Ilex opaca Ait. American Holly

Aquifoliaceae Holly family

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When the Pilgrims landed the week before Christmas in 1620 on the coast of what is now Massachusetts, the evergreen, prickly leaves and red berries of American holly *(Ilex opaca)* reminded them of the English holly *(Ilex aquifolium)*, a symbol of Christmas for centuries in England and Europe *(13,26)*. Since then American holly, also called white holly or Christmas holly, has been one of the most valuable and popular trees in the Eastern United States for its foliage and berries, used for Christmas decorations, and for ornamental plantings.

Habitat

Native Range

From the maritime forests of Massachusetts, holly (fig. 1) is scattered along the coast to Delaware. It

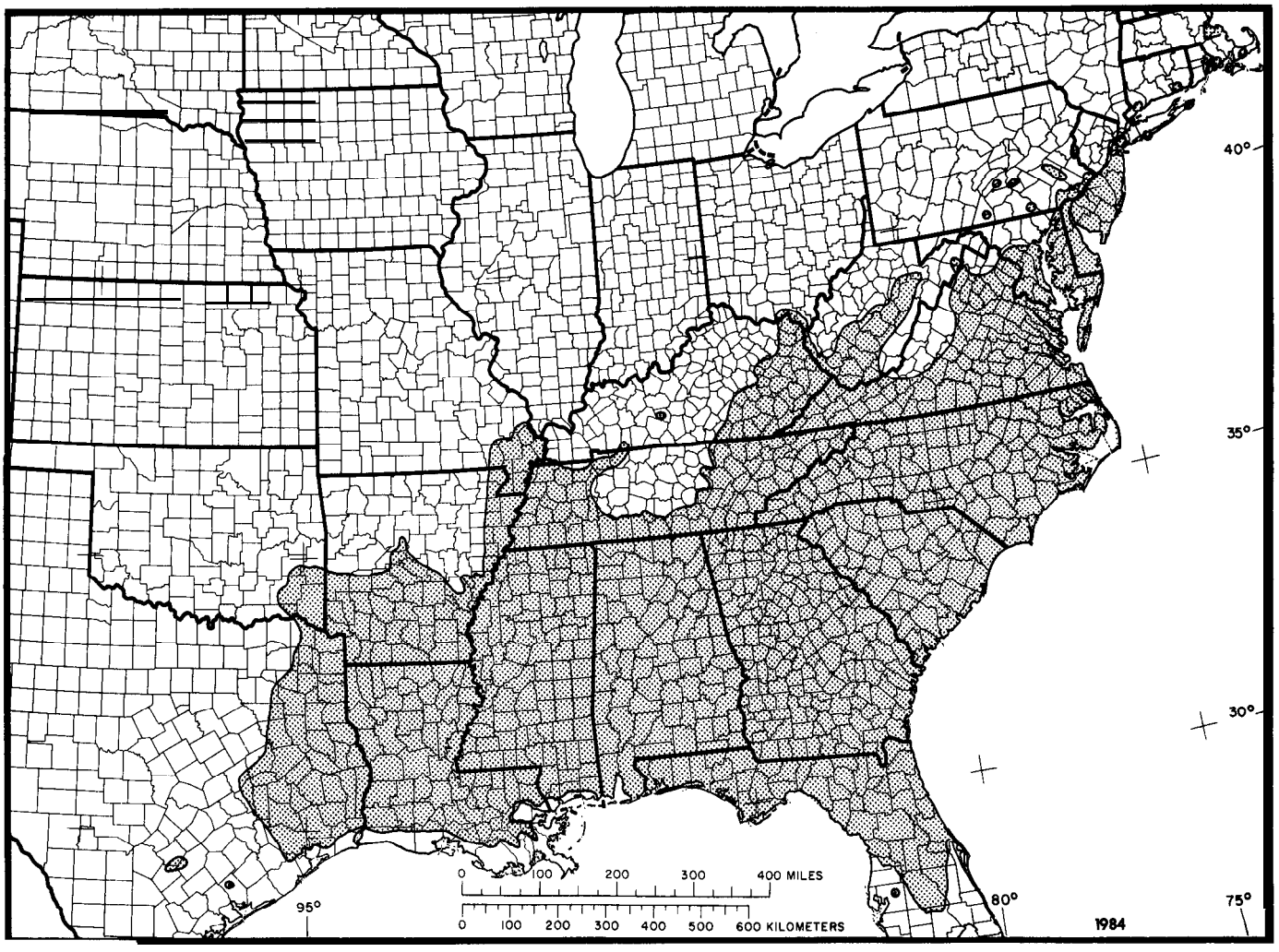

Figure *l-The native range of American holly.*

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grows inland into several Pennsylvania counties and abundantly southward throughout the coastal plain, Piedmont, and Appalachian system. The range extends south to mid-peninsular Florida, west to eastern Texas and southeastern Missouri *(20).* It corresponds roughly to the combined ranges for loblolly and shortleaf pines.

Climate

Like the southern pines, American holly is primarily a plant of the humid Southeast. Annual precipitation throughout its range is 1020 to 1650 mm (40 to 65 in) with over 2030 mm (80 in) in the southern Appalachians. Growing season varies from about 150 days in the Appalachian Mountains, the northeastern limit of the range, to almost yearlong in the central Florida peninsula. Average minimum temperature in the coastal plain portion of its range is above -18" C (0° F) but in the mountains of West Virginia, holly grows where the average low temperature is below -23" C (–10° F) *(20).* Holly cultivars in a northern Ohio arboretum, north of its natural range, have survived -29" C (-20" F) ***(12).*** American holly is the hardiest known broadleaf evergreen tree (23).

Soils and Topography

Holly survives on a wide variety of soils from near sterile Inceptisols of Atlantic sandy beaches to fertile but thin mountain Ultisols to an elevation of approximately 915 m (3,000 ft) (8). Largest trees are found in the rich bottom lands and swamps of the coastal plain (fig. 2). Growth is best on moist, slightly acid, well-drained sites such as upland pine sites and hammocks. Trees will not survive flooding or saturated soils for more than 17 percent of the growing season ***(31).*** In the northeastern portion of its range, holly is found on sandy coastal soils or dry gravelly soils farther inland ***(16).***

