A Review of the Taxonomic Status of *Quercus ellipsoidalis* and *Quercus coccinea* in the Eastern United States

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Photos of acorns were taken by Doug and Dave Shepard for the COCC & Ell paper.

The current taxonomic status of *Q. ellipsoidalis* Hill, Hill's oak or northern pin oak, and *Q. coccinea* Muenchh., scarlet oak, in the midwestern states of Indiana, Michigan, Illinois, Wisconsin, Iowa, and Minnesota has been controversial among field botanists and systematists for over one hundred years (**Fig 1**). Field and herbarium study have revealed unresolved discrepancies in attempting to define clear morphological distinctions between these two taxa. Currently there is no uniform agreement among biologists as to the range or the actual taxonomy of both species in the upper midwestern United States. Many of the taxonomic problems concerning both species have centered historically in Illinois and have been discussed most recently by Hipp (2006).

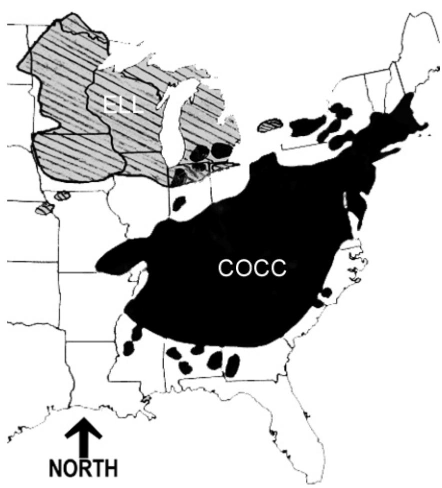

Figure 1. Range map of *Quercus coccinea* (COCC) and *Quercus ellipsoidalis* (ELL).

Quercus coccinea was first described and named by the German botanist Muenchhausen in 1770 from a New England population of the taxon. The species was first recognized in the Illinois flora by Vasey (1870) and later, in 1872, H. H. Babcock cited the taxon for the flora of the Chicago area (Jones and Fuller 1955). In 1876, *Q. coccinea* was listed in the flora of the Wabash River Valley in southern Illinois by Schneck (Jones and Fuller 1955). *Quercus ellipsoidalis* was discovered growing near the Little Calumet River of southern Chicago in southeastern Cook County Illinois by E.J. Hill.

The description of the morphologically similar *Q. ellipsoidalis* by E. J. Hill (1899) and subsequent publications by Trelease (1919) and Wadmond (1933) prompted botanists to question the validity of populations of *Q. coccinea* in northern Illinois, Iowa, Minnesota, and Wisconsin. *Quercus coccinea* was deleted from the Chicago flora and subsequently northern Illinois by Buhl (1934) leaving only records for southern Illinois. *Quercus coccinea* was, however, recognized as occurring in nearby Michigan and northwest Indiana (Deam 1953). Later, Overlease (1977) presented a detailed morphological study on variation in the red oak group (Lobatae) in the states of Wisconsin, Illinois, Indiana and Michigan, concluding that *Q. ellipsoidalis* was a northern small fruited expression of *Q. coccinea* showing a similar pattern of clinal variation displayed by *Quercus rubra* and *Quercus velutina*. Voss (1985) concurred with the findings of Overlease (1977) by omitting *Q. ellipsoidalis*, and extending the range of *Q. coccinea* throughout the state of Michigan. Swink and Wilhelm (1994) concurred with Voss and Overlease by eliminating *Q. ellipsoidalis* from the flora of the Chicago region but still recognized alternative interpretations by other botanists.

In a numerical taxonomic study on the *Lobatae* group, (Jensen 1977b) found no support for Overlease's conclusions and suggested that *Q. coccinea* and *Q. ellipsoidalis* are two phenetically distinct taxa. Jensen further countered Overlease's clinal concept in a study on geographic spatial autocorrelation in *Q. ellipsoidalis* in the states of Illinois, Wisconsin, Michigan and Indiana (Jensen 1986). In his analyses Jensen concluded that trees growing near the type locality of *Q. ellipsoidalis* (*i. e.*, southeastern Cook County) and northward most reflected the morphological characters diagnostic of the taxon. His results also indicated that the type locality populations were more related to those of Wisconsin and northern Michigan than the populations of nearby northwest Indiana where he presumed the ranges of *Q. coccinea* and *Q. ellipsoidalis* overlap and introgression between the two taxa is likely. Jensen (1997) in the *Flora of North America* has *Q. coccinea* ranging through most of Illinois and southern Wisconsin and maintains the original distribution of *Q. ellipsoidalis*. Shepard (1993) found northern Illinois populations of *Q, ellipsoidalis* to be morphologically similar to southern Illinois populations of *Q. coccinea* and not a product of hybridization with *Q. velutina* or *Q. palustris*.

Quercus coccinea ranges from southern Maine south through the Appalachians to Georgia, Mississippi, and into the Ozarks of northern Arkansas, southern Missouri, and extending into southern Illinois. Disjuncts occur in upstate New York and in several states along the southern Atlantic coastal plain. One isolated population recently discovered in the Tinley Creek Forest Preserve of northern Illinois grows with southern forests associates in a flatwoods community.

Quercus ellipsoidalis was described by E. J. Hill (1899) from populations observed in the south Chicago region of Cook County Illinois. The species is predominately Midwestern and is presumed to range from extreme northwest Ohio through northern Indiana, Michigan, Illinois, Wisconsin, Iowa, and Minnesota. Disjunct populations occur in southern Ontario near Lake Erie, northern Missouri, and extreme northeast Kansas. The current distinction between *Q. ellipsoidalis* (abbreviated as ELL) and *Q. coccinea* (abbreviated as COCC) is outlined in **Table 1**. Additional differences botanists have used in distinguishing ELL are its shiny, striated acorns and yellowish cotyledons versus dull, unstriated acorns with white cotyledons for COCC.

This paper is a synopsis of key points encompassing twenty five years of unpublished data collected on these two taxa. It includes statistical, herbarium, ecological, annual variation (plasticity), and general field observations of populations of both taxa throughout most of their range. Studies were performed to find out whether the range of morphological variability seen in populations of COCC encompasses the range of variability seen in populations of ELL. It was to be determined whether observable morphological differences were genetic or due to climatic variation. The relationship between the ELL/COCC complex and

Table 1. Current Characters distinguishing COCC and ELL based on the Flora of North America (Jensen, 1997) and Palmer (1942). Asterisk* indicates key characters from Jensen (1997).

Quercus coccinea	*Quercus ellipsoidalis*
Dead branches absent	Dead branches present
Nut oblong, subglobose	Nut mostly ellipsoidal to oval
*One or more concentric rings of pits at apex	*Occasionally with one or more rings of pits at apex
Buds 4-7 mm conic to ovoid pubescent above middle	Buds 3-5mm nearly glabrous/ pubescent above middle
Cupule 16-30mm, bract scales broad at base	Cupule 11-19mm, bract scales narrow
*Scales with a broad glossy base, scale (bract) margins often strongly concave	* Scales pubescent with straight or slightly concave margins

Illinois populations of *Quercus velutina,* black oak (VEL) and *Quercus palustris,* pin oak (PAL) was also analyzed.

