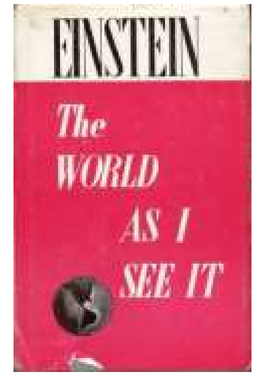
Using Light to Keep Track of Time and Determine Orientation in Space:

Photomorphogenesis in Plants



"*What is the meaning of human life, or of organic life altogether? To answer this question at all implies a religion. Is there any sense then, you ask, in putting it? I answer, the man who regards his own life and that of his fellow-creatures as meaningless is not merely unfortunate but almost disqualified for life*." From *The World as I See It* by Albert Einstein (1949).

What is life? **Life** can be **operationally defined** by a biologist as 1) the ability to **assimilate sustenance** in the form of matter and energy from the environment; 2) the ability to **transform** this environmental input at **ambient temperature and pressure** into **usable energy** (chemical, electrical and radiant) as well as the **common and unique molecules** (including pigments, luciferins and luciferases) that make up the body; 3) the ability to **expel any waste material** that would be toxic; 4) the **ability to move** using its own energy source; 5) the ability to **reproduce the information** in the form of DNA that directs all the above processes with **near perfect fidelity** such that the near-perfect reproduction gives rise to variation; and 6) the **ability to sense** and **respond** appropriately to the environment. This operational definition of life does not subsume the additional requirements that contribute to our own definition of **a good and well-lived life**.

Life is a Journey by Rabbi Alvin Fine (https://vimeo.com/42921067)

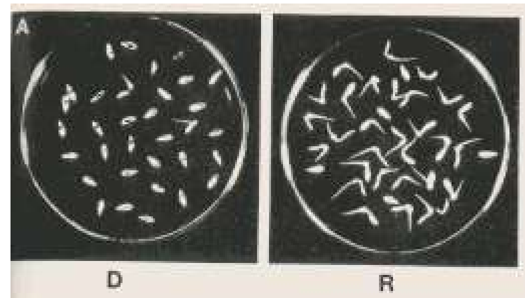
Birth is a beginning and death is a destination. And life is a journey.
From childhood to maturity and youth to age;
From innocence to awareness and ignorance to knowing;
From foolishness to discretion and then, perhaps, to wisdom;
From weakness to strength or strength to weakness. And often, back again;

From loneliness to love, from joy to gratitude, from pain to compassion,
From grief to understanding, from fear to faith,
From defeat to defeat to defeat. Until looking backward or ahead,
We see that victory lies not at some high place along the way,
But in having made the journey, stage by state a sacred pilgrimage.
Birth is a beginning and death is a destination.
And life is a journey, a sacred pilgrimage—to life everlasting.

Consciousness, as defined as **an awareness of the external environment** is the first step in responding appropriately to the environment. It is a characteristic of life and may have begun with the first cell. Remember that Jerome Wolken described *Euglena* as a **photo-neurosensory cell**. Consciousness differs from **conscience**, which means a **knowledge within oneself**, an inner sense of **right and wrong**, a **moral** sense, **intention**. Here we are touching on the origin of conciousness and the science that describes and explains it. A **Law of Nature** that describes the origin of conscience is still forthcoming and may be a place where science and theology meet.

Plants do not have a conscience but are conscious in that they sense the external environment and respond appropriately to the sensations. If we were to ramble through a meadow, hike through the woods, walk along the seashore, climb a mountain, or walk quietly and observantly through a garden at the **Cornell Plantations**, it would become increasingly clear that it is a normal and ubiquitous property of plants to **sense** and **respond** to their environment.

Plants depend on sunlight to power photosynthesis, where **radiant energy acts as a substrate** that is transformed into chemical energy. However, plants also depend on the **information content of sunlight** to **catalytically** affect their structure and function.



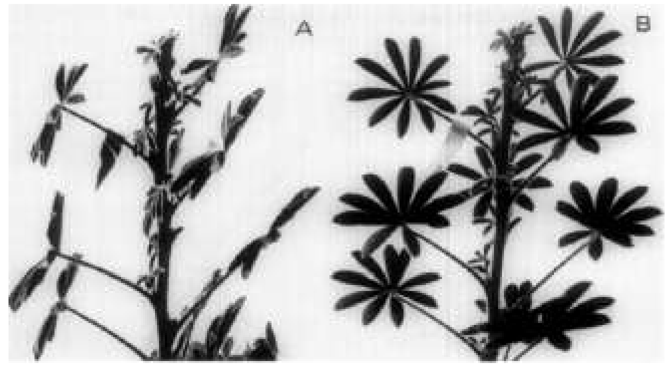
For example, some seeds, particularly those of weeds, do not **germinate** in the dark (D) but require a short burst of red light (R) to **germinate**.

Once the seeds germinate, many seedlings require light to retard stem growth and to promote leaf expansion and greening. Development in the dark, where the seedling appears pale and drawn out (**etiolated**) is known as **skotomorphogenesis**. Development in the light is known as **photomorphogenesis**.

Plants also develop differently depending on whether they grow in the **shade** (where the red part of sunlight has been absorbed by the chlorophyll in the leaves above) or in **full sun** (which has plenty of red light). The **shade-avoidance response** involves stem elongation. Thinking of the etiolation response or the shade-avoidance response, we see the general biological principle of **compensatory growth**, **compensation**, or **variation on the archetype**. There is no single best way for a plant to grow because there is no single environment. In the real world, having a variety of good ways to respond to a variable environment leads to the successful life of a plant.

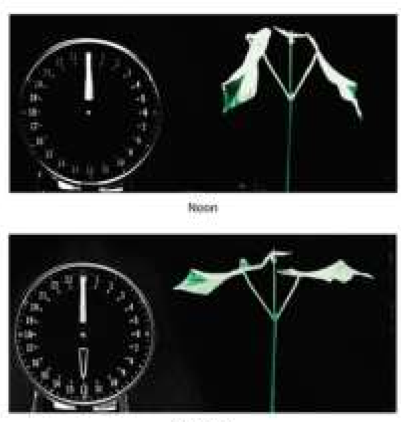
Some plants sense the **direction of light** and the whole plant bends or turns towards the light in a process known as **phototropism**.

