

STUDIES IN THE QUERCUS UNDULATA COMPLEX. IV. THE CONTRIBUTION OF QUERCUS HAVARDII¹

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A B S T R A C T

Scrub oak populations in the semidesert area of northeastern Arizona and southeastern Utah are ordinarily identified in regional manuals as *Quercus undulata*. They are very similar, both morphologically and ecologically, to *Q. havardii* of the Staked Plain of the Texas Panhandle and southeastern New Mexico. They differ, however, in a number of inconspicuous characters. Population sample analyses indicate that most of these differences are suggestive of *Q. gambelii*, and the deviant populations are thus interpreted as having been derived from ancestral *Q. havardii* through introgression by *Q. gambelii*. Two differences are not in accord with this interpretation; these are regarded as possible cases of transgressive segregation. Considering the evolution of these hybridized populations, it is speculated that the ancestral *Q. havardii* occurred to the south and west of the present range of this species during the Kansan period of the Pleistocene. During subsequent northward dispersal, it became split in two. The eastern portion ultimately came to occupy the present range of the species in the Staked Plain; the western portion—lying to the west of a north-south mountain barrier in central New Mexico—became introgressed by *Q. gambelii* (and locally by *Q. turbinella*), resulting in the present populations of Arizona and Utah.

IN THE FIRST PAPER in this series (Tucker, 1961) the *Quercus undulata* complex was discussed in general terms as being putatively of hybrid origin between *Q. gambelii* and six other species. *Quercus havardii* Rydb. was indicated as one contributor to the complex, notably in the semidesert country of northeastern Arizona and southeastern Utah. The scrub oak populations of this region are very similar to *Q. havardii* both morphologically and ecologically, but all populations studied by the writer differ in a number of characters from typical *Q. havardii*. They are probably best interpreted as introgressed populations of the latter. In the most obviously hybridized populations, these differences clearly reflect the genetic influence of *Q. gambelii*. (In a few limited areas the influence of *Q. turbinella* is also apparent.) But even where the differences are less conspicuous, they seem best interpreted on the same basis. Therefore, this whole series of populations has been included in the writer's study of the *Q. undulata* complex. It may be noted that they are ordinarily identifiable as *Q. undulata* in the botanical manuals for this region (Tidestrom, 1925; Kearney and Peebles, 1960). The purpose of this paper is to document the preceding statements and to offer some suggestions in regard to the origin and evolution of these introgressed populations.

¹ Received for publication 9 May 1969.

This study has been supported by National Science Foundation grants G-9088, G-18634, and GB-147.

The author is indebted to Walter P. Cottam and Rudy Drobnick for assistance throughout this study; to Chester M. Rowell, Jr. and Stanley L. Welsh for phytogeographic data; and to Harry D. MacGinitie and Robert J. Lyon for reading critically portions of the manuscript.

DISTRIBUTION AND HABITAT OF PARENTAL SPECIES AND HYBRIDS—The distribution of these hybridized populations was shown in a very general way in a previous paper (Tucker, 1961, Fig. 5), as was, also, the distribution of *Q. gambelii* (Tucker, 1961, Fig. 2). Locations of hybrid collections included in the present study are shown in this paper in Fig. 1. The distribution of *Q. havardii* is shown, in part, in papers by Muller (1952, Fig. 2) and by Wiedeman and Penfound (1960, Fig. 2). The species ranges from southeastern New Mexico eastward across the southern Panhandle of Texas into western Oklahoma. Nowhere are *Q. gambelii* and typical *Q. havardii* sympatric today, although they come to within about 75 miles of each other in southeastern New Mexico. In the region of the hybridized populations in southeastern Utah and northeastern Arizona, typical *Q. havardii* is absent. *Quercus gambelii*, however, occurs in the mountains peripheral to the area, and small outlying stands occur in sheltered sites along water courses at considerably lower elevations than usual and at distances of only a few miles from hybrid populations.

In addition to being geographically isolated, *Q. gambelii* and *Q. havardii* are very different ecologically. As indicated previously (Tucker, 1961), *Q. gambelii* is the common oak of the ponderosa pine zone in the higher mountains of the Southwest. Where its range approaches that of *Q. havardii* most closely today, i.e., in the Guadalupe Mountains of Eddy County, New Mexico, it seldom occurs much below 6,500 ft. Some 75 miles to the northeast, *Q. havardii* may be found at ca. 3,800 ft. It ranges across the

Llano Estacado, or Staked Plain, of the Texas Panhandle and southeastern New Mexico, often growing in areas of shifting sand. Typically it grows as a low, rhizomatous sub-shrub, often no more than 1-2 ft in height, forming extensive clones by vegetative growth. The ecological setting of the hybridized populations in southeastern Utah and northeastern Arizona is remarkably similar to that of typical *Q. havardii* in the Staked Plain—a flat, sandy, treeless expanse with here and there areas of shifting,

partially stabilized dunes (Fig. 2). The hybridized populations occur at elevations from ca. 4,600 ft (Tucker 2820) to 5,800 ft (Tucker and Haskell 2932). I have observed *Q. havardii* on the Staked Plain at elevations from ca. 2,900 ft (Tucker 2971) to 4,300 ft (Tucker 2961). Thus the altitudinal range of the hybrids is approximately 1,500 ft higher than that of *Q. havardii*. Latitudinally, the distribution of the hybrids is almost entirely north of the northern limits of *Q. havardii* (as shown by Wiedeman and Penfound,