Associated Forest Cover

In longleaf pine-slash pine *(Pinus palustris—P. elliottii)* forests of the coastal plain, frequent prescribed fires are more limiting to the presence of American holly than site. Within that timber type, therefore, association is mainly with trees of bottom lands, swamps, or other sites not subject to burning. In the loblolly pine-shortleaf pine and upland hardwood types where fire is not so common, holly, as well as numerous other hardwoods, is found beneath the pines on a wide range of sites. Because of its slow growth and relatively short stature, holly is seldom dominant. It is an understory component of a number of forest cover types ***(10).*** Common associates of holly in various parts of its geographic range are shown in table 1.

Figure 2—*Mature* ***American holly in the Mississippi River Delta of Arkansas. This female tree*** is about ***15.2 m (50 ft) in height and 38.1 cm (15 in) d.b.h.***

Life History

Reproduction and Early Growth

Flowering and Fruiting-Hollies are dioecious; male (staminate) and female (pistillate) flowers, similar in appearance, with four to six small white petals, are produced on separate plants on the current season's growth. The male-to-female ratio for

Table l-Trees commonly associated with American holly on various sites throughout its range

Tree species	Range[1]
Sweetgum *(Liquidambar styraciflua)*	A, C, D, F, G, I
Flowering dogwood *(Cornus florida)*	A, B, D, G,
American beech *(Fagus grandifolia)*	A, B, E, G,
Red maple *(Acer rubrum)*	A, F, G, I-I
White oak *(Quercus alba)*	B, C, F, G
Water oak *(Quercus nigra)*	A, C, G, I
Hickory *(Carya spp.)*	C, D, G
White ash *(Fraxinus americana)*	C, D, F
Yellow-poplar *(Liriodendron tulipifera)*	D, F, G
Black tupelo *(Nyssa sylvatica)*	A, D, G
Southern red oak *(Quercus falcata)*	A, F, G
Post oak *(Quercus stellata)*	A, C, I-I

Key to range symbols:
A. East Texas *(15,25).*
B. Southeast Louisiana (7).
C. Mississippi River Delta (24).
D. Georgia Piedmont (24).
E. Kentucky; western hills (24).
F. Southeast Pennsylvania *(24).*
G. Virginia Coastal Plain (35).
H. New Jersey and New York: maritime forests (28).
I. North–central Florida (29).