The leaves of some plants can track the movement of the sun throughout the day. The process of **solar tracking** is known as **heliotropism**.



Some plants are also able sense the **duration of sunlight**, which is a measure of day length. The response to the duration of day length or **photoperiod** is known as **photoperiodism**. Plants respond differently to **day length**. For example, **skunk cabbage** flowers in the spring when the days are short, and **chicory** flowers in the summer when the days are long.

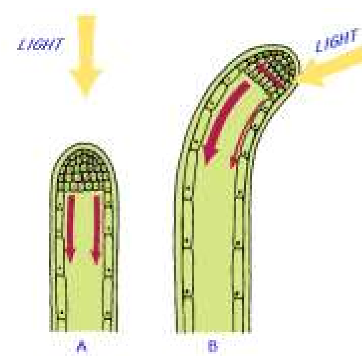
Many flowers, including the daylily and *Crocus*, can tell when the daylight begins and ends. They open in the morning and close at night. Perhaps they open for insect pollinators and close to protect the flowers from insect pests. Some leaves also change their position during the day and at night. They spread out in the day to catch the sunlight and close at night. Such daily responses may be part of a daily rhythm, known as a **circadian rhythm**,

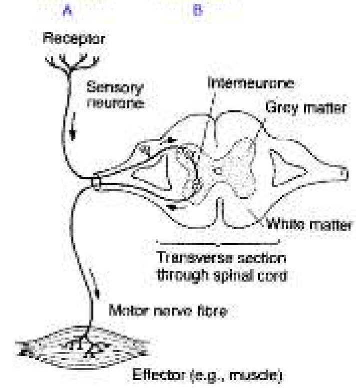


which will persist in continuous darkness, but which is reset each morning when the sun rises. **Circadian** means, about a day.

Roger Hangarter has captured many video clips that show "**plants in motion**" where many of the motions are responses to light (http://plantsinmotion.bio.indiana.edu/).

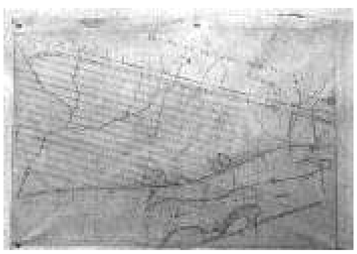
In order for plants to sense and respond to the **information** held by the environmental light, they must have **photoreceptor pigments**. When activated, these pigments must activate **signal transduction chains** (like the one we discussed that participated in vision) that lead to the **physical and/or chemical changes** that result in the appropriate **response.** Stimulus response coupling in plants has a surprising number of similarities with stimulus response coupling in humans.

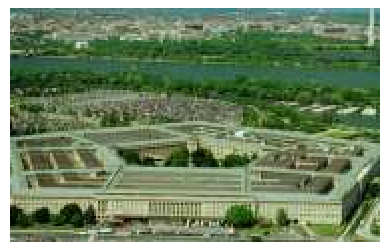




Raoul Francé (1905) wrote, *"What grander lesson could the speechless plants give than that which they have taught us: that their sense life is a primitive form, the beginning of the human mind... it tells us that after* ***all the living world is but mankind in the making****, and that we are but a part of all."*

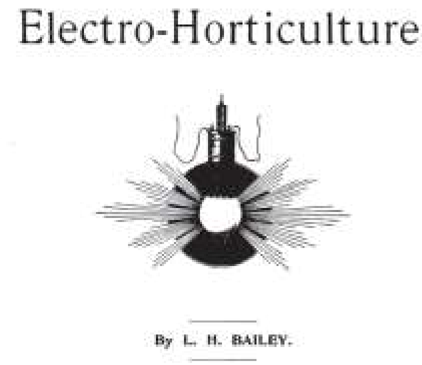
I am now going to discuss the **discovery of photoperiodism**—something that occurred at the present location of the **Pentagon**. A **United States Department of Agriculture** research farm known as the **Arlington Experimental Farm** once stood where the Pentagon now stands.

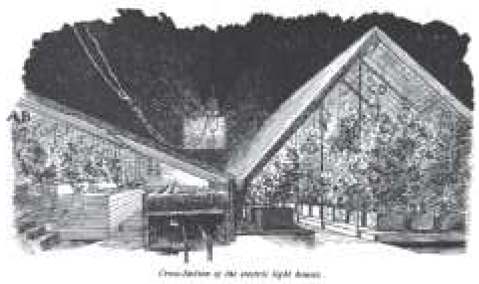


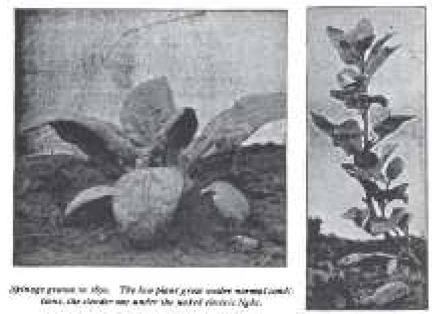


In order to make room for the military's growing needs during World War II, President Franklin D. Roosevelt signed an order to move the Experimental Farm to Beltsville, Maryland. Ground breaking for the Pentagon occurred at the Arlington Experimental Farm site on September 11, 1941 and **Colonel Leslie Groves**, who would later oversee the Manhattan Project, oversaw the project. The **Pentagon** building was designed to have a pentagonal shape because the original Arlington Experimental Farm had a pentagonal shape.

Photoperiodism is ***not*** primarily a response to the intensity of light or the total quantity of light but to the **duration** and **timing** of the light and dark conditions. **Liberty Hyde Bailey**'s (Cornell; 1892) use of artificial light in greenhouses led to an awareness that the **duration** of illumination has various effects on plant growth.





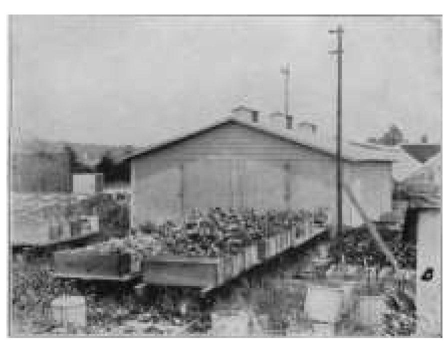


Very tall and leafy mutants of **tobacco** plants occasionally appeared in an experimental plot at the Arlington Experimental Farm. Getting seed to propagate one of these gigantic mutants, which was known as **Maryland Mammoth**, was difficult.

