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Distribution of common oaks (*Quercus* spp.) and regional forest types in New England

by

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Introduction

The distribution and ecology of common forest trees of eastern North America are still poorly known. Information on the regional variations in the total forest flora, particularly on the quantitative differences in the regional abundance or frequency of various tree species or combinations of these species, is even scantier. Whatever the reasons for this incomplete record, somewhat paradoxical in an area that has been settled and studied for several centuries, the need for accurate geographical and ecological data seems clear. Accurate maps of the distribution of Linnaean species, the basic units of vegetation, reflect the influence of topographic and climatic diversity on species distribution. Such botanical maps, when compared with same-scale maps of the various components of the physical environment, such as geological or geomorphological factors, may also provide partial explanations for the distribution of plants and stimulate useful questions in physiological-experimental plant ecology. Other fields that may profit from accurate knowledge of the distribution and field relations of tree species are forestry, Pleistocene and other branches of geology, hydrology, climatology, zoogeography, and remote sensing. Recent revisions in the fundamental concepts of the development of soils and landforms have also focused attention on the vegetation as an integral part of a dynamic landscape (Hack and Goodlett, 1960; Chorley, 1962; Zimmermann and Thom, 1982). There is, finally, the need to know accurately the present vegetation as a key to the past. Paleoecological or paleoclimatic interpretations based on fossil remnants of modern species must rely on knowledge of present-day ranges and ecology of the same species. Incomplete or inaccurate knowledge may lead to interpretations of the past that are partly, if not wholly, false (Davis, 1965).

The present study emphasized the oaks because these common canopy trees of the eastern deciduous forest have the northern limit of their ranges in New England. In addition, in New England as well as elsewhere in the northeastern United States (Goodlett, 1954), the oaks are useful key species in plant-geographical work because important differences in the total species composition of the forest coincide with their presence or absence. The oaks may thus be used to delimit and define important regional forest types.

A floristic map was compiled from data collected during continuous traverses through most of Massachusetts, Vermont, New Hampshire, and the southern half of Maine. Map units are based on the presence or absence of a few key species. These key species were chosen by the criterion that a species of value in interpretive plant geography is one that is common, conspicuous, and having a wide but discontinuous range. Species that are ubiquitous or rare are not used. The map units used in this study were formulated from large-scale floristic studies made in the ethol 7 1/2′ quadrangle of north-central Massachusetts by the senior author. The data were recorded on U.S. Geological Survey 1:24,000, 1:31,680, and 1:62,500 quadrangle sheets. The original field maps are on deposit at the Harvard Forest. The data were recorded in the field as color codes representing the various oaks, or combinations of oaks, present along the reconnaissance routes.

The density of the map coverage varied somewhat from quadrangle to quadrangle, depending upon the terrain, the road network, and the botanical interest of a particular area. A dense map coverage is one in which each square mile of a quadrangle was crossed at least once, except in areas lacking public roads or a forest cover. This map coverage was achieved only in parts

of north-central Massachusetts, where certain distributions and ecological relationships were studied in detail. In most other quadrangles, each quadrant, or quarter of the quadrangle, was crossed along at least one route or, more typically, along two routes (see Davis and Goodlett, 1960, figs. 1, 4). In northern New Hampshire and northern Maine, where detailed mapping revealed that oaks are absent, reconnaissance was confined to single routes, which were followed to the Canadian border. Most of the quadrangle sheets used were at a scale of 1:62,500.

The limits of the ranges shown on the present map are the lines connecting the lowest altitudinal or northernmost observed points of occurrence of the oaks, whether adult or seedling. In preparing the map, a certain amount of inter- and extra-polation has inevitably occurred; however, as the scale of the present map is smaller than that of the maps used in the field, the distributions shown are considered to be accurate. Land use was found to have remarkably little effect on the regional abundance of the oaks. At approximately the same distance from the limit of the range, and without marked differences in topography and geology, the number of points or stretches of route at which oaks were observed varied but little regardless of the total area of forest cover.