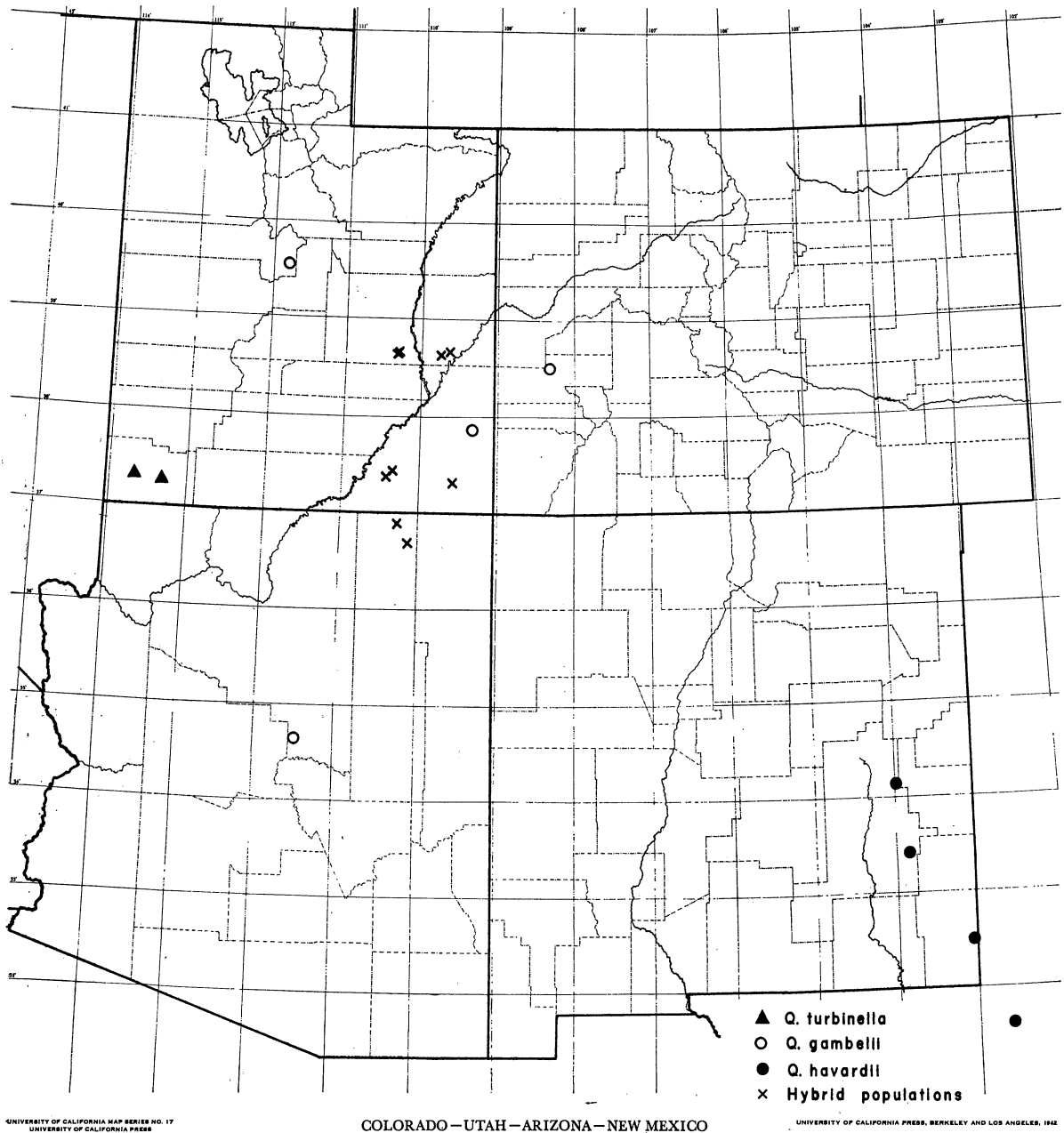


Fig. 1. Locations of hybrid populations and the collections of *Q. gambelii*, *Q. havardii*, and *Q. turbinella* included in this study.

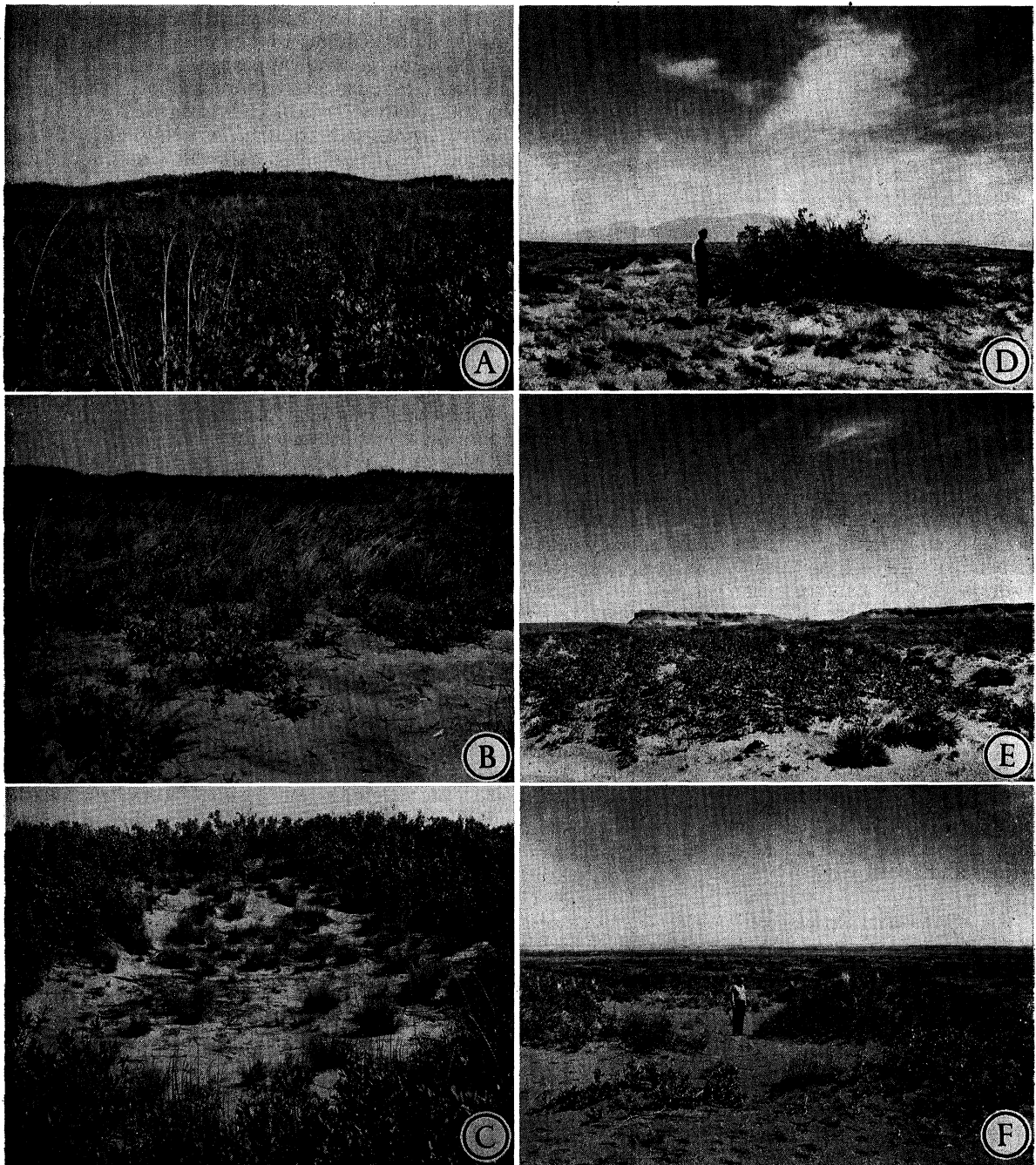


Fig. 2. Habitat of *Q. havardii* in the Staked Plain, Bailey Co., Texas (A - C), and of a hybrid population in the San Rafael Desert, Emery Co., Utah (D - F). Photographs A - C by Chester M. Rowell, Jr., D - F by Walter P. Cottam.

1960, Fig. 2) and extends at least 150 miles farther northward.