1,930 seedlings from 10 randomly chosen, open-pollinated pistillate trees was 1.03 to 1.00 after 9 years had elapsed and all seedlings had produced flowers. Flowering began as early as age 3 and the latest bloomed at age 9, staminate plants flowering somewhat earlier on the average than pistillate. For this reason, the male-to-female ratio at age 5 was about 5 to 1 (5).

Flowering begins in April in the southern part of the range of American holly, and in June at the northern limits. Pollination is accomplished by insects, including bees, wasps, ants, yellowjackets, and night-flying moths (3). Staminate trees should be planted close to fruit-producing trees *(34).* Although some female hollies are apparently isolated by distance from pollen-bearing trees, good fruit crops are produced regularly. The fruit, commonly called "berries," are technically four-seeded drupes or pyrenes. They ripen from September through December and remain on the tree through most of the winter unless consumed by birds or other wildlife. The fruit is round to ellipsoid, about 6 to 12 mm (0.25 to 0.50 in) in diameter, and bright-but not shiny-red, orange, or occasionally yellow in color.

The four seeds in each fruit are bony with a coarsely reticulated, ridged surface (34). Seed germination is very slow, requiring from 16 months to 3 years in nature. Germination tests over a 2.5-year period indicated only 33 to 56 percent germination capacity. Overwinter storage or cold, moist stratification improves germination. Sowing immediately after collection has been recommended although complete germination does not occur until the second or third spring *(4).*

Seed Production and Dissemination-Seed production may be low in years of heavy spring rain, as rain can diminsh the wide dissemination of pollen. A late frost can kill the spring flowers, eliminating a fruit crop. Frequent prescribed burning also drastically reduces fruit production. Such crop failures are rare and localized, however, and an abundance of seed can be found each year *(19,24).* Clean seeds average approximately 61,730/kg (28,000/lb) and about four units (by weight) of fruit yield one unit of clean seeds (4). Seeds are dispersed mainly by birds and small mammals.

Seedling Development-Germination is epigeal. Following germination, holly seedlings rapidly develop a taproot and numerous lateral roots. American holly is very shade tolerant and may become established from bird droppings in the understory of upland pine plantations or bottom land hardwoods. It is very susceptible to fire and may be completely lacking in regularly or even occasionally burned forests (35). Initial growth is slow, averaging about 1.8 m (6 ft) in 16 years under medium shade (32). The bark is easily injured by fire and even large trees may be killed by light fires in the understory. Fastest growth of American holly was probably achieved in a North Carolina holly plantation; after 9 years of cultural practices such as mowing, mulching, and fertilizing, lo-year-old hollies averaged about 6.7 m (22 ft) in height and 3.7 m (12 ft) in crown spread and produced abundant fruit (24).

Vegetative Reproduction-Young holly trees usually sprout if the tops are removed by cutting or burning. Because of a taproot and a profilic lateral root system, young hollies can be transplanted without much difficulty (6). Transplanting should be done during the dormant season, usually November through March. Small plants may be dug bare-rooted if roots are kept moist, but larger plants should be balled and burlapped (34). When wild hollies are transplanted from the woods, tops should be severely pruned and most of the remaining leaves removed *(16).* Small trees should be allowed to flower before transplanting to ensure the selection of fruit-bearing individuals. Root pruning to a depth of 0.6 to 0.9 m (2 to 3 ft), a year before lifting, improves transplanting success (27). In Ohio, outside the natural range of American holly, better outplanting success has been obtained with plants 60 to 120 cm (24 to 48 in) tall than those 30 cm (12 in) or less, because of winterkill of the younger plants *(11).* Holly can be

produced from cuttings taken in August or September and December. Cuttings should be taken from the current season's ripened wood, with a small section of 2-year-old wood including several leaves. Cuttings should be set slanting in about 15 cm (6 in) of peatmoss and soil moisture, with the leaves lying flat on the surface. Treating with indolebutyric acid (IBA) and growing under high humidity with bottom heat is also recommended *(6,24)*. "Quick dips" in IBA at high concentrations (up to 20,000 p/m) are recommended for cultivars that are normally hard to propagate (27). Root cuttings are unsatisfactory.

