Chromosome numbers in ten species of Quercus, with some remarks on the contributions of cytology to taxonomy

Ray C. Friesner

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Chromosome Numbers in Ten Species of Quercus,
With Some Remarks on the Contributions
of Cytology to Taxonomy

By Ray C. Friesner

INTRODUCTION

It is becoming increasingly more apparent that for the solution of
many of the difficult problems in the field of taxonomy, we must take
into consideration the work of the cytologist. A very large number of
what we may call cytological-taxonomic studies have appeared during
the past decade. These have thrown much light upon such taxonomic
problems as the origin, evolution, and relationship of species within
polymorphic genera; the determination of the limits of subgenera and
of variable species with numerous supposed variations, and the probable
relationship of supposed natural hybrids.

CYTOLOGICAL CHARACTER OF POLYMORPHIC GENERA

When we turn to the cytological character of genera containing large
numbers of species, particularly those which contain many taxonomic
entities which are puzzling to know whether they should be considered
species, or varieties, or hybrids, and if the latter two, the problem of
determining just which particular species should claim a particular form
as its variety, or just which species were the probable parents of a
hybrid, we find that these genera fall into four cytological categories.
There are (1) polyploid genera, (2) genera with both polyploid and
aneuploid species, (3) genera with species containing chromosome num-
bers so variable that it is difficult to place them in either group (1) or
(2), and (4) genera in which all species appear to have the same
chromosome numbers.

Polyploid genera. Table I gives a list of ninety-six genera in which
species occur with chromosome numbers forming a geometrical series
with some small number as the basic number. This table is a complete
list of such genera studied to date where the publication is known to the
writer. There are undoubtedly others. In the third column, figures refer
**TABLE I**

**Genera with polyploid species**

<table>
<thead>
<tr>
<th>GENUS</th>
<th>POLYPLOID GROUPS</th>
<th>AUTHORITY</th>
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<tbody>
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<td>Elodea</td>
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</tr>
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<td>Valliniera</td>
<td>2x, 4x</td>
<td>85, 217</td>
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<tr>
<td>Triticum</td>
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<td>Zea</td>
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<td>Aegilops</td>
<td>2x, 4x, 8x, 6x</td>
<td>1, 46, 160, 179</td>
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<td>Euclidean</td>
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<td>Anthurium</td>
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<td>Tradescantia</td>
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<td>Allium</td>
<td>2x, 4x</td>
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<td>Tulipa</td>
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<td>Spiranthus</td>
<td>(Gynostachys)</td>
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<td>Patanthera</td>
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<td>Dendrobiu</td>
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<td>Oncidium</td>
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<td>Vanda</td>
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<td>Betula</td>
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<td>Alnus</td>
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<td>Morus</td>
<td>2x, 3x</td>
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1Numbers in parentheses refer to titles in bibliography. No attempt has been made to give a complete list of titles. Latest titles which will serve as leads to students working on particular genera are all that are given.
<table>
<thead>
<tr>
<th>GENUS</th>
<th>BASIC CHROMOSOME NUMBERS</th>
<th>POLYPLOID GROUPS</th>
<th>AUTHORITY</th>
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<td>2x, 4x, 6x, 10x, 16x+2</td>
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<td>7x, 8x, 9x</td>
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<table>
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<td>8 4x</td>
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<td>Primula</td>
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<td></td>
<td>11 2x, 4x</td>
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<td></td>
<td>12 2x, 3x</td>
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<td>4 2x, 3x</td>
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<td>Mentha</td>
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<td>Galeopsis</td>
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<td>Datura</td>
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<tr>
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<td>Solanum</td>
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<td>Digitalis</td>
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<td>Veronica</td>
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<td>9, 10, 17 2x</td>
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<td>Plantago</td>
<td>6 (4, 5, 10) 2x, 4x</td>
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<td>Lonicera</td>
<td>9 2x, 4x</td>
<td>208</td>
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<td>Valeriana</td>
<td>7 2x, 4x, 8x</td>
<td>183</td>
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<td>Campanula</td>
<td>8, 17 2x, 4x, 6x</td>
<td>47, 63, 208</td>
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</tr>
<tr>
<td></td>
<td>(10, 13)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lobelia</td>
<td>7 (9) 2x, 4x, 6x</td>
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<td>Crepis</td>
<td>3, 4, 5, (67) x, 2x, 3x, 4x, 5x, 6x, 8x</td>
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<td>Aster</td>
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<tr>
<td>Senecio</td>
<td>5 7 x, 4x, 3x, 10x, 12x, 18x</td>
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<td>Lactuca</td>
<td>(5, 7, 9)</td>
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<td></td>
<td>8 2x, 3x, 4x, 6x</td>
<td>63, 80</td>
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<td>Hieracium</td>
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<td>Chrysanthemum</td>
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<td>Erigeron</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>(8, 13) 2x, 4x, 6x</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td>Taraxacum</td>
<td>8 (12) 2x, 4x</td>
<td>181, 192</td>
<td></td>
</tr>
<tr>
<td>Dahlia</td>
<td>16 (18) 2x, 4x</td>
<td>102</td>
<td></td>
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</tbody>
</table>

