Gymnocarpium dryopteris

Oak Fern

Dryopteridaceae

Gymnocarpium dryopteris by Karen Johnson, 2019

Gymnocarpium dryopteris 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

Gymnocarpium dryopteris (Oak Fern) is a deciduous perennial fern. Taxonomic uncertainty regarding *Gymnocarpium* has led to its placement in a number of families over the years including Aspleniaceae, Woodsiaceae, and Dryopteridaceae (eg. Crabbe et al. 1975, Bremer 1994a, Pellinen et al. 1999) but the genus was recently transferred to Cystopteridaceae after molecular studies revealed an unexpected close relationship to *Cystopteris* and *Acystopteris* (Rothfels et al. 2013). As with most other ferns, the life cycle of *Gymnocarpium* includes two independent generations. Spores produced by mature plants initially develop into tiny free-living gametophytes with structures that produce male and female reproductive cells (gametes). Male gametes (sperm) develop in an antheridium and a female gamete (egg) develops in an archegonium. Fertilized female cells develop into the leafy plants (sporophytes) that produce the spores for the next generation, and once the sporophytes are large enough to be self-sufficient the gametophytes disintegrate (Raven et al. 1986).

Although Nayar and Kaur (1971) did not specifically address *Gymnocarpium* in their comprehensive review of gametophyte morphology, the prothallia of *G. dryopteris* are probably similar to those described for related genera. The gametophytes of comparable ferns are generally thin, flat, and oval in shape with a notch on one side and a median midrib that may be 4–8 cells thick. They typically have a short life span, producing sporophytes in less than eight months. When propagated in a controlled setting, *Gymnocarpium dryopteris* gametophytes appeared about 2–3 weeks after the spores were sown and the sporophytes developed 4–5 months later (Luna 2000).

Left: Britton and Brown 1913, courtesy USDA NRCS 2023a. Right: Bob Cunningham, 2015.

The sporophytes of *Gymnocarpium dryopteris* are rhizomatous with branching underground stems that are long, slender, scaly, and blackish in color. The fronds may be up to 5 dm in height and the thin petioles are longer than the blades. A few scales are often present near the stem base. The blades are broadly triangular and the lowest pair of pinnae (primary leaflets) is notably larger than the others and long-stalked, making the leaves look three-parted. The stalk (rachis) and blade are usually smooth but a few glands may be present. Leopold (2005) noted that Oak Fern's frond structure is similar to that of *Pteridium* species but the bracken ferns are larger and more coarsely textured. The uppermost pinnae on the fronds of *G. dryopteris* are pinnate-pinnatifid and the lower ones are more deeply divided (bipinnate-pinnatifid). The sori, which are situated near the leaf margins, are round and uncovered. (See Britton and Brown 1913, Fernald 1950, Boivin 1962, Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992, Pryer 2020).

Gymnocarpium dryopteris is a summer-green species that spends a relatively short time above ground. Frond expansion typically begins during early to mid-spring and the leaves die back in the fall (Snyder 1993, Bremer 1994b). A study in Japan found that the sporophytes only remained green for about four months (Sato 1982). In comparison to some other ferns the leaves of *G. dryopteris* have a relatively heavy coating of wax, which can help to prevent water loss and also to protect the fronds from insects, pathogens, or ultraviolet radiation. A detailed analysis of the compounds present in the waxy coating is available in Guo et al. (2018). The water-repellency conferred by the wax also facilitates the removal of particles such as dust and fungal spores by rain, dew, or fog. However, Neinhuis and Barthlott (1997) reported that the protective waxes on *G. dryopteris* leaves are mainly present while the fronds are unfolding and they wear away as the season progresses.

Gymnocarpium dryopteris is a monomorphic fern, meaning that the fertile and sterile leaves are similar in appearance, although the fertile fronds may be larger. Monomorphic ferns often produce more fertile fronds than sterile ones (Britton and Watkins 2016) but in *G. dryopteris* the percentage of fertile fronds in a colony was found to increase with stand size (Bremer 1994a). Spores may be present from June through September (Hough 1983, Weakley et al. 2022). Stone (1911) observed that the spores of one specimen collected during early July had already been released. When germination occurs soon after the spores are dispersed the plants overwinter as gametophytes (Sato 1982). Mature *G. dryopteris* plants are also able to reproduce vegetatively. Their frequently branching rhizomes can form large clones which may remain connected or break up into patches (Gartmann 1988, Bremer 2010a).