The initial research for this paper began in 1990 with an extensive herbarium study of populations of COCC and ELL across the eastern United States. Six major herbaria were utilized in the study, with over 200 specimens examined. Soil surveys from each site were obtained along with associated climatic information. Forest associations were studied in the field along with supplementary research articles on each site. Portions of this research and statistical analysis of Illinois populations of ELL, COCC, VEL, and PAL were presented at the Transactions of Illinois Academy of Science meetings in 1991 and 1993. Data for the statistical analysis is derived from a yet unpublished manuscript.

Statistical Methods: Morphology comparisons utilizing multivariate statistical designs employing scatter plots can be useful tools in comparing and sorting out closely related species groups. Morphological variation seen can be associated with climate and local site conditions and thus be useful in determining clines or allopatric speciation.

Discriminate Functions Analyses (SYSTAT 1997, SPSS Inc., Chicago, IL.) were performed on quantitative and qualitative morphological data of leaves, buds, twigs, and acorns of COCC and ELL. A total of 174 trees were used in the study, segregated into twenty populations. Two different statistical assays were performed: one attempting to separate ELL, COCC, VEL, and PAL; and the other separating individual COCC and ELL populations. The first test involved a comparative analysis with VEL, PAL, COCC, and ELL using twelve morphological characters involving leaves, buds, and acorns (**Fig 2.**). Eighteen populations representing 154 trees of the *Q. ellipsoidalis*/*Q. coccinea* complex were studied, encompassing a

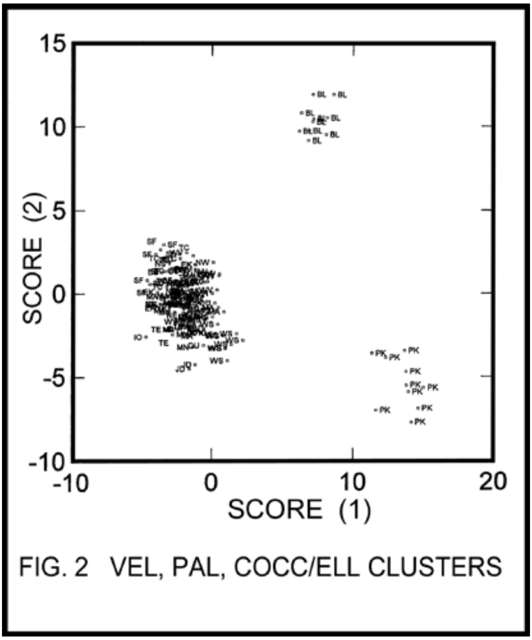

Fig 2. Discriminate Functions Analysis. Discriminate Functions One and Two Comparing COCC, ELL populations, PAL, and VEL. Twelve morphological variables.

distance of 1375 kilometers east to west from Massachusetts to Minnesota and an 830-kilometer distance north to south from Minnesota to southern Illinois/West Virginia (**Fig. 3**). Twelve populations of ELL from the states of Michigan, Indiana, Illinois, Wisconsin, Iowa, and Minnesota, and seven populations of COCC from the states of Illinois, Indiana, West Virginia, Pennsylvania, and Massachusetts were analyzed. Likewise, one population of ten trees representing VEL from central Illinois and one population of ten trees representing PAL from southern Illinois were studied.

The second DFA analysis involved thirty-four morphological characters attempting to segregate populations of ELL and COCC. Eighteen characters dealt directly with bud and nut/cupule characters, fourteen related to leaf and twig morphology, and two analyzed growth form and dead branching patterns.

Specimens that could be located in the natural areas of the study sites were assigned a number and deposited in a plastic bag. Leaves from each specimen were then pressed and dried. Acorns, both viable and non viable, were refrigerated until analyzed. Leaves, buds, and acorns were collected from late summer and early fall through late winter from the various sites during the years 1990 to 2008. Sampling from each location generated an average subsample of five mature buds, five mature acorns (nuts with cupules), and five mature leaves from each tree. Leaves and mature buds exposed to full sun were collected by various methods. Nuts with cupules were collected directly from mature trees and from twigs lying on the ground from recently broken upper crown exposed branches with the aid of binoculars to avoid misidentification. Photographs of individual trees and associated leaves, buds, and acorns were made for reference. Forest associations, soil types, and climate were noted and recorded taken at each site. Terminal buds, twigs, nuts, and cupules were measured using either a binocular scope or hand lens using 7X and 30X magnification. Viable acorns from the sampled trees were collected and planted in pots with potting soil, germinated, moved, and studied.

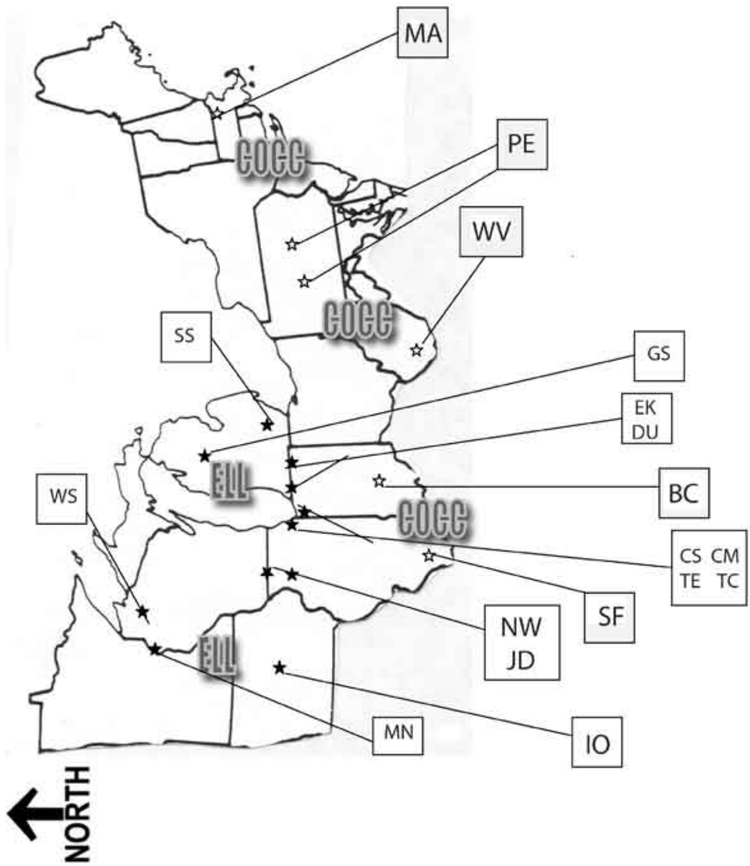

Figure 3. Study sites of *Quercus ellipsoidalis* and *Quercus coccinea*. Number of trees analyzed in parenthesis.

