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EASTERN AND WESTERN SPECIES.

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RELATIONSHIPS OF TWO ISOLATED GROUPS OF SUGAR MAPLE IN
CENTRAL OKLAHOMA TO EASTERN AND WESTERN SPECIES

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Norman, Oklahoma

1969

RELATIONSHIPS OF TWO ISOLATED GROUPS OF SUGAR MAPLE IN
CENTRAL OKLAHOMA TO EASTERN AND WESTERN SPECIES

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RELATIONSHIPS OF TWO ISOLATED GROUPS OF SUGAR MAPLE IN CENTRAL OKLAHOMA TO EASTERN AND WESTERN SPECIES

CHAPTER I

INTRODUCTION

The genus Acer was divided into thirteen sections by Pax (1902). Those which are apetalous and have connate sepals, were placed in the section Saccharina. This group, commonly called "sugar maple," is also referred to as "hard maple." The first designation arises from the high economic importance associated with the refinement of syrup from the sugary sap. The latter distinction is one of commercial lumbering origin and refers to qualities of hardness, strength and stiffness not possessed by the other maples. The arrangement of wood elements yields a firm, close-grained product of high commercial value.

In the prairies of central Oklahoma, small to medium size populations of sugar maple are found in protected places in the Caddo Canyons, Caddo and Canadian counties and in the Wichita Mountains, Comanche County. The population aggregations occur in moist micro-climatic habitats mostly in the deeper parts of the more stabilized canyons and in the draws of north facing slopes or on well protected bottom lands in the mountains. The closest Eastern North American relative is 150 to 200 miles away where the irregular fringe of the range of Acer saccharum Marsh. var. saccharum penetrates a short distance into

the state. Acer grandidentatum var. sinuosum Sarg. is one of the nearest Western North American relatives. It is found in the canyons of the Sabinal River and those of other of the Edwards Plateau Balcones Escarpment waterways in Bandera, Kendall and Uvalde counties, Texas. This is approximately 400 miles south of the central Oklahoma stations. A. grandidentatum Nutt. var. grandidentatum is reported from approximately 300 miles directly west in the Monzano Mountains of New Mexico.

The designation A. s. var. saccharum has been applied without contestation to the Caddo Canyon plants. Sargent (1922) assigned those of the Wichitas to Acer grandidentatum Nutt. var. grandidentatum mentioning G. W. Stevens. Stevens (1916) had cited the plant from the Wichitas. The Oklahoma question, then, has been focused on the assignment of the specific epithet, saccharum, by some investigators to the Wichita plants.

A comparison of the two groups to Eastern and Western references by numerical analysis has been used. This was augmented by the integration of other observations. The conclusions emerged as a limited interpretation which directs attention to another perplexing aspect of the Western sugar maple complex.

CHAPTER 11

THE SUGAR MAPLES OF CENTRAL OKLAHOMA, A COMPARISON

Introduction

The discussions of two commentators can be used as an outline to illustrate the trend of the thinking concerning the sugar maples of central Oklahoma.

Hopkins (1943) started the dialogue when he stated that in the Wichita Mountains there occur ". . . such eastern plants as Arabis missouriensis (in the greatest abundance, so that one almost thinks of it as a weed), Acer saccharum (in that region treated by most Oklahoma botanists as A. grandidentatum, but clearly not that, although further study may reveal it to be merely an isolated variety of the typical New England sugar maple). . . ." The defense of this part of a sentence was included in a footnote ". . . first identified (erroneously ?) by G. W. Stevens (about 1915-16)." Hopkins earlier (1938) had hailed Stevens as one ". . . whose familiarity with the flora of northern and north-central Oklahoma was greater than that of any other local botanist of his time" His competence in southwest Oklahoma apparently was not considered equally adequate.

Hopkins also admitted in the footnote (1943) that his field experience with the plant was very brief. In spite of this and the

imposing list of other botanists which he included who independently specified the material as A. g. var. grandidentatum, he stated that he is convinced that these plants were probably only ". . . ecological (or genetic) variants of the eastern sugar maple."

Little (1944) attempting to vindicate his earlier (1939) use of the epithet, A. g. var. grandidentatum, answered with an abundance of factual information. He mentioned a number of authorities who had made independent and corroborating identifications (additional to those produced by Hopkins). From these, special emphasis was given to four men.

1. He found it difficult to believe that Sargent (1922) would include the species citation from the Wichitas with the name G. W. Stevens beside the Oklahoma distribution, without actual verification of the authenticity.

2. Palmer (1934) decided the Wichita maple was A. grandidentatum based on his observations from his Hobart camp.

3. Eskew (1938) noted the plant as one of the most unusual disjuncts of that region.

4. Alfred Rehder was then mentioned as rendering an identification from specimens sent to the Arnold Arboretum in 1930. He pronounced those from the Caddo Canyons as A. s. var. saccharum and the ones from the Wichitas as A. g. var. grandidentatum.

Several other points were offered to reinforce Little's argument. One given considerable importance was his reference to his earlier (1939) discussion of the combinations of Eastern and Western plants found in both of the Oklahoma locations. This is

evaluated elsewhere (p. 12).

Hopkins' only recorded answer to Little's (1944) defense occurred as marginal notations in red pencil in the copy of *Rhodora* in the library of The University of Oklahoma. On the first occasion was written "by their fruits ye shall know them" with the initials "M. H." following. This was beside a statement in which Little suggested that distinctions between sugar maples are largely based on leaf morphology. A "yes," "no," and "Much higher" were the final three comments. The first was in agreement with the observation that, although only 50 miles apart, the plants were very different in growth habit in the field. Disagreement was expressed with the statement that distinction can be made from herbarium specimens. Little had placed a high value on this type of determination as rendered by Rehder for the materials sent from the two areas. The last comment concerned Little's concurrence with Stevens' description that the trees are ". . . shrubby, branched and only about 10 feet high." One is inclined to agree with Hopkins' criticism since the field habit of a number of trees, especially those on well protected bottom lands, doesn't fit the description.

The situation has remained relatively unchanged since Little's last (1944) publication. The problem has been referred to by others with some deciding for A. s. var. saccharum in the Wichitas and others A. g. var. grandidentatum. Most recently Paul Buck (1964) designated the plants A. s. var. saccharum.

Phytogeography

Geological Formations

Caddo Canyons. The Caddo Canyon area was described by C. Taylor

(1961) as occurring principally in northeast Caddo County and southeast Canadian County. There are a number of deep, steep walled canyons from Binger to several miles north of Hinton into Blaine County. The boxheads of these, some with plunge pools at the headwater basins, are cut in the Permian Rush Springs sandstone sediment of the Whitehorse formation. These runoff waterways are the tributary creeks which drain into both Sugar Creek, a branch of the Washita River, and the Canadian River. Boggy Creek, with some deep lateral canyons, is another larger branch waterway which lies between the Canadian and Sugar Creek. It eventually joins Sugar Creek with both then contributing to the Washita River drainage basin.

Some of the canyons were formed by runoff from a ridge which separates the Canadian from the Boggy-Sugar Creek complex. From this highland, drainage and canyon cutting are in a northeasterly direction into the Canadian, southwesterly into Sugar Creek and from both directions into Boggy Creek. Some canyons are also present on the north side of the Canadian and the south side of Sugar Creek. The wider mouth ends of the Sugar Creek drainages are cut into the more easily eroded Marlow member.

