# Comparative Morphology of Red Oak Taxa in Landscape Ecosystems in Lower Michigan

by Edward H. Trager

## ABSTRACT

The taxonomy and range limits of scarlet oak, *Quercus coccinea* Muenchh., and northern pin oak, *Q. ellipsoidalis* E.J. Hill, in the Lake States have been much debated, and recent authors continue to arrive at different conclusions regarding the segregation of these two taxa. The problem is compounded because *Q. ellipsoidalis* has also often been confused with northern red oak, *Q. rubra* L., and black oak, *Q. velutina* Lam. An ecosystem approach was used to investigate the morphology of the two well-characterized taxa, *Q. rubra* and *Q. velutina*, in relation to the poorly-characterized *Q. coccinea* in southeastern and northern Lower Michigan. *Q. ellipsoidalis* is hypothesized to be a northern, smaller-fruited race of *Q. coccinea*. To test this hypothesis, characters thought to be most conserved in evolution —flowers, fruits, and terminal buds— were examined in order to establish baseline references for distinguishing *Q. coccinea*, *Q. rubra*, and *Q. velutina*. Populations of each taxon were then examined to document differences along a south-to-north gradient.

Significant differences in female flower shape and pubescence, fruit size and shape, and terminal bud size and pubescence were found among the three taxa. There were no differences in female inflorescences among populations of *Q. coccinea*. However, acorn and terminal buds are smaller in the northern populations of *Q. coccinea*, and acorn and bud size is correlated with growing degree days, growing season length, and spring and summer precipitation. Differences in fruit and terminal bud morphology among populations of the taxa appear to be associated with differences in the ecosystems, and the diversity of form may reflect the process of natural selection at work within the mosaic of landscape ecosystems in Michigan. The lack of significant differences in female floral morphology leads me to suggest that *Q. ellipsoidalis* be treated as a northern race of *Q. coccinea*.

For Sue and Cattleya

# AKNOWLEDGEMENTS

I would foremost like to thank my advisor, Dr. Burton V. Barnes, and committee members, Dr. Gary W. Fowler, and Dr. Warren H. Wagner, Jr. of the University of Michigan, for their advice and guidance throughout the preparation of this thesis. All three gentlemen have been mentors to me throughout my graduate study in many more ways than they realize.

I am indebted to the McCleary and Perkins families of Monroe County for their gracious permission to sample on their lands. I am also grateful to Dr. Anton A. Reznicek of the University of Michigan, and to Dennis Albert and Michael Penskar of the Michigan Department of Natural Resources Natural Features Inventory for valuable information and help at various times during the study.

In the preparation of this thesis, and throughout my graduate study, I have benefited from the loving support of my wife, Sue, and daughter, Cattleya, who share a keen interest in nature, and from the encouragement of my brother, James, and uncle, William, who assured me that the study of biology is a fine pursuit.

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# PROBLEM STATEMENT

The taxonomy and range limits of scarlet oak, *Quercus coccinea* Muenchh., and northern pin oak, *Q. ellipsoidalis* E.J. Hill, in the Lake States have been the subject of much debate ever since the Reverend E.J. Hill, an amateur botanist from Chicago, named *Q. ellipsoidalis* in 1899. *Q. ellipsoidalis* has been repeatedly confused with northern red oak, *Q. rubra* L. (Shetron, 1974), and black oak, *Q. velutina* Lam. (Palmer, 1942). It has been suspected of being a hybrid with one or the other of these two taxa and even with pin oak, *Q. palustris* Muenchh. (Jensen, 1984). This situation has led to continued confusion among foresters, botanists, and natural resource managers to this day. The problem continues to exist because:

1. The extent of variation between and within these red oak taxa in the lake states is not well known.
2. Authors of older studies relied primarily on herbarium specimens (Trelease, 1919; Wadmond, 1933).
3. Some recent studies have been based on leaf characters alone (Jensen, 1984; Jensen et al., 1993), even though the leaves of red oaks are quite variable.
4. Some researchers have failed to include specimens from Michigan, among other areas, where red oaks with characters intermediate between *Q. ellipsoidalis*, *Q. coccinea*, *Q. rubra*, and *Q. velutina* are common.
5. These taxa have not been compared using an ecosystem approach in order to understand on what types of landforms, in what soils, and under what hydrological regimes they might be expected to occur.

To increase our understanding of these oaks, an ecosystem apporach was used to investigate the morphology of *Q. rubra*, *Q. velutina*, and *Q. coccinea* in southeastern and northern Lower Michigan. *Q. rubra* and *Q. velutina* are two well characterized taxa. However, *Q. coccinea* is poorly characterized in Michigan and authorities such as Voss (1985) include *Q. ellipsoidalis* as part of the *Q. coccinea* complex.

# OBJECTIVES

The general objective of this study was to arrive at a better understanding of morphological and ecological variation in Michigan populations of *Q. coccinea*, including populations commonly referred to as *Q. ellipsoidalis*, in comparison to the closely-related but better characterized *Q. rubra* and *Q. velutina*. The specific objectives were to:

1. Compare the flowers, fruits, and terminal buds of *Q. coccinea*, *Q. rubra*, and *Q. velutina* to determine baseline distinctions that consistently separate these taxa.
2. Study how differences in the expression of characters between populations of these taxa might be related to clinal changes in seasonal precipitation, growing season length, growing season heat sum, and soil composition.
3. Determine whether small-fruited populations commonly referred to as *Q. ellipsoidalis* in Michigan should be treated as a northern race of *Q. coccinea*, as Voss(1985) and Overlease (1964, 1977) have suggested.
4. Contrast morphological traits of northern and southern populations of *Q. coccinea*, *Q. velutina*, and *Q. rubra*.
5. Suggest methods and avenues for further investigation.

To accomplish these objectives, background material was assembled, and field studies were conducted over a three-year period from 1994 to 1996. Background information that amplifies the problem statement is presented below.

# BACKGROUND

Trelease (1919), Wadmond (1933) and Palmer (1942) provide accounts of the long-standing controversy concerning the taxonomy and distribution of *Q. ellipsoidalis* and *Q. coccinea*. Trelease (1919) was unable to find any region where *Q. coccinea* and *Q. ellipsoidalis* overlap in distribution. He noted that all the more northern material he had examined could be assigned to *Q. ellipsoidalis*. Wadmond (1933), relying primarily on herbarium material, also could not find a region where the two taxa overlap, although he guessed that if the ranges did overlap, it would most probably occur in northwestern Ohio.

However, Palmer (1942) suggested that the ranges of *Q. coccinea* and *Q. ellipsoidalis* barely overlap in a narrow belt, principally in southern Michigan and northern Indiana and extending into northern Illinois. Palmer felt that the acorns of the two species were "very dissimilar" and notes that the trees grow in "entirely different habitats." It is not clear how many field populations of these taxa Palmer examined, and no explanation of the entirely different habitats is provided.

Little (1971) provided maps of the distribution of *Q. ellipsoidalis* and *Q. coccinea* that suggest some overlap in distribution in northern Indiana, northwestern Ohio, and southeastern Michigan. According to Little's maps, the two taxa would appear to overlap in Michigan in Livingston, Oakland, Washtenaw, and Wayne counties. However, the data for Michigan in Little's maps must be considered incomplete. For example, Little does not show *Q. coccinea* or *Q. ellipsoidalis* as occurring in either Jackson or Genesee counties, two counties where I have sampled populations. Thus, Little's maps more likely represent the distribution of herbarium specimens that he was able to examine rather than the true limits of distribution in Michigan.

In the most extensive field study to date to specifically examine populations of these two taxa in the Lake States, Overlease (1964, 1977) concluded that *Q. ellipsoidalis* should be treated as a small-fruited form of *Q. coccinea* with the acorn less covered by the cup. Overlease examined leaves, fruits, winter twigs, and buds in the field. Also, he conducted common garden studies of juvenile plants. Overlease concluded that the morphological differences he observed among the *Q. coccinea-Q. ellipsoidalis* populations were no greater than the differences he observed in his parallel studies of *Q. velutina* and *Q. rubra* (1964, 1975a, 1975b).

In a comparative study of leaf, bud, and acorn characters of taxa in the red oak group, Jensen (1977) found no support for Overlease's conclusion. Jensen sampled *Q. ellipsoidalis* from Wisconsin and Illinois, and *Q. coccinea* from southern Ohio, Pennsylvania, Rhode Island, and Tenessee. Thus, no collections of *Q. coccinea* or *Q. ellipsoidalis* were from Michigan, Indiana, or any of the northern counties of Ohio bordering Michigan. In another study, Jensen (1984) compared leaf characters of some of Hill's *Q. ellipsoidalis* type specimens with recent collections of red oak taxa and concluded that some of Hill's type material may have come from hybrid trees, with *Q. velutina* and *Q. palustris* as possible parental taxa and with *Q. coccinea* possibly involved as well. Jensen's reliance on leaf characters and absence of corollary acorn or winter bud data limit the value of his conclusions. The suggestion of *Q. palustris*, a tree of low, wet or seasonally inundated ground, as a putative parental taxon is clearly at odds with what we know of the ecological traits of *Q. ellipsoidalis*, a tree of excessively well-drained sandy upland soils.

Voss (1985) includes *Q. ellipsoidalis* with *Q. coccinea*. He notes that C.C. Deam, E.J. Palmer, and W.H. Camp, who all studied oaks extensively over many years, did not reach uniform conclusions regarding these two taxa. He accepts Overlease's (1977) conclusion and believes the best solution, short of a detailed genetic analysis, is to treat these oaks as a single, variable complex. Voss suggests that some of the variability in the complex is due to genetic exchange with *Q. velutina*, *Q. rubra*, and possibly other taxa over thousands of years.

Over 20 years ago, Burton V. Barnes (pers. comm.) discovered three relatively large-fruited populations on the old Maumee lake plain in far southeastern Michigan which he and Warren H. Wagner identify as *Q. coccinea* in **Michigan Trees** (1981). Noting that these populations were quite different from *Q. ellipsoidalis* as he knew it from northern Lower Michigan and Upper Michigan, Barnes felt that the *coccinea* epithet would serve to distinguish and call attention to these large-fruited lake plain populations. Nevertheless, he recognized that the appellation should be conditional upon further study.

The old glacial Lake Maumee plain (Dorr and Eschman, 1970, p. 169) in southeastern lower Michigan supports populations of woody plant species that are rare in Michigan. This regional ecosystem (Fig. 1), identified as the Maumee Subdistrict within the Washtenaw District of southeastern Michigan by Albert et al. (1986), is distinctive due to its long growing season (the longest in Michigan), its generally flat physiography, and its patterns of lacustrine clay and sandy soils created by postglacial events. Outwash sands veneer the less permeable lacustrine clay bed in depths ranging from centimeters to tens of meters, giving rise to a unique hydrological cycle characterized by high spring and fall water tables.

Barnes originally identified three populations of *Q. coccinea*, and other populations have been observed at several localities by Michael Penskar and Dennis Albert (pers. comm.) of the Michigan Department of Natural Resources Natural Features Inventory. Barnes (pers. comm.) distinguishes the lake-plain populations he identifies as *Q. coccinea* from populations of *Q. ellipsoidalis* elsewhere in the state on morphological and ecological grounds. In addition to relatively larger fruit size, Barnes notes that acorn caps have a distinctive orange cast unlike the darker reddish-brown cast that he observed for *Q. ellipsoidalis* near Mio in the Grayling Subdistrict of northern Lower Michigan and elsewhere in northern Michigan and Wisconsin. Barnes also felt that the redder fall leaves and apical rings seen on some acorns accorded better with descriptions of *Q. coccinea* than with those of *Q. ellipsoidalis*.

Barnes notes intriguing differences in ecosystem requirements between the larger-fruited lake plain populations of *Q. coccinea* and the smaller-fruited *Q. ellipsoidalis* populations found in northern Lower Michigan. The larger-fruited populations appear to grow exclusively in the Maumee Subdistrict of the regional landscape ecosystem classification of Albert et al. (1986). This regional ecosystem is

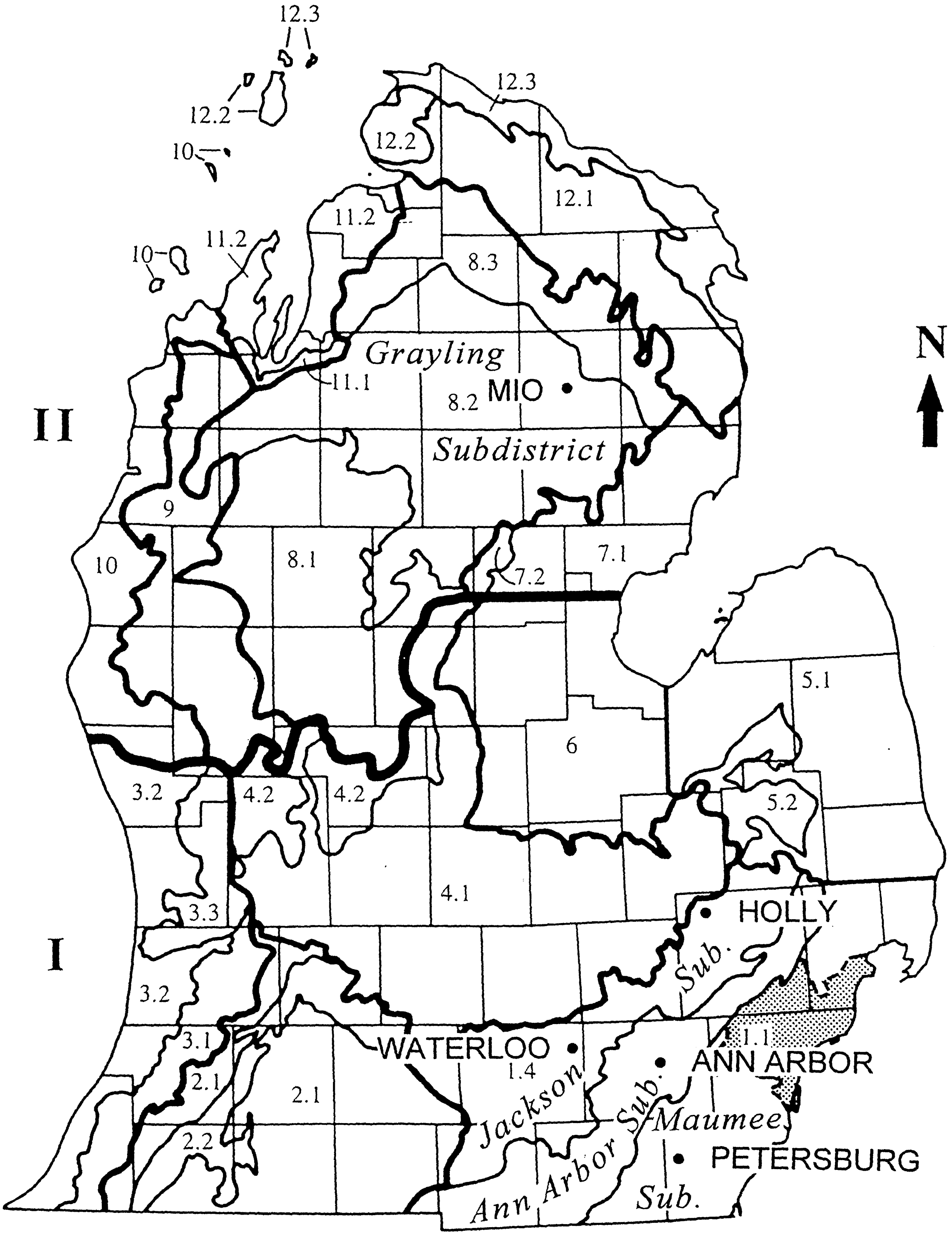

Fig. 1. Regional landscape ecosystem map of Michigan (adapted from Albert et al., 1986). Approximate locations of the Maumee, Ann Arbor, Waterloo, Holly and Mio red oak populations sampled in this study are shown in relation to the regional landscape ecosystem subdistricts of Albert et al. (1986). The Maumee populations are located in the vicinity of Petersburg.

markedly different from the adjacent Ann Arbor and Jackson Subdistricts in landforms and soils, and the climate may be different as well (Albert, pers. comm.). The Maumee Subdistrict is characterized by lacustrine deposits of clay interspersed by areas where the glacial rivers Huron and Raisin broke through the Defiance Moraine and carried large quantities of well-rinsed sand onto the lake plain.

The larger-fruited populations occur on these broad outwash channels on low and medium sand beach ridges and plains that were formed as the old Lake Maumee receded to the east (Barnes, pers. comm.). Low beach ridges and plains are defined as those approximately 0.3 to 1.0 m above the standing spring water table, while medium ridges and plains are approximately 1.0 to 2.5 m above the standing spring water table. Adjacent local ecosystems on such sand plains support *Q. palustris* and *Q. bicolor* Willd. in the low wet depressions where the water table is at or above ground level in early spring. *Q. alba* L. occurs on medium to high (>2.5 m) beach ridges, and *Q. velutina* on the highest and driest beach ridges. *Q. rubra* appears rarely in ecosystems where the sand veneers the lacustrine clay very thinly (0.4 m in one measured location: Barnes, pers. comm.) but does not appear to be a component of the sand-veneered ecosystems. However, in the lake plain area, Gerald Waldron, Anton Reznicek, and Warren H. Wagner, Jr. have identified *Q. shumardii*, a taxon closely related to *Q. rubra*, on low, wet sites with heavy clay soils, and *Q. rubra* also occurs on upland sites with clay soils on the lake plain (Reznicek, pers. comm.).

Mottling at a depth of 0.3-1.0 m in the soils of low beach ridge ecosystems indicates the standing level of the seasonally high water table. *Q. coccinea* here appear to tolerate the partial inundation of their root systems in early spring . Barnes (pers. comm.) hypothesizes that the roots of these trees below the water table are able to withstand low oxygen levels better than those of either *Q. alba* or *Q. velutina*, although not as well as roots of *Q. palustris* can. The roots are impeded by the water table from ever reaching the deeper neutral or slightly basic horizons that retain moisture longer. The trees are, thus, uniquely adapted to survive in a site that is excessively wet in spring and excessively dry in summer.

In contrast, smaller-fruited populations referred to as *Q. ellipsoidalis* typically grow on excessively-drained outwash or ice-contact landforms (plains, eskers, kames) in the coldest areas of Michigan (Archambault et al., 1990). Although the sandy Maumee lake plain beach ridges are droughty in summer when precipitation is infrequent, drainage of spring and fall precipitation is impeded by the less permeable underlying lacustrine clays. This unique hydrological cycle influences Maumee ecosystems in ways that are very different from the ice-contact and outwash ecosystems of the nearby Ann Arbor and Jackson Subdistricts, or the more distant Grayling Subdistrict where typical Michigan *Q. ellipsoidalis* occurs in abundance.

# METHODS

## Field And Laboratory Methods

### SITE SELECTION

Photocopies of Farrand's (1982) map of the quaternary geology of Michigan were scaled and superimposed over maps from a 1991 DeLorme Michigan Atlas and Gazetteer to produce composite maps showing the occurrence of lacustrine clay and outwash sand plains, major beach ridges, and other geologic features in relation to roads, public lands and private woodlots. Potential sites for sampling were selected based on these maps and the advice of Burton V. Barnes of the School of Natural Resources and Environment (SNRE), University of Michigan, Warren H. Wagner, Jr. and Tony Reznicek of the Department of Botany, University of Michigan, and Michael Penskar and Dennis Albert of the Michigan Department of Natural Resources Natural Features Inventory.

A field reconnaissance was conducted in early spring, 1994, of 24 of the most promising sites distributed in four regional landscape ecosystem subdistricts defined by Albert et al. (1986), the Maumee, Ann Arbor, Jackson and Grayling Subdistricts (Fig. 1). Each regional landscape ecosystem represents a region of relatively homogenous climate and physiography at a given geographic scale. The spring reconnaissance included sampling of emergent male and female flowers from 16 of the 24 sites. From these 16 sites, 12 sites were chosen for detailed study (Table 1). Site selection criteria were the presence of a sufficient number of mature individuals of the selected taxa with branches at a height that could be sampled with a pole pruner, absence of recent disturbance as indicated by overstory and understory composition, and landowner permission on private lands.

## SITE SAMPLING

Site locations from south to north, the taxa sampled, and the number of soil pits excavated at each site are listed in Table 1. At each site, an average of three (range 1-8) trees of each taxon present were sampled within local ecosystems where the taxon typically occurred to represent a local population. Three local populations of *Q.coccinea* and one local population of *Q.velutina* were sampled in the Maumee Subdistrict in outwash plain ecosystems at Petersburg State Game Area (PETR) and at two sites on private land, Perkins' Farm (PERK), and McCleary's Farm (MCCL). One local population each of *Q. rubra* and *Q. velutina* were sampled in an oak-hickory ecosystem on clay loam soil at the University of Michigan's Radrick Forest (RADR) in the Ann Arbor Subdistrict. Three local populations of *Q. coccinea*, two local populations of *Q. velutina*, and one local population of *Q. rubra* were sampled at Waterloo State Recreation Area in the southwestern section of the Jackson Subdistrict on sandy ice-contact landforms in the vicinity of the Gerald E. Eddy Geology Center (GEOC), the Potowatomi trail (POTO), and Sugarloaf Lake (SUGR), respectively. A local population of each of the three taxa was sampled in ice-contact ecosystems at Holly State Recreation Area (HOLL) in the northeast section of the Jackson Subdistrict. Three populations of *Q. coccinea*, and one population each of *Q. velutina* and *Q. rubra* were sampled in outwash plain and ice-contact ecosystems in the Huron National Forest in Oscoda County near Mio in the Grayling Subdistrict. These local ecosystems were designated as MIO1, MIO2, MIO3 and MIO4, respectively.

Table 1. Sampling locations in Southern Michigan.

| No | Acronym | Location | Taxa sampled [1] | No. of soil pits |
|---|---|---|---|---|
| **Region I, Maumee Subdistrict** | | | | |
| Maumee populations | | | | |
| 1. | PERK | Private land, Monroe County | QC, QV | 2 |
| 2. | PETR | Petersburg State Game Area., Monroe County | QC | 1 |
| 3. | MCCL | Private land, Monroe County | QC | 1 |
| **Region I, Ann Arbor Subdistrict** | | | | |
| Ann Arbor populations | | | | |
| 4. | RADR | Radrick Forest, Washtenaw County | QR, QV | 2 |
| **Region I, Jackson Subdistrict** | | | | |
| Waterloo populations | | | | |
| 5. | GEOC | Waterloo State Recreation Area, Washtenaw County | QC | 1 |
| 6. | POTO | Waterloo State Recreation Area, Washtenaw County | QC, QR, QV | 1 |
| 7. | SUGR | Waterloo State Recreation Area, Washtenaw County | QC, QV | 1 |
| Holly populations | | | | |
| 8. | HOLL | Holly State Park., Genesee County | QC, QR, QV | 0 |
| **Region II, Grayling Subdistrict** | | | | |
| Mio populations | | | | |
| 9. | MIO1 | Huron National Forest, Oscoda County | QC | 2 |
| 10. | MIO2 | Huron National Forest, Oscoda County | QV | 1 |
| 11. | MIO3 | Huron National Forest, Oscoda County | QC, QR | 1 |
| 12. | MIO4 | Huron National Forest, Oscoda County | QC | 1 |

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[1] QC: *Quercus coccinea*; QR: *Q. rubra*; QV: *Q. velutina*

Local populations were grouped for analysis. Two or more local populations of a taxon that were sampled within 20 km (12 miles) of one another within the same Subdistrict were treated as geographically proximate replicates of a larger population. Thus, as shown in Table 1, the GEOC, POTO, and SUGR populations of *Q. coccinea*, which were all sampled within the same general vicinity of southwestern Jackson Subdistrict, are together treated as the Waterloo population of this taxon, while the HOLL population, sampled from the northeastern section of the same Subdistrict, is treated as a distinct population, the Holly population. *Q. coccinea* has not been observed to occur in the Ann Arbor subdistrict, and *Q. rubra* occurs only rarely in the sand-veneered clay-plain Maumee ecosystems. Thus, a total of four populations of *Q. coccinea*, five populations of *Q. velutina*, and four populations of *Q. rubra* were available for study. Although broadly categorized by the Subdistrict in which they occur, these populations are regarded as representative of local ecosystems and not necessarily of the Subdistricts as a whole. Geographic locations and directions to the sites are listed in Appendix A.

Female inflorescences were sampled in spring while acorns and terminal buds were sampled from fall to early winter of 1994. A total of 82 trees were selected for sampling. Trees selected in spring were reassessed in fall for winter bud and acorn sampling, and additional trees were added in fall. Due to variations in flower and mast production and branch accessibility, not all trees were sampled in each collection. The number of trees of each taxon sampled in each collection is summarized in Table 2.

Site physiography, overstory, understory, and ground-cover vegetation were recorded for each site. Soil pits were excavated to a depth of 1.3 to 1.8 m. Soil samples were collected from each horizon. Cores of the top 20 cm of soil were also collected. In addition, two cores were augered to a depth of apx. 3 m from the two soil pits dug at the PERK site. Mechanical soil analyses were performed in the soil laboratory at SNRE on all cores and on samples taken from each soil horizon. Soil sampling and analysis generally followed the methods described by Spies and Barnes (1985). Field pH, laboratory pH, and percent sand, silt and clay using the hydrometer method were measured

Table 2. Number of trees of each taxon sampled in each population for female flower, winter bud, and acorn collections.

| No. | Site | Number of trees sampled | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Female flower collection | | | Winter bud collection | | | Acorn collection | | |
| | | QC[1] | QR | QV | QC | QR | QV | QC | QR | QV |
| | Maumee populations[2] | | | | | | | | | |
| 1. | PERK | | | | 1 | | 2 | 6 | | 3 |
| 2. | PETR | 2 | | | 7 | | | 8 | | |
| 3. | MCCL | | | | 6 | | | 7 | | |
| | **Total ...** | **2** | **-** | **0** | **14** | **-** | **2** | **21** | **-** | **3** |
| | Ann Arbor populations[3] | | | | | | | | | |
| 4. | RADR | **-** | **0** | **0** | **-** | **3** | **3** | **-** | **3** | **2** |
| | Waterloo populations | | | | | | | | | |
| 5. | GEOC | | | | 5 | | | 5 | | |
| 6. | POTO | 2 | 3 | 3 | 1 | 3 | 2 | 2 | 4 | 4 |
| 7. | SUGR | | | | 4 | | 2 | 4 | | 2 |
| | **Total ...** | **2** | **3** | **3** | **10** | **3** | **4** | **11** | **4** | **6** |
| | Holly populations | | | | | | | | | |
| 8. | HOLL | **2** | **1** | **1** | **5** | **2** | **3** | **5** | **2** | **2** |
| | Mio populations | | | | | | | | | |
| 9. | MIO1 | 3 | | | 4 | | | 4 | | |
| 10. | MIO2 | | | 3 | | | 3 | | | 3 |
| 11. | MIO3 | | 2 | | 1 | 2 | | 1 | 2 | |
| 12. | MIO4 | | | | 2 | | | 2 | | |
| | **Total ...** | **3** | **2** | **3** | **7** | **2** | **3** | **7** | **2** | **3** |
| **Grand total ...** | | **9** | **6** | **7** | **36** | **10** | **15** | **44** | **11** | **16** |

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[1] QC: *Quercus coccinea*; QR: *Q. rubra*; QV: *Q. velutina*.