Quercus coccinea: MA (16) = Massachusetts, PE(6)=Pennsylvania, WV(11)=West Virginia, EK(11)=Elkhart, Indiana, BC(6)=Brown County, Indiana, TC(10)=Tinley Creek Woods/ Chicago, SF(10)=Southern Illinois.

Quercus ellipsoidalis: SS(6)=Waterloo, Michigan, GS(9)=Northern Michigan, CS(7)=Chicago Sand Ridges, CM(5)=Chicago Moraine, TE(3)= inley Creek/ Chicago, DU(3)=Indiana Dunes, NW(5)=Northwest Illinois, JD(5)=Jo Daviess Co., IO(11)=Hardin County, WS(10)=Wisconsin, MN(12)=Minnesota

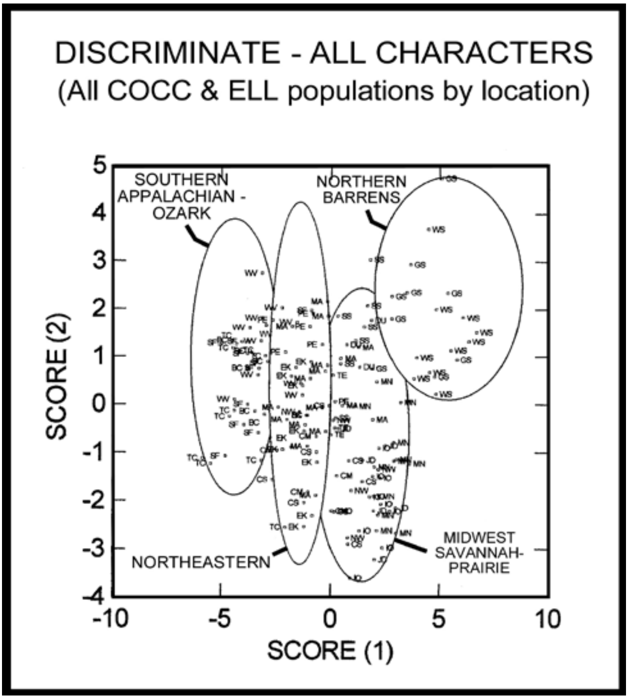

Fig 4. Discriminate Functions Analysis. Discriminate Functions One and Two Comparing COCC/ELL Populations. Ecotypical complexes illustrated.

Statistical Results of DFA (Fig 2)

Figure 2 shows the results of the first study comparing the populations of ELL, COCC, PAL, and VEL in attempt to clarify morphological differences. Canonical coefficients within groups and canonical loadings for Discriminate Functions One and Two indicated that bud length, bud pubescence, scale length, scale shape, cup pubescence, rings present or absent, nut width, aristae (bristle tip) number, leaf length, amount of cupule covering nut, and percent scar width divided by nut width, separated VEL and PAL into distinct entities. ELL and COCC grouped into an amorphous mass with overlapping COCC and ELL populations but showed a wide separation from VEL and PAL. Two extremes show southern Illinois COCC trees (SF) at one end and the northern Michigan and Wisconsin trees (WS) at the other with all other populations in the middle.

Statistical Results of DFA (Fig. 4)

Fig 4 shows the results of the second study comparing just the populations of ELL and COCC using all thirty-four morphological characters. Canonical coefficients within groups and canonical loadings for Discriminate Functions One and Two indicated width of the widest leaf lobe, percent of the widest leaf lobe in relationship to leaf length, leaf width, leaf length, percent leaf width to leaf length, sinus length, cup width, nut length, and total nut size (length plus width). Four clustering patterns are discernable showing rather loose regional affinities in a left to right pattern. Southern populations group on the far left followed by northern Appalachian, Midwestern, and finally northern Wisconsin and Michigan on the far right. The southern COCC populations were illustrated by WV, BC, SF, and TC. The second clustering showed a mix of COCC and ELL with MA, PA, EK dominating, but with individual trees of WV, CS, CM, NW, and SF. It is notable that individual trees of Massachusetts and Pennsylvania populations grouped more closely to ELL populations of Minnesota and northwest Illinois than the southern trees of COCC in the DFA plot. The third clustering was dominated by ELL with MN, IO, JD, NW,CS, CM, SS, and DU dominant but with trees of MA and GS. The fourth cluster represented the northern population of ELL and was represented by GS and WS.

Discussion

Diagnostic morphological characters attributed to ELL were common in populations of COCC from the Northern Appalachians (**Photos 2, 3, 4, 5,and 8**). DFA plots and field observations show COCC and ELL as highly polymorphic and variable taxa that appear to be closely related and conspecific. Characters attributed to both COCC and ELL were found in all populations studied. The key diagnostic characters -- presence or absence of rings, ellipsoid versus globular nuts, and scale shape of involucre (cupule) bracts (Table 1) -- used in segregating these two taxa were not statistically significant. Field work revealed by this study shows that both COCC and ELL produce globular and ellipsoidal nuts, many without the presence of rings or pits about the stylar end, and may have acute bracts with slightly concave margins.

Northern Appalachian COCC possess ELL morphological characters.

Hill's oak has been classically defined by the shape of its ellipsoid acorn, yet in this study COCC was found to produce ellipsoid acorns in PE , MA, and WV. These smaller ellipsoid nuts were most prevalent at the MA study site of Mt. Lincoln at 1000 ft (310 m) near Pelham, Massachusetts and at the Clearfield County, Pennsylvania site. Those collected in this study were viable and germinated to produce seedlings. Populations of COCC at these sites exhibited ELL characters such as dead branches, smaller buds, and striated nuts with slightly yellowish cotyledons.

E.J. Palmer noted this variability among COCC in New England and termed it "ellipsoidalis forms" on an annotated herbarium specimen from Arnold Arboretum collected in 1945 from Essex County Massachusetts. ELL was reported from Long Island, New York by Grier (1924) but later dismissed because it was presumed out of its range. Hill's oak populations in Iowa, Wisconsin, Northwest Illinois, and Minnesota produce acorns with diagnostic characters for COCC (**photos 3, 4, 5, 7, and 11**).

Trees producing nuts with concentric arcs, pits and ring patterns were observed in all populations of ELL. Representative specimens with these characters used in this study were collected from southeastern Cook County (**photos 7 and 11**), northwestern Wisconsin, Minnesota, and Jo Daviess County and deposited at the Field Museum. **Photo three** (3) shows acorns collected from Central Iowa, Northern Wisconsin and Northern Michigan with broad-based cupule bracts not discernible from a MA specimen. Leaf morphology was similar in COCC and ELL (**Photos 14 and 15**). It was also observed that leaf morphology was unique to

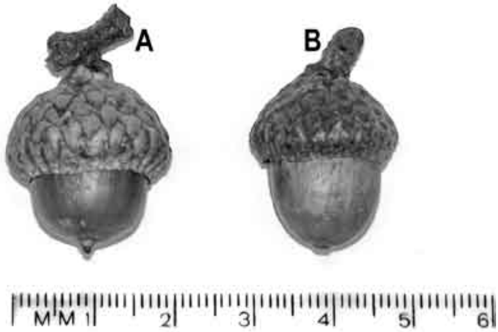

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Photo 1. Annual Cupule plasticity of ELL from Southern Cook County, Ill. Acorn A coll. 1991 glossy broad scales; Acorn B coll. 1992 narrow puberulent scales.