80
to the number by which the basic number must be multiplied to give
the number of chromosomes occurring in sporophyte tissues of different
species within the genus. It will be seen that multiples run more often
4, 6, and 8, but occasionally run as high as 16, 18, or 20. Numbers in
the fourth column refer to literature citations. No attempt has been
made to give a complete bibliography. This would be both too costly
of time and space as well as entirely unnecessary, since citations given
are “key” references.

Aneuploid (dysploid) species. Table II lists six genera in which spe-
cies have chromosome numbers which are slightly more or slightly less
than exact multiples of the basic number. In the table, 2x+1 indicates
that some one particular pair is represented by three chromosomes
forming what has been called a “trisome,” 2x+1+1 indicates that one
each of two different pairs is so represented, thus forming two “tri-
somes,” while 2x+2 indicates that some one particular pair is repre-
sented by four chromosomes, thus forming a “tetrasome.” The rela-
tively small number of genera listed in this table may or may not be
significant. If it is significant, it would indicate that there is a much
greater tendency for all members of a chromosome set or complement
to double than for individual chromosomes so to behave.

TABLE II

<table>
<thead>
<tr>
<th>GENERA</th>
<th>BASIC CHROMOSOME NUMBERS</th>
<th>ANEUPLOID GROUPS (Number of chromosomes in sporophyte tissues)</th>
<th>AUTHORITY</th>
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</thead>
<tbody>
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<td>Hyacinthus</td>
<td>8</td>
<td>3n-1, 2n+3, 3n+3, 3n+4</td>
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<tr>
<td>Betula</td>
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<td>6x+6, 3(2x+2)*</td>
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<tr>
<td>Rosa</td>
<td>7</td>
<td>2x+1, 2x+2</td>
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<tr>
<td>Enothera</td>
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<td>2x+1, 3x+1, 4x+2</td>
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<td>Lycopersicum</td>
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<tr>
<td>Datura</td>
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<td>2x+1, 2x+1+1, 2x+2, 4x+1, 4x+2, 4x-1</td>
<td>14, 15</td>
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</tbody>
</table>

Genera with chromosome numbers irregular. Table III lists twelve
genera in which the chromosome number is so irregular that further

"This arrangement is suggested by the present writer as possible. It was not proposed by
Woodworth (26)."
study will be necessary in order to determine which are basic numbers and to determine the condition with respect to polyploidy or aneuploidy. Some of these genera (e.g., Campanula, Lactuca, Viola, Oxalis, and Plantago) belong also to the polyploid group, and it is entirely possible that further study will reveal two or more basic numbers, as is true in the genus Crepis (and possibly others), and the apparent irregular numbers will be found to fall in line with polyploidy and aneuploidy which is so common.

### TABLE III

<table>
<thead>
<tr>
<th>Genera with chromosome numbers so irregular that further study is necessary to determine which are basic numbers and to determine the condition with respect to polyploidy and aneuploidy</th>
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<tbody>
<tr>
<td>GENERA</td>
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<td>Cyperus...</td>
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<tr>
<td>Eleocharis...</td>
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<td>Scirpus...</td>
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<td>Carex...</td>
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<td>Tradescantia...</td>
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<td>Linum...</td>
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<td>Oxalis...</td>
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<td>Callitriche...</td>
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<td>Viola...</td>
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<td>Begonia...</td>
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<td>Plantago...</td>
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<td>Campanula...</td>
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<td>Senecio...</td>
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<tr>
<td>Lactuca...</td>
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<td>Erophila...</td>
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</tbody>
</table>

**Genera with but one chromosome number.** Table IV lists ten genera in which five or more species have been studied and but a single chromosome number found applicable to all species. In only two cases, viz., Philadelphus and Corylus, has the number of species studied been large. It may, therefore, well be that these genera will, after further study, also be transferred to groups I and II. The relatively small number of genera in this group at least serves to indicate how relatively frequent is the condition, polyploidy. Further study upon these genera...
will be necessary before constancy of chromosome number, with whatever it may imply from a phylogenetic standpoint, may be a definitely proven condition in these genera.