[2] *Q. rubra* occurs only rarely on the sand-veneered clay plain ecosystems of the Maumee Subdistrict.

[3] *Q. coccinea* has not been observed to occur in the Ann Arbor Subdistrict.

for all horizon and core samples. Standard sieves were used to measure percent very fine, fine, medium, coarse, and very coarse sand. Measured soil variables are shown in Table 3. Soil moisture desorption curves were estimated based on texture data from the top 20 cm cores using Saxton's regression (1986). Soil profiles and summary data for each soil pit are presented in Appendix B.

Thirty-year averages of climatic data from weather stations closest to the study sites were obtained from the Michigan Department of Agriculture Division of Climatology at Michigan State University (http://climate.geo.msu.edu). Data from the following weather stations were used to represent the climate in the ecosystems of the respective Subdistricts: Monroe Waterworks station for the Maumee Subdistrict ecosystems, University of Michigan station for the Ann Arbor Subdistrict ecosystem, Jackson FAA Airport station for the Waterloo ecosystems in southwestern Jackson Subdistrict, Flint WSO Airport station for the Holly ecosystems in northeastern Jackson Subdistrict, and the Mio Hydro Plant station for the Mio ecosystems in the Grayling Subdistrict.

Growing degree days at base 7.2 degrees Celsius (45 degrees Fahrenheit), growing season length at base 0 degrees Celsius (32 degrees Fahrenheit), and seasonal and total annual precipitation variables were selected for use in regression analyses (Table 4).

## TAXON DETERMINATIONS AND TREE SELECTION

Taxon determinations were made based on the most reliable winter condition characters and on examination of physiographic characters of the growth site. Winter buds, outer bark form and color, inner bark color, acorn and acorn cap form and color, the landform where a tree occurred, soil, position of the tree on the landform, and aspect of the position were all used to distinguish taxa in the field (Table 5).

Of the 82 trees sampled, a total of 7 were either suspected to be hybrids when initially sampled in spring, or were reclassified as such when revisited in fall for additional sampling. Of these seven, four were classified as putative hybrids between *Q. coccinea* and *Q. velutina*, and three as hybrids between *Q. coccinea* and *Q. rubra*. All seven were excluded from the study.

Table 3. Soil variables measured on top 20 cm soil cores and on samples from each soil horizon.

| No. | Description | Top 20 cm soil cores | Each soil horizon |
|---|---|---|---|
| 1. | Field pH | ■ | ■ |
| 2. | Laboratory pH | ■ | ■ |
| 3. | Percent sand | ■ | ■ |
| 4. | Percent silt | ■ | ■ |
| 5. | Percent clay | ■ | ■ |
| 6. | Percent very fine sand | ■ | |
| 7. | Percent fine sand | ■ | |
| 8. | Percent medium sand | ■ | |
| 9. | Percent coarse sand | ■ | |
| 10. | Percent very coarse sand | ■ | |

Table 4. Climatic Variables used in analyses.

| No. | Description |
|---|---|
| 1. | Growing degree days base 7.2 degrees Celcius |
| 2. | Growing season base 0 degrees Celcius |
| 3. | Total annual precipitation, mm |
| 4. | Total winter precipitation, mm |
| 5. | Total spring precipitation, mm |
| 6. | Total summer precipitation, mm |
| 7. | Total fall precipitation, mm |

Table 5. Winter Condition Field Key.

| Taxon | Expected growth site | Outer bark color and texture | Inner bark color | Winter bud pubescence and size | Acorn cap size, form, pubescence |
|---|---|---|---|---|---|
| Maumee populations of *Quercus coccinea* | sand beach ridges of low to intermediate height on the old Maumee lake plain | silver gray; relatively smooth textured bark even on large individuals | whitish to pinkish-tan | tip of bud pubescent, bud smaller than in *Q. rubra* or *Q. velutina* of the same geographic area | cap deeply turbinate, external cap width often > 15 mm, cap scales not pubescent |
| Populations of *Quercus coccinea* in northern Lower Michigan | excessively well drained sandy soils on outwash plains, esker or kame ridge tops, mid to upper slope on south or southwest facing slopes | silver gray; relatively smooth textured bark on young individuals, becoming blocky on larger individuals | whitish to pinkish tan | tip of bud pubescent, bud smaller than in *Q. rubra* or *Q. velutina* from the same geographic area | cap deeply turbinate, external cap width usually < 15 mm, cap scales not pubescent |
| *Quercus rubra* | often lower to mid slope on mesic north and northeast facing slopes | silver gray; relatively smooth-textured or with long, vertical ridges, the edges of the ridges generally beveled so that the grooves between ridges appear v-shaped | whitish to pinkish tan | bud glabrous or tip slightly pubescent, relatively larger than in *Q. coccinea* of the same geographic area | cap saucer shaped, cap scales not pubescent |
| *Quercus velutina* | often with white oak and hickories on well drained sandy soils; on the highest sand beach ridges on the old Maumee lake plain | dark gray to black, very blocky, the edges of the ridges usually rougher and less beveled than in Q. rubra. | yellowish to deep yellow-orange (yellow color often less pronounced in Mio specimens) | bud uniformly pubescent, the pubescence imparting a dull tawny or light golden color to the entire bud | cap turbinate, cap scales loose along the margin of the cap, cap scales uniformly pubescent, imparting a dull tawny or light golden color to the entire cap of fresh specimens |

## TREE SAMPLING METHODS

In both spring and fall, southern populations were sampled first. In stands with relatively open canopies, mature individuals of each taxon accessible with a pole pruner were randomly selected from the interior of stands. In stands with dense canopies, accessible trees were more often than not located along the edges of the forest adjacent to fields or roads. The most open stands were kame and esker ridges at Waterloo State Recreation Area and outwash plains at Huron National Forest near Mio. Stands with moderate to dense canopies occurred in the Maumee lake plain ecosystems and in the RADR, MIO2 and MIO3 ecosystems with *Q. rubra* and *Q. velutina*.

Selected trees were tagged at the base of the trunks with numbered nails. Diameter at breast height was measured, and inner bark color scored using Munsell color chips. Tree locations were mapped so they could be easily relocated in fall for acorn and terminal bud sampling.

In both spring and fall, a pole pruner was used to sample an average of three branches from each tree. Branches were sampled from lower-mid to upper-mid crown, depending upon the size and accessibility of the tree, and preferentially from the south and southwest sides of the tree to insure consistency in sampling. Only outer branches were sampled. Branches were 0.6 to 1.2 m long and up to 3 cm in diameter where cut. In both spring and fall, only vigorous and healthy shoots were selected for measuring flowers or winter buds, respectively. Adventitious shoots that arose as a result of leader dieback from frost or insect damage were avoided.

## FLOWER SAMPLING

Mature female inflorescences were sampled from mid May to early June, 1994. Male inflorescences were also examined, but morphological differences among taxa were too slight to justify large-scale sampling and quantification. Because of the relatively short temporal window of flowering, individual variation in flowering time and duration, and the necessity of taking all measurements within hours of cutting samples that would not store or refrigerate well, it was decided to sample female inflorescences from only a subset of the sites, as documented in Table 2.

Female inflorescences develop on shoots of the current year at the base of leaf axils. In North American oaks, the female inflorescences are reduced spikes only a few millimeters long consisting of an inflorescence axis, or peduncle, normally with two (rarely 3-5) individual gynoecious flowers. The natural unit of observation chosen for sampling was, thus, the entire inflorescence.

The female flowers on a tree only begin to reach maturity after the male catkins have begun to dehisce pollen. Therefore, the disposition of the male catkins, which are easily observed at a distance, served as a quick indicator of the probable maturity of the minute and cryptically displayed female inflorescences.

Observations of stigma recurvature were used to confirm female floral maturity (Fig. 2). In immature flowers, the stigma lobes protrude from the bracts, but are not yet reflexed, as illustrated in the upper drawing in Fig. 2. In mature flowers, the stigma lobes both protrude from the bracts and are spread or reflexed, as illustrated in the lower drawing.

An average of 16 to 17 female inflorescences were sampled from shoots randomly selected from among the three branches sampled per tree. To avoid problems with wilting and discoloration of the delicate flowers, measurements were made directly in the field or, more rarely, in the lab within four to eight hours of collecting. Characters were recorded for fertile shoots, individual inflorescences on shoots, and individual flowers on inflorescences.

In the usual case when more than one flower was present on an inflorescence, scored variables (such as perianth red color coverage) were recorded as the average of the scores of the individual flowers, but measured variables (such as stigma length) were recorded by randomly sampling just one of the normally two mature flowers present.

The following shoot characters were recorded: current and previous year's shoot length and width at the base of the shoot, number of leaves and number of inflorescences on the shoot, and shoot sex. Shoot sex was

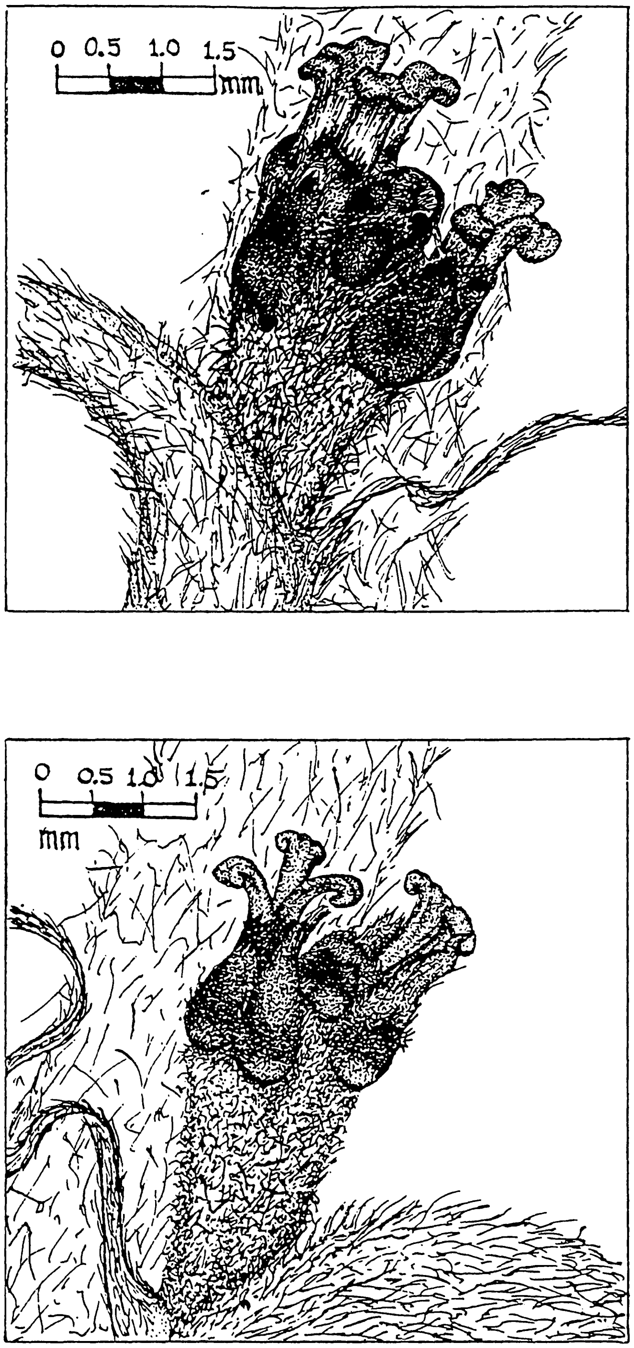


Fig. 2. Female inflorescences of Maumee *Q. coccinea* in two stages of maturity. Female flower maturity was ascertained by inspecting the degree of recurvature of the stigma lobes, as illustrated in these drawings. Upper drawing, the stigma lobes protrude from the bracts significantly in both flowers, but are not yet reflexed. This inflorescence is still immature and would have been scored as 2 on the five-point scale of stigma recurvature (Fig. 4). Lower drawing, the stigma lobes on the mature flower on the left are clearly reflexed and would have been scored as 3.

recorded as female if the shoot bore only female flowers, or bisexual if the shoot also bore some male catkins (not an infrequent condition).

The following inflorescence-specific characters were recorded: leaf axil ordinal counting from the base of the shoot, distance from shoot base to leaf axil, shoot width at the leaf axil, peduncle pubescence, distance from base of inflorescence to first flower, distance from first flower to second flower (when present), and the inflorescence shape.

Inflorescence shape represented an abbreviated notation for recording the number and arrangement of the fully developed flowers in relation to vestigial flowers that frequently appear on the reduced inflorescence spike. (Vestigial flowers appear as minute knobby structural extensions toward the terminus of the vestigial spike axis. They tend to be glabrous and somewhat tinged with red in *Q. rubra*, but more likely appear as pubescent tufts in *Q. coccinea* and *Q. velutina*; floral vestigia are apparent in the drawings of inflorescences of all three taxa in Fig. 3). Only the number of fully developed flowers was extracted as a quantitative variable analyzed in this study.

The following flower-specific characters were recorded: number of stigma lobes, stigma lobe length, stigma recurvature class, the color and red color coverage of the stigma, perianth collar, and bracts, respectively, and the pubescence of the bracts.

Stigma recurvature class was scored on a scale of one to five (Fig. 4). In stage (1) in Fig. 4, stigma lobes are just beginning to emerge from bracts and are not yet reflexed. A score of (2) represents a slightly more developed immature stage in which the stigma lobes are protruding significantly but are still not reflexed. Stages (3),(4), and (5) represent mature stages in which stigma lobes are reflexed and completely receptive to pollen. In the study, only flowers that were scored at 2.5 or above were considered mature and included in analyses.

Colors on flowers were scored in comparison to a series of red, maroon, and red-brown embroidery floss colors.

Red color coverage on flowers was scored separately for stigmas, perianths, and bracts using a five-point scale (Fig. 5). No appreciable red coverage was scored as *none*. Red coverage less than yellow-green coverage was scored as *low*. Red coverage about equal to yellow-green

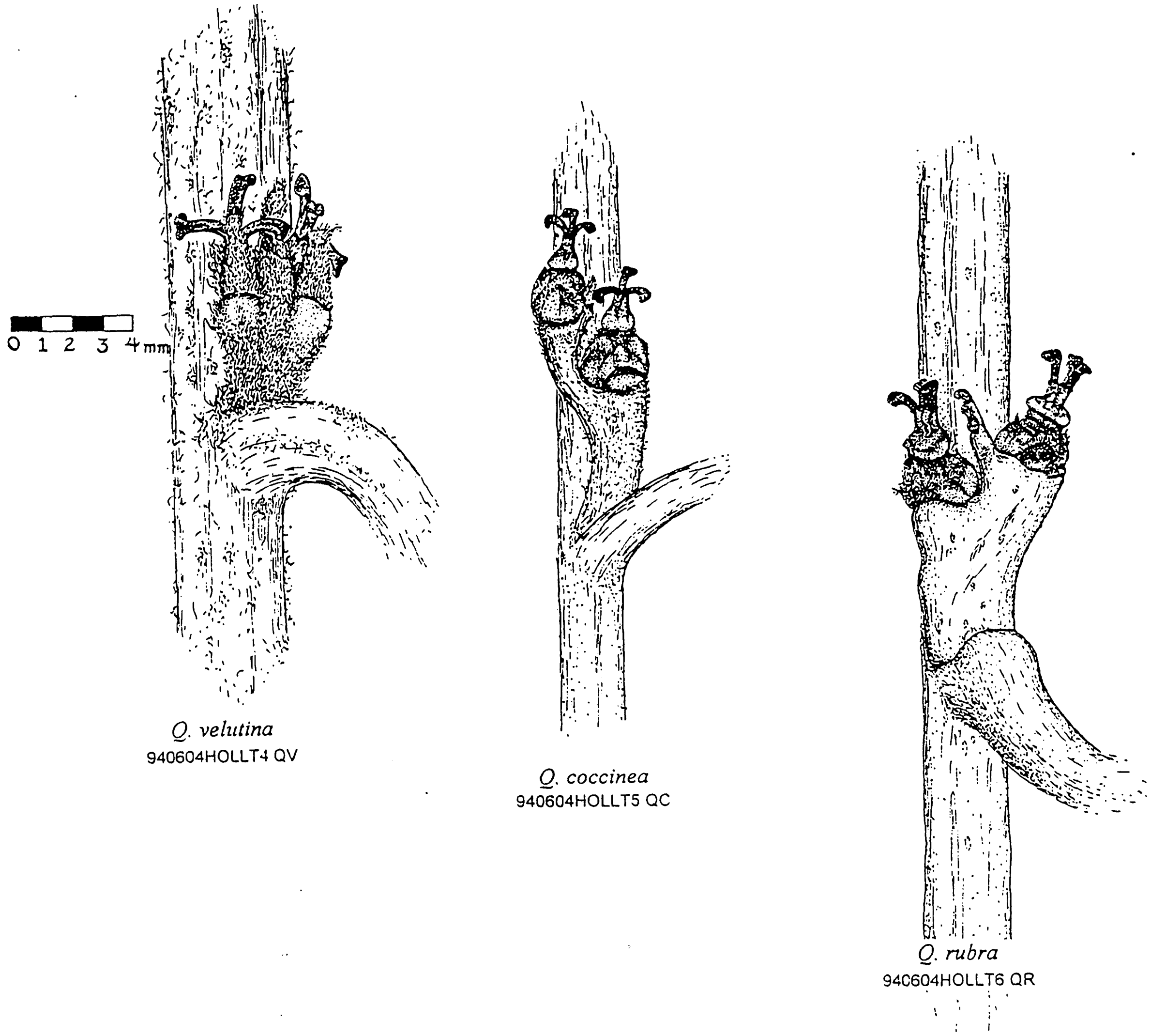


Fig. 3. Female inflorescences of *Q. velutina*, *Q. coccinea*, and *Q. rubra* drawn from specimens collected at Holly State Park on June 4, 1994. Inflorescences of *Q. velutina*, left, are characterized by dense pubescence and the stockiest peduncles of the three taxa. Inflorescences of *Q. coccinea*, middle, are the longest and most gracile of the three taxa and are slightly pubescent. Inflorescences of *Q. rubra*, right, are generally glabrous. Although the peduncles in *Q. rubra* are sometimes as long as those in *Q. ellipsoidalis*, they are relatively thicker and thus easily distinguished by the trained eye. Note that vestigial flowers are present on the reduced spikes of all three taxa in these drawings. In *Q. velutina* and *Q. ellipsoidalis*, the vestigial flowers often appear as pubescent tufts, while in *Q. rubra* they more frequently appear as tiny somewhat reddish bract-covered globular protruberances.

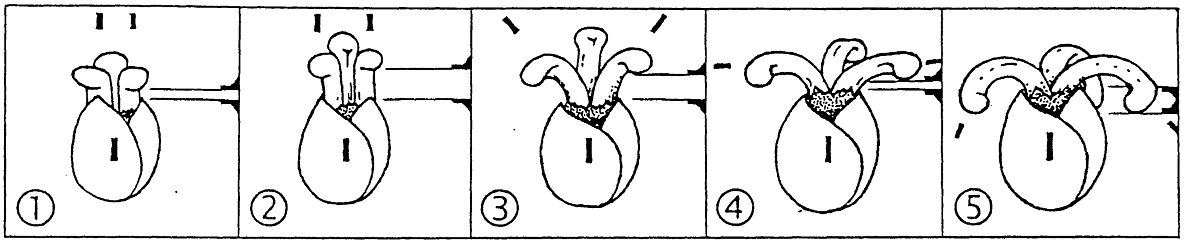


Fig. 4. Illustration of categories used in scoring stigma recurvature in female oak flowers. Stigma recurvature was scored on a scale from one to five. In (1), stigma lobes are just beginning to emerge from bracts and are not yet reflexed. (2) represents a slightly more developed immature stage in which the stigma lobes are protruding significantly but still not reflexed. Categories (3), (4), and (5) represent mature stages in which stigma lobes are reflexed and completely receptive to pollen. In the study, flowers that were scored at 2.5 or above were considered mature and included in analyses.

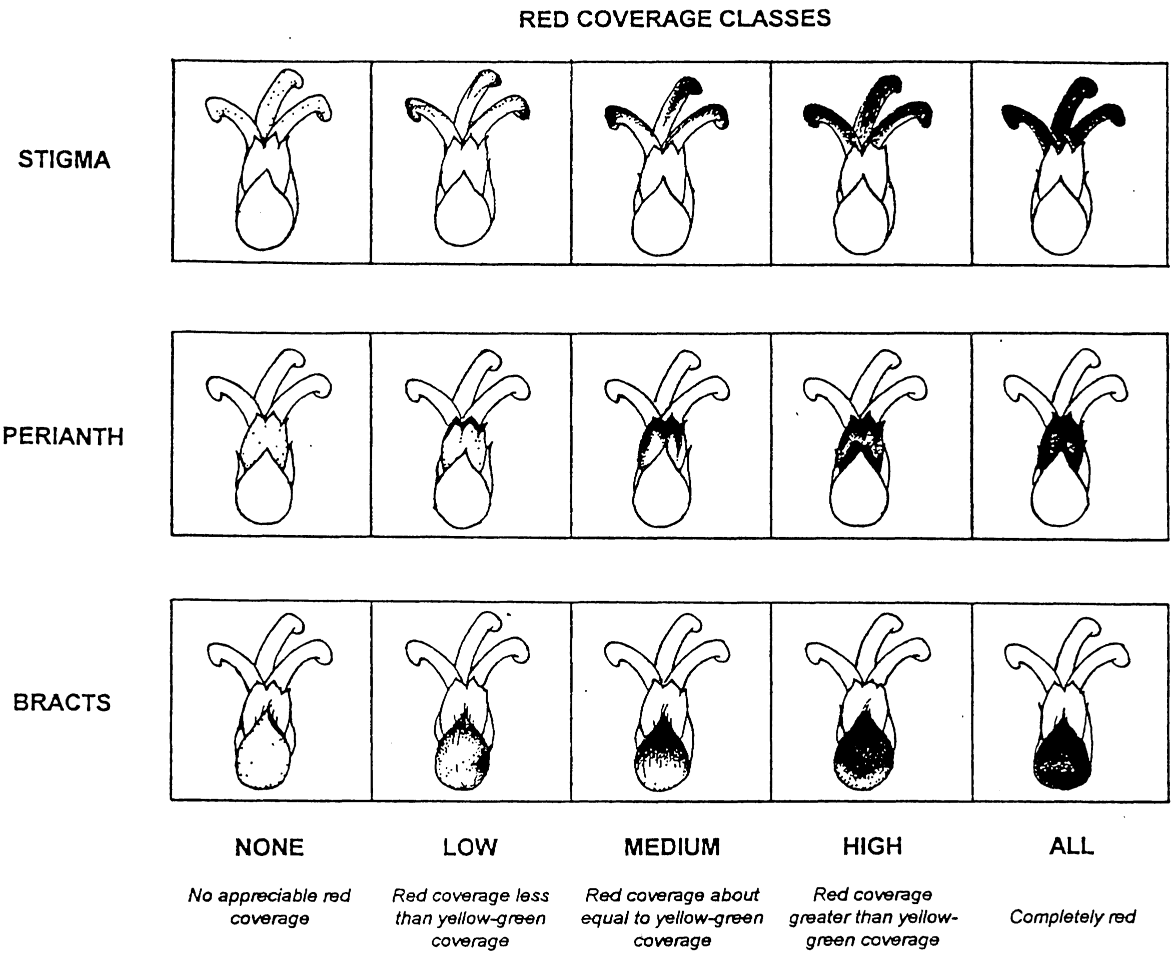


Fig. 5. Illustration of categories used in scoring the degree of red color coverage on female oak flowers. Red color coverage on flowers was scored scored separately for stigmas, perianths, and bracts using a five-point scale. No appreciable red coverage was scored as *none*. Red coverage less than yellow-green coverage was scored as *low*. Red coverage about equal to yellow-green coverage was scored as *medium*. Red coverage greater than yellow-green coverage was scored as *high*, and complete red coverage was scored as *all*. These scores were converted to 0.0, 0.25, 0.50, 0.75, and 1.0 respectively for use in analyses.

coverage was scored as *medium*. Red coverage greater than yellow-green coverage was scored as *high*, and complete red coverage was scored as *all*. These scores were converted for analysis to 0.0, 0.25, 0.50, 0.75, and 1.0, respectively.

Pubescence was scored as glabrous (**g**), slightly pubescent (**s**), pubescent (**p**), or very pubescent (**v**) and transformed for analysis to 0, 1/3, 2/3, and 1, respectively (Table 6). All length and width measurements were interpolated to the nearest 0.033 mm using dial calipers with lines to 0.1 mm.

Most of the measured floral characters are illustrated in Fig. 6. In addition to quantitative sampling of female flowers, notes on floral position on crown, male catkin morphology, spring shoot tomentum, trichome characteristics examined under a dissecting microscope, and flowering phenology were made.

## ACORN, WINTER BUD, AND SHOOT SAMPLING

Acorns and winter buds and shoots were sampled from late September to late November, 1994. An average of 25 to 30 acorns were collected from directly below the crown of each tree. Masking tape was used to secure nuts into caps. An average of 30 to 45 shoots bearing healthy terminal and peripheral winter buds were trimmed from the three branches collected per tree. Acorns and shoots bearing winter buds were bagged and placed in a freezer at SNRE until measured.