There are climatic differences between the two regions, and these may well be significant in considering the genetic makeup of the hybrid populations. When climatic data for the Staked Plain (U. S. Weather Bureau records for Hobbs and Portales, N. M., and Muleshoe, Texas)

are compared with data for the region of the hybrids (Moab and Bluff, Utah, and Kayenta, Ariz.), the climate of the Staked Plain is seen to be somewhat less extreme than the region of the hybrids, with higher daily maximum temperatures during the winter months. In other respects the temperature regimes of the two regions are quite similar. Total precipitation is

TABLE 1. Total precipitation

| Station | Total precipitation (annual average in inches) | Number of years of record |
|------------------------------|--|---------------------------|
| <i>Region of the hybrids</i> | | |
| Moab, Utah | 8.98 | 72 |
| Bluff, Utah | 7.42 | 45 |
| Kayenta, Ariz. | 8.25 | 42 |
| <i>Staked Plain</i> | | |
| Portales, N.M. | 17.27 | 53 |
| Muleshoe, Texas | 17.70 | 40 |
| Hobbs, N.M. | 15.38 | 43 |

roughly twice as much as in the region of the hybrids (Table 1). High winds, however, are characteristic of the Staked Plain: "... the annual average velocity is 12 to 15 mph, but it is a rare month which does not have winds in excess of 30 mph, and usually more than 40 mph. These velocities are considerably greater than in adjacent areas; ..." (Wendorf, 1961). The region of the hybrids is, of course, also subject to winds (Greene and Sellers, 1964). Nevertheless, prolonged winds of high velocity seem to be much more prevalent in the Staked Plain, and their desiccating effect could well offset to some extent the higher precipitation of the region.

MORPHOLOGICAL DIFFERENCES BETWEEN *Q. GAMBELII* AND *Q. HAVARDII*—The principal differences between these very distinct species are summarized in Table 2. The most conspicuous of these are in stature, leaf size and degree of indentation, and acorn size.

TABLE 2. Principal morphological differences between *Q. gambelii* and *Q. havardii*

| | <i>Q. gambelii</i> | <i>Q. havardii</i> |
|--|---|---|
| Growth Habit | shrub or small tree (or infrequently a medium-sized tree 12–15 m in height) | low, rhizomatous shrub or sub-shrub, commonly under 1.2 m in height (often no more than 0.5 m tall) |
| Leaves | | |
| width | commonly 3.0–6.0 cm | commonly 1.3–3.5 cm |
| degree of indentation | moderately to deeply lobed | subentire to undulate, toothed, or infrequently distinctly lobed |
| length of petiole | 3–(usually) 10, or even 20 mm | 2–7 mm |
| color | upper surface dark to bright green, and commonly glossy | upper surface light bluish-green; glossy, or often dull |
| density of pubescence on lower surface | sparse to moderate | moderately dense |
| number of rays per stellate hair | 4 or fewer | 8 or more |
| Acorns | | |
| cup | 7–15 mm diam, 5–8 mm high; deeply cup-shaped | 15–25 mm diam, 10–12 mm high; deeply cup-shaped to goblet-shaped |
| nut | 12–15 mm long, 8–10 mm diam | 12–25 mm long, 14–18 mm diam |

The populations of hybrid origin are mostly much more similar to *Q. havardii* than to *Q. gambelii* in general appearance, growth habit, stature, leaf size and color, and other morphological characteristics. Nevertheless, even the most *havardii*-like populations are readily distinguished from typical *Q. havardii*. One population (no. 2820) included at least one individual identifiable as *Q. gambelii* growing with intermediate and *havardii*-like forms. Hence, the occasional individuals in other populations throughout this region that have larger, more deeply lobed and darker green leaves, or that have a taller, more arborescent growth habit, can easily be interpreted as showing *Q. gambelii* influence. Thus, on the basis of gross morphology and field observation, I suspected that these populations represent remnants of a formerly more or less continuous distribution of ancestral *Q. havardii*, which have become introgressed by *Q. gambelii*.

With this as a working hypothesis, several population samples of *Q. gambelii* and of *Q. havardii* were analyzed in detail, attention being focused on a number of their more nearly constant differences. A number of samples from populations of hybrid derivation were analyzed in the same way. The collections included in this study, and their locations, are given in Table 3. The characters studied, and the methods of analysis, were as follows:

1. *Leaf size*—In assessing the character of leaf size, both length and width were measured, although *Q. gambelii* and *Q. havardii* are more sharply separated on leaf width. Data on the latter character are used in the scatter diagrams

TABLE 3. Population samples illustrated in Fig. 3-5

| Taxon | Collection | No. of individuals | Location |
|--------------------------------|--|--------------------|---|
| <i>Q. gambelii</i> | <i>J. M. T. 2773</i> 5 August 1955 | 14 | 11.5 miles northwest of Jacob Lake, beside Highway 89, Coconino Co., Ariz. |
| <i>Q. gambelii</i> | <i>J. M. T. 2775</i> 6 August 1955 | 20 | Chicken Creek Canyon, 2 miles east of Levan, Juab Co., Utah |
| <i>Q. gambelii</i> | <i>J. M. T. 2821</i> 18 August 1955 | 12 | 2 miles west of Monticello, beside North Creek Rd., San Juan Co., Utah |
| <i>Q. gambelii</i> | <i>J. M. T. 2830</i> 2 September 1955 | 28 | 6.4 miles north of Columbine Pass, beside road from Delta, Uncompahgre Plateau, Montrose Co., Colo. |
| <i>Q. gambelii</i> and hybrids | <i>J. M. T. 2820</i> 18 August 1955 | 9 | In canyon near road, 0.9 mile north of Bluff, San Juan Co., Utah |
| hybrids | <i>J. M. T. and H. S. Haskell 2933</i> 9 October 1955 | 15 | 15 miles north of Kayenta, Navajo Co., Ariz., beside road to Mexican Hat |
| hybrids | <i>J. M. T. 2815-2816</i> 17 August 1955 | 14 | Vicinity of road to Arches National Monument, 4-4.2 miles east of Highway 160, Grand Co., Utah |
| hybrids | <i>J. M. T. 2817-2819</i> 17 August 1955 | 7 | Beside road to Dead Horse Point, ca. 9-9½ miles west of Highway 160, Grand Co., Utah |
| hybrids | <i>J. M. T. and H. S. Haskell 2932</i> 8 October 1955 | 25 | 12 miles southeast of Kayenta, beside road to Chilchinbito, Navajo Co., Ariz. |
| hybrids | <i>J. M. T. 3993</i> 13 September 1966 | 2 | 6.6 miles east of Jeffrey Wells, and 13 miles (by road) southeast of its junction with Highway 24, Emery Co., Utah |
| hybrids | <i>J. M. T. 3994</i> 13 September 1966 | 23 | 5.3 miles east of Jeffrey Wells, Emery Co., Utah |
| hybrids | <i>J. M. T. 4000</i> 14 September 1966 | 12 | ½ mile north of Nakai Dome to ca. 5 miles north, beside road to Fry Canyon, San Juan Co., Utah |
| hybrids | <i>J. M. T. 4001-4005</i> 14 September 1966 | 5 | Ca. 5.5 miles north-northwest of Nakai Dome to ca. 6.6 miles north-northwest, beside road to Fry Canyon, San Juan Co., Utah |
| <i>Q. havardii</i> | <i>J. M. T. 2961</i> 23 October 1955 | 21 | Ca. 21 miles south of Taiban, DeBaca Co., N. M. |
| <i>Q. havardii</i> | <i>J. M. T. 2963</i> 24 October 1955 | 25 | 0.2-0.4 mile north of Highway 380, and ca. 8 miles west of Caprock, in Chaves Co., N. M. |
| <i>Q. havardii</i> | <i>J. M. T. 2967</i> 25 October 1955 | 17 | Highway 18, 5.3-5.4 miles north of road to Eunice (Road 176), Lea Co., N. M. |
| <i>Q. havardii</i> | <i>J. M. T. 2971</i> 26 October 1955 | 25 | Road 1053, 5 miles south of its junction with Highway 80, Crane Co., Texas |
| <i>Q. turbinella</i> | <i>J. M. T. 2810</i> 15 August 1955 | 22 | Ca. 2½ miles north of Gunlock, beside road to Veyo, Washington Co., Utah |
| <i>Q. turbinella</i> | <i>J. M. T. 2813</i> 16 August 1955 | 24 | Ca. 1 mile northeast of Leeds, Washington Co., Utah |

