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On the Movements of Petals

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I.—On the Movements of Petals

BY ESTHER PEARL HENSEL

INTRODUCTION

The following paper has to do with an investigation of the physical causes which bring about opening and closing movements, periodic or otherwise, of certain flowers. With that end in view, seven different species of flowering plants have been experimented upon directly, a much larger number being simply observed with respect to the nature, time, etc., of their anthotropic movements.

Movement consists in the corolla taking upon itself either the open or closed position for certain periods of the day or night; for example, the morning glory (*Ipomoea purpurea*) opens early in the morning (from 4:00 to 5:00 A.M., in the greenhouse) and closes from II:00 A.M. to 2:00 P.M., or even 5:00 P.M. on cool days, while the common dandelion (*Taraxacum taraxacum*) opens from 7:00 to 8:00 A.M. and closes from 5:00 to 6:00 P.M.

In the closed position, the petals or florets may assume practically the same position as that of the bud, as in the gentians, asters, dandelions, etc.; often, however, the edges of the petals only touch, forming a dome inside of which the stamens and pistil are well protected, as in the wild rose and in the tulip. In

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some genera, as in Mentzelia, the sepals may stay reflexed after the first opening.

For convenience, flowers which are influenced in their opening and closing by the amount of heat present may be grouped into four classes as follows:

- I. Day-bloomers.
 - Those that open only during the day, but for two or more (sometimes several) days in succession (hemeranthous).
 - 2. Those that open only during one day or part of a day, then the corolla withering, deliquescing, or dropping at once (ephemeral-hemeranthous).

II. Night-bloomers.

- 3. Those that open only during the night, but for successive nights (nyctanthous).
- 4. Those that open for only one night or part of one night (ephemeral-nyctanthous).

All flowers not included in these types open at any time of the day or night and stay in this condition through day and night until the end of their existence, irrespective of the amount of heat present. Whether a flower is a day-bloomer or a nightbloomer seems to depend upon nothing so much as habit, the conditions surrounding the plant, its environment, in no way influencing this aspect. The purpose of this paper is to explain the causes of opening and closing in any type by means of experiments.

The form of the corolla and its physical condition when mature, i. e., dry shriveling, deliquescing, deciduous when yet fresh, etc., do not seem to influence the kind of movement; any type, for instance day-bloomers, may have the extreme variety of forms of corolla, from undivided, as in the morning glory, to divided, as in the tulip; the corolla itself may vary in its physical characteristics, e. g., in ephemeral day-bloomers from dry shriveling in the spring lily (*Erythronium albidum*) to deliquescing in the spiderwort (*Tradescantia bracteata*) and deciduous.

in flax (*Linum usitatissimum*). The corolla may also change in color upon withering, as in the evening primrose (*Pachylophus caespitosus*), the waxy white petals turning a dull pink upon withering.

The life of an individual flower varies from a few hours, as in the ephemeral species, to many days. According to Kerner and Oliver, the range is from 3 hours (in *Hibiscus trionum*) to 80 days (in *Odontoglossum rossii*). Whether the length of life of an individual flower and the closing at certain hours have anything to do with the pollination of the flowers by certain insects is not a question to be discussed here, however interesting it may be. The two are closely connected but are not cause and effect.

Following is a list of plants which show these movements, those preceded by a * having been experimented upon directly; the others were simply observed. The list is very small when compared with the cases actually known, since it simply includes those coming under personal observation within the last two or three years:

· I. Day bloomers.	DAYS	OPEN A.M.	CLOSED P.M.
1. Opening and closing repeatedly.			
Agoseris greenei, (Gray) Rydb.	1 - 2	7:00- 8:45	2:00-3:00
Claytonia virginica L.	2	8:00- 9:00	6:30-7:30
Crocus vernus All.	12	9:00-10:00	4:00-5:0 0
Erigeron flagellaris Gray	2	9:30-10:30	5:00-7:30
Gentiana acuta Michx.	4	8:00-10:00	5:00-6:00
Gentiana frigida Haenke	4	8:00-10:00	5:00-6:00
Gentiana parryi Engelm.	4	8:00-10:00	5:00-6:00
Lactuca scariola L.	2+	8:00- 9:00	3:00-4:00
Machaeranthera aspera Greene	4+	7:00-10:00	4:00-6:00
Rosa woodsii Lindl.	4	6:00-10:00	7:00
*Ta axacum taraxacum	2 - 5	6:00- 8:00	5:00-7:00
Tulipa gesneriana L.	5-7	9:00-10:00	5:00-6:00
2. Opening and closing but once, 1 d	ay or less		
Epilobium adenocaulon Haussk.	•	9:00	3:00-5:00
Erythronium albidum Nutt.		8:00- 9:00	6:00-7:00
Specularia perfoliata (L.) A.DC.		7:00- 8:00	3:00-7:00
*Linum usitatissimum L.		5:00- 8:00	10 а.м2
*Oxalis stricta L.		8:00- 9:00	3:00-4:00
Portulaça oleração I		10.00 11.00	3.00 4.00

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	OFEN A.M.	CLOSED I.M
Sisyrinchium angustifolium Miller	9:30-11:00	5:00-6:45
Tradescantia bracteata L.	5:00- 6:00	4:00-5:00
II. Night bloomers	OPEN P.M.	CLOSED A.M.
3. Opening and closing repeatedly.	01	
*Mentzelia nuda (Pursh.) T. & G. 4-5 days	3:00-5:00	5:00- 6:00
4. Opening and closing but once. 1 day or less	•	
Allionia linearis Pursh.	5:00-6:00	8:00- 9.00
Allionia nyctaginea Michx.	4:00-5:00	9:00-10:00
Cereus grandiflorus Mill.	8:00-9:00	2:00- 3:00
Datura stramonium L.	5:00 6:00	8:00-11:00
*Ipomoea purpurea (L.) Roth.	4-5 А.М.	10:30 a.m3 p.m.
*Mirabilis jalapa L.	6:00-9:00	10 а.м4 р.м.
Onagra biennis (L.) Scop.	5:00-6:00	9:00-10:00
*Pachylophus caespitosus (Nutt.) Raimann	5:00-8:00	9:00-11:00
Silene hallii Wats.	5:00-7:30	9:00-12.00
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All flowers not included in the previously stated types stay open through the day and night during their period of existence. Such flowers do not open because of temperature changes but because they have reached a certain period of growth; the largest number of flowers belong here. Of the other classes, a very large number are day bloomers, a smaller number night bloomers.

Ephemeral flowers behave much as those flowers which open and close for several days, that is, they are influenced by temperature variations; in their opening, however, they show a close relation to the large number of flowers which open only once and stay open until they die (generally after several days); the chief difference is that the ephemeral species are more regular in the time at which this process occurs.

HISTORICAL REVIEW (FROM 1686 TO 1905)

So much has been written on the subject of flower movement, and with such different views as to its cause, that it seems advisable to give a rather detailed account of the work of the different investigators.

Pfeffer reports Cornutus as having said as early as 1686 that heat caused, or at least hastened, the opening of the anemone.

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Whether this was a theory or had really been found out from experimentation, I am not able to ascertain, as I do not have access to the original paper.

Linné in 1751 gave many instances of flower movement. He made a list of forty-six species with the time of opening and closing of each. These he called "sun flowers" ("solares flores") and divided them into (a) those which the conditions of shade, humidity of the air, and atmospheric pressure affect directly ("meteorici"); these do not open during cloudy or rainy weather; (b) those that open in the morning but close before evening, at different times according to the light ("tropici"); (c) those that open and close at a certain hour of the day ("aequinoctiales"). These last he grouped into his "Floral Clock" according to the hours of the day at which they open and close their flowers, every hour being represented by two or three opening or closing flowers; composites were also included here since the ray florets act much as the petals of simple flowers. It is quite significant of the importance of the subject that it should have been known even thus well over two hundred years ago.

According to Royer, Duhamel (a contemporary of Linné's) attributed opening to heat and turgescence, but said that heat rarified the cell sap, quite contrary to the later view that turgescence is due to an excessive flow of liquids to certain regions.

Dutrochet in 1836 gave as the cause of the opening and closing of four-o-clocks (*Mirabilis jalapa* and *Mirabilis longiflora*), the morning glory (*Ipomoea purpurea*), and the dandelion (*Taraxacum taraxacum*) turgescence and the filling of the fibrous tissue with oxygen. He attempted to explain the process in this way: on the external side of the corolla nerves, parenchymatous tissue is arranged in longitudinal rows, while on the internal side there is fibrous tissue, the two tissues tending to curve in opposite directions and thus draw along the other tissues surrounding them. Opening and closing result from the alternately predominant action of one or the other tissue. The parenchymatous tissue tends to curve outward by filling with water, thus causing opening in flowers of Mirabilis; the fibrous tissue curves outward by the chemical action of the oxygen in the water, causing closing

of the flower. The reason that Mirabilis closes earlier than Convolvulus is because it is easier for Mirabilis to fill its fibrous tissue with oxygen under the influence of light and heat. In the case of flowers opened and closed for several days, as the dandelion, etc., the fibrous tissue becomes gradually filled with oxygen during the day when the flower is open. At the same time, the sap current is diminished because of the decreasing light, thus decreasing turgescence; in consequence, the cellular tissue curves inward and the flower closes.