Gymnocarpium dryopteris is very similar to *G. disjunctum* (Rupr.) Ching, Pacific Oak Fern, and in the past the two ferns were viewed as a single species although subtaxons were often recognized (see Synonyms and Taxonomy section). Around the middle of the 20th century, Wagner (1966) determined that the Pacific variety was diploid while the more widespread form was tetraploid and Sorsa (1966) confirmed his findings. Ongoing investigations determined that the species were distinct and also identified another close relative in the eastern United States (*Gymnocarpium appalachianum*) that had previously been undetected (Pryer and Haufler 1993). Subsequent genetic studies indicated that *Gymnocarpium dryopteris* had originated as a hybrid, with *G. disjunctum* and *G. appalachianum* as the diploid parent species (Rothfels et al. 2014). Triploid offspring resulting from crosses between *G. dryopteris* and both of its parent species have been reported, although the resulting plants appear to be sterile (Pryer 2020). Neither *G. appalachianum* nor any *Gymnocarpium* hybrids have been documented in New Jersey (Montgomery and Fairbrothers 1992, Kartesz 2015) but both have been found in Pennsylvania (Rhoads and Block 2007). In places where they co-occur, *G. dryopteris, G. appalachianum,* and their hybrids can be difficult to distinguish (Bartgis et al. 2015).

Pollinator Dynamics

Because *Gymnocarpium dryopteris* is a non-flowering plant, pollination does not take place. Fertilization is dependent on water, which facilitates the movement of the multiflagellate sperm toward a receptive egg cell (Raven 1986). Fern gametophytes can be functionally female (producing only archegonia), male (producing only antheridia) or hermaphroditic (producing both types of reproductive cells). Each spore is capable of following multiple developmental paths, and the sex of a gametophyte is not determined until after the spore has germinated (Banks 1999).

The female gametophytes of many ferns release a hormone (antheridiogen) that induces male development in nearby undifferentiated gametophytes. Antheridiogen can also stimulate the germination of nearby spores beneath the soil surface, which then develop as male or bisexual (Banks 1999). Gartmann (1988) inferred the presence of antheridiogen in *Gymnocarpium dryopteris* after observing gametophytes that were developing in close proximity. Gartmann also noted that the sperm of *G. dryopteris* were able to move rapidly—achieving velocities of 0.1–4.5 millimeters per minute—but only remained mobile for a short time, and he suggested that the strategy could promote outcrossing. Studies of the closely related *Gymnocarpium disjunctum* documented the presence of antheridiogen and also reported that the species had high rates of outcrossing and that fertilizations by unrelated gametophytes were significantly more likely to result in sporophytes (Kirkpatrick et al. 1990, Soltis and Soltis 1990 and 1992).

Seed Dispersal and Establishment

Dispersal in *Gymnocarpium dryopteris* is carried out by spores rather than seeds. Fern spores are transported by wind and the majority are likely to be deposited locally although some can end up thousands of kilometers away (Kessler 2010). Larger spores typically travel for shorter distances (Raynor et al. 1976). Kirkpatrick et al. (1990) indicated that the spores of the similar *G. disjunctum* were particularly well adapted for wind dispersal due to their small size and surface characteristics.

Spores of *Gymnocarpium dryopteris* that do not germinate immediately may remain below ground until conditions become more suitable (Mladenoff 1990, Bremer 2010b). A deeply buried viable spore bank was found at a site in Norway where the strong presence of *G. dryopteris* propagules in the soil contrasted with the species' absence in the aboveground vegetation (Rydgren and Hestmark 1997, Rydgren et al. 1998).

Corio et al. (2009) observed that *Gymnocarpium dryopteris* was more likely to be found at sites with high earthworm density. In places where earthworms were abundant enough to reduce the litter layer, the resulting loss of soil moisture led to a significant decrease in woody seedlings so the ferns might have benefited from a reduction in competition. Other advantages to ferns from earthworm activity may include the repositioning of buried spores in the soil or the removal of certain fungi and algae that could inhibit the growth of the young plants (Hamilton and Lloyd 1991).