(Fig. 3); data on leaf length are presented in the form of frequency polygons (Fig. 5). One representative leaf of each specimen was measured with a millimeter scale.

2. *Leaf length: width ratio*—Not only is the absolute width typically less in *Q. havardii* than in *Q. gambelii* (see Table 2), but there is also a general tendency for the relative width to be less in the former (i.e., for *Q. havardii* to have relatively narrower leaves). This is expressed by the ratio of length to width, which was computed from

measurements obtained as in the preceding character.

3. *Relative depth of marginal indentation*—The longest lobe (or tooth) of one representative leaf on each specimen was measured (Tucker, Cottam, and Drobnick, 1961, Fig. 2). Total length of the secondary vein and length of the lobe proper were recorded. Depth of indentation was expressed as the ratio of the length of the vein to the length of the lobe.

4. *Relative length of petiole*—Of the differences chosen for detailed analysis, this was perhaps the subtlest and least obvious. The mean petiole length and lamina length were computed for each specimen using five representative leaves. The ratio of these means—petiole length to lamina length—was used as an expression of relative petiole length.

5. *Density of stellate pubescence on lower leaf surface*—Five representative leaves per specimen were examined with a compound microscope at 100 × magnification using reflected light. Two sites on the lower side of each leaf and near its center, free of major veins and necrotic areas, were inspected in turn. All stellate hairs whose centers fell partially or entirely within the area of an ocular micrometer scale were counted. Thus 10 areas were counted for each specimen. The mean of the 10 counts was taken as an individual specimen's score on this character.

6. *Number of rays per stellate hair*—As in the analysis of the preceding character, two 100 × fields were examined on the underside of each leaf. Ray numbers were determined for five trichomes in each field, giving a total of 10 counts per leaf. In analyzing population samples of the pure species, if most of the ray numbers were well within the limits (and none exceeded the limits) characteristic of the species, i.e., four or fewer in *Q. gambelii* and eight or more in *Q. havardii*, then usually only one leaf was checked. If any count fell outside these ranges, a second (and some times a third) leaf was checked. In all the hybrid population samples at least two, and often three, leaves were checked. The mean of all counts for each specimen was taken as the individual's score on this character.

Data derived from the analyses are presented in the form of scatter diagrams (Fig. 3) or frequency polygons (Fig. 4, 5). It should be noted that only three characters are used in the scatter diagrams—leaf width, depth of marginal indentation, and number of rays per stellate trichome. *Quercus gambelii* and *Q. havardii* are better

separated on these three than on any of the other character differences analyzed. In the population samples studied there was no overlap between these species in values for indentation and number of rays per stellate trichome, and only very slight overlap in leaf width.

In all other characters analyzed, the two species overlapped to some extent. Overlapping character differences do not lend themselves to use in a pictorialized scatter diagram, or in any system of scoring or graphic presentation of data that requires delimitation of (1) a range of values characteristic of one species, (2) a range characteristic of a second species, and (3) an intermediate range. If the normal range of variation for a character in one species overlaps the normal range in a second species, the overlapping part of the ranges cannot be designated realistically an "intermediate" range, which would imply intermediacy due to hybridization. Data from these overlapping characters, therefore, are shown as frequency polygons.

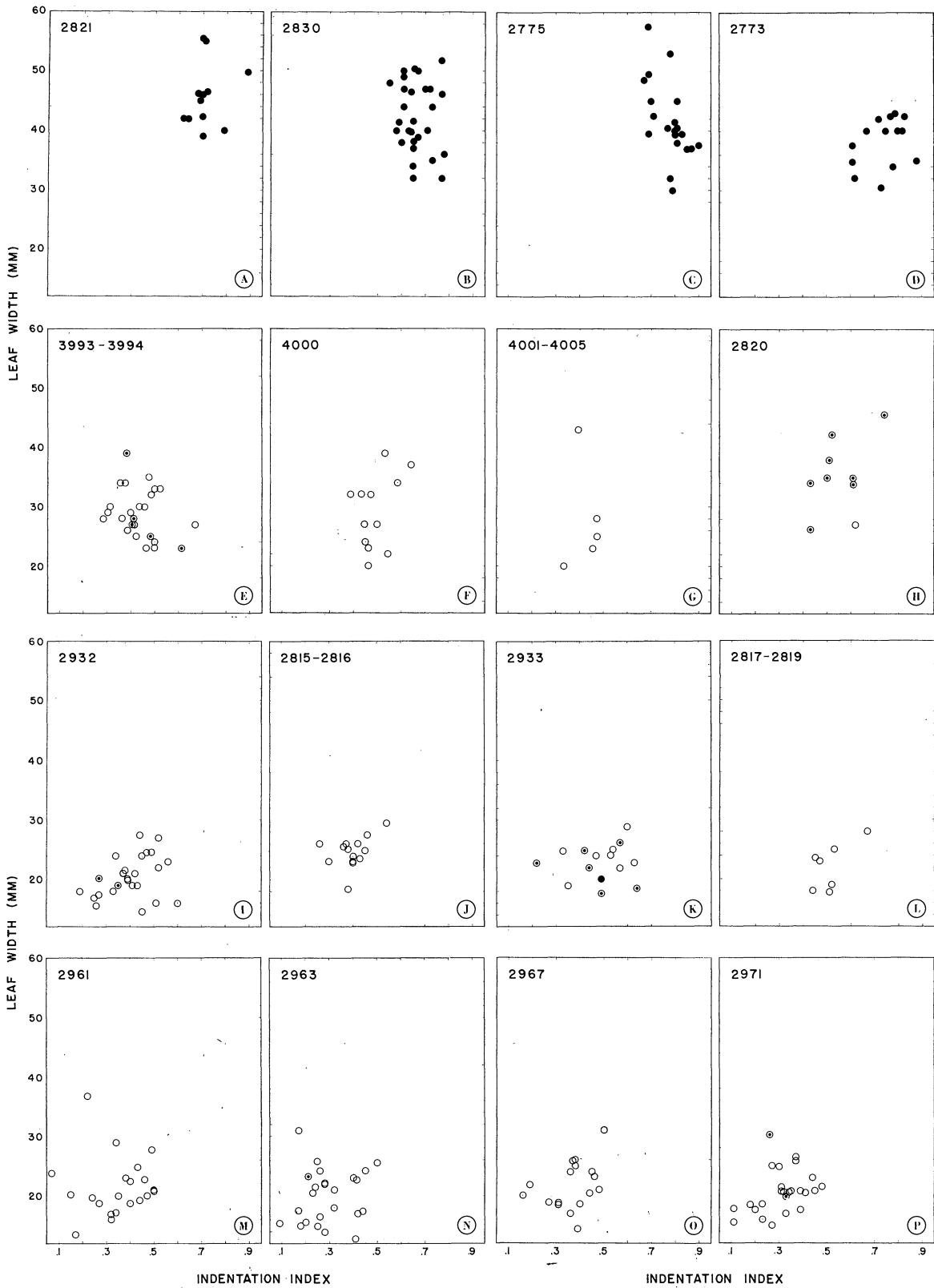
EVIDENCE OF HYBRIDITY—As stated previously, the general appearance of the hybridized populations in the field is very similar to that of *Q. havardii*. The scatter diagrams (Fig. 3) bear this out. Also, they indicate that most of these populations are only slightly more variable than populations of either parental species. Most of the hybrid populations, however, vary at least slightly in the direction of *Q. gambelii*. Thus on the basis of the three characters used in the diagrams, they might well be taken as slightly introgressed *Q. havardii*.