## ACORN DIGITIZATION AND EXTRACTION OF DISTANCE MEASURES

Acorn and acorn cap outlines were digitized in a multi-step process using a PC-based video image capture system at the University of Michigan Herbarium, Morphosys software (Meacham and Duncan, 1989), and custom software that I developed. A random sample of usually 12 acorns was selected from the pool of 25 to 30 that had been collected per tree. Selected acorns and matching caps were first numbered, and the caps were then separated from the nuts. Caps were sliced transversely in order to accurately capture cross-sectional outlines. No special preparation of

Table 6. Scale used for scoring pubescence.

| Letter | Description | Numeric Assignment |
|---|---|---|
| **V** | Very pubescent | 1 |
| **P** | Moderately pubescent | $^{2}/_{3}$ |
| **S** | Slightly pubescent | $^{1}/_{3}$ |
| **G** | Glabrous | 0 |

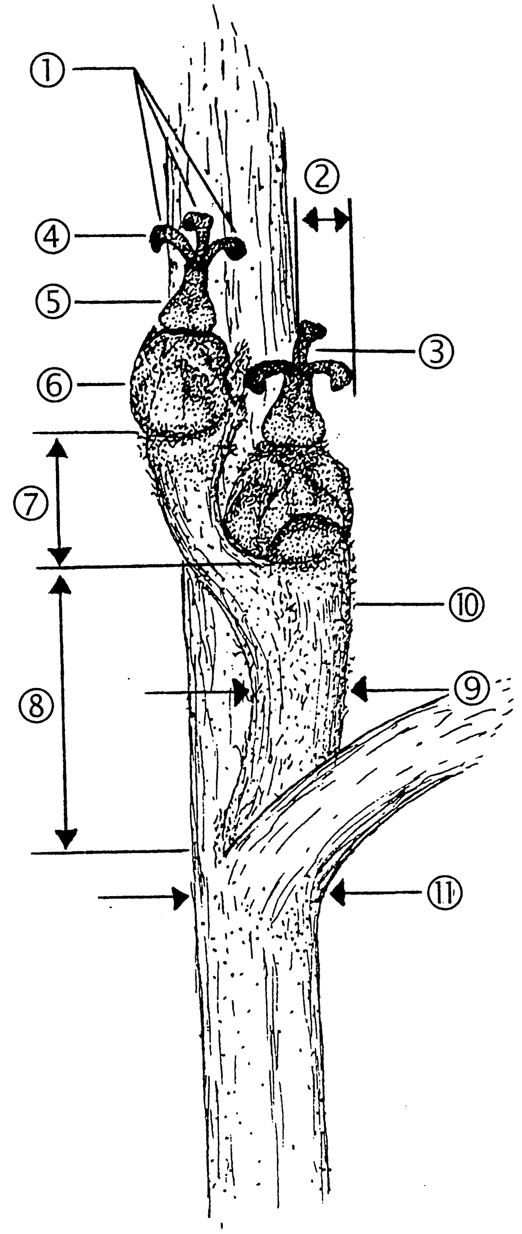


Fig. 6. Female oak inflorescence illustrating characters measured in the study. Characters of inflorescences measured in this study include: number of stigma lobes (1), stigma lobe length (2), stigma recurvature class (3), the color and red color coverage of the stigma (4), perianth collar (5), and bracts (6), bract pubescence class (6), distance from base of the first flower to base of second flower when present (7), peduncle length from base of inflorescence to base of first flower (8), peduncle width (9), peduncle pubescence class (10), and width of shoot at the leaf axil at the base of each inflorescence (11).

acorns was necessary. After outlines were digitally captured from silhouettes, forelighting was increased to reveal structural details necessary for accurate placement of cap and acorn landmarks. I wrote a utility in C (Kernighan & Ritchie, 1988) to then electronically attach matching cap and nut outlines and extract inter-landmark distance measurements into a cumulative database. These steps are summarized in Fig. 7.

The following distances were recorded for each fruit: cap width, cap neck length, depth of cap involucre, total cap length, acorn width, length of the acorn nipple, acorn length, and total fruit (cap+acorn) length. From these, the following ratios were calculated: ratio of cup depth to acorn length, ratio of acorn nipple length to acorn length, ratio of acorn length to width, and ratio of cap width to acorn width. Acorn distance variables are illustrated in Fig. 8.

## WINTER BUD AND SHOOT CHARACTERS

On average 12 shoots bearing terminal buds were randomly selected from the pool of 30 to 45 that were collected per tree. The largest and most apical of the several buds normally clustered at the terminus of an oak shoot was considered the *terminal bud*. The two to four axillary buds that normally surround the terminal bud in the apical bud cluster were termed *peripheral buds*. Characters of the terminal buds, peripheral buds, and the shoots bearing the buds were recorded.

The following winter bud and shoot characters were recorded: shoot length and basal width, previous year's shoot length and basal width, terminal bud length and width, shoot width just below the base of the terminal bud, distance from the base of the terminal bud to its widest width, terminal bud pubescence density and pubescence coverage, and the averaged length of the two largest peripheral buds when present. Distance measurements were interpolated to 0.033 mm using a dial caliper with lines to 0.1 mm. From these measurements, the following ratios were calculated: ratio of terminal bud length to width, ratio of terminal bud length to peripheral bud length, ratio of shoot length to width, ratio of previous year's shoot length to width, and ratio of two

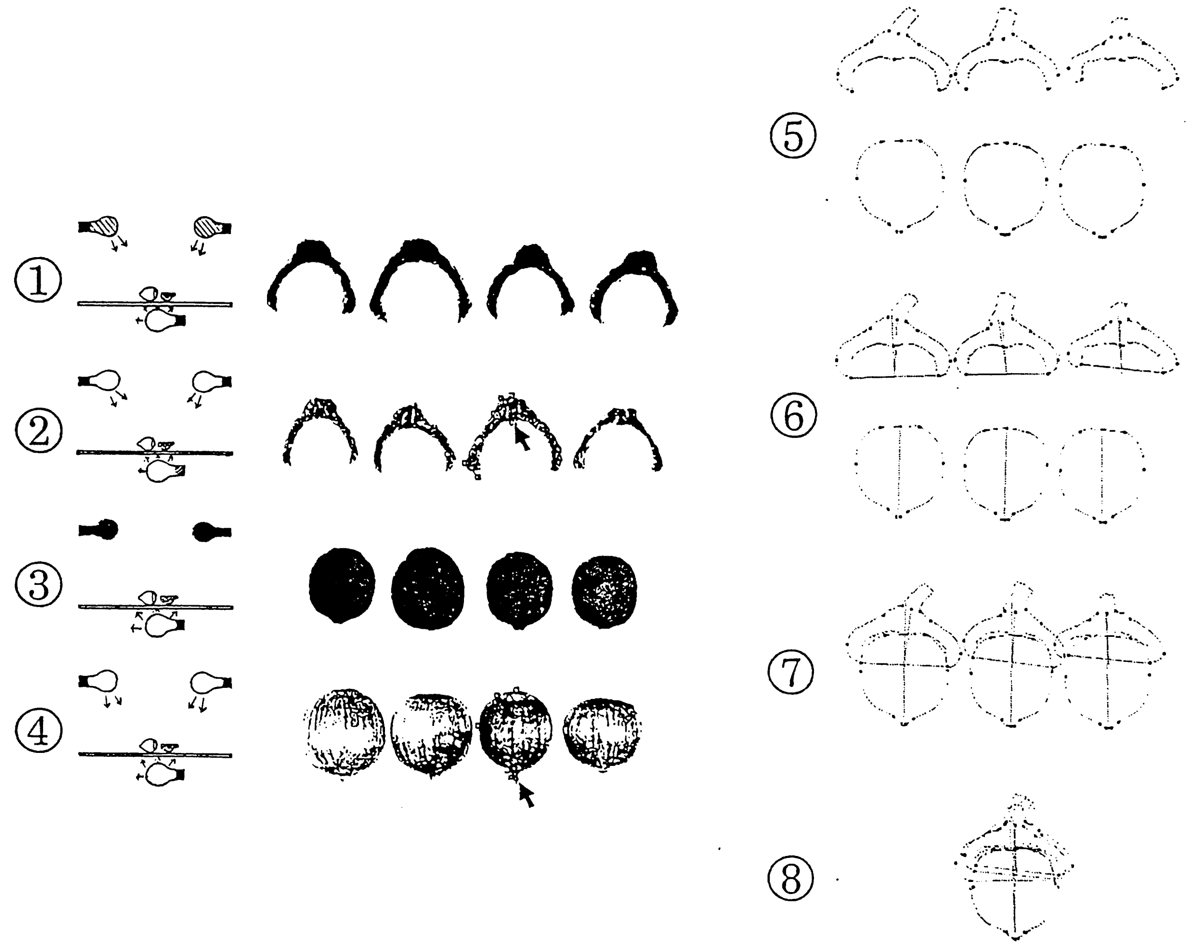


Fig. 7. Illustration of steps used to digitize acorns and caps. Caps and acorns were digitized using a PC-based video image capture system, Morphosys software (Meacham, 1989) and custom software that I wrote. Acorns and transversely-sliced caps were placed on a light table with a video camera (not shown) overhead. Outlines were captured from back-lit silhouettes (1, 3). Forelighting was increased to reveal structural details for accurate placement of landmarks (2, 4). Digitized outlines and landmarks (5) were read from Morphosys files (5). Labels (not shown) were assigned to each landmark and guidelines drawn (6). Cap outlines were then digitally aligned and reattached to matching acorn outlines (7),and inter-landmark distances were written to a cumulative database after outlines had been translated and rotated to the origin (8).

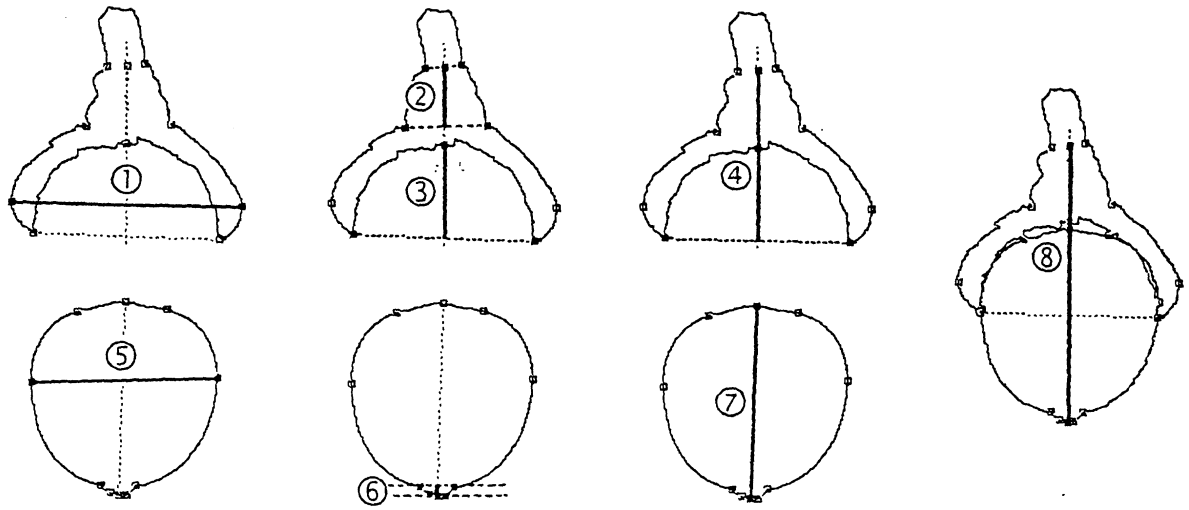


Fig. 8. Cross sections of acorns and caps illustrating measured size variables. Acorn size variables were extracted from inter-landmark distances of digitized cap and acorn outlines. Cap measures are cap width (1), cap neck length (2), depth of cap involucre (3), and total cap length (4). Acorn measures are acorn width (5), acorn nipple length (6), and acorn length (7). Total fruit length was also recorded (8).

year's shoot length to width. Measured characters are illustrated in Fig. 9.

Terminal bud pubescence density and coverage were scored as follows: the number of bud scale *rows* were counted by starting at the tip of the bud and counting to the base along one *column* of scales (Fig. 10). Each scale row was scored for pubescence using the same notation and scale already described for inflorescence pubescence as glabrous (**g**=0), slightly pubescent (**s**=1/3), pubescent (**p**=2/3), or very pubescent (**v**=1) to arrive at a scale formula, from tip to base, like **psgg** or **vpsggg** (Table 6).

To arrive at average pubescence *density*, the values assigned to the scored category for each scale row were summed up and divided by the total number of scale rows scored for that bud. For the formula **psgg**, the value is (2/3+1/3+0+0)/4=0.25. The numeric scale was designed to go from zero to one using equally-spaced increments, hence the use of 1/3 and 2/3.

Approximate pubescence *coverage* was calculated by adding one to a running sum for each non-glabrous score (one scored as **s**, **p**, or **v**) and then dividing by the total number of scale rows. For the formula **psgg**, the coverage value is (1+1+0+0)/4=0.50. Scored pubescence coverage is only an approximation of actual pubescence coverage because the scales do not expose equal areas on the bud. In particular, the most apical and most basal scale rows expose lesser areas than those in the middle.

## Analytical methods

A nominal significance level of $\alpha=0.10$ was chosen for statistical analyses.

### ANALYSIS OF VARIANCE MODELS

One-way analysis of variance (ANOVA) and analysis of covariance (ANCOVA) mixed-models were fit to contrast taxa and, separately, to contrast populations of each taxon on flower, acorn, and winter bud

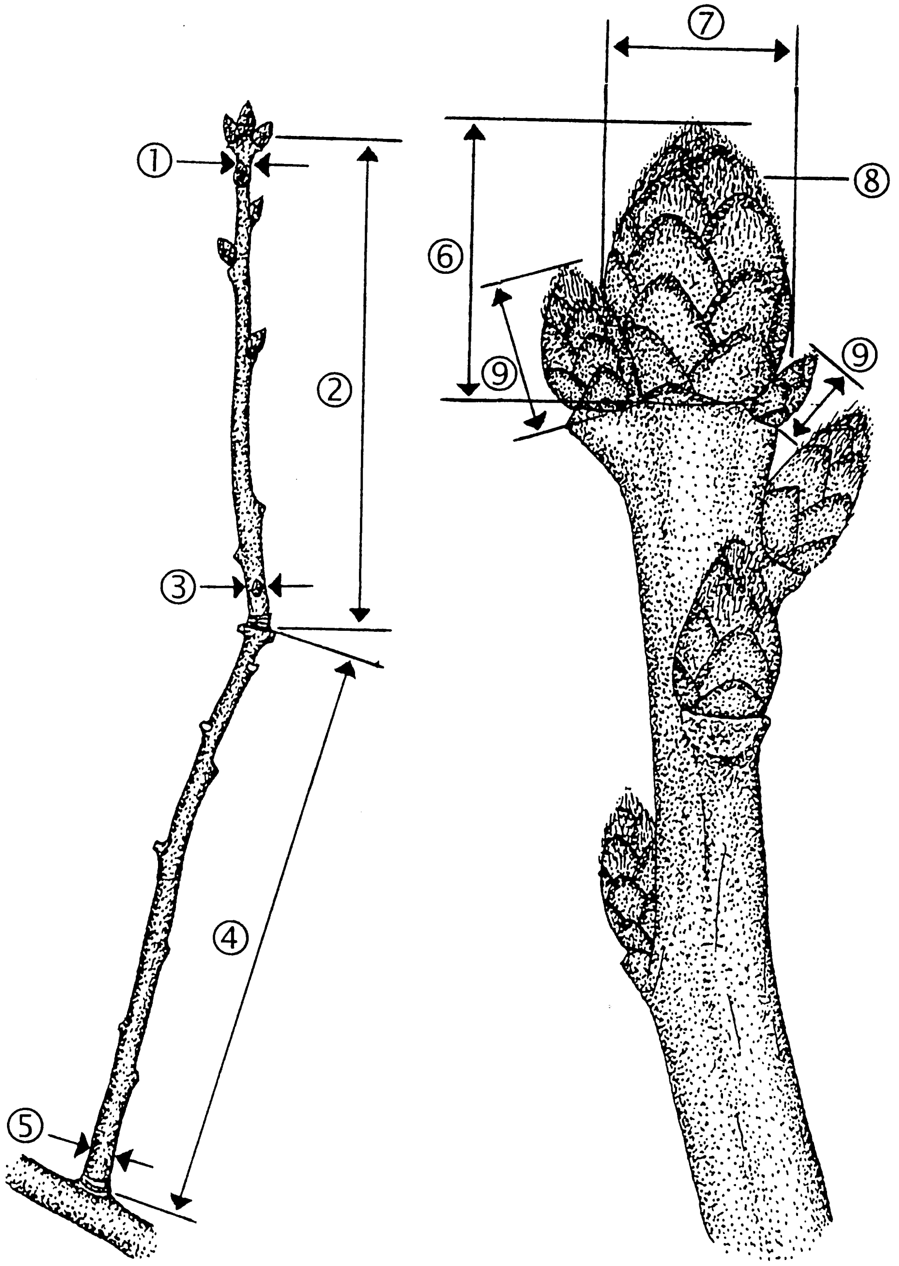


Fig. 9. Winter condition oak shoot (left) and enlargement of terminal bud (right) illustrating characters measured in the study. The following winter bud and shoot characters were recorded: shoot width just below the base of the terminal bud (1), shoot length (2), shoot width at the base of the shoot (3), previous year's shoot length (4), previous year's shoot width at the base of the shoot (5), terminal bud length (6), terminal bud width (7), terminal bud pubescence density and pubescence coverage (8), and the averaged length of the two largest peripheral buds when present (9).

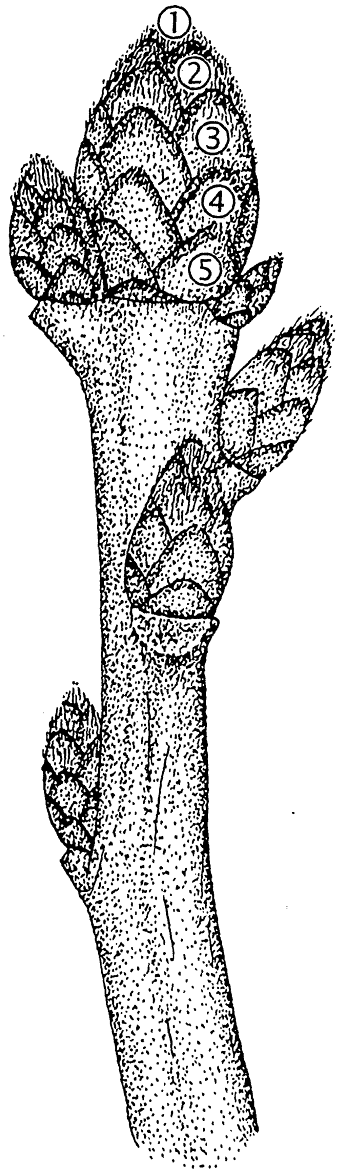


Fig. 10. Winter condition terminal bud showing how bud pubescence was scored. Terminal bud pubescence density and coverage were scored as follows: the number of bud scale *rows* were counted by starting at the tip of the bud and counting to the base along one *column* of scales, as illustrated. Each scale row was scored for pubsecence as glabrous (**g**), slightly pubescent (**s**), pubescent (**p**), or very pubescent (**v**) to arrive at a scale formula from tip to base. See text and Table 6 for further explanation.

characters. All models were fit using the mixed-model procedure, PROC MIXED (SAS Institute, 1996). Either taxa or populations within each separate taxon were defined as fixed effects, and trees were defined as random subjects in mixed effects models. Trees were defined as subjects in order to correctly model variance due to individual trees. Following the advice of Wolfinger (1993), the restricted/residual maximum likelihood method (REML) was used to fit all final models used for inference. Unstructured covariance matrices were used in all models (Wolfinger, 1993; Diggle, 1988). Satterthwaite's approximation (Satterthwaite, 1946) was used to calculate degrees of freedom for the unbalanced models.

Stigma recurvature class was used to ascertain female flower maturity. Only inflorescences that scored 2.5 or above on the stigma recurvature scale were included in floral character analyses.

Inflorescences originating from leaf axils toward the base of a shoot are usually longest and generally become progressively shorter closer to the apex of the shoot (Fig. 11). This is especially noticeable in *Q. coccinea* which has the longest and most gracile peduncles among the three taxa investigated, but the phenomenon also occurs in *Q. rubra* and *Q. velutina*. Only the three most basal inflorescences per shoot were included in analyses of inflorescence peduncle length, peduncle width, and distance from first flower to second flower. Any basal inflorescence scoring below 2.5 on stigma recurvature class was excluded.

When appropriate, a measure of shoot width was used as a covariate in ANCOVA analyses of inflorescence and winter bud size characters to reduce extraneous variability due to differences in shoot size. For size characters of inflorescences, shoot width at the leaf axil of the inflorescence (character no. 11 in Fig. 6) was used. For size characters of terminal buds, shoot width at the base of the shoot (character no. 3 in Fig. 9) was used. PROC MIXED was used to test the slopes-equal-to-zero and common-slopes hypotheses prior to fitting common-slope and unequal-slope models used for inference (Littell, 1996, Ch. 5). In cases where the covariate was not significant, models were reparameterized without the covariate.

Fig. 11. Spring shoots of *Q. rubra* (left) and *Q. coccinea* (right) with blooming female inflorescences. Inflorescences originating from leaf axils toward the base of a shoot are usually longest and generally become progressively shorter closer to the apex of the shoot. This is most noticeable in *Q. coccinea* which has the longest and most gracile peduncles among the three taxa investigated, but the phenomenon also occurs in *Q. rubra*, and in *Q. velutina* (not illustrated).

Bonferroni comparison tests were performed to investigate significant differences between pairs of taxa and pairs of populations of each taxon, respectively. The Bonferroni method was chosen in order to control for Type I error in the family of all pairwise contrasts investigated for each ANOVA. Separate ANOVAs were conducted to investigate differences between the Mio populations and all other populations, between the Maumee populations and all other populations and, finally, contrasting the Maumee, Jackson, and Ann Arbor populations with the Holly and Mio populations of each respective taxon. For all analyses, the number of trees, number of observations, means, and standard deviations of the variables were tabulated by level.

## REGRESSIONS ON CLIMATIC AND SOIL VARIABLES

Weighted simple linear least-squares regressions were fit to examine relationships between measured bud and acorn characters and climatic and soil variables which might affect the expression of these characters. Regressions were limited to *Q. coccinea* which comprised the largest subset of the data. Models were fit using the general linear models procedure, PROC GLM (SAS Institute, 1989). Mean values of the dependent variables were first computed for each tree. Values for climatic data were obtained at the population level, while soil characters were measured at the ecosystem level. Therefore, regressions on climatic variables were weighted by the number of trees sampled in each population, while those on soil variables were weighted by the number of trees in each ecosystem. All acorn and bud variables shown in Figs. 8 and 9 and all climatic and soil variables shown in Tables 3 and 4 were considered.

## ADDITIONAL STATISTICAL METHODS

Multivariate Analysis of Variance (MANOVA) was used to test for differences in inner bark color. MANOVA was run using the general linear models procedure, PROC GLM, and the MANOVA statement (SAS Institute, 1989) to model group differences in inner bark hue, value, and chroma. The Kolmogorov-Smirnov test statistic was used to formally test for differences between two distributions. Kolmogorov-Smirnov statistics were generated using the EDF option of PROC NPAR1WAY (SAS Institute, 1989).

## CHECKING STATISTICAL ASSUMPTIONS

Deviations from the assumptions of the statistical models were investigated informally by examining scatterplots, moments (mean, variance, skewness, and kurtosis), Box plots and normal probability plots of the residuals.

Box's correction of Bartlett's test (Neter et al., 1990, p. 617) was used to formally investigate equality of population variances for the ANOVA and ANCOVA models. When possible, PROC MIXED was used to directly model unequal group variances (Littell et al., 1996, Section 4.4.7). However, some problems were too large for PROC MIXED to handle. Regression lack of fit was formally investigated using F tests (Neter et al., 1990, p. 131). Bartlett's tests and regression lack-of-fit F-tests were calculated using a utility I wrote in C incorporating algorithms described in Press et al. (1988).

In the small number of cases where a problem of heterogeneity of variances was suspected, appropriate transformations (Neter et al., 1990, p. 145) were not found to substantially improve normality of the residuals, nor to substantially affect the calculated significance levels obtained using the MIXED procedure. In the cases where the problem was not too large for PROC MIXED to model the variance components directly, I found few differences in the significance levels obtained using an unequal-variance model vs. an equal-variance model. All reported probability values are from analyses of untransformed variables.

# RESULTS AND DISCUSSION

## Characteristics of the Ecosystems

### ECOSYSTEMS OF THE MAUMEE SUBDISTRICT

The Maumee ecosystems experience the warmest and wettest climate of the three regional ecosystems investigated. The growing season averages 180 days between frosts and annual precipitation averages 831 mm. (Table 7). The trees are generally large in stature and form a closed forest canopy. The A horizons are relatively deep (10 cm or greater in depth in MCCL and PERK ecosystems: see soil profiles in Appendix B). The highly rinsed, acid sand soils in the three Maumee ecosystems are rapidly permeable and have low available water content. However, drainage in these soils is often poor due to the lacustrine clay substratum which results in a standing water table apparent at the surface or within about a meter of the soil between four to eight months of the year (USDA Soil Survey, 1981). This high water table is an important factor affecting soil characters, such as pH, and the distribution and growth of plants in these ecosystems.

In all Maumee ecosystems, *Q. coccinea* generally dominates the overstory on the low beach ridges and is codominant with *Q. alba* on medium beach ridges. Low beach ridges are approximately 0.3 to 1.0 m above the standing spring water table, while medium beach ridges are approximately 1.0 to 2.5 meters above the spring water table. *Q. velutina* begins to replace *Q. coccinea* on the higher beach ridges where it competes with *Q. alba*. Typically *Q. velutina* completely dominates the highest ridges above approximately 2.5 m. In contrast in the low, wet depressions where the water table is at the surface in spring, *Q. palustris* is the dominant red oak. Other overstory taxa of the wet depression ecosystems include *Q. bicolor*, *Nyssa sylvatica*, and *Acer saccharinum*.

Table 7. Growing degree days, growing season length, and annual and spring precipitation by ecosystem.

| Ecosystem | Growing degree days base 7.2$^{o}$ C | Growing season length base 0$^{o}$ C | Annual precipitation (mm) | Spring precipitation (mm) |
|---|---|---|---|---|
| Maumee | 2246 | 180 | 831 | 222 |
| Ann Arbor | 2196 | 178 | 833 | 220 |
| Waterloo | 2062 | 156 | 755 | 204 |
| Holly | 1910 | 160 | 769 | 197 |
| Mio | 1573 | 117 | 691 | 160 |

The Maumee populations of *Q. coccinea* may be able to tolerate partial inundation of its root system in spring when the water table is highest (Barnes, pers. comm.). This tolerance for low oxygen levels is assumed to be not as great as in *Q. palustris*, but greater than in *Q. velutina*, and, thus, *Q. coccinea* occupies an intermediate position on the beach ridge ecosystems. At MCCL in a soil pit on a low sand rise adjacent several large individuals of *Q. coccinea*, I measured fine rooting to a depth of 36 cm and coarse rooting to a depth of 44 cm, coinciding with the development of a more chromatic, concreted $B_{w2}$ horizon that spans the approximate fluctuating depth of the high spring water table (see soil profile for MCCL in Appendix B). Root development, hence, appears to be largely restricted to the upper horizons of strongly acidic soil --pH values for A and $B_{w1}$ horizons at MCCL are 4.53 and 5.11, respectively. With their roots restricted to the uppermost horizons of soil, the *Q. coccinea* here are subject to extremely droughty conditions in summer.

The influence of the high water table and the underlying clay substratum is evident in the C horizon which becomes progressively less acidic at increasing depths. In the second soil pit at PERK dug in a wet depression ecosystem dominated by *Q. palustris*, pH in the C horizon was still moderately acidic just below 1 m, neutral at 2.4 m, and alkaline at 2.8 m. However, as the example at MCCL illustrates, there appears to be little opportunity for roots of *Q. coccinea* to tap this supply of Calcium. The presence of acid indicator species *Vaccinium angustifolium* and *Gaultheria procumbens* in the ground cover of these low and medium ridge ecosystems attests to the lack of significant calcium pumping by the oaks (Barnes, pers. comm.). "Pumping" refers to the ability of deep-rooted oaks to acquire and "pump" Ca++ laden water to the crown. When the calcium-rich leaves fall, they decompose more rapidly than those on sites where shallow roots fail to reach the Ca++ zone.

## ANN ARBOR, WATERLOO, AND HOLLY ECOSYSTEMS

The RADR ecosystem in Ann Arbor consists of an oak-hickory forest on clay loam till. Major overstory constituents are *Q. rubra*, *Q. alba*, *Q. velutina*, *Carya glabra* and *C. ovata*. *Q. coccinea* is not present. The climate is quite similar to that of the Maumee ecosystems. The three Waterloo ecosystems and one Holly ecosystem consist of oak-hickory forests on sandy ice-contact landforms. The Waterloo and Holly ecosystems experience a growing season that is about 20 days shorter than that of the Ann Arbor region, and precipitation is also less, as indicated in Table 7.