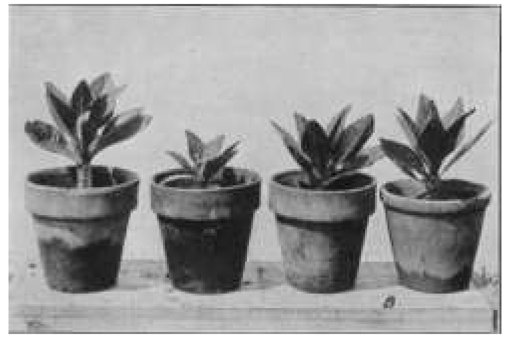
According to Harry Allard (1919), "*The great increase in number of leaves, together with a greatly elongated main stem, is accompanied by a period of vegetative vigor of such long duration that blossoming does not normally take place when the plants are growing in the field. In order to obtain seed from such plants, the usual practice has been to transplant the roots and stub, or even the plants entire, to the greenhouse in the fall, where vegetative vigor is resumed with the final production of normal blossoms and seed during the winter*."

Wightman Garner and Harry Allard found that it did not matter what size pot they grew the Maryland Mammoth tobacco plants in or how well they were fertilized, the experimental plants, no matter what the treatment, would never flower in the summer even though they reached a height of 10-15 feet; and would all flower at the same time in the winter even though the plants were not yet 5 feet tall. Garner and Allard (1920) wrote, "*Obviously, then,* ***the time of year*** *in which the Mammoth tobacco develops determines whether the growth is of the giant character*."

While the **difference in temperature** was an obvious potential cause of the difference between the behavior of plants in the summer and in the winter, the **length of daylight** could also be the cause of the difference in plant behavior in the summer and the winter. Garner and Allard (1920) could study the influence of day length in four different ways. They could compare the behavior of plants growing at different latitudes or at different seasons of the year; or they could supplement the daylight with artificial light or prevent the daylight from reaching the plant. They chose the latter experimental treatment. In the summer of 1918, they built a **dark chamber** to limit the length of daylight experienced by the Maryland Mammoth tobacco plants and in 1919 they expanded the experimental treatment by building a **dark house** to limit the length of daylight experienced by the plants. The plants could be moved in and out of the dark house every day with trucks on steel tracks.



The plants grown in 8-inch pots that were exposed to **seven hours of sunlight** from 9AM to 4PM and then wheeled into the dark house flowered by August 15, 1919. The control plants grown in 8-inch pots that were kept outdoors, exposed to the **long days** of summer, had not flowered by August 15, 1919.

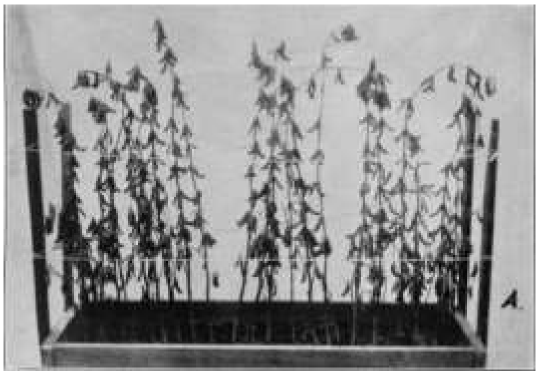



Likewise, Maryland Mammoth plants grown in 12-quart buckets that were exposed to **7 hours of sunlight** flowered and produced seeds by August 19, 1919 while the ones exposed to **12 hours of sunlight** or left outdoors did not.



Garner and Allard had solved the problem of the Maryland Mammoth. Once they understood the role of **photoperiod**, they could get the plants to flower and set seed by growing them during the **long days of summer by using the dark house** or during the **short days of winter in a greenhouse**.

Garner and Allard experimented with many plants, including **Peking soybeans**. Peking soybeans exposed to **7½ hours of daylight** before being put in a dark house already had matured pods ready for harvest on September 13, 1919, while the control plants that had been left outside exposed to the **long days of summer** had seed pods that were still green and leaves that were just beginning to yellow.

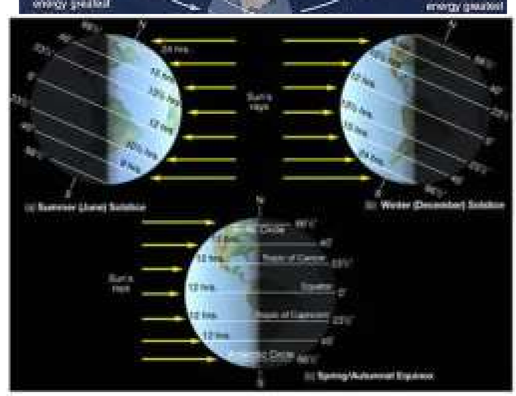


Garner and Allard began to realize that each variety of soybean had its own "***critical length of day*** *required for furnishing the stimulus which brings into expression the processes of sexual reproduction*." Others would define **short-day plants** as plants that ***will not*** flower if the photoperiod is extended beyond the **critical photoperiod** and they would define **long-day plants** as plants that ***will*** flower if the photoperiod is extended beyond the **critical photoperiod**.