TABLE IV

*Genera in which five or more species or varieties (all studied to date) show the same chromosome numbers*

<table>
<thead>
<tr>
<th>GENERA</th>
<th>NO. OF SPECIES</th>
<th>CHROMOSOME NUMBER</th>
<th>AUTHORITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinus</td>
<td>7</td>
<td>12</td>
<td>40</td>
</tr>
<tr>
<td>Lilium</td>
<td>6</td>
<td>12</td>
<td>30, 130, 175, 176, 177</td>
</tr>
<tr>
<td>Cypripedium</td>
<td>5</td>
<td>11</td>
<td>156</td>
</tr>
<tr>
<td>Corylus</td>
<td>17</td>
<td>14</td>
<td>210</td>
</tr>
<tr>
<td>Quercus</td>
<td>10</td>
<td>6</td>
<td>Present Paper</td>
</tr>
<tr>
<td>Ficus</td>
<td>7</td>
<td>13</td>
<td>29, 217</td>
</tr>
<tr>
<td>Philadelphus</td>
<td>37</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Wisteria</td>
<td>7</td>
<td>8</td>
<td>160</td>
</tr>
<tr>
<td>Scabiosa</td>
<td>8</td>
<td>8</td>
<td>162</td>
</tr>
<tr>
<td>Penstemon</td>
<td>8</td>
<td>8</td>
<td>63</td>
</tr>
</tbody>
</table>

**CYTOLOGICAL DATA BEARING ON THE LIMITS OF SUBGENERA**

Clausen (25) has shown how well cytology may help in the determination of the limits of subgenera groups. He has shown, for example, that the Nominium section of Viola should be divided into two subsections, one with species having chromosomes in multiples of 10 and the other with species having chromosomes in multiples of 12, that the Chamaemelanium section includes only forms with numbers of $x=6$ and $x=12$, while section Melanium contains species with such variable counts as $x=7, 8, 10, 11, 13, 17, 18, 20, 24, 30$.

In the wheats it is found that members of different sections of the genus have different chromosome numbers, viz., Monococcum wheats have 7 as the haploid number, Emmer wheats have 14 and Spelt wheats have 21 as the reduced number. In the roses (63): Section Caninae species have $7 \times 2=14, 7 \times 2+14=28, 7 \times 2+21=35$, and $14 \times 2+28=56$; in section Cinnamomea species have 7, 14, 21, and 28 pairs. In Lactuca (63) subgenus Lactuca has 9 pairs, subgenus Crepidastrum has 5 pairs, and subgenus Ixeris has 7, 8, 12, 16, and 24 pairs. Afzelius (2)
has shown in the genus Senecio that species in the section Objejacoileae have 10 pairs of chromosomes, in section Objejaceae and in a number of others the haploid number is 20, while in section Tephroseris it is 25. Numerous other examples occur in the literature.

**CYTOLOGICAL DATA BEARING ON SPECIES LIMITS**

All attempts to define and therefore definitely delimit the term species break down sooner or later in their application. The term will undoubtedly best serve its purpose by continuing to denote "an aggregate of more or less similar individuals which may be considered a kind." I would not advocate any basis of delimitation which did not embody the element of "convenience" in observational determination. Nevertheless, cytological data has something to offer—only substantiating evidence, it is true—toward determining species limits when a particular species has a wide range of variability and what may seem to be more or less distinct entities within the supposed single species. An example is found in the case of *Betula alba* L. (*B. pubescens* Ehr.). *B. verrucosa* Ehr. and *B. papyrifera* Marsh. are often considered to be extreme forms of *B. alba*. It has been shown by Helms and Jorgensen (66) that *B. verrucosa* has 14 and *B. alba* has 28 as the haploid chromosome numbers, while Woodworth (218) has found *B. papyrifera* to be pentaploid, with 35 as the reduced number. From this it would seem that *B. verrucosa* and *B. papyrifera* should each be considered as species coordinate with, and not forms of, *B. alba*.