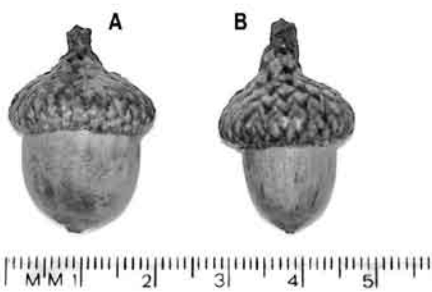

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Photo 2. Acorn A COCC Pelham Mass. Ellipsoidalis form; Acorn B ELL glossy-scale form.

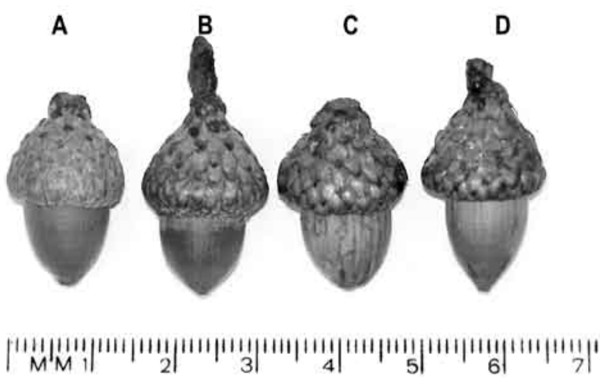

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Photo 3. Ellipsoidalis forms. Acorn A ELL Minn; Acorn B ELL N. Wisc.; Acorn C COCC Mass.; Acorn D COCC Mass.

ELL and COCC but distinct from PAL and VEL. Northwestern Illinois and central Minnesota specimens deposited at Western Illinois University and the Field Museum showed striking leaf morphology to southern Illinois trees.

Variability and Plasticity (Photos 1 and 9)

It has been known that the genus *Quercus* shows a great deal of plasticity and variability in its morphological characters. In the Chicago area both *Quercus alba* and *Quercus macrocarpa* will produce atypical ellipsoid acorns in any given year. After several years of observations, it was noted that leaf, bud, and acorn morphology can fluctuate considerably in size, pubescence, and form among the COCC/ELL complex. Statistically significant changes in bud, leaf and acorn morphology were noted on several trees collected in Cook, Will, Dupage, and Pope Counties in Illinois and recorded (Shepard, 1993). Trees in Cook County can fluctuate annually in the intensity of ring patterns, bud size, and cupule. Many trees produced acorns, and buds with "ellipsoidalis" characters (puberulent cupules) one year and then "coccinea" characters the next year (tuberculated and glossy cupules). Recent higher annual rainfall in northern Illinois has apparently induced many trees in southern Cook County to produce typical COCC characters.

E. J. Hill's syntype and "authentic type" material deposited at the University of Illinois and St. Louis Botanical Garden possess diagnostic characters of COCC (Photos 12 and 13)

Definitive separation of ELL from COCC becomes obscure with further examination of E. J. Hill's herbarium collections of ELL. It is clear that E.J. Hill and William Trelease did not attempt to study the range of northeastern populations of COCC and neither used the concentric rings or pits or strongly concave bracts as diagnostic for any species of *Quercus*. While Hill did not specify a holotype, he did leave a large collection of what he felt were typical examples of specimens labeled "authentic type" material housed at the University of Illinois (UI). The lectotype specimen for ELL was made from these collections by Jensen (1979).

It should be noted that three of Hill's "authentic type" specimens; *Hill 62, 1902* UI, *Hill 150 1895* UI, *Hill 175 1895* UI collected at the type locality (CS) possess nuts with concentric rings and pitting at the stylar end and buds falling within the size range of COCC. Hill's syntype specimen (collected off the lectotype tree) *Hill 176, 1895* (*97, 1896* UI) is a nearly identical replicate of a COCC specimen collected by Agnes Chase from Beltsville, Maryland (photo 13). Likewise, another "authentic type" specimen from Gardner's Park, Chicago (*Hill 129, 1896* UI) exhibits leaf forms, buds, and acorns falling in COCC range of variability to a COCC specimen from Anderson County South Carolina (*Davis 899360* MO). The acorns from this South Carolina specimen possess the same ring pattern as specimen *Trelease 16073* UI collected by William Trelease in southern Cook County (Glenwood), Illinois.

Ecological differences can define species

Along these same lines, oak species can be segregated on ecological habitat differences, forest associations and related habitat requirements. Outside of the obvious morphological discrepancies presented in this document, segregating ELL/COCC populations based on habitat likewise has not been observed where both are purported to grow. No specific soil or site preference differences exist

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Photo 4. COCC acorn form. Acorn A Minn. Glossy strongly concave bracts.

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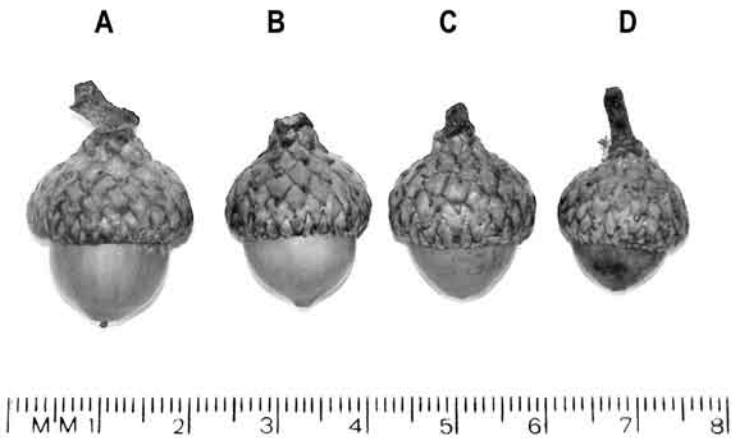

Photo 5. Globular acorns with glossy bract scales. Acorn A ELL Central Iowa; Acorn B COCC Mass; Acorn C ELL N. Wisc; Acorn D ELL N. Michigan.