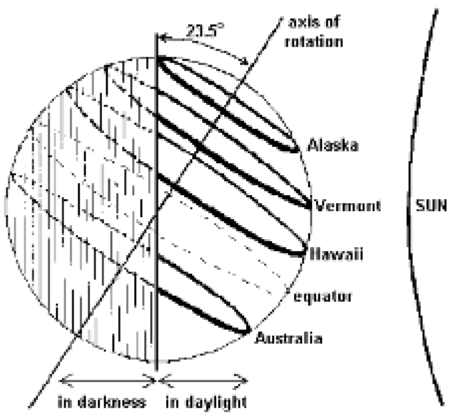
These are convenient definitions for horticulturalists and plant physiologists. However, the distinction between short-day plants and long-day plants is based on whether or not flowering is promoted or inhibited by increasing the light period about a critical value and not based on the absolute day length as it would be defined by a naturalist. For example, *Xanthium* **(cocklebur)** is a **short-day plant with a critical**

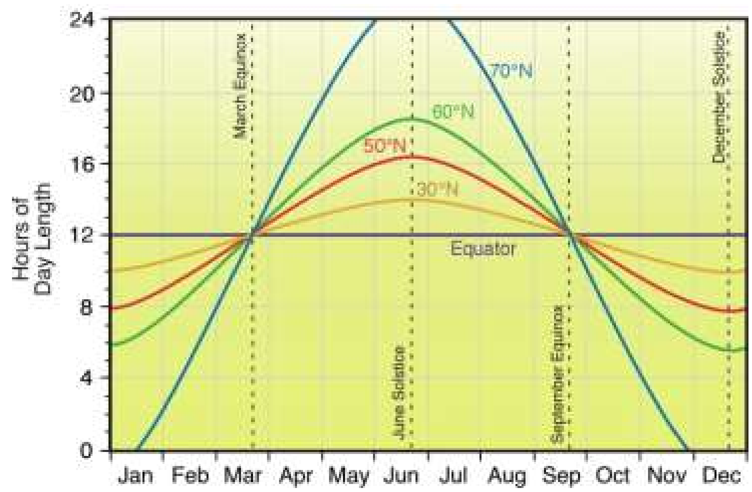
photoperiod of 15½ hours and will ***not*** flower if the light period is extended beyond the critical photoperiod. *Hyoscyamus* **(Henbane)** is a **long-day plant with a critical photoperiod of 11 hours** but ***will*** **flower when the photoperiod is extended beyond the critical photoperiod**.

Garner and Allard (1920) ended their paper by coining the term **photoperiod** "*to designate the favorable length of day for each organism*" and **photoperiodism** "*to designate the response of organisms to the relative length of day and night*." Furthermore they wrote about the possibility of photoperiodism in animals, "*As to **animal life**, nothing definite can be said, but it may be found eventually that the animal organism is capable of responding to the stimulus of certain day lengths. It has occurred to the writers that possibly the **migration of** birds furnishes an interesting illustration of this response. Direct response to a stimulus of this character would seem to be more nearly in line with modern teachings of biology than are theories which make it necessary to assume the operation of instinct or volition in some form as explaining the phenomena in question*."

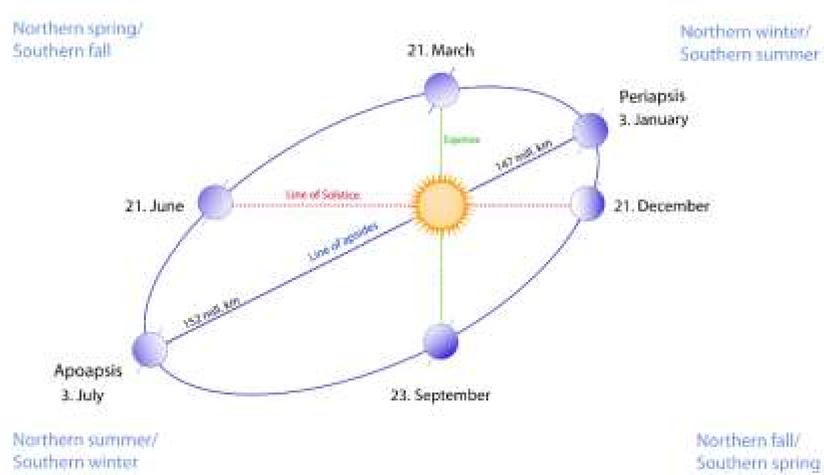


The **day lengths** of the growing regions of earth depend on **astronomical factors**. The **day length** or **photoperiod** in the temporal regions of earth changes seasonally as a result of the **23½ degrees tilt of the earth's axis**. During **summer** in the northern hemisphere, the earth is tilted toward the sun so that the days are longer than the nights. During **winter** in the northern hemisphere, the earth is tilted away from the sun so the days are shorter than the nights. To get a real picture of the seasonal changes imagine what would happen if the axis were tilted 90 degrees. The **summer solstice** (≈ June 21) marks the longest day of the year and the **winter solstice** (≈ December 21) marks the shortest. On the **autumnal equinox** (≈ September 21) and **vernal equinox** (≈ March 21), the day lengths and night lengths are equal.

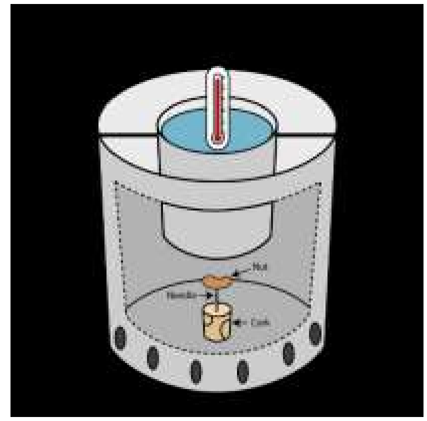


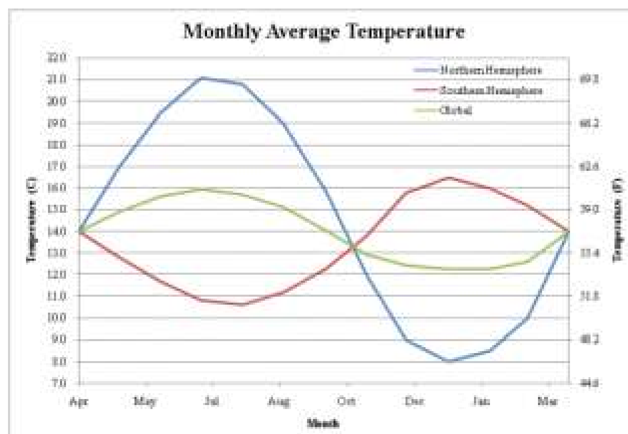


Even though the photoperiods in the northern and southern hemispheres are complementary during the year, the two hemispheres are not complementary in terms of solar radiation and temperature—two factors that also affect plant growth and development. Because the **earth's orbit** is **elliptical** and not a perfect circle, the northern hemisphere gets less solar radiation than the southern hemisphere. This is because the northern hemisphere tilts towards the sun when it is farthest from the sun during the long days of its summer and the southern hemisphere tilts towards the sun when it is closest to the sun during our winter and during its long days of its summer.