In the Waterloo and Holly ecosystems, *Q. coccinea* was observed to dominate on ridge tops and on the south and southwest-facing slopes where *Q. velutina* was also usually present, although in fewer numbers than *Q. coccinea*. *Q. rubra* was present at POTO on an east and northeast-facing slope along with *Q. velutina* and *Q. alba*.

Of the three Waterloo ecosystems, the GEOC kame ecosystem appeared to have the lowest productivity. Trees here are widely spaced with very little canopy closure, especially on the kame top and steep southwest face. This ecosystem also has extremely gravelly and cobbly soil. Canopy closure in the two other Waterloo ecosystems and in the Holly ecosystem was considerably more closed, although all the ecosystems show evidence of former disturbance and are now in the process of aggrading.

## MIO ECOSYSTEMS

Compared to the other areas studied, Mio experiences a much harsher, more continental climate characterized by larger temperature swings, minimal lake effect, and a shorter growing season averaging just 117 days between late spring and early fall frosts. The 30-year average for annual precipitation is 690 mm, 140 mm less than the Maumee average.

The MIO1 and MIO4 ecosystems occur on excessively drained nearly-level outwash plain. The ground cover in both ecosystems is dominated by shade-intolerant, xeric acid-indicator species, notably *Comptonia peregrina*, *Ceanothus americanus*, *Vaccinium angustifolium*, *Arctostaphylos uva-ursi*, and lichens.

In MIO1, *Pinus banksiana* and *Quercus coccinea* dominate the overstory where they form a very open canopy of widely-spaced trees in this least-productive of the four Mio ecosystems sampled. *Q. velutina* and *Q. alba* both occur in the ground cover, but *Q. alba* does not appear to enter the understory at all, while the occasional understory specimens of *Q. velutina* showed noticeable frost damage on the expanding shoots when visited in early June, 1994. No specimens of *Q. coccinea* examined here showed any signs of frost damage.

*Pinus resinosa* occurs with *P. banksiana* as a dominant component of the overstory, and *Q. alba* appears in the understory, in the slightly more productive MIO4 ecosystem. Canopy closure here ranges from moderately-open to moderately-closed. Canopy closure is uneven due to selective logging which appears to have adversely affected overall productivity. The relatively more mesophytic, moderately shade-tolerant *Pinus strobus* occurs in the more protected spots in the ground cover here, but it does not appear in the understory. Although the A horizon in MIO4, with a measured depth of just 3.5 cm, is as shallow as that of MIO1 (2 to 4 cm: see soil profiles in Appendix B), the substantially greater proportion of fine sand in the top 20 cm of soil (34% here vs. only 8 to 12% in MIO1) may partially account for the better productivity seen here. No *Q. velutina* trees were found in MIO4.

The moderately-productive MIO2 ecosystem, on sandy ice-contact slopes of 2 to 6%, was the only ecosystem with mature fruiting individuals of *Q. velutina*. *Q. velutina*, *Q. alba*, *Pinus banksiana*, *P. resinosa*, and *Populus grandidentata* form a moderately closed-canopy overstory here. Most of these overstory taxa are also present in the understory and ground cover. Additional taxa such as *Pinus strobus*, *Hamamelis virginiana*, *Populus tremuloides*, *Prunus serotina* and *Prunus virginiana* in the understory, and *Acer rubrum* in the ground cover, contribute to the relatively more diverse flora of this ecosystem. Sand comprises 84% of the top 20 cm of soil here, compared to over 90% in both MIO1 and MIO4, and the A horizon, at 5 cm, is slightly deeper (Appendix B). No individuals of *Q. coccinea* were found here.

The MIO3 ecosystem, on a north to northeast-facing sandy ice-contact slope of 5 to 10%, represents a biotically rich, mesophytic northern hardwoods ecosystem. Measured from a soil pit on the upper slope, the A horizon spans 7 cm. Fine roots penetrate the BC horizon to a depth of approximately 67 cm, and the C horizon is alkaline (pH 8.0) at a depth of 105 cm. *Pinus resinosa*, *P. strobus*, *Picea glauca*, *Betula papyrifera*, *Quercus rubra*, *Q. alba*, and *Populus grandidentata* are all present in the overstory which forms a predominantly closed canopy. This was the only Mio ecosystem found to contain *Q. rubra*.

Around Mio, *Q. coccinea* appears confined to the acidic, fire-prone, excessively drained outwash plain ecosystems where it codominates with *Pinus banksiana*. *Q. rubra* appears confined to the mesic northern hardwood ecosystems which develop on moist sites with loamy soils. *Q. velutina* only appeared in large numbers in an ecosystem of intermediate productivity where it occurred with *Q. alba* and *Pinus resinosa*. A few putative individuals of *Q. velutina* were seen on the xeric outwash plain ecosystems with *Q. coccinea*, but no fruiting specimens of *Q. velutina* were found there.

## Regressions of Acorn and Bud Characters

Results of regression analyses support the hypothesis that populations of *Q. coccinea* exposed to longer, warmer, and wetter growing seasons have larger buds and acorns (Figs. 12, 13). Four climatic variables were found to consistently produce moderate coefficients of determination ($r^2$ as high as 0.49, $r^2>0.30$ in 48% of the cases) on 10 size measures of the acorn and terminal bud (Table 8). The regressions were highly significant ($0.0001 \le p \le 0.0034$). Growing degree days was, on average, most highly correlated with the 10 measures, followed closely by spring precipitation, growing season length, and summer precipitation, respectively.

Growing degree days measures two factors important to plant growth, the amount of heat received by a plant, and the duration of time over which that heat is received. Growing season length only measures the second factor, the duration of time during which growth can occur. Therefore, it is not surprising that growing degree days was consistently more correlated with the size measures than was growing season length.

In 8 out of 10 cases (Table 8), spring precipitation is more highly correlated with the size measure than is summer precipitation. Coefficients of determination of these 10 size variables with fall and

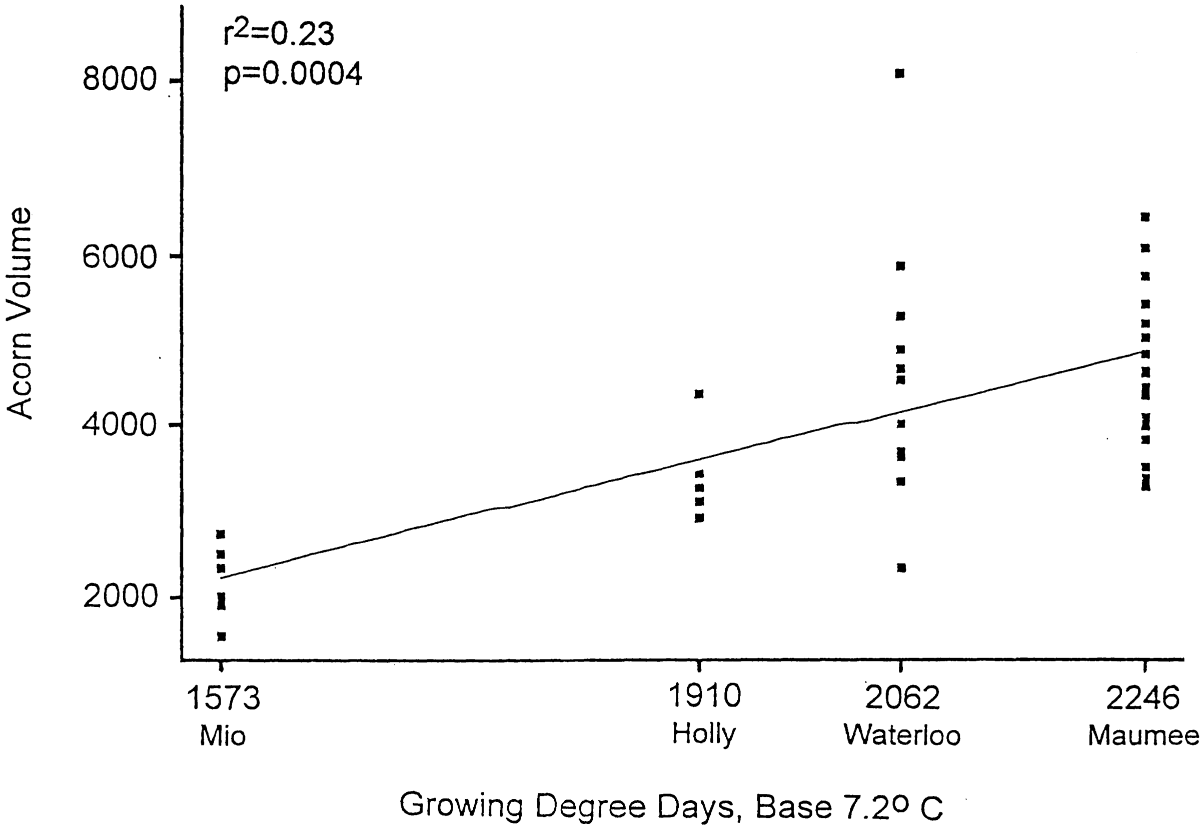


Fig. 12. Relationship of acorn volume to growing degree days in four populations of *Q. coccinea*. Mean acorn volume of individual trees is plotted against growing degree days for the Maumee, Waterloo, Holly and Mio populations of *Q. coccinea*. Acorn volume was calculated as (acorn length)×(acorn width)$^2$.

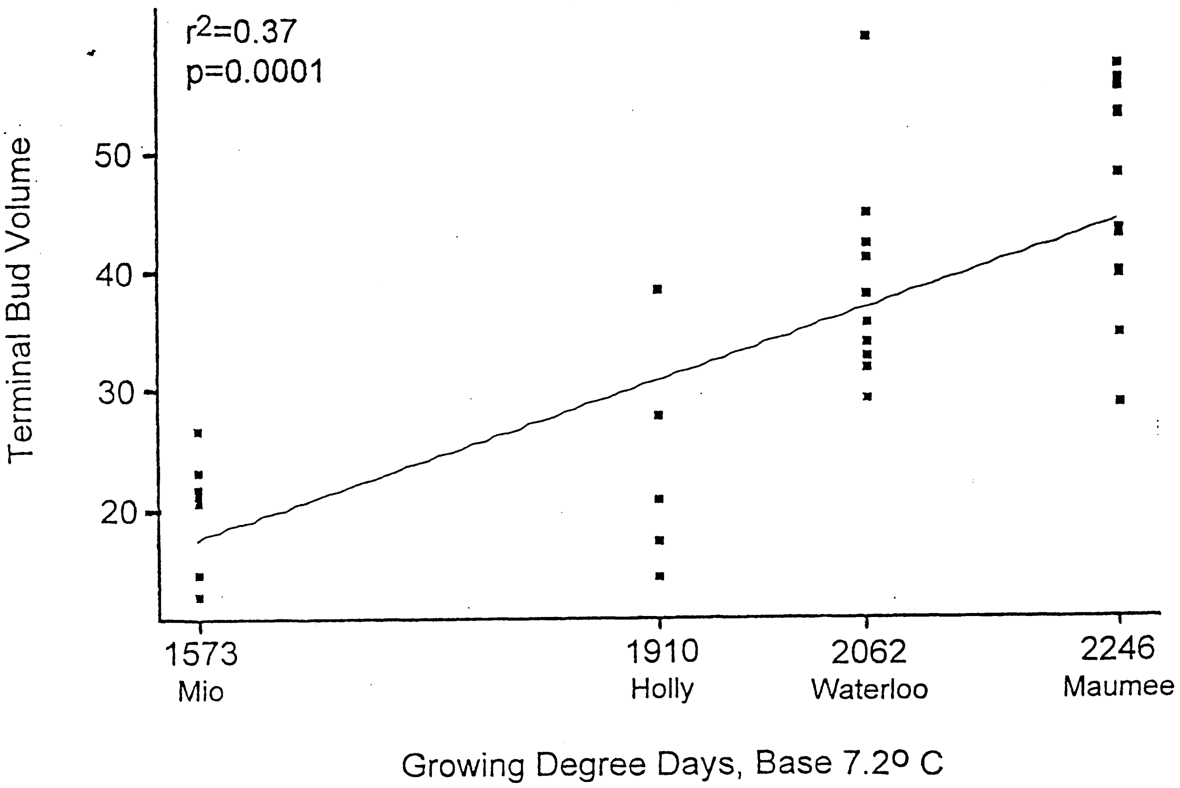


Fig. 13. Relationship of terminal bud volume to growing degree days in four populations of *Q. coccinea*. Mean terminal bud volume of individual trees is plotted against growing degree days for the Maumee, Waterloo, Holly, and Mio populations of *Q. coccinea*. Bud volume was calculated as (bud length)×(bud width)$^2$.

Table 8. Relationships of size characters of the acorns and terminal buds of *Q. coccinea* to four climatic factors.

| | | Weighted Linear Regression Coefficient of Determination ($r^2$) values | | | |
|---|---|---|---|---|---|
| No. | Variable | Growing degree days, base 7.2° C | Growing season length, base 0° C | Spring precipitation mm | Summer precipitation mm |
| 1. | Terminal bud width | 0.49 | 0.46 | 0.48 | 0.48 |
| 2. | Terminal bud length | 0.29 | 0.21 | 0.27 | 0.21 |
| 3. | Terminal bud volume[1] | 0.37 | 0.34 | 0.36 | 0.36 |
| 4. | Acorn cap width | 0.37 | 0.32 | 0.36 | 0.29 |
| 5. | Depth of cap involucre | 0.37 | 0.38 | 0.38 | 0.35 |
| 6. | Acorn cap length | 0.36 | 0.35 | 0.36 | 0.31 |
| 7. | Acorn width | 0.26 | 0.21 | 0.25 | 0.18 |
| 8. | Acorn length | 0.21 | 0.17 | 0.20 | 0.14 |
| 9. | Total fruit length | 0.25 | 0.20 | 0.24 | 0.17 |
| 10. | Acorn volume[2] | 0.23 | 0.18 | 0.22 | 0.15 |

[1] Terminal bud volume was calculated as (bud length)×$(\text{bud width})^2$.

[2] Acorn volume was calculated as (acorn length)×$(\text{acorn width})^2$.

winter precipitation (not shown) were in general lower, and often very much lower for fall precipitation in particular.

No soil variables were found to be correlated with measures of the bud and acorn in a consistent or biologically interpretable manner.

# Differences Among Taxa

## DIFFERENCES IN FEMALE INFLORESCENCES AMONG TAXA

Eight of 12 characters of female inflorescences were significant among taxa ($p \leq 0.049$, Table 9). The most striking differences were in characters of the peduncle, the part of the inflorescence most easily seen by the unaided eye.

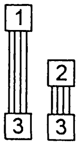
The most striking difference was in density of pubescence on the peduncles of inflorescences ($p=0.0001$, Table 10). Inflorescence peduncles in *Q. velutina* were very pubescent, whereas those of *Q. rubra* were usually glabrous. Inflorescence peduncles of *Q. coccinea* were almost never scored as very pubescent. About 2/3 of the peduncles of *Q. coccinea* were scored as slightly pubescent and 1/3 as glabrous, resulting in the mean density of 0.20 shown in Table 10. The lack of a statistically significant difference between *Q. coccinea* and *Q. rubra* is probably due to the small sample size for *Q. rubra*. In the field, the difference in peduncle pubescence between these latter two taxa is usually apparent, as I have illustrated in Fig. 3.

Trelease (1924) noted that the degree of peduncle stalking often affords a good specific or group character. The length of the peduncle in *Q. velutina* is about half that of *Q. rubra* or *Q. coccinea* (Table 11). Although *Q. rubra* and *Q. velutina* do not appear to differ much in peduncle length, the width of the peduncle in *Q. rubra* is 1/3 to 1/2 times wider than in *Q. velutina* or *Q. rubra* (Table 12). Thus, when length and width are considered together, as in Table 13, it is apparent that *Q. coccinea* has by far the most gracile inflorescence peduncles, whereas those of *Q. velutina* are the stoutest. In *Q. rubra*, the inflorescence peduncles are often as long as in *Q. coccinea*, but they

Table 9. Characters of the female inflorescence and probability values of statistically significant ANOVAs comparing *Q. coccinea*, *Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

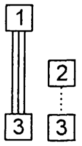
| No. | Character | ANOVA P-value |
|---|---|---|
| 1. | Density of pubescence on the peduncle | 0.0001 |
| 2. | Peduncle length | 0.0003 |
| 3. | Peduncle width | 0.0405 |
| 4. | Ratio of peduncle length to width | 0.0034 |
| 5. | Distance from first to second flower on the inflorescence | 0.0254 |
| 6. | Number of flowers on the inflorescence | 0.0105 |
| 7. | Recurvature of stigma lobes | 0.0367 |
| 8. | Coverage of red color on the perianth | 0.0490 |

Table 10. Comparison of density of pubescence on the peduncles of female inflorescences in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 158 | 0.20 | 0.23 |  |
| 2 | *Q. rubra* | 6 | 77 | 0.11 | 0.16 | |
| 3 | *Q. velutina* | 7 | 119 | 0.90 | 0.15 | |

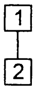
[1] Quadruple line: $p < 0.00005$.

Table 11. Comparison of peduncle length of female inflorescences in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 125 | 6.26 | 2.92 |  |  |
| 2 | *Q. rubra* | 6 | 64 | 5.54 | 2.02 | | |
| 3 | *Q. velutina* | 7 | 106 | 3.27 | 1.67 | | |

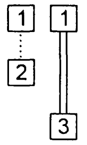
1 Bar length indicates mean peduncle length of female inflorescences.
2 Dotted line: $p<0.10$; triple line: $p<0.0005$.

Table 12. Comparison of peduncle width of female inflorescences in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 125 | 1.02 | 0.25 |  |  |
| 2 | *Q. rubra* | 6 | 62 | 1.63 | 0.50 | | |
| 3 | *Q. velutina* | 7 | 106 | 1.22 | 0.29 | | |

1 Bar length indicates mean peduncle width of female inflorescences.
2 Single line: $p<0.05$.

Table 13. Comparison of the ratio of peduncle length to width of female inflorescences in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 125 | 6.64 | 3.84 |  |
| 2 | *Q. rubra* | 6 | 62 | 3.96 | 2.56 | |
| 3 | *Q. velutina* | 7 | 106 | 2.91 | 1.80 | |

1 Dotted line: $p<0.10$; double line: $p<0.005$.

differ in being relatively thicker (p=0.0405, Table 12). This difference becomes readily apparent with field experience. Recall that peduncle length and width data are based on examination of the three most basally positioned inflorescences on each shoot. These inflorescences are usually the longest and are not only easier to see in the field, but are the most useful in distinguishing these taxa.

In Table 14, the distance from first to second flower on female inflorescences (character no. 7 in Fig. 6) of the three taxa is compared. The results suggest that the pair of flowers which normally make up the mature inflorescence tends to be most symmetrically opposed in basal inflorescences in *Q. rubra*, and least so in *Q. coccinea*. The divergence is, on average at least, quite small for all three taxa. However, the variance of this character, like the variance of peduncle length itself, is greatest for *Q. coccinea*. The character is thus diagnostic in the field: inflorescences in which the pair of flowers are separated by 2 or more millimeters (see Fig. 3) should certainly be suspected as belonging to *Q. coccinea*, but examination of additional characters should be used to confirm the diagnosis.

In Table 15, the mean number of mature flowers on female inflorescences is compared among the three taxa. *Quercus rubra* averages more than two flowers per inflorescence. Although the sample size for *Q. rubra* was small, in the field I noticed that *Q. rubra* appeared much more likely than the other two taxa to have three or more (four, five) flowers on the reduced inflorescence spike. Twenty-one percent of inflorescences of *Q. rubra* had three mature flowers on the spike, versus just 8% for *Q. coccinea* and 6% for *Q. velutina*. I did not encounter any inflorescences of either *Q. velutina* or *Q. coccinea* with more than three mature flowers.

Stigma lobes on mature inflorescences of *Q. velutina* are distinctly more recurved than those of *Q. rubra* ($p<0.05$, Table 16). No real difference in recurvature is apparent between *Q. velutina* and *Q. coccinea* (p=0.95), nor between *Q. coccinea* and *Q. rubra*, although this latter result (p=0.20) might have been different were more data available.

To an extent, stigma lobe recurvature is an indication of floral maturity. If *Q. velutina* were to mature earlier, stigma lobes in *Q.*

Table 14. Comparison of distance from first to second flower on female inflorescences in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 109 | 1.42 | 1.04 |  | $\boxed{1}$ |
| 2 | *Q. rubra* | 6 | 62 | 0.74 | 0.73 |  | $\boxed{2}$ |
| 3 | *Q. velutina* | 7 | 74 | 1.05 | 0.72 |  | |

[1] Bar length indicates mean distance from first to second flower on female inflorescences.

[2] Single line: $p<0.05$.

Table 15. Comparison of the number of flowers on female inflorescences in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 158 | 1.93 | 0.48 | |
| 2 | *Q. rubra* | 6 | 77 | 2.22 | 0.62 | $\boxed{2}$ |
| 3 | *Q. velutina* | 7 | 119 | 1.74 | 0.56 | $\boxed{3}$ |

[1] Single line: $p<0.05$.

Table 16. Comparison of recurvature of stigma lobes on mature female flowers in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 158 | 3.49 | 0.74 | |
| 2 | *Q. rubra* | 6 | 77 | 3.03 | 0.47 | $\boxed{2}$ |
| 3 | *Q. velutina* | 7 | 119 | 3.69 | 0.79 | $\boxed{3}$ |

[1] Single line: $p<0.05$.

*velutina* would appear more recurved relative to those of *Q. coccinea* or *Q. rubra*. However, my field observations were exactly the opposite: *Q. velutina* appeared to mature later than both *Q. rubra* and *Q. coccinea*. The different taxa in each population were collected and measured at most one day apart. In the field at both HOLL and POTO, male catkins of *Q. velutina* were often still green and not yet dehiscent, or were just beginning to dehisce on some trees, when those of *Q. rubra* and *Q. coccinea* in the same or nearby ecosystems were already senescent or shriveled. In some cases, the stigma lobes of female inflorescences of *Q. rubra* and *Q. coccinea* were already beginning to blacken while those of *Q. velutina* still showed no signs of senescence. Peak flowering in *Q. velutina* may generally occur somewhat later than in *Q. coccinea* and in *Q. rubra*, although clearly there is close overlap. In any case, the later flowering observed in individuals of *Q. velutina* indicates that the greater recurvature readily seen in *Q. velutina* represents a real morphological distinction. I again refer the reader to Fig. 3 which shows representative inflorescences of the three taxa drawn to scale from fresh specimens that were all collected from one site on the same day (HOLL on June 4, 1994).

In addition to greater recurvature, the stigma lobes of *Q. velutina* were often observed to be larger than those of *Q. coccinea* and *Q. rubra*, as I have illustrated in Fig. 3. The ANOVA of stigma lobe length was not statistically different among the taxa (p=0.22, Table 17). However, the distribution of stigma lobe length in *Q. velutina* is significantly different from the combined distribution of *Q. coccinea* and *Q. velutina* (Kolmogorov-Smirnov test statistic=3.28, p=0.0001). Forty-one percent of observations for *Q. velutina* had a stigma lobe length greater than or equal to 1.5 mm, versus just 9% for *Q. coccinea* and 3% for *Q.rubra* (Table 18). At the 75th percentile of the distributions, *Q. velutina* has stigma lobes that are on the order of a half a millimeter longer than for the other two taxa, a size difference that is readily apparent to an observer in the field.

Differences in red color coverage between taxa were significant only for perianths (p=0.049) where *Q. velutina* had much lower coverage scores than either *Q. coccinea* or *Q. rubra* (Table 19). In practice, the perianth collar in *Q. velutina* is more generally obscured by the densely

Table 17. Comparison of length of stigma lobes on female flowers in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 9 | 158 | 1.10 | 0.24 |  | |
| 2 | *Q. rubra* | 6 | 77 | 1.14 | 0.18 |  | |
| 3 | *Q. velutina* | 7 | 119 | 1.31 | 0.43 |  | |

[1] Bar length indicates mean length of stigma lobes on female flowers.

[2] No pairwise contrasts were statistically significant.

Table 18. Distributions of stigma lobe length (mm) in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Minimum | 25th Percentile | Median | 75th Percentile | Maximum | Percent of observations with lobe length >= 1.5 mm |
|---|---|---|---|---|---|---|
| *Q. coccinea* | 0.55 | 0.95 | 1.10 | 1.21 | 1.80 | 9 |
| *Q. rubra* | 0.70 | 1.00 | 1.20 | 1.30 | 1.50 | 3 |
| *Q. velutina* | 0.60 | 0.90 | 1.30 | 1.70 | 2.40 | 41 |

Table 19. Comparison of coverage of red color on perianths of mature female flowers in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Inflor. | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 4 | 59 | 0.27 | 0.19 | |
| 2 | *Q. rubra* | 4 | 44 | 0.44 | 0.20 | $\boxed{2}$ |
| 3 | *Q. velutina* | 4 | 46 | 0.05 | 0.10 | $\boxed{3}$ |

[1] Dotted line: $p<0.10$.

pubescent bracts (see Fig. 3). Therefore, perianth red color coverage is not a generally useful diagnostic trait.

In summary, mature female inflorescences of *Q. velutina* are easily distinguished from those of the other two taxa by their greater pubescence, stocky peduncles, and more greatly reflexed stigma lobes. The differences between *Q. coccinea* and *Q. rubra* are more subtle, but examination of peduncle characters are sufficient to distinguish the taxa: peduncles are generally more gracile and more pubescent in *Q. coccinea.* When flowers are available, use of these characters can be extremely helpful in diagnosing specimens, especially in situations where vegetative or fruit characters appear confounding. A case in point will be found under the discussion of the Mio population of *Q. velutina*.

## DIFFERENCES IN ACORNS AMONG TAXA

Ten of 12 analyzed acorn characters were highly significant among taxa (p=0.0001), and one was significant at p=0.0765 (ratio of acorn length to acorn width, Table 20).

As expected, acorn width (Table 21) and length (Table 22) are greatest in *Q. rubra*. Acorns of *Q. velutina* are on average smaller than those of *Q. coccinea* in the populations studied. The latter result may simply reflect the populations that were sampled: the morphologically larger Maumee and Waterloo populations comprise 73% of the *Q. coccinea* sample.

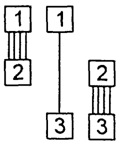
The ratio of acorn length to width (Table 23) is significant at p=0.0765 for the contrast between *Q. coccinea* and *Q. rubra*, and no difference in means is seen between *Q. coccinea* and *Q. velutina*. *Q. rubra* has the most globular acorns, whereas the latter two taxa have acorns that are on average 1 1/4-times longer than wide.

There is a small difference between *Q. coccinea* and *Q. velutina* in the median tree-averaged acorn length-to-width ratios (Table 24), but no difference in the 75th percentile ratios. Although some specimens in this study did have noticeably elliptical acorns, *Q. coccinea* does not in general appear to have acorns that are substantially more elongate than those of *Q. velutina* in the populations studied.