The ridge was described by Foreman (1939) as that along which Captain R. B. Marcy traveled. Marcy mentioned in his diary the presence of sugar maple within a distance of 10 miles from his May 22, 1849 camp site near the head of Boggy Creek. He was probably much closer to the plants than he estimated. The cuts into Marcy's Ridge, except for the Boggy Creek complex, were the canyons in which the most populations of sugar maple were found. The aggregations were usually in the deeper canyons and in the direction of the boxheads. A few plants were

reported in the waterway cuts from the north into the north side of the Canadian and from those which drain into the south side of Sugar Creek. The canyons from which population samples were taken were: Devil's, Methodist, Widder Maker, Kickapoo, Medicine Creek, Water, Wildcat Creek, Red Rock and Salyor Lake.

Taylor (1961) summarized one of the most widely accepted hypotheses concerning the geological evolution of the canyons as proposed by Norris (1951). Briefly the proposition was that four cycles of cutting occurred in conjunction with the periods of glacial advance and recession during the ice age. Rounded valleys appeared during the Kansan with the oldest canyons widened and deepened during the Illinoian. During the final Wisconsin cutting period, the boxheads were extended upstream.

The increased water flow during the inter-glacial recession periods was suggested as the cutting mechanism. It was also proposed that the canyons refilled between cuttings except where the topography was conducive to a fairly regular runoff. Re-excavation followed each filling. The agricultural procedures of more recent times have been implicated in the topographical alteration activities which have led to the re-excavation of some of the younger canyons. A crevice near Lookeba was observed by Norris (1951) to have enlarged due to this. Taylor (1961) stated that the erosion of the sediment from another old canyon, which was only a slight draw depression, is now known as the Activity Branch of the Water Canyon complex. This activity is known to have been specifically started by a heavy rainfall on May 31, 1932, following a cotton planting. Grokett Canyon has had a similar history. The more stable vegetation, including the sugar maple, has not yet become

established in these younger re-excavations.

Wichita Mountains. A composite of the formation of the Wichita Mountains can be made from Ham, Denison and Merritt (1962) and Vaughn (1899). This began with the sink formation of a Cambrian sea basin 550 to 600 million years ago. The only remnants of this event are the small outcrops of Meer's quartzite along Medicine Creek north of Mount Sheridan. Two separate intrusions then occurred, one forming a dark igneous rock and the other a pink granite. Faulting and folding following another sea sedimentation deposit were accompanied by uplifting. Since this time in the Pennsylvanian period the major effect has been erosional. Sedimentary deposits have been stripped away leaving the granite protrusions and the black gabbro outcrops prominent in the topography.

The draws, crevices and bottomlands formed by the uplifts have functioned as catch basins for eroded materials which have developed into flora-supporting soils. The sugar maple is found in the most protected of these soil pockets, in north facing draws and in bottomlands. Population samples were secured from: Mount Scott, Elk Mountain, Hollis Canyon, Mount Pinchot, Baker Peak, Panther Creek, Greenleaf Canyon, Boulder Camp and Halley's Canyon.

Vegetational Occupation

The natural range of the sugar maple today is confined to the temperate and subtropical North American continent. The limits of the distribution were reviewed by Martin and Harrell (1957). The northern extreme includes the continuous east to west occurrence of A. s. var. saccharum in the southern regions of several of the Eastern Canadian provinces. The presence of A. skutchii Rehder in Guatemala apparently represents the southern-most member of this hard maple complex.

Pax (1902) cited the reported presence of a European Tertiary Paleosaccharina. He only mentioned A. hispidum Schwerin, a cultivated variety of A. s. var. saccharum, as the living representative in that area today. No Asian kin, fossil or extant, was noted.

Chaney (1936) reviewed the proposed Tertiary circumpolar distribution of the pre-glacial deciduous element in North America. Asa Gray's (1859) recognition of a past interchange among members of the element in Eastern North America through a continuous range into eastern Asia was pointed out.

A symposium, sponsored by the Paleobotanical and Systematic sections of the Botanical Society of America (1947), provided a comprehensive review of the proposed mechanisms of dispersal involved in the distribution of this Tertiary circumpolar flora. T. Just, R. W. Chaney, G. L. Stebbins, W. H. Camp, S. A. Cain, H. L. Mason, E. L. Braun and H. M. Raup contributed, through this symposium, hypotheses to account for the southern migration of a north temperate flora as well as propositions suggesting subsequent redistributions. The relict flora hypothesis is one of the ideas further developed.

Braun (1950) posulated the emergence of a drying interior separating a continuous deciduous forest into an Eastern and Western faction by the end of the Tertiary. This forest could be derived either from the radiating spread of plants surviving glacial pressures in eastern refugia or from north advancing elements of a glacial pushed southern located temperate flora. The question is then posed whether the Rocky Mountain sugar maple (A. g. var. grandidentatum) either represents the selected remnant of a Tertiary east from west segregation of a continuous element arising as suggested above or the

northward migrants of a western arm of post-glacial plant invasion as discussed below.

Little (1939) proposed migration by combining the glacial pushing of northern plants southward, as suggested by Clements (1936), with the advance and retreat fluctuations of the North American floral community caused by reciprocating xeric and mesic climate changes as proposed by Sears (1932, 1933). Hall (1952) reviewed the theory concerning the northeastward expansion of a more xeric Southwestern U. S. flora which is similar to the mechanism proposed for the activity of a mesic element. If the Great Plains Province were already too dry to support a mesic flora when southern located temperate plants moved north and the area west of it moist enough, a north advancing eastern and western arm would be active. Eastern and Western species would then be separated from common southern ancestors rather than by a mesic to xeric climate shift elimination of the central part of a continuous east to west distribution.

Sears (1961) reinforced the proposition of a succession of advances and retreats of southern located temperate floral elements. He correlated this activity with alternating humid and dry climatic periods resulting from the readvance and retreat phenomena related to the irregular withdrawal of the Wisconsin ice sheet to the north.

These observations supported an expansion of Little's (1939) accounting for the presence of A. s. var. saccharum in the Caddo Canyons which he coupled with Palmer's (1934) observation of A. g. var. grandidentatum indicating a former invasion of the Wichitas by Rocky Mountain representatives. The relict flora hypothesis quoted from Sears (1932, 1933) and applied specifically to the Oklahoma plants,

placed the last humid period of plant invasions from east and west at about 4,000 B.C. Welbourne (1962) stated from personal communication with Ireland that fossil remnants indicated the existence of a mesic forest between the last extensive canyon cutting and the more recent vegetational stabilization in the Caddo Canyon area to be as long as 9,000 years ago. This comes close to a realistic approximation for the initial establishment of stabilized vegetation since it seemingly could not occur until after the disruptive effect of the canyon cutting suggested by Norris (1951).

The mechanism, as proposed by Little (1939), effected the elimination of all of the plants of the central area by an intense xeric condition. This led to a wide gap between the eastern and western aggregations. Subsequently, in the wake of the return of a slightly more humid condition, the separated mesic eastern and western factions approached each other. The elimination of all but relict plant groups in the sheltered microhabitats of the two Oklahoma locations followed due to a return to a more xeric condition. Little's conclusion was: "These maples of eastern and western forests thus are separated by only 50 miles and almost meet across the grassland of Oklahoma."

Hopkins' rebuttal (1943) is supported if the plants in both central Oklahoma locations were separated from a continuous eastern distribution and each other by a single xeric event. Since the Wichita environments tend to be drier, the plants eventually selected there would then be ". . . only ecological (or genetic) variants of the eastern sugar maple."

Little (1939) pointed out herbaceous representatives of Eastern

species which appear to be at or close to their western range in the canyons. He also mentioned several Southwestern plants at or near their northeastern range. Rice (1960) added to the list of Eastern species and included a group which is described as having a disjunct distribution similar to the sugar maple. Little observed that there are Eastern herbs found in the Wichitas which are not seen in the canyons. The final piece to this complex picture is that in both the Wichitas and Caddo Canyons there are no other distinctively Eastern or Western woody species associated with the maple as disjunct.