Data from the continuous reconnaissance traverses were supplemented by data obtained in sample plots or at sampling points. These data are, in part, basal area measurements, or measurements of the cross-sectional area of tree boles at 1.5 m above ground. Basal area is a direct measure of the relative local abundance of species in a given area. An indirect measure of the relative importance of a species in an area is the frequency of occurrence of that species in a given number of sampling points. This frequency, which is expressed as a percentage of the total number of sampling points, is derived from inventories of all species in sight at a sampling point or of all species within a unit area.

The two basic methods of continuous reconnaissance mapping of selected species and of quantitative sampling of the total forest flora at selected locations are mutually reinforcing. Together they provide a reliable picture of the vegetation at regional scales in an area the size of New England. The generalizations given below are based on data obtained by these methods. The map itself is based on the reconnaissance traverses.

The distributions of black and white oaks are very similar to previously published distributions (Fowells, 1965). The boundary of red oak, however, is considerably south of Fowells' boundary. The discrepancy is probably best explained by comparing the methods of compiling the two maps. Fowells' map is based on state and local vegetation maps and herbarium specimens and uses a very small scale. The present map is based on road transects, and isolated occurrences of red oak north of the generalized boundary are mapped separately. Another possible northern boundary could be drawn by connecting all the very northernmost occurrences of red oak in which case the boundary would be much nearer to Fowell's boundary.

The distribution of red oak

Red oak is the most widely distributed oak in New England (Plate 1). It is present throughout Connecticut, Rhode Island, and most of Massachusetts. In western Massachusetts, it is rare or absent only above 460 m in Berkshire

County. In Vermont, red oak is present in the valley of the Connecticut River as far north as Essex County, and in the Champlain Valley it extends north across the Canadian border. The altitudinal limit of red oak in Vermont varies with latitude. In the southern Green Mountains, red oak is common to altitudes of 490 m, but scattered trees or small stands were observed as high as 670 m. In central Vermont, in Addison and Windsor counties, red oak was seen only at altitudes of 340 m or lower. Near the Canadian border, red oak apparently grows only below 270 m.

In New Hampshire, red oak is present throughout the southern half of the state, except in the west-southwest at altitudes generally above 580 m. On the southeast-facing slope of Mt. Monadnock, red oak was seen, however, at a maximum altitude of 790 m. In the White Mountains, red oak is apparently absent or rare above 400 m. Red oak is missing from most of Coos County, northern New Hampshire.

In Maine, red oak occurs south of a diagonal line running roughly from the Androscoggin River at the Maine-New Hampshire line to the Washington County-Aroostook County line. South of this line, red oak is, however, largely absent from Washington County, in the eastern-most part of Maine. The range of red oak extends northward of the the diagonal line by more than 30 km in the valleys of the Kennebec and Penobscot Rivers. In northern Maine, a striking feature of the distribution of red oak is the occurrence of many isolated stands well to the north of the main area of occurrence of this species. The northernmost of these stands were found in northern Penobscot County, along Moosehead Lake in Piscataquis County, and in southern Aroostook County. Planted red oaks were seen as far north as northern Aroostook County.

In Vermont and Maine, the range of red oak was found to coincide roughly with areas having an average annual frost-free period of 120 days or longer (fig. 1). Extreme temperatures do not seem to control the range of red oak (or of the other oaks), because this species occurs in areas where the minimum temperatures are as low or lower than those occurring in areas lacking red oak. The range of oaks seems to be controlled primarily by the length and temperature regime of the growing season; the frost-free period shown on climatic maps approximates an indirect measure of the length of this season. More accurately, the amount of energy available for the completion of the flowering and fruiting cycle is probably an important climatic-physiological relationship controlling the geography of plants.