Number 2820, however, quite obviously bridges the intermediate range. Furthermore, the frequency polygons show that in such characters as leaf length/width ratio, and petiole/lamina ratio (Fig. 4), the hybrid populations are distinctly intermediate or even more similar to *Q. gambelii* than to *Q. havardii*. These two last-mentioned characters are rather subtle and not nearly so obvious as such parental differences as degree of lobing (indentation) or gross size (width) of the leaves. Thus despite the very *havardii*-like

Fig. 3. Scatter diagrams based on three characters: leaf width, indentation index, and number of rays per stellate hair. Scores on the latter character are indicated as follows: values representative of *Q. gambelii* (4.0 or lower) ●; *Q. havardii* (8.0 or higher) ○; values in the intermediate range (4.1–7.9) ⊙. A–D, *Q. gambelii*; E–L, hybrid populations; M–P, *Q. havardii*.

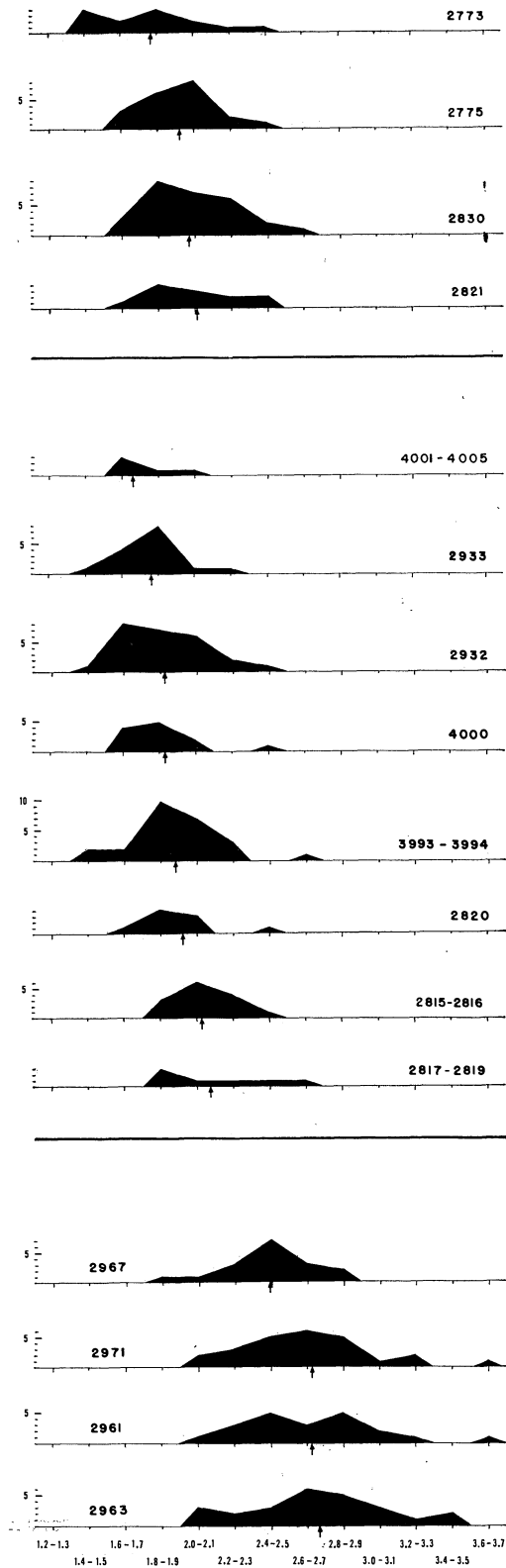
Fig. 4. Frequency polygons for leaf length/width ratio, and petiole/lamina ratio. The vertical scale at left indicates number of individuals; the small arrow under each polygon indicates the population mean.

Fig. 5. Frequency polygons for leaf length and density of pubescence. The vertical scale at left indicates number of individuals; the small arrow under each polygon indicates the population mean.