Seed transportation to the central Oklahoma sites by aeolian or alluvial mechanisms is a remote possibility. This might have occurred rather regularly and when a favorable microclimate and soil structure finally developed, germination, ecesis and plant establishment took place.

Biodynamics Survey

Ecology

Pedology. In Eastern United States the presence of sugar maple is sometimes associated with limestone derived soils. Some populations encountered in West Virginia and Maryland seemed to be consistently related to limestone outcroppings. The plant is also found on a variety of other soil types throughout the East. Rice (1960 and 1962) verified the well known sand stone derived nature of the Caddo Canyon bottoms. Buck (1964) found the Wichita plants associated with a rough stony land type derived from Quanah and Lugert granites. The habitat soils of the Western United States where the sugar maple was found, were also similarly generated from igneous or sedimentary parent materials.

The chemical processes contributing to pedogenesis in these various habitats were extremely variable from one location to another. Texture and combination of particles, as suggested by Fralish (1968), along with climatic and other ecologic conditions seem then to be of primary importance to plant success with parent material and chemical composition somewhat secondary.

Climatology. The precipitation/evaporation ratio which favors the development of mesic habitats was an essential condition. Precipitation in Oklahoma was in an inverse relationship to elevation. The Yearbook of Agriculture, "Climate and Man" (1941, p. 1073), reported an annual 44-46 inches in the southeast to 18 inches in the northwest. Shirley (1937) approximately concurred giving a decline from about 40 inches in the low lying southeast to some 30 inches in the central Wichita and Canyon areas with about 20 inches reached in the western high plains. These figures are based on gross weather bureau statistics which were unreliable for specific, isolated areas. Evaporation activity was observed in a general manner by noting the distribution of mesic and arid sites proceeding respectively from east to west.

The accurate, comparative study made by Rice (1960, 1962) of microclimates of sugar maple stands in eastern and western Oklahoma produced relatively the same results for both research sites. The Caddo Canyons and a farm in Muskogee County were the study areas. Air movement, soil temperature, and daily minimum air temperatures were consistently lower in Devil's Canyon than in the eastern stand after about the middle of June each summer. There was, overall, a striking similarity between the mesic microclimates of the two environments. Studies of this type have not been made in the Wichitas or Rocky

Mountains but one would expect comparably similar results with a shift toward more xeric conditions.

Miscellaneous. Other ecological aspects have only been cursorily observed. Shade tolerance contributes to successful ecesis beneath the parent canopy. Invader activity has been noticed from the lower slopes of a mesic mountain indentation in northern Utah into the encompassed sage brush flat. Westman (1968) reported a similar phenomenon into a fir forest in Itasca Park, Minnesota. Nixon (1967) concluded from exclosure studies in the Wasatch Mountains that the Rocky Mountain sugar maple was increasing at the expense of the other woody dominant, Gambel oak.

Limited age establishment with bore cores from the four general research areas seemed to indicate trees of the same dbh to be older in the more xeric western locations. Other than that included in the studies mentioned above and from numerous eastern investigations, no phytosociological sampling or other ecological analyses have been attempted.

Physiology

Growth. Seed germination was accomplished for three of the general study areas, Wichita Mountains, Caddo Canyons and eastern Oklahoma. The fruits gathered in Utah were a full year older and there were fewer of them. None of these germinated. A cold treatment with stratification in moist sand was most effective of several methods tried. The seedlings, with long cotyledons, elongated hypocotyls but very small epicotyls, emerged after 60 days stratification at ca. 8° C. They were still in good transplant condition 5 months later.

Risser (personal communication) conducted respiration and growth experiments. The sample was limited but indicated that further research with the Caddo and Wichita plants may yield significant differences.

Kriebel (1957) reported general variation in growth form to be genetically controlled but also subject to phenotypic plastic modification. The bushy habit of A. floridanum (Chapm.) Pax was investigated in these transplant studies at the Ohio Agricultural Research Development Center, Wooster, Ohio. A lack of apical dominance promoted forking in the plants which resulted in multiple main stems. A. s. var. saccharum and A. nigrum Michx. were usually represented by single stemmed individuals indicative of strong apical dominance. Frost and temperature conditions abnormally different from the native habitat produced intensified forking which led to bushy individuals.

The tendency toward the shrubby form increases from plants of the Northeastern United States and reaches a maximum in the A. floridanum representatives in the Southeast and finally persists in the A. grandidentatum complex of the Rocky Mountains. The characteristic pattern described above indicates weaker apical dominance and therefore more bushiness associated with the more severe environments. Some of the factors of such habitats which would lead to damage, removal or inactivation of a main apical meristem would include; frost, freezing or protracted cold, extremely hot and dry conditions and mechanical damage from activities such as browse, storm, etc. The plants of the Caddo Canyons are mostly single-trunked while those of the Wichitas tend toward the multi-stemmed southeastern and western relatives.

Physiochemistry. Peattie (1950) declared "... plant physiologists tell us that the very glory of the maple's autumn leaves is due

in part to the sweetness of its sap, no less than to the acidity of New England soils . . ." Tolerable soil pH seems also to vary since, as previously mentioned, specific association with alkaline types is encountered.

The commercial utilization of the sap of the eastern plants has stimulated rather extensive and careful chemical analyses for that group. Harris (1934) processed a number of samples of leaf extractions from A. g. var. grandidentatum for freezing point depression, conductivity and chloride and sulphate content. Bailey (1949) reported distillation of syrup, comparable to eastern products, from the sap of A. g. var. grandidentatum. Older residents of the Caddo Canyon area reported a similar experience. Particular climatic fluctuations associated with the spring sap rise in some of the more northeasterly states seems necessary to make procuring and processing of these chemically similar fluids profitable. A synthesis of these data with information derived from more recent chromatographic and analytical techniques, could add significantly to the picture.

A very general survey to determine fall coloration tendencies from east to west was conducted in 1967. The results indicated a trend from a stronger representation of yellows in the east to more predominant reds in the west. The reports received on A. nigrum and A. floridaeum were for 100% yellow displays. Much is not known about the variation in fall color. Single individuals will not only vary throughout but will vary from year to year. The survey involved numerous respondees and can only be regarded as indicating another aspect of significant difference which requires a more thorough and scientific treatment.

Mr. William Garee (personal communication) grew stock in his nursery at Noble, Cleveland County, Oklahoma from seedlings of eastern and Caddo Canyon *A. s.* var. saccharum. A row of each, adjacent to each other, yielded a striking illustration of differing drought resistance characteristics. The leaves of the eastern trees turned brown before the Caddo maples would loose their green color, whether from water deficit or the approach of winter.

Reproduction. Christensen and Nixon (1964) pointed out the probability of a strong vegetative reproductive process. Stems from layering and root shoots were observed as more effectively persistent than seedling originated individuals. Production of viable seed seems to be erratic. There are "good" and "bad" years from two points of view. Viable embryo production may fluctuate as indicated by Christensen and Nixon (1964) or flowering be abbeyed. Many viable seeds were produced in the Wichita and Caddo Canyon stands in the summer of 1967. Seedling germination in both places was profuse in the spring. There was, however, in that same spring (1968), a great reduction (almost nil) in flowering and fruiting in both areas.