At its northern or upper altitudinal limit, red oak is consistently found in well-drained habitats throughout New England. These habitats include glacio-fluvial sands and gravels, steep and south-facing slopes, high river banks, and sandstone rubble. In southern New Hampshire, however, red oak was found on valley bottoms. In southern New York State, only 480 km south of its northern limit in northern Vermont, red oak is most common in relatively moist coves (Davis and Goodlett, 1960; Davis, 1965).

The distribution of white oak

White oak is probably the second most common and conspicuous oak in New England. It is common in Connecticut, Rhode Island, and most of Massachusetts. In north-central Massachusetts, it is apparently absent above 290 m, whereas in the western part of the state it is rare above 370 m. Along the Massachusetts-Connecticut line, white oaks were observed at altitudes as

high as 480 m.

White oak ranges far into northern New England, but apparently grows north of the Canadian border only in the Champlain Valley of northwestern Vermont. In the Connecticut Valley, white oak was seen as far north as the northern border of Orange County, at altitudes below 210 m. In New Hampshire, white oak was found at maximum altitudes of about 270 m, but it is generally common only below 180 m. Along the Maine-New Hampshire line in Carroll, Strafford, and York counties, the upper limit of the range of white oak coincides with the 180-m contour in a strikingly consistent fashion.

In Maine, white oak was seen as far north as the southern end of Oxford County and the southern end of Franklin County, at an altitude of about 200 m. In the Kennebec Valley, white oak apparently ranges as far north as the northern edge of Kennebec County, but occurs in stands only from southern Kennebec and southward.

In Maine, and elsewhere in New England, white oak generally grows in areas with an average annual frost-free period of at least 140 days.

In central and northern New England, white oak grows in well-drained gravelly deltaic deposits (northwestern Vermont), on sandy outwash plains (southeastern New Hampshire and southern Maines), on gravelly-cobbly eskers (for example, near Lake Sebago, Maine), and on steep banks and bluffs along large rivers such as the Connecticut and the Kennebec.

The distribution of black oak

The distribution of black oak in New England is similar to that of white oak. The northern or upper limit of black oak is commonly less than 30 km south of or less than 180 m below that of white oak, particularly in southern New Hampshire and Vermont and in central and western Massachusetts.

In western Vermont, black oak has its northernmost known area of occurrence along Lake Champlain, on sands and gravels of the Winooski River delta. Across Lake Champlain, in New York State, black oak has, similarly, its northern limit on the sandy gravelly Pleistocene-early Recent delta of the Ausable River. In the Connecticut Valley, the northern limit of black oak is apparently along the Cheshire and Sullivan County line. Elsewhere in New Hampshire, the northern or upper limit of black oak is strikingly similar to that of white oak. In Maine, on the other hand, the range of black oak is more restricted than that of white oak, as black oak apparently does not occur north of the Lake Sebago area. In western Massachusetts, black oak was not observed above 270 m.

In New England, as elsewhere, black oak grows primarily in well-drained habitats such as steep or convex landforms or on coarse-grained glacio-fluvial deposits.

The distribution of other oaks

Other oaks that have the northern limit of their ranges in New England are scarlet, bur, scrub, chestnut, and swamp white oak. The distribution of these oaks was not mapped as systematically as that of red, white, and black oak, and therefore the data shown on figure 2 give only partial indication of the ranges of these oaks.

The northern limit of scarlet oak is poorly known, partly because this

species is not easily identified. Scarlet oak may occur in the Champlain Valley of Vermont as far north as the Winooski River and in the Connecticut Valley as far north as Orange County, Vermont. In New Hampshire, scarlet oak was identified at least as far north as Carroll County. In these two states the northern limit of the range of scarlet oak seems to coincide approximately with that of white oak. In Maine, however, scarlet oak apparently ranges farther north than white oak, and of the limit previously reported (fig. 2 and Plate 1; Munns, 1938, p. 100). Scarlet oak was positively identified in the Androscoggin Valley in Oxford County and in south-central Franklin County. Scarlet oak may also be present in the Kennebec Valley in southern Somerset County. Thus in western Maine, scarlet oak ranges almost as far north as red oak.