A slightly different aspect of this same type of contribution of cytology to taxonomy is found in the aid it may give in helping determine the status of a supposed taxonomic variety. An example is found in the case of *Betula papyrifera* var. *cordifolia* (Regal) Fernald. It has been shown by Woodworth (218) that *B. papyrifera* is pentaploid (x=35) while *B. papyrifera* var. *cordifolia* is tetraploid (x=28). From this it would seem that *B. cordifolia* should be recognized as a species distinct from *B. papyrifera*.

Blackburn (10) found two races of *Silene ciliata* to yield 12 and 48 respectively as haploid numbers, and, in case these chromosome differences are correlated with constant visible morphological differences, it would seem justifiable to separate the species into two species.
CYTOLOGICAL DATA IN RELATION TO NATURAL HYBRIDS

The cytological behavior of known hybrids has been studied by many workers. In some cases hybrids behave perfectly normally cytologically: in others the chromosome number of the hybrid is twice as many as the sum of the two gametes instead of being equal to the sum of the two; and in many, while chromosome numbers equal the sum of the two gametes, the cytological behavior of the hybrid is very abnormal. Doubling of the number of chromosomes by hybrids is found in such genera as Papaver (170), Rosa (13), Nicotiana (26) and others. Among the cytological behaviors which are commonly looked upon as evidence of past hybridity, the following may be cited: abnormal meiosis, chromosome lagging in meiotic anaphase, imperfect pairing in meiosis, chromosome extrusion and formation of dwarfed and degenerate microspores, cytomyxis, pollen sterility, and polyploidy.

Cytology may offer evidence bearing upon possible relationships of supposed natural hybrids. Example is found in the case of Betula coerulea Blanchard, as pointed out by Woodworth (218). This form is variously considered a natural hybrid between B. coerulea grandis and B. populifolia and between B. papyrifera and B. populifolia. Cytological data, according to Woodworth, makes the latter relationship improvable, since B. coerulea is diploid (x=14), while B. papyrifera is pentaploid (x=35) and B. populifolia is diploid (x=14). The former relationship is cytologically possible, since B. coerulea grandis is also diploid. Numerous other illustrations might be given.

CHROMOSOMES IN THE GENUS QUERCUS

Chromosome studies in the Fagales have been made upon Betula (66) (218), Corylus, and Alnus (213) (219). In Betula a polyploid series (2x, 3x, 4x, 5x, 6x), with 14 as the basic haploid number, is found. In Corylus three species according to Wetzel (213), show 11 as the haploid number, while in Alnus five species show 14 as the haploid number. In a paper which appeared just as this paper was ready for the press, Woodworth (219) finds 14 as the haploid number in 17 species of Corylus and 14 as the basic number of a 2x and 4x series in Alnus. No member of the Fagaceae has been studied to date. Acorns from the following species of oaks were collected in the

These acorns were planted in moist sawdust in the greenhouse at varying dates during the autumn and early winter. Acorns of *Q. Prinus* had already germinated in the field before they were collected. The radicle and most of the hypocotyl were severed from each and they were then planted in the moist sawdust with approximately 2 centimeters of the hypocotyl protruding from the acorn. In all cases these hypocotyls regenerated 2-5 vigorous new radicles. When the radicles from any particular acorns reached 4-5 centimeters they were removed and washed free from sawdust particles and the root tips were killed in strong chromo-osmic-acetic solution according to Flemming's formula. Germination and regeneration data collected during this work will be presented in a subsequent brief paper, since it has no direct bearing upon the question at hand in this paper.

Root tips were washed free from the killing solution, dehydrated, and brought into paraffin. They were sectioned 12 microns thick and stained in iron haematoxylin. All chromosome counts were made with a Spencer research microscope equipped with apochromatic objectives and aplanatic condenser, and at a magnification of 1900 X. Counts were made from both side and polar views of both the metaphase and early anaphase stages of somatic mitosis.

**OBSERVATIONS**

*Q. alba* (2x=12). Figures 1, 2, 15, 16. Chromosome behavior is apparently normal. Figure 2 shows one chromosome in metaphase plate split before the remaining members have begun to divide. Figure 1 shows four daughter chromosomes (1 pair) considerably larger than the others. This was not a constant feature of this species.