The twig layering and root shooting observed for the western plants is also present in the other three general study areas. These phenomena seem to occur móre frequently among the plants in the more severe environments. The diffuse root system of the western sugar maple as described by Christensen (1962) is probably characteristic of the other hard maples thus enhancing the tendency for adventitious root shooting in all of them. Observations of shooting from roots exposed by erosion have been made in the Caddo Canyons and are reported by Barclay (personal communication) for eastern species.

Percentages of seedling ecesis seem to be lower in the more demanding sites. In the Wichitas there was a pronounced lack of intermediate sized individuals. The only profuse seedling persistence noted was in Hollis Canyon which is one of the more protected bottomlands. These appeared to be approximately 3 or 4 years old. The new seedlings from the 1968 spring germination were also present. A large gap occurs and there were few individuals intermediate between the smallest saplings and the seedlings. The absence was even more pronounced in the more exposed slope populations. There seem to be more intermediate representatives in the Caddo Canyon groups and there is a continuous distribution from smallest to large in many of the eastern forests.

Cytology

A basic $n = 13$ is reported for all maples. Sugar maples fall into the consistently diploid species of the group of which there are, with reported numbers, 27 according to Santamour (1965) or 24 as suggested by Wright (1957). Wright summarized 5 ploidy conditions as diploid or triploid (A. platanoides L. $2n = 26$ or 39); tetraploid (A. caprinifolium Sieb. and Zucc., A. pseudoplatanus L., and A. saccharinum L. $2n = 52$); or hexaploid and octoploid (A. rubrum L. $2n = 78, 104$).

Of the sugar maples, A. s. var. saccharum has been officially reported by W. Taylor (1920) and A. nigrum by Heiser (1949). Kriebel (1957) adds A. floridanum to the diploid list. The limited cytological work done as a part of this research has confirmed A. g. var. grandidentatum and the plants of both central Oklahoma areas to be $2n = 26$.

As suggested by Santamour (1965), meiotic activity is difficult to observe since pollen formation time apparently is variable. Flower

buds sent by Christensen from spring 1968 seemed to contain only reduced microspores and pollen grains. The chromosome count for A. g. var. grandidentatum is from sterile anther tissue. Those for the Caddo Canyons and Wichita Mountains were observed in embryonic epicotyl cells. No satisfactory mitotic figures were encountered in root tip preparations of the central Oklahoma material.

As experienced by other investigators, the size of the chromosomes (2 to 5 microns long) make construction of karyograms difficult and so they were not attempted. Taylor (1920) published a number of these in which the chromosomes appeared in forms of typical rod shapes or contracted spheres. An unpublished karyogram of A. nigrum by Anderson (personal communication), drawn with camera lucida at 3200X, showed knob-like satellites associated, apparently as organizers, with each one of the pair involved in nucleolus formation during prophase.

Relative Distribution

The sugar maples of North America today fall into two large groups. The Great Plains extending from Texas northward into Canada form an east from west separator.

Desmarais (1952) established the ranges of the species of the Eastern sugar maple complex. A. s. var. saccharum reached its greatest density in Northeastern United States and Canada. The northernmost extension of range occurred in the southern portions of the lower Canadian provinces from the southeastern tip of Manitoba to Nova Scotia. It was found throughout Minnesota and along the eastern edges of Iowa, Kansas, Oklahoma and Texas. The irregular southern extension of its range was through Virginia, North Carolina, Tennessee, Arkansas, and Texas. The western occurrences become more confined and local as

suitable habitats become fewer upon approaching the central grasslands.

A. nigrum is contained fairly well within the distribution of A. s. var. saccharum. It begins to occur a little west of the easternmost A. s. var. saccharum locations. It does not range as far north or south but Aikman and Smelser (1938) indicated that it bulges beyond the western range of A. s. var. saccharum approximately 120 miles into central Iowa. A. nigrum has a density distribution inverse to that of A. s. var. saccharum with its most profuse occurrence in the western locations. It seems to be more xerically adapted and is suggested by Anderson and Hubricht (1938) as possibly representing an introgressive hybrid of A. s. var. saccharum and A. s. var. rugelii Rehd.

A. floridanum has a northern range which slightly overlaps that of the southern extension of A. s. var. saccharum. It is found as far south as central Florida and west in eastern Texas.

A. s. var. rugelii, A. s. var. schneckii Rehd. and A. leucoderme Small occur approximately along the demarcation of the overlap mentioned. A. s. var. rugelii is rare and local in its extreme leaf shape and extends north of the overlap to Canada. It is generally agreed that there is an introgressive genetic continuity among all of these.

The Western complex lies to the south, west, and northwest of the Oklahoma disjuncts. The Guatemalan A. skutchii is probably the most southern. Small, isolated groups of A. mexicanum Gray range through central Mexico northward. Along the northern Mexican border A. g. brachypterum Woot. and Standl. is found to the west in Arizona and A. g. var. grandidentatum eastward in New Mexico and Texas. A. g. var. sinuosum occurs farther east of these as disjunct in central Texas. It is separated by several hundred miles from the local and

spotty mixtures of A. s. var. saccharum and A. floridanum of the eastern timbers near the Louisiana border. Similarly local populations of A. g. var. grandidentatum proceed northward through Arizona and New Mexico to the southwestern tip of Colorado and southern Utah.

The canyons of the Wasatch Mountains in northern Utah harbor the most extensive western populations of A. g. var. grandidentatum at 5,000 to 6,000 ft. elevations. As the distribution extends into the mountains of Idaho, one west central location in Wyoming and at scattered stations in Montana, the aggregations again become local and more isolated from each other.

Taxonomic Characteristics

A brief treatment of selected, general taxonomic characters is given below. These were synthesized from a number of descriptive sources and field and herbarium observations.

Leaves

These organs have been heavily relied upon to separate the species of hard maple. The numerical analysis of this research was based on them. Although variable in form and represented by a variety of intergrading intermediates, the characteristic differences are neither so subtle nor so uncorrelated as is the case with some of the other indicators mentioned below.

Leaf dimorphism does occur in addition to intergrading variability and is often especially noticeable on fertile as opposed to sterile branches. The descriptions below pertain to the leaf types most commonly encountered on sterile branches.

Base. The A. saccharum - nigrum complex most consistently

has a cordate base which is also found as subcordate to rounded truncate. A. floridanum rarely exceeds subcordate and frequently is quite truncate. A. g. var. grandidentatum and A. g. var. brachypterum are mostly a broad cordate form with A. g. var. sinuosum almost uniformly truncate. The Caddo plants are mostly subcordate while those in the Wichitas are a rounded truncate with regular intermediates approaching subcordate and even close to cordate.

Lobes. All species are found in 3 lobed forms but the most predominant occurrence is as 5 lobed. Intermediate projections, or lobules, are present in all species. These range from undulations or bumps to well defined, pointed emergences. The highest numbers occur in the A. saccharum complex with the tips mostly acuminate as is the case also with the tips of the major lobes. Major and minor lobe tips in all other species are acute unless the lobules have been reduced to undulations as is the case commonly with A. nigrum, A. g. var. brachypterum and A. g. var. sinuosum. The type form of A. g. var. sinuosum is divided into 3 ovate-triangular lobes whose margins are practically entire. A similar condition is reported for A. g. var. brachypterum.

Sinuses are mostly considered to be open. The exceptions here occur in some of the A. saccharum complex where narrower and deeper ones are found. This is especially characteristic of A. s. var. schneckii. The sinuses of the Caddo plants frequently are deeper and more closed than those of the Wichita specimens. The sides of the central lobe vary from uniformly parallel in A. floridanum and A. s. var. saccharum to strongly divergent at the lower lobule tips in A. s. var. schneckii and A. g. var. grandidentatum. The central Oklahoma plants consistently tend toward the divergent tips. This condition, of course, is not

observed in the entire lobed vars. of A. grandidentatum.