Gymnocarpium dryopteris sporophytes often form mycorrhizae, although fungal associations are probably not necessary for establishment as both mycorrhizal and non-mycorrhizal Oak Fern plants have been found (Wang and Qui 2006). Variable rates of root colonization have been reported for the species, ranging from 5–95% in one study and 61–80% in another (Berch and Kendrick 1982, Lee et al. 2001).

In addition to the clonal growth of sporophytes, another potential mechanism of vegetative reproduction has been described for *Gymnocarpium dryopteris*. Doposcheg-Uhlar (1911) successfully grew Oak Fern from short (1–1.5 cm) sections of stem. When placed on a suitable substrate, cortex cells in the cut sections proliferated and formed buds which eventually developed into new plants. The results of that experiment suggest that some vegetative dispersal might be also achieved by the relocation of broken stem or rhizome fragments.

Habitat

Gymnocarpium dryopteris has been recorded at elevations of 0–3000 meters above sea level, although it is more frequently located at medium to high elevations. It is typically found in cool forested sites. The canopy may be dominated by hardwoods, coniferous trees, or mixed species. Oak Fern can also grow along the edges of woods, swamps, or bogs (McFarland 1916, Hough 1983, Meidinger and Pojar 1991, Rhoads and Block 2007, Guo et al. 2018, Pryer 2020, NJNHP 2022, Weakley et al. 2022). *G. dryopteris* is a characteristic species of mature forests in Europe (Bader et al. 1995, Hermy et al. 1999) and the fern has also been associated with climax forests in the Rocky Mountains (Cormack 1953). In the Netherlands *G. dryopteris* sometimes establishes on canal walls (Bremer 1994b). An occurrence in northernmost Canada was found in a *Betula/Alnus* thicket (Cody et al. 2003) while the habitat of an occurrence at the extreme southern end of the fern's range was described as a sandstone ledge adjacent to the bottom of a perennial creek in a canyon (Boucher 1988). At one New Jersey site the fern was noted to be growing on rotting logs or *Sphagnum* mosses (NJNHP 2022).

Gymnocarpium dryopteris flourishes in shade (Gartmann 1988, Leopold 2005, NJNHP 2022). Bremer (2010b) reported that populations in the Netherlands were located in sites that were at least 75% shaded. Although the fern is classified as an upland species throughout much of the eastern United States (see next section) the places where it grows are frequently described as moist or occasionally as wet (Gartmann 1988, Meidinger and Pojar 1991, Bremer 1994b, Leopold 2005, NJNHP 2022, Weakley et al. 2022). *G. dryopteris* often favors acidic substrates (Hough 1983, Leopold 2005): Gartmann (1988) suggested that Oak Fern was an indicator of acid soil and would only occur over limestone if the surface was acidified. Exceptions have been noted in the Netherlands, where *G. dryopteris* is usually associated with acidic sites but also grows on walls with alkaline mortar and in transition zones between calcareous and acid soils on the forest floor (Bremer 2010a). Salinity inhibits spore germination and establishment (de Groot and During 2013).

Wetland Indicator Status

The U. S. Army Corps of Engineers divided the country into a number of regions for use with the National Wetlands Plant List and portions of New Jersey fall into three different regions (Figure 1). *Gymnocarpium dryopteris* has more than one wetland indicator status within the state. In the Northcentral and Northeast region the fern is a facultative upland species, meaning that it usually occurs in nonwetlands but may occur in wetlands. In other parts of New Jersey *G. dryopteris* is an upland species, meaning that it almost never occurs in wetlands. In the central and western United States Oak Fern is facultative, indicating that it is equally likely to occur in wetlands or nonwetlands (U. S. Army Corps of Engineers 2020).