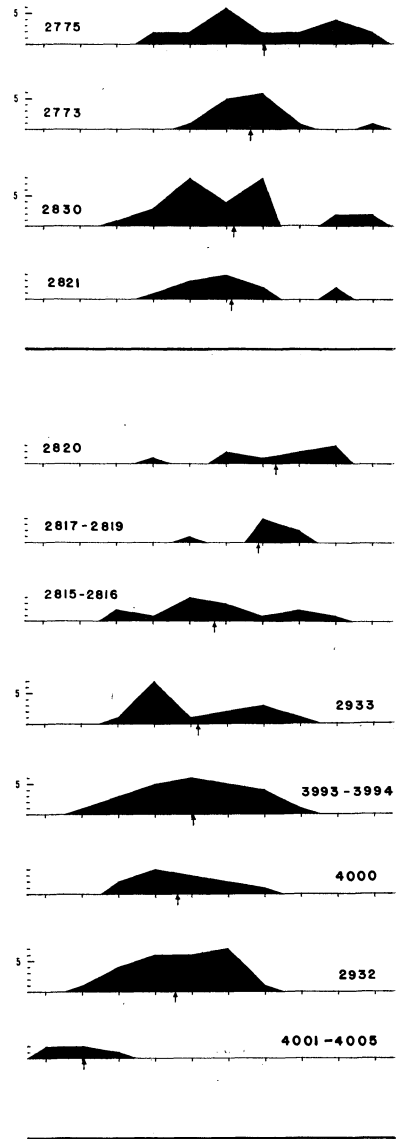


LEAF LENGTH:WIDTH RATIO

PETIOLE:LAMINA RATIO

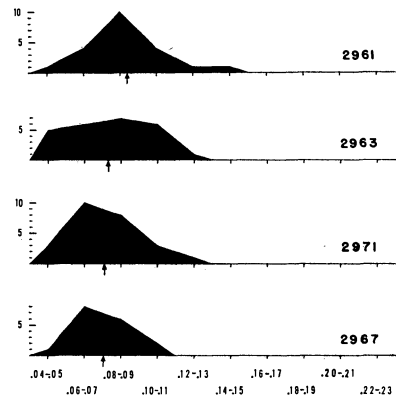


Q. gambelii

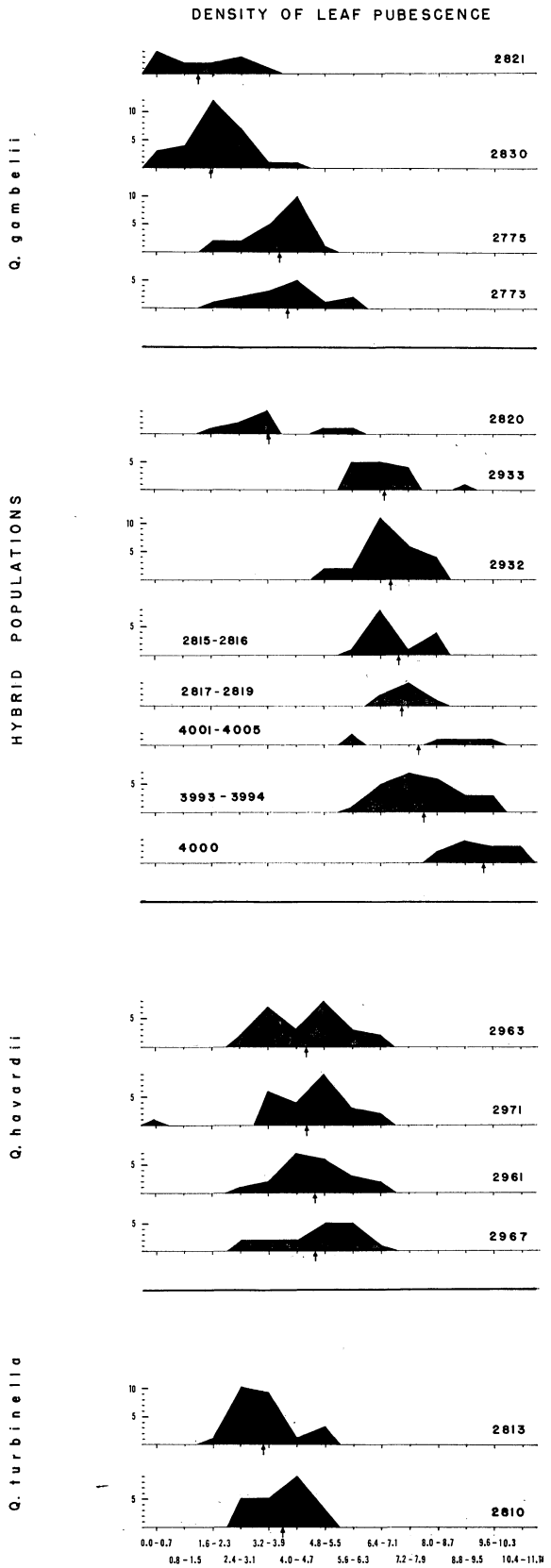
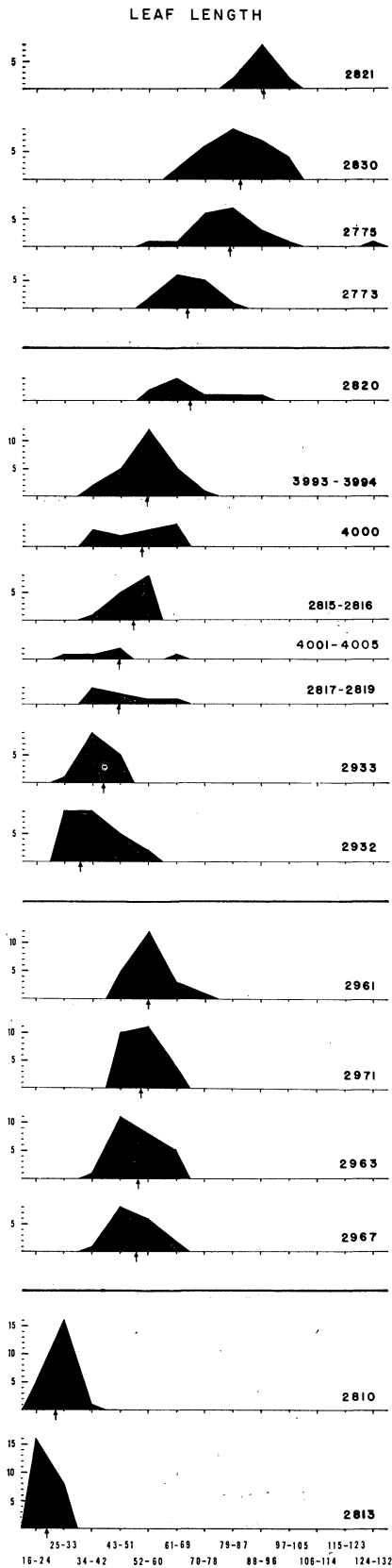


HYBRID POPULATIONS

Q. havardii



See page 76 for caption.



Q. gambelii
 HYBRID POPULATIONS
Q. havardii
Q. turbinella

See page 76 for caption.

general appearance of most of the hybrid populations—in stature, growth habit, leaf size, and other characteristics—they are sufficiently different in other, less obvious characters that the individuals can be readily distinguished from typical *Q. havardii*.

Still other characters depicted in the frequency polygons do not seem to fit a picture of simple hybridity between *Q. gambelii* and *Q. havardii*. Neither leaf length nor density of pubescence on the lower leaf surface (Fig. 5) is intermediate in the hybrid populations (except for no. 2820). Leaf length, in general, is even smaller than in *Q. havardii*; and leaf pubescence is more dense than in the latter species.

Apparently either of two explanations could apply: (1) these extreme character conditions could be examples of transgressive segregation, or (2) they could be the result of the genetic influence, via introgression, of a third species. Transgressive segregation seems to be the more plausible explanation. Admittedly, introgression of *Q. turbinella* could account for the small leaf size in the hybrid populations, for this species does have smaller leaves than either *Q. gambelii* or *Q. havardii*. In density of foliar pubescence, however, the hybrid populations exceed all three species.