Upper Surfaces. Upper surfaces are glabrous and color range is from dark green to yellowish-greens. The darker color and an opaque appearance are more often associated with the eastern trees and those located in the more protected, mesic western sites. The lustrous surface and lighter color occurs mostly in the more open and severe habitats. The more xeric A. nigrum is a consistent exception to this and there are regular deviations among the other species.

Lower Surfaces. Glaucescence is most pronounced in eastern species with its most consistent correlation being to A. floridanum. A thin layer is often observed in the others leading frequently to descriptions of a "pale" appearance.

Surface color variation from dark green to light yellowish-green is effected by the amount of pubescence and glaucescence. The glaucous deposit is often difficult to detect as such even in non-dried materials. Pubescence is variable but has some specific correlations. A. s. var. saccharum is generally glabrous but hair occurs on the main veins and in some local situations a longer, silky, appressed covering is found in varying densities. A. nigrum is consistently characterized by a short, erect pubescence which is generally very dense on the veins and the surface. The close introgressive nigrum-saccharum relationship leads to numerous intermediates. A. floridanum is also rather uniformly pubescent. An unusual continuum exists with the hairs of A. floridanum in the Southeastern United States having erect, nigrum-like but shorter appearance which gradually gives way to a longer appressed saccharum-like type with a sinuous rather than silky quality. A. s. var. schneckii is described as

densely covered, including the petiole, with long, silky, appressed hairs.

In the far west, A. g. var. grandidentatum has a relatively dense, nigrum-like covering. The hairs are erect but, unlike A. nigrum, seem to curl with a sinuous hook at the tip. The two varieties of A. g. var. grandidentatum are interesting since A. g. var. sinuosum is relatively glabrous at maturity while A. g. var. brachypterum is densely pubescent. The pubescence density in A. g. var. grandidentatum is noticed to diminish south of Utah. More observation from the Arizona, New Mexico, and Texas sites is needed to firmly establish this.

Domatia in the axils of the main veins is almost universally present. Significant glabrescence is only noted with any consistency in populations of A. floridanum from parts of Crowley's Ridge in Arkansas and Missouri.

The Caddo and Wichita plants were sparingly pubescent, frequently on the veins and occasionally with small patches of surface hair. The surface hair seemed to be more erect and shorter in the mountain plants with the position intermediately appressed in both. There was a tendency toward less denseness in the canyon plants.

Petioles. The eastern plants have slender petioles while A. s. var. schneckii has long hairs as mentioned earlier. A. floridanum has a short tomentum which is often lost as the leaf matures. The petioles of the western plants tend to be stouter and also essentially glabrous with the exception of the rather uniformly pubescent A. g. var. brachypterum. The central Oklahoma plants were essentially glabrous also with the petioles of those from the mountains tending toward the stouter

characteristic and those from the canyons having a strong slender representation.

General. The palmately veined leaves demonstrate a total width to length ratio which is close to unity (slightly wider than long). Higher ratios are found in some local eastern situations and with A. g. var. sinuosum.

Flowers

Calyx. The 5 yellowish-green sepals are connate with obtuse tips.

Corolla. The corolla is absent.

Stamens. 7 or 8 stamens with glabrous filaments are inserted on the inner margin of a staminal disk. Sterile stamens are present in pistillate flowers but the filaments do not elongate.

Pistil. The pistil is pale green with 2 long, exserted stigmas. 2 ovules, one of which develops into a seed, are present in each compartment of the 2 loculed superior ovary.

Pedicel. The long pedicels are slender and hairy. They elongate in early spring as the leaves expand. The inflorescence is a nearly sessile corymb.

General. The flowers may occur as staminate or pistillate in the same or different clusters on the same or different trees.

Fruit

The fruit matures into 2 separable, one seeded keys. Each carpel of the samara bears a wing. There is great variation in size and color even within species. A tendency toward divergent wings is characteristic of all species except A. floridanum. The calyx has

been observed to persist only on two groups, A. g. var. grandidentatum and the Wichita Mountain plants.

Miscellaneous

Bark. Trunk bark is variable in texture and color. It is generally smooth in most younger trees with longitudinal furrowing beginning earlier in the northern and western species. The southern plants (excepting A. g. var. grandidentatum) have a tendency toward limited furrowing and separating of the old bark and seldom develop the prominent plate-like scales of the northern trees. Lichens, fungi and general exposure to the factors of the habitat influence this characteristic to a degree which makes correlation with species unreliable. Twig characteristics are also variable.

Winter Buds. The differences here are subtle and minute. A careful contrast study, well correlated with plant aggregations which are characteristically strongly pure for a particular species, would likely yield some good separation differences.

Growth Habit. The huge growth habit of the single-trunked northern A. s. var. saccharum and A. nigrum was contrasted earlier to the smaller, shrubby habit of those species of the more severe or xeric sites.

CHAPTER III

A NUMERICAL ANALYSIS

As previously illustrated, the characteristics used to separate the sugar maples are often subtle and intergrading. The objectivity of a numerical analysis was applied to leaf characteristics to help clarify the relationship of the central Oklahoma plants. A complete numerical taxonomic treatment would involve the use of many diverse characteristics.

Method

This research was early directed toward the use of Anderson and Hubricht's (1938) average leaf technique. The same lengths and angles were used (Fig. 1). These measurements were taken for population samples from the Wichita Mountains, Caddo Canyons, Southwestern United States and Utah. Approximately 4,000 leaves were included. Also used were a number of Eastern populations containing approximately 3,000 leaves and selected from the pooled mass collections of Anderson and Hubricht (1938), Dansereau and LaFond (1941), Dansereau and Desmarais (1947) and Desmarais (1952). These populations were loaned by Dr. Yves Desmarais. The sampling procedure for the Oklahoma and western material was the same one used for the eastern collections. Populations were examined for mature leaves which were selected from

older sterile branches at about shoulder height in semi-shade.

In addition to the measurements, average pubescence and lower surface color values were determined by scoring after the system of Desmarais (1952). Pubescent (P) was evaluated at 0, intermediate (I) and 1 and glabrous (G) at 2. Green undersurface (V) was 0, yellow-green (Y) at 1 and glaucous (G), 2.

The analysis is a modification of the method of Russell (1964). The 24 characters used (Table I, A - X) were angular measurements, linear ratios, pubescence scores, undersurface color score, number of lobules, sinus relationships and main lobe divergence. These characters were indexed for the two large reference groups with a "0" assigned to the eastern end and a "1" to the western. The 50 populations included for the West were collection samples from the northern Utah canyons of the Wasatch Mountains. The 80 populations of the Eastern reference were mostly made up of those which Desmarais (1952) had coded as pure A. s. var. saccharum, A. floridanum and A. s. var. schnechii. One large group consisted of populations from the states immediately adjacent to Oklahoma.

Large group relationships were being studied, so the units used were the averages of the characteristics for a given population. Characters were retained and used if their indexing represented at least 51% in each group of the index value assigned that group. The overlap percentages (Table I) were equalized in each group by appropriate setting of the indexing ranges. The Wichita Mountain and Caddo Canyon populations were then indexed by these range criteria.

A definite and wide separation would have been made between the four groups if actual linear dimensions had been used. This would

be due to size variation resulting from habitat selection pressures. For this reason, the average linear dimensions were converted to ratios (Table I). In addition to these, ratios were constructed to indicate depth of sinuses and divergence of the main lobe. Average lobule numbers, angle measurements and the pubescence and lower surface color values were indexed directly.