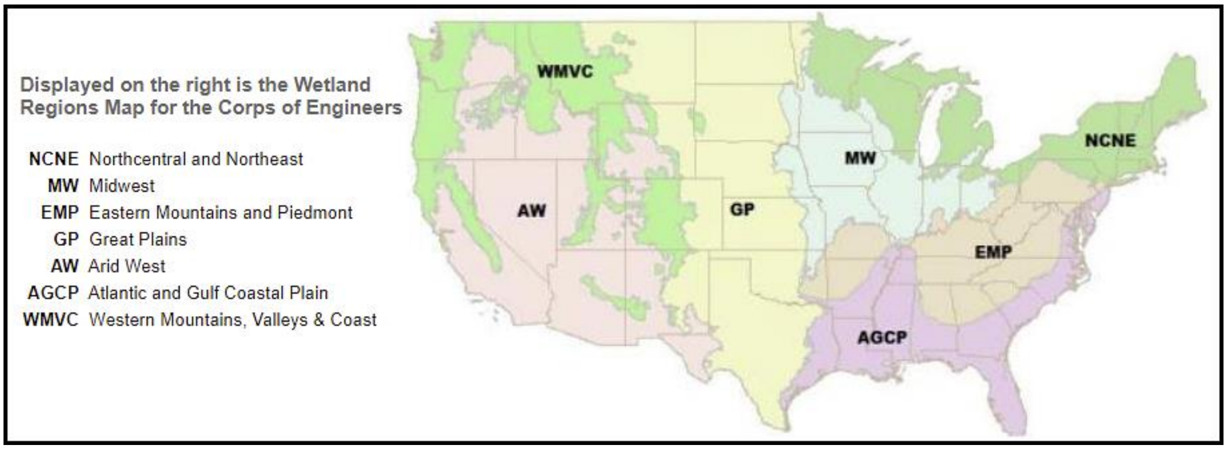

Figure 1. Mainland U. S. wetland regions, adapted from U. S. Army Corps of Engineers (2020).

USDA Plants Code (USDA, NRCS 2023b)

GYDR

Coefficient of Conservancy (Walz et al. 2020)

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

Distribution and Range

The global range of *Gymnocarpium dryopteris* extends throughout the northern hemisphere (POWO 2023). The map in Figure 2 depicts the extent of *G. dryopteris* in North America.

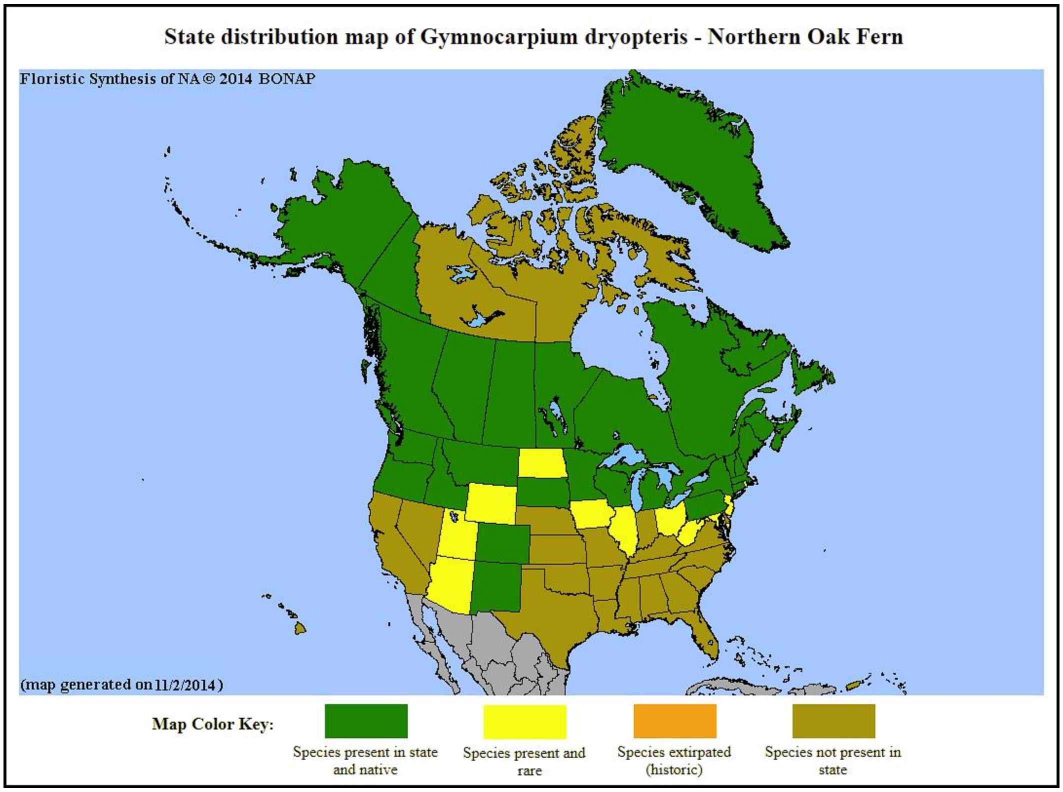

Figure 2. Distribution of G. dryopteris in North America, adapted from BONAP (Kartesz 2015).