Hermann Hoffmann (1850) brought together results showing that temperature was the all-important factor in opening and closing, light influencing the processes only as it contained heat rays. His experiments were conducted upon foliage leaves of Oxalis tetraphylla and Mimosa pudica, and the flowers of Tolpis barbata, Oenothera lindleyana, Onagra biennis, Lotus peregrinus, Ipomoea purpurea, and Eschscholtzia. These were the principal species experimented upon; several others, however, were used to help disprove that sleep movements are caused by moisture in the air, electricity, or the expansion of gas within the plantcauses to which opening had been ascribed. He further proved that opening can be caused artificially at the hour of most profound sleep by simple increase of heat without the aid of light, but that the prolongation or excess of heat caused sleep. He stated also that the dilatation of the sap by the action of heat could not cause the daily expansion of a flower, since water expands only 1/22 of its volume between 0° and 100° C.

Royer (1868) affirmed that variations of heat and turgescence --complements of each other-were the cause of all flower movements. Taraxacum taraxacum, Crocus, Tulipa gesneriana, Ficaria ranunculoides, and Bellis perennis were experimented upon by him as examples of sleeping flowers, i. e., those that open and close several times. He made a close distinction, however, between sleeping flowers and ephemeral ones, such as Convolvulus arvensis, C. sepium, Glaucium flavum, Stellaria media, and several Veronicas, which sleep only in appearance and close only when their existence is ended. These latter, he said, could be transformed into sleeping flowers by humid earth, shade, late

flowering, etc.; and, vice versa, sleeping flowers could be made ephemeral by increased heat and dryness, or when the whole flow of sap toward the flower was hindered. In his opinion, turgescence and heat caused opening and closing by the unequal dilatation of the faces; without heat there was no dilatation, without turgescence no elasticity. The internal face, on account of its position, was less exposed to the action of the air and dilated more than the outer, causing opening. Prolonged and abundant transpiration diminished turgescence, and sleep occurred; then the internal face was shortened and the outside became plane and convex.

De Candolle, a contemporary of Royer, has been stated by the latter as having emphasized light as the factor causing opening and closing movements.

Light and moisture, and a certain law of periodicity, were stated by Balfour (1875) to be the cause of sleep movements of flowers, periodicity (or habit) being given almost first place.

Darwin (1881), as we should expect, held to the latter view, saying that movement was a quality inherited by both plants and animals. He agreed with Pfeffer that nyctitropic movements of flowers are caused by unequal growth of the two sides of the petals due to temperature changes.

Gustav Zacher (1881) ascribed floral movement of *Lotus or*nithopodiodes to light, but more especially to the variability of the amount of water in the water vessels.

Pfeffer reports Hofmeister to have said that temperature changes caused movements in garden tulips.

According to Sachs (1882 and 1887) light was the all-important factor; temperature and humidity were given a secondary place, it being only occasionally, as in Tulipa and Crocus, that they were the important factors. However, Pfeffer's experiments (1876) were mentioned by him, and he certainly considered them valuable. Pfeffer's experiments on Tulipa, Crocus, Adonis vernatus, Ornithogalum umbellatum, and Cochicum autumnale make heat the most important element. He considers opening and closing mere growth movements; heat and light, as they diminish at night, cause the outer surface to grow faster

than the inner, and the flower closes, or, in the case of flowers remaining open at night, meteoric influences affect the internal and external surfaces in the opposite way.

It is due to Anton Hansgirg, first in 1890, and then later, that we have such exhaustive lists of plants possessing what he calls "gamotropic" and "carpotropic" movements, principally the latter. Under the former term he includes movements that serve to protect the ovary and stamens and to make cross-fertilization easy; under the latter, those growth movements of flower stems by which the flower is placed in a certain position at one period of its growth, and in a different one at a later period; for example, the morning glory bud and flower are erect, while the fruit is pendulous. Movements of the calyx, involucre, etc., to protect the fruit, are also included under "carpotropic" movements. The real cause of what he terms "gamotropic" movements, those serving to protect the ovary, stamens, etc., he does not state directly, but in a later paper he remarks that carpotropic nutation movements are not so dependent upon the daily change of light as the nyctitropic and gamotropic appearances. He also makes the statement that carpotropic movements must be distinguished from those similar to nyctitropic and gamotropic ones which occur through epinasty and hyponasty-the merely passive movements without growth. In a still more recent article (1892) he adds a few facts on the subject, but offers no explanation, saying that it is yet to be proven whether periodic opening and closing are caused by changing epinastic and hyponastic growth of flowers. He states that such movements are inconstant in different genera of the same family. The same lists of species were continued in 1896 when he assigned to gamotropic and to nyctitropic movements light and heat as causes. He divides gamotropic flowers into: (a) those periodically opened and closed, (b) ephemeral, day or night, (c) those that open only once and stay thus until withering (agamotropic), and (d) those that are pseudocleistogamous and hemicleistogamous. Light is given importance, for ephemeral flowers can be made to become two-day flowers if deprived of light. In 1902 still further additions were made to these lists of species possessing types of car-

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potropic and gamotropic movements. Here, as in earlier publications, he concludes by saying that the exact causes are unknown.

In a paper published in 1890, Hermann Vochting treats of the influence of temperature upon the flower movements of *Anemone stellata*—those of the flower pedicel especially—but he also mentions that the opening and closing are connected with the unequal growth of the upper and under sides of the basal portion of the floral leaves.

Friedrich Oltmanns (1895) gives to light the most important place in causing nyctitropic movements of flowers, the more intense the light, the earlier the closing or opening, a certain quantity of light being necessary for the withering of ephemeral flowers or the closing of periodically moving ones. He makes the statement that Royer, De Candolle, Dutrochet, and Meyen have all thought light an important factor, while Pfeffer considers that heat works with light in causing flowers to open in the morning.

Kerner and Oliver (1895) say that the opening of flowers is promoted by sunshine, but whether it is light or heat is to them a question. Kerner says that the amount of pollen produced and the number of flowers on a plant directly affect the length of time a flower stays open. As to the physical cause, the sun's rays' affect the tension of the tissues, but just how is not known. The movement of flowers—the change in the position of the petals—is only another expression of heat energy. The author suggests that, since anthocyanin converts light into heat, if the petals or sepals are white on the inside, the under surface must be tinged red, violet, or blue in order to cause opening.

From Strasburger and Schimper (1898) it is to be inferred that light and temperature variations are the cause of opening and closing. The same two factors are said by Ludwig Jost (1898) to cause nyctitropic movements. They work together, the two sides of a petal reacting in an opposite manner due to internal causes. His experiments were made principally upon tulip and dandelion flowers. He gives three possibilities as to the growth of the two sides. The first is Pfeffer's: the growth of the concave side is hindered by the growth of the convex side,

i. e., the concave side is passive. It is affected, later, as much by temperature changes as the convex side. The second (the most probable according to the author) is that the opposite sides react in an opposite manner to temperature changes, the restraint of the concave side being recognized as an active retardation in growth. The third possibility is that the concave side is not usually influenced by temperature changes.

Reynolds Greene's view (1900) as to the nervous mechanism of a plant is especially interesting, although flower movement is not discussed by him in his *Vegetable Physiology*, in which the former discussion is given. He says that a plant has a nervous mechanism, and that stimuli are conducted from cell to cell through the connecting strands of protoplasm which pass through the cell walls, and contrasts this with the nervous system of animals. The root tip, at a short distance from the apex, the three hairs on the leaf of "Venus' Fly Trap," etc., are special sense organs or regions, which, however, are not anatomically differentiated. The protoplasm in those parts receives the stimulus due to the physiological differentiation of the protoplasm; hence plants can respond to a more delicate stimulus than animals. The lack of coordination, however, may cause the stimulus to produce a harmful effect on the plant.

J. Bretland Farmer, in an article which appeared in the New Phytologist for March 19, 1902, refuses to accept the theory that epinasty and hyponasty cause opening and closing of the tulip flower. He attributes movement to a localized irritable tissue (as in Dionaea) on the outer surface of the petals. This area consists of active cells capable of altering their state of turgescence, or, at any rate, their size, more readily and effectively than the cells which form the more internal tissue layers. The intercellular spaces are large in these perianth leaves, and the cells so arranged that they give a certain amount of shearing action without damaging the cells themselves. One experiment, made by Farmer, is to put a median longitudinal section in dilute KNO₃ solution, which causes the petals to straighten out (open). To prove that there is an irritable tissue, he puts the petal in water, when it closes, or, rather, curves in, then in alcohol to kill

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it, and finally in water or salt solution, when it straightens out again. He considers that this shows that movement is due to the life and activity of the protoplasm.

Detmar, in his recent *Plant Physiology* (1903), devotes some space to nyctitropic movements of flowers, citing a few experiments with *Leontodon hastilis, Tulipa gesneriana, Crocus vernus, Adonis vernalis,* and *Taraxacum taraxacum.* Those with Leontodon heads show, as he thinks, that light variations are very important in the opening and closing, while in the experiments with all the others, temperature variations alone cause the movements. His experiment, cited for *Leontodon hastilis,* was about as follows: he cut off during the day several stalks possessing open flowers and put them in water in the dark. They closed as usual in the evening and opened again the next morning (in the dark). The following night they closed, but would not open the next morning until placed in the light. In the evening they closed again, thus proving to his satisfaction that light in no way affects opening.