As in Russell's (1964) method the index scores for each characteristic were then added to give the total specific index value to each population. Each population was then tallied within the group to which it belonged over the total specific index range (Table II). The modes and extremes of each group tally were used to plot a curve of each of the four groups across a common index range scale (Fig. 2).

The index distribution curves were each compared with the other as shown by example (Fig. 2) for the Caddo Canyon and western groups and as explained below. The sum of the four percentage relationships for each pair of curves becomes the total index difference of Russell (Table III).

- 1.* Percentage of the portion of the total specific index range (common to both groups) covered from the mode of one group to the extreme value of the other.
2. Percentage of their common total specific index range not covered by the curve of the reference group to which the other group is being compared.
3. Percentage of their common total specific index range not occupied by either of the two groups being

*See example (Fig. 2) and final results of all curve comparisons (Table III).

compared (this will be negative if the pairs overlap).

4. Percentage of their common total specific index range between the modes of the two groups.

A different total difference index value is obtained when the second curve of the pair is used as the reference. This results from a change in percentages 1 and 2 due to the differing distance of the extreme of each curve of the pair from the reference mode.

Results

The total difference indices were entered into a double matrix (Table IV). These were then averaged and placed in a single matrix (Table V). The lower the total difference value, the closer is the total relationship of the leaf characteristics of the two groups. A spatial relationship was shown by polar graphing (Fig. 3) of the double matrix (Table IV). The geometric model (Fig. 4) illustrates the single matrix relationships (Table V).

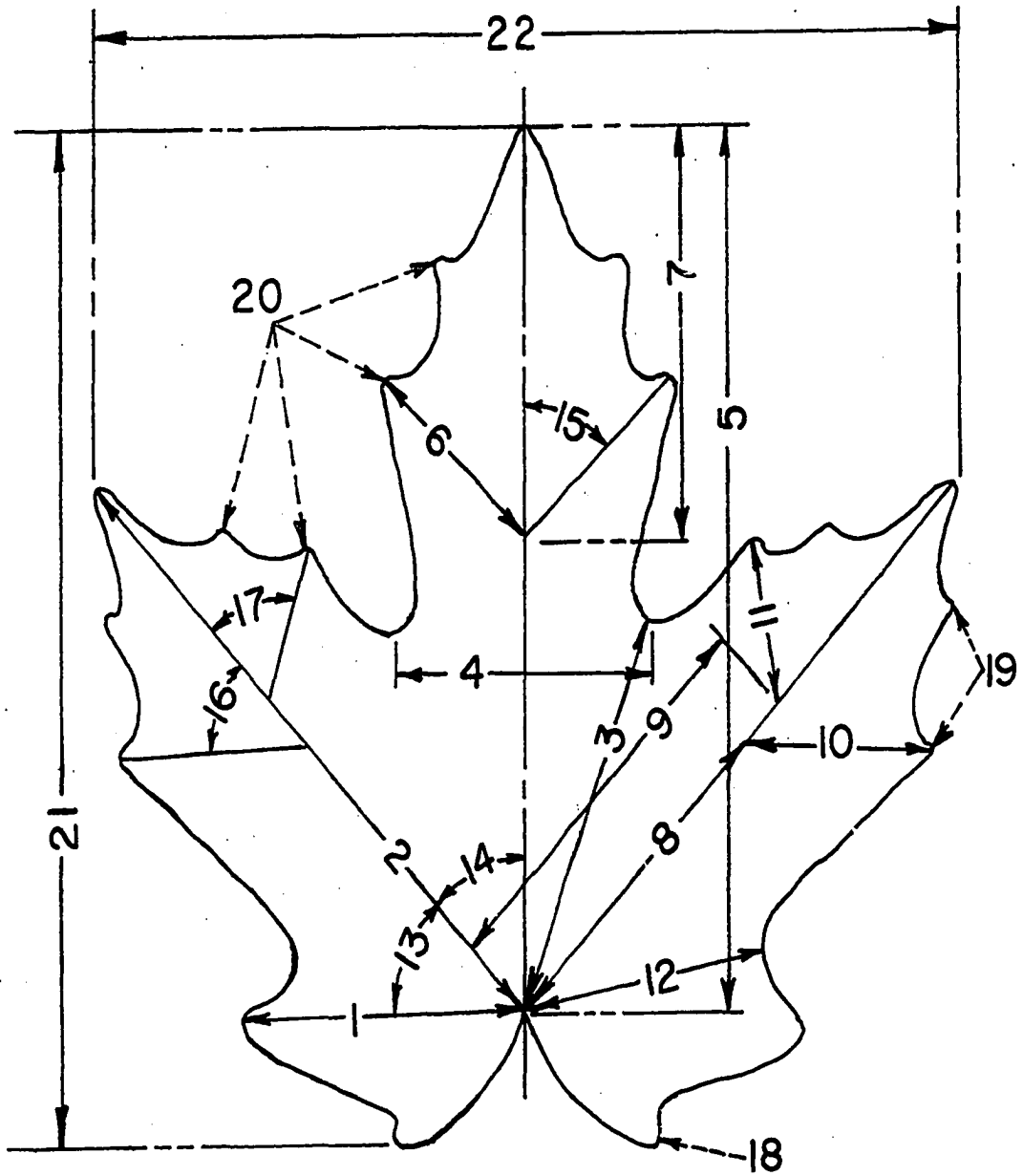
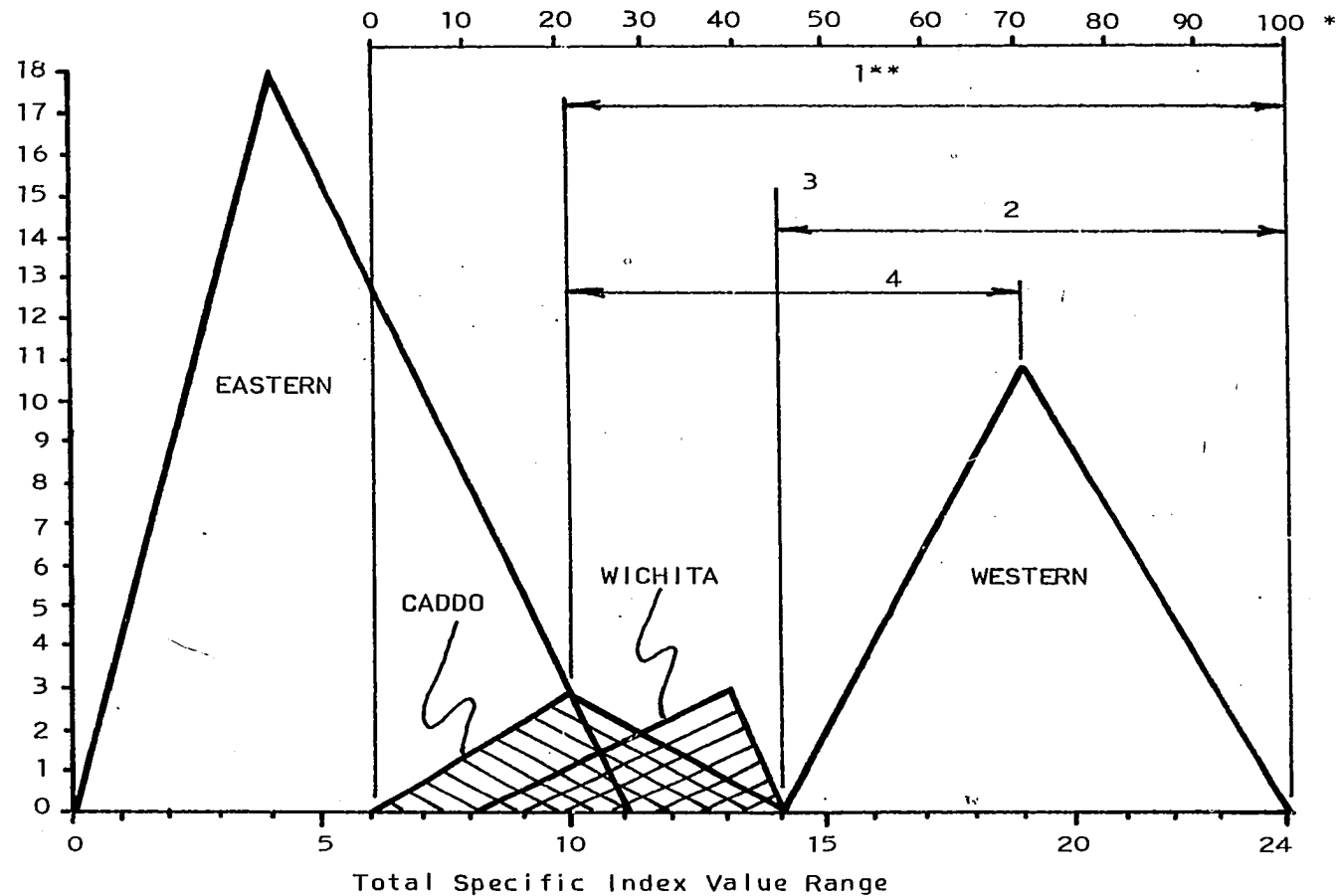
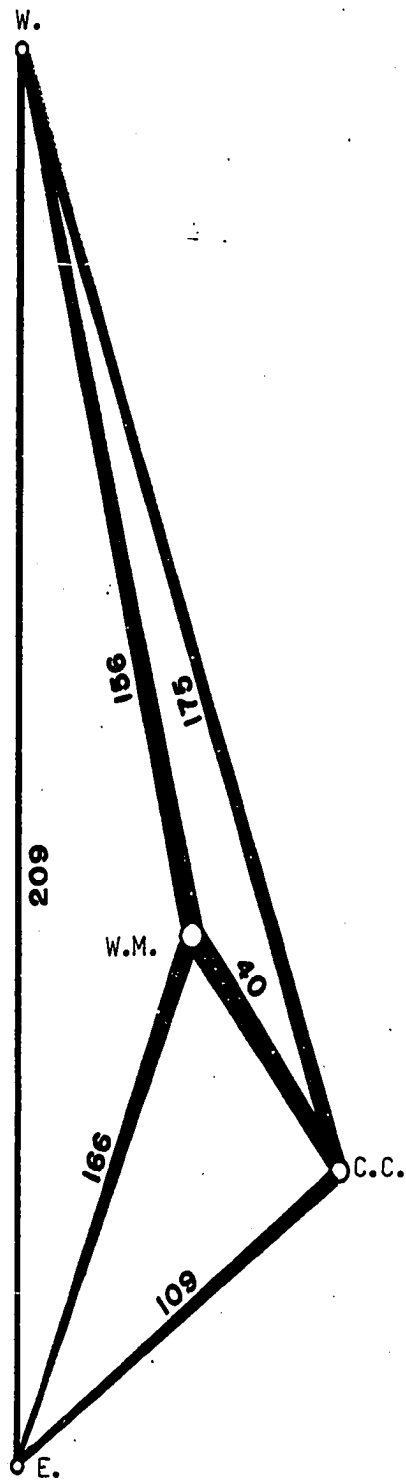