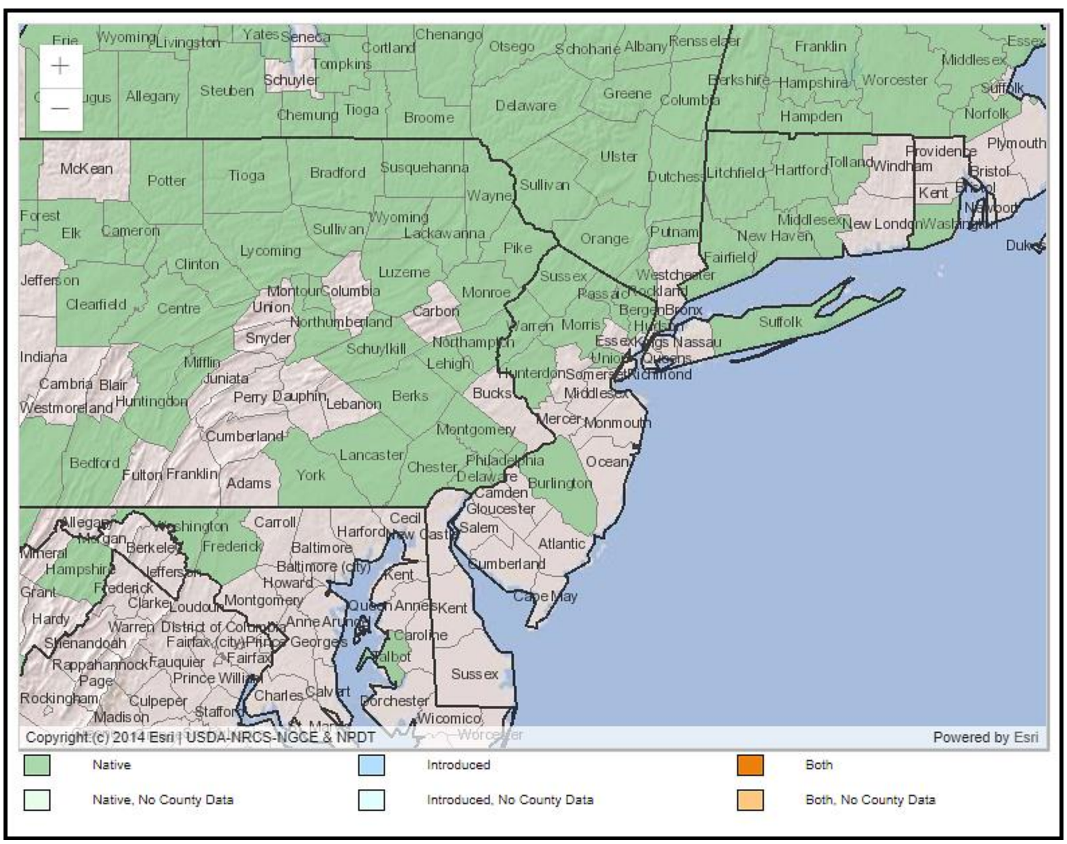

Figure 3. County records of G. dryopteris in New Jersey and vicinity (USDA NRCS 2023b).

The USDA PLANTS Database (2023b) shows records of *Gymnocarpium dryopteris* in eight New Jersey counties: Bergen, Burlington, Hunterdon, Morris, Passaic, Union, Sussex, and Warren (Figure 3 above). The data include historic observations and do not reflect the current distribution of the species. The Burlington County record, which is the southernmost report of the species in the state, was based on a single 1899 specimen collected in an abandoned well shaft so that occurrence was considered anomalous (Stone 1911, Taylor 1915).