Bur or mossy-cup oak is common in the Champlain Valley of western Vermont. It is particulary common on fine-grained lacustrine or marine deposits. Bur oak has also been observed near Bangor, Maine, where this species has well-documented isolated distribution (see Davis, 1965, p. 378, 384).

In northern New England, scrub or bear oak is particularly common on sandy-gravelly outwash plains in east-central and southeastern New Hampshire. It is also common on the same materials in southern Maine, south of a line running from southern Oxford County to the city of Portland on the coast. In Carroll County, New Hampshire, in southern Oxford County, and in York County, Maine, scrub oak commonly forms dense understory thickets in stands of pitch pine growing on outwash plains. This distinctive type of vegetation occurs, for example, on lake shores along the New Hampshire-Maine line in Carroll and York Counties. White pine, red pine, trembling aspen, and gray birch are also common in this pitch pine-scrub oak forest. Scrub oak has not been observed in Vermont.

Chestnut oak was observed in western Vermont, in the Connecticut Valley near the Massachusetts-Vermont-New Hampshire state lines, and in Hillsboro County, south-central New Hampshire. In western Vermont, chestnut oak grows as far north as southern Addison County. Chestnut oak is relatively abundant on the steep, west-facing slope overlooking the southern end of St. Catherine Lake, southern Rutland County. This slope, which is underlain mainly by Cambrian St. Catharine slate and phyllite (Doll, 1961), rises about 110 m in 0.3 km. In the Connecticut Valley, chestnut oak was seen on steep banks of the Connecticut River about 20 km north of the Massachusetts state line.

Swamp white oak was seen in Rockingham County, New Hampshire, and in Maine as far north as a point in the Androscoggin River valley in Androscoggin County. At this northernmost point, swamp white oak is growing on a ridge above the floodplain of the Androscoggin River. Swamp white oak was also seen near the mouth of the Winooski River along the shore of Lake Champlain in Vermont.

Regional forest types in New England

In New England, as in other parts of eastern North America, there has been little agreement on the number, nature, and geographic extent of forest types. The general lack of agreement stems mainly from the subjective, deductive nature of much of the early ecological work done in the eastern forest (see Davis, 1965). Many boundaries have been drawn on the basis of "communities" that are difficult to define and next to impossible to delimit on the ground. Many of these "communities" are also based on subjective

notions of what the forest should be rather than on data concerning the existing forest. In addition, forest types depicted at certain scales are based on data collected at different scales; typically, regional forest types are defined on the basis of species that are abundant only in relatively rare habitats within a particular region. Regional forest types should be based on species that are regionally common, that is, on species that at a particular latitude occur frequently and abundantly in most sites. In practice, species that are regionally common and abundant are for the most part those that are common and abundant on side slopes, which, in most regions, are the landforms that contribute by far the greatest proportion of the total land area. It is these species that determine the general appearance of the mantle of vegetation covering the landscape. The pines of the Coastal Plain of the southeastern United States or the spruces and firs of the Canadian boreal forest belt are well-known examples of regionally common species that strongly influence the general appearance and composition of the regional forest cover.

A simple test of the relative regional frequency of occurrence of species used in the present study of New England forests was to inventory species at about 50 points evenly distributed in a 15-minute quadrangle having at least 30 percent forest cover. As the sampling points fall in habitats ranging from valley floors to side slopes, the test, though it may fail to detect rare species, reveals which species are regionally common because of their presence in most habitats of the particular region. These are the species that have been used to characterize the regional forest types described next. The simplicity and rapidity of the test are considered its strengths, for too elaborate and detailed local sampling may prevent not only the coverage of large land areas, but also the emergence of vegetation patterns that are important at regional scales.