Fig. 1 Key to average leaf dimensions



- *Example - Percentage divided portion of the total specific index range occupied in this example by the Caddo Canyon and western group.
- **Example - Percentage relationships (1,2,3, and 4) shown in this example for the Caddo Canyons and western group. Determined for each pair of curves (see text p. 34 and Table III, p. 43).

Fig. 2 Group Modal Curves



E.- East
W.- West
C.C.- Caddo Canyons
W.M.- Wichita Mountains

Fig. 4 Geometric model of single matrix (Table V)

TABLE I

INDEX RANGES OF LEAF CHARACTERS

Character		"0" Eastern	Overlap %	"1" Western
A.	13* Angle	0° to 54.3°	14	54.4° to 80.0°
B.	14 Angle	0° " 46.7°	14	46.8° " 70.0°
C.	15 Angle	0° " 34.3°	21	34.4° " 40.0°
D.	16 Angle	0° " 39.7°	15	39.8° " 45.0°
E.	17 Angle	0° " 32.7°	3	32.8° " 40.0°
F.	18 Lobules from petiole to lower lobe tip	0 " .7	18	.8 " 2.5
G.	19 Lobules between lower lobe tip and lateral lobe tip	0 " 1.8	12	1.9 " 4.5
H.	20 Lobules between lateral lobe tip and central lobe tip	0 " 2.9	8	3.0 " 5.0
I.	Petiole pubescence	1.92 " 2.00	40	0 " 1.91
J.	Main vein pubescence	.41 " 2.00	10	0 " .40
K.	Undersurface pubescence	.76 " 2.00	16	0 " .75
L.	Type of pubescence	.05 " 2.00	0	0 " .04
M.	Color of undersurface	.16 " 2.00	15	0 " .15
N.	5/2 Main vein to lateral vein	1.10 " 1.20	25	0 " 1.09
O.	5/1 Main vein to lower vein	0 " 2.19	33	2.20 " 2.70
P.	5/7 Main vein to lower main vein	0 " 1.85	45	1.86 " 2.30
Q.	7/6 Upper main lobe	1.28 " 1.80	23	0 " 1.27
R.	2-9/11 Upper, upper lateral lobe	1.47 " 2.35	20	0 " 1.46
S.	2-8/10 Upper, lower lateral lobe	1.40 " 2.00	22	0 " 1.39
T.	22/21 Total width to total length	0 " 1.16	15	1.17 " 1.55
U.	3/12 Upper sinus to lower sinus	1.45 " 1.70	42	0 " 1.44
V.	5-3/2-3 Depth of upper sinus	1.22 " 2.30	23	0 " 1.21
W.	2-12/1-12 Depth of lower sinus	0 " 5.00	43	5.01 " 8.30
X.	sin 15-4/2** Divergence of main lobe	-2.70 " 2.50	42	2.51 " 8.00

* Numbers in this column are from Fig. 1.

Dashes (-) in character column above mean "minus."

Slashes (/) in character column above mean "divided by."

** Not from Fig. 1, indicates half of the value of 4 from Fig. 1.

TABLE II

TALLY OF TOTAL SPECIFIC INDICES

Total Specific Index Value	Caddo	Wichita	Western	Eastern
0				
1				1
2				1111111
3				11111111
4				1111111111111111
5				11111111111111
6				1111111111
7	1			111111111
8	1			1111111
9	111	1		11
10	1	11		1
11	111	11		
12	11	11		
13	1	111		
14				
15			1	
16			111	
17			11111	
18			111111111	
19			11111111111	
20			111111111	
21			11111111	
22			111	
23			1	
24				

1 - Each designation represents a population within the group with the Total Specific Index indicated.