*Q. macrocarpa* (2x=12). Figures 3 and 4. Chromosome behavior normal in every way. Chromosome count of 12 as the diploid number is certain. Figure 3 must have been drawn from a cell in early metaphase. Nuclear membrane had already disappeared but the nu-

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*Acorns from *Q. Prinus*, *Q. velutina*, and *Q. marilandica* were collected by Mr. Ralph Wilcox, Indiana State Forester, and those of *Q. prinoides* were supplied by Mr. Charles Dean from his Arboretum at Bluffton, Indiana.
cleolus marked "n" had only begun to disorganize. The conclusion that it was disorganizing is based upon the ragged contour which it exhibited.

Q. Primus (2x=12). Figures 17 and 18. Chromosome behavior apparently normal. One chromosome in figure 17 marked "a" has begun division earlier than others. No other abnormalities were observed in this species.

Q. Michauxii (2x=12). Figures 19-21. Chromosome behavior apparently normal. One chromosome in figure 17 marked "a" has begun division earlier than others. No other abnormalities were observed in this species.

Q. muhlenbergii (2x=12). Figures 5, 22, and 23. Chromosome behavior somewhat abnormal. Figures 5 and 22 show normal behavior with 12 daughter chromosomes for each pole of the dividing cell. Figure 23 shows only 16 chromosomes. Eight are widely separated while 8 others are in close proximity to each other. It is possible that 8 of these represent daughter chromosomes and the other 8 represent chromosomes tardy in their longitudinal division. In that case the normal number of 24 daughters would ultimately be produced. A number of cases of tardy separation of daughter halves were found and this is a bit of evidence in favor of the probability that 8 of the chromosomes in figure 23 are undivided and 8 divided.

Q. borealis maxima (2x=12). Figures 6, 7, and 24. Chromosome behavior slightly abnormal. Figures 6 and 7 show normal behavior in polar views of metaphase and early anaphase respectively. Figure 24 shows a slight tardiness in the separation of three sets of daughter chromosomes.

Q. velutina (2x=12). Figures 8 and 25. Chromosome behavior normal. Figure 8 shows 14 daughter chromosomes in polar view of early anaphase and figure 25 shows 12 daughters moving toward each pole.

Q. coccinea (2x=12). Figures 9-11. Chromosome behavior somewhat abnormal. Figure 9 shows polar view of an early anaphase with 25 daughter chromosomes. This must have been due to an extra longitudinal split on the part of one chromosome or it could have resulted from failure to divide on the part of a thirteenth chromosome which could have been present before nuclear division as a result of previous non-disjunction. Figures 10 and 11 show normal behavior in
polar views in anaphase and metaphase. Figure 11 shows the disorganizing nucleolus marked "n."

Q. marilandica (2x=12). Chromosome behavior normal. Figure 12 shows polar view of early anaphase with 24 daughter chromosomes.

Q. prinoides (2x=12). Figures 13, 14, and 26. Chromosome behavior normal. Figure 13 shows 12 daughter chromosomes in polar view of late anaphase. Figure 14 shows 24 daughters in polar view of very early anaphase. Figure 26 shows side view of very early anaphase, with 12 longitudinally split chromosomes.

DISCUSSION

A haploid number so low as 6 is interesting when the other three genera studied in the order Fagales show 11 and 14 as their reduced numbers. If polyploidy is absent in the genus Quercus, this will also be a significant fact. Too few species, however, have been studied to warrant any such conclusion at present.

Just as the manuscript for this paper was going to print a paper appeared by Woolworth (219) in which he found that the basic number 14 also holds for Alnus, and that tetraploid species have 28 as the reduced number. Wetzel (213) had previously reported 14 as the reduced number, but found only diploids. Wetzel had reported 11 as the reduced number for Corylus, but Woolworth finds the number to be 14 in his studies. Seventeen species, varieties, and hybrids indicated no evidence of polyploidy. This is of considerable interest, in view of the lack of evidence for polyploidy in Quercus. An attempt will be made to secure material for study of many other species as well as of some of the numerous hybrids which have been described.

It has been pointed out by Osawa (152), Longley (116) and others in Taraxacum, Fragaria, Rosa, Rubus, et al., that within any closely related group, species with smaller chromosome numbers are more primitive and those with larger numbers are more recent in their phylogeny. If this is true, the genus Quercus is more primitive than Betula, Corylus and Alnus. It has, however, been claimed with equal reason in the case of Maize and its relatives (Longley, 112) that more primitive and less specialized members have higher chromosome numbers and more recent and more highly specialized members have lower chromosome numbers. Heilborn (63) expresses the opinion that in case one
group of species is considered for other reasons to be derived from another, the group with the lower chromosome number should be regarded as the more primitive and that with the higher number as the more recent. While phylogenetic lines may be drawn from groups with low to groups with higher chromosome numbers, chromosome numbers alone are insufficient for constructing a phylogenetic structure and are only valuable as supplementary evidence.