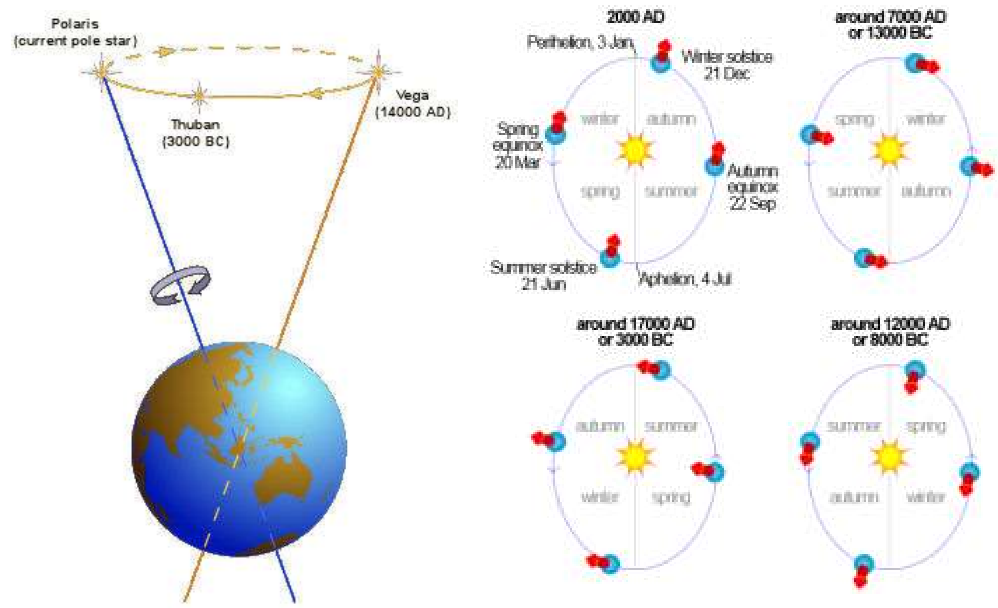
Because of the differences in the relative proportions of land, the northern hemisphere heats up and cools more quickly than the southern hemisphere. This is because the proportion of water to land is greater in the southern hemisphere than in the northern hemisphere and water has a greater **heat capacity** than land. Remember from our **calorimetry experiment with the peanut**, the change in temperature (ΔT) in response to an input of thermal energy (TE) depends in the heat capacity (c) and mass (m) of the water according to the following equation: $TE = c\, m\, \Delta T$. The northern hemisphere has an **ocean to land ratio** of 60.7% to 39.3% while the southern hemisphere has a ratio of 80.9% to 19.1%. Consequently annual temperature variation is moderated in the southern hemisphere compared with the northern hemisphere. Because of the heat capacity of water, summer in the northern hemisphere is hotter than summer in the southern hemisphere even though the earth is closer to the sun during summer in the southern hemisphere than it is during summer in the northern hemisphere; and winter in the northern hemisphere is colder than winter in the southern hemisphere even though the earth is closer to the sun during winter in the northern hemisphere than it is during winter in the southern hemisphere. The heat capacity of water also explains why the average temperature of the earth is lowest when the earth is closest to the sun and warmest when the earth is farthest from the sun.



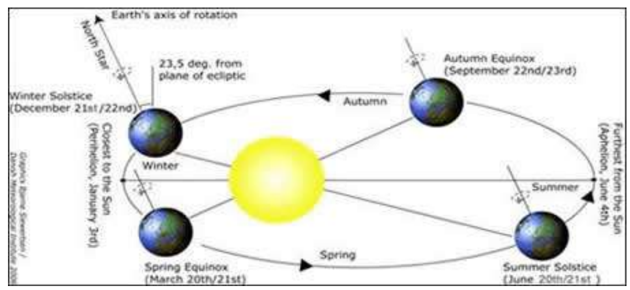


Water is important for plant growth in many ways!!!!!

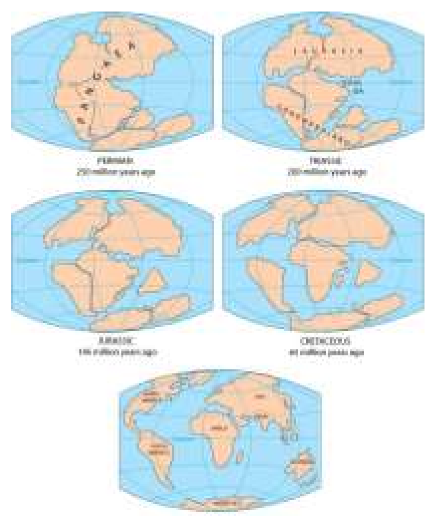
Because the earth is not a perfect sphere (the radius at the equator and the poles is 6378 km and 6357 km, respectively), the gravitational forces from the sun and the moon create a torque on the axis of the earth that causes the tilt to change. The change in tilt has a period of 25,765 years and results in a precession of the position of the sun on the first day of spring (vernal equinox). In other words, while winter currently occurs in the northern hemisphere when the earth is closest to the sun (**perihelion**), around 12000 AD, as a result of the **precession of the equinoxes**, winter will occur when the earth is farthest from the sun (**aphelion**).

