The Distribution and Ecology of *Dryopteris* in Southeastern Virginia and Adjacent North Carolina¹

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The pteridophyte flora of southeastern Virginia and northeastern North Carolina has received considerable study during the past century. Such notable botanists as Chickering, Palmer, Kearney, Small, Wherry, and Fernald have botanized in this region (see the literature review in Kirk et al., 1978). More recently, the Dismal Swamp and contiguous areas have been studied, and the results of these efforts have been included in the Floras published for North Carolina (Radford et al., 1968) and Virginia (Harvill et al., 1977). The genus *Dryopteris* has received special attention, for it was in 1899 that Palmer first collected *D. celsa* (Palmer) Small in the Dismal Swamp. More recent studies on the genus in the Dismal Swamp through 1973 are summarized in Wagner and Musselman (1978).

The present paper presents new information on the distribution of *Dryopteris* species and hybrids collected since 1974, not only in the Dismal Swamp but throughout the Virginia counties of Norfolk (now the City of Chesapeake), Nansemond (now the City of Suffolk), Southampton, Isle of Wight, and Surry, as well as the North Carolina counties of Hertford, Gates, Chowan, Perquimans, Pasquotank, and Camden. This is an area roughly delimited by the James River to the north, the Atlantic Ocean to the east, the Chowan River to the west, and Albemarle Sound to the south (Fig. 1). This work indicates that *Dryopteris* is more widely distributed in the area than formerly thought.

Our field observations indicate that in this area *Dryopteris* species always are ecotone plants. Although they are invariably found in areas contiguous with swamps, they seldom grow in inundated sites. A description of the habitat at the study location in Gates County illustrates such a habitat best. The Suffolk escarpment rises abruptly to the west. Along the slope of the escarpment are *Pinus taeda*, *Liquidambar styraciflua*, *Fagus grandifolia*, *Quercus michauxii*, *Osmunda cinnamomea*, and *Polystichum acrostichoides*.

The wet, low area which forms the eastern boundary of this *Dryopteris* site has frequent periods of inundation, especially during the winter months. As in the well drained slopes of the escarpment, no *Dryopteris* is found in this area. Dominant tree species here are *Nyssa aquatica*, *Taxodium distichum*, *Acer rubrum*, *Salix nigra*, and *Populus heterophylla*. The herbaceous vegetation is characterized by *Saururus cernuus*, *Pilea pumila*, *Arundinaria gigantea*, *Lorinseria areolata*, and *Smilax* spp.

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The ecotone where *Dryopteris* occurs contains elements from both the escarpment and the low areas. *Nyssa aquatica*, *Acer rubrum*, and *Taxodium distichum* usually are the dominant trees. The understory consists of *Ilex opaca* and *Asimina triloba*. *Lonicera japonica* (the weedy Japanese Honeysuckle) is common throughout the swamp; however, it serves as a good indicator of a *Dryopteris* site when present with the woody plants noted above. Other ferns, such as *Athyrium asplenoides* and *Lorinseria areolata*, also are abundant here. This area has high leaf litter accumulation throughout the year, usually is damp, and receives very little light.

FIG. 1. County map and the study region. FIG. 2A-H. Distribution of *Dryopteris* taxa in the study area.

The center of *Dryopteris* distribution in our study region is the Gates County site, where all eight taxa found in our area occur within a few acres (Figs. 2 and 3). The sexual species are *D. celsa* (Palmer) Small (Log Fern), a tetraploid with the genome GLL (see Wagner, 1971, for a discussion of this system of genome designation); *D. spinulosa* (Muell.) Watt (Spinulose Wood Fern), a tetraploid with IISS; *D. intermedia* (Muhl.) Gray (Fancy Fern), a diploid with II; and *D. cristata* (L.) Gray (Crested Shield Fern), a tetraploid with LLSS. Also present at this site are the hybrids *D. X separabilis* (Palmer) Small (*D. celsa* × *intermedia*), ILG; *D. X triploidea* Wherry (*D. intermedia* × *spinulosa*), IIS; *D. X australis* (Wherry) Small (*D. celsa* × *ludoviciana*), GLL; and the unnamed hybrid *D. celsa* × *cristata*, GLLS.

DISTRIBUTION OF SEXUAL SPECIES

The following list summarizes the distribution of each sexual species by county (Fig. 2). Voucher specimens cited in this paper are deposited in the herbaria of Old Dominion University (ODU) and the University of Michigan (MICH).

***Dryopteris celsa* (Palmer) Small**

Figs. 2A and 3A.

Harvill et al. (1977) listed *D. celsa* as occurring in Norfolk, Nansemond, and Southampton counties in Virginia. Two additional counties may now be added:

Isle of Wight: Two plants at margin of upland forest and small tributary of the Blackwater River, *Musselman* 5055. **Surry:** About ten plants at bottom of steep slope along small stream, *Musselman et al.* 4948.