The view held by Ludwig Jost in his recent *Plant Physiology* (1904) is that not all flowers act nyctitropically to temperature variations; some react to light variations. I infer from his statements that it is variations in light that cause opening and closing in composite heads, while in Crocus it is temperature. He states that darkness has the same effect on composites as coolness has on Crocus, and that light has the same effect as heat. He adds that, generally in nature, it is the receiving of light accompanied by a rise in temperature, or the taking away of light with lowering of temperature, that causes these movements.

In the Prantl-Pax Lehrbuch der Botanik (1904), rising temperature and light are said to cause the inner side of floral leaves (such as Tulipa, Crocus, Adonis) to grow more than the outer; hence the flower opens. Lower temperature and light cause the outer to grow more, and the flower closes. There is a caution not to confuse these movements with those of ephemeral flowers. The author seems to make two divisions of floral movement: those caused by outside forces (autonomous), and those caused by internal forces, turgor changes, brought about by stimuli acting on the protoplasm and influencing growth (paratonic).

It is to Pfeffer more than to any one else that we owe the most of our knowledge on the subject of plant movement, more in respect to leaves than to flowers, however. Temperature, according to his view, causes the flowers of Crocus and Tulipa to open and close by certain variations. A sudden rise opens them. They then turn gradually back to a lesser opening, which position is kept constantly while the temperature remains stationary. When the temperature is lowered a similar reaction occurs. The flowers of Crocus luteus, C. vernus, and Tulipa gesneriana react in a few minutes, he says, to a rise of $\frac{1}{2}^{\circ}$ C. The flowers of Adonis vernalis, Ornithogalum umbellatum, and Colchicum autumnale react less strongly, while those of Ranunculus ficaria, Anemone nemorosa, and Malope trifida respond to changes of 5°-10° C. Flowers of Oxalis rosea, Nymphaea alba, and Leontodon show only a common thermonastic movement with this change $(5^{\circ}-10^{\circ} \text{ C.})$.

In volume I of his *Plant Physiology*, Pfeffer states that osmotic pressure varies with temperature according to the same laws that influence gaseous pressure, and hence, by a rise in temperature of 15° C. the pressure is only raised from 100 to 105.5. Thus temperature can never exercise any marked direct effect upon turgor in plants.

The most recent publication on this subject is by Walther Wiederscheim (1904). Movements of petals are said by him to be caused by variations in temperature. The flowers experimented with were Tulipa and Crocus. Burgerstein and Farmer say that the movement in these flowers is a variation movement that occurs, not on account of growth, but by the changing, lengthening, and shortening of certain tissue complexes. Jost, Schwendener, the author, and Pfeffer consider them to be growth movements, the latter saying that growth produces movement by a change in the force of expansion occurring "simultaneously and equivalently" in the two halves, but unequally fast. The other three agree in saving that growth, one phase of it, either opening or closing, occurs as a result of light or temperature stimulus but unequally, the second movement, the counter-reaction, occurring from interior causes, due to the stimulating action set up by increase in growth of the first side.

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The foregoing summary of the work done on this problem since 1686 shows how very varied have been the theories as to the cause of the movement of floral leaves, and the great need for further investigation. Many of the articles which support good theories show evidence of a small or inexact amount of experimentation. This, I have tried to avoid by endeavoring to prove all statements by actual experiment, so that the final result should be conclusive. As to the exact processes which are carried on within the flower, or plant, to bring about movement, there is yet much to be done.

EXPERIMENTAL METHODS.

Information as to the cause of floral movements was sought in two ways: first by means of field observations, and second by means of experiments performed either in the field or greenhouse, mostly the latter because of the greater ease with which the surrounding conditions could be controlled. The aim was to eliminate the possible physical factors, such as light, humidity, etc., one after the other. For example, in order to prove that humidity could not cause the opening of the flowers of the morning glory, light, heat, and the water-content of the soil were made the same in three instances: in one of these the air was made very dry, in another very moist, and in the third it was kept normal. The procedure was the same for the elimination of the other factors. The apparatus used for these experiments was very simple. For example, in the humidity experiment cited above, two large bell jars, thermometers, a psychrometer, calcium chloride for absorbing moisture, and a piece of sheet rubber to tie around one flower pot were used. Water-content and light require tin cans for soil samples, thermometers, photometers, and a shade tent. To ascertain whether heat influences opening and closing of flowers, several simple pieces of apparatus were necessarv. A tin box, 2 x 2 x 2 ft., collapsible like the small tin dinner boxes, was constructed to be used in field work, but was also found useful in indoor experiments. The top and one side were made of glass; a hole 3/4 of an inch in diameter was cut in

another side to admit a cork for holding the thermometer in place. Two alcohol lamps were also found necessary, one to heat the box in which the plants were placed, the other to heat water in a retort, and thus pass water vapor into the box and produce a moist atmosphere. Self-registering thermometers and psychrometers were of great aid in taking readings of control conditions. Besides taking advantage of low temperatures in the open, or in cold rooms, double-walled bell jars packed with snow or ice were used to obtain low temperatures.

In all the experiments, strong, healthy plants were used, and no experiments were performed with flowers cut off from the plant. Wiederscheim, in his researches of 1904 on the crocus and tulip, and also Pfeffer and Jost, have affirmed that they have obtained the same results with flowers cut off from the plant as with those on the plant. Wiederscheim has even performed experiments successfully with all but one perianth leaf removed. However, unless this fact is thoroughly proved as in the instance just mentioned, it is much safer to work with the plant intact.

Unless otherwise stated, all observations apply to flowers in the greenhouse.

EXPERIMENTS

The plants directly experimented with were the common dandelion (*Taraxacum taraxacum*), the cultivated four o'clock (*Mirabilis jalapa*), the cultivated morning glory (*Ipomoea purpurea*), the evening star (*Mentzelia nuda*), the large evening primrose (*Pachylophus caespitosus*), and the common flax (*Linum usitatissimum*). Four of these are ephemeral types, one hemeranthous (the dandelion), and one nyctanthous (the evening star).

Hemeranthous and nyctanthous flowers open and close because of temperature variations, and temperature variations alone. They undergo a resting period, they sleep, while ephemeral flowers in closing end their existence, and therefore temperature variations only prolong or hasten this process with them. Hemeranthous and nyctanthous types can be made ephemeral, or at least shorter lived, by the addition of more heat than

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is normal. This is shown by the difference in the actual life of a flower blooming in the spring or in midsummer: the common dandelion lasts three to five days in the spring, while in midsummer two days is normal, on account of the more intense life of the flower at that time. On the other hand, ephemeral flowers can be made longer lived by the opposite process, the life processes going on less intensely than normal, as numerous experiments with the morning glory have shown.

The dandelion, four o'clock, morning glory, and flax were experimented with in the greenhouse, the plants being grown from sced, and the evening star and evening primrose in the open, since it was impossible to grow them in the greenhouse either from seeds or by transplanting the young seedlings. The difficulty probably lay in the fact that the change of climate, altitude, etc., was too great, from 9,000 ft. above the sea at Halfway, Colorado, to 1,200 ft. at Lincoln. At any rate, it was impossible to grow them at all from seeds, even when these were seasoned. The young seedlings of Mentzelia, transplanted in the fall from the mountains in Colorado to the university greenhouse at Lincoln, grew for a short time, but soon died, while those of the evening primrose grew fairly well during the whole year but showed no tendency to flower.

The experiments which follow seem to me to prove quite conclusively that variations in the amount of heat present are the causes of opening and closing movements among hemeranthous and nyctanthous types which are not ephemeral, and also secondarily in the latter. It is the sudden variations within a few hours which cause flower movement. Seasonal variation in temperature effects opening and closing scarcely at all, even in types of flowers (ainthous) which bloom throughout an entire season or more as the dandelion. In May it opens between 7:00 and 8:00 o'clock in the morning, in July between 5:00 and 7:00, ir August between 7:00 and 8:00, and in September between 7:0c and 9:00. The plant accommodates itself gradually to these changes, and opening and closing occur regularly with, perhaps, only a few hours difference in time.

The reason why cloudiness has been considered by some investigators as an important factor in movement is probably because a reduction in the amount of light (cloudiness) is nearly always accompanied by a lower temperature. The factors have not been carefully separated.

Movement can not be brought about by an increase of turgor within the cells, for with a rise of 15° C. the pressure is only raised from 100 to 105.5, and this, according to Pfeffer, could not cause a movement. Fifteen degrees of temperature, Centigrade, are, in no case that I know of, necessary to effect opening, and hence sufficient power could not be obtained in this way. Experiments were made with flowers cut off from the plant to determine whether turgescence was efficient in closing them. Some were immersed in water, others in different per cents of sugar solutions—all with the same results—opening and closing at the usual times.

It seems not at all probable that the expansion of the gases in the plant could increase turgidity by the rise of temperature, and hence cause opening, since, as far as temperature is concerned, gaseous pressure and osmotic pressure are governed by the same laws. Moreover, how can night blooming flowers be explained by this theory? Lack of time prevented experimentation on such an improbable cause.

