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SEASONAL DEVELOPMENT IN SUN AND SHADE LEAVES

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INTRODUCTION

It is generally agreed that the same species of plants growing under different environmental conditions often produce leaves that are strikingly different. Light is thought to be one of the most important, if not the chief factor, in producing these leaf differences—hence, the term "sun" leaves for plants growing in full sunlight, in contrast to "shade" leaves for plants growing under less intense light. Wylie (1949, 1951) has demonstrated the occurrence of sun and shade leaves at different locations in the crown of isolated trees by intensively studying differences in tissue volume per unit area of blade and in vein spacings. Although other studies, the results of which are summarized by Burkholder (1936) and Daubenmire (1947), have been made on the ecological anatomy of mature leaves, little work has been done in tracing foliar development of sun and shade leaves from their initial stages in the bud to the fully matured leaf. Consequently, the time and manner in which the characteristic differences arise are not well known. The purpose of this study has, therefore, been to undertake such an investigation and to relate certain environmental factors, namely, temperature and light to the developmental morphology of sun and shade leaves.

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oration with Dr. Murray F. Buell, in furnishing the data on light measurements used in this paper.

METHODS

Data reported in this paper have been obtained from *Cornus florida* L. which seems to grow about equally well in full sunlight as in shady woods, and *Viburnum prunifolium* L. which attains maximum vigor and size in open fields. In early October, a fairly mature specimen of each species growing in the dense shade of Mettler's Woods, an oak-hickory forest of central New Jersey, and two other plants of comparable size and age found nearby on an abandoned field of the same soil type as Mettler's Woods were selected for study. Bud or leaf measurements, collections of material for histological examination, and temperature readings were made from October 9, 1952, to July 13, 1953, at approximately monthly intervals in the winter, and at biweekly or weekly visits later in the growing season.

Growth was followed by measuring the length of a series of 5 to 6 vegetative buds along a tagged branch on each plant with a vernier caliper. When this was no longer possible due to the unfolding of the leaves, measurements were made with a mm. ruler. The several buds or pairs of leaves from each branch were averaged to obtain the growth measurements recorded in this paper.

Bud or leaf collections were made by removing a twig close to the median peripheral portions of the plant. The twigs were immediately wrapped

with wet towelling and put into a vasculum. Except for the first few collections when the buds were stored in this condition overnight, the majority of buds and leaves were brought to the laboratory to be fixed within the same day. Buds were descaled, removed from the twigs, and fixed in FAA (5 cc. formaldehyde, 5 cc. glacial acetic acid, 90 cc. of 50% ethyl alcohol). In older leaves, which were always confined to the first pair, small rectangles were removed from the middle of the blade and then fixed in FAA. The leaves from the last two collections were fixed in a formalin-pyrogallol solution (Marengo 1952). The tissues were aspirated, and after fixation they were dehydrated in a n-butyl alcohol series, embedded in paraffin, sectioned transversely with a microtome at 10 microns, and stained with safranin and fast green (Johansen 1940). Serial sections were considered necessary only for the buds.

Temperature records were made with a pair of maximum-minimum thermometers in the woods and with a similar pair in the open field. The thermometers rested on wooden blocks in aluminum shields which were nailed to a post or tree trunk about one meter above ground level. They were oriented so that the bulb pointed in a northerly direction. The thermometers were reset after each reading.

At approximately 1 P.M. on January 17, 1953, a bright cloudless day, light readings were taken with a Weston illumination meter. The photocell was held in a horizontal position about 1.8 m. above the ground. Averages of 36 light readings obtained at 1 m. spacings along a 5 m. square grid were taken in the open, in the woods, and again in the open. The readings which were taken twice in the open were averaged. Further data on light readings for use in this paper were obtained through the courtesy of Dr. M. F. Buell and Dr. J. A. Small.

RESULTS

Growth

There was little growth in both shade and sun leaves of *Cornus florida* and *Viburnum prunifolium* during November, December, January, and most of February. This may be seen in Fig. 1 in which the average length of buds and the average area (length x width) of unfolded blades for the various dates on which they were measured are plotted. Although in both species, the buds of sun plants were slightly longer than those in the shade at the beginning of the experiment, this difference was not considered significant. Early in the experiment, the abandoned field was plowed for cultivation, resulting in the destruction of the

sun plants. Buds of sun plants which were newly selected on February 28 were somewhat shorter than buds of the shade plants.

In *Cornus florida*, no change in bud size was observed until about March 30 for the shade plants and April 8 for the sun plants, when significant increases in length occurred as is evident from Fig. 1. Leaves did not begin emerging from their bud scales until two weeks later, April 8 for the shade plant and April 13 for the sun plant. Growth continued at a fairly steady rate so that by April 27, two pairs of leaves from each bud were completely unfolded, and measured an average of 34 mm. long for the shade leaves and 21 mm. for the sun leaves. Although the rate of leaf expansion increased markedly in both *Cornus* plants during the early part of May, the difference of growth rate between sun and shade plants was even more striking, as may be seen by the sharp divergence in their growth curves in Fig. 1. By the first week in June, growth gradually levelled off. At this time the shade leaves of *Cornus florida* were 1.4 times as long and 1.3 times as wide as the sun leaves. The total area of the shade leaves was about 1.9 times greater than that of the sun leaves (Fig. 1).