Sapling and Pole Stages to Maturity

Growth and Yield-Because of its intolerance of fire, holly is found as scattered trees, even on good holly sites. Its slow growth and limby habit detract from its timber value. American holly under intensive culture is capable of 0.9 to 1.2 m (3 to 4 ft) of height growth per year (3).

Holly dominates some of the maritime forests of the Atlantic coast near the northern limit of its range, associated with salt-intolerant species such as black cherry *(Prunus serotina)*, eastern redcedar *(Juniper-us virginiana)*, and hackberry *(Celtis occident&is)*. One of the best developed coastal stands reported was at Sandy Hook in New Jersey, where 97 percent of the tree basal area of a 30-ha (74-acre) forest was American holly. The oldest holly was 144 years old and 62 cm (24 in) in d.b.h. Height of holly trees in these sandy coastal forests ranges from 4.6 to 9.1 m (15 to 30 ft). Older trees or those on better sites may reach 15.2 m (50 ft) (28).

The "national champion" American holly, in the Congaree Swamp of South Carolina, is 30.2 m (99 ft) tall, with a circumference of 248 cm (98 in), a trunk diameter of 79 cm (31 in), and a crown diameter of 12.2 m (40 ft) (2). Hollies 30 to 90 cm (24 to 36 in) in diameter measured near the ground are common in the Mississippi River Delta (24). Trees 30.5 m (100 ft) tall and 122.0 cm (48 in) in d.b.h. have been recorded *(18)*, but such trees were over 100 years old.

Rooting Habit-No information available.

Reaction to Competition-Holly is classed as very shade tolerant and can survive in the understory of most forest canopies, but growth may be slowed and flowering and fruit set reduced under shade (22). Leaf area increased and leaves were greener under shade *(30)*. In a mesic pine-hardwood forest of east Texas, dominated by loblolly pine *(Pinus taeda)*, southern magnolia *(Magnolia grandiflora)*, American beech *(Fagus grandifolia)*, white oak *(Quercus alba)*, and water oak *(Q. nigra)*, holly was the principal understory species *(15)*. Its slow growth allows faster growing species of the same age to overtop it. Shade and root competition in natural stands reduced average height of hollies at age 16 by about 0.3 m (1 ft) in medium shade and 0.61 m (2 ft) in heavy shade, compared with those growing in full sunlight. Crown area was reduced by one-third under medium shade and by more than one-half under heavy shade (32).

Damaging Agents-The greatest damage to holly trees is indiscriminate harvesting of foliage with berries for Christmas decorating. Before laws were passed in Maryland and Delaware to protect the holly, there was a "roadside" market for holly vandalized from trees that did not belong to harvesters. Trees were left mutilated and many died *(17)*.

Fire is another deadly enemy of American holly. Most commercial pine timberland is burned often enough to eliminate holly seedlings or sprouts, especially where livestock graze. Burning where hollies are in the midstory can seriously damage the bark and kill trees. Three annual fires in a southern pine forest reduced the number of fruit-producing holly trees by 95 percent *(19)*.

The thick evergreen leaves, which remain on the trees until the spring of their third year *(18)*, are year-long hosts to many foliage diseases and insects. Few threaten the health of the trees, but many may reduce the esthetic and commercial value of the foliage. Diseases include 14 species of leaf spot fungi, six species of black mildews, two powdery mildews, and one rust. The most common and widespread of the leafspots are caused by the fungi *Cercospora pulvinula, Phacidium curtissii, Phyllosticta opaca,* and *Physalospora ilicis.* The rust *Chrysomyxa ilicina* is known only from the southern Appalachian area. Hollies of the northeast are subject to a serious leaf and twig blight caused by *Corynebacterium ilicis (16)*.

Although nearly 30 species of insects are known to attack holly, only a few are serious pests. The southern red mite *(Oligonychus ilicis)* causes a reduction in leaf and twig growth and undesirable foliage color. The native holly leafminer *(Phytomyza ilicicola)* can damage foliage severely, causing leaves to drop prematurely. The holly midge *(Asphondylia ilicicola)* feeds on the berries causing them to remain green in color. Several species of scale insects feed on holly, including the holly scale *(Asterolecanium puteanum) (1,24)*.