That the protoplasm of the cells within the plant could be stimulated by temperature is the last and only plausible explanation. Just how this is done can not be understood, but that flowers are positively or negatively thermotropic to certain temperature extremes seems evident. Why a certain flower is ephemeral while others are hemeranthous or nyctanthous seems to me to be only partially answerable. It is doubtless true that the character is inherent, but the original causes must have been climatic, a flower closing for biological reasons, such as protection of pollen against unfavorable weather conditions, etc., and loss of water by excessive heat. An attempt was made by Dutrochet in 1836, and Farmer in 1902, to explain movement by means of the corolla (of Taraxacum and Mirabilis in the case of the former, and of Tulipa in that of the latter). Dutrochet gives tur-

gescence as the cause. Farmer gives to a localized tissue on the outer face of Tulipa petals the power of causing the perianth to open as a result of irritation. He says the opening is, however, due to the stimulus (he does not state what, but denies epinastic and hyponastic growth here) affecting the protoplasm and producing movement. Sections that I have made through the nerves of the corolla of Mirabilis do not show the differences in structure, indicated by Dutrochet, sufficient to cause opening and closing. He states that the cellular tissue on the outside would tend to curve out by filling with water in excess-opening, the fibrous tissue on the inner side tending to curve in by oxidation-closing. Cross-sections through the nerves of the corolla of Mirabilis show about this proportion of the different tissues: 145 μ of parenchyma on the outside of the nerve, exclusive of epidermis, 72μ of fibrous tissue, and on the inner side, 102μ of parenchyma, exclusive of the epidermis. We could scarcely expect movements such as Dutrochet speaks of to occur as results of turgescence of the parenchymatous tissue when it is present on both sides of the fibrous tissue and in such proportions. He states also that the morning out-curving of parenchymatous tissue (opening) of the dandelion is brought about by a strong rise of sap under the influence of light, causing turgescence. The closing, he says, is due to the diminution of this force, and to the gradual filling of the fibrous tissue with oxygen during the day. This could not occur, since the osmotic pressure of the cell sap is increased only 5 per cent with a rise in temperature of 15° C., and the temperature never need change this much to induce closing; hence, some other cause must be sought.

HEMERANTHOUS TYPE

Experiments with Taraxacum taraxacum. The flowers of the dandelion open from 7:00 to 8:00 A.M. in the greenhouse or in the open in May, and close from 5:00 to 6:00 P.M. On cool, cloudy days they may not open at all, and in a sudden lowering of the temperature, usually accompanied by cloudiness, as upon the approach of a storm, they may close at once. Temperature

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is in all cases, however, the cause of movement, light and the humidity of the air in no way influencing it except in so far as they are necessary to the continued growth of the plant. The composite head acts as the simple flower.

Experiments showing that light does not influence opening and closing. Plants with buds that were ready to open, or that were open for the first time, were at 6:00 P.M. put into shade tents made of black cambric and of sufficient darkness so that there was not the slightest coloration of solio paper at 3:00 P.M. after 5 minutes exposure, when the sun was shining brightly upon the tent. The next morning, the flowers in the shade tents were open as wide as those in normal sunlight. In other experiments, the same results were obtained; in nearly every case, the temperature in the shade tent was the same as in the sunlight, or a little higher.

Experiments showing that humidity has no direct effect upon flower movement. Plants with flowers open one day only were used. At 5:00 P.M. after the flowers had closed, one plant, well watered, was placed in a bell jar with the sides of the bell jar wet with water and the pot standing in water. A thermometer was suspended in the jar. Another plant was placed in a bell, jar, which had been dried by lying on its side in a very dry room with an air temperature of 23° C. and a relative humidity of 25 per cent. The pot was wrapped in rubber cloth so that there could be no evaporation from the pot or soil, and a flat dish filled with calcium chloride placed beside it to absorb any moisture given off. A thermometer was suspended in this jar also. The following morning, both flowers were open at 8:00 A.M., as were those left in normal conditions. The temperature in the dry jar was 27.6° C., in the moist one 25.6° C., and in the normal one 21° C. with a relative humidity of 54 per cent. The same results were obtained several times, so that this experiment also seems to prove conclusively that opening is not dependent directly upon the humidity of the air.

Experiments showing that variations in temperature produce opening and closing. I have been able to open and close dandelion flowers before the usual time by varying the amount of her

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present, but never to make the flowers stay open longer than usual by increasing the amount of heat to a little more than normal. The point at which opening occurs seems to be from 15° to 18° C., in the greenhouse, generally nearer the higher limit.

In the experiments which follow, relative humidities will usually accompany the temperatures, simply as additional proof that they are not influential in causing movement. For convenience, different parts of the greenhouse in which experiments were performed will be indicated, especially in those cases where the plants are transferred from one part to another to obtain the different conditions present there, thus: south house, north house, east house, middle house. The situation of plants placed out of doors will be indicated as *open*, that of those placed in the tin box with increased temperature as *warm chamber*, those placed in double walled bell jars packed with snow or ice, *cold chamber*, those in bell jars with saturated air, *moist chamber*, those in dry bell jars, *dry chamber*, while that of those in the compartment made of black cambric will be indicated as *shade tent*.

Flowers which do not open at the usual time in the morning because of low temperature, can be opened in from fifteen minutes to an hour by placing the plant in the warm chamber described on page 13.

		sot	тн ноц	SE	WARM CHAMBER		
Date	Hour	Condition	Temp.	Rel. Hum	Condition.	Temp	Rel. Hum.
Mar. 25, 1904 Mar. 25, 1904 Mar. 25, 1904	1С:45 а.м. 11:: 0 ам. 12:00 м.	% open % open Wide open	15.5°C. 21.8°C.	67.4% 26%	% open Wide open	36.5°C.	39 4%

On March 30, 1904, a cloudy day, dandelion flowers remained closed all the morning in the greenhouse. When the temperature was artificially increased in the warm chamber, in dry air or with vapor, opening occurred as in the several cases cited below.

Esther Pearl Hensel

		so.	UTH HO	USE	WARM CHAMBER		
Date	Hour	Condition	Temp	Rel. Hum.	Condition	remp.	Rel. Hum
Mar 30, 1904 Mar. 30, 1904 Mar. 30, 1904 April 7, 1904 April 7, 1904 April 7, 1904 April 15, 1904 April 15, 1904 April 15, 1904	11:00 A.M. 11:30 A.M. 12:00 M. 8:00 A.M. 8:15 A.M. 8:40 A.M. 11:00 A.M. 10:20 A.M. 11:00 A.M.	Closed Closed Closed Closed Closed Opening Closet Closed Open	16° 16° 13° 14.8° 17° 17°	83% 83% 83% 81% 	Closed Open Closed ¼ Open Ciosed Open	43° 43° 29° 29° 29° 29° 22°	Dry Dry Dry Dry Dry 3%

		SO	игн но	Us 18	WAI	RM CHAP	ABER
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp	Rel. Hum.
Jan. 30, 1905. Jan. 30, 1905. Jan. 30, 1905.	10:30 а.м. 10:55 а.м. 11:12 а.м.	Bud ½ open Bud ½ open Bud ½ open	19.8° 19 8° 20°	63% 62% 60%	Bud ½ open ½ + open Open	23° 25.9° 28°	Moist Moist Moist

Open dandelions when put into the cold chamber do not ordinarily close at night in the manner of those under normal conditions. They look perfectly natural and do not wither on removal, but seem to be in a rigid condition. The change from normal temperature to that of the cold chamber (19° or 21° to 2° or 5° C.) is probably so extreme that the flower is unable to react to the stimulus of the variation in temperature, for, when a plant with open flowers is put out of doors or in another room where the temperature difference is not so great, closing occurs very readily at any time of day. When the temperature in the cold chamber was not too low, closing occurred in certain instances at about the normal time.

Following are two instances of this sort with figures showing normal closing:

		SO	отн но	USE	COLD CHAMBER		
Date	Hour	Condition	Temp	Rel Hum.	Condition	Temp.	Rel. Hum,
Feb. 22, 1905 Feb. 22, 1905 Feb. 22, 1905 Feb. 22, 1905 Feb. 22, 1905 Feb. 22, 1905	9:00 A.M. 10:30 A.M. 11:30 A.M. 2:30 P.M. 5:00 P.M	Open Open Open Open ½ closed	19.4° 25.6° 27.3° 31.7° 2; °	57.5% 56% 51% 44 5% 57%	Open Open % closed . % + closed	10° 10° 10° 10°	

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		sou	тн нот	JSE	COLD CHAMBER		
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. Hum.
Feb. 27, 1905 Feb. 27, 1905 Feb. 27, 1905 Feb. 27, 1905 Feb. 27, 1905 Feb. 27, 1905 Feb. 27, 19.5	10:00 A.M. 10:45 A.M. 12:(0 M. 1:25 P.M. 3:00 P.M. 5:00 P.M.	Open Open Open Open ¼ closed	24.8° 25° 26° 23° 19°	45% 41% : 8.5% 35% 43%	Open Open Open ½ closed	$12.5^{\circ} \\ 12.5^{\circ} \\ 12.4^{\circ} \\ 14.4^{\circ}$	

The following data show the effect of a lowering of temperature such that closing occurs from 2 to 6 hours earlier than normal. In certain cases the lower temperature of a different part of the greenhouse was made use of, in others, the open:

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		sot	ли ног	JŞE	EAST HOUSE		
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. / um.
Jan. 21, 1905 Jan. 21, 1905 Jan. 2 ¹ , 1905 Jan. 24, 1905 Jan. 24, 1905 Jan. 24, 1905 Jan. 24, 1905 Jan. 24, 1905	10:00 A.M 11:00 A.M. 41:45 A M. 10:30 A.M. 12:00 M 1:30 P.M. 5:(40 P.M.	Open ¼ open	18.6° 	52%	Open ¼ closed . ¼ closed . ¼ open ¼ open Closed	$ \begin{array}{r} 12^{\circ} \\ 14^{\circ} \\ 17^{\circ} \\ 7.8^{\circ} \\ 5^{\circ} \\ 65^{\circ} \\ 1.4^{\circ} \end{array} $	9 3. ! % 88 4%
Feb. 2, 1905 Feb. 2, 1905 Feb. 2, 1905	10:30 A.M. 12:00 M. 3:00 P.M.	1/4 open	18° 	55%	¼ open ¼ open	8° 16° 8.6°	
Feb. 2, 1905 Feb. 4, 1905 Feb. 4, 1905 Feb. 9, 1905	5:30 P.M. 10:00 A.M. 5:00 P.M. 9:30 A.M.	Open Open	16.8° 18.6° 12.8°	58% 63% 55%	Closed Not open. Closed Open	7 5° 13.5° 16.2° 10.5°	
Feb. 9, 1905 Feb. 9, 1905 Feb. 9, 1905	11:00 A M. 2:40 P.M. 5:00 P.M.	Open Open ¼ closed .	2).5° 20° 18.2°	20% 41% 63.5%	Closing Closed Closed	13° 14.8° 9°	

,		sou	ли нот	JSE	NORTH HOUSE		
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. Hum.
Feb. 25, 1905. Feb. 25, 1905. Feb. 25, 1905. Feb. 25, 1905.	9:30 a.m. 10:30 a m. 1:10 p.m. 5:00 p.m.	Open Open Open Open	23.4° 16.4° 29.9° 16.4°	51% 49% 52.5% 54%	Open (pen % closed	19.4° 16.8° 23°	, 82.6% 73.4% 68.1%

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Esther Pearl Hensel

		្រ៍ ទ០។	UTH HOU	JSE	OPEN		
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. Hum.
Feb. 25, 1903 Feb. 21, 1905 Feb. 21, 1905 Feb. 21, 1905	9:33 A.M. 10:33 A.M. 11:33 A.M. 1:15 P.M. 2:00 P.M. 2:15 P.M. 2:15 P.M. 4:00 P.M. 5:00 P.M. 6:00 P.M. 10:00 A.M. 11:10 A.M. 12:00 M. 3:0 P.M.	¼ open Open	19° 19° 20° 19° 19° 19° 18° 18° 18° 17° 15° 14° 25° 	53%	Closed Closed Closed 4 open 9 open 0pen 4 closed 4 closed 4 closed 9 closed 0pen 0 pen 14 closed	3.5° (Taken 19° 19° 18° 18° 17° 15° 14° 14° 13° 14°	into green [house

		SOUTH HOUSE		OPEN			NORTH HOUSE			
Date	Hour	Cond.	Temp.	Rel. Hum.	Cond.	Temp.	Rel. Hum.	Cond.	Temp.	Rel. Hum
[†] eb. 27, 1905 [†] eb 27, 1905 [†] eb. 27, 1905	10:00 A.M. 10:30 A.M 10:45 A.M 12:00 M. 1:25 P.M. 3:00 P.M. 5:00 P.M	Open Open Open Open Open M clo'd	24.8° 25° 26° 23° 19.4°	45% 41% 38.5% 35% 4.%	Open Open Open % clo'd Closed.	11° 13° 12.5° 13.5° 13.5°	82% 74% 58.4% 68.4% 53.8%	Open Open Open Open 3⁄3 clo'd	21.8° 21.2° 20.8° 17.4°	56.2% 71.8% 64.6% 68.9%

		so	отн нос	JSE	OPEN		
Date	Hour	Condition	Тетр.	Rel. Hum.	Condition	Temp.	Rel. Hum.
March 1, 1905 March 1, 1905 March 1, 1905	8:30 A.M. 9:30 A.M. 10:30 A.M.	Open Open Open	250	61%	Open ¹ / ₃ closed	50 120	78.4% 63.4%
March 1, 1905 March 1, 1905 March 1, 1905 March 2, 1905 March 2, 1905	11:50 A.M. 2:30 P.M. 4:35 P.M. 8:35 A.M. 9:45 A.M.	Open Open Open	21.6° 21.6° 17.2° 23.4°	54.5% 47.5% 54.5% 60% 61%	% closed Closed Open	14° 16° 15.5° 11° 15°	13.3% 52% 52%
March 2, 1905 March 6, 1905 March 6, 1905	5:00 P.M. 9:00 A.M. 11:00 A.M.	Open Open Open	24° 21 2° 24 5°	40% 65.5% 66%	% closed Open Open	20° 1 8° 3°	92.2 % 77.5 %
March 6, 1905 March 6, 1905	3:45 р.м. 5:00 р.м.	Open Closing	20° 22°	62% 63.5%	% +closed ¾ +closed ¾ +closed	6° 6.8°	81.2% \ 74.44

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		SOU IH HOUSE			OPEN			NORTH HOU.E		
Date	Hour	Cond	Temp.	Rel. Hum.	Cond.	Temp.	Rel. Hum	Cond.	Temp.	Rel. Hum.
Ma ch 9, 1905 March 9, 1905 March 9, 1905 March 9, 1915 March 9, 1905	8:45 A.M 11:00 A.M 1:30 P.M 2:30 P.M 5:00 P M.	Open Open Open Open ¾ clo'd	19.2° 23.6° 24° 22.8° 16°	59% 53% 38½% 41% 47½%	Closed. Open . Open Open	7° 14° 13° 10° 7°	 	1% open 1% open 1% open 1% open 10 open	18.4° 19.4° 21.6°)8.9° 17.2°	

Light readings also were taken by exposing solio paper to the light to show that the intensity did not influence opening or closing. Following are some data regarding the amount of light present at the times of opening and closing. If we take the tables just preceding, giving temperature and humidity values, and observe the time at which closing occurs in the different situations, and note at the same time the relative light values, light can be seen at once to be of no value in effecting closing, since it is strongest where flowers close earliest. The relative values are obtained by comparing the exposures on solio paper in a photometer, for the different situations, with a sun standard taken at noon on a certain clear day, e. g., March 21, 1905.

On February 27, 1905, dandelions were not closed in the greenhouse at 3:00 P.M. when the relative light value was .05, while out of doors they were two-thirds closed and the light value was .1. At 5:00 P.M., dandelions in the greenhouse were one-third closed with a light value of .02, while out of doors they were entirely closed, and the light was .05. In the stronger light they closed earlier.

On March I, 1905, open dandelions put out of doors at 9:30 A.M. were one-third closed at 10:30 A.M. with a light value of .5, while indoors they were open, and the light was .I. At 4:35 P.M., those in the greenhouse were still open, with light at .03, while out of doors they were closed with light at .06.

On March 6, 1905, at I:30 P.M., the open dandelions put out of doors at 9:00 A.M. were two-thirds or more closed, the light being .15, while indoors at the same time, where the light was .03, they were open as usual.

OTHER HEMERANTHOUS TYPES

The flowers of *Gentiana parryi*, the large blue gentian, open for two or more days only during the day from 8:00 to 10:00 A.M. and close from 5:00 to 6:00 P.M. It is very noticeable that they do not open on cloudy, cold, or rainy days and that they close on the approach of rain. Detached flowers will stay open in the house at night but will close out of doors; if brought indoors they will open in the dark. *Gentiana acuta* behaves in much the same way, and opens at about the same time. It also stays open for almost the same number of days, possibly a little longer.

I carried on a few experiments with tulip flowers, but was unable to do much with them as they did not seem to close at night. They were forced bulbs potted for me by a local greenhouse. I did succeed in opening a few with increased temperature but not with $\frac{1}{2}^{\circ}$ C. difference, such as Pfeffer says is possible; nor was it possible to close the flowers with either a moderate or extreme degree of cold.

NYCTANTHOUS TYPES

Experiments with Mentzelia nuda. The flowers of this plant open from 3:00 to 5:00 P.M. and are closed again the following morning between 5:00 and 6:00 A.M. This is repeated for 3 to 5 days. The sepals do not close around the corolla after once opening, but stav reflexed. When first opened, the flower emits a fragrance which is lacking after a few hours, a fact probably in some way connected with pollination. On rainy days, when it is cool and cloudy, the opening is two hours or more earlier than on bright sunshiny days. The experiments which I was able to carry on were all performed in the fields, in the mountains at Halfway, Colorado. The gravel slides on which Mentzelia grows experience very great extremes of temperature on their surface: during a single day, from 10° C. between 6:00 and 7:00 A.M. to as high as 46° C. at 11:00 A.M. or 25° to 35° C. between 2:00 and 3:00 P.M. On account of this fact, I took soil samples of the gravel at the time the flowers opened or a little

before, and also a little before their closing, in order to determine whether the water-content of the soil had anything to do with the phenomenon. No differences in per cents were obtained that could be construed as influencing movement by increasing the turgescence of the cells. The per cents varied very little, from 4-5 per cent being the normal in July and August for root depth.

