Red River Gorge Geological Area of the Daniel Boone National Forest, Kentucky, total frequency of herbaceous groundlayer species, which included large whorled pogonia, was greater on burned plots than on unburned control plots. Frequency of groundlayer species was greater on twice-burned than single-burned plots. Plots on a scarlet oak-white oak-pitch pine/red maple-blackgum forest were burned in late winter (March) using single (1993 or 1995) or repeat (1993 and 1995) prescribed fire (n = thirty 1-m^2 plots) [3].

On Whittleton Ridge on the Daniel Boone National Forest, large whorled pogonia was present on both burned and unburned sites the year following a mid-March prescribed fire [41]. Percent cover or frequency was not measured.

In at least one case, prescribed fire apparently reduced large whorled pogonia in the short term. Large whorled pogonia was noted as present before a prescribed fire on the Fernow Experimental Forest in

West Virginia, but it was not present in postfire month 6 [66]. Timing of fire and cover and frequency of large whorled pogonia were not provided.

FUELS AND FIRE REGIMES

Fuels

Small whorled pogonia grows in substrates with litter, decaying organic matter, and a sparse to dense shrub layer [19, 91], and it is found growing in or near decaying wood [53, 91]. Accumulations of fallen trees, branches, small twigs, and bark and leaf litter are often substantial in small whorled pogonia habitats [91].

Large whorled pogonia also grows in substrates with litter and decaying organic matter [7, 34]. Herbaceous and shrubby fuels in plant communities with large whorled pogonia may be highly variable. In Fredericksburg and Spotsylvania National Military Park, the white oak-scarlet oak-black oak/black huckleberry forests in which large whorled pogonia occurs have patchy to dense shrub layers. Even when shrub layers are dense, groundlayer vegetation can be abundant [80]. In Berkshire County, Massachusetts, large whorled pogonia grows in open chestnut oak-black oak-pitch pine forests with a dense shrub layer and a sparse ground layer [96].

Fire Regimes

Isotria: Small whorled pogonia and large whorled pogonia occur in forests that have regimes of frequent surface fires (e.g., oak-hickory [85] and oak-pine [83]) and in forests with regimes of infrequent stand-replacement fire (e.g., mixed-hardwood swamps [84]). Their place in postfire succession in these widely ranging fire regimes is undocumented. Weatherbee (1992) notes that in Berkshire County, Massachusetts, succession in chestnut oak-black oak-pitch pine forests with large whorled pogonia leads to a closed-canopy forest, but this progress "may easily be set back by the occurrence of an occasional fire, to which this community is particularly susceptible" [96].

Find fire regime information for the plant communities in which these species may occur by entering "small whorled pogonia" or "large whorled pogonia" in the FEIS home page under "Find Fire Regimes".

FIRE MANAGEMENT CONSIDERATIONS

Isotria: Postfire or postthinning grazing pressure on *Isotria* species may be high (see Other Management Considerations.

Studies are needed on the possible fire adaptions of *Isotria* species, including burial depth of perennating organs (root crowns and, for large whorled pogonia, rhizomes), presence/absence of a seed bank, and depth of seed burial. Case studies are needed to document their postfire response. Closely monitoring postfire response, and subsequently modifying burn plans as needed, will increase understanding of the fire ecology of and may promote *Isotria* species.

Small whorled pogonia: No recommendations for or against using prescribed fire in plant communities with small whorled pogonia were provided in the literature as of 2019.

Large whorled pogonia: The Shawnee National Forest reports that prescribed fire and/or selective thinning of trees and shrubs can benefit large whorled pogonia by opening the overstory canopy [82]. Fire exclusion has been noted as one of the threats to large whorled pogonia populations. Hill (2017) points out that the postfire influx of nutrients, rather than opening of the canopy, may be what promotes postfire flowering in large whorled pogonia. He states that the "periodicity and optimum seasonality of fires is incompletely known and the precise reason why fires benefit the species is also a mystery" [31].

Frequent fire may not benefit large whorled pogonia. In Louisiana, frequent fires on sweetbay-blackgum forest seeps with large whorled pogonia have converted the seeps to unforested bog communities that are unsuitable habitat for large whorled pogonia [31, 43]. Given the uncertainty of fire effects to and postfire response of large whorled pogonia, carefully controlled prescribed fire and vigilant postfire monitoring are recommended for this species. Although allowing natural fire regimes to function is likely beneficial, effects of other fire management of large whorled pogonia habitats is uncertain, and research is needed on fire adaptations of and fire effects to large whorled pogonia before specific recommendations for fire use in large whorled pogonia habitats can be made [31].