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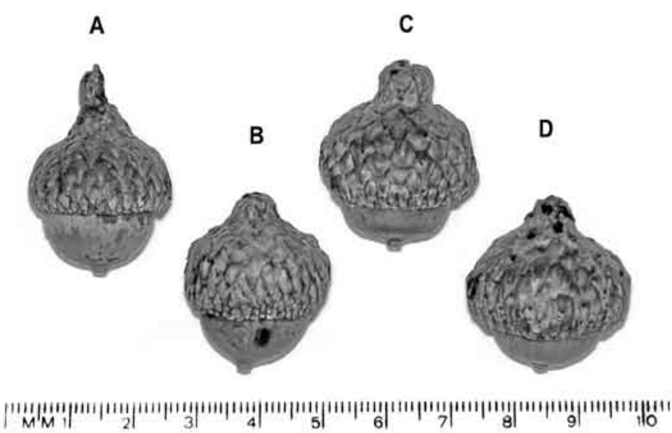

Photo 6. Southern COCC forms. Acorn A West Virginia; Acorn B Missouri Ozarks Acorn C Tinley Creek N. Ill.; Acorn D South Carolina.

between trees with COCC characters and trees with ELL characters in the Chicago region. On the other hand, sympatric species PAL and VEL, which can be found growing on the same acidic sand loams in southern Cook County as do COCC/ELL, segregate out morphologically and ecologically. Typically, PAL is most tolerant of wet sites, growing to the exclusion of VEL, COCC, and ELL on flood-prone Gilford Sand Loam. VEL grows commonly on dry sandy ridges on well drained Oakville Sand Loam while COCC/ELL grow in between moisture gradients on somewhat poorly drained Watseka Sand Loam. COCC/ELL appear to reproduce out of the same gene pool with a multiplicity of acorn forms, leaf forms and bark variation induced by local climatic conditions. This character is found throughout all populations of COCC/ELL.

DNA correlations with morphological results

There is no question that genetic differences exist between populations of oak taxa. This is true with the COCC/ELL dilemma. The question is how much is enough and what warrants a species designation. DNA studies have not shown to be conclusive on speciation of oak taxa and even other woody taxa. The DNA results recorded by Hipp and Weber (2008) revealed a strong genetic separation between populations of VEL and ELL and COCC alluding support of the hypothesis that COCC and ELL be regarded as segregate species. Several aspects of that study, which was published in ts entirety in *Systematic Botany* (Hipp and Weber, 2008), need to be examined.

First, ELL populations used were restricted to only Illinois, Wisconsin, and Indiana. Comparisons were also made in a circumscribed range of COCC that included only three states in southerly locations; Ohio, Illinois and Missouri. The study did not include northern Appalachia or other eastern populations including the type locality of COCC. A conclusion is made based on a limited a populational study that assessed a comparison between two extreme points of distribution where there is no apparent gene flow as there is between populations of VEL. ELL populations showed no gene flow with COCC populations because the variety or race of COCC used in the study is not sympatric with it. Except for the disjunct Tinley Creek population, southern COCC does not exist in the upper Midwest. The study used one genetic populational type as a representative for the whole species ignoring all the rest. From the view point of this paper essentially, two COCC populations were analyzed with expected genetic differences.

Another aspect of the study assumes that two species exist in the Chicago area. The results from the study were not clear as to whether DNA or morphology was used in ultimately determining ELL from COCC. Specimen labeled TAG-027 collected in northwest Indiana grouped genetically with ELL but morphologically possessed the diagnostic characters of COCC in its nut and bract cupules. The study grouped this tree as COCC, not ELL, despite the contradictory results. One explanation was that backcrossing with ELL populations could have resulted in the genotype but with selection for the phenotype of COCC. The question still remains as to what ELL are being referred to. What would southern Illinois tees be called without rings and elliptical nuts?

A third question regarding the paper involves VEL and its relationship with ELL and COCC. Continuous gene flow is seen in the southern and northern populatons of VEL . Gene flow is expected with populations from VEL where

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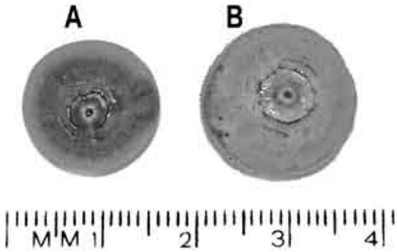

Photo 7. Concentric rings. Acorn A ELL Cook County, Illinois; Acorn B West Virginia

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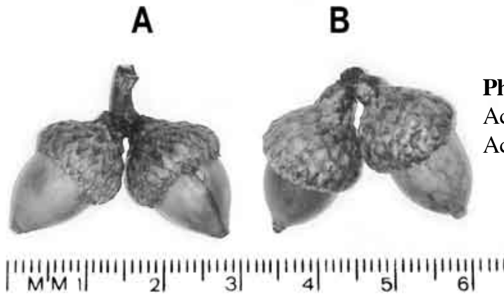

Photo 8. Ellipsoidalis forms. Acorn set A ELL N. Wisc.; Acorn set B COCC Mass.

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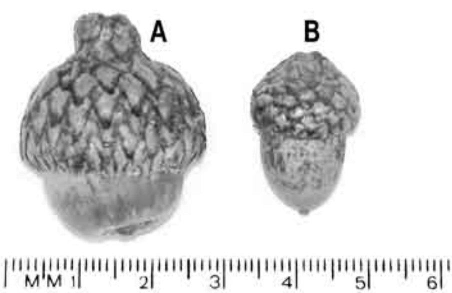

Photo 9. Annual variation S. Illinois COCC on same tree. Acorn A 1994; Acorn B 1995.

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Photo 10 Concentric Rings. COCC Tinley Creek N. Illinois.

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Photo 11. Concentric Rings. ELL Will Co. N. Illinois.

populations are continuous north to south and there is sympatry. The analysis is based upon an inordinate number of trees sampled from each population. While VEL showed no genetic break in clustering patterns between northern and southern populations as did COCC and ELL, only three trees out of a total of forty four represented southern populations. All the remaining trees studied were from the upper Midwest. VEL is also less polymorphic and probably more stable genetically than COCC, but caution should be used when there is such a dichotomy.

Finally, DNA inconsistencies have been noted in other studies done in the Chicago area. A recent study by Ashley (2006) involving *Quercus alba* L. white oak, *Quercus bicolor* L. swamp white oak, and *Quercus macrocarpa* L. bur oak, showed two Chicago-area populations of *Quercus alba* as genetically distinct even though morphologically similar. Ashley also noted that there was as much difference between the members of the same species as there was between members of different species. Another study by Gutman and Weigt (1988) involving electrophoretic allozyme analysis of the red oak group showed COCC and ELL to be more closely related to each other than to VEL or PAL as proposed by Jensen (1977). A small sample size warranted them to be tentative on their results.

DNA can and will continue to be a useful tool in helping taxonomists solve speciation. It is not the ultimate solution to plant taxonomy, however. This study recognizes genetic and morphological differences in COCC/ELL populations. The DNA study by Hipp and Weber substantiates this. However, speciation needs to be correlated with many other factors. Another aspect to the ELL/COCC controversy is the recognition of ecotypes or varieties.

Regional Ecotypes

The morphological variability of ELL and COCC is interpreted from this study to be attributed in part to local site conditions, current climatological influences, and dramatic climate shifts during the Pleistocene epoch. Statistical and ecological data suggest a COCC complex forming a clinal continuum with regional ecotypes ranging from the southern Appalachian/Ozarks through the northern Appalachians to the western upper Great Lakes and extending into Iowa and beyond. The statistical DFA of all characters reveals four major groupings: a southern Appalachian/Ozark scarlet complex; a northeastern complex; a prairie/savannah complex; and a northern sand barrens complex. Discussion on the four types follows.