Dryopteris celsa was described as being "rare and sporadic" and occurring no farther north than Martin County in North Carolina (Radford et al., 1968). Our field studies have shown, however, that *D. celsa* is considerably more widespread than once thought, at least in the northeastern section of the state. Recently, Hardin (1977) recorded *D. celsa* as threatened throughout all floristic provinces of North Carolina. The following list gives new county records for this fern not recorded in Wagner and Musselman (1978) or Musselman et al. (1977). In each county, the habitat is very much like the one described for the Gates County site.

Hertford: A large population of ca. 50-75 plants growing with *D. cristata*, *Nickrent* 1271. **Chowan:** A large population of ca. 75-100 plants growing with *D. spinulosa*, *Nickrent* 1295. **Perquimans:** Two small populations of less than 20 plants, one with *D. × separabilis*, *Nickrent* 1298, 1299. **Pasquotank:** Two small populations of less than 20 plants, *Nickrent* 1301, 1302. **Camden:** Many scattered populations along a creek bank; one site with four plants of *D. spinulosa*, *Nickrent* 1278. **Nansemond:** A population of ca. 500 plants near Whaleyville, *Musselman* 4944.

***Dryopteris cristata* (L.) Gray**

Figs. 2B and 3B.

Harvill et al. (1977) recorded *D. cristata* from Norfolk and Southampton counties. Efforts to find a population in the interposed Nansemond County have so far not been successful. Hardin (1977) considered this species to be threatened in the mountain and piedmont portions of North Carolina. *Dryopteris cristata* was first collected in Gates County in 1974 (*Teulings s. n.*, NCU, ODU). Since then, the Crested Shield Fern has been discovered in adjacent Hertford County (*Musselman* 5472). Only two plants were found here among a large *D. celsa* population near Parker's Ferry. Aside from the presence of *Pinus taeda*, this habitat was generally like the ecotone described earlier.

***Dryopteris spinulosa* (Muell.) Watt**

Figs. 2C and 3C.

The Spinulose Wood Fern previously was known from only Cabarrus and Mecklenburg counties in North Carolina (Radford et al., 1968), until Wagner and Musselman (1978) found it in Gates County. Hardin (1977) considered this fern to be threatened in the southern Piedmont area. The range of this fern is now extended to two more counties within our study area.

Camden: About four plants among a large *D. celsa* population, *Nickrent* 1274. **Chowan:** Only two plants among a large *D. celsa* population, *Nickrent* 1296.

The rarity of this species makes the possibility of finding the hybrid between it and *D. celsa* somewhat remote. If the hybrid is to be found, however, the most probable location would be where the two parents are abundant: in the Dismal Swamp (Wagner & Musselman, 1978).

Dryopteris intermedia* (Muell.) A. Gray*Figs. 2D and 3D.**

In our study area, the Fancy Fern is found in the Virginia counties of Norfolk and Nansemond and in Gates County, North Carolina. Apparently this fern has more restricted habitat requirements than the other *Dryopteris* taxa.

DISTRIBUTION OF DRYOPTERIS HYBRIDS***Dryopteris* × *australis* (Wherry) Small****Figs. 2E and 3E.**

The postulated parents of the Southern Wood Fern Hybrid are *D. celsa* (GGLL) and *D. ludoviciana* (Kunze) Small (LL) (Wagner, 1971). To date, *D. ludoviciana* has not been collected in the Dismal Swamp area. This would be an important discovery, since only *D. celsa* is currently known to exist in the vicinity of the hybrid. In this area, *D. × australis* is known only from the Gates County site. The distribution and cytology of this hybrid will be published separately (Wagner, pers. comm.).

Dryopteris* × *triploidea* Wherry*Figs. 2F and 3F.**

Two sites in Gates County are the only known locations for the Glandular Spinulose Fern Hybrid in our study area. The rarity of the parents, *D. intermedia* and *D. spinulosa*, and the difficulty in proper identification probably account for the fact that this hybrid is seldom seen or collected. If the two parents existed together in great enough numbers, hybridization should occur, for *D. × triploidea* is common and even abundant elsewhere in its range (Wagner, 1971). For example, Montgomery (1976) mentions that this hybrid may be even more abundant than either parental species in New Jersey.

Dryopteris* × *separabilis* (Palmer) Small*Figs. 2G and 3G.**

Previous collections of the Glandular Log Fern Hybrid have been made from Norfolk and Gates counties. A new site in Perquimans County (Nickrent 1297) was especially interesting, for it contained only two plants of *D. × separabilis* and only about 15 plants of one of the parents, *D. celsa*. A thorough search revealed no *D. intermedia*, the other parent. This raises the question of how plants of this "sterile" triploid originated at this site.

Dryopteris celsa* × *cristata**Figs. 2H and 3H.**

This hybrid is one of the more interesting fern discoveries made in the Dismal Swamp in recent years. Its genomic formula is GLLS, and the plants yield mainly sterile spores. This hybrid has been reported from only three other locations in the United States, each of which is many hundreds of miles distant from the others.