Table 20. Characters of the acorn and probability values of statistically significant ANOVAs comparing *Q. coccinea*, *Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| No. | Character | ANOVA P-value |
|---|---|---|
| 1. | Acorn width | 0.0001 |
| 2. | Acorn length | 0.0001 |
| 3. | Ratio of acorn length to acorn width | 0.0765 |
| 4. | Acorn cap width | 0.0001 |
| 5. | Acorn cap length | 0.0001 |
| 6. | Total fruit (acorn plus cap) length | 0.0001 |
| 7. | Neck length of acorn cap | 0.0001 |
| 8. | Cup depth of acorn cap | 0.0001 |
| 9. | Ratio of acorn cup depth to acorn length | 0.0001 |
| 10. | Length of acorn nipple | 0.0001 |
| 11. | Ratio of acorn nipple length to acorn length | 0.0001 |

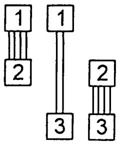
Table 21. Comparison of acorn width in *Q. coccinea*, *Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 14.83 | 2.09 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 19.55 | 1.88 |  | |
| 3 | *Q. velutina* | 16 | 202 | 13.44 | 2.07 |  | |

1 Bar length indicates mean acorn width.

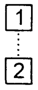
2 Single line: $p<0.05$; quadruple line: $p<0.00005$.

Table 22. Comparison of acorn length in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 18.26 | 2.16 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 22.55 | 1.40 |  | |
| 3 | *Q. velutina* | 16 | 202 | 16.41 | 1.60 |  | |

1 Bar length indicates mean acorn length.
2 Double line: $p<0.005$; quadruple line: $p<0.00005$.

Table 23. Comparison of the ratio of acorn length to acorn width in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 1.24 | 0.15 |  |
| 2 | *Q. rubra* | 11 | 111 | 1.16 | 0.13 | |
| 3 | *Q. velutina* | 16 | 202 | 1.24 | 0.15 | |

1 Dotted line: $p<0.10$.

Table 24. Distributions of tree-averaged ratios of acorn length to width in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Minimum | 25th Percentile | Median | 75th Percentile | Maximum | Range |
|---|---|---|---|---|---|---|
| *Q. coccinea* | 0.99 | 1.15 | 1.25 | 1.35 | 1.59 | 0.61 |
| *Q. rubra* | 0.96 | 1.07 | 1.09 | 1.23 | 1.36 | 0.41 |
| *Q. velutina* | 1.05 | 1.14 | 1.19 | 1.35 | 1.54 | 0.48 |

Acorn caps of *Q. rubra* were typical, being on average the widest (Table 25) and shortest (Table 26) of the three taxa. The smaller cap dimensions of *Q. velutina* relative to *Q. coccinea* concord with what we have already seen for the acorns. Not surprisingly, total fruit length (Table 27) is greatest in *Q. rubra*, while the lengths for *Q. coccinea* and *Q. velutina* concord with what we have already seen for the acorns and caps separately.

Cap neck length is extremely short in *Q. rubra* and is longest in *Q. coccinea* (Table 28). Although the difference in neck length is significant (p=0.0211) between *Q. coccinea* and *Q. velutina*, the difference in length is probably too small to be useful in distinguishing these two taxa in the field.

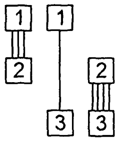
Cup depth (Table 29) in *Q. rubra* averages just under 5 mm and the caps on average cover a little over 20% the nut (Table 30). Cap depth in *Q. velutina* averages 2 mm less than in *Q. coccinea*. Much of this difference is due to the smaller average size of the acorns in *Q. velutina*, so that the difference in acorn coverage between *Q. velutina* and *Q. coccinea*, while significant (p=0.092, Table 30), is quite modest: the quantiles shown in Table 31 confirm this.

The most striking measured difference in acorns between *Q. coccinea* and *Q. velutina* is in the length of the nipple which is quite prominent in *Q. velutina* (Table 32). As shown in Table 33, the nipple averages 9% of the acorn length in *Q. velutina*, versus only 5% to 6% in *Q. coccinea* and *Q. rubra*, respectively.

In summary, distinguishing acorns of *Q. rubra* from those of *Q. coccinea* or *Q. velutina* is a trivial task. In contrast, *Q. velutina* and *Q. coccinea* do not differ strikingly on the majority of acorn size and shape characters examined here, with the notable exception of nipple length which is quite prominent in *Q. velutina*.

In the field, however, pubescence and color supplement size and shape characters to distinguish these latter two taxa. *Q. velutina* has relatively large, loose, tawny-colored pubescent cap scales that form a distinct fringe along the lower cap margin, while the cap scales of *Q. coccinea* are in general smaller, tightly appressed, glabrous and orange (in Maumee populations) to red brown (in Mio populations) in color. Acorn color in *Q. velutina* is usually a noticeably light dull tawny

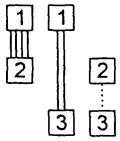
Table 25. Comparison of acorn cap width in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 18.39 | 3.19 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 22.14 | 2.99 |  | |
| 3 | *Q. velutina* | 16 | 202 | 15.80 | 2.77 |  | |

[1] Bar length indicates mean acorn cap width.

[2] Single line: $p<0.05$; triple line: $p<0.0005$; quadruple line: $p<0.00005$.

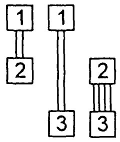
Table 26. Comparison of acorn cap length in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 13.58 | 2.67 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 8.70 | 2.22 |  | |
| 3 | *Q. velutina* | 16 | 202 | 10.86 | 2.51 |  | |

[1] Bar length indicates mean acorn cap length.

[2] Dotted line: $p<0.10$; double line: $p<0.005$; quadruple line: $p<0.00005$.

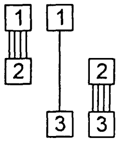
Table 27. Comparison of fruit (acorn plus cap) length in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 23.40 | 2.77 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 26.48 | 1.85 |  | |
| 3 | *Q. velutina* | 16 | 202 | 20.81 | 2.06 |  | |

[1] Bar length indicates mean fruit (nut plus cap) length.

[2] Double line: $p<0.005$; quadruple line: $p<0.00005$.

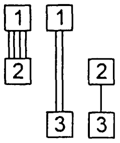
Table 28. Comparison of neck length of acorn caps in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 3.07 | 1.06 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 0.96 | 0.84 |  | |
| 3 | *Q. velutina* | 16 | 202 | 2.45 | 0.80 |  | |

[1] Bar length indicates mean neck length of acorn caps.

[2] Single line: $p<0.05$; quadruple line: $p<0.00005$.

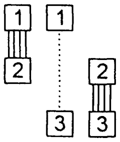
Table 29. Comparison of cup depth of acorn caps in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 8.70 | 2.00 |  |  |
| 2 | *Q. rubra* | 11 | 111 | 4.94 | 1.35 |  | |
| 3 | *Q. velutina* | 16 | 202 | 6.77 | 1.87 |  | |

[1] Bar length indicates mean cup depth of acorn caps.

[2] Single line: $p<0.05$; double line: $p<0.005$; quadruple line: $p<0.00005$.

Table 30. Comparison of the ratio of acorn cup depth to acorn length in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

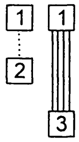
| Taxon | Name | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 44 | 540 | 0.48 | 0.10 |  |
| 2 | *Q. rubra* | 11 | 111 | 0.22 | 0.06 | |
| 3 | *Q. velutina* | 16 | 202 | 0.41 | 0.11 | |

[1] Dotted line: $p<0.10$; quadruple line: $p<0.00005$.

Table 31. Distributions of tree-averaged ratios of acorn cup depth to acorn length in *Q. coccinea*, *Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Minimum | 25th Percentile | Median | 75th Percentile | Maximum | Range |
|---|---|---|---|---|---|---|
| *Q. coccinea* | 0.18 | 0.44 | 0.49 | 0.54 | 0.61 | 0.43 |
| *Q. rubra* | 0.15 | 0.18 | 0.21 | 0.28 | 0.35 | 0.17 |
| *Q. velutina* | 0.22 | 0.36 | 0.41 | 0.50 | 0.66 | 0.44 |

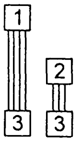
Table 32. Comparison of length of acorn nipples in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Q. coccinea | 44 | 540 | 0.85 | 0.45 |  |  |
| 2 | Q. rubra | 11 | 111 | 1.30 | 0.57 |  | |
| 3 | Q. velutina | 16 | 202 | 1.55 | 0.48 |  | |

[1] Bar length indicates mean length of acorn nipple tips.

[2] Dotted line: $p<0.10$; quadruple line: $p<0.00005$.

Table 33. Comparison of the ratio of acorn nipple length to acorn length in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Q. coccinea | 44 | 540 | 0.05 | 0.02 |  |
| 2 | Q. rubra | 11 | 111 | 0.06 | 0.02 | |
| 3 | Q. velutina | 16 | 202 | 0.09 | 0.03 | |

[1] Triple line: $p<0.0005$; quadruple line: $p<0.00005$.

color and is consistent across populations, while in *Q. coccinea* it varies from orange in the Maumee and Waterloo populations to red-brown in the Holly and Mio populations.

Other acorn characters that are frequently mentioned for distinguishing *Q. coccinea* are the presence of apical rings and dark vertical striping on the nut. The former character is present in some populations, such as the Maumee population, but lacking in others. The latter character was not observed in the southern populations examined in this study (Maumee and Waterloo) and its presence in the Holly and Mio populations is unreliable. More importantly, vertical striping is frequently also seen in *Q. velutina*, and, thus, cannot serve as a reliable character to distinguish *Q. velutina* from *Q. coccinea*.

## DIFFERENCES IN TERMINAL BUDS AMONG TAXA

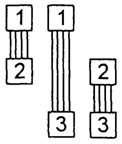
Five of six analyzed characters of the terminal buds were highly significant ($p \leq 0.00011$) among taxa (Table 34). Terminal buds of *Q. velutina* are on average completely covered with dense pubescence (Tables 35 and 36). *Q. rubra* is frequently tipped with pubescence (coverage = 0.31; Table 35), but the pubescence is sparse (density = 0.09; Table 36). Coverage in *Q. coccinea* is intermediate (0.52) and pubescence density is slight (0.33). Pairwise contrasts between all three taxa are highly significant ($p<0.0005$ or better) for both pubescence coverage and density.

Terminal bud length and width are presented in Tables 37 and 38, respectively. Terminal buds are smallest in *Q. coccinea* and largest in *Q. velutina*. Terminal buds in *Q. rubra* are on average nearly as long as those of *Q. velutina*, but are noticeably narrower ($p<0.0005$ in Table 38). Thus, *Q. rubra* has the most gracile buds (Table 39). The buds of *Q. coccinea* and *Q. velutina* do not differ in ratio of bud length to width ($p=1.0$, Table 39), but this is nearly irrelevant since they differ so obviously in terms of size and pubescence. No differences were found in the ratio of terminal bud length to peripheral bud length which averages close to 1.5 for all three taxa (Table 40).

Table 34. Characters of the terminal bud and probability values of statistically significant ANOVAs comparing *Q. coccinea*, *Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

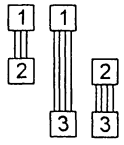
| No. | Character | ANOVA P-value |
|---|---|---|
| 1. | Coverage of pubescence on terminal bud | 0.00011 |
| 2. | Density of pubescence on terminal bud | 0.00010 |
| 3. | Terminal bud length | 0.00010 |
| 4. | Terminal bud width | 0.00010 |
| 5. | Ratio of terminal bud length to width | 0.00010 |

Table 35. Comparison of coverage of pubescence on terminal buds in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 0.52 | 0.21 |  |
| 2 | *Q. rubra* | 10 | 118 | 0.31 | 0.19 | |
| 3 | *Q. velutina* | 15 | 196 | 0.99 | 0.04 | |

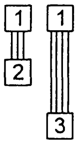
[1] Quadruple line: $p<0.00005$.

Table 36. Comparison of density of pubescence on terminal buds in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 0.33 | 0.18 |  |
| 2 | *Q. rubra* | 10 | 118 | 0.13 | 0.09 | |
| 3 | *Q. velutina* | 15 | 196 | 0.95 | 0.11 | |

[1] Triple line: $p<0.0005$; quadruple line: $p<0.00005$.

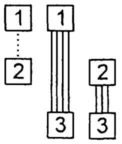
Table 37. Comparison of terminal bud length in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Buds | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 4.59 | 0.82 |  |  |
| 2 | *Q. rubra* | 10 | 118 | 6.24 | 0.97 |  | |
| 3 | *Q. velutina* | 15 | 196 | 6.56 | 1.46 |  | |

1 Bar length indicates mean bud length.

2 Triple line: $p<0.0005$; quadruple line: $p<0.00005$.

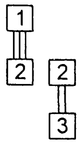
Table 38. Comparison of terminal bud width in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Buds | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 2.76 | 0.45 |  |  |
| 2 | *Q. rubra* | 10 | 118 | 3.23 | 0.44 |  | |
| 3 | *Q. velutina* | 15 | 196 | 3.80 | 0.66 |  | |

1 Bar length indicates mean bud width.

2 Dotted line: $p<0.10$; triple line: $p<0.0005$; quadruple line: $p<0.00005$.

Table 39. Comparison of the ratio of terminal bud length to width in *Q. coccinea, Q. rubra,* and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 1.67 | 0.20 |  |
| 2 | *Q. rubra* | 10 | 118 | 1.94 | 0.20 | |
| 3 | *Q. velutina* | 15 | 196 | 1.72 | 0.23 | |

1 Double line: $p<0.005$; triple line: $p<0.0005$.

Table 40. Comparison of the ratio of terminal bud length to peripheral bud length in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 32 | 346 | 1.45 | 0.49 | |
| 2 | *Q. rubra* | 9 | 106 | 1.48 | 0.41 | |
| 3 | *Q. velutina* | 15 | 189 | 1.55 | 0.40 | |

[1] No pairwise contrasts were statistically significant.

### RELATIONSHIPS BETWEEN TERMINAL BUD SIZE AND SHOOT SIZE

On biological grounds, we expect the size of terminal buds to be correlated with the size of the shoots, and in particular with the width of the shoot since the cross sectional area of a shoot directly indicates the vascular capacity of that shoot. Shoot width was highly significant ($P=0.0001$) as the covariate in the ANCOVAs of bud length and width. Thus, a discussion of terminal bud size characters is incomplete without mentioning differences in shoot size among the taxa.

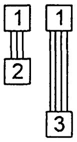
Shoot width, measured just above the base of the most recent year's growth, averages less than 3 mm in *Q. coccinea* (Table 41). This width is significantly different from the nearly 3.5 mm for *Q. rubra* and *Q. velutina* ($p<0.0005$). In contrast, shoot length is only marginally different ($p<0.10$) between *Q. rubra* and *Q. coccinea* or *Q. velutina* (Table 42). Shoot length is, however, an extremely plastic character. The coefficient of variation ranges from a high of 0.70 for *Q. velutina* to a low of 0.57 for *Q. rubra*. Shoot width, with an average coefficient of variation of just 0.18, is much less plastic. The results for previous year's shoot width (Table 43) agree with the results for current year's shoot width. The same does not hold for shoot length: compare Tables 42 and 44. Shoot width, therefore, appears to be a taxonomically more informative character. The relatively narrower width of *Q. coccinea* appears to reflect a true difference that distinguishes this taxon from the other two and influences terminal bud size.

## Differences Among Populations of Each Taxon

### DIFFERENCES AMONG POPULATIONS OF *Q. coccinea*

The female inflorescences of *Q. coccinea* show many more similarities than differences among populations. There were no significant differences in peduncle length (Table 45), peduncle width, distance from first to second flower, nor in stigma length or stigma

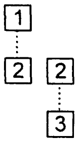
Table 41. Comparison of current year's shoot width in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Shoots | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 2.85 | 0.51 | ├┤ |  |
| 2 | *Q. rubra* | 10 | 118 | 3.44 | 0.60 | ├┤ | |
| 3 | *Q. velutina* | 15 | 196 | 3.46 | 0.61 | ├┤ | |

1 Bar length indicates mean width of current year's shoot.

2 Triple line: $p < 0.0005$; quadruple line: $p < 0.00005$.

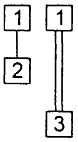
Table 42. Comparison of current year's shoot length in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Shoots | Mean *(cm)* | Standard Deviation | 1/10th Actual Size[1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 5.83 | 3.44 | ├──┤ |  |
| 2 | *Q. rubra* | 10 | 118 | 7.46 | 4.31 | ├───┤ | |
| 3 | *Q. velutina* | 15 | 196 | 5.57 | 3.92 | ├──┤ | |

1 Bar length indicates mean length of current year's shoot.

2 Dotted line: $p < 0.10$.

Table 43. Comparison of previous year's shoot width in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Shoots | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 3.62 | 0.76 | ├┤ |  |
| 2 | *Q. rubra* | 10 | 118 | 4.12 | 1.01 | ├┤ | |
| 3 | *Q. velutina* | 15 | 196 | 4.08 | 0.89 | ├┤ | |

1 Bar length indicates mean width of last year's shoot.

2 Single line: $p < 0.05$; double line: $p < 0.005$.

Table 44. Comparison of previous year's shoot length in *Q. coccinea, Q. rubra*, and *Q. velutina* in southeastern and northern Lower Michigan.

| Taxon | Name | No. of Trees | No. of Shoots | Mean *(cm)* | Standard Deviation | 1/10th Actual Size[1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | *Q. coccinea* | 36 | 410 | 7.98 | 5.19 | ├────┤ | |
| 2 | *Q. rubra* | 10 | 118 | 8.44 | 5.56 | ├────┤ | |
| 3 | *Q. velutina* | 15 | 196 | 6.01 | 4.07 | ├──┤ | |

1 Bar length indicates mean length of last year's shoot.
2 No pairwise contrasts were statistically significant.

Table 45. Comparison of peduncle length of female inflorescences in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Inflor. | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 2 | 23 | 8.33 | 3.82 | ├────┤ | |
| 3 | Waterloo | 2 | 25 | 3.92 | 1.84 | ├─┤ | |
| 4 | Holly | 2 | 25 | 6.75 | 2.29 | ├───┤ | |
| 5 | Mio | 3 | 52 | 6.23 | 2.37 | ├──┤ | |

1 Bar length indicates mean peduncle length of female inflorescences.
2 No pairwise contrasts were statistically significant.

recurvature. These results must be viewed with the small size of the sample in mind. Nevertheless, using the results for peduncle length (Table 45) as an example, no trends in the data are apparent to support any taxonomically useful hypothesis about differences in female inflorescences between populations of *Q. coccinea*.

Differences in acorn and terminal bud characters are much more apparent. In general, there is a gradual decrease in size along a south-north gradient from the most southern population (Maumee) to the most northern population (Mio). Acorn width (Table 46) in the Mio population of *Q. coccinea* averages just under 12 mm, compared to over 15 mm for the Maumee and Waterloo populations ($p<0.0005$). Acorn length (Table 47) in the Mio population, at just over 15 mm, is significantly less than in the three other populations, and the contrast with the Maumee population, which averages 19 mm, is highly significant ($p<0.00005$).

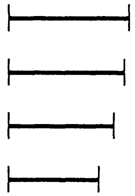
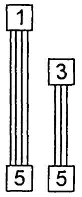
There were no differences in the ratio of acorn length to width (Table 48). I, thus, found no support for the hypothesis that acorns are more elliptical in the northernmost population (Mio) of *Q. coccinea* compared to southern populations (Maumee, Waterloo, Holly).

The results for acorn cap width (Table 49) correspond with the trend already described: there is a general decrease in size as one moves from the Maumee to the Mio population. In this case, however, the Bonferroni contrasts also confirm field observations of a distinction between the wider caps of the Maumee and Waterloo populations on the one hand, and the narrower caps of the Holly and Mio populations on the other.

The results for acorn cap length and total fruit length (Tables 50 and 51) indicate that acorns of Mio *Q. coccinea* are significantly smaller, whereas there are no significant differences among the remaining three populations.

Cup depth of acorn caps in the Mio population (Table 52) averages just under 6 mm which is significantly less than the mean of just over 8 to nearly 10 mm in the three southern populations. As a result, caps in the Mio population appear, on average, to cover only 2/5 of the acorn versus about half the acorn in the other populations (Table 53),

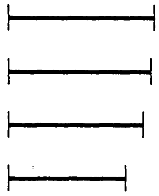
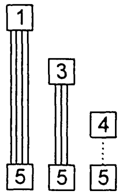
Table 46. Comparison of acorn width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 15.78 | 1.47 |  |  |
| 3 | Waterloo | 11 | 156 | 15.23 | 2.13 | | |
| 4 | Holly | 5 | 67 | 13.85 | 1.01 | | |
| 5 | Mio | 7 | 76 | 11.88 | 1.09 | | |

[1] Bar length indicates mean acorn width.

[2] Triple line: $p<0.0005$; quadruple line: $p<0.00005$.

Table 47. Comparison of acorn length in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 19.10 | 1.76 |  |  |
| 3 | Waterloo | 11 | 156 | 18.64 | 1.93 | | |
| 4 | Holly | 5 | 67 | 17.62 | 1.33 | | |
| 5 | Mio | 7 | 76 | 15.37 | 1.71 | | |

[1] Bar length indicates mean acorn length.

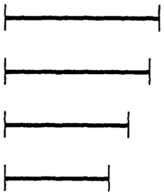
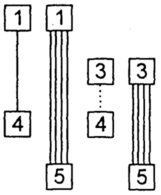
[2] Dotted line: $p<0.10$; triple line: $p<0.0005$; quadruple line: $p<0.00005$.

Table 48. Comparison of the ratio of acorn length to acorn width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 1.22 | 0.14 | |
| 3 | Waterloo | 11 | 156 | 1.24 | 0.17 | |
| 4 | Holly | 5 | 67 | 1.28 | 0.11 | |
| 5 | Mio | 7 | 76 | 1.30 | 0.19 | |

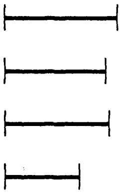
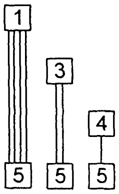
[1] No pairwise contrasts were statistically significant.

Table 49. Comparison of acorn cap width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 20.15 | 2.41 |  |  |
| 3 | Waterloo | 11 | 156 | 18.89 | 2.68 | | |
| 4 | Holly | 5 | 67 | 16.22 | 1.03 | | |
| 5 | Mio | 7 | 76 | 13.66 | 1.23 | | |

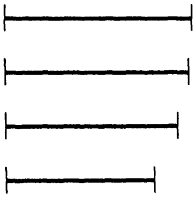
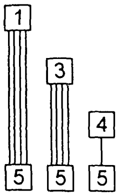
[1] Bar length indicates mean acorn cap width.
[2] Dotted line: $p<0.10$; single line: $p<0.05$; quadruple line: $p<0.00005$.

Table 50. Comparison of acorn cap length in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 14.84 | 1.73 |  |  |
| 3 | Waterloo | 11 | 156 | 13.38 | 2.88 | | |
| 4 | Holly | 5 | 67 | 13.76 | 1.36 | | |
| 5 | Mio | 7 | 76 | 9.86 | 1.95 | | |

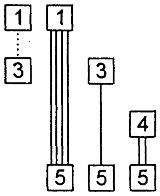
[1] Bar length indicates mean acorn cap length.
[2] Single line: $p<0.05$; double line: $p<0.005$; quadruple line: $p<0.00005$.

Table 51. Comparison of fruit (acorn plus cap) length in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 24.47 | 2.16 |  |  |
| 3 | Waterloo | 11 | 156 | 24.00 | 2.49 | | |
| 4 | Holly | 5 | 67 | 22.53 | 1.50 | | |
| 5 | Mio | 7 | 76 | 19.53 | 2.25 | | |

[1] Bar length indicates mean fruit (nut plus cap) length.
[2] Single line: $p<0.05$; quadruple line: $p<0.00005$.

Table 52. Comparison of cup depth of acorn caps in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 9.73 | 1.42 |  |  |
| 3 | Waterloo | 11 | 156 | 8.27 | 2.03 |  | |
| 4 | Holly | 5 | 67 | 9.07 | 1.06 |  | |
| 5 | Mio | 7 | 76 | 5.96 | 1.11 |  | |

[1] Bar length indicates mean cup depth of acorn caps.

[2] Dotted line: $p<0.10$; single line: $p<0.05$; double line: $p<0.005$; quadruple line: $p<0.00005$.

Table 53. Comparison of the ratio of acorn cup depth to acorn length in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 0.51 | 0.08 |  |
| 3 | Waterloo | 11 | 156 | 0.45 | 0.11 | |
| 4 | Holly | 5 | 67 | 0.52 | 0.07 | |
| 5 | Mio | 7 | 76 | 0.39 | 0.08 | |

[1] Single line: $p<0.05$.

although only the extreme contrast between the Mio and Maumee populations is statistically significant ($p<0.05$).

Reduced coverage of the acorn by the cap in the northern form of *Q. coccinea* may partially account for the perception that acorns are "more elliptical" in northern populations, such as the Mio population, when in fact no differences in the ratio of acorn length to width were detected in the populations examined (Table 48). Some Mio trees do in fact have very elliptical acorns, but many others have ovoid or globular acorns. I also found that although short-ovoid or globular acorns are typical in the Maumee populations, some Maumee trees also have very elliptical acorns.

The ratio of acorn cap width to nut width (Table 54), provides a measure of the thickness of the walls of the acorn cap at the widest point relative to acorn width. The results indicate that caps are relatively thicker at their widest point in the Maumee population compared to the Holly and Mio populations ($p<0.05$). The greater accentuation of the cap at its widest point is visually evident in a more turbinate appearance in the Maumee phenotype. The mean for the Waterloo population is intermediate, but closer to the mean of the Maumee population than to the mean of the Holly population. This again correlates with field observations: I noticed that the wall of the involucre first thickens before finally tapering off at the rim in typical Waterloo and Maumee trees, whereas it typically decreases monotonically in the Holly and Mio populations (Fig. 14). In addition to the turbinate shape, acorn cap scales often appeared somewhat larger and were often relatively light orange in color in many of the Waterloo specimens examined, once again appearing similar to the Maumee population. In contrast, caps of the Holly population typically had smaller, dark reddish or mahogany colored scales typical of Mio *Q. coccinea*.

Coverage of pubescence on the terminal buds is consistent in the Maumee, Waterloo, and Mio populations, with an average of 0.55, but is significantly less in the Holly population (Table 55, $p<0.05$). The Holly population also had the smallest mean score for pubescence density (Table 56).

Table 54. Comparison of the ratio of acorn cap width to nut width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Maumee | 21 | 241 | 1.28 | 0.08 | $\boxed{1}$ $\boxed{1}$ |
| 3 | Waterloo | 11 | 156 | 1.24 | 0.11 | |
| 4 | Holly | 5 | 67 | 1.17 | 0.07 | $\boxed{4}$ |
| 5 | Mio | 7 | 76 | 1.15 | 0.07 | $\boxed{5}$ |

[1] Single line: $p<0.05$; double line: $p<0.005$.