Bud and leaf growth in *Viburnum prunifolium* followed a similar pattern to that in *Cornus florida*. The buds of *Viburnum* began to show growth considerably earlier, however, as increased bud length measurements in late February indicated. The first pair of shade leaves had completely emerged by the end of March and measured an average of 19.3 mm. in length while sun leaves were only 11.1 mm. long at the time when they emerged two weeks later. Most rapid growth took place throughout April and early May. The final difference between the two types of *Viburnum* leaves was even greater than that of *Cornus*. The shade leaves of *Viburnum prunifolium* were 1.5 times as long and 1.5 times as wide as the sun leaves. The total area of the shade leaves was about 2.3 times greater than that of the sun leaves.

In addition to larger size, shade leaves were considerably darker green in color, smoother and thinner in texture than sun leaves in both *Cornus florida* and *Viburnum prunifolium*.

Leaf thickness

Total leaf thickness showed considerable variation in the individual leaves. This may be seen from the sharp dips, which are most frequent at the time of greatest morphological change, in the curves of leaf thickness in Fig. 1. Any decrease in leaf thickness from one date to another was

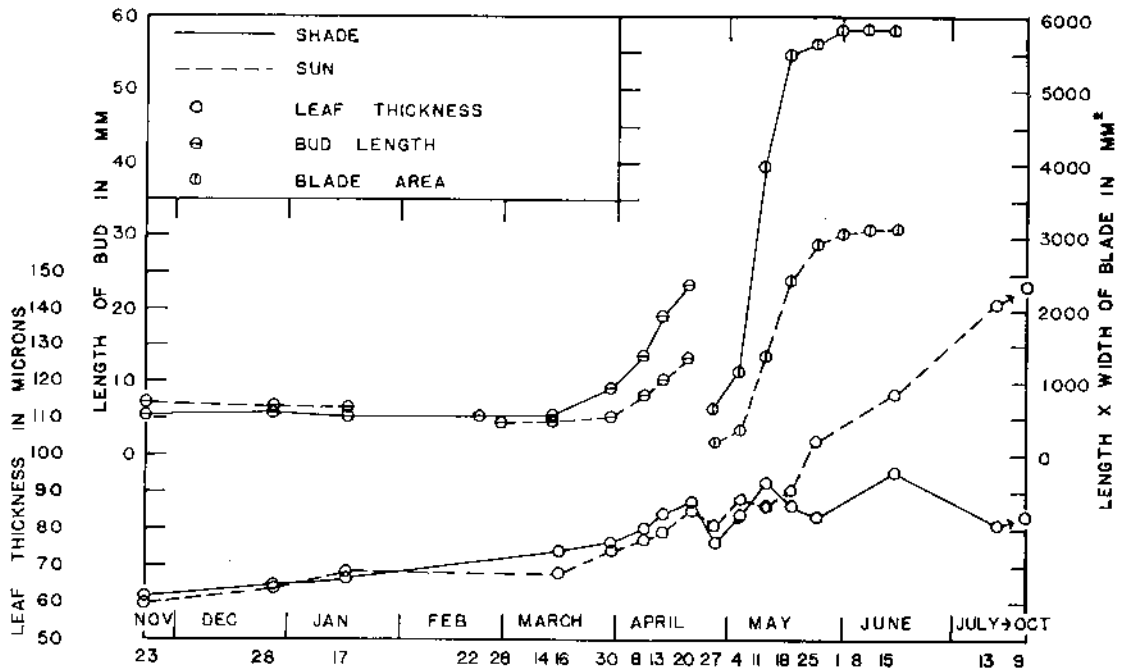


FIG. 1. *Cornus florida*. Growth of sun and shade leaves as measured by length of bud and by area (length x width) of unfolded blade. The break in the curve of bud measurements in the sun plant is due to the interval between which the first experimental plant was destroyed and another sun plant was selected for study. The second part of the curve of bud measurements in the sun plant represents, therefore, the averages of an entirely new set of buds.

Leaf thickness of sun and shade leaves. Mature leaves collected on October 9, 1952 were used to compare leaf thickness with leaves collected on July 13, 1953.

probably due to individual variation in the leaves rather than to the method of measurement, since the average standard deviation for the latter was relatively small, ± 2 microns.

About May 6 for *Viburnum* and May 16 for *Cornus*, the rate of increase in thickness for sun leaves began to exceed those in the shade to such an extent that by July 13 leaf thickness had become obviously greater in sun leaves. Shade and sun leaves for *Cornus* had increased 19.9 microns and 89.4 microns, respectively, from the earliest buds collected to the completely mature leaf, while for *Viburnum* the increases were 45.3 microns for shade leaves and 113.9 microns for sun leaves. Comparison of blade thickness in leaves collected on July 13 with that in leaves collected on October 9 of the previous year indicated that significant increases did not occur in either *Cornus* or *Viburnum* after July 13.

A comparison of the thickness or height of the different cell layers was made between "embryonic" and mature leaves as one of the methods in determining the manner in which the layers contribute to the over-all thickness of the leaf. Leaves referred to as "embryonic" were from fall and winter buds in which some differentiation had already occurred, as will be described later.

Early stages in primordia development are not considered here. There was an increase in thickness in all layers, except the lower epidermis, in shade as well as in sun leaves with the approach toward maturity. However, the total thickness of sun leaves, which was greater at maturity than that of shade leaves in about the same proportion in the two species, was due to a relatively larger increase of cell layer thickness. The palisade, in which marked elongation occurred, was the most important layer in producing this effect. Increased height of spongy mesophyll and upper epidermis also contributed to the final difference, but to a lesser extent. The cells of the lower epidermis measured the same in all four plants both in embryonic and mature stages.

Since the thickness of a leaf depends not only on the height but on the number of cell layers as well, an attempt was made to determine whether there was any significant difference in this respect between embryonic and mature leaves and between sun and shade leaves. In *Cornus florida*, the embryonic leaf consisted typically of 6 layers. However, in some places it was possible to count 7 layers due to additional periclinal divisions in the first layer of the spongy mesophyll. The numerous and closely spaced veins may have been

responsible for this, since increased number of cell layers is usually associated with vein formation. The primarily 6-layered condition persisted throughout the bud stage. In early April, when the leaf cells were undergoing rapid division and cytological changes, 7 layers became as common as 6. In the later collections and in mature leaves, 7 layers predominated, and although intercellular spaces interfered with accurate counting, there were places along the lamina which seemed to consist of 8 layers. There was no apparent difference between sun and shade leaves in the number of cell layers in a comparable stage of development.

The development of cell layers in *Viburnum prunifolium* was similar to that of *Cornus*, except for one additional layer of mesophyll. As in the dogwood, embryonic leaves consisted of 6 layers, although 7 were quite common since there was a great abundance of periclinal divisions in the first spongy mesophyll layer. The 7-layered condition became increasingly noticeable after the emergence of the leaves. During the rapid expansion of the leaf, both 7 and 8 layers (4 or 5 layers of spongy mesophyll) were present. In the final stages, 8 to 9 layers were most common, with sun and shade leaves alike.

Internal structure

Changes in the internal structure of sun and shade leaves at various stages of development were observed primarily in regard to the size, shape, and staining intensity of the cells. Although shade and sun leaves underwent the same general morphological changes during their development, the differences arose principally in the time at which the processes were initiated and the extent to which they were carried out. Most rapid changes in cellular structure coincided with the time when rapid growth and increased leaf thickness were recorded. The embryonic leaves remained in much the same condition for both leaf types and for both species from the time when the buds were first collected in early October to the time when the splitting of the bud scales occurred in March and April.

Cornus florida.—In *Cornus florida*, the embryonic leaves lay folded lengthwise along the midrib with their adaxial surfaces facing each other, so that one half of each blade was inserted between the folded blade of its mate. Veins formed from periclinal divisions in the upper layers of the spongy mesophyll were abundant and close to one another. Three or four major veins, many of which contained well-lignified xylem, were conspicuous along either side of the prominent midrib. Illustrations of the embryonic leaves in Figures 2

and 3 show that the cells of the epidermal and two inner rows of spongy mesophyll layers were similar in size and shape and in having large nuclei and dense cytoplasm. In contrast to the cells just described, those of the palisade and last layer of spongy mesophyll layers were considerably larger and highly vacuolate. A conspicuous mass of cytoplasm surrounded the nuclei in these highly vacuolate cells and stained so intensely with safranin that the nuclei were obscured.

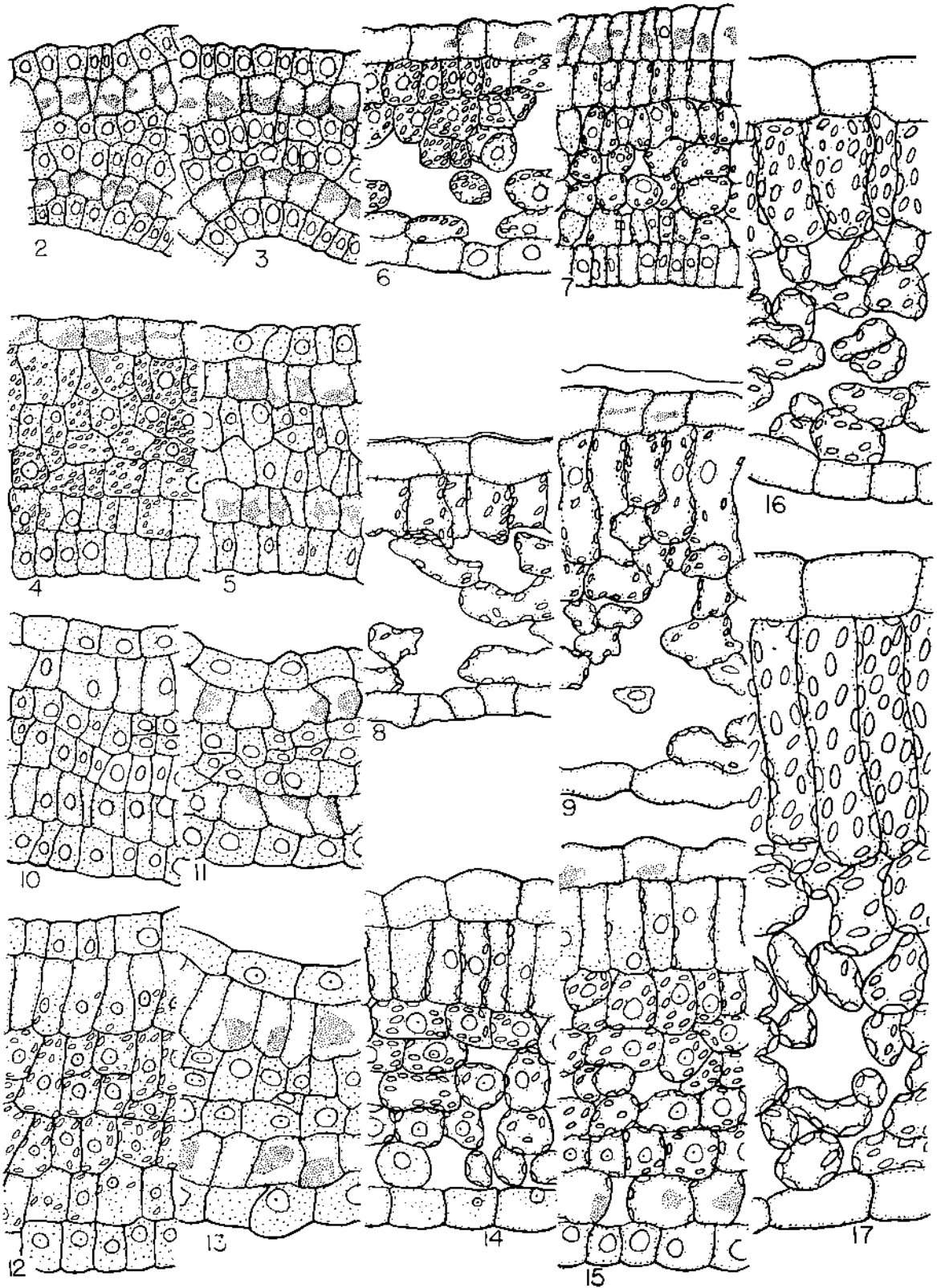
No change was noted from this condition in the shade leaves until March 16 when mitotic figures had become abundant and the staining intensity of the palisade and lower mesophyll layers had decreased. Cell divisions were primarily anticlinal although the first layer of spongy mesophyll had often doubled, as mentioned before.

In the shade leaves of March 30, the sub-marginal cells had lost their densely cytoplasmic appearance and had become similar to the vacuolate cells of the palisade and lower layer of the spongy mesophyll.

Shade leaves collected on April 13 were the first to show early stages in cellular configuration and differentiation which would later characterize the mature leaf (Fig. 4). The majority of the cells were densely cytoplasmic, except for those of the upper epidermis in which conspicuous vacuolation had taken place. Chloroplasts were recognized for the first time at this date. Although the shape of the cells remained approximately the same, there had been an increase in cell size as well as an enormous multiplication of cells between veins. Cells of leaves collected previous to April 13 had been closely compact, but now occasional intercellular spaces among the spongy mesophyll were found for the first time.

Not until April 27 did the cells typical of the mature leaf appear in the shade plants. The upper and lower epidermal cells had broadened and vacuolated considerably by this time as may be seen in Figure 6. The spongy mesophyll cells had also lengthened in a horizontal direction and their corners had become less angular as they were pulled apart, producing large intercellular spaces. The cells beneath the upper epidermis had assumed the characteristics of a distinct palisade layer. The majority of cells had enlarged and vacuolated to such an extent that the cytoplasm was largely confined to the periphery. Chloroplasts had become abundant in both palisade and spongy mesophyll layers.

Except for larger intercellular spaces and cellular enlargement, mature leaves of July 13 (Fig. 8) did not appear to be considerably different from those collected on April 27 (Fig. 6).



FIGS. 2-9. *Cornus florida*. FIGS. 10-17. *Virburnum prunifolium*. Transverse sections of developing leaves. Dark stippling represents shrunken cytoplasm which is stained intensely red so that the nuclei are obscured. Light-

Sun leaves lagged in their development about one or two weeks behind those in the shade. Thus, the cells of the sun leaves were still typical of those of embryonic leaves on April 13 (Fig. 5) though they had become somewhat larger than in earlier collections. The submarginal cells, however, had become vacuolate on April 8 so that they became continuous in appearance with the highly vacuolate subepidermal cells. Small intercellular spaces and increase in vacuolation in some of the upper epidermal cells did not appear in sun leaves until April 20. In this collection, the nuclei of the conspicuously vacuolated cells did not stain as intensely as in some of the earlier leaves.

Sun leaves of April 27 (Fig. 7) had elongated palisades and conspicuous chloroplasts. The cells had become quite vacuolate and the cytoplasm and chloroplasts stained dark red. In contrast to the shade leaves of April 27, the intercellular spaces were considerably smaller, however. Indeed, it was not until May 11 that the intercellular spaces had become large and conspicuous, and the epidermal cells had broadened out to their mature state. Otherwise, further important changes did not occur in the later collections of sun leaves, except for continued elongation of the palisade cells and the development of a thick cuticle, as comparison with the mature leaf in Fig. 9 shows.

Viburnum prunifolium.—Leaf veneration in *Viburnum prunifolium* was involute with an average of 2 to 3 pairs of decussately arranged leaves within the bud. Except for the midrib, the major veins of these embryonic leaves were less prominent than those of *Cornus florida*. Cellular detail was, however, remarkably similar as Figs. 10 and 11 show. However, the vacuolate subepidermal cells did not continue as far out to the margins as in *Cornus* leaves but were replaced by the densely cytoplasmic cells of the submarginal meristem. A difference between sun and shade leaves in staining intensity was evident in the very darkly stained nuclei of the embryonic sun

leaves in contrast to the lighter staining nuclei in shade leaves.

Early stages in differentiation corresponding to those that had occurred in the shade leaves of *Cornus florida* on April 13 were first observed in *Viburnum prunifolium* on March 16. In this latter collection (Fig. 12), the palisade and last layer of spongy mesophyll had become less vacuolate than previously. Chloroplasts appeared to be present, and the palisade cells had elongated to such an extent that they were easily recognized as such.

Definite chloroplasts were seen in shade leaves collected on March 30. The epidermal cells, especially the upper ones, had broadened and vacuolated by this time. The submarginal cells had also become highly vacuolate.

The configuration of the cells as seen in transverse view of shade leaves collected on April 8 appeared to be that of mature leaves. However, extensive cell enlargement and the formation of intercellular spaces continued to occur in older leaves (Fig. 16).

The sun leaves collected on March 16 (Fig. 13) were still in a relatively embryonic condition at the time that shade leaves, which were collected on the same day (Fig. 12), were undergoing conspicuous differentiation. However, the sun leaves rapidly overtook the shade leaves, so that by April 8, sun and shade leaves were not unlike in morphological structure (compare Figs. 14 and 15). The first sun leaves to show marked differentiation were those of March 30—the extent of development being almost identical to that of shade leaves collected on March 16. Definite chloroplasts and conspicuous vacuolation in the submarginal layer had occurred by April 8 for the sun leaves (Fig. 15). As in the shade leaves, there was little difference between April 8 and the last collection made on July 13 in cell shape or content, though cell size and intercellular spaces

er stippling is used to indicate less intensely stained cytoplasm. X520. FIGS. 2, 3. Embryonic shade and sun leaves respectively, collected on October 9. Note the highly vacuolated cells in the subepidermal layers. Epidermal and inner mesophyll layers are densely cytoplasmic. FIGS. 4, 5. Emerging shade and sun leaves respectively, collected on April 13. Note that in contrast to the sun leaf which still remains in a relatively embryonic condition, the shade leaf has differentiated to the extent that the upper epidermis is conspicuously vacuolate and chloroplasts are recognizable. FIGS. 6, 7. Completely unfolded shade and sun leaves respectively, collected on April 27. Cells are vacuolate in both leaves but the sun leaf has considerably smaller intercellular spaces. FIGS. 8, 9. Mature shade and sun leaves respectively, collected on July 13. Greater blade thickness in the sun leaf, due chiefly to the marked elongation of the cells and thicker cuticle, is evident. FIGS. 10, 11. Embryonic shade and sun leaves respectively, collected on November 23. The cytoplasm of the subepidermal layers in the shade leaf is somewhat lighter in staining intensity than in the other embryonic leaves. FIGS. 12, 13. Emerging shade and sun leaves respectively, collected on March 16. Note that the cells of the shade leaf are undergoing noticeable differentiation while those of the sun leaf are still embryonic in appearance. FIGS. 14, 15. Completely emerged shade and sun leaves respectively, collected on April 8. Both leaves appear to consist of mature cells. The shade leaf shows less intercellular space and there are remnants of the intensely staining cytoplasm in the last row of spongy mesophyll. FIGS. 16, 17. Mature shade and sun leaves respectively, collected on July 13. Cell elongation, especially in the palisade layer, is evidently responsible for the considerably thicker lamina in the sun leaf.

were considerably larger in the fully matured leaves (compare Figs. 15 and 17).

Upper epidermis

Paradermal examination revealed differences in size and shape in the upper epidermal cells between sun and shade leaves of *Cornus florida* as the series of drawings in Figures 18-25 show. This difference corresponded to the time and extent to which growth in leaf area occurred in the two types of plants. The contrast between the epidermal cells of sun leaves and those of shade leaves was most striking on May 4 (Figs. 20 and 21). At this time, their slightly larger size and waviness in the shade leaf, which had been noticed on April 27 (Figs. 18 and 19), had become greatly exaggerated. Epidermal cells of sun leaves collected on May 11 (Fig. 23) were not as small and as angular as those from earlier sun leaves. By June 15 (Figs. 24 and 25), the difference between the two leaf types had diminished although the epidermal cells of the sun leaves continued to be smaller and less contorted in shape than those of shade leaves.

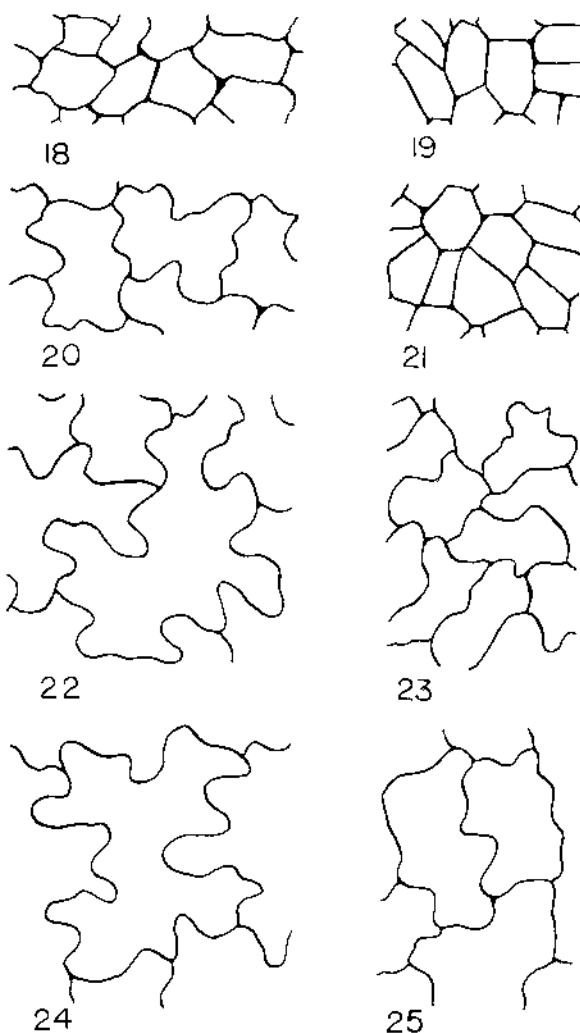
Temperature

The minimum temperature in the woods was generally higher and the maximum temperature generally lower than corresponding temperatures in the open. While the differences varied from 0 to 11.6° F., the minimum temperature in the woods was 6.3° F. higher on the average than that in the open, and the average difference in maximum temperatures between the two areas was 6.5° F.

There was little difference in mean temperature between open and wooded conditions. The mean temperature in the woods was slightly higher during most of the cooler months, however. Although there was fluctuation from one date to another there was a gradual upward trend in all temperature readings with the approach of spring.

Light

The light reaching the 1.8 m. level in Metter's Woods on January 17, 1953, was 44.9% of that of maximum sunlight in the open field. Light readings taken on December 13, 1950 by Buell and Small yielded a similar result, 44.8%. The recorded light readings in the spring of 1950, April 22, as the angle of incidence of the sun increased, thus decreasing the amount of light intercepted by branches and tree trunks, resulted in a relatively high figure of 67.6%. All during the month of May, there was a rapid decline from this percentage of light penetration, with a gradual levelling off in June and July. By July 21, the typical



FIGS. 18-25. *Cornus florida*. Paradermal views of the upper epidermis. X520. FIGS. 18, 19. Shade and sun leaves respectively, collected on April 27. FIGS. 20, 21. Shade and sun leaves respectively, collected on May 4. FIGS. 22, 23. Shade and sun leaves respectively, collected on May 11. FIGS. 24, 25. Shade and sun leaves respectively, collected on June 15. Note that the cells of the sun leaf remain relatively small and regular in shape while those of the shade leaf increase in cell size and in waviness of outline to a marked extent and at a greater rate.

figure for light penetration through a completely foliated deciduous forest was reached—about 3%.

DISCUSSION

There is a gradual increase in growth in the winter buds of *Cornus florida* and *Viburnum prunifolium* during March after a winter period of relatively little growth, and then a rapid advance in April, as curves plotted from the growth measurements seem to indicate. Similar growth curves were obtained by Moore (1909) who studied the

winter buds of the common tree and shrub species of Massachusetts.

One of the few papers concerned with the anatomy of the embryonic leaf is that by Smith (1934) who made an intensive study of about 20 common deciduous trees and shrubs. He concludes that embryonic leaves consist of "... densely protoplasmic parenchymatous cells which are of uniform size." He notes that cells of *Cornus florida* dissected in April which presented a typically embryonic structure were 6-layered and similar in size and shape and closely compact. The present study of *Cornus florida* and *Viburnum prunifolium* does not completely agree with his observations, however. In the embryonic leaves of both species, the cells are not all alike in size, shape, and staining intensity but are arranged in distinctive layers. The upper and lower subepidermal layers consist of large, highly vacuolate cells and darkly staining nuclei, in contrast to the epidermal and innermost cells which are smaller and more densely cytoplasmic.

Growth of shade leaves of *Cornus florida* and *Viburnum prunifolium* begins earlier in the spring and is manifested by more rapid increases in bud length and by general changes in internal structure one or two weeks in advance of sun leaves. Nordhausen (1903) also observed that buds of shade branches taken from the interior of the crown of trees begin earlier growth than sun buds. However, Watson (1942) states that sun leaves of *Hedera helix* completed their development in 4 weeks while shade leaves did not finish until 11 weeks.

Shade leaves of *Cornus florida* and *Viburnum prunifolium* were also found to be larger in area than those growing under full sunlight. Paradermal views show that the epidermal cells of these shade leaves are not only more distorted in shape but considerably larger. Shank (1938) also observed that shade leaves of *Cornus florida* were larger in size than sun leaves. Isanogle (1944), on the contrary, obtained a smaller area from *Cornus florida rubra* and *Acer platanoides* shade leaves. Her experiment was based on shading to varying degrees one bud from each pair of opposite buds on a twig. Besides the difference in total leaf area, the size and shape of the epidermal cells as recorded by her do not agree with those of the present investigation. She observed that the epidermal cells of the shade leaves were smaller and there were more cells in a given area than sun leaves. Hanson (1917), Clements (1904), and Bergen (1904), all of whom considered a wide variety of species also noted that leaves of plants growing under reduced

light were larger in every case. Although greater area was also obtained from shade leaves in such plants as *Renanthera* (Groom 1893), tobacco (Hasselbring 1914) and castor bean (Penfound 1932), there have been other studies made which indicate that sun leaves are larger in *Cucumis* (Gregory 1928) and *Cornus stolonifera* (Marsh 1941). Whether the maximum size attained is greater for shade or for sun leaves, therefore, remains an open question, subject to differences in species and in methods employed by the various investigators.

Mature sun leaves of *Cornus florida* and *Viburnum prunifolium* are definitely thicker than mature shade leaves. Since there is not a significant difference in the number of cell layers between the two leaf types, thickness in these two species, at least, is contributed mainly by vertical cell elongation. Similar results were obtained by Isanogle (1944) using *Cornus florida rubra* and *Acer platanoides*. In some plants, however, such as *Helianthus* (Clements and Long 1935) and *Pistacia lentiscus* (Bergen 1904) a doubling of the palisade layer has been observed in sun leaves. Snith (1934) is of the opinion that while the mature shade leaf retains the same number of cell layers characteristically found in the embryonic condition, the mature sun leaf may have a greater number of layers than originally.

There is little apparent difference between embryonic sun and embryonic shade leaves of *Cornus* and *Viburnum*. Sun and shade characters are present in mature leaves probably in response to differences in the environment. Cormack and Gorham (1953) found that mature leaves of *Menziesia glabella* and *Lonicera glaucescens* developed sun and shade characters corresponding to the environment in which the leaves expanded and matured rather than to the environment in which their buds developed. Nordhausen (1903) believed that sun and shade characters are already predetermined in the bud. He observed the development of leaves from sun and shade buds by keeping twigs cut from beech plants immersed in water. Sun and shade leaves retained their characteristic features even though shade buds were allowed to develop in full sunlight while sun buds developed in the shade.

The importance of light as a factor in determining sun and shade characters is a well-known fact. Less attention is generally paid to other factors which may be equally or more important in a study of this type where the plants are not grown under controlled laboratory conditions. Temperature differences between the woods and the open field may be important in determining the differ-

ences between sun and shade plants in the time at which leaf development is initiated. The narrower range in maximum and in minimum temperatures as well as a generally higher mean temperature in the woods may influence the early growth of shade leaves. This belief is largely based on the findings of Gregory (1928) who thought that the unfolding of the first foliage leaves at suboptimal (70.8° F.) levels is controlled largely by temperature. He also demonstrated that temperatures above the optimum (76.8° F.) inhibit cell division in the leaf primordia and there is a decline in rate of growth accompanying supraoptimal (90.3° F.) temperature increases. The smaller leaf area of both species in the present investigation may possibly be due to exposure of the plants growing under direct insolation to supraoptimal temperatures.

Although soil moisture conditions were not considered here, a number of workers (Clements and Long 1935, Penfound 1932, Bergen 1904, Hasselbring 1914) have shown that there is often a close relationship between this environmental factor and plant structure. Plants growing in their natural habitat are continually being subjected to a complex of environmental factors. Therefore the differences observed in plants of the same species growing in different environments can best be understood by analyzing the effect of each factor individually and by varying the factors in as many different combinations as possible. Further research in following the developmental sequence in sun and shade leaves should thus be made in the laboratory under controlled conditions and in the field where as many different environmental factors as possible should be measured.

SUMMARY

1. The development of sun and shade leaves of *Cornus florida* and *Viburnum prunifolium* growing under contrasting light intensities was studied for differences in growth, thickness, and morphological structure. Temperature and light conditions in Mettler's Woods and in an open field, where the plants were found to occur, were compared.

2. Leaves of *Viburnum* emerged and unfolded earlier than those of *Cornus* in the spring. In both species, larger leaf area, which was produced by earlier and larger increases in growth rate (especially at the time of most rapid leaf expansion), was attained by shade leaves.

3. Mature sun leaves were considerably thicker than mature shade leaves. Sun and shade leaves increased in thickness in about the same proportions during the period of early growth incre-

ments. The greatest divergence between leaf thickness in the two leaf types occurred later than the corresponding differences in leaf area.

4. Cell elongation, especially that of the palisade tissue, was found to be responsible for increases in blade thickness. There was no difference in the number of cell layers between sun and shade leaves, though it was greater in the mature rather than in the embryonic leaf.

5. Embryonic leaves of sun and shade plants were basically alike in cell structure. The palisade and lowest spongy mesophyll were distinctly different from other layers. Changes in vacuolation of the embryonic cells were most marked during the time of leaf emergence and unfolding. Chloroplasts were also recognizable at this time. The initiation and formation of cells characteristic of the mature leaf was decidedly earlier in shade leaves, as was the case for increase in bud length and leaf expansion.

6. Paradermal views showed the cells of the upper epidermis in shade leaves to be considerably larger and more distorted in shape than those in sun leaves.

7. The drastic reduction of light penetration during and after the canopy had closed in the woods was associated closely with the appearance of differences between sun and shade leaves in blade thickness.

8. Temperature, which was on the average higher and less extreme in the woods, may be one of the determining factors in producing earlier development in shade rather than sun leaves.

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THE SEASONAL LIFE HISTORY OF DAPHNIA IN AN ARCTIC LAKE

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INTRODUCTION

The purpose of the present paper is to discuss in some detail the population of *Daphnia* in Imikpuk, a shallow lake near the Arctic Research Laboratory, Point Barrow, Alaska. Of the planktonic animals present, *D. pulex* var. *tenebrosa* Sars 1898 is the most important in terms of bulk, although two others are much more numerous. The material consists of quantitative samples taken on 11 dates in 1951 and 30 dates in 1952, and some additional qualitative samples. This is one of a number of papers being prepared on the results of a study of Arctic limnology, a preliminary report of which has been published (Comita and Edmondson 1953). These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and the University of Washington, NR 165-080.

The entire responsibility for the conduct of the field work was undertaken by Dr. G. W. Comita, then a graduate student, who served as Chief Scientist on the project. The author is glad to take this opportunity to express his appreciation of Dr. Comita's initiative and painstaking work which was carried through successfully under Arctic conditions, and work in connection with all phases of the project in Seattle.

In the 1951 field work, Dr. Comita was assisted by Mr. Robert A. Main, and in 1952 by Mrs. G. W. Comita. A number of other assistants have contributed to the present paper by making counts, measurements and calculations; to Mr. Curt Wiberg, Mr. Robert Black, Mr. Russell Zimmer, and Mrs. H. E. Broadbooks, the author expresses his thanks for their careful work. Thanks are due others who provided help. Dr. John L.

Brooks of Yale University identified the *Daphnia*, made special examinations of material, and has been very generous with information. Mr. John J. Koranda kindly took plankton samples after the lake had frozen in 1952. Dr. John L. Mohr sent living animals and ephippia in 1954. Mrs. R. G. Merritt helped prepare figures for publication. Special thanks are due Miss Patricia Dudley who made the photographs in Figure 2.

LIMNOLOGICAL CONDITIONS

A paper now in preparation will give a detailed discussion of the limnology of Imikpuk. To avoid duplication, only the necessary minimum of general information will be presented here. Imikpuk is approximately elliptical in shape, 1065 meters long, 680 meters wide, with a maximum depth of 2.8 meters. It contains no higher vegetation, but there are areas on the bottom where *Vaucheria* forms mats. The bottom material near shore is composed of silt and gravel, while the deeper deposits are much softer. Imikpuk is freely exposed to the high winds that blow all summer with varying intensity and direction. (Fig. 1A).

In 1952, when the first sample was taken on July 6, the lake had only partly melted around the edge. It was not possible to take a quantitative sample then nor on July 8, but by July 10 the floating block of ice was small enough to permit launching of the boat and operation of the sampler. The last ice was observed on July 21. During the summer samples were taken frequently, the longest interval being 5 days, until September 21 when the last quantitative sample was taken.

The temperature rose rapidly after the lake