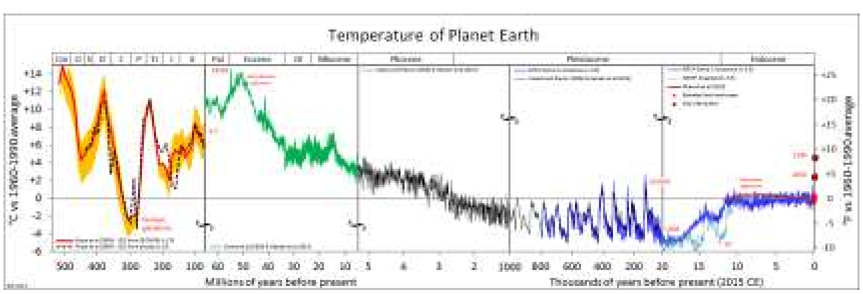


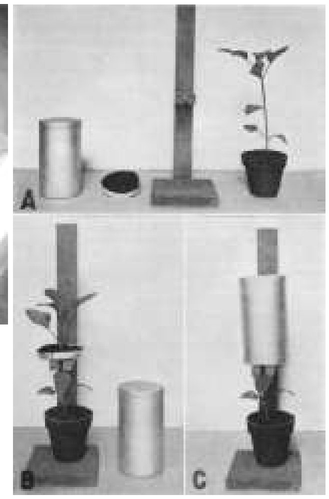
The **photoperiod** of a region, along with its temperature, water availability and light intensity, are important factors in determining the **natural geographical distribution** or **biogeography** of plants in terms of their northward and southward distribution. Harry Allard (1948) realized that day length is a part of **climate change** that occurs over **geological time** when he wrote, "*Length of day must, therefore, always be a function of every climate. Geologists inform us that there have been great changes in world climate throughout all the great geological eras. Some climates have been characteristically warm and weakly zonal and others have been cool and strongly zonal.* ***That there have been profound local, regional and even world-wide changes in climate involving length of day as well as temperature cannot be denied****. The* ***astronomical relations*** *responsible for earth* *climate are very complex and involve many factors including the earth's obliquity, the rate of rotation, the distance and eccentricity of the path of revolution around the sun, the length of time required to complete the revolution, as well as various conditions pertaining to the intensity of the solar energy and many physical conditions obtaining upon the earth itself. The astronomer, on purely mathematical grounds, may theorize about changes in the obliquity of the axis. However, were this obliquity actually to approach zero, with the same daily rotation that we have at present, causing a uniform length of day of 12 hours to prevail over all the earth, accompanied by weak zonations of temperature, there is every reason to believe that profound changes would take place in the floristic life-form and vegetation of the earth."*

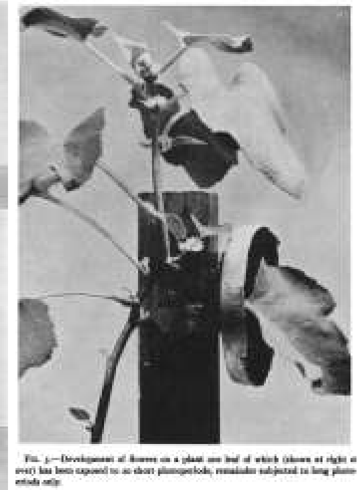


The **photoperiodic responses** of plants on earth are adapted to the **astronomical relations** between the earth and the sun. However, the profound changes that have occurred in the vegetation on earth over geological time are ***not*** due to a change in the obliquity of the axis, but due to other factors that have a major effect on climate such as meteorite impact and the movement of land masses proposed by **Alfred Wegener** (1915) and known as **plate tectonics**. Plate tectonics explains the shape of the continents and the similarities of fossils on different continents.









Working together for one summer, Karl Hamner and **James Bonner** (1938) found that the **leaves**, as opposed to the stems, are the organs of the *Xanthium* plant that sense the length of the day. When they removed all the leaves from a plant, the cocklebur would not flower under short days. It would flower under short days when they left one leaf. In fact they could grow the plant under long days, slide a light-tight cylinder over one leaf so that only one leaf was exposed to short days. Even though only one leaf was exposed to short days, the whole plant flowered.

Karl Hamner and James Bonner (1938) exposed plants to various day lengths with a constant night length or to various night lengths with a constant day length and found that the length of the day was not very important for flowering in *Xanthium* but that it was essential that the dark period exceeded 8½ hours. They wrote that "*It seems probable that the manufacture of the substance or substances responsible for the initiation of the flowering condition in Xanthium is* ***not*** *primarily* ***a response to duration of the photoperiod, but rather a response to duration of the dark period***."

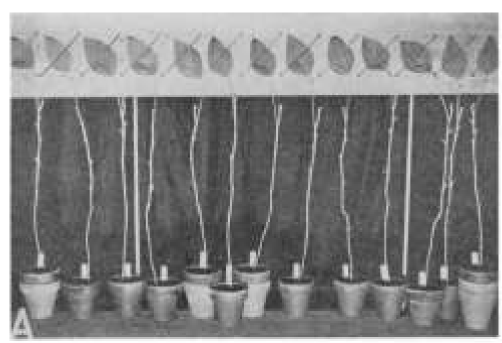
Indeed realizing that the **photoperiod** and **dark period** are **complements** of each other, Vernon H. Blackman (1936) had already pointed out that, "*Duration of illumination rather than quantity of light is the important thing, and this is exceedingly difficult to interpret in terms of physiology. In the case of short-day plants there is some reason for believing that it is the* ***corollary of the period of***

***illumination, namely the period of darkness**, to which attention should be directed.”*

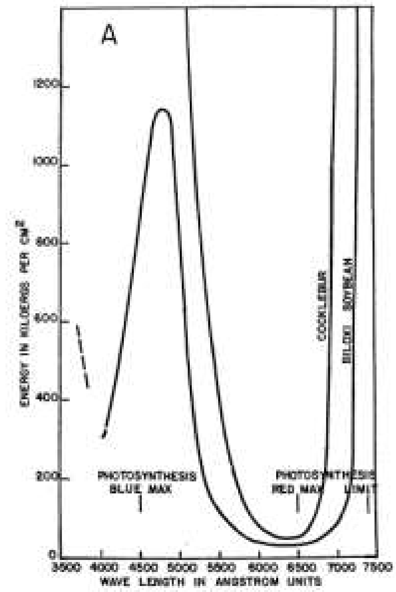
Then Karl Hammer and James Bonner serendipitously discovered that a ***single*** dark light period was enough to stimulate flowering when Edith Neidle, a graduate student of Karl Hamner’s, went to the greenhouse and found that all the *Xanthium* plants were flowering. The greenhouse manager reluctantly told her that the power had been off for one night and consequently, all the plants had received a single long night. Building on this lucky find, Karl Hamner and James Bonner (1938) compared plants that had a 9 hour dark period with plants that experienced a one minute flash of light 4.5 hours into the dark period. The plants that had a 9 hour dark period flowered (mac fl & fr = macroscopic flowers and fruits) as usual while the plants whose dark period was interrupted by a one minute flash of light remained vegetative.