Southern Scarlet Oak (Photos 6, 7, 10, 12, 13, 14)

The origin of ELL revolves around the nominate species COCC. It reaches its apex of development and greatest size in the southern Appalachians where it has attained heights of 50+ meters and circumferences of over 7m at breast height (Godfrey, 1988). It has been recorded as living over 400 years by some accounts (Harlow, 1984). It is here that the best examples of the species can be observed. Optimal growth is attained on deep, acidic, silt loams supplemented by annual rainfall patterns of over 50 inches (127cm) and high relative humidity. This form of COCC is restricted to the unglaciated regions of the lower Midwest and southern Appalachian/Ozark Mountains. The study populations included SF, WV, BC, and a disjunct TC. They are typified with an open growth form with or without dead branches, possessing large dull brown globular nuts with white cotyledons. The nuts reveal consistent ring patterns, with bowl shaped or turbinate cupules with

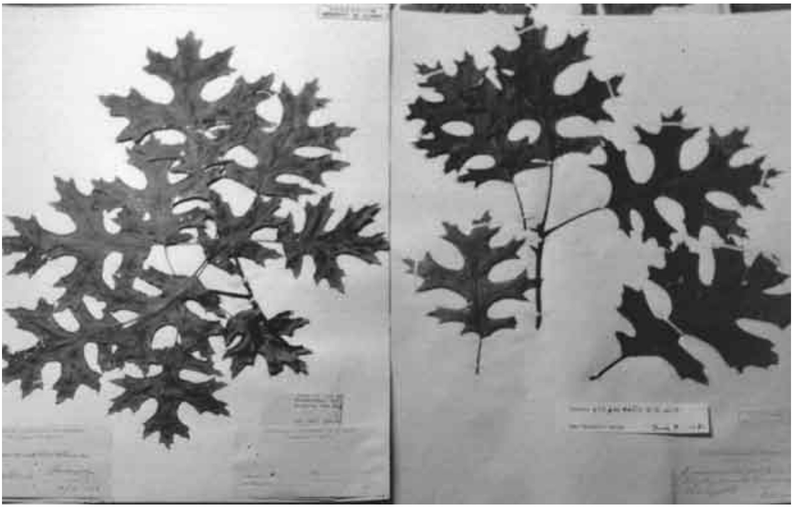

Photo 12. E.J. Hill's type material. Left photo South Carolina; Right Photo ELL "Authentic type" Chicago Illinois.

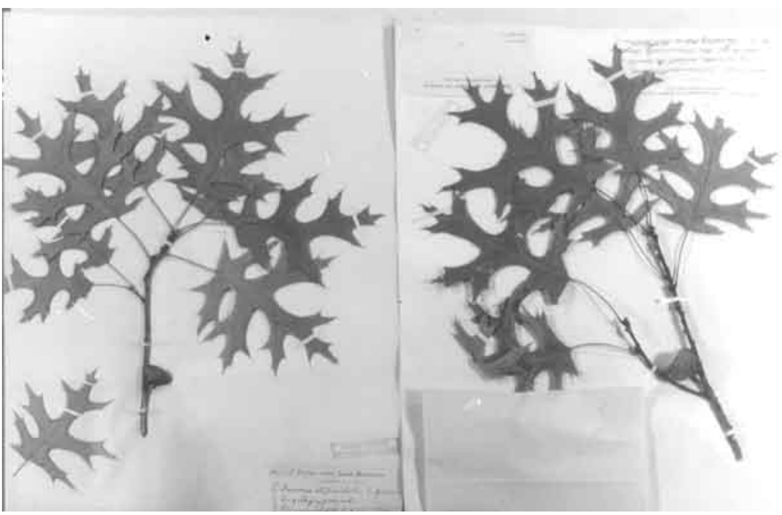

Photo 13. Syntype of ELL. Left photo Syntype of ELL Chicago, Illinois; Right Photo COCC Maryland

broad-based bracts frequently over 6mm. The buds range can range to 9mm (larger than many VEL) with elongated leaves over 200mm with 5-9 lobes. The Tinley Creek population is a population of over one hundred acorn-producing trees and represents a rare disjunct that grows with other southern taxa in a flatwoods near the lower end of Lake Michigan. Migrations of southern oaks along routes with silt loam deposits of the Mississippi River Valley from the unglaciated South in post glacial times has been suggested as its origin (Shepard, 2005).

Eastern Appalachian Scarlet Oak/ Origin of Hill's Oak (Photos 1, 3, 5, and 8)

Northern Appalachian populations of COCC presumably arose from post-glacial migration from the South and are represented by the study sites in Pennsylvania and Massachusetts. These forms of COCC are particularly common on the sand barrens of New Jersey, Massachusetts and Long Island of the Atlantic coastal plain. The populations of the northern Appalachians grow in high rainfall with cold winters. They represent northern variants of those to the south with slightly smaller, frequently tapered, cylindric, ellipsoidal nuts often lacking rings or pits. At elevations over 1000 feet in Massachusetts trees produce striated acorns with yellowish cotyledons and narrow, acute 4-5mm bracts. This is believed to

Photo 14. Leaf Morphology. Pope Co. Southern Illinois

Photo 15. Leaf Morphology. Whiteside Co. N.W. Illinois

be a response induced by cooler and dryer growing conditions and such trees have been grouped as "ellipsoidalis forms." All statistical studies showed a close relationship between the northern Appalachian populations of COCC and ELL. The DFA results indicate that Pennsylvania (PE) and Massachusetts (MA) populations are most closely related morphologically to those of ELL, suggesting ELL's origin. It is hypothesized here that populations of ELL of the western Great Lakes arose from a northwesterly migration of COCC originating from the northern Allegheny-Appalachian Mountains and Atlantic Coastal Plain following extensive sand deposits of the post-glacial stages of ancient glacial lakes from Lake Ontario and Erie in the East and continuing west and northward into Lakes Huron, Michigan, and Superior. Subsequent populations of ELL established themselves along the sand plains of northern Ohio, Michigan, northern Indiana, northern Illinois, Wisconsin, Minnesota, and Iowa. Populations of ELL reach their greatest abundance in the northern sections of Michigan, Wisconsin, and Minnesota. The absence of ELL/ COCC from central Illinois, northern Missouri (except for Harrison county), southern Iowa, central Indiana, and most of western Ohio suggests this. In northern Illinois, populations become increasingly scarce moving south from the Wisconsin/ Illinois border, indicating that major migrations originated from the north/northeast. Many coastal plain disjuncts in the genera *Carex*, *Eleocharis*, *Styrax,* and *Panicum* followed this presumed east/west path and occur in northwest Indiana, southern Michigan, northwest Wisconsin, and northeastern Illinois. This was documented by Peattie (1924), Curtis (1959), Swink and Wilhelm (1994), and Reznicek (1994). It is worth noting that woody taxa *Comptonia peregrina, Vaccinium angustifolium,* and *Amelanchier arborea* occurring at the Montague Massachusetts sandplain also occurred at the sites in northwest Wisconsin and northern Michigan. *Betula populifolia,* another disjunct, common in Montague and Pelham Massachusetts, grew as far west as northeastern Illinois on ancient beach sand a few kilometers east of the Tinley Creek Preserves (TE and TC) (Bartel, 1979) .