In New England, the regional frequency of occurrence of common canopy trees varies with the ranges of the three common oaks, red, white, and black. Thus, by using the ranges of these oaks, regional forest types (which, like all classifications, will always be more or less arbitrary) can be defined and delimited on the basis of an objective criterion. Use of the common oaks for this purpose allows the field worker to identify by rapid inspection the regional forest types. Rigid quantitative definitions of regional forest types based on the entire forest flora were considered neither possible nor desirable. For the forest types or geographical areas strictly defined or delimited on the basis of the common oaks, statements concerning the probability of finding certain species at any one location are, however, possible. The regional forest types suggested are revisions of classical New England forest types.

The Central Hardwoods.

The area of New England south of the northern limit of white oak supports the Central Hardwoods regional forest type, composed mainly of oaks (white, red, black, scarlet, chestnut, and others), red maple, pitch and white pine, and hickories. The range of the white oak is chosen as the boundary of this forest type because white oak is more conspicuous than black oak, and because black oak is not as invariably present as white oak.

The northern or upper limit of the range of white oak marks an important biogeographic boundary in New England. Chestnut and scrub oak, the hickories, pitch pine, yellow poplar, red cedar, sassafras, flowering dogwood, and black gum are among the species that have their northern limit at or immediately

south of this boundary. Thus many so-called Southern species range only as far north as white oak. South of this limit, red maple is nearly ubiquitous (nearly 100 percent frequency of occurrence or, conversely, of probability of occurrence in any one site). Formerly the forest also contained the American chestnut, now present only here and there as sprouts in the understory. Scarlet oak and black birch are rare north of the limit of white oak. On valley floors, a common and easily recognized tree with a northern limit regionally coincident with that of white oak is the sycamore. Valley floors and other moist habitats also support most of the northern hardwoods (see below) found within the range of white oak.

The Central Hardwoods forest is distinctive in appearance. The presence of four or more species of oak, with their characteristic lateral and crooked branching, causes the forest to be relatively open, in contrast to the denser, more northerly forest. The open oak forest commonly has, on the other hand, a dense, tangled understory composed mainly of heath (ericaceous) shrubs.

There is probably more variation within the Central Hardwoods than within the other regional forest types described below, mainly because many southern species have the northern limit of their ranges within the range of white and black oak. Most northern tree species also occur, however rarely, in the Central Hardwoods forest. Most of the variation within this floristically rich forest occurs, however, over relatively short distances, and this variation should not be given the rank of regional forest types. The variation within the Central Hardwoods can perhaps be shown by means of forest sub-types based on the presence or abundance of, for example, chestnut oak, yellow poplar, scrub oak/pitch pine, red cedar, or black birch. These are "physiographic" rather than regional forest types; they are best mapped at scales of 1:24,000 or larger, that is, at scales at which vegetation may be related to such terrain features as concave or convex slopes, ridges, valley floors, or coastal sand plains. The presence of these forest sub-types does not detract from the generalization that from southern Maine to Cape Cod and across southern Massachusetts and in Connecticut, the vegetation that most characterizes the landscape is an oak/red maple/
pine/hickory forest.

The Transition Hardwoods.

The area of New England where red oak is the only common oak is designated a transitional zone supporting Transition Hardwoods. In this zone, white pine, red oak, hemlock, paper birch, and black cherry apparently reach their maximum regional frequency of occurrence in New England. At roughly the mid-latitude of this zone, white pine is nearly ubiquitous (nearly 100 percent frequency), and red maple and sugar maple have approximately the same regional frequencies of occurrence. To the north of this mid-point, the regional frequency of red maple declines, whereas that of sugar maple rises sharply. In general, the northern half of this transitional zone supports many northern hardwoods (see below). However, the abundance of white pine, red oak, and hemlock seems sufficient reason for retaining a transitional regional forest type between the oak/red maple/hickory/pine Central Hardwoods forest to the south and sugar maple/beech/yellow birch, or classical Northern Hardwoods forest, to the north. The presence of red oak alone is enough to impart distinctive appearance to this forest (Goodlett, 1954, p. 30). In moist habitats such as valley floors and bogs, several species have, in addition, their northern or upper altitudinal limit generally coincident with that of red oak. These species are Eastern cottonwood, silver maple, blue-beech

(hornbeam), and box-elder.