MANAGEMENT CONSIDERATIONS

FEDERAL LEGAL STATUS

Small whorled pogonia

United States: Threatened [87, 88]

Small whorled pogonia was initially listed as Endangered in 1982. That listing was revised to Threatened in 1992 based on discovery of new sites, achievement of protection for many existing sites, and additional life history and population information [97].

Large whorled pogonia

United States: none [88]

Canada: Critically Imperiled (N1) [35]

OTHER STATUS

Small whorled pogonia: NatureServe (2019) ranked the overall threat impact to small whorled pogonia as medium to high due to vulnerability to habitat loss from land-use conversion to residential and commercial property [58].

As of 2019, small whorled pogonia had state-level protection status in 18 states, and large whorled pogonia had state-level protection status in 7 (table 3).

Large whorled pogonia: NatureServe (2019) considers large whorled pogonia "highly threatened" by land-use conversion, habitat fragmentation, and forestry management practices [58]. It is considered particularly at risk at the margins of its distribution, and it is listed as an "At Risk" species on the Shawnee, Mark Twain, and Green Mountain national forests [31].

Table 3—Protection and conservation status of small whorled pogonia and large whorled pogonia in the United States and Canada.

---------- Small whorled pogonia ----------		
State or province	Protection [86] or conservation status [58]	
	PLANTS Database (2019) [86]	NatureServe (2019) [58]
Connecticut	Endangered	S1, Critically Imperiled
Delaware	None	S1, Critically Imperiled
District of Columbia	None	SX, Presumed Extirpated
Georgia	Threatened	S2, Imperiled
Illinois	Endangered	S1, Critically Imperiled
Maine	Endangered	S2, Imperiled

Maryland	Endangered, extirpated	SH, Possibly Extirpated
Massachusetts	Endangered	S1, Critically Imperiled
Michigan	Endangered	SX, Presumed Extirpated
Missouri	Endangered	SH, Possibly Extirpated
New Hampshire	Endangered	S2, Imperiled
New Jersey	Endangered	S1, Critically Imperiled
New York	Endangered	S1, Critically Imperiled
North Carolina	Endangered	S1, Critically Imperiled
Ohio	Endangered	S1, Critically Imperiled
Pennsylvania	Endangered	S1, Critically Imperiled
Rhode Island	Endangered	S1, Critically Imperiled
South Carolina	None	S2, Imperiled
Tennessee	Endangered	S1, Critically Imperiled
Vermont	Endangered	SX, Presumed Extirpated
Virginia	Endangered	S2, Imperiled
West Virginia	None	S1, Critically Imperiled
Ontario	None	S1, Critically Imperiled
--**Large whorled pogonia** ---		
State or province	Protection [86] or conservation status [58]	
	PLANTS Database (2019) [86]	NatureServe (2019) rank [58]
Alabama	None	S2, Imperiled
Arkansas	None	SNR, Unranked
Connecticut	None	S3, Vulnerable
Delaware	None	SNR, Unranked
District of Columbia	None	SNR, Unranked
Florida	Endangered	S1, Critically Imperiled
Georgia	None	S3, Vulnerable
Illinois	Endangered	S1, Critically Imperiled
Indiana	None	S3, Vulnerable
Kentucky	None	S4-S5, Apparently Secure-Secure
Louisiana	None	S3, Vulnerable
Maine	Possible extirpated	SX, Presumed Extirpated
Maryland	None	SNR, Unranked
Massachusetts	None	S3, Vulnerable-S4
Michigan	Threatened	S2, Imperiled
Mississippi	None	S3, Vulnerable
Missouri	None	S1- S2, Critically Imperiled-Imperiled
New Hampshire	Endangered	S1, Critically Imperiled
New Jersey	None	S4, Apparently Secure
New York	Exploitably vulnerable	S3-S4, Vulnerable-Apparently Secure
North Carolina	None	S2-S3, Imperiled-Vulnerable
Ohio	None	SNR, Unranked
Oklahoma	None	S1, Critically Imperiled
Pennsylvania	None	SNR, Unranked
Rhode Island	None	S3, Vulnerable
South Carolina	None	SNR, Unranked

Tennessee	None	SNR, Unranked
Texas	None	S1, Critically Imperiled
Vermont	Threatened	S2, Imperiled
Virginia	None	S5, Secure
West Virginia	None	S5, Secure
Ontario	None	SH, Possibly Extirpated

IMPORTANCE TO WILDLIFE AND LIVESTOCK

Palatability and Nutritional Value

Isotria species are palatable to white-tailed deer [9, 31, 73, 87]. Other known grazers include feral pigs [87], rabbits [31, 87], turtles [31], camel crickets, and slugs [11, 31, 73, 87]. White-tailed deer in particular graze *Isotria* species, and may seek them out preferentially [31]. Overgrazing by white-tailed deer [23, 31, 87], feral pigs, and rabbits [87] sometimes causes considerable damage or mortality to these orchids.