The first report of *D. celsa* × *cristata* was from the East Bergen Swamp in Genesee County, New York (Wagner & Wagner, 1965). The presence of aborted spores and later the recognition of 164 chromosomes confirmed the identification. In 1968, while exploring a swamp in Kalamazoo County, Michigan, W. H. Wagner and D. J. Hagenah again discovered this Log Fern hybrid (Wagner et al.,

FIG. 3. Representative silhouettes of fronds of *Dryopteris* taxa from the study area. FIG. 3A. *D. celsa* (Nickrent 1271). FIG. 3B. *D. cristata* (Pitchford 1023). FIG. 3C. *D. spinulosa* (Pitchford 102). FIG. 3D. *D. intermedia* (Sampson 135). FIG. 3E. *D. × australis* (Nickrent 1292). FIG. 3F. *D. × triploidea* (Pitchford 2004). FIG. 3G. *D. × separabilis* (Pitchford 2031). FIG. 3H. *D. celsa* × *cristata* (Pitchford 1005). Bar=5 cm.

1969). The third report was by Montgomery (1975) from Bergen County, New Jersey.

In 1975, this hybrid was collected from Gates County (*Musselman 4911*). *Figure 3H* shows a frond of *D. celsa* $\times$ *cristata* from this site. As with most *Dryopteris* hybrids, it is intermediate in morphology between its parents.

DISCUSSION

Data presented here indicate that *Dryopteris* taxa are much more common in southeastern Virginia and adjacent North Carolina than previously was realized. Among the sexual species, one of the more significant findings of this study is the collection of *D. spinulosa* in Camden and Chowan counties, North Carolina. With the Gates County report of Wagner and Musselman (1978) and the two Piedmont counties recorded by Radford et al. (1968), the Spinulose Wood Fern is now known from five North Carolina counties.

Certainly the rarest taxon included in this study is the unnamed hybrid *D. celsa* $\times$ *cristata*. This hybrid will be given a specific epithet for consistency in referring to *Dryopteris* hybrids (Wagner, pers. comm.). The large population (ca. 100 plants) of the hybrid is located in the midst of a huge *D. celsa* stand (over 1,000 plants) and about 25 plants of *D. cristata*.

At this same site are a few scattered plants of *D. intermedia* and abundant *D. spinulosa*, yet the only *D. cristata* hybrid found here is the one noted above. We have searched carefully for *D.* $\times$ *boottii* Underw. (*D. cristata* $\times$ *intermedia*) and *D.* $\times$ *uliginosa* Druce (*D. cristata* $\times$ *spinulosa*) to no avail.

The Glandular Log Fern Hybrid (*D.* $\times$ *separabilis*) is a very rare fern, but one which will grow in disturbed habitats. We have been able to grow large numbers of sporophytes of this triploid from its "giant" spores. While we have yet to determine with certainty the chromosome makeup of either the "giant" spores or the sporophytes, it appears that spores may play an important role in the reproduction of this plant. Wagner (1971) has proposed a mechanism which he termed "hybridization by remote control," which may be an explanation for the hybrid's occurrence. This mechanism, as opposed to others, is in agreement with field observations, for the habitat of the hybrid can only be described as weedy. The plants of *D.* $\times$ *separabilis* grew along the roadside among *Rubus cuneifolius*, *Phytolacca americana*, and abundant *Lonicera japonica*. This habitat may be unfavorable for *D. intermedia* sporophytes, but adequate for the gametophytes to persist and provide the necessary gametes for hybridization. A third alternative, which we consider unlikely, is that both parents once existed at this site but only *D. celsa* persisted.

The Log Fern (*D. celsa*) has long been the most intriguing vascular plant of the Dismal Swamp, one of the few areas where it is truly common and found in large populations. Our work indicates, however, that the Log Fern is much more common in the geographical region under consideration than was realized previously. It is to be expected in well drained soil at the border between swamps and upland areas. An exception to this is its absence along any large river. This may be due to the fact that it cannot tolerate inundation. In fact, the Log Fern appears to be an

aggressive invader of disturbed areas in swamp systems. It regularly spreads to roadbanks within the Dismal Swamp. Large, vigorous plants were abundant on dredge spoils from a drainage canal at the Camden County site. Activities which impede water movement, thus making a drier habitat, favor the spread of the Log Fern. The construction of U.S. Highway 158 in Gates County apparently blocked water movement to the south, with resultant drying and the spread of *D. celsa*. Similar examples could be given from the sites noted earlier in this paper. It may be significant that of the eight county records reported in this paper, we consider only two sites (Isle of Wight and Chowan counties) to be relatively undisturbed. In these areas, *D. celsa* does not form large stands, but rather occurs scattered among plants of *Woodwardia areolata*, *Athyrium asplenoides*, and *Onoclea sensibilis*. Thus, we consider *D. celsa* to be more abundant now than at any other time in recent history.

Dryopteris celsa is morphologically quite variable within our study area. One of us (DWS) has begun a study of variability in *D. celsa* using such characters as the pinna angle in relation to the rachis and the shape of the pinnules closest to the rachis. Of particular interest is the presence of aborted and "giant" spores in morphologically typical *D. celsa* plants.

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