The Northern Hardwoods.

The forest immediately north of or above the limit of red oak is a predominantly deciduous forest composed mainly of sugar maple, yellow birch, and beech, with local concentrations of paper birch, white ash, black cherry, and basswood. This forest type has long been known as Northern Hardwoods; it is here strictly defined as lacking oaks.

The Northern Hardwoods forest is generally composed of dense stands, and the heavily shaded floor of this forest supports a numerically rich flora of flowering herbs, ferns, and mats of club-moss. On valley floors and in bogs, common species are American elm, balsam poplar, mountain-maple, and conifers such as northern white cedar, spruces (mainly red and white), balsam fir, and larch. Conifers also form pure stands on recently abandoned land within the zone occupied by the Northern Hardwoods. The presence of these conifers makes it difficult to separate the Northern Hardwoods from the Spruce-Fir regional forest type that occupies the highest and northernmost parts of New England. Attempts to define the boundary between these two forest types are beyond the scope of the oak study undertaken; however, selection of the range of one deciduous species, however arbitrary, seems preferable to attempts to define the boundary by means of a limited number of quantitative samples. Species whose northern limit might be useful as a concrete boundary between the Northern Hardwoods and the Spruce-Fir regional forest types are beech, white ash, or possibly sugar maple.

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Table 1. Common and scientific names of plants cited in the text. Nomenclature follows Fernald, 1950.

Common Name	Scientific name
Ash, White	Fraxinus americana L.
Aspen, trembling	Populus tremuloides Michx.
Balsam fir	Abies balsamea (L.) Mill.
Balsam poplar	Populus balsamifera L.
Basswood	Tilia americana L.
Beech, American	Fagus grandifolia Ehrh.
Birch:	
Black	Betula lenta L.
Gray	B. populifolia Marsh.
Paper or white	B. papyrifera Marsh.
Yellow	B. lutea Michx. f.
Black gum, tupelo	Nyssa sylvatica Marsh.
Black locust	Robinia pseudo-acacia L.
Blue-beech, American hornbeam	Carpinus caroliniana Walt. (in northern Vermont, Carpinus caroliniana Walt. var. virginiana (Marsh.) (Fern.)
Box-elder	Acer negundo L.
Cedar:	
Northern white, arborvitea	Thuja occidentalis L.
Red	Juniperus virginiana L.
Cherry, black	Prunus serotina Ehrh.
Chestnut, American	Castanea dentata (Marsh.) Borkh.
Cottonwood, Eastern	Populus deltoides Marsh.
Dogwood, flowering	Cornus florida L.
Elm, American or white	Ulmus americana L.
Hemlock	Tsuga canadensis (L.) Carr.
Hickory:	Carya spp.
Larch, tamarack	Larix laricina (Du Roi) K. Koch
Maple:	
Mountain	Acer spicatum Lam.
Red	A. rubrum L.
Silver	A. saccharinum L.
Sugar	A. saccharum Marsh.
Oak:	
Black	Quercus velutina Lam.
Bur, mossy-cup	Q. macrocarpa Michx.
Chestnut	Q. prinus L.
Red	Q. rubra L.
Scarlet	Q. coccinea. Muenchh.
Scrub, bear	Q. ilicifolia Wang.
Swamp white	Q. bicolor Willd.
White	Q. alba L.
Pine:	
Pitch	Pinus rigida Mill.
Red	P. resinosa Ait.
White	P. strobus L.
Sassafras	Sassafras albidum (Nutt.) Nees
Spruce:	

Black	*Picea mariana* (Mill.) BSP.
Red	*P. rubens* Sarg.
White	*P. glauca* (Moench) Voss
Yellow poplar	*Liriodendron tulipifera* L.