EFFECT OF INTERRUPTION OF DARK PERIOD BY VARYING EXPOSURES TO LIGHT ON FLOWERING OF XANTHIUM. EXPERIMENTS X-43, X-60, X-71; UNTREATED CONTROLS ALL VEGETATIVE

LENGTH OF PHOTO-PERIOD (HOURS)	LENGTH OF DARK PERIOD (HOURS)	LIGHT EXPOSURE DURING DARK PERIOD	NO. OF PLANTS	CONDITION OF PLANTS AT END OF TREATMENT
15.............	9	None	12	mac fl & fr
15.............	4.5+4.5	1 minute after 4.5 hours	10	veg



What is the **photoreceptor** that **absorbs** the one minute pulse of light that inhibits flowering? At the new USDA center in Beltsville that replaced the Arlington Experimental Farm where Garner and Allard discovered photoperiodism, **Harry Borthwick**, **Sterling Hendricks** and Marion Parker built a **large spectrograph** to irradiate leaves of *Xanthium* or Biloxi soybean with a brief pulse of light with different wavelengths during the dark period and compare the ability of the pulse of light of a given wavelength to **inhibit** flowering. They used the large spectrograph to obtain an **action spectrum**. An action spectrum is a plot of the effectiveness or the amount of radiant energy of a given wavelength of light needed to cause a given response.



To construct the **large spectrograph**, Parker et al. (1946) used the prisms that **Samuel Pierpont Langley** used to measure the solar insolation and determine the solar constant, a carbon arc lamp that was cadged from a Baltimore movie theatre, and a large resistor that had been discarded from the Georgetown streetcar system. Admirably, this government-run spectrograph construction project had an outside cost of $50.

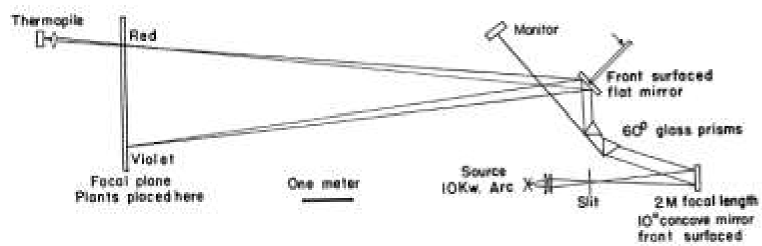


FIG. 1.—Diagram of optical path in spectrograph used for irradiation of plant leaves

The **Grotthuss-Draper Law** also known as the **First Law of Photochemistry** states that the radiant energy that causes a response must be absorbed by the pigment that mediates the response. Consequently, a **comparison** of the **action spectrum** for the inhibition of flowering with the **absorption spectrum** of known pigments would indicate which pigment was involved in photoperiodism. Parker et al. (1946) found that blue light was not effective and that red light from 600-680 nm was most effective. This ***did not*** coincide with the absorption spectrum of any ***known*** pigment, including chlorophyll.

Borthwick et al. (1952) also found that when the pulse of red light irradiation is followed by a pulse of far-red (722-745 nm) irradiation, the inhibiting pulse of red light is nullified and flowering occurs.

EFFECT OF VARIOUS WAVE-LENGTHS OF RADIATION ON PROMOTION OF FLOWERING OF *Xanthium saccharatum* PLANTS THAT HAD PREVIOUSLY RECEIVED RADIATION INHIBITORY TO FLOWERING

WAVE-LENGTH, Å	INCIDENT POWER (ERGS × 10³/CM.²/MIN.)	NUMBER OF FLOWERING PLANTS PER LOT OF 4 AFTER IRRADIATION FOR INDICATED TIME			
		16 MIN.	8 MIN.	4 MIN.	2 MIN.
6820–7020	87	0	0	0	0
7020–7215	93	1	3	0	0
7215–7450	99	3	3	3	1
7450–7700	102	1	1	1	0
7700–8010	105	0	0	0	0
8010–8300	111	0	0	0	0

Robert J. Downs (1956), also at Beltsville, showed that the pigment that inhibited flowering in *Xanthium* **could be turned on and off like a switch**. Flowering would be determined by the last irradiation. If the last irradiation was red light, flowering would be inhibited and if the last irradiation was far red light, flowering would occur.

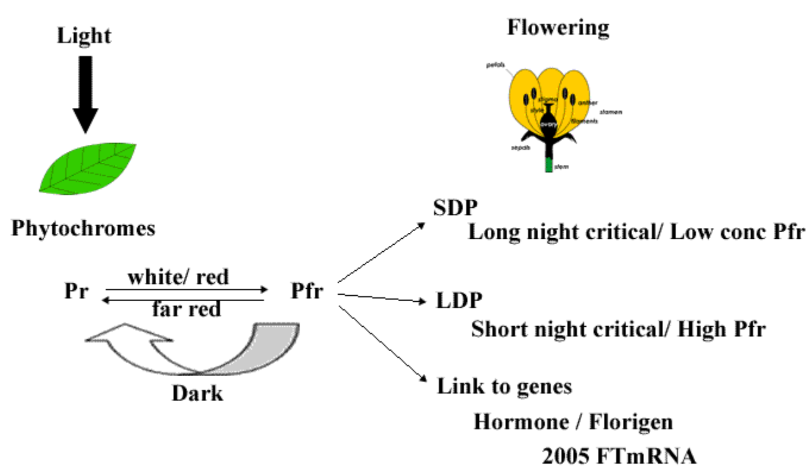
TABLE III

EFFECT OF DAILY INTERRUPTIONS OF THE DARK PERIOD WITH SEVERAL CONSECUTIVE IRRADIATIONS WITH RED AND FAR-RED IN SEQUENCE ON FLOWER INITIATION OF COCKLEBUR AND SOYBEAN

TREATMENT	MEAN STAGE OF FLORAL DEVELOPMENT IN COCKLEBUR *	MEAN NO. OF FLOWERING NODES IN BILOXI SOYBEAN **
Dark control	6.0	4.0
R	0.0	0.0
R, FR	5.6	1.6
R, FR, R	0.0	0.0
R, FR, R, FR	4.2	1.0
R, FR, R, FR, R	0.0	...
R, FR, R, FR, R, FR	2.4	0.6
R, FR, R, FR, R, FR, R	0.0	0.0
R, FR, R, FR, R, FR, R, FR	0.6	0.0

* Two min far-red from the sun. Values are for lots of 5 plants.
** Eight min of far-red from three 300-watt internal reflector flood lamps. Values are for lots of 4 plants.