From the standpoint of mitotic behavior it would seem that abnormalities and irregularities are too infrequent to indicate anything against considering all of the forms studied in this paper to be bona fide species. It is true that most of the mitotic criteria used for such conclusions are determined only in meiotic divisions, and hence conclusions of this nature based upon mitotic behavior above described are of little value. It should also be noted that chromosome counts based upon cells of roots may be misleading, since it has been shown by Breslawetz (20) and Langlet (101) that individual root cells may have as high as 4x and 8x chromosome numbers and entire roots may exhibit 4x numbers. This could hardly be misleading in the case of Quercus, however, since the number in root cells is already low. No cells were found in this study illustrating the above situation as Langlet found it in *Spinacea oleracea*, *Thalictrum spp.*, and *Cannabis sativa*.

**SUMMARY**

1. Chromosome studies reveal 12 as the diploid number of chromosomes in the roots of each of ten species of oaks.

2. Mitotic behavior is regular and normal in six of the ten species.

3. Four species show such mitotic abnormalities as somatic nondisjunction, tardy separation of daughter halves, and extra longitudinal division of a single chromosome.

4. Tables are included listing 96 genera with references in which polyploidy and aneuploidy has been found.

5. Other tables list genera exhibiting variable chromosome numbers and genera having all species with the same numbers.


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1928. YARNE; S. H. Notes on the somatic chromosomes of the seven-chromosome group of Fragaria. Genetics 14: 78-84. 1929.
EXPLANATION OF FIGURES

Fig. 1. *Q. alba*: polar view of early anaphase showing 24 daughter chromosomes.
Fig. 2. Same: polar view of metaphase. 13 chromosomes, probably one at "a" already split.
Fig. 3. *Q. macrocarpa*: polar view of metaphase showing 12 undivided chromosomes together with disorganizing nucleus marked "n." Nuclear membrane had entirely disappeared.
Fig. 4. Same: polar view of early anaphase showing 24 daughter chromosomes.
Fig. 5. *Q. muelenberga*: polar view of early anaphase showing 24 daughter chromosomes.
Fig. 6. *Q. borealis maxima*: polar view of metaphase.
Fig. 7. Same: polar view of early anaphase.
Fig. 8. *Q. velutina*: polar view of early anaphase.
Fig. 9. *Q. coccinea*: polar view of early anaphase showing 25 daughters.
Fig. 10. Same: showing normal number (24) of daughters.
Fig. 11. Same: polar view of metaphase showing 12 undivided chromosomes with disorganizing nucleus, marked "n."
Fig. 12. *Q. marilandica*: polar view of early anaphase showing 24 daughters.
Fig. 13. *Q. prinoides*: polar view of late anaphase showing 12 daughter chromosomes.
Fig. 14. Same: polar view of very early anaphase showing 24 daughter chromosomes.
EXPLANATION OF FIGURES

Fig. 15. *Q. alba*: side views of anaphase. Each show 12 daughters going to each pole of the dividing cell.

Fig. 17. *Q. primus*: oblique view of metaphase. Longitudinal split is visible in chromosome marked "a."

Fig. 18. Same: side view of anaphase. Twelve daughter chromosomes are moving toward each pole.

Fig. 19. *Q. Michauxii*: polar view of early anaphase. Twenty-four daughter chromosomes.

Fig. 20. Same: side view of anaphase. Twelve daughter chromosomes moving toward each pole.

Fig. 21. Same: side view of anaphase. Non-disjunction apparently affected two chromosomes, 14 daughters going to one pole and 10 to the other.

Fig. 22. *Q. mukdenbergii*: side view of anaphase. Twelve daughter chromosomes moving toward each pole.

Fig. 23. Same: side view of very early anaphase. Only 16 chromosomes present.

Fig. 24. *Q. borealis marina*: side view of early anaphase. Twelve daughter chromosomes moving toward each pole. Tardy separation shown in three cases.

Fig. 25. *Q. velutina*: side view of anaphase showing 12 daughter chromosomes moving toward each pole.

Fig. 26. *Q. pensiades*: side view of very early anaphase showing 12 chromosomes each split longitudinally.