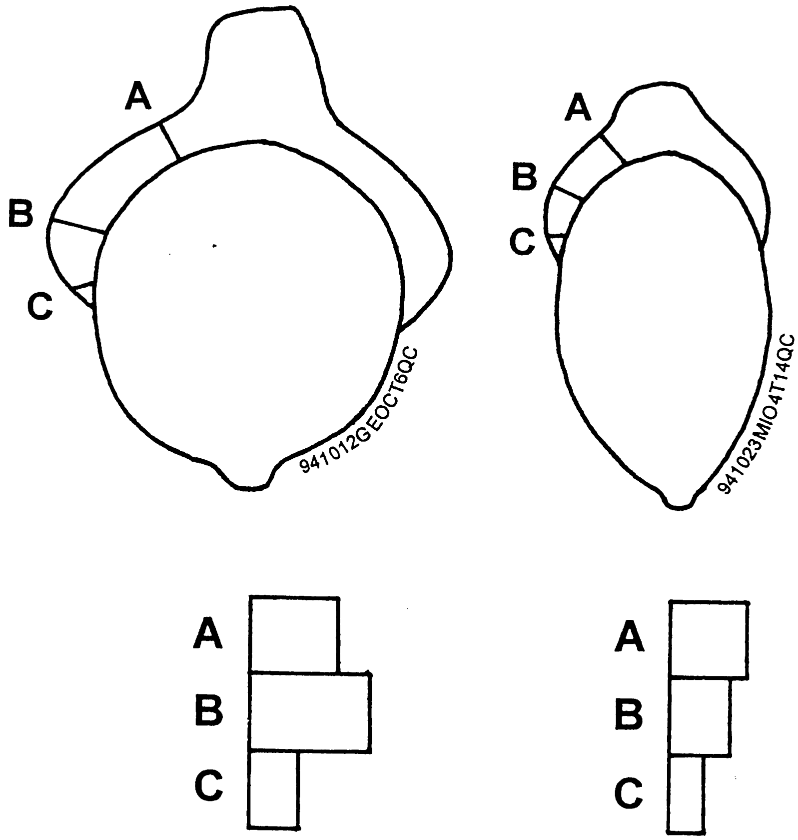


Fig. 14. Cross-sectional views of representative acorns from two populations of *Q. coccinea*. The wall of the involucre thickens between points **A** and **B** before tapering off at the rim, point **C**, in typical Waterloo and Maumee *Q. coccinea*, whereas wall thickness typically decreases monotonically in Holly and Mio trees of the same taxon. The acorn on the left is from a Waterloo tree; on the right, from a Mio tree.

Table 55. Comparison of coverage of pubescence on terminal buds in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Maumee | 14 | 160 | 0.57 | 0.20 | $\boxed{1}$ |
| 3 | Waterloo | 10 | 121 | 0.53 | 0.16 | $\boxed{3}$ |
| 4 | Holly | 5 | 58 | 0.33 | 0.17 | $\boxed{4}$ $\boxed{4}$ $\boxed{4}$ |
| 5 | Mio | 7 | 71 | 0.55 | 0.25 | $\boxed{5}$ |

[1] Single line: $p<0.05$.

Table 56. Comparison of density of pubescence on terminal buds in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Maumee | 14 | 160 | 0.42 | 0.17 | $\boxed{1}$ $\boxed{1}$ |
| 3 | Waterloo | 10 | 121 | 0.37 | 0.15 | $\boxed{3}$ $\boxed{3}$ |
| 4 | Holly | 5 | 58 | 0.12 | 0.07 | $\boxed{4}$ $\boxed{4}$ |
| 5 | Mio | 7 | 71 | 0.21 | 0.11 | $\boxed{5}$ $\boxed{5}$ |

[1] Dotted line: $p<0.10$; double line: $p<0.005$; triple line: $p<0.0005$.

Results for terminal bud length (Table 57) and width (Table 58) show a general decrease in size along a south-north gradient from the Maumee population to the Mio population, similar to the trend already seen for acorn characters. Not surprisingly, the trend in bud size is also apparent in shoot width between the populations (Table 59), where we again see that the geographically most distant populations show the most statistically significant differences. When the previous year's shoot width is also investigated (Table 60), the Mio population is once again seen to be smaller than the the three other populations which do not differ from one another.

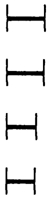
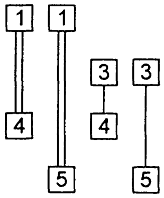
In summary, there is a clear trend along the south-north gradient from the southern Maumee population to the northern Mio population of *Q. coccinea*: acorn and terminal bud size decrease progressively in the ecosystems examined. This result is consistent with Overlease's (1977) findings. These changes appear to coincide with climatic changes in growing season length, heat sum, precipitation, and soil water stress, as the results of the regression analyses indicate. The Mio population is geographically most distant from the remaining three populations and is in a separate Subdistrict in Albert et al.'s (1986) regional landscape ecosystem classification system. So, not surprisingly, the most striking size differences were in contrasts with the Mio population.

In addition to the overall clinal trend, the Maumee and Waterloo populations appear to share some morphological features as a group distinct from the Holly and Mio populations. This is quantitatively most evident in the pattern of statistically significant contrasts in the analyses of acorn cap width (Table 49), density of pubescence on terminal buds (Table 56), bud length (Table 57), and bud width (Table 58). This pattern was, however, also evident in the size and color of acorn cap scales observed in the field, as well as in the shape of the acorn caps which has been quantified indirectly via size measurements.

## DIFFERENCES IN *Q. rubra* AMONG POPULATIONS

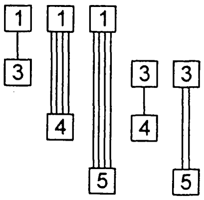
No meaningful differences were found between populations of *Q. rubra* in flower, acorn or winter bud characters, confirming field

Table 57. Comparison of terminal bud length in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Buds | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 14 | 160 | 4.98 | 0.66 |  |  |
| 3 | Waterloo | 10 | 121 | 4.88 | 0.64 | | |
| 4 | Holly | 5 | 58 | 3.93 | 0.65 | | |
| 5 | Mio | 7 | 71 | 3.74 | 0.58 | | |

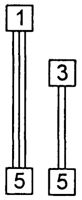
1 Bar length indicates mean bud length.
2 Single line: p<0.05; double line: p<0.005.

Table 58. Comparison of terminal bud width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Buds | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 14 | 160 | 3.08 | 0.34 |  |  |
| 3 | Waterloo | 10 | 121 | 2.81 | 0.31 | | |
| 4 | Holly | 5 | 58 | 2.43 | 0.38 | | |
| 5 | Mio | 7 | 71 | 2.25 | 0.18 | | |

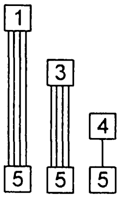
1 Bar length indicates mean bud width.
2 Single line: p<0.05; double line: p<0.005; quadruple line: p<0.00005.

Table 59. Comparison of current year's shoot width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Shoots | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 14 | 160 | 2.99 | 0.50 |  |  |
| 3 | Waterloo | 10 | 121 | 2.96 | 0.47 |  | |
| 4 | Holly | 5 | 58 | 2.77 | 0.43 |  | |
| 5 | Mio | 7 | 71 | 2.39 | 0.32 |  | |

1 Bar length indicates mean width of current year's shoot.
2 Double line: $p < 0.005$; triple line: $p < 0.0005$.

Table 60. Comparison of previous year's shoot width in four populations of *Q. coccinea* in southeastern and northern Lower Michigan.

| Pop. | Name | No. of Trees | No. of Shoots | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Maumee | 14 | 160 | 3.83 | 0.77 |  |  |
| 3 | Waterloo | 10 | 121 | 3.75 | 0.71 |  | |
| 4 | Holly | 5 | 58 | 3.60 | 0.61 |  | |
| 5 | Mio | 7 | 71 | 2.93 | 0.51 |  | |

1 Bar length indicates mean width of last year's shoot.
2 Single line: $p < 0.05$; quadruple line: $p < 0.00005$.

observations that specimens of *Q. rubra* even from geographically distant ecosystems in this study were similar in appearance. For example, acorns and terminal buds of Mio *Q. rubra* were very comparable in size to those in other populations. However, note that the sample of *Q. rubra* had only 1/4 the number of trees compared to that of *Q. coccinea*, and so the power to detect differences was much less.

## DIFFERENCES IN *Q. velutina* AMONG POPULATIONS

Relative to other populations, Mio *Q. velutina* have less intensely colored inner bark, smaller and less densely pubescent terminal buds, and smaller but more densely pubescent inflorescences. Unlike the clear patterns of clinal variation that were found for *Q. coccinea*, when the Mio population of *Q. velutina* was excluded, I found no evidence for clinal trends along a south-north gradient in size or pubescence characters among the four remaining populations of *Q. velutina*.

In southern Lower Michigan, the inner bark of *Q. velutina* is characteristically bright yellow-orange. However, in all the Mio *Q. velutina* I examined, the inner cambium layer was pale-yellow, more yellow than is typical of *Q. coccinea* or *Q. rubra* (which both typically have very pale pink or tan-colored inner bark), but nevertheless not necessarily diagnostic. In Mio *Q. velutina*, inner bark color averages close to 10YR 8/7 using Munsell color chips, compared to an average of 10 YR 7/8 for *Q. velutina* in all other ecosystems. This difference is significant (MANOVA, n=20 trees, Wilk's Lambda p=0.0375). In contrast, inner bark color for *Q. coccinea* and *Q. rubra* in all ecosystems averaged between 7.5 YR 8/4 to 10 YR 8/4. Note that Munsell color chips designed for soil colors provide a handy, but subjective approximation for gauging inner bark color.

Terminal buds are also smaller and less densely pubescent in Mio *Q. velutina*. Bud length averages just under 5 mm for Mio trees, significantly less than the 7 mm average for all other populations (p=0.0133, Table 61). Bud width is also significantly less (p=0.0387, Table 62). While pubescence coverage averaged nearly 100% in all populations of *Q. velutina*, pubescence density scored only 0.85 for the Mio trees versus nearly 1.00 for other populations (p=0.0005, Table 63).

Table 61. Comparison of terminal bud length in the Mio population contrasted with all other populations of *Q. velutina* in southeastern Michigan.

| Level | Description | No. of Trees | No. of Buds | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Mio | 3 | 54 | 4.93 | 0.77 | ├──┤ | $\boxed{1}$ |
| 2 | All other pops | 12 | 142 | 7.18 | 1.16 | ├────┤ | $\boxed{2}$ |

1 Bar length indicates mean bud length.

2 Single line: $p<0.05$.

Table 62. Comparison of terminal bud width in the Mio population contrasted with all other populations of *Q. velutina* in southeastern Michigan.

| Level | Description | No. of Trees | No. of Buds | Mean *(mm)* | Standard Deviation | Actual Size [1] | Significant Contrasts [2] |
|---|---|---|---|---|---|---|---|
| 1 | Mio | 3 | 54 | 3.06 | 0.32 | ├┤ | $\boxed{1}$ |
| 2 | All other pops | 12 | 142 | 4.08 | 0.53 | ├─┤ | $\boxed{2}$ |

1 Bar length indicates mean bud width.

2 Single line: $p<0.05$.

Table 63. Comparison of the density of pubescence on terminal buds in the Mio population contrasted with all other populations of *Q. velutina* in southeastern Michigan.

| Level | Description | No. of Trees | No. of Buds | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Mio | 3 | 54 | 0.85 | 0.13 | $\boxed{1}$ |
| 2 | All other pops. | 12 | 142 | 0.98 | 0.06 | $\boxed{2}$ |

1 Double line: $p<0.005$.

Despite these differences in bark and bud characters, there were few differences in characters of the acorns. Only two of thirteen acorn characters were significantly different, with the ratio of acorn cup depth to acorn length (Table 64) and ratio of cap width to acorn width (Table 65) both being somewhat less in the Mio population. Overall acorn size was not different. Although the characters quantified here are based on only a few trees, I observed many more trees than I measured and found no notable distinctions in other characters of the acorns. In particular, all Mio *Q. velutina* examined in the field displayed the typical loosely-appressed, tawny-pubescent cap scales that form a distinct fringe along the bottom edge of the cap. Acorn coloration was also typical of *Q. velutina*.

Peduncle length on female inflorescences averaged just 2.28 mm in Mio, compared to 4.26 mm for all other populations of *Q. velutina*. Peduncle pubescence density averaged 1.00, compared to 0.80 for all other populations. Although the inflorescences are smaller, their stout and densely pubescent character is consistent with other populations of *Q. velutina* and entirely unlike the long, gracile, and only slightly pubescent inflorescences of *Q. coccinea*. Expanding shoots of Mio *Q. velutina* observed in spring were also stout and densely pubescent, as is typical for this taxon.

In summary, the female inflorescences of Mio *Q. velutina* are smaller but are otherwise very similar in appearance to inflorescences in other populations of *Q. velutina*. The acorn and shoot characters of the Mio *Q. velutina* are entirely consistent with *Q. velutina* elsewhere in the state. However, the terminal bud and inner bark characters appear almost intermediate between *Q. velutina* and *Q. coccinea*. A range of variation was found in acorn, terminal bud, and inflorescence size and pubescence among the four other populations of *Q. velutina*, but no clear pattern was seen to support a clinal trend hypothesis.

Table 64. Comparison of the ratio of acorn cup depth to acorn length in the Mio population contrasted with all other populations of *Q. velutina* in southeastern Michigan.

| Level | Description | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Mio | 3 | 40 | 0.30 | 0.07 | $\boxed{1}$ |
| 2 | All other pops. | 13 | 162 | 0.44 | 0.11 | $\boxed{2}$ |

[1] Single line: $p<0.05$.

Table 65. Comparison of ratio of acorn cap width to acorn width in the Mio population contrasted with all other populations of *Q. velutina* in southeastern Michigan.

| Level | Description | No. of Trees | No. of Acorns | Mean | Standard Deviation | Significant Contrasts [1] |
|---|---|---|---|---|---|---|
| 1 | Mio | 3 | 40 | 1.08 | 0.11 | $\boxed{1}$ |
| 2 | All other pops. | 13 | 162 | 1.20 | 0.07 | $\boxed{2}$ |

[1] Single line: $p<0.05$.

# GENERAL DISCUSSION AND CONCLUSIONS

The female inflorescences of the three taxa differ in density of peduncle pubescence and degree of peduncle stalking and, thus, provide diagnostic characters that should not be overlooked when present in the field. In addition to peduncle characters, stigma lobes in *Q. velutina* appear more recurved than in the other two taxa. Inflorescences of *Q. velutina* were also observed to mature later than those of *Q. coccinea* and *Q. rubra* in the populations studied.

The acorns of *Q. rubra* are easily distinguished from those of *Q. coccinea* and *Q. velutina* by virtue of their larger size and much shallower cups. Based on shape characters alone, *Q. velutina* can be distinguished from *Q. coccinea* by the presence of a more pronounced acorn nipple. In general, however, acorn and cap color, cap scale appression along the fringe of the cap, and cap pubescence appear more useful than size and shape in distinguishing acorns of *Q. velutina* and *Q. coccinea*. The degree of acorn eccentricity did not appear useful in distinguishing *Q. coccinea* from *Q. velutina* in any of the populations. Terminal buds are smallest in *Q. coccinea*, largest and most densely pubescent in *Q. velutina*, and most gracile and most glabrescent in *Q. rubra*.

Overlease (1964, 1977) found that northern populations of the *Q. coccinea--Q. ellipsoidalis* complex had smaller acorns and terminal buds compared to southern populations. I found the same thing. Overlease also found that acorns were less covered by the acorn cap in more northern populations, which is also consistent with my finding. Unlike Overlease, however, I did not find that acorns of *Q. coccinea* are narrower (i.e., elliptically more eccentric, which appears to be what Overlease means) in more northern populations.

Northern populations of *Q. coccinea*, such as the Mio population examined in this study, not only have smaller terminal buds and acorns, but also tend to have very small leaves (Fig. 15). The Maumee, Waterloo, and Holly populations of *Q. coccinea* typically had larger

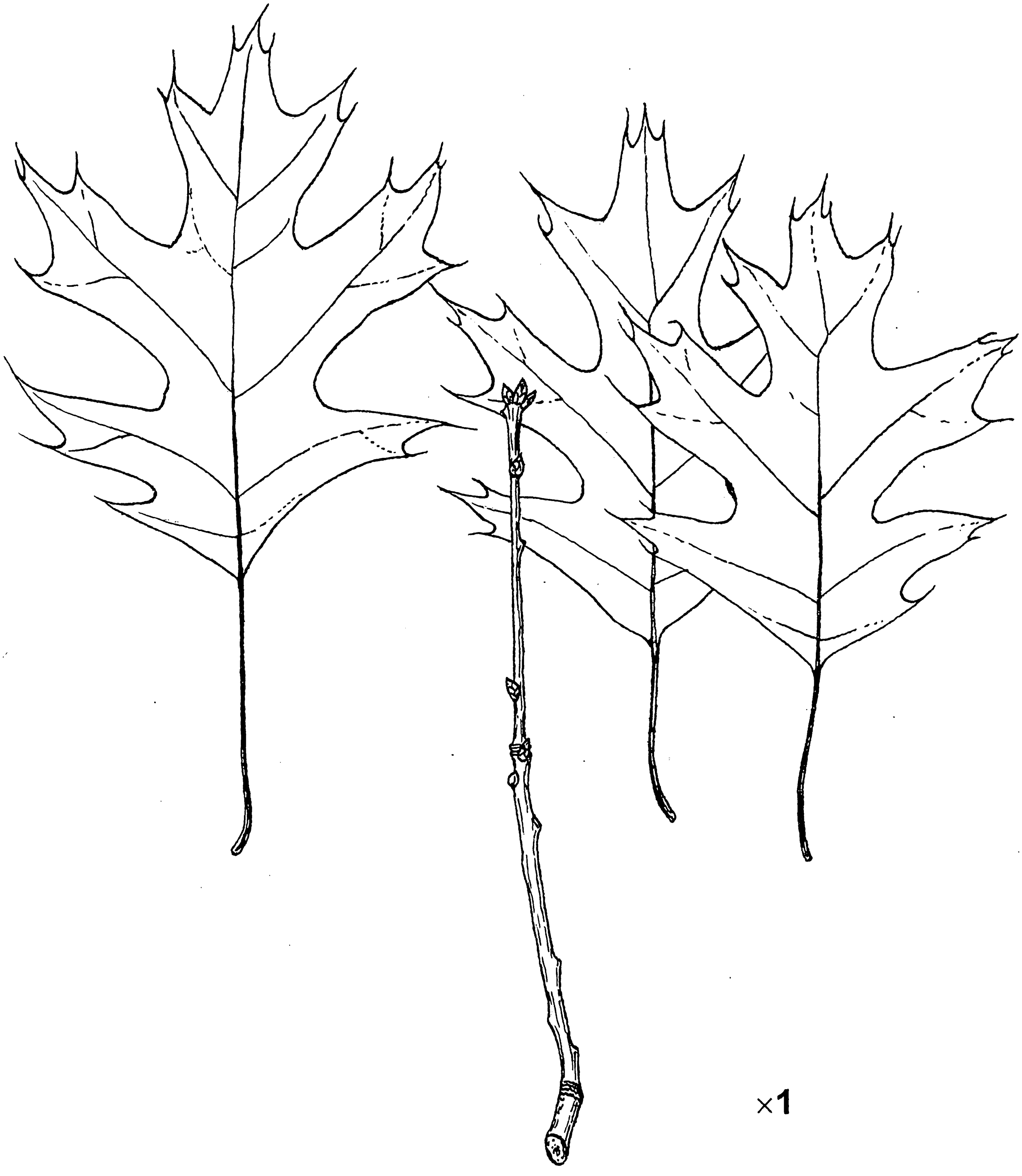


Fig. 15. Leaves and winter condition twig of a typical specimen of *Q. coccinea* from the Mio population. Leaves are from shoots collected from mid-crown position.

leaves (Figs. 16 and 17). Plants of extremely xeric and nutrient-limited environments typically have small leaves. In the case of *Q. coccinea* in the Grayling Subdistrict, one can argue that smaller buds, leaves, and acorns all represent specific adaptations for conservation of water and nutrients in the very harsh environment of the outwash sand plain ecosystems.

The very small buds seen in the Mio population of *Q. velutina* may, likewise, reflect adaptation for survival in northern outwash sand ecosystems that may be only marginally better in water and nutrient retention than those where *Q. coccinea* is found. However, leaves and acorns of Mio *Q. velutina* (Fig. 18) were not observed to be any smaller than those of more southern populations of *Q. velutina*. Hence, I cannot make as strong a case for specific water or nutrient-conserving adaptations in the Mio population of *Q. velutina* as that which can be made for *Q. coccinea* there.

Overlease (1975) found that northern populations of *Q. velutina* had smaller, narrower acorns which were less covered by the cup, lighter yellow inner bark color, smaller winter buds, and, in certain populations, less pubescent twigs. I too found acorns less covered by the cup, lighter yellow inner bark color, and smaller winter buds in the northernmost population of *Q. velutina*. However, acorns of Mio *Q. velutina* did not appear to be either smaller or narrower than acorns in other populations of *Q. velutina*. I also did not find clinal patterns in the expression of acorn, terminal bud, or inflorescence characters among the four other populations of *Q. velutina* studied. *Q. velutina* was represented by 15-16 trees in this study, and my findings may partially reflect the relatively small sample size.

*Q. rubra* was represented by even fewer trees than *Q. velutina*, and so not much power was available to detect differences between populations. Overlease (1975) found that northern populations of *Q. rubra* tended to have smaller and somewhat narrower acorns. He also found that poor site populations had smaller, narrower acorns, and presence of fringe pubescence on the cups compared to better site populations. Overlease's poor site populations were typified by the presence of *Pinus banksiana* or *P. resinosa* in the stands: Overlease characterized these populations as *Q. rubra* var. *borealis*. All

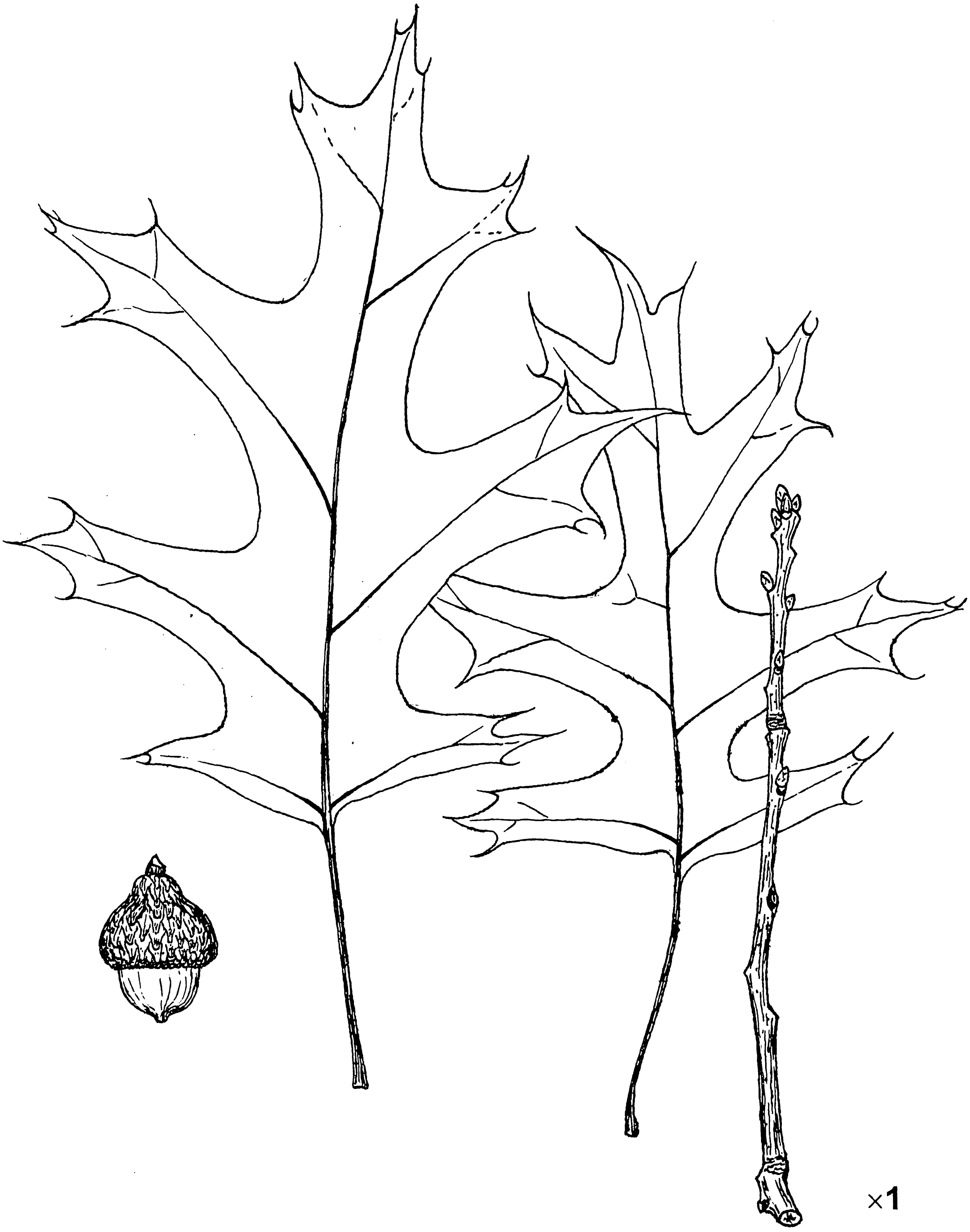


Fig. 16. Acorn, leaves, and winter condition twig of a typical specimen of *Q. coccinea* from the Waterloo population. Leaves are from shoots collected from mid-crown position.