According to Borthwick et al. (1952), reproduction in many plants is controlled by the length of the dark cycle and "*A dark reaction affords the measure of time and this reaction can be quickly stopped or reversed by light such as that from the rising sun.*" After reading about the **business cycle** in Arnold Tustin's (1953), *The Mechanism of Economic Systems*, Sterling Hendricks realized the importance of **connected linear systems that oscillate** and proposed that the pigment itself may be **photoreversible**. He also suggested



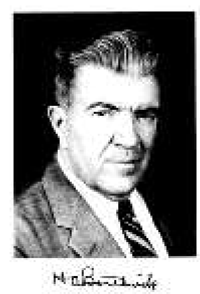
that the **dark transformation** or **reversion** of the far red-absorbing form of the pigment to the red-absorbing form of the pigment may be the **basis of the timing mechanism** that enabled photoperiodic plants to measure the length of the dark period. During the light period, the red light-absorbing form of the pigment is converted to the far red light-absorbing form and at the onset of the dark period; the pigment begins to revert to the red light-absorbing form. A flash of red light during the dark period converts the pigment to the far red light-absorbing form and the dark period has to start again. If the dark period does not last longer than the critical dark period, no flowering occurs. On the other hand, if the red light flash is followed by a far red light flash, the pigment reverts to the red light-absorbing form and flowering results. Whereas short-day plants (long-night plants) require a **low concentration of the far red light-absorbing form** of the pigment to trigger the plant to flower in response to the dark period, long-day plants (short-night plants) require **a high concentration of the far red light-absorbing form** of the pigment to trigger the plant to flower in response to the dark period.

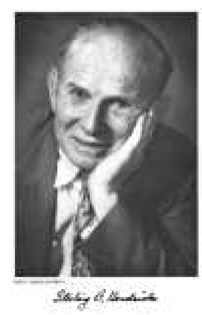
Looking back, Harry Allard (1948) realized that "*So long as there is light, terrestrial rotation, the sun, cycles of length of day will continue to operate upon plant and animal life upon the earth*." The plant leaves sense the day length with a photoreversible photoreceptor pigment.

By 1959, it was time to begin to isolate and purify the pigment that was involved in **photoperiodism** and many other red light-stimulated **photomorphogenetic responses**. Since the pigment absorbs reddish light, it probably reflects and transmits blue light and therefore looks blue. So the members of the Beltsville group, including Warren Butler, Karl Norris, Bill Siegelman and Sterling Hendricks built a **special spectrophotometer** to assay the **photoreversible pigment**, and then extracted a red light-absorbing

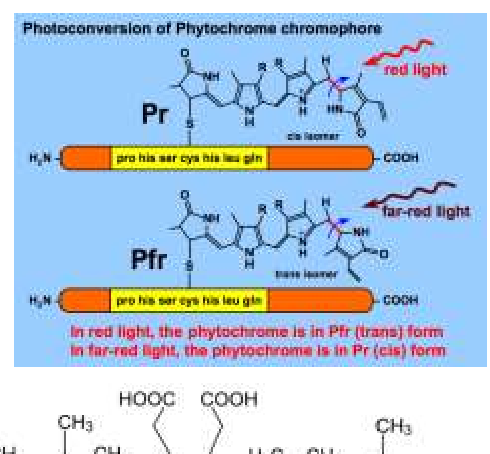
photoreversible blue pigment that could be transformed to a far red-absorbing greenish pigment.

Excited to show the photoreversible pigment at the Ninth International Botanical Congress in Montreal in the summer of 1959, Sterling Hendricks, Warren Butler and Bill Siegelman drove from Beltsville, Maryland to Montreal. Every time they stopped for gas, they would check the pigment sample in the trunk. They did not realize that exposing the extracted pigment to light when they opened the trunk resulted in the conversion of the stable red light-absorbing form to the less stable far red light-absorbing form. By the time they got to the meeting, the pigment sample had degraded and the demonstration was a dud. The photoreversible pigment became known as “*the pigment of the imagination*.”



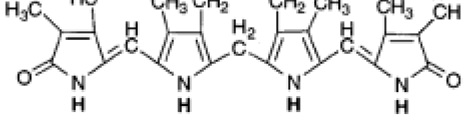


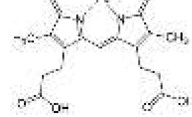
Following the suggestion by Warren Butler to call the yet unpurified photoreversible pigment **phytochrome** from the Greek for “plant color,” **Harry Borthwick** and **Sterling Hendricks** named it in 1960. Phytochrome was finally purified in the 1980s.



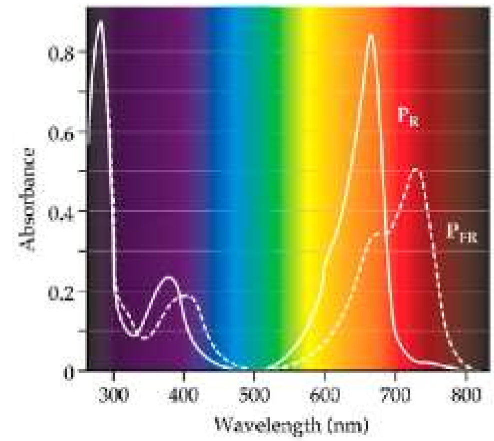
Phytochrome is a biliprotein with the following red-far red reversible structures:

Biliprotein is named after **bilirubin** (l), which is a component of bile. Bilirubin is a breakdown product of the **heme** (c) from hemoglobin that is recycled from aged red