It seems highly probable that *Q. turbinella* was widely distributed through the region of the hybrids in past time. This is indicated by several disjunct, and probably relict, occurrences of the species: Courthouse Wash (Jones 16 June 1913, POM) and Moab (Jones 7 June 1913, POM), both in Grand County, Utah, and Canyon del Muerto, Apache County, Arizona (Culler, Goodman, and Payson 2937, 2946, DS); and by occurrences of hybrids between *Q. turbinella* and *Q. gambelii* (Tucker et al., 1961, Fig. 1).

The obvious genetic influence of *Q. turbinella* in these hybrid populations has indeed been noted but in only a few instances. At two locations (Table 3, collections 2818 and 4001-4005) individuals were observed which were very *turbinella*-like in overall appearance as well as in the distinctive morphological characters that mark this species: small, oblong-ovate leaves with dull, gray-green upper surfaces, spinose marginal teeth, and subcordate bases. Several collections (Drobnick 1 April 1962) from the area of Hole-in-the-Rock, Kane County, Utah, also show *turbinella* influence. Elsewhere, however, evidence of genetic influence of this species has been very infrequent. Other characters sometimes seen in the hybrid populations that could be the result of *Q. turbinella* influence are the acute and sometimes mucronate teeth of the leaf margin and the moderately stellate-tomentose twigs (*Q. turbinella* has spinose-dentate leaves and densely short-tomentose twigs). However, these appear usually as individual characters and therefore the evidence is not entirely unequivocal. Thus it

would appear that introgression by *Q. turbinella* in this segment of the *Q. undulata* complex has been only very slight and localized.

DISCUSSION—If the thesis is tenable that the present populations of Arizona and Utah represent *Q. havardii* introgressed by *Q. gambelii* (and locally by *Q. turbinella*), it would be logical to assume that at some time and place in the past there was a single system of populations, more or less geographically continuous, that was ancestral both to these hybridized populations and to the populations of *Q. havardii* presently in the Llano Estacado. Several questions then arise. What region did this ancestral *Q. havardii* occupy? How can we account for the wide geographic gap between the populations now? At what period in geological time did this separation occur?

Unfortunately, there is little evidence on any of these points, and if we are to propose answers of any sort they must be largely speculative. Since these questions are obviously interrelated, it is probably better to attempt a single integrated answer, rather than to consider them separately.

First, it seems doubtful that the distribution of *Q. havardii* extended continuously from southeast to northwest across the region between the two groups of populations. I know of no relict occurrences of *Q. havardii* in this region, nor of any evidence indicating it had introgressed other species there. Furthermore, the series of mountains that extend north to south through the middle of New Mexico form an almost continuous barrier across this region—from the Sangre de Cristo Mountains on the north, to the Sacramento and Guadalupe Mountains on the south.

There is abundant evidence that during the Wisconsin glacial period biotic zones occurred at generally lower altitudes and latitudes than at present. That this was also the case during the other glacial periods of the Pleistocene can scarcely be doubted. The distribution of *Q. havardii* doubtless fluctuated accordingly, extending farther southward during the glaciopluvial periods than it does today. Indeed, during the Wisconsin Full Glacial, this species may not have occurred in the Llano Estacado at all but probably occupied a region to the south. The fossil pollen record of this period from several sites in the Llano Estacado is characterized by abundant pine, continuous occurrence of spruce, and an almost total lack of juniper, ephedra, oak and herbs. "The most probable interpretation of the consistent high pine pollen percentages, is that they reflect an open pine forest, or woodlands, with a very poor field vegetation covering the Southern High Plains" (Hafsten, 1961, p. 85). Although the difficulties and problems confronting the palynologist working in the Southwest are numerous, as recently emphasized by Hafsten (1961, p. 75, 76), Leopold (1964), and Potter (1964), in the present case a logical inference would be that the

habitat and climatic conditions required by *Q. havardii* were not at hand in the area during this period.

At what period of the Pleistocene *Q. havardii* extended *farthest* south is a matter of conjecture. The most extreme climatic conditions in the Llano Estacado, as inferred from the fossil pollen record, evidently occurred during the Wisconsin Full Glacial. Pre-Wisconsin events in the Southwest, however, are not clearly revealed by palynological evidence and are difficult to correlate with the classical picture of multiple glaciations in other regions (Martin and Mehringer, 1965). Evidence from glaciation, however, indicates that the Kansan Period may have been even more extreme than the Wisconsin in the Southwest. In the Rocky Mountains, glaciers of Kansan (Cedar Ridge) age were more widespread than those of any other Pleistocene glaciation (Richmond, 1965, p. 220), and in the La Sal Mountains of southeastern Utah, Kansan (Middle Harpole Mesa) glaciation was much more extensive than that of Wisconsin age (Richmond, 1962; see especially Plate 6). Thus it may be suggested that the range of *Q. havardii* lay farthest to the south during the Kansan Period. Then, spreading northward during the following interglacial period, the species became split into two populations, one to the east and one to the west of the mountain barrier mentioned previously. The western population was ancestral to the present hybrid populations of southeastern Utah and northeastern Arizona; the eastern population was ultimately to occupy the Llano Estacado.

Several things suggest this long period of separation. For instance, certain of the present hybrid populations are moderately homogeneous, and not nearly so variable as the typical "hybrid swarm" so often noted in cases of hybridization in *Quercus* (Tucker, 1952; Tucker and Muller, 1956; Silliman and Leisner, 1958; Tucker et al., 1961). Presumably this reduction in variability

would have necessitated a relatively long period of selection. Another point suggesting a long separation is the low degree of floristic similarity between the two regions. To make this determination, the plants of the Arches National Monument, in southern Utah (Harrison, Welsh, and Moore, 1964), were compared with those listed for the Texas High Plains (which coincides, in large part, with the Llano Estacado) in Gould's checklist (1962). Harrison et al. noted (1964) that, aside from species of wide distribution in the western states, "other elements of the flora with a more limited distributional range show a close relationship with the flora of the region to the south, especially to the southeast." Such an observation seems suggestive in considering the case of our oaks. These authors do not, however, cite any particular regions to the south or southeast, nor do they mention the elements of the flora showing the close relationship. In any event, a floristic comparison reveals a relatively low (18.8%) coefficient of similarity between the two regions inhabited by these oaks (Table 4).

When the comparison includes only the species commonly associated with the oaks in the two regions, even less floristic similarity is apparent (Table 4). For the purpose of this comparison, a list was drawn up with the assistance of Chester M. Rowell, Jr., of the species associated with *Q. havardii* in the Staked Plain. A comparable list was drawn up with the assistance of Stanley L. Welsh of the associates of the hybrids (at least for the area of the Arches National Monument).

In making these comparisons, no attempt was made to cross-check the various lists for synonyms or for the possibility that very closely related (and perhaps conspecific) forms were listed under different species names. Conceivably, a critical check for these factors might have raised the percentage of similarity slightly. However, the level would probably still have been quite low, which suggests—again—that these oak popula-

TABLE 4. Floristic comparison of the regions occupied by *Q. havardii* and the hybrids, and of their associated species

| | Regional flora | | Associates of the oaks | |
|---|------------------------------------|---|--------------------------------|--------------------|
| | Texas High Plains (Gould, 1962) | Arches National Monument (Harrison et al., 1964) | <i>Q. havardii</i> (Rowell) | Hybrids (Welsh) |
| No. of species and varieties of vascular plants | 655 | 320 | 97 | 60 |
| Taxa in common | | 92 | | 8 |
| Coefficient of similarity ^a (Sorensen, 1948) | | 18.8% | | 10.2% |

^a $\frac{2c}{a+b} \times 100$, where a and b are the numbers of species in the areas being compared, and c is the number of species in common.