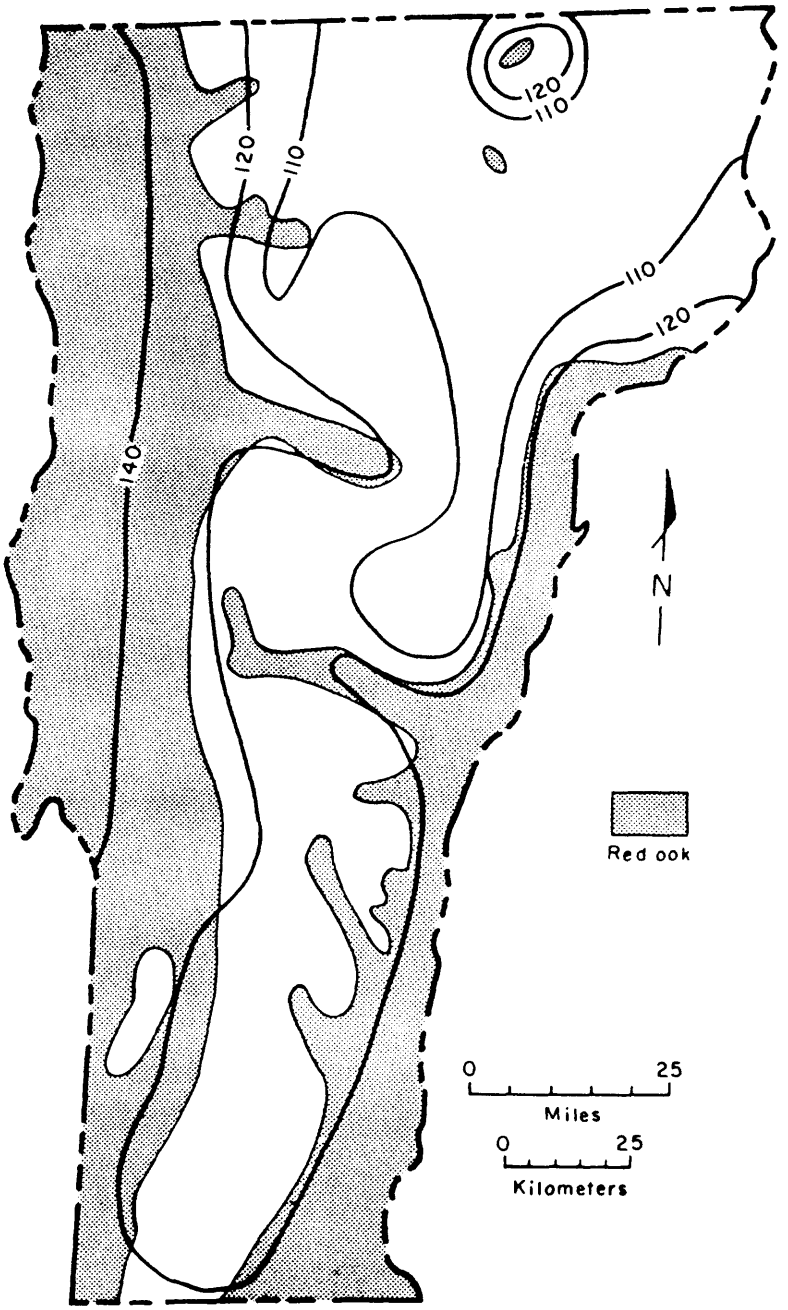

Fig. 1. Range of red oak and areas in Vermont with an average annual frost-free period of 110, 120, and 140 days. Climatic data from Hopp et al. (1964, p. 10)