Conservation Status

Gymnocarpium dryopteris appears to be 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 2023). The map below (Figure 4) illustrates the conservation status of *G. dryopteris* in the United States and Canada. Oak Fern is critically imperiled (very high risk of extinction) in six states, imperiled (high risk of extinction) in four states, and vulnerable (moderate risk of extinction) in one state. The fern is also vulnerable in Nunavut, although it is secure or apparently secure throughout all of the other Canadian provinces.

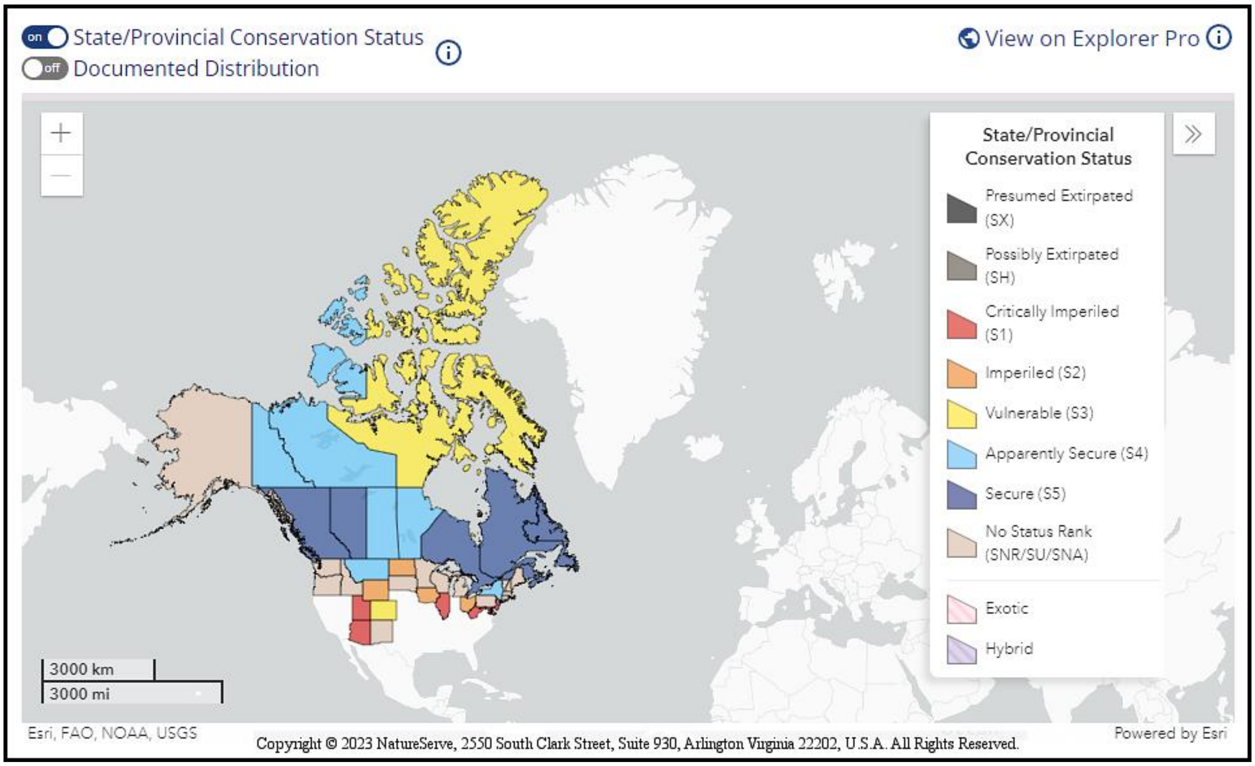

Figure 4. Conservation status of G. dryopteris in the United States and Canada (NatureServe 2023).

Gymnocarpium dryopteris is critically imperiled (S1) in New Jersey (NJNHP 2022). The rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *G. dryopteris* has also been assigned a regional status code of HL, signifying that the species is eligible for protection under the jurisdiction of the Highlands Preservation Area (NJNHP 2010).

The first documented populations of *Gymnocarpium dryopteris* in New Jersey were located in Passaic and Warren counties (Britton 1889). Setting aside the spurious record from Burlington County, Taylor (1915) characterized the state distribution of the species as rare and local from Hunterdon, Somerset, Union, and counties to the north. Hough (1983) noted that *G. dryopteris* was decreasing in New Jersey and Natural Heritage Program records indicate that the fern's status in the state has transitioned from imperiled to critically imperiled during the 21st century (NJNHP 2001, 2010, and 2014). Two-thirds of the documented populations are now ranked as historical or extirpated and the five extant occurrences are restricted to two counties (NJNHP 2022).