Rather crude experiments were also carried on to measure the amount of transpiration in shoots bearing flowers about to open, and also those about to close. Vigorous blooming shoots were cut off and placed in large test tubes well stoppered, the shoot fitting into the stopper through a split in the latter, the end resting for an inch or more in the water. The amount of water transpired was practically the same during the day and night, showing that turgescence is not the efficient stimulus.

I also tried shading the plants continuously to induce an earlier opening, but it was not possible to get a sufficient change in temperature by this means.

Relative humidities taken just at the top of the plant at the time of opening vary extremely, as also those taken at the time of closing. When the flowers were opening, relative humidity values from 17.1 per cent to 95.6 per cent were obtained between 2:45 and 6:45 P.M.; when the flowers were closing in the morning, between 6:00 and 7:00 A.M., values from 54.2 per cent to 63.8 per cent were obtained. It is evident, then, that the watercontent of the air does not influence opening, as neither do watercontent of the soil nor light. That temperature is the controlling factor can only be deduced from temperature readings taken at the times of opening and closing, for, as mentioned earlier in the paper, it was impossible to grow Mentzelia in the greenhouse, and in the field conditions were extremely hard to control. As to figures showing temperatures at which the flowers open in the afternoon from 2:45 to 7:45 P.M., the range is from 141/4° to 23° C., while the corresponding range of temperatures when they close in the morning is from 8° to 16.8° C.

EPHEMERAL TYPES

Only three ephemeral, day blooming flowers were experimented with: the morning glory (*Ipomoea purpurea*), the common flax (*Linum usitatissimum*), and the yellow wood sorrel (*Oxalis stricta*); the other two were night bloomers, the evening primrose (*Pachylophus caespitosus*) and the four o'clock (*Mirabilis jalapa*).

Experiments with Ipomoea purpurea. Ipomoea opens from 5:00 to 6:00 A.M. and closes as early as 10:00 or 11:00 A.M. when it is quite warm. (All experiments were performed in the greenhouse.) Generally, however, closing occurs between 1:00 and 3:00 P.M. Contrary to the results with the dandelion, it was always possible to keep the flowers open for a considerable time (24 hours at least) beyond the normal, by placing the plant in a temperature as low as 3 to 4° C.; also to close the flowers earlier than their time by increased temperature (28 to 32° C.) with dry air or with water vapor introduced. On the other hand, heat does not work here as a direct stimulus, but rather only to hasten the growth processes. The following tables show how closing is hindered in temperatures lower than the normal:

		SOUTH HOUSE		EAST HOUSE			NORTH HOUSE			
Date	Hour	Cond.	Тетр.	Rel. Hum.	Cond.	Temp.	Rel. Hum.	Cond.	Temp.	Rel. Hum
Dec. 16, 1904 Dec. 16, 1904	10:30 A.M. 11:00 A.M. 12:00 M. 1:30 P.M. 3:00 P.M. 5:00 P.M. 6:00 P.M. 9:30 P.M.	Open Open Open Open % clo'd % clo'd .losed.	23° 20.7° 23.2° 20° 17.4° 15.4° 16.2° 15°	54.5% 53% 50.5% 49.5% 49.5% 50.5% 51.5% 41%	Open Open Closing Closing Closing Closing Closing Closed.	17.2° 17.2° 17.2° 16.2° 13.8° 13.8° 13.8°		Open Open Open Open Open Open Closed	17.7° 17° 19° 18 9° 17.8° 17.4° 16.2°	·····

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		SO1	отн нот	JSE	EA	ST HOU	SE
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. Hum
Dec. 19, 1904 Dec. 20, 1904 Dec. 21, 1904 Dec. 21, 1904 Dec. 21, 1904	10:30 A. M. 12:00 M. 2:30 P.M. 4:00 P.M. 6:00 P.M. 9:00 P.M. 3:30 P.M. 3:30 P.M. 10:00 A.M. 12:00 M. 2:45 P.M.	Open Open Open % of fls cl. % of fls cl. All closed. Bud op'ng	22° 16° 20° 21° 22.6° 23° 24.7° 13°	50% 55% 63% 59% 57% 56.5% 5.5% 53.5% 58%	Open Open Open Open Open Bud op'ng Open Beg to cl. ½ closed 2 closed	$\begin{array}{c} 15^{\circ} \\ 10 \ 4^{\circ} \\ 11.2^{\circ} \\ 11.6^{\circ} \\ 16.4^{\circ} \\ 17.5^{\circ} \\ 10.6^{\circ} \\ 16.5^{\circ} \\ 12.2^{\circ} \\ 13.4^{\circ} \\ 15.4^{\circ} \end{array}$	55.5% 82.8% 68.5% 73% 63.2% 63.2% 60.8% 85.2% 81.1% 88.2% 83.8% 85.2% 83.8%

		SOUTH HOUSE		NOR	тн ноц	SE	COLD CHAMBER			
Date	Hour	Cond.	Тетр.	Rel. Hum.	Cond.	Тетр.	Rel. Hum.	Cond.	Temp.	Rel. Hum.
Feb. 25, 1905 Feb. 25, 1905 Feb. 25, 1905 Feb. 25, 1905 Feb. 25, 1905 Feb. 25, 1905	9:30 A.M. 10:30 A.M. 10:35 A.M. 1:10 P.M. 5:00 P.M.	Open ¼ clo'd ¼ clo'd ¾ + cld Closed.	22.8° 26.4° 27° 29.9° 26.4°	51% 49% 50% 52.5% 54%	Open ¼ clo'd ¾ + cl	16.8° 23°	 73.4% 68.5%	Open Open Open	9° 7° 11°	Moist Moist Moist

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		SOUTH HOUSE		NORTH HOUSE			OPEN			
Date	Hour	Cond	Temp.	Rel. Hum	Cond.	Temp.	Rel. Hum.	Cond.	Тетр.	Rel. Hum.
March 6, 1905 March 6, 1905 March 6, 1905 March 6, 1905 March 6, 1905 March 6, 1905	9:00 A.M. 11:00 A.M. 1:30 P.M. 3:45 P.M. 5:00 P.M.	Open Open ¼ clo'd Closed Closed	21.2° 24.5° 27.4° 20° 22°	65.5% 66% 64% 62% 68.5%	Open Open ¼ clo'd % clo'd Closed.	$19.4^{\circ} \\ 19.6^{\circ} \\ 20.8^{\circ} \\ 17.4^{\circ} \\ 17.6^{\circ}$	40.1% 73.5% 82.4% 81% 68%	Open Open Open *Chil'd	1.8° 3° 5.4° 6°	92.2% 77.5% 79.7% 87.2%

* Taken into the south house, where it opened in perfect condition at a temperature of 22° and a relative humidity of 68.5%.

		sou	TH HOU	SE	NOR	NORTH HOUSE			SHADE TENT		
Date	Hour	Cond.	Temp.	Rel. Hum.	Cond.	Temp.	Rel. Hum.	Cond.	Temp.	Rel. Hum.	
March 8, 1905 March 8, 1905	8:30 A.M. 10:00 A.M. 10:30 A.M. 11:45 A.M. 1:45 P.M. 2:45 P.M. 4:45 P.M.	Open Open Open Nearly all cl'd Closed. Closed.	18.6° 19 5° 22° 27.2° 26.8° 25.8° 19.1°	57% 56% 54% 45% 50% 46% 43%	Open Open Open Open Closing Closing Closed .	19° 19° 19° 20.4° 20.8° 18.5°	63 2 [%] 69.3 [%]	Open Open Open Closing Closed. Closed.	23° 25° 32 4° 31.8° 31.2° 23°	57.9%	

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The third column of the last series, March 8, 1905, shows very well the negative effect of light. The tent was made of black cambric, which produced so diffuse a light that an exposure of solio paper for five minutes at 3:00 P.M. on a bright day, December' I, 1904, resulted in no coloration whatever of the sensitive paper. Here, the flowers close as early as those situated where the light is more intense.

Following are three instances out of a dozen or more showing the effect of increased temperature:

		sor	ли ног	SE	WAF	м снам	IBER
Date	Hour	Condition	Temp.	Rel. Hum	Condition.	Temp.	Rel. Hum.
Dec. 31, 1904 Dec. 31, 1904 Dec. 31, 1904 Dec. 31, 1904 Jan. 11, 1905 Jan. 11, 1905 Jan. 11, 1905 Jan. 11, 1905 Jan. 11, 1905 March 6, 1905 March 6, 1905 March 6, 1905 March 6, 1905 March 6, 1905 March 6, 1905	9:45 A.M. 10:00 A.M. 12:15 P.M. 9:00 A.M. 10:45 A.M. 11:00 A.M. 12:00 M. 11:00 A.M. 12:00 M. 11:00 A.M. 9:30 A.M. 9:33 A.M. 10:00 A.M. 11:00 A.M. 13:0 P.M. 3:45 P.M.	Open	18° 19° / 21° 23° 22° 22.4° 20.8° 21.2° 24.5° 27.4° 26°	57% 56% 51.5% 60.5% 61.5% 59% 57.5% 65.5% 66% 64% 62%	Open ¼ closed Open ½ closed Closed Closed Closed Open Open Øpen Øpen Člosed Closed	30° 37.2° 37.2° 37.2° 31° 31° 31° 31° 31° 31° 32° 28° 50° 32°	Moist Moist Moist Moist Moist Moist Moist Moist

The relative light values may be considered here also. On February 25, 1905, at 10:30 A.M., light was o in the north house, and .33 in the south house; in the former the flowers were still open, while in the latter they were beginning to wither. At I:10 P.M. in the north house, the flowers were beginning to close in darkness (0), while in the south house they were nearly closed in a light value of .33. At 5:00 P.M. in the north house, with light o, flowers were nearly closed, while in the south house, light .01, they were entirely closed.