Information on the nutritional value of *Isotria* species was not available in the literature as of 2019.

Cover Value

Predatory spiders use ***Isotria*** flowers as hideouts for capturing floral visitors [51].

VALUE FOR RESTORATION OF DISTURBED SITES

Isotria: Small whorled pogonia and large whorled pogonia are not used for restoration. Cultivation from seed has not been successful [10, 38, 40], possibly because associated mycorrhizae fail to establish [10]. Transplanting has met with little success [31, 40]. In New Hampshire, 147 small whorled pogonia plants were moved from a site slated for development to protected state land that already had an existing small whorled pogonia population. The effort was "an almost total failure": 96% of the transplants (141 plants) failed to emerge in the last 4 years of 8 years of monitoring, and they were considered dead. Season of transplanting (July or September) did not affect survivorship. The authors concluded that "transplanting of *Isotria medeoloides* should not be considered a viable alternative to protection of plants *in situ*" [10].

Mycorrhizae associated with *Isotria* are not well studied, and a better understanding of these fungi is essential for management and restoration of sites with *Isotria* [47, 64, 91]. Ectomycorrhizal Russulaceae species are associated with small whorled pogonia [47, 64], and *Rhizoctonia* fungi have been isolated from large whorled pogonia roots ([77], Mehrhoff 1983, personal communication cited in [91]). A honey mushroom (*Armillaria mellea*) [91] may be associated with small whorled pogonia as well. Efforts to cultivate known mycorrhizae associated with Isotria have not been successful (McCormick 2013, unpublished data cited in [40]).

OTHER USES

No information is available on this topic.

OTHER MANAGEMENT CONSIDERATIONS

Protection of ***Isotria*** species is highly dependent upon safeguarding existing and historical habitats [31]. Small populations are at risk of winking out due to stochastic events such as severe wildfire, major storms, or drought [35]. Use of fungicides or herbicides is likely to harm *Isotria* [31]. Nonnative invasive plant species (e.g., garlic mustard, Japanese honeysuckle, and Nepalese browntop) are potential threats

[35, 82], although effects of invasive plants species to *Isotria* were not well studied as of 2019. On the Shawnee National Forest, Nepalese browntop is replacing large whorled pogonia in seep springs [82].

Losses of **small whorled pogonia** populations are attributed to residential and commercial development [10, 31, 93], grazing by white-tailed deer [10, 23, 31, 93] and rabbits [31]; soil compaction from logging or other heavy equipment [31]; habitat fragmentation and consequent poor seed dispersal; trampling by feral pigs [31]; and illegal plant collection [10]. Surveys across small whorled pogonia's distribution showed declines in many populations over 8- to 15-year periods. Causes of these declines were not due to "obvious environmental changes" and could not be determined [91]. Loss of historical populations in Maryland and the District of Columbia was due to land development [91]. White-tailed deer can greatly reduce small whorled pogonia populations [23, 31]. In Maine , for example, about 96% of plants severely grazed by white-tailed deer herbivory died within 4 years, compared to 58% of ungrazed plants (n = 100 paired plants) [23, 31]. Hill (2017) stated that in Virginia "the magnitude of threat from deer browse of *Isotria medeoloides* populations may be second only to development of its habitat". White-tailed deer exclosures have protected an small whorled pogonia population in Virginia from overgrazing [31]. Regionally, there are more populations in decline in the Southeast than in the Northeast [53]. Most small whorled pogonia populations in the Southeast contain <25 individuals, and are subject to local extinction [87].