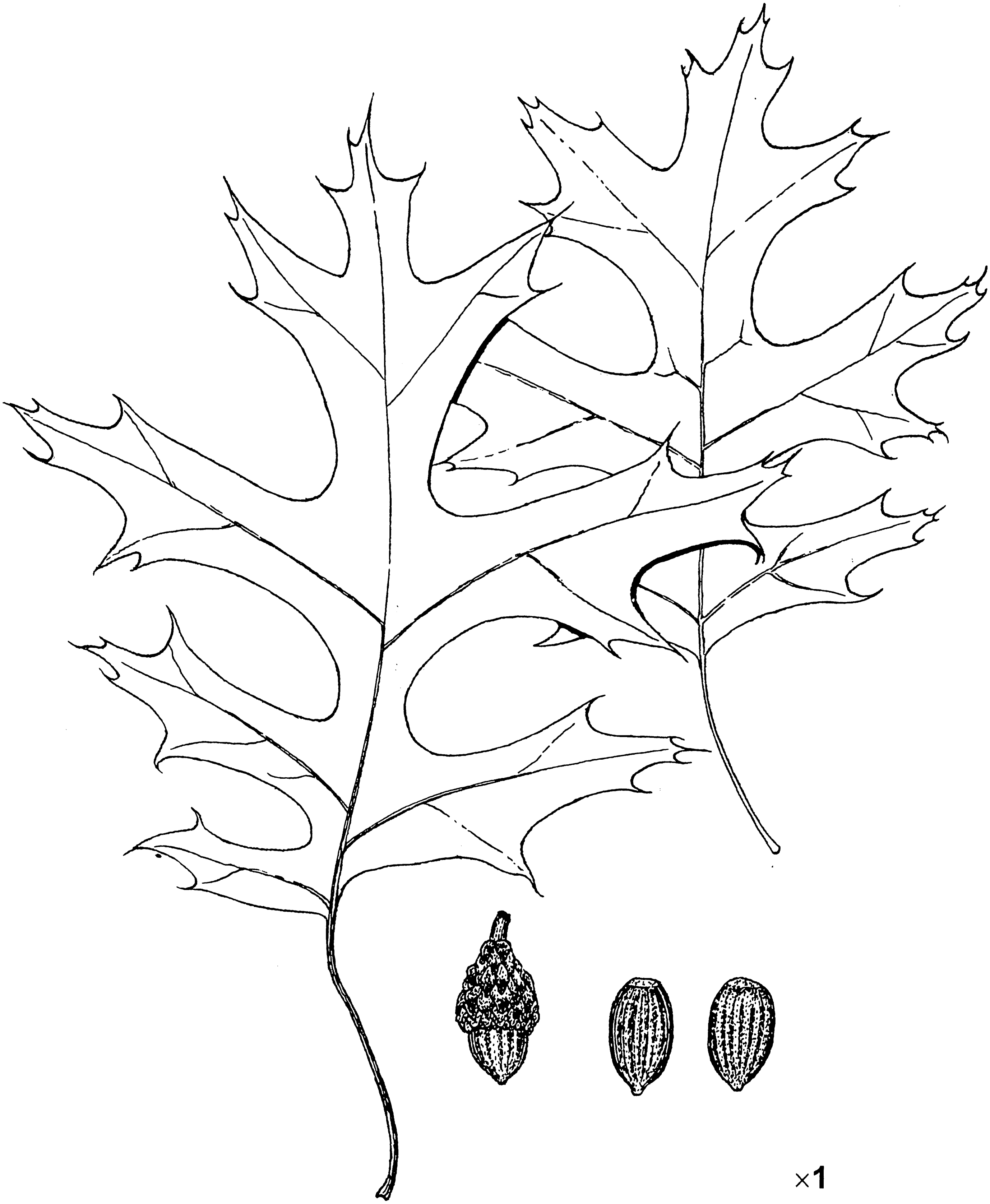


Fig. 17. Leaves and acorns of a typical specimen of *Q. coccinea* from the Holly population. Leaves are from shoots collected from mid-crown position.

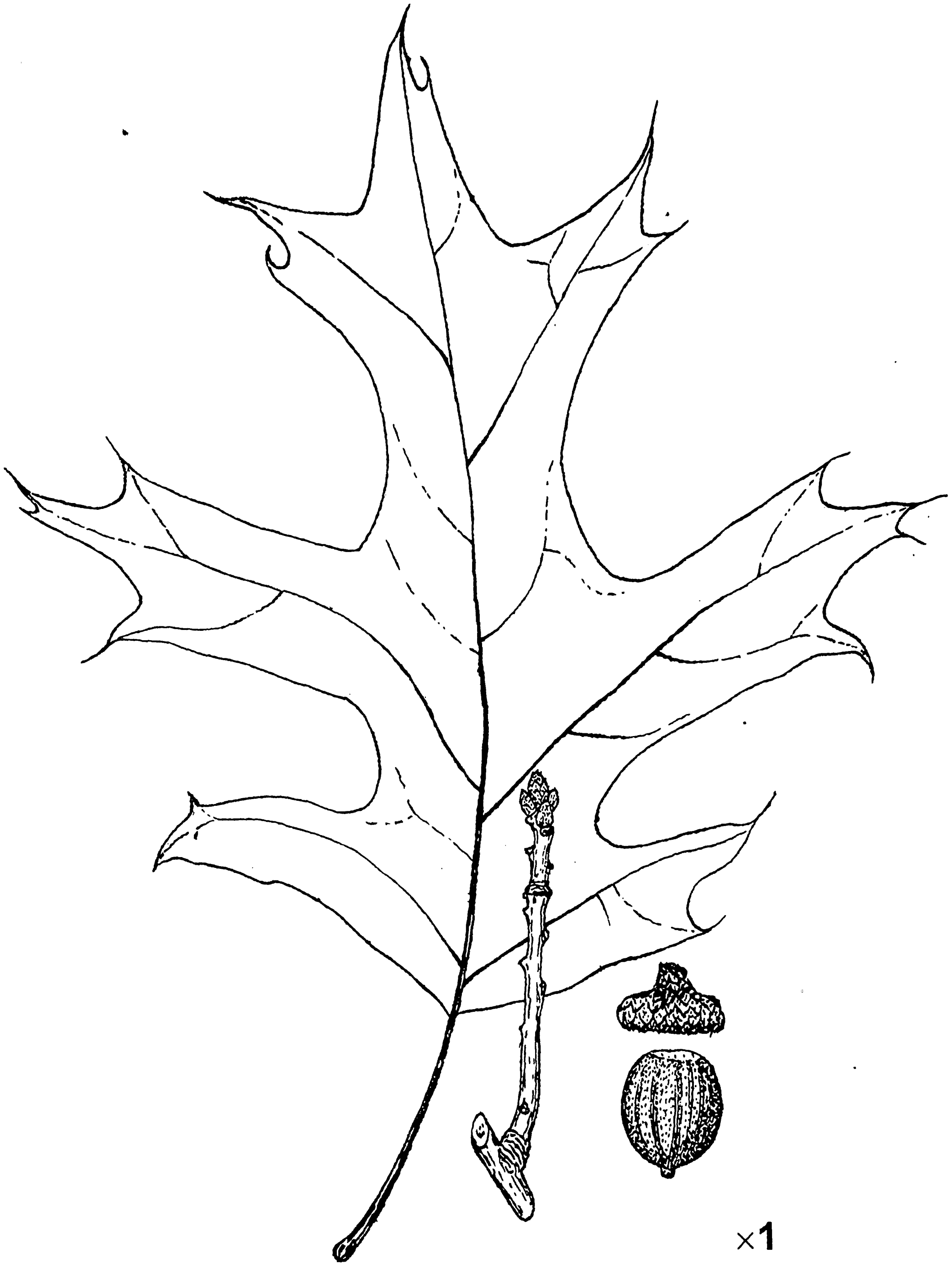


Fig. 18. Leaf, winter condition twig, and acorn of a typical specimen of *Q. velutina* from the Mio population. Leaf is from a shoot collected from mid-crown position.

populations of *Q. rubra* that I examined were on dry-mesic to mesic sites, and so it may have been much less likely that I would have seen the sorts of differences that Overlease saw. I did not find any trees that I would classify as *Q. rubra* on the outwash sites with *P. banksiana* or *P. resinosa* that I examined.

Floral characters are considered highly conserved in evolution, and, thus, are frequently used to distinguish difficult taxa. I uncovered no statistical differences in female inflorescences among populations of *Q. coccinea*, nor did I observe any other notable differences in female inflorescences in the field among the many other trees that I examined but did not measure. There is a gradual decrease in acorn and terminal bud size along a south-north gradient, but there do not appear to be any sharp breaks along this continuum of readily discernible variation. Some populations, especially the POTO and SUGR populations at Waterloo Recreation Area, exhibited a wide degree of variation among individual trees, especially in acorn size, eccentricity, and shape (bullet-shaped vs. blunt-tipped, etc. -- note that the standard deviations for acorn size characters shown in tables 46, 47, 49, 50, and 51 are consistently higher for the Waterloo population). The floral characters of these same trees were, however, remarkably consistent. Therefore, I suggest that populations commonly referred to as *Q. ellipsoidalis* in Michigan should be treated as a northern race of *Q. coccinea*, as Voss (1985) and Overlease (1964, 1977) have suggested.

There are differences in terminal bud, fruit, and leaf morphology between populations of *Q. coccinea* that appear to be associated with ecological differences in the ecosystems. The Maumee lake plain ecosystems are characterized by highly rinsed, acidic outwash sands over less-permeable lacustrine clay which results in poor drainage and a seasonally high water table. Populations of *Q. coccinea* with large buds, large, deeply sinuate leaves and large, distinctively orange, globose acorns (the largest acorns of all populations examined) occur here on low to medium sand ridges. Waterloo and Holly populations of *Q. coccinea* dominate on ridge tops and on south and southwest-facing slopes of outwash and ice-contact landforms. Some Waterloo trees exhibit a phenotype that is quite close to the Maumee phenotype, but, in general, there appears to be greater variation in fruit and leaf form in Waterloo populations. Mio populations of *Q. coccinea* have the smallest terminal buds, acorns and leaves of the populations studied, and are confined to acidic, fire-prone, excessively drained outwash plain ecosystems with *Pinus banksiana*.

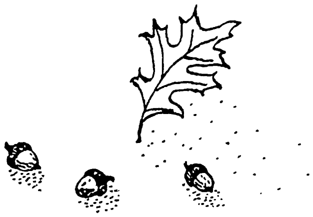
Part of the difficulty that has historically arisen in distinguishing red oak taxa in the field in the Lake States may be attributed to a failure to adequately consider the physical site conditions of the population studied. Historically, taxonomic studies have generally emphasized the visible traits of plants, while neglecting the equally real but less visible ecosystem requirements of plants. The great advantage of an ecosystematic approach is that it can provide information about where plants are expected to grow. These expectations can then be used as testable hypotheses: we can go out in the field and see whether plants with specific traits do in fact grow where we expect them to grow.

In the study of difficult taxa such as *Q. coccinea*, an ecosystem approach should be considered the only viable approach that can be expected to truly increase our knowledge and understanding of the taxa. As this study has shown, there are morphological differences between populations of red oak taxa that appear to be associated with ecological differences in the ecosystems.

Palmer (1942) concludes his treatment of the *Coccineae* by noting:

> The variable and unstable character of several of the red oaks considered here suggests that in some cases —particularly in that of *Quercus shumardii* and its varieties— we are dealing with incipient species or with a complex of various forms of one polymorphic species, all derived from a common and not very remote ancestral type that became widely dispersed in eastern and central North America, and that several segregates are now in the process of development in different parts of the range under more or less diverse ecological conditions.

Palmer was apparently speaking with particular reference to *Q. shumardii* and its varieties, but it seems that the statement could be applied equally well to the diverse populations of *Q. coccinea* in Michigan, a few of which have been examined in this paper. During the past 2 million years of the Quaternary, there were 18 to 20 glaciations, each lasting about 100,000 years. Davis (1983) hypothesizes that the taxa that have survived the very unstable environments of the interglacials must necessarily have been selected for their abilities to rapidly colonize deglaciated terrain. The great diversity of form we see in *Q. coccinea* may very well reflect the process of natural selection at work within the vast mosaic of ecologically distinct local and regional landscape ecosystems in Michigan.



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# APPENDIX A
# SAMPLING LOCATIONS IN SOUTHEASTERN AND NORTHERN LOWER MICHIGAN

## Region I, Maumee Subdistrict

### Maumee Populations

1\. PERK. Perkins Farm, privately owned land, southeast of Petersburg in Monroe Cty. On the west side of Secor Rd. between Stein Rd. to the north and Morocco Rd. to the south (SE¼NE¼SEC30T7SR7E).

2\. PETR. Petersburg State Game Area, southeast of Petersburg in Monroe Cty. Enter on the south side of Lulu Rd. between Teal Rd. to the west and Summerfield Rd to the east. (W½NE¼SEC14T7SR6E).

3\. MCCL. McCleary's Land, privately owned land, northeast of Petersburg in Monroe Cty. on the south side of the railroad tracks between Ida West Rd to the south and Wells Rd to the east (SE¼SE¼SEC36T6SR6E).

## Region I, Ann Arbor Subdistrict

### Ann Arbor Population

4\. RADR. Radrick Forest of the University of Michigan, east of Ann Arbor in Washtenaw Cty. To the north of the University of Michigan Golf Course on Geddes Rd. between Dixboro Rd. to the west and Gale Rd. to the east (NW¼NW¼SEC30T2SR7E ).

## Region I, Jackson Subdistrict

### Waterloo Populations

5\. GEOC. Waterloo State Recreation Area, west of Chelsea in Washtenaw Cty. On the east side of the road to the Gerald E. Eddy Geology Center (SW¼NE¼SEC4T2SR3E).

6\. POTO. Waterloo State Recreation Area, west of Chelsea in Washtenaw Cty. Trail just west of Walsh Lake between Bush Rd. to the south and Waterloo Rd. to the north (S½S½SEC33T1SR3E).

7\. SUGR. Waterloo State Recreation Area, west of Chelsea in Washtenaw Cty. West of Sugarloaf Lake on the southeast side of the road to the lake (E½SW¼SEC31T1SR3E).

### Holly Population

8\. HOLL. Holly State Park east of Holly in Genesee Cty. Southwest of Valley Lake between McGinnis Rd to the north, Wildwood Rd to the east, and Dixie Rd to the southwest.

# APPENDIX A

(CONTINUED)

# SAMPLING LOCATIONS IN SOUTHEASTERN AND NORTHERN LOWER MICHIGAN

## Region II, Grayling Subdistrict

### Mio Populations

9. MIO1. Huron National Forest southeast of Mio in Oscoda Cty. Apx. 2 miles east of Hoy Rd. on M489.

10. MIO2. Huron National Forest southeast of Mio in Oscoda Cty. Apx. 8 miles east of Hoy Rd. on the north side of M489.

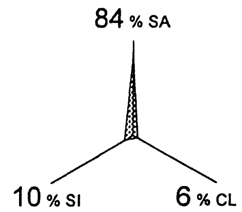
11. MIO3. Huron National Forest southeast of Mio in Oscoda Cty. Enter on the east side of M33 apx. 1 mile north of Hughes Lake Rd.

12. MIO4. Huron National Forest southeast of Mio in Oscoda Cty. Just east of Hoy Rd. on the north side of M489.

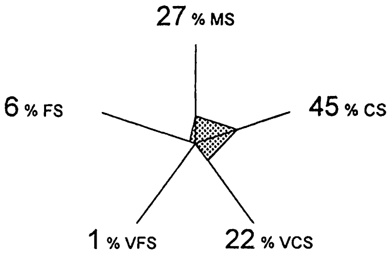
# APPENDIX B
# SOIL PROFILES

# MCCL Ecosystem Soil Pit No. 1
## Top 20 cm Core

### Percent Sand, Silt & Clay

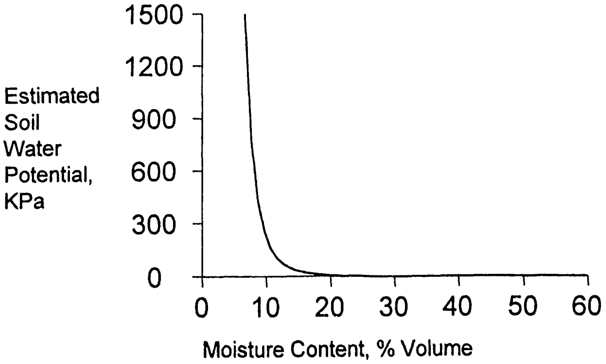


### Sand Particle Size Distribution

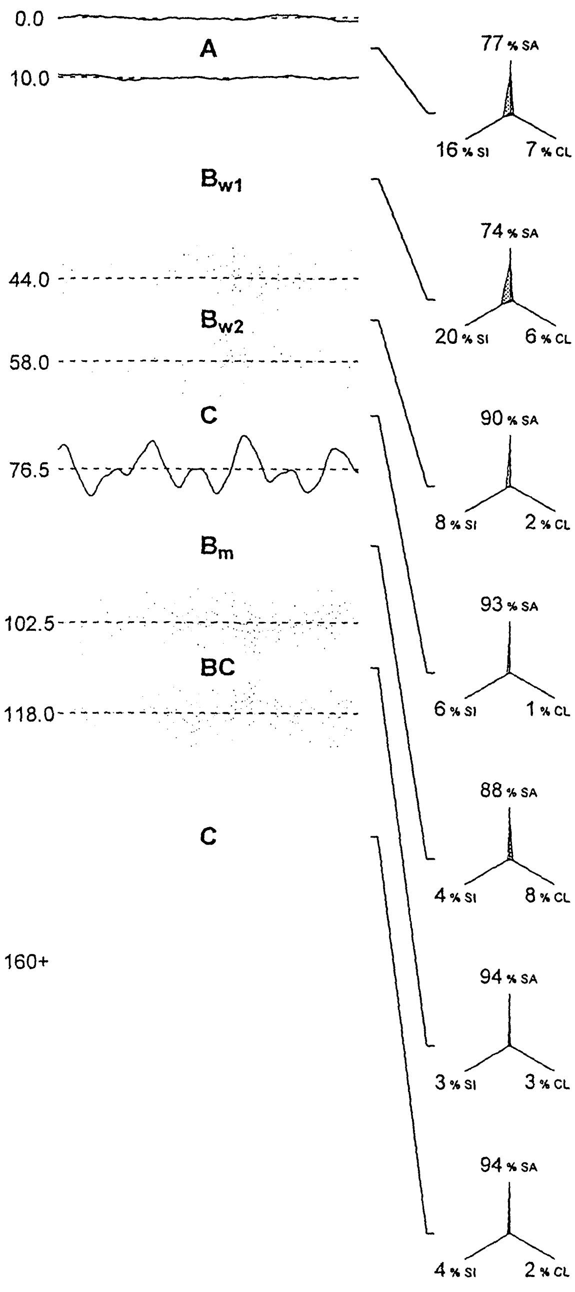


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 1 | 6 | 27 | 45 | 22 |
| 6 | | 27 | 67 | |

### Estimated Soil Water Potential (Saxton's Regression)



# MCCL Ecosystem Soil Pit No. 1
## Profile of Mineral Horizons



**A horizon**

- sandy loam
- 7.5 YR 3/1 dark grayish brown (PCCS)
- lab pH 4.53 very strongly acid
- very friable weak fine granular peds
- abrupt smooth boundary

**$B_{w1}$ horizon**

- sandy loam
- 7.5 YR 5/8 strong brown
- lab pH 5.11 strongly acid
- single grain to very friable weak fine granular peds
- becoming somewhat concreted toward boundary with Bw2
- gradual wavy boundary

**$B_{w2}$ horizon**

- sand
- 10 YR 6/6 brownish yellow
- lab pH 5.16 strongly acid
- single grain to very friable weak fine granular peds
- noticeably more concreted than Bw1
- concretions firm to very firm
- gradual wavy boundary

**C horizon**

- sand
- 10YR 7.5/6
- lab pH 5.85 medium acid
- single grain
- projections and mottles of circum-neutral (pH 7.0) concreted sand
- concretions of deeper chroma (7.5YR 5/6) as in Bm horizon
- abrupt irregular boundary

**$B_m$ horizon**

- loamy sand
- 7.5YR 5/6 strong brown
- lab pH 5.99 medium acid
- extremely firm concreted medium to coarse subangular blocky peds
- gradual wavy boundary

**BC horizon**

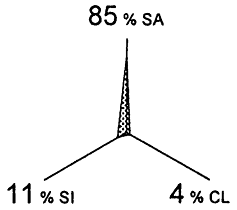
- sand
- 10 YR 6/8 brownish yellow
- lab pH 6.90 very slightly acid
- friable to firm weak to moderate fine granular peds
- numerous but discontinuous bands of deeper chroma
- somewhat banded boundary delimits end of highly concreted material
- gradual wavy boundary

**C horizon**

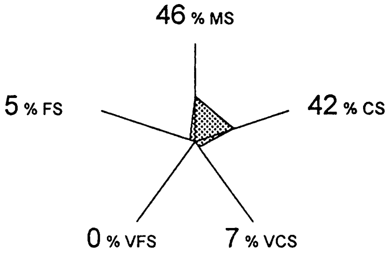
- sand
- 2.5 Y 5/3 grayish olive (PCCS)
- lab pH 7.42 neutral
- single grain
- very wet

# PERK Ecosystem Soil Pit No. 1
## Top 20 cm Core

### Percent Sand, Silt & Clay

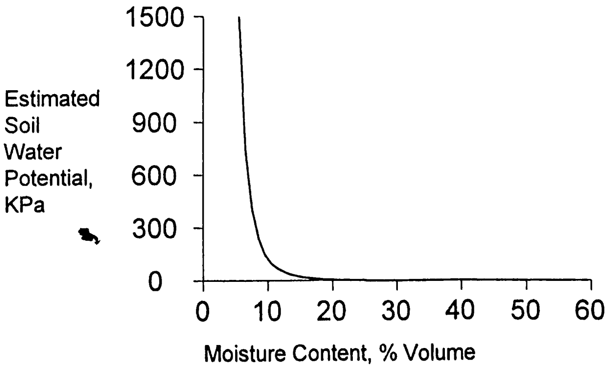


### Sand Particle Size Distribution

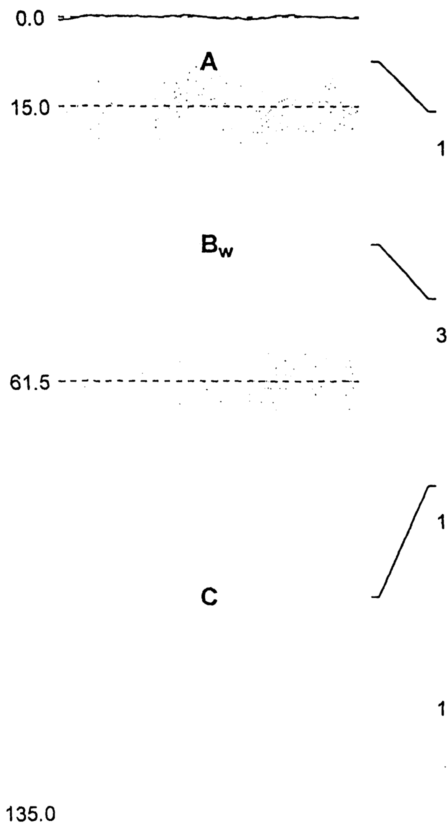


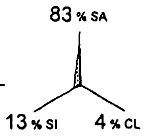
| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 0 | 5 | 46 | 42 | 7 |
| 5 | | 46 | 49 | |

### Estimated Soil Water Potential (Saxton's Regression)



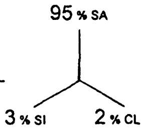
# PERK Ecosystem Soil Pit No. 1
## Profile of Mineral Horizons





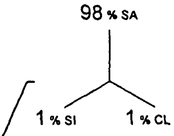
**A horizon**

* loamy sand
* 10 YR 4/4 dark yellowish brown
* lab pH 5.23 strongly acid
* single grain to very friable weak coarse granular peds
* gradual wavy boundary



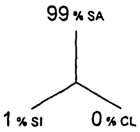
**$B_w$ horizon**

* sand
* 10 YR 6/8 brownish yellow
* lab pH 6.72 very slightly acid
* single grain to very friable weak medium granular peds
* becoming less acid (pH 6.5 very slightly acid) at 56 cm.
* gradual smooth boundary



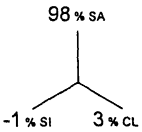
**C horizon**

* sand
* 10 YR 7/3 very pale brown
* lab pH 5.69 medium acid
* single grain
* mottling at 210 cm



**$C_{3.0M}$ core**

* sand
* 2.5Y 6/6
* lab pH 5.80 medium acid
* single grain

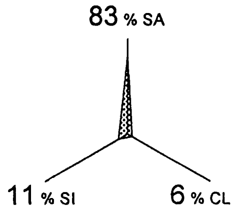


**$C_{3.1M}$ core**

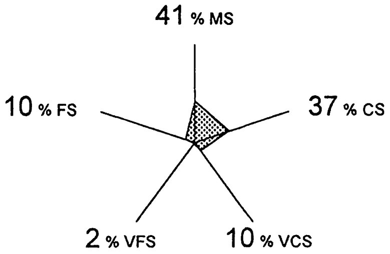
* sand
* 2.5Y 4/4 olive brown
* lab pH 6.03 slightly acid
* single grain

# PERK Ecosystem Soil Pit No. 2
# Top 20 cm Core

## Percent Sand, Silt & Clay

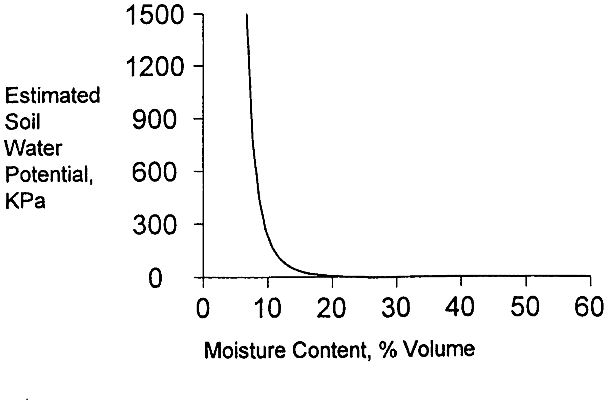


## Sand Particle Size Distribution

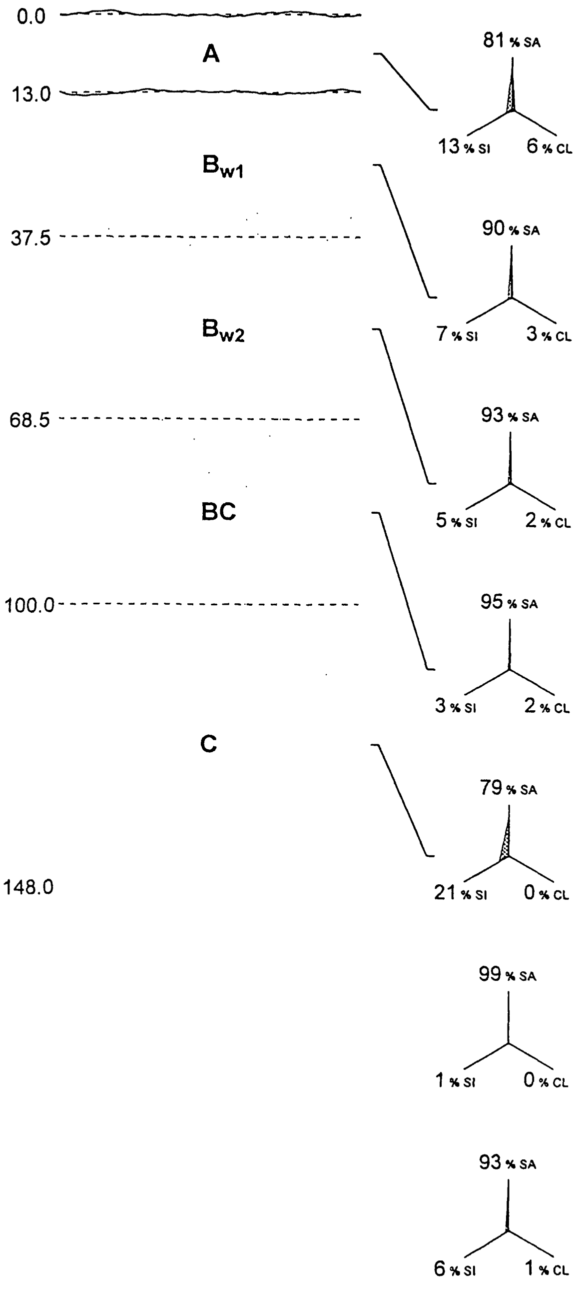


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 2 | 10 | 41 | 37 | 10 |
| 11 | | 41 | 47 | |