Threats

New Jersey's two largest populations of *Gymnocarpium dryopteris* face some potential threats from invasive plants. Species of concern noted in the vicinity of the occurrences included *Alliaria petiolata, Berberis thunbergii, Rosa multiflora*, and *Microstegium vimineum* (NJNHP 2022). Once established, all of those non-indigenous species can become dominant and replace native flora. There is some indication that *G. dryopteris* may be a poor competitor: Bremer (2010b) observed that Oak Fern was able to "colonize bare soils and thrive until eliminated by competition" and that *G. dryopteris* was outcompeted by another native fern (*Athyrium filix-femina*).

One former New Jersey occurrence was destroyed by development, and in other parts of its range reported threats to *Gymnocarpium dryopteris* have included habitat destruction, groundwater depletion, herbivory, and trampling (Snyder 1993, Bråthen and Oksanen 2001, Bremer 2010a). The application of herbicides (eg. Glyphosate) during the growing season is harmful to the fern (Snyder 1993) and some decreases in vigor may result from pollution (Trubina 2009).

The response of *Gymnocarpium dryopteris* to canopy removal can vary depending on the type and scale of the disturbance. For example, Mladenoff (1990) found that small gaps were favorable for the establishment and growth of *G. dryopteris* but Rydgren et al. (1998) noted that the species was absent from disturbed patches despite the presence of abundant propagules in the soil. When trees are uprooted buried spores may become closer to the surface, creating an opportunity for germination (Rydgren and Hestmark 1997). *G. dryopteris* has been known to initially increase following gap formation but its persistence may depend on the subsequent trajectory of succession, so small gaps that promote emergence of the fern but not of woody species may be the most beneficial (Bremer 1994a and 2010b, Mladenoff 1990). Large scale canopy removal such as that resulting from logging often results in drying of the soil, which can benefit *G. dryopteris* at sites that were initially wet but trigger a decline in the species at drier sites (Snyder 1993).

Gymnocarpium dryopteris appears to be somewhat tolerant of fire but it does not usually benefit from burns. McFarland (1916) observed that it was one of the few forest ferns which remained in areas that had been cut over and burned although Engelmark (1987) found that it was more likely to become prevalent at sites that had experienced low fire frequency. Fire destroys standing fronds but *G. dryopteris* can regenerate from rhizomes and banked spores, although frequent fires are likely to take a greater toll (Snyder 1993). The local impact of a burn might also depend on the post-fire community composition.

Gymnocarpium dryopteris produces some oils and proteins that may provide some protection against disease or pests. High levels of antifungal activity were detected in essential oils extracted from the fern (Sunar et al. 2019). Protein extracts derived from *G. dryopteris* were found to cause high levels of mortality in one common insect herbivore, although they had no effect on another (Markham et al. 2006). Bremer (2010a) noted that Oak Fern rarely experiences significant damage as a result of invertebrate herbivory. However, the chemical defenses do not appear to deter mammalian herbivores. *G. dryopteris* is a preferred forage species of European Reindeer (*Rangifer tarandus*) and losses from browsing can be exacerbated by trampling (Bråthen and Oksanen 2001). Snoksrud (2020) similarly reported detrimental effects of herbivory and associated trampling by Moose (*Alces alces*) and Red Deer (*Cervus elaphus*). Grizzly Bears (*Ursus arctos*), Elk (*Cervus canadensis*), and livestock have also been known to consume Oak Fern fronds (Snyder 1993, Bremer 2010a). However, herbivores that preferentially browse on woody species may actually benefit the fern in certain situations (Bremer 2010b). Increases in *G. dryopteris* have been reported in places where heavy browsing by White-tailed Deer (*Odocoileus virginianus*) and Moose have suppressed the growth of more competitive species (Frerker et al. 2013, Bachand et al. 2015).