Plant communities of the western Great Lakes and upper Midwest have undergone dramatic climatic changes over several thousand years. A region including the states of Ohio, Illinois, Iowa, Wisconsin, Minnesota, northern Indiana, and portions of southern

Michigan comprised the Prairie Peninsula, an extension of the tall grass prairie, expanding 8,000 YBP during the hot and dry Hypsithermal Period (Transeau, 1935). Oak taxa migrating into these regions some 3-11,000 YBP incorporated themselves into these drier savannah / prairie communities. Climate in the Prairie Peninsula was and currently is not as suitable for development of complex forest communities as those further east or south (Braun, 1950). Forest species adapting to these shifting spells of extreme drought and extreme cold and wetness have had to survive by various changes genetically and through hybridization. Both COCC and ELL are

Photo 16. Bud Morphology. Pope Co. Southern Illinois

Photo 17. Bark Morphology. Lucas Co. Ohio

species that prefer open sites and are frequently pioneers in secondary succession, thus morphological responses to adverse climatic conditions seems likely. Scrubby oak populations of *Quercus alba* and *Quercus velutina,* growing alongside COCC, are associated with these savannahs.

Sand Plain Scarlet Oak

The region from Ohio through northeastern Illinois represents a vegetative ecotone from the complex mixed mesophytic forests of the east and south to the prairie/oak/savannahs of the west. Rainfall is annually under 100 cm (40in). It is typified by beech/maple on the moist sites and oak/hickory/savannah on the more upland drier areas. This area marks the eastern edge of the Prairie Peninsula. Populations across Lower Michigan, northern Indiana, and southeastern Cook County Illinois represented by SS, DU, CS, and CM represent transitional forms and have characteristics of both extremes of this continuum. Their members group morphologically between those of Appalachia and prairie groups. Scattered trees closely resembling those of the northern Appalachians can be found across northern Indiana and Lower Michigan. The Indiana counties of Elkhart (EK), Jasper, Cass, and White are a few of the counties representing these populations between the sand outwashes of the Kankakee and Wabash Rivers (Deam, 1953). Trees in this region have a more open growth form with fewer dead branches.

Prairie Scarlet Oak (Photos 1, 3, 4, 5, 7, 11, and 15)

The prairie/savannah region is represented by trees with generally poorer growth form, compacted branching patterns, smaller leaves, and shiny, striated nuts with yellow cotyledons. The populations of SS, CS, CM, DU, TE, NW, JD, IO and MN from southern Michigan, Illinois, Indiana, Iowa, and Minnesota are represented. Most of these populations lie on the west side of Lake Michigan, a region ecologically and vegetatively different than the Indiana/Michigan side (Swink and Wilhelm, 1994). Many eastern species drop out at this division, notably *Fagus grandifolia* and *Cornus florida*. The combinations of lower, unpredictable rainfall, high evapotranspiration rates, silty clay soil, and drought are environmental factors that can affect growth form and promote dead branching patterns and smaller buds (Cochrane and Iltis, 2000) (Nixon, et al. 1994). Hybridity between

COCC/ELL and VEL producing *Quercus* x*paleolithicola* is common on dry, sandy ridges near Lake Michigan. Alternately, locally moist conditions adjacent to Lake Michigan (CS, CM, DU, TE) offer more suitable sites and foster morphological characteristics of the complex in the form of larger buds, leaves, and nuts with concentric rings. Likewise, growing on better soil, trees of central Minnesota exhibit similar characteristics.

Northern Boreal Scarlet Oak (Photos 2, 3, 5, and 8)

Populations representing GS and WS represent northerly populations growing in the coldest climates in excessively dry sandy soil with the poorest nutrient capacity. These populations have the smallest acorns and buds, and thus position far statistically from the Appalachian groups. Individual trees at these sites frequently are stunted and scrubby and are sometimes called "grubs" (Curtis, 1959). Local site conditions play a role in separating northern populations of ELL. Moist loamy prairie soil of the Minnesota population (MN) supporting large trees contrasts with the stunted population in northwest Wisconsin (WS) growing almost directly across the Mississippi River in poor sandy soil. Nonetheless, Wisconsin trees showed COCC characters with cupules with acuminate bracts and broad bases, nuts with ring patterns, and COCC leaves.

Conclusion

The statistical, herbarium, and ecological observation from this study question the legitimacy of *Quercus ellipsoidalis* as a valid species. *Quercus ellipsoidalis* and *Quercus coccinea* are considered as infraspecific taxa with loosely based regional varieties comprising a complex. Four regional ecotypes of this *Quercus coccinea* complex are recognized, following the key below:

1a. Nuts frequently ellipsoid/subglobose with a pale yellow pigmented cotyledon, frequently shiny and striate, concentric rings often absent; Cupules mostly turbinate/conical; Buds mostly pubescent 25-75% of upper bud surface(rarely glabrous); Growth form compact, dense with dead branches, upper crown leaves frequently less than 125mm;
Midwestern in distribution.. **3**

1b. Nuts mostly globose with predominately white or occasionally pale yellow cotyledons, frequently dull and weakly striate. Cupules turbinate/ bowl shaped; Buds pubescent 25-75% of upper bud surface (rarely glabrous); Concentric rings often present; Growth form open, coarse with dead branches reduced; Upper crown leaves frequently over 125mm in length.
Mostly Appalachian and Ozarks in distribution **4**

2a. Buds 2-4 (6) mm, narrow, glabrous to sparsely pubescent, conical/turbinate cupules less than 19mm in width ,mostly glabrous, Tree often scrubby and stunted; growing on sand plains, boreal forest, edges of bogs in northern Michigan, northern Wisconsin, Minnesota, and southern Canada
....**Northern Scarlet Oak**

2b. Buds 3-6 (7.5) mm narrowly ovate, sparsely to moderately pubescent, Cupules mostly 13-28mm in width; Cupule bracts mostly 3-5mm frequently pubescent Tree to 30 meters; prairies, savannahs, hedgerows, oak woodlands, N.Illinois, NW. Indiana, Iowa, S. Mich., Minn, and Wisc.......... **Savannah Scarlet Oak**

3a. Buds 4-8mm narrowly ovate/bulbous, sparsely to densely pubescent. Cupules mostly 13 to 30mm, Cupule bracts 4-6mm mostly glabrous Nuts globular, cylindric and ellipsoid, concentric rings present or absent Northern Appalachian Mountains and associated sand plains, oak woodlands, pine barrens of New England, Penn, NJ, NY, Disjunct populations on sand savannahs; northern Indiana , extreme northeastern Illinois, northwest Ohio, lower Michigan.. **Eastern Scarlet Oak**

3b. Buds 5-9mm broadly ovate/bulbous, sparsely to densely pubescent Cupules frequently 20-30+mm, mostly bowl shaped, Cupule bracts 5-8mm Nuts globular to cylindric mostly with prominent rings or pits. Dominant in Ozarks and southern Appalachian Mountains, also southern Illinois, southern Ohio, and southern Indiana; Disjunct in northern Illinois and southern Atlantic Coastal Plain... **Southern Scarlet Oak**

LITERATURE CITED

Braun, E. L. 1950. Deciduous Forests of Eastern North America. The Blakiston Co., Philadelphia, Pa. 596 pp.