Overstory thinning apparently increases small whorled pogonia abundance [9, 23, 38, 82]. In New Hampshire, light transmittance to the forest floor approximately doubled after a winter, over-snow treatment that removed all shrubs and thinned basal area of mixed conifer-deciduous forest by 25%. On thinned plots, tree basal area was reduced from 173.7 ft^2/acre to 44.0 ft^2/acre (39.9 m^2/ha to 10.1 m^2/ha), with shade-tolerant species such as eastern hemlock and red maple targeted for thinning. In posttreatment year 2, the number of small whorled pogonia stems and seed capsules on thinned plots was about twice that on untreated plots ($P < 0.01$). It was the first increase in stem production in 14 years of monitoring. Stem heights of plants on thinned plots remained longer than those of plants on unthinned plots through 11 posttreatment years. On all plots, plants did not produce seed capsules in the first year of treatments. After that, plants on thinned plots produced more seed capsules than plants on untreated plots. Over 11 posttreatment years, the mean annual proportion of stems with seed capsules averaged 22% on thinned plots and 5% on untreated plots. Prior to treatments, seed capsule production was negligible in both plot groups [9].

However, Brumback et al. (2011) suggest that potential gains in small whorled pogonia reproduction and density by thinning could be offset by losses to grazing on sites with high white-tailed deer populations. In their New Hampshire, heavy grazing by white-tailed deer was anecdotally "very evident" on small whorled pogonia plants in thinned plots but not on untreated control plots [9]. In Frederick County, Maryland, density of orchid species, including small whorled pogonia, was negatively associated with large numbers of white-tailed deer (R = -0.93) [39].

The U.S. Fish and Wildlife Service (2008) notes that while experimental and anecdotal evidence indicated that small whorled pogonia density *may* increase with thinning of the overstory canopy, those "data are preliminary and are based on observations over a limited time period" [87]. Cairn (2006, unpublished report cited in [87]) states that "natural variation found in small whorled pogonia populations, the effects of weather, seed banking, and age structure of the experimental population are unknown and may have a greater effect on the number of stems emerging annually than habitat management".

The National Park Service (2011) identified these knowledge gaps and management priorities for small whorled pogonia:

- Develop consistent method for monitoring populations and develop protocols for data collection
- Research growing conditions that lead to high dormancy and low emergence rates, including mycorrhizal associations and light and climate conditions
- Identify patterns and duration of the belowground life stage and its underlying causes
- Isolate and identify associated symbiotic mycorrhizae; identify their potential to support seed germination and seedling establishment
- Determine patterns of genetic relatedness among individuals in primary population centers [47]

In general, **large whorled pogonia** has not been studied as extensively as the Federally Threatened small whorled pogonia [31]. Hill (2019) reports that such "basic facts as the means of establishment of fungal associations, longevity, and yearly variations in colony size over a long period are not precisely known for populations of this species [large whorled pogonia], and conclusions have so far been based upon infrequent visits and the infrequent flowering observed in known populations" [31]. Overall, large whorled pogonia populations are in decline. Large populations of large whorled pogonia are apparently secure [31], but large whorled pogonia is vulnerable in areas with small, isolated populations (e.g., the Midwest). It is ranked fully secure only in Virginia and West Virginia) [31] (see Other Status). Overstory thinning has been suggested as a tool to promote large whorled pogonia [38], but its efficacy has not been tested in the field.

Threats to large whorled pogonia include habitat fragmentation, development [31, 35], fire exclusion [31], clearcutting or heavy logging [31, 35], soil compaction, conversion to pine plantations, changes in hydrology [31, 35, 43], overgrazing, and trampling by feral pigs [31]. Exotic earthworms may be a threat because they consume litter layers that help maintain large whorled pogonia and its associated mycorrhizae [35]. In 1909, Batchelder noted the conversion of a site in New Hampshire where large whorled pogonia was locally abundant to a potato field that was "doubtless more profitable to the owner, but less interesting to the botanist" [6].

The Ontario Ministry of Natural Resources (2012) identified these knowledge gaps and management goals for large whorled pogonia populations, which can also apply to populations in the United States:

- Access current status of extant and historical populations
- Provide detailed mapping of existing populations to guide habitat protection
- Identify potential areas of large whorled pogonia expansion
- Identify specific associated mycorrhizae
- Study ecological requirements of large whorled pogonia pollinators
- Study impacts of nonnative earthworms and plant species
- Study impacts of pollution [35]

Given the uncertainty of large whorled pogonia habitat requirements, management recommendations are difficult to make [31]. The Michigan Natural Features Inventory (2019) states that "Very little is known of the population dynamics of this species, thus no specific management recommendations can be suggested. Monitoring and avoidance of cutting in the immediate area of colonies are recommended at this time. It like requires the maintenance of hydrology where it occurs in or near wetlands" [52].