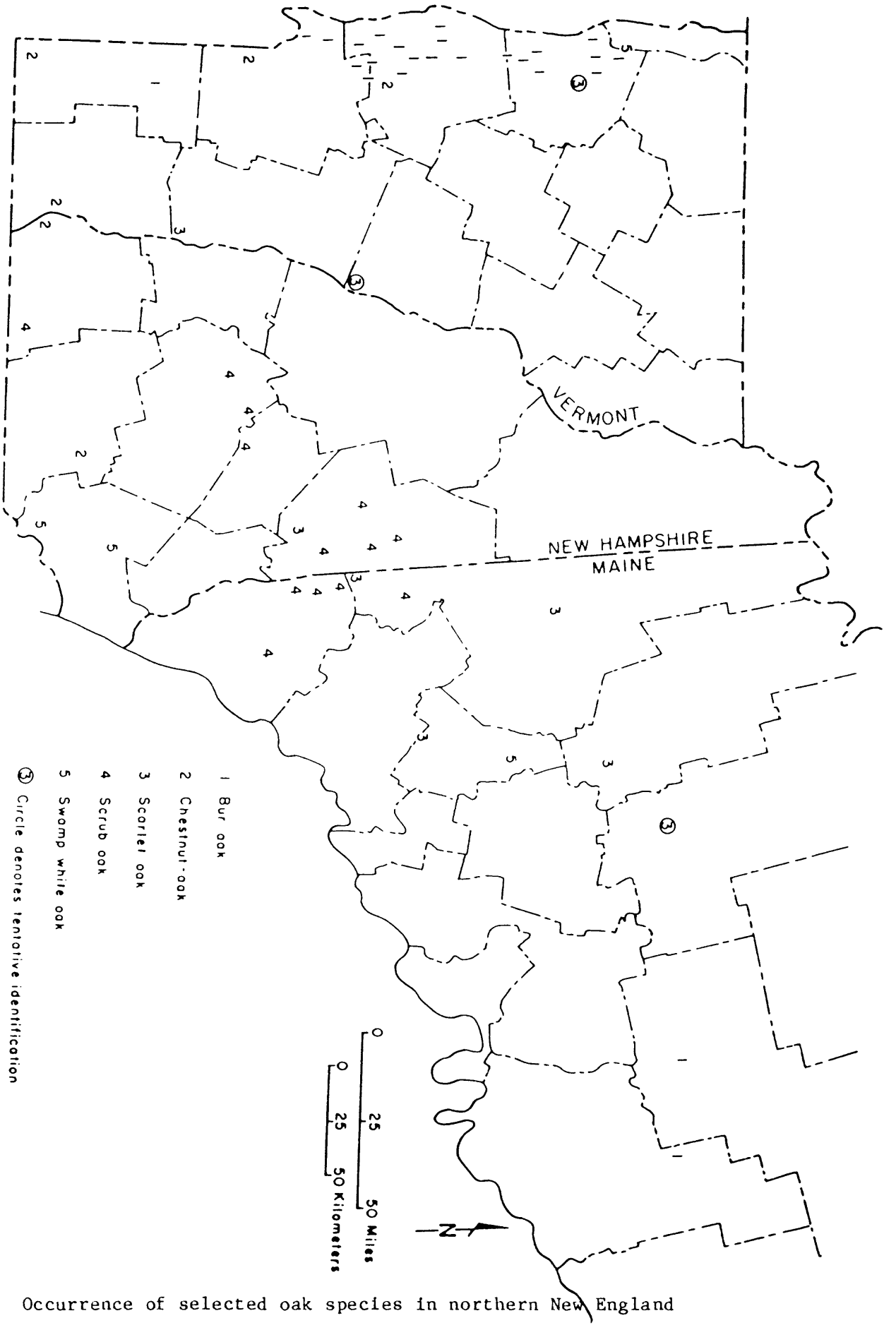

Figure 2. Occurrence of selected oak species in northern New England