On March 6, 1905, at 9:00 A.M., morning glories were open in the north house with light o, in the south house with light .012, and in the open with light .o6. At 1:30 P.M., they were

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beginning to close in the north house with light .003, and in the south house with light .04, while in the open, with light .15 they were still open.

These figures all go to show that light is not effective in opening and closing flowers, for closing takes place latest in nearly every instance where there is the most light, this being where it is also coldest. The experiment of March 8, 1905, in the shade tent, given on page 27, shows that closing occurs as soon in the darkness as in the light. Morning glories, ready to open, when put in a dark tent at night and kept there all of the following day, behave exactly in opening and closing as they do in normal light with the same temperature.

It was quite noticeable that when buds ready to open were put in too low a temperature (13° or less) they did not open at all but assumed the closed position as normally after opening; the temperature was too low for the ordinary processes of life to be carried on.

Experiments to show that humidity of the air is not the cause of opening and closing. On November 10, 1904, at 5:00 P.M., three plants, each with buds almost open, were put into different bell jars with light and heat practically the same in all three cases. One was a moist bell jar and one a dry bell jar, with the pot wrapped in a rubber cloth, etc. Still others were left out from under the bell jars. At 8:00 A.M. on November 11, 1904, all the buds were open with a temperature of 21° C. On November 14, 1904, at 5:00 P.M., a similar experiment was performed with the same results.

Experiments with Linum usitatissimum. The flowers of this plant open from 5:00 to 8:00 A.M. and close from 10:00 A.M. to 2:00 P.M., or, rather, they drop their petals at that time if there is sufficient movement of the air to bring about the process. Otherwise, the petals wither and dry in place. Flax flowers can be caused to drop their petals sooner than normal by increasing the temperature. Following are tables showing the results of such experiments:

Esther Pearl Hensel

	•	SO	итн но	USE	WARM CHAMBER		
Date	Hour	Condition	Temp	Rel. Hum	Condition	lemp.	Rel. Hum
April 6, 1905 April 6, 1905 April 6, 1905 April 6, 1905 April 6, 1905 April 29, 1905 April 29, 1905 April 29, 1905 April 29, 1905 April 29, 1905	9:45 A.M. 9:50 A.M. 10:15 A.M. 10:45 A.M. 11:25 A.M. 2:30 P.M. 8:35 A.M. 9:00 A.M. 9:25 A.M. 11:00 A.M. 12:00 M.	Open Open Open Pet. fal'ng Open Open Open Open Pet. fal'ng	26° 28.5° 28.5° 28.2° 21.2° 21.2° 21.5° 22° 23.5°	38% 36% 33% 36% 36% 35.5% 35% 32.5%	Open Open Pet. fal'ng Open Pet. fal'ng	30° 33° 34.5° 35° 20° 24.5°	Moist Moist Moist Moist Moist Moist

Temperature, when lower than the normal, prolongs the existence of the flower, as is readily seen on mornings when it is cooler than usual because of cloudiness, etc. In this event, the flower lives on into the afternoon.

		SOUTH HOUSE						
Date	Hour	Condition	Тетр.	Rel Hum				
Feb. 1, 1905	8:40 а.м.	½ open	10°	62.5%				
Feb. 1, 1905 Feb. 1, 1905	12:00 M. 3:00 P.M.	$\frac{3}{3}$ open $\frac{3}{3}$ + open.	19° 16.4°	1 51% 4(%				
Mar 28, 1905	8:30 A.M.	Open	17.5° 19.1°	50% 71%				
Mar. 28, 1905	10:20 A.M.	Open	17.4°	61%				

		sor	отн ноч	JSE	-	OPEN	
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. Hum
Mar. 28, 1905	11:20 A.M.	Open	18.4°	60%			
Mar. 28, 1905	1:45 P.M.	Open	18°	61%			
Mar. 28, 1905	5:00 р.м.	Pet. fal'ng	15.6°	62.5%			
Mar. 24, 1905	10:00 A.M.	Open	27.8°	53%	Open	220	
Mar. 24, 1905	12:00 m.	Pet, fal'ng	26°	51%	Open	22°	
Mar. 24, 1905	2:30 р.м.	Pet fal'ng	26.8°	41%	Closed	220	
May 4, 1905	9:55 A.M.	Open	24.5°	32%		1	
May 4, 1905	10:00 A.M.	Open			Open	12.5°	
May 4, 1905	11:00 A.M.	Open	25°	35%	Open	12.5°	
May 4, 1905	12:00 M	1 flr. with			•		100 C
		fall'g pets.	24.5°	36%	Open	14.5°	
May 4, 1905	1:30 p.m.	All petals		- •/-			
		falling			Open	16 ⁰	
May 4, 1905 i	2:0 P.M.	All retais					
,		falling.	23.4°	31.5%	Closing	170	

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. . .

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In the following instance opening was not complete at any time during the day:

		so	тн но	JSE
Date	Hour	Condition	Temp.	Rel. Hum.
April 10, 1905	10:00 а.м.	Opening a	12.60	60%
April 10, 1905	1:30 р.м.	Opening a	12.80	684
April 10, 1905	4:30 р.м.	Opening a trifle	20.5°	70%

This late closing is always associated with a late opening in the morning accompanied by a low temperature.

Experiments with Oxalis stricta. The flowers of Oxalis stricta open from 9:30 A.M. to II:00 A.M., and close for the first and only time between I:30 and 3:00 P.M. The same phenomena are to be observed as in the other ephemeral day blooming species studied, i. e., a low temperature hinders opening and also prolongs it when there has been a temperature high enough to induce opening. Opening can be made to occur earlier than normal also, as in the case of the other flowers studied, by increasing the amount of heat to a few degrees above the normal. As evidences of the effect of low temperatures on the time of opening, the following figures are conclusive. Table I shows the normal condition of the flowers under normal temperatures; table II, the effect of a lower temperature continuing more or less throughout the day:

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- 1		

Date	Hour	Condition	Temp.	Rel. Hum.
March 21, 1905 March 21, 1905 March 21, 1905 March 21, 1905 March 21, 1905	8:30 A.M. 9:30 A.M 11:30 A.M. 1:30 P.M.	Not open. % open. Open . Only 2 flowers still open.	$\begin{array}{c} 22.4^{\circ} \\ 24.6^{\circ} \\ 27.2^{\circ} \\ 28.4^{\circ} \end{array}$	5f% 54% 54% 50%

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II.

Date	Hour Condition		Temp.	Rel. Hum.	
March 28, 1905	8:30 A.M.	Not open	17.5°	71% -	
March 28, 1905	9:30 A M.		19.1°	59%	
March 28, 1905	10:20 A.M.		17.4°	61%	
March 28, 1905	11:20 A.M.		18.4°	60%	
March 28, 1905	1:45 P.M.		18°	61%	
March 28, 1905	5:00 P.M.		15.6°	61%	

The effect of a temperature slightly higher than normal in inducing a more rapid opening is shown by the following table:

Date		so	отн но	USE	WARM CHAMBER			
	Hour	Condition	Тетр.	Rel. Hum.	Condition	Temp	Rel. Hum.	
April 26, 1905 April 26, 1905 April 26, 1905 April 26, 1905 April 26, 1905	9:30 A.M. 10:15 A.M. 1'):40 A.M. 10:45 A.M. 11:00 A.M.	Not open. Not open. ½ open ½ + open. % + open.	25.3° 23° 16 2° 14.5° 14.8°	57.5% 60% 63% 74% 63%	Not open % open 1 flr. wide open All flow'rs wide open	22° 22° 27.5° 27.5°	Moist Moist Moist Moist	
April 26, 1905 April 29, 1905 April 29, 1905 April 29, 1905 May 3, 1905 May 3, 1905 May 3, 1905	11:15 A.M. 8:35 A.M. 9:00 A.M. 9:25 A.M. 8:40 A.M. 9:20 A.M. 9:40 A.M.	Open Not open I flower % open Not open % open % open	14.5° 21.2° 22° 23.5° 22° 22 6° 23.2°	64% 36% 34% 31% 82% 78% 77%	Not open. All open. Not open. Wide open Wide open	21° 24.5° 22° 26.8° 26.8°	Moist Moist Moist Moist Moist	

That Oxalis flowers should not yet be open at 8:35 A.M., April 29, 1905, and at 8:40 A.M., May 3, with the same temperature or practically so, 21.2° and 22° , and the light practically the same, shows that the widely different relative humidities do not count for much, 36 per cent in the first instance, and 82 per cent in the other. Opening occurs at practically the same time, 9:30 A.M., with temperature and light the same, but the relative humidities still widely different, 31 per cent and 78 per cent.