An assessment of rare species in Illinois, another state where *Gymnocarpium dryopteris* is at the southern end of its range and ranked as critically imperiled, concluded that the fern is moderately vulnerable to climate change (Molano-Flores et al. 2019). A vulnerability score of Moderate indicates that the abundance or range of the species within that state is likely to decrease by 2050. Changing climactic conditions are also likely to significantly increase the vulnerability of *G. dryopteris* populations in New Jersey, where shifting precipitation patterns are resulting in higher temperatures, more intense storms, and lengthier droughts (Hill et al. 2020). Oak Fern can tolerate brief periods of submergence as long as the roots do not remain waterlogged for too long (Bremer 2010a). However the species is sensitive to drought stress (Winkel and Wood 2022) and even in near-drought conditions the withering and discoloration of fronds has been observed in a New Jersey population (NJNHP 2022). *G. dryopteris* plants that grow in drier habitats sometimes develop fewer and smaller stomata to limit water loss but Winkel and Wood (2022) found that the adaptation did not increase drought tolerance in the fern. The authors suggested a critical water stress threshold of 15% soil moisture combined with a relative air humidity below 75% for the species. The delicate fronds of *G. dryopteris* can also be destroyed by severe storms, although early in the season the plants may produce some smaller replacement leaves (Bremer 1994a). A West Virginia population was apparently extirpated in 2012 by Superstorm Sandy, which uprooted and downed many trees at a site where the fern had previously been found (Fox 2018).

Management Summary and Recommendations

An updated statewide status assessment is recommended for *Gymnocarpium dryopteris*. Only one of New Jersey's five extant populations has been monitored within the past decade, one occurrence has not been observed since 1956, and two of the other colonies were relatively small when last seen. Eight occurrences which were last observed between 1886 and 1958 have been ranked as historical based on the presence of potentially suitable habitat so diligent searches might turn up a few that are still extant. More frequent monitoring of known populations is suggested in order to document current risk levels from nonindigenous plant species and identify any other emerging threats. Some site-specific plans for the management of invasive flora may be needed since the fern appears to be a poor competitor.

Synonyms and Taxonomy

The accepted botanical name of the species is *Gymnocarpium dryopteris* (L.) Newman. Orthographic variants, synonyms, and common names are provided below (ITIS 2021, POWO 2023, USDA NRCS 2023b). Although the generic name *Gymnocarpium* was established in 1851 it was largely overlooked for more than a century, and in the interim Oak Fern was assigned to an assortment of genera due to a lack of clarity regarding the relationship between *Gymnocarpium* and other fern taxa (Wagner 1966, McNeill and Pryer 1985).

Probably the most confusing synonym that has been assigned to *G. dryopteris* is Morton's (1941) *Dryopteris disjuncta*. As discussed in the Life History section, *Gymnocarpium dryopteris* and *G. disjunctum* are now recognized as distinct species. At the time, however, Morton did not feel that their differences were worthy of nomenclatural distinction so he lumped them all under *D. disjuncta* and Fernald (1950) followed his lead in applying the name broadly. Some later authors designated *Gymnocarpium dryopteris* as the "common" oak fern and treated *G. disjunctum* as either a subspecies or variety (eg. Boivin 1962, Wagner 1966, Sarvela 1978).

Botanical Synonyms

Aspidium dryopteris (L.) Baumg.
Carpogymnia dryopteris (L.) Á. Löve & D. Löve
Currania dryopteris (L.) Wherry
Dryopteris disjuncta (Ledeb.) C. V. Mort.
Dryopteris dryopteris (L.) Britton
Dryopteris linnaeana C. Chr.
Dryopteris pulchella (Salisb.) Hayek
Dryopteris pumila V. Krecz
Dryopteris triangularis Herter
Lastrea dryopteris (L.) Bory
Nephrodium dryopteris (L.) Michx.
Phegopteris dryopteris (L.) Fée
Phegopteris dryopteris f. *interrupta* Jewell
Phegopteris dryopteris var. *minor* Farw.

Common Names

Oak Fern
Common Oak Fern
Northern Oak Fern
Western Oakfern

Phegopteris triangularis St.-Lag.
Polypodium conjunctum Schur
Polypodium dryopteris L.
Polypodium dryopteris var. *glabrum* Neilr.
Polypodium dryopteris var. *glandulosum* Neilr.
Polypodium dryopteris var. *rigidius* Hook.
Polystichum dryopteris (L.) Roth
Thelypteris dryopteris (L.) Sloss.

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