## Estimated Soil Water Potential (Saxton's Regression)



# PERK Ecosystem Soil Pit No. 2
# Profile of Mineral Horizons



**A horizon**

- * loamy sand
- * 10 YR 4/4 dark yellowish brown
- * lab pH 4.90 very strongly acid
- * very friable weak fine to medium granular peds
- * abrupt smooth boundary

**$B_{w1}$ horizon**

- * sand
- * 7.5YR 5/8 strong brown
- * lab pH 5.01 strongly acid
- * single grain to very friable weak coarse granular peds
- * gradual smooth boundary

**$B_{w2}$ horizon**

- * sand
- * 10 YR 6/8 brownish yellow
- * lab pH 5.04 strongly acid
- * single grain to very friable weak coarse granular peds
- * diffuse smooth boundary

**BC horizon**

- * sand
- * 10 YR 7/8 yellow
- * lab pH 4.88 very strongly acid
- * single grain to very friable weak coarse granular peds
- * prominent deep red chroma (5YR 3/4-5/8) mottling begins at 79.5 cm
- * diffuse smooth boundary

**C horizon**

- * loamy sand
- * 10YR 6/3 pale brown
- * lab pH 5.58 medium acid
- * single grain
- * pH 7.5 at 2.0 m; pH 8.0 at 2.4 m
- * prominent mottling continues to 113 cm

**$C_{2.4M}$ core**

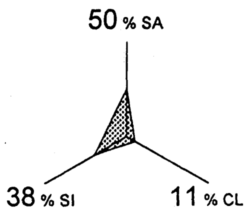
- * sand
- * 2.5Y4/4 olive brown
- * lab pH 7.74 neutral
- * single grain

**$C_{2.8M}$ core**

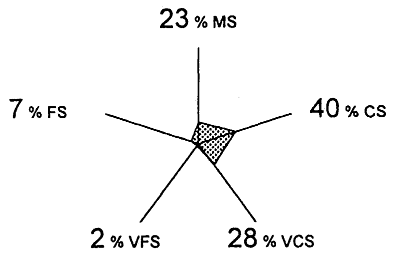
- * sand
- * 2.5 Y 5/3 grayish olive (PCCS)
- * lab pH 8.12 alkaline
- * single grain

# RADR Ecosystem Soil Pit No. 2
# Top 20 cm Core

## Percent Sand, Silt & Clay

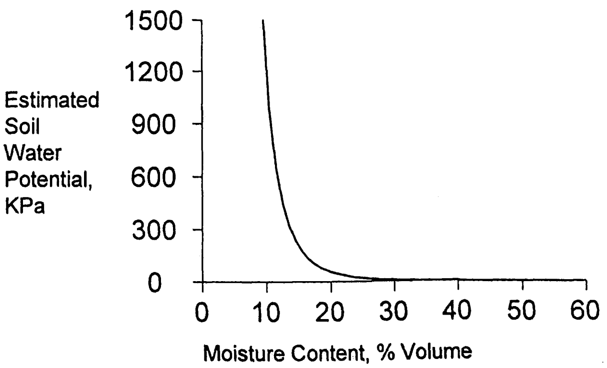


## Sand Particle Size Distribution

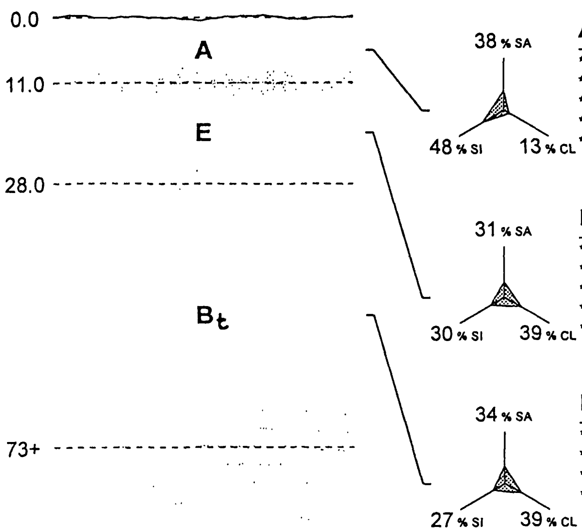


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 2 | 7 | 23 | 40 | 28 |
| 9 | | 23 | 68 | |

## Estimated Soil Water Potential (Saxton's Regression)



## RADR Ecosystem Soil Pit No. 2
## Profile of Mineral Horizons



**A horizon**

- loam
- 10YR 2/2 very dark brown
- lab pH 5.97 medium acid
- moderate fine to medium subangular blocky peds
- clear smooth boundary

**E horizon**

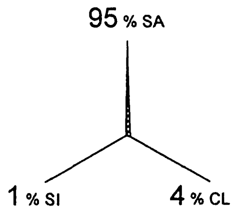
- clay loam
- 10 YR 5/4 yellowish brown
- lab pH 4.82 very strongly acid
- moderate to firm coarse subangular blocky peds
- clear smooth boundary

**$B_t$ horizon**

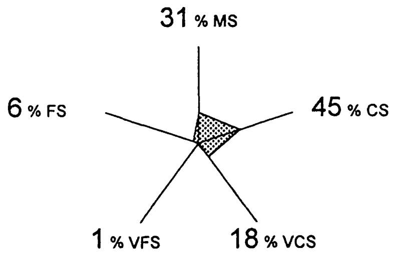
- clay loam
- 10YR 4/4 dark yellowish brown
- lab pH 7.07 neutral
- moderate to strong coarse subangular blocky peds

# GEOC Ecosystem Soil Pit No. 1
## Top 20 cm Core

### Percent Sand, Silt & Clay

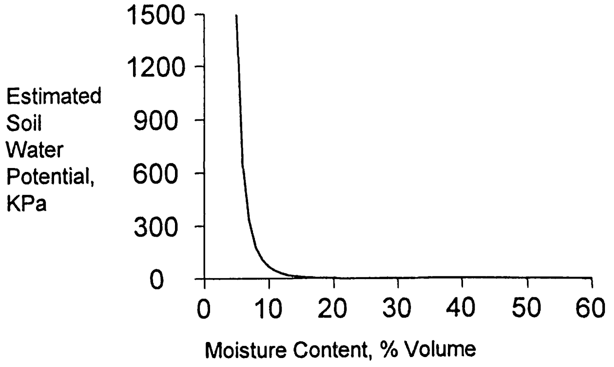


### Sand Particle Size Distribution

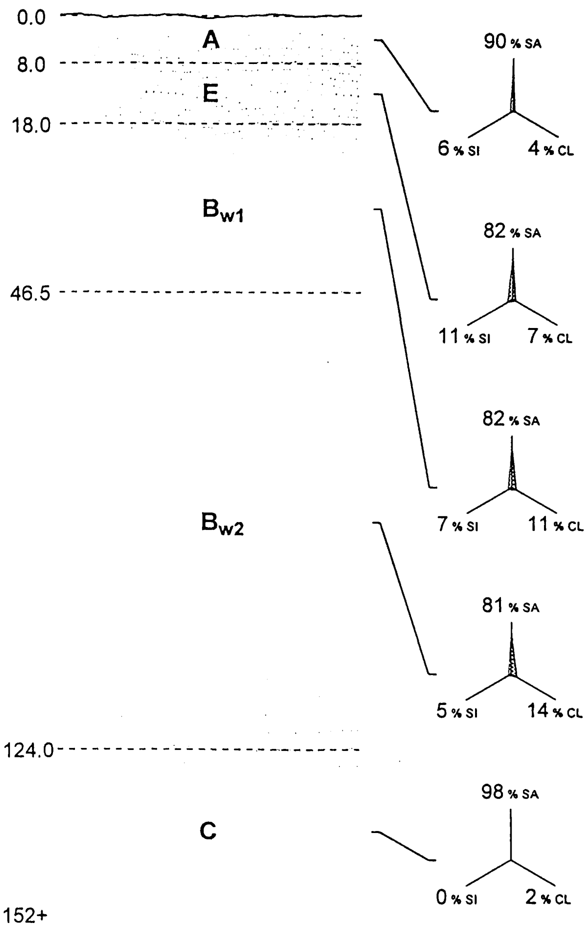


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 1 | 6 | 31 | 45 | 18 |
| 7 | | 31 | 62 | |

### Estimated Soil Water Potential (Saxton's Regression)



# GEOC Ecosystem Soil Pit No. 1
# Profile of Mineral Horizons



**A horizon**

* sand
* 7.5 YR 3/3 dark yellowish brown (PCCS)
* lab pH 4.66 very strongly acid
* very friable weak medium to coarse granular peds
* gravelly; gravel 0.5-1.0 cm diam.
* gradual smooth boundary

**E horizon**

* loamy sand
* 10 YR 4/6 yellowish brown (PCCS)
* lab pH 5.35 strongly acid
* very friable weak medium to very coarse granular peds
* gravelly; gravel 0.5-1.0 cm diam.
* gradual smooth boundary

**$B_{w1}$ horizon**

* loamy sand
* 7.5 YR 5/6 strong brown
* lab pH 5.56 medium acid
* single grain to very friable weak fine to medium granular peds
* gravelly with cobbles; gravel coarse, cobbles 3.5-7.5 cm diam.
* diffuse smooth boundary

**$B_{w2}$ horizon**

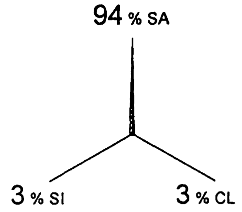
* sandy loam
* 7.5 YR 4/8
* lab pH 5.64 medium acid
* single grain to very friable weak medium to coarse granular peds
* gravelly and very cobbly; cobbles 3-7.5 cm diam.
* diffuse smooth boundary

**C horizon**

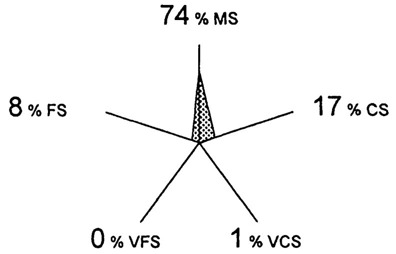
* sand
* 10 YR 6/4 lightyellowish brown
* lab pH 7.68 neutral
* single grain
* cobbly; cobbles 3.5-4.5 cm diam.

# MIO1 Ecosystem Soil Pit No. 1
# Top 20 cm Core

## Percent Sand, Silt & Clay

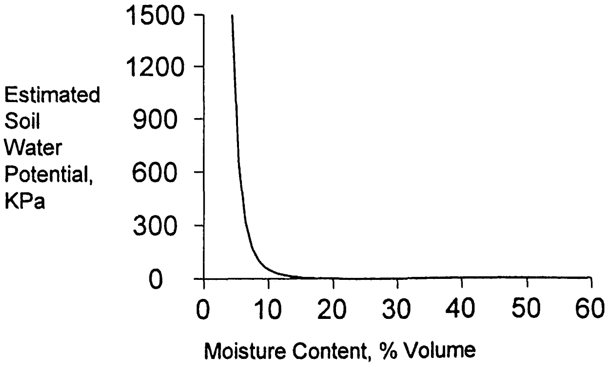


## Sand Particle Size Distribution

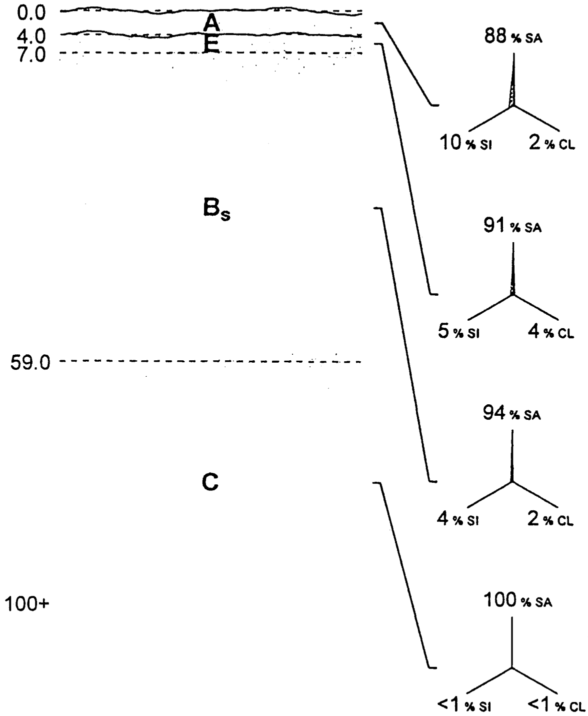


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 0 | 8 | 74 | 17 | 1 |
| 8 | | 74 | 18 | |

## Estimated Soil Water Potential (Saxton's Regression)



## MIO1 Ecosystem Soil Pit No. 1
## Profile of Mineral Horizons



**A horizon**

- sand
- 7.5YR 2/1 dark grayish brown (PCCS)
- lab pH 4.66 very strongly acid
- single grain to weak fine to medium granular peds
- charcoal present
- many fine and medium roots present
- abrupt smooth boundary

**E horizon**

- sand
- 7.5 YR 4/2 dark brown
- lab pH 4.61 very strongly acid
- single grain
- presence of charcoal creates a "salt and pepper" appearance
- gravel present; gravel 1.0-1.5 cm diam.
- gradual smooth boundary

**$B_s$ horizon**

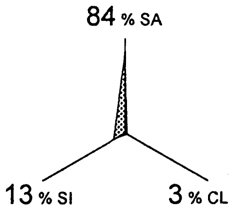
- sand
- 10 YR 5/6 yellowish brown
- lab pH 5.06 strongly acid
- single grain
- gravel present; gravel 0.7-1.2 cm diam.
- occasional cobbles, 2.8-7.0 cm diam.
- gradual smooth boundary

**C horizon**

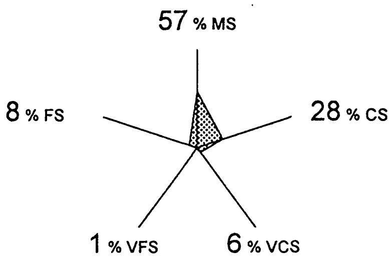
- sand
- 10 YR 5/6 yellowish brown
- lab pH 5.20 strongly acid
- single grain
- occasional cobbles up to 9 cm diam.

# MIO2 Ecosystem Soil Pit No. 1
# Top 20 cm Core

## Percent Sand, Silt & Clay

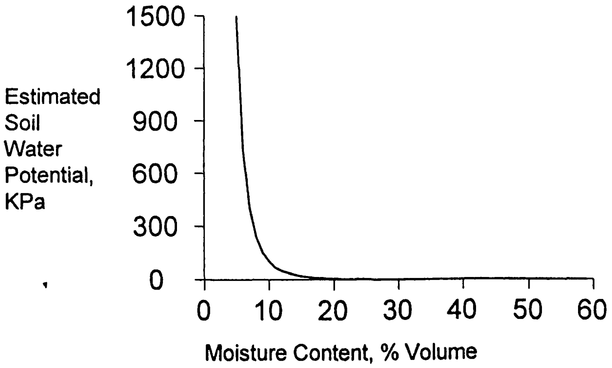


## Sand Particle Size Distribution

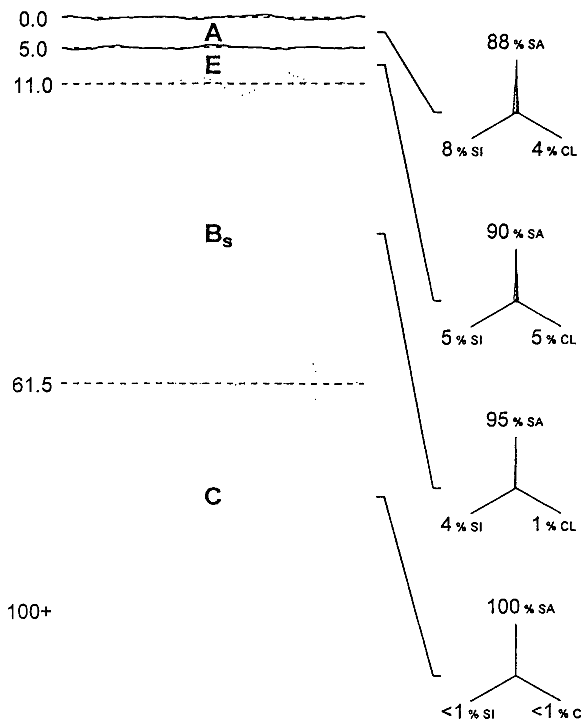


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 1 | 8 | 57 | 28 | 6 |
| 9 | | 57 | 34 | |

## Estimated Soil Water Potential (Saxton's Regression)



## MIO2 Ecosystem Soil Pit No. 1
## Profile of Mineral Horizons



**A horizon**

* sand
* 10YR 2/2 very dark brown
* lab pH 4.71 very strongly acid
* single grain to very friable weak fine granular peds
* charcoal present
* fine roots and rootlets abundant
* abrupt smooth boundary

**E horizon**

* sand
* 10 YR 4/6 yellowish brown (PCCS)
* lab pH 4.68 very strongly acid
* single grain
* presence of charcoal contributes to "salt & pepper" appearance
* roots abundant
* clear smooth boundary

**$B_s$ horizon**

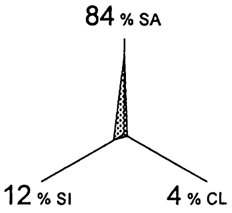
* sand
* 7.5 YR 5/6 strong brown
* lab pH 4.81 very strongly acid
* single grain
* roots (0.7-2.0 cm diam.) present throughout
* occasional smooth rounded cobbles 4.0-5.0 cm diam.
* gradual smooth boundary

**C horizon**

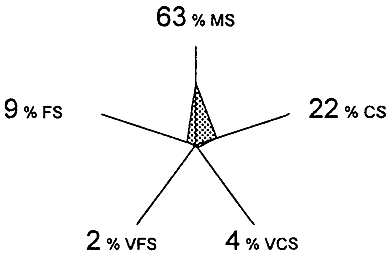
* sand
* 10 YR 6/6 brownish yellow
* lab pH 5.43 strongly acid
* single grain
* small percentage of gravel
* occasional cobbles

# MIO3 Ecosystem Soil Pit No. 1
## Top 20 cm Core

### Percent Sand, Silt & Clay

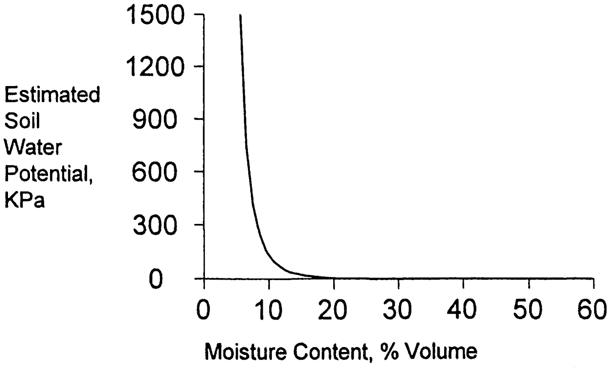


### Sand Particle Size Distribution

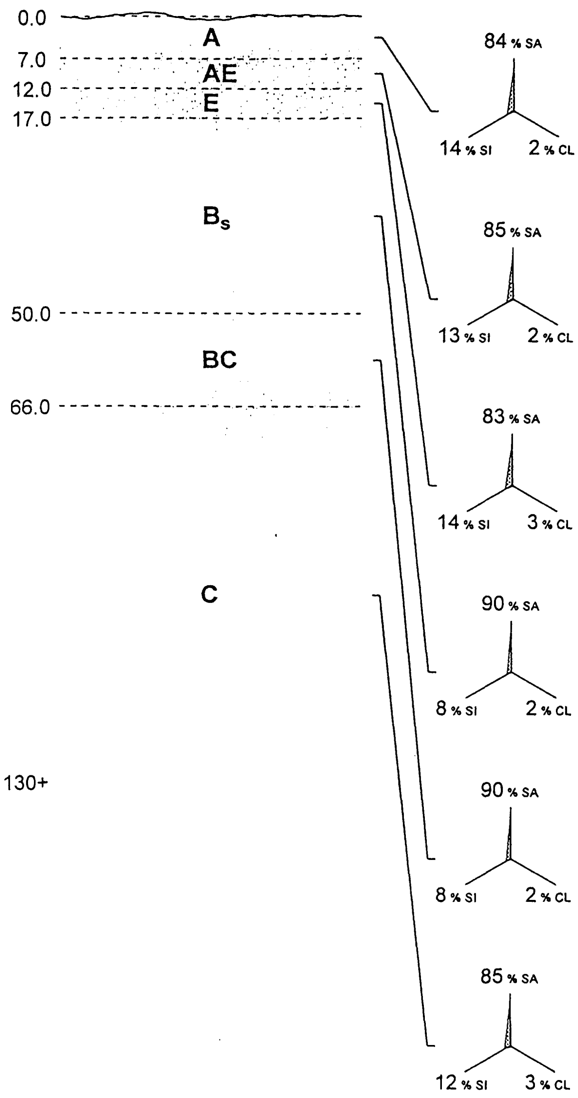


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 2 | 9 | 63 | 22 | 4 |
| 11 | | 63 | 26 | |

### Estimated Soil Water Potential (Saxton's Regression)



# MIO3 Ecosystem Soil Pit No. 1
## Profile of Mineral Horizons



**A horizon**

- * loamy sand
- * 10 YR 4/1 dark gray
- * lab pH 4.38 extremely acid
- * very friable weak fine granular peds
- * charcoal present
- * roots and rootlets abundant
- * clear smooth boundary

**AE horizon**

- * loamy sand
- * 10 YR 6/2 light brownish gray
- * lab pH 4.57 very strongly acid
- * very friable weak fine granular peds
- * charcoal present
- * gradual wavy boundary

**E horizon**

- * loamy sand
- * 7.5 YR 6/3 beige (PCCS)
- * lab pH 5.01 strongly acid
- * single grain
- * no charcoal found
- * gradual wavy boundary

**$B_s$ horizon**

- * sand
- * 7.5 YR 6/8 reddish yellow
- * lab pH 5.91 medium acid
- * single grain
- * occasional smooth rounded erratics to 5.5 cm diam.
- * gradual smooth boundary

**BC horizon**

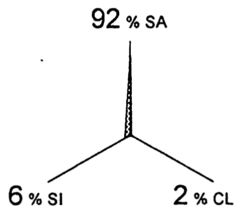
- * sand
- * 10 YR 7/6 yellow
- * lab pH 5.77 medium acid
- * single grain
- * occasional smooth rounded erratics 10-15 cm diam.
- * fine and medium roots to 67 cm.
- * gradual smooth boundary

**C horizon**

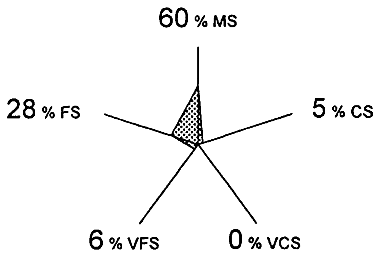
- * loamy sand
- * 10 YR 8/2 white
- * lab pH 5.73 medium acid
- * single grain
- * alkaline (pH 8.0) at 105 cm

# MIO4 Ecosystem Soil Pit No. 1
# Top 20 cm Core

## Percent Sand, Silt & Clay

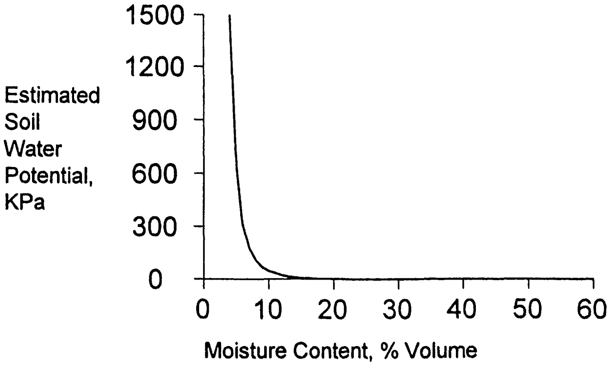


## Sand Particle Size Distribution

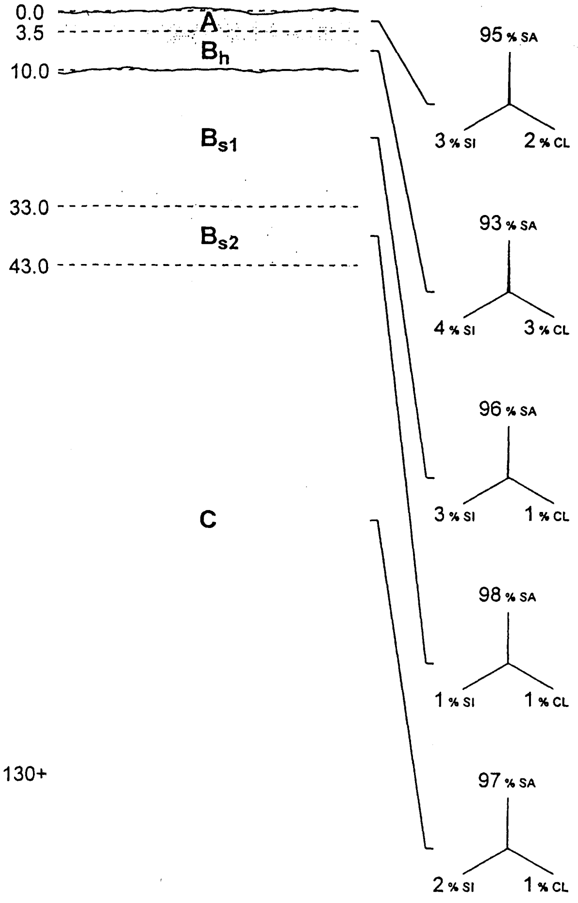


| Sand Particle Size Distribution, % | | | | |
|---|---|---|---|---|
| Fine Sand | | Medium Sand | Coarse Sand | |
| VFS | FS | MS | CS | VCS |
| 6 | 28 | 60 | 5 | 0 |
| 34 | | 60 | 5 | |

## Estimated Soil Water Potential (Saxton's Regression)



# MIO4 Ecosystem Soil Pit No. 1
## Profile of Mineral Horizons



**A horizon**

- sand
- 10 YR 3/3 dark brown
- lab pH 5.52 medium acid
- very friable weak fine granular peds
- clear smooth boundary

**$B_h$ horizon**

- sand
- 10 YR 3/4 dark yellowish brown
- lab pH 5.52 medium acid
- very friable weak fine granular peds
- weak Bh with some humus accumulation
- 2-5% small gravel (0.3-1.0 cm diam.)
- abrupt smooth boundary

**$B_{s1}$ horizon**

- sand
- 10 YR 4/6 yellowish brown (PCCS)
- lab pH 5.71 medium acid
- single grain
- occasional small round cobbles
- 2-5% small gravel (0.3-1.0 cm diam.)
- gradual smooth boundary

**$B_{s2}$ horizon**

- sand
- 10 YR 5/6 yellowish brown
- lab pH 5.90 medium acid
- single grain
- occasional small round cobbles
- 2-5% small gravel (0.3-1.0 cm diam.)
- gradual smooth boundary

**C horizon**

- sand
- 10 YR 7/4 very pale brown
- lab pH 5.90 medium acid
- single grain
- apx. 5% small cobbles (1.5-4.0 cm diam.); pH 7.5 @ 110 cm
- 5-10% small gravel (0.3-1.0 cm diam.)