TABLE III
TOTAL DIFFERENCE INDICES

REFERENCE GROUP	1	PERCENTAGE*			COMPARED GROUP	TOTAL DIFFERENCE INDEX
		2	3	4		
E.	84	45	13	63	W.	205
W.	79	58	13	63	E.	213
C.C.*	79	55	0	50	W.	184
W.	71	45	0	50	C.C.	166
W.M.	69	62	0	38	W.	169
W.	69	38	0	38	W.M.	145
C.C.	71	42	-37	43	E.	119
E.	72	21	-37	43	C.C.	99
W.M.	93	58	-21	65	E.	195
E.	72	21	-21	65	W.M.	137
C.C.	42	0	-76	39	W.M.	5
W.M.	87	24	-76	39	C.C.	74

E. - Eastern
W. - Western
W.M. - Wichita Mountains
C.C. - Caddo Canyons

*See example (Fig. 2) and explanation in text (p. 29).

TABLE IV
DOUBLE MATRIX
(Read horizontally only)

	E.	W.	C.C.	W.M.
E.	X	205	99	137
W.	213	X	166	145
C.C.	119	184	X	5
W.M.	195	169	74	X

E. - Eastern
W. - Western
W.M. - Wichita Mountains
C.C. - Caddo Canyons

Matrix values are total difference indices (Table III). The lower the value for any two indicated groups, the closer their total relationship. See Table V for single matrix.

TABLE V
SINGLE MATRIX

	E.	W.	C.C.	W.M.
E.	X			
W.	209	X		
C.C.	109	175	X	
W.M.	166	156	40	X

E. - Eastern
W. - Western
W.M. - Wichita Mountains
C.C. - Caddo Canyons

Matrix values are averages from double matrix (Table IV).

CHAPTER IV

DISCUSSION

A numerical analysis, although based on the characteristics of the leaf only, indicated a close relationship between two isolated groups of sugar maple in central Oklahoma. When both groups were considered together they were shown to relate more closely to an Eastern reference, which included representative samples of major species, than to a Western reference from northern Utah. The Caddo Canyon group was shown to be shifted more toward the main Eastern reference while the Wichita Mountain aggregations tended toward the western end of the range. These relationships were demonstrated by a set of modal curves and a total difference index derived from them.

The modal curves (Fig. 2) emerged from total specific indices for the various population samples when they were tallied (Table II) according to the four major groups involved over their total specific index range. The total specific index for each population was the summation of index values assigned to the selected, measured characters. An "0" was assigned for those which predominated the eastern end of an indexing range and a "1" to those which were western.

The total difference indices (Table III), derived from relationships of the curves to each other (Fig. 2), reinforced the

conclusion. These values when placed in matrices (Tables IV and V) revealed the closest relationship (lowest difference index) to be between the Caddo Canyon and Wichita Mountain groups. Their stronger correlation to the Eastern reference was indicated by the intermediate difference index values with a tendency for the Caddo group to be shifted east and the Wichita group farther west. The large value reflecting the relationship of the Eastern to the Western reference, indicates them to be least similar.

A check was also made to determine if different or the same characters were involved within each of the Oklahoma groups in establishing this intermediate position. Many of the influencing items were shared by both. This would indicate a common ancestor. It was also determined that of these shared items, approximately 12 were common to or also shared with that part of the Eastern group which was from eastern Oklahoma and the states proximate to that border. There were 8 items shared with the main Western reference and only 7 with the one population representing the Uvalde Sugar Maple of the Edwards Plateau in Texas. This then indicates it as likely that the central Oklahoma groups were separated from the segment most directly east of them and isolated to mesic microhabitats when the eastern deciduous forests were retreating as the Great Plains became more xeric.

The localized West-southwestern groups present a puzzling picture. In addition to the Uvalde sample mentioned above, only 5 others, widely scattered, were available. Because of the small size of the sample, the total specific indices for these were not included in the analysis. They were used, however, to propose the existence of two separable western factions.

All but one of the groups of the more eastern of these two western factions have generally been referred to as the western A. g. var. grandidentatum. The grouping begins with A. g. var. sinuosum, the exception, which had a specific index value of 6 which placed it within the western end of the index range of the Eastern reference. Proceeding west from the protected canyons of the Edwards Plateau it joins a north-south axis of groups ranging through the mountains which begins in the Sierra del Carmens of Mexico and the Chisos of the Big Bend of Texas and proceeds northward through central and perhaps western New Mexico. It reaches a northern limit in southwestern Colorado at Mesa Verde. This suggests circumstances which either eliminated representatives from the high Rockies of Colorado or stopped a northward migration. Similarly a possibly xerically severed western connection or deterred expansion would account for the separation from the nearest western relatives in southern Utah. The components of this group range from the Eastern specific index value of 6 for the Uvalde group to barely Western value of 15.

Physiographically the aggregation mentioned above can be seen to be separated from an approximately parallel mountain chain farther west in which the more western representatives are associated. This more western group extends from Montana southward through its main concentration in the canyons of the Wasatch Mountains in northern Utah and then along a line south which follows the mountains approximately through Zion National Park in southern Utah. Finally it runs diagonally across Arizona from west to east starting in the mesic microhabitats in the vicinity of Grand Canyon. It possibly then extends into the western Sierra Madre Occidental of Mexico. These more western plants

make their closest approach to the other proposed western strain in the southeast corner of Arizona as A. g. var. brachypterum. One small population sample from Coronado National Memorial in this area had a specific index of 16 indicating an affinity to the eastern end of the main Western reference of A. g. var. grandidentatum.

The total difference index produced indicated a tendency for the Uvalde Sugar Maple to relate to the more western representatives of the Eastern A. floridanum. The total difference indices from the few population samples from southwest Texas and one from Colorado did follow a trend which was progressively more Western but they just reached the eastern index extreme of the Utah reference.

The populations processed from the West-southwest are too few to strongly suggest the combination of this group with the more eastern A. g. var. sinuosum. The total index value of the one sample from southeastern Arizona indicating a stronger identification with the more western plants, would reinforce such a proposal. Either the proposed northern mesic migration or the east-west xeric separation concept of plant distribution would account for a two armed Western phytogeographic pattern.

Sugar maple has an ability to persist in marginal moisture environments which has made it one of the good indicators of relict mesic microhabitats. These are useful in evaluating the distribution movements of past floras.

Of the other factors considered in this investigation, only a few offer enough significance to suggest reinforcement for one position or the other. Bushy habit is a characteristic more correlated with xeric or severe habitats than it is with east to west distribution and

so is not a reliable indicator. The fact that a number of Eastern plants disjunct, or at their western range, are found in both Oklahoma locations as opposed to relatively few Western examples, reinforces the argument for an Eastern predecessor. Characteristics of significant specificity, such as the persistence of the calyx on the fruit of Western plants, were few and difficult to evaluate.

CHAPTER V

CONCLUSIONS

Specific index ranges and total difference indices produced by a numerical analysis, were the primary factors used to examine the relationship of two isolated groups of sugar maple in central Oklahoma to Eastern and Western North American references. The average leaf characteristics used were reliable separators for large geographic groups in the section *Saccharina* of the *Aceraceae*.

The Caddo Canyon and Wichita Mountain groups are indicated as derived from a common ancestor associated with the segment of the Eastern reference occurring in eastern Oklahoma and adjacent states. Hopkins' designation of the plants from both areas as *Acer saccharum* Marsh. was indicated more valid than Little's specification of those from the Caddo Canyons as *Acer saccharum* Marsh. and those from the Wichita Mountains as *Acer grandidentatum* Nutt. The total difference index values were large enough to suggest that the central Oklahoma plants are varietally distinct from *A. s.* var. *saccharum*. The values also emphasized differences between the Caddo Canyon and Wichita Mountain groups.

The study also suggests the possibility of including the Bigtoothed Maples of Colorado, New Mexico and west Texas with *A. g.*

var. sinuosum of the Edwards Plateau Balcones Escarpment canyons.

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