Buhl, C. A. 1934. Supplement to an annotated flora of the Chicago Area by H. S. Pepoon. Bull. Chicago Acad. Sci. 5(2):5-12.

Craft K. J. and Ashley M. V. 2006. Population differentiation among three species of white oak in northeastern Illinois. Canadian Journal of Forest Resources 36: 206-215.

Curtis, J. T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin. 657 pp.

Deam, C. C. 1953. Trees of Indiana. The Bookwalter Co., Inc. Indianapolis, Indiana. 355 pp.

Godfrey, R. K. 1988. Trees, Shrubs, and Woody Vines of Northern Florida and adjacent Georgia and Alabama. University of Georgia Press. Athens, Georgia. 734 pp.

Grier, N. M. 1924. Unreported plants from Long Island. Torreya 24:71-76.

Gutman, S. I. and Weigt. L. A. 1989. Electrophoretic evidence of relationships among *Quercus* (oaks) of eastern North America. Canadian Journal of Botany 67: 339-351.

Harlow, W. M., E. S. Harrar, F. M. White. 1984. Textbook of Dendrology. 6th Ed. McGraw-Hill Book Company, New York, New York. 510 pp.

Hill, E. J. 1899. A new biennial fruited oak. Bot. Gaz. 27:204-208. Illinois Natural History Survey. 1976. Inventory of flora and fauna of Thornton

Hipp, A. L. and Weber, J. A., 2008. Taxonomy of Hill's Oak (*Quercus ellipsoidalis:* Fagaceae): Evidence from AFLP Data. Systematic Botany: 33(1) pp. 148-158.

Jensen, R. J. 1977a. A preliminary numerical analysis of the red oak complex in Michigan and Wisconsin. Taxon 26:399-407.

Jensen, R. J. 1977b. Numerical analysis of the scarlet oak complex (*Quercus* subgen. *Erythrobalanus*) in the eastern United States: Relationships above the species level. Syst. Bot. 2:122-133.

Jensen, R. J. 1979. Lectotypification of *Quercus ellipsoidalis* E. J. Hill. Taxon 29:154-155.

Jensen, R. J. 1997. *Quercus* Linnaeus sect. *Lobatae* Loudon. Pp. 447-468 in Flora of North America Editorial Committee, eds. *Flora of North America, North of Mexico,* Vol. 3 Oxford University Press, New York.

Jones, N., and G. D. Fuller. 1955. The Vascular Plants of Illinois. University of Illinois Press, Urbana, and the Illinois State Museum, Springfield, Museum Scientific Series (6). 55pp.

Little, E. L., Jr. 1971. Atlas of United States trees. Volume 1., Conifers and important hardwoods. United States Department of Agriculture, Forest Service, Miscellaneous Publication Number 1146. 200 pp.

Overlease, W. R. 1977. A study of the relationship between scarlet oak (*Quercus coccinea* Muenchh.) and Hill oak (*Quercus ellipsoidalis* E. J. Hill) in Michigan and nearby states. Proc. Penn. Acad. of Sci. 51:47-50. Palmer, E. J. 1942. The red oak complex in the United States. Amer. Midl. Naturalist 27:732- 740.

Peattie , D. C. 1922. The Atlantic Coastal Plain element in the flora of the Great Lakes. Rhodora 24: 57-88.

Reznicek, A. A. 1994. The disjunct coastal plain flora in the Great Lakes region. Biol. Conservation 68: 203-215.

Shepard, D. A. 1991. The occurrence of the scarlet oak, *Quercus coccinea* in northern Illinois. Trans. Ill. State Acad. Sci. 84 (Suppl. 35) (Abstract).

Shepard, D. A. 1993. The Legitimacy of *Quercus ellipsoidalis* based on a Populational study of *Quercus coccinea* in Illinois. Unpublished Thesis. Western Illinois University. 168pp.

Shepard, D. A. 2005. The land that time forgot; southern flatwood oaks and associates of the Tinley Creek Forest Preserve of Cook County, Illinois. International Oak Journal 16: 47-60.

Swink, F.and G. Wilhelm. 1994. Plants of the Chicago region, 2nd Edition. The Morton Arboretum, Lisle, Illinois. 922 pp.

Transeau, E. N. 1935. The prairie peninsula. Ecology 16:423-437.

Trelease, W. 1919. The Jack Oak (*Quercus ellipsoidalis*). Trans. Ill. State Aca. Sci. 12:108-

Vasey, G. 1870. Our native oaks. American Entomol. and Bot. 1:344-345.

Voss, E. G. 1985. Michigan Flora Part II, Dicots (Saururaceae-Cornaceae). Cranbrook Institute of Science and University of Michigan Herbarium 724 pp.

Wadmond, S. C. 1933. The *Quercus ellipsoidalis-Quercus coccinea* complex. Trans. Wisc. Acad. Sci Arts and Lett. 28:197-203.

Wilkenson, L. 1990. Systat: The System for Statistics. SYSTAT Inc., Evanston, Illinois. 677 pp.

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An Interesting Hybrid Oak Population in Southeastern Colorado and Adjacent Areas

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Farmers and ranchers in southeastern Colorado in Las Animas and Baca Counties have long been aware of unusually large oak trees growing in the bottomlands along creeks in the local "canyons," which are more properly gulches or draws in the context of the High Plains. Cottonwood (Creek) Canyon, located in western Baca County, is perhaps the best known of these.

On the drier, rocky hillsides above and away from the creeks are a different set of oaks entirely, short, twisty, and scrubby, certainly "scrub oaks" in the classical sense. These scrub oaks, which vary from short shrubs to trees up to 15 or more feet high, have been designated as *Quercus* x *undulata* (Tucker 1961-1971). These oaks are characterized generally by smallish, somewhat holly-like, sometimes prickly gray-green leaves which are very unlike the deeply-sinused, dark green leaves which most people associate with oaks. The acorns are also small, with shallow, rather smooth caps, often but not always on peduncles.

The large trees are another matter: they DO have typical "oak leaves," with deep sinuses. The leaves are a rich green and can be quite large ranging from 8.5-15 cm length and 4.5-10 cm width with up to 5-7 lobes per leaf, and some have a blunt terminal lobe with an obovate to elliptical leaf blade in outline (Figure 1). The acorns are rather large, and virtually always have a smooth cap without fringes. Since the leaves in particular do not match those of any of the more familiar oaks of the area—*Q. gambelii* to the west and north, *Q. macrocarpa*, *Q. stellata* to the south and east, there has always been speculation as to just what they could be.

Figure 1. Foliage of an apparent *Q. macrocarpa* x *Q. gambelii* in Cottonwood Creek Canyon, Baca County located in SE Colorado.