APPENDIX

Table A: Common and scientific names of plant species. Links go to FEIS Species Reviews.	
Common name	Scientific name
Trees	
American basswood	*Tilia americana*
American beech	*Fagus grandifolia*
American holly	*Ilex opaca*
American witchhazel	*Hamamelis virginiana*
beech	*Fagus* spp.
blackgum	*Nyssa sylvatica*
black oak	*Quercus velutina*
black spruce	*Picea mariana*
chestnut oak	*Quercus montana*
eastern hemlock	*Tsuga canadensis*
eastern white pine	*Pinus strobus*
eastern hemlock	*Tsuga canadensis*
hickory	*Carya* spp.
hophornbeam	*Ostrya virginiana*
mockernut hickory	*Carya tomentosa*
northern red oak	*Quercus rubra*
oak	*Quercus* spp.
paper birch	*Betula papyrifera*
pine	*Pinus* spp.
pitch pine	*Pinus rigida*
red maple	*Acer rubrum*
scarlet oak	*Quercus coccinea*
sassafras	*Sassafras albidum*
scarlet oak	*Quercus coccinea*
shagbark hickory	*Carya ovata*
shortleaf pine	*Pinus echinata*
sourwood	*Oxydendrum arboreum*
striped maple	*Acer pensylvanicum*
sugar maple	*Acer saccharum*
swamp chestnut oak	*Quercus michauxii*
swamp tupelo	*Nyssa biflora*
sweetbay	*Magnolia virginiana*
sweet birch	*Betula lenta*
sweetgum	*Liquidambar styraciflua*
tamarack	*Larix laricina*
tuliptree	*Liriodendron tulipifera*
Virginia pine	*Pinus virginiana*
white oak	*Quercus alba*

Shrubs	
alternateleaf dogwood	*Cornus alternifolia*
American hazelnut	*Corylus americana*
black huckleberry	*Gaylussacia baccata*
black raspberry	*Rubus occidentalis*
Blue Ridge blueberry	*Vaccinium pallidum*
common serviceberry	*Amelanchier arborea*
common winterberry	*Ilex verticillata*
deerberry	*Vaccinium stamineum*
eastern teaberry	*Gaultheria procumbens*
flame azalea	*Rhododendron calendulaceum*
flowering dogwood	*Cornus florida*
great laurel	*Rhododendron maximum*
highbush blueberry	*Vaccinium corymbosum*
Japanese honeysuckle	*Lonicera japonica*
laurel	*Kalmia* spp.
lowbush blueberry	*Vaccinium angustifolium*
mountain laurel	*Kalmia latifolia*
northern spicebush	*Lindera benzoin*
partridgeberry	*Mitchella repens*
sheep laurel	*Kalmia angustifolia*
southern bayberry	*Morella carolinensis*
Forbs	
Canada mayflower	*Maianthemum canadense*
brown widelip orchid	*Liparis liliifolia*
downy rattlesnake plantain	*Goodyera pubescens*
fiveleaf orchid	*Isotria* spp.
garlic mustard	*Alliaria petiolata*
green adder's-mouth orchid	*Malaxis unifolia*
heartleaf foamflower	*Tiarella cordifolia*
Indian cucumber	*Medeola virginiana*
large whorled pogonia	*Isotria verticillata*
liverleaf wintergreen	*Pyrola asarifolia*
moccasin flower	*Cypripedium acaule*
rattlesnakeroot	*Prenanthes* spp.
rattlesnakeweed	*Hieracium venosum*
small whorled pogonia	*Isotria medeoloides*
smooth Solomon's-seal	*Polygonatum biflorum*
whorled yellow loosestrife	*Lysimachia quadrifolia*
white snakeroot	*Ageratina altissima*
wild sarsaparilla	*Aralia nudicaulis*
Graminoids	
Nepalese browntop	*Microstegium vimineum*
sedges	*Carex* spp.

Ferns and fern allies	
Christmas fern	*Polystichum acrostichoides*
cinnamon fern	*Osmunda cinnamomea*
clubmoss	Lycopodiaceae
eastern hayscented fern	*Dennstaedtia punctilobula*
netted chainfern	*Woodwardia areolata*
New York fern	*Thelypteris noveboracensis*
osmunda	*Osmunda* spp.
royal fern	*Osmunda regalis* var. *spectabilis*
sensitive fern	*Onoclea sensibilis*
western brackenfern	*Pteridium aquilinum*
Mosses	
Lescur's sphagnum	*Sphagnum lescurii*
sphagnum	*Sphagnum* spp.

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