TABLE 5. *Cynipid gall-makers on Quercus gambelii, Q. havardii, Q. turbinella, and hybrids*

| Gall-maker | Host oak species | | | | |
|-------------------------------------|------------------|---------|-----------------|-------------------|---|
| | <i>gambelii</i> | hybrids | <i>havardii</i> | <i>turbinella</i> | others (see master list, p. 27, Weld, 1960) |
| <i>Neuroteras howertoni</i> Bass. | — | + | + | + ^a | arizonica oblongifolia toumeyii |
| <i>Atrusca bella</i> Bass. | — | + | + | + | arizonica oblongifolia rugosa ^b toumeyii |
| <i>Andricus</i> (undescribed sp.) | + | + | — | + | arizonica grisea oblongifolia pungens rugosa |
| <i>Callirhytis juvenca</i> Weld. | + | + | + | + | arizonica oblongifolia rugosa |
| <i>Disholcaspis rubens</i> (Gill.) | + | + | + | + | arizonica fendleri (=undulata) oblongifolia rugosa toumeyii |
| <i>Disholcaspis edura</i> Weld. | — | + | — | — | arizonica oblongifolia rugosa |
| <i>Xanthoteras eburneum</i> (Bass.) | + | + | — | + | grisea rugosa (incl. submollis) |

^a Listed by Weld as *Q. subturbinella*, a synonym.

^b Listed by Weld as *Q. reticulata*, a synonym.

tions have been separated for a considerable period of time.

The region occupied by the ancestral population of *Q. havardii* before it split into two was most likely an area south of the Llano Estacado and the mountain barrier mentioned previously. Also, its range probably extended farther to the west than it does at present. This latter point is inferred from the present location of the hybrid populations. It is also suggested by the distribution of certain oak gall wasps.

The oak gall wasps (about 31 genera in the Family Cynipidae) are highly specialized Hymenoptera that are obligate parasites on oaks. They are relatively sedentary, often short-lived, and probably unable to travel long distances. Some species are restricted to a single oak species, although most gall wasps have been recorded from several different host species. Because of their relatively sedentary mode of life, the occurrence of one gall wasp species on two or more

allopatric oak species is a strong indication that the oaks have existed sympatrically at some time in the past and have harbored the parasite in common. When two allopatric oaks have several cynipids in common, there is even a stronger basis for an assumption of former sympatry. In this and other ways, host records of gall wasps can provide clues to past associations of different oak species (Tucker and Muller, 1958; Maze, 1965).

Much cynipid collecting remains to be done in the regions with which we are concerned—especially the southern High Plains (see Weld, 1960, p. 34). For example, as recently as 1963 a general collection of galls (*Cavagnaro 251*) from several clones of *Q. havardii* at a single location in De Baca County, New Mexico, yielded five species of gall-makers not previously recorded from this oak. In fact, only two gall wasp species had been recorded from this oak previously (R. J. Lyon, personal communication). The only

cynipids definitely recorded from our hybrid populations, as far as we are aware, are a series collected in 1963 by Mr. David Cavagnaro. The gall-makers from this series, identified by R. J. Lyon, are listed in Table 5. Records of these same species from other oaks are also included, the information having come from Weld (1960), other Cavagnaro collections, and Lyon. It may be noted that none of the cynipids in Table 5 have been recorded from any of the oaks of the eastern United States (see Weld, 1959).

Two points merit our attention in Table 5. First, of the seven gall-makers recorded from the hybrids, four are also recorded from *Q. gambelii*, six from *Q. turbinella*, and four from *Q. havardii*. Such a community of cynipid parasites is, of course, to be expected if our postulate is valid that the hybrid populations have involved these three species as parents. Second, and fully as important, is the distribution of the other oaks from which these same cynipids have been recorded. Of these other hosts, the four most frequently involved—*Q. arizonica*, *Q. oblongifolia*, *Q. rugosa* (*Q. reticulata*), and *Q. toumeyii*—are all species mainly of southern Arizona, southwestern New Mexico, and adjacent northern Mexico. Two other hosts, *Q. grisea* and *Q. pungens*, occur mainly to the south of *Q. havardii*, but they also extend westward to Arizona. The only exception to this pattern is the one record of *Disholcaspis rubens* on *Q. fendleri* (a form in the *Q. undulata* complex.)

Still other cynipid species (as yet not known from the hybrids and not included in Table 5) are recorded from *Q. havardii* and from these other southwestern oaks, as well. Thus, *Callirhytis frequens* (Gill.) is found on *Q. havardii* and *Q. gambelii*; and *Disholcaspis spissa* Weld is recorded from *Q. havardii* and from *Q. turbinella*, *Q. arizonica*, and *Q. rugosa* (*Q. reticulata*) (Weld 1960). The cynipid distributions, therefore, clearly imply a sympatric existence of *Q. havardii* and these other oaks at some time in the past, and it may be suggested that this sympatry occurred during a time when the range of *Q. havardii* extended considerably farther to the south and west than it does today.

If we assume, then, that this time was the Kansan Period of the Pleistocene, as the climate became warmer in the following interglacial period, the ancestral *Q. havardii* population spread northward over a progressively broadening front. In the process, however, it was channelled into two migration lanes, one east and one west of the series of mountains (mentioned previously) that extend north to south through central New Mexico.

Infrequent and widely scattered contacts between the western population and *Q. gambelii* provided repeated opportunities for hybridization. Not so with the eastern population, which lay to the east of the range of *Q. gambelii*. In the western

population, introgression by *Q. gambelii* remained at a low level but became ever more general and widespread with repeated migrations and withdrawals contingent upon the climatic changes in subsequent pluvial and interpluvial periods. Ultimately the western population was introgressed throughout, although by no means uniformly so. Thus the situation was attained that we find today—nothing recognizable as pure *Q. havardii* remains. Introgression by *Q. turbinella* in the western population has been much more localized.

As we have noted previously, the region of the hybrids is subject to somewhat more severe winters than is the Llano Estacado. Thus an increase in winter hardness, which *Q. gambelii* genes could have contributed, would have obvious selective advantage. Nevertheless, on the flat, open plains of deep sand, subject to xeric climate as these oaks are, selection would still be preponderantly for traits of *Q. havardii* rather than those of *Q. gambelii*, although no pure populations of *havardii* occur here today. It may well be inferred, therefore, that given a slight infiltration of germ plasm of the more cold-adapted *Q. gambelii*, the introgressed populations have been able to persist in the inhospitable semi-desert environments of the Navajo country, after the pure ancestral *Q. havardii* was eliminated.

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