Strong winds cause spines of mature leaves to puncture other leaves, rendering the foliage less valuable for decoration (24). In northern portions of

its range, twigs and branches can be killed during extreme cold periods *(12)*, although holly is quite hardy (23).

Holly is more resistant to damage from salt spray than associated woody species in the maritime forests of New England, enabling it to dominate coastal stands (29). Hollies are intolerant of flooding and may die if their roots are inundated for a period of several weeks *(31)*.

Special Uses

The attractiveness of its foliage is American holly's principal value, whether as a forest tree, planted ornamental, or Christmas decoration. The development of commercial holly orchards and the education of landowners in the value and harvesting of holly foliage have lessened the exploitation of wild hollies *(13)*.

The wood of American holly is tough and hard but not strong. It is close-grained and moderately heavy, weighing about 640.7 kg/m^3 (40 lb/ft^3). Specific gravity is 0.61 (oven-dry) and about 0.50 green. It is one of the whitest woods known, with white sapwood and ivory-white heartwood. Growth rings are almost indistinct. The wood is used for veneer and to a limited extent as pulpwood and lumber. Greatest use of the wood is for specialty items such as fancy cabinet inlays, small pieces of furniture, brush backs, handles, novelties, wood engravings, scroll work, woodcuts and carvings, and measuring scales and rules for scientific instruments; when dyed black to resemble ebony, it is used for piano keys, violin pegs, and fingerboards *(6,18,33)*.

Birds are the principal consumers of the fruit, although deer, squirrels, and other small mammals also eat them. Cattle sometimes browse the foliage. At least 18 species of birds including songbirds, mourning doves, wild turkeys, and the bobwhite are known to eat the fruit *(14,34)*. Perhaps the most important in seed dispersal, however, are the large winter-migrating flocks of small birds such as the cedar waxwing and American goldfinch. The complete stripping of all berries from a 10.7 m (35 ft) tall holly in a few seconds by a flock of cedar waxwings has been observed.

Despite the presence of saponins in the leaves and berries, American holly is not considered poisonous to man or animals (36). Although not as well known as gallberry *(Ilex glabra)* as a honey plant, its nectar makes excellent honey (24).

Figure 3—*Two branches from the same American holly tree, showing variation in leaf spininess. Branch with spineless leaves* and *fruit is from upper canopy; branch with toothed leaves is from basal sprout. (Courtesy Dr. Clair A. Brown)*

Genetics

Population Differences

American holly has 36 chromosomes, differing from the basic number for the genus *Ilex* of 9 or 10 *(24)*. Although leaf spininess and fruit colors vary, the coastal-dune hollies are usually smaller than those on the rich bottom lands of the Mississippi River Delta. Only one botanical variety other than the typical variety is recognized *(21)*. Dune holly *(Ilex opaca* var. *arenicola)* grows on deep sandy soils in north and central Florida. It has lanceolate or oblanceolate leaves with forward-pointing teeth and oval, shallowly grooved nutlets. Yellow-fruited holly, once named a variety, is now considered only the expression of the recessive yellow color gene present in nearly all red-fruited hollies. Spineless leaves were once the basis for segregating another variety but the trait is highly variable; spiny and spineless leaves often grow on the same plant (34) (fig. 3).

More than 1,000 cultivars of American holly have been named, although not all have been registered with the International Registration Authority. These do not necessarily represent different forms of *Ilex opaca;* many were selected because of unusual

growth habit, fruit color, size or shape, or degree of leaf spininess (9).

Hybrids

Topel holly *(I. x attenuata* Ashe) is a hybrid of I. *opaca* and dahoon holly *(I. cassine)*, with long spiny-pointed leaves, that grows in South Carolina and northwestern Florida *(21,34)*. Several cultivars registered under *Ilex opaca*, such as Foster, Hume, Savannah, and East Palatka, are actually I. x *attenuata* (9). Crosses have occurred between American holly and myrtle dahoon *(I. myrtifolia)*, which, like dahoon holly, is an evergreen, red-fruited shrub or small tree found on wet sites of the coastal plain (24).

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