Several experiments, a half dozen at least, relative to the effect of light in opening flowers, show, as for the other flowers experimented upon, that opening occurs as well when plants were put into the shade tent as when in the open with full light.

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EPHEMERAL TYPES

Night bloomers

Experiments with Pachylophus caespitosus. Field conditions, rather than controlled experiments, were made use of here to obtain information as to sleep movements, since it was impossible to grow the plants in the greenhouse. The plant as observed grew on the gravel slides of the mountains around Halfway, Colorado. Its delicate fragrant white flowers open from 4:50 P.M. to 8:00 P.M., and close from 10:00 to 11:00 the next morning, when they become a dull pink color. It often happens that the flower stays open the entire day when it is cool and cloudy, and, rarely, on to the next day. The early or late opening in the evening is not due so much to the immediate temperatures as to those that have prevailed during the day, thus enabling growth to go on faster and opening to occur sooner. This is shown by the varied temperatures at which opening and closing occur. On certain days, the flowers are still open in the morning when the temperature rises as high as 31°, while in other cases they are closed when the temperature is as low as 13.5° C. or as high as 23.5° C. Opening in the evening occurs when the temperature is as high as 19.5° C. while, when it remains as low as 16.5° C., they may still remain unopened.

Plants copiously watered showed no earlier opening than those normally treated.

Experiments with Mirabilis jalapa. In the greenhouse, in March and April, these flowers stay open until noon or after, sometimes 2:00 or 3:00 o'clock, but occasionally are closed or almost closed by IO:30 A.M. when the day has been warm and bright. The opening almost never occurs at 4:00 o'clock, as tradition goes, but at 6:00 or 9:00 o'clock or later. It is possible to prolong the period of opening by lowering the temperature below the normal. This is illustrated by the following tables:

		sou	TH HOU	JSE	NORTH HOUSE			
Date	Hour	Condition	Temp.	Rel. Hum.	Condition	Гетр.	Rel. Hum.	
April 15, 1903 April 15, 1903	10:00 A M 10:15 A.M. 10:30 A.M. 11:05 A.M. 12:00 M. 2:30 P.M. 3:00 P M.	Open Open Open ½ closed Closed Closed	$12.8^{\circ} \\ 13^{\circ} \\ 17.4^{\circ} \\ 17^{\circ} \\ 21^{\circ} \\ 25^{\circ} \\ 26^{\circ} \\ 26^{\circ} \\ 12^{\circ} \\ 26^{\circ} \\ 12^{\circ} \\ 12^{\circ}$	55% 50% 41.5% 16% 28% 26% 26%	Open Open Open ¼ closed ¼ closed	12.5° 12.5° 13° 14.5° 13° 13°	51% 61% 33% 49% 35% 62%	

1		sot	ли ног	ISE	EAST HOUSE			
Date ,	Hour	Condition	Temp.	Rel. Hum.	Condition	Temp.	Rel. Hum	
an. 24, 1905 [an. 24, 1905 [an. 24, 1905 [an. 24, 1905	10:30 A.M. 12:00 M. 1:30 P.M. 3:15 P.M.	Open	13°	43 .5%	Open Open Open Open	7.8° 5° 6.5° 1.6° 1.4°	93.3% 88.4%	
an. 24, 1905 an. 25, 1905 Jan. 25, 1905 Feb. 2, 1905 Feb. 2, 1905 Feb. 2, 1905	5:03 P.M. 11:30 A.M. 2:20 P.M. 10:30 A.M. 12:00 M 3:00 P.M 5:00 P.M	Open Closed Open	21.4° 25.8° 18°	42% 30% 55%	Open Open Open Volored	1.4° 		

*The flower which was open on the morning of January 24, 1905, was still open the next morning at 11:30 A.M., but closed at 2:20 P.M.

When the temperature is raised above the normal, closing can be brought about earlier than usual, a fact shown by the following table:

		sou	тн ног	IS 3	WARM CHAMBER			
Date	Hour	Condition	Temp.	Rei. Hum.	Condition	Temp.	Rel. Hum.	
April 15, 1904 April 15, 1904 April 15, 1904 April 15, 1904 April 15, 1994 April 29, 1905 April 29, 1905 April 29, 1905 April 29, 1905 April 29, 1905	10:00 A.M. 10:20 A.M. 10:30 A.M. 11:05 A.M. 2:30 P.M 8:35 A.M 9:00 A.M. 9:25 A.M. 10:30 A.M. 12:00 M.	Open Open Open Ya closed Closed Open Open Open Closing	$12.8^{\circ} \\ 16^{\circ} \\ 17.4^{\circ} \\ 21.4^{\circ} \\ 25^{\circ} \\ 21.2^{\circ} \\ 22^{\circ} \\ 23.5^{\circ} \\ 24.2^{\circ} \\ 23^{\circ} $	55% 51% 41.5% 28% 27% 36% 35% 34% 34% 32%	Open ¾ closed Open Closing Closed	17° 22.5° 20° 24.5° 24.5° 24.5°	51% 34% Moist Moist Moist	

Humidity in no way influences closing as evidenced by the following:

On the Movements of Petals

		MIDDLE HOUSE			MOIST CHAMBER			DRY CHAMBER			
Date	Hour	Cond.	Temp.	Rel. Hum.	Cond.	Temp.	Rel Hum.	Cond	Temp.	Rel. Hum	
April 15, 1904 April 15, 1904 April 15, 1904 April 15, 1904 April 15, 1904 April 20, 1905 April 20, 1905 April 20, 1905	10:00 A.M. 10:30 A.M. 11:05 A.M. 12:00 M. 2:30 P.M. 10:00 A M. 11:30 A.M. 3:00 P.M	Open Open ½ clo'd Closed. Open Open	12.8° 17.4° 17° 21.4° 15.4° 16.8° 16.2°	55% 41.5% 16% 28% 57.5% 55.8% 51%	Open Open Øpen ½ clo'd Closed. Open Open	16.8° 14.5° 15° 16.8°	66%	Open Open Open	14.5° 14.5° 14.5° 15.4°		

Variations in the amount of light present do not seem to affect closing, for, when a plant with open flowers is put into the tin box with increased temperature, and practically no light, except the small amount from the non-luminous alcohol flame, closing occurs as readily as in the open, if not more so. Opening and closing also occur as in the open when the plants are put in the black shade tents. Closing may take place at as low a degree of temperature as 7.5° C., when the flower has been kept open beyond its usual time by several hours, as in the case cited on page 34, for February 2, 1905. This is to be explained on the basis that, since the flower's existence is normally only one day or a part of it, the flower has remained open its usual time according to its hereditary habits, its activities were completed, and hence closing occurred. Whenever closing occurs in the morning between 11:00 and 12:00, the temperature is nearly always 19° to 26° C., while, when it is delayed until 2:00 to 4:00 P.M., it is as low as 13° or 17° C. with high humidities, showing that it is not the extremely low temperature, but the constantly low temperature, continued for a considerable time, which is the cause of the late opening.

SUMMARY

I have been able to control the opening and closing of dandelion flowers in so far that I can close them permanently with lower temperature than normal, and open them when temperature has continued too low, by the application of either dry or moist heat. It is also possible to close any ephemeral flower be-

fore its time by an extra amount of heat, with either dry or moist air. It is impossible, however, to open an ephemeral flower by placing the plant in a lower temperature, since this checks growth, and opening is here rather a growth movement than a stimulatory one as in the other types.

In the careful study by experiment of Taraxacum taraxacum, Mentzelia nuda, Ipomoca purpurea, Linum usitatissimum, Oxalis stricta, Mirabilis jalapa, and Pachylophus caespitosus, light, humidity of the air, and water-content of the soil have been successfully eliminated as possible physical factors likely to cause the opening and closing of flowers by the movement of the petals (or florets). Heat, on the other hand, by its variations during twenty-four hours, is the direct cause of movement in hemeranthous and nyctanthous types that bloom for more than one day. In the case of those ephemeral flowers which open very early in the morning before the temperature has risen to any extent, as the morning glory, in contrast to those like purslane which open as the temperature rises, or those like the evening primrose which open a short time after the higher temperatures of the day have given place to the lower ones of night, the phenomenon is not to be explained so easily; it is possible that they react to a smaller variation in temperature than do the others mentioned.

The closing of ephemeral flowers is, however, a different process from that of periodic flowers, since it signifies the end of the existence of the flower. This closing, as has been shown, can be delayed for several hours by a temperature constantly lower than normal, showing that the two are closely connected. It would seem to be a tenable theory that ephemeral types of flowers have arisen by an extra need for protection of the flower against excessive heat and evaporation, e. g., in a dry or warm climate, for it is true in nearly every instance that the ephemeral type of flower either blooms at night or for only a few hours during the day. The differentiation into these types in the past generations must have come about in some such way, and they have persisted because of this favorable adaptation.

The cause of the periodic movements of hemeranthous and nyctanthous types is, however, explainable through the influence

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of variations in temperature, acting, not through turgescence, but by stimulation of the protoplasm.

To Professor Doctor C. E. Bessey and Professor Doctor F. E. Clements, under whose guidance the work embodied in this thesis has been carried on, I owe my most sincere thanks for encouragement and for suggestions and advice concerning instruments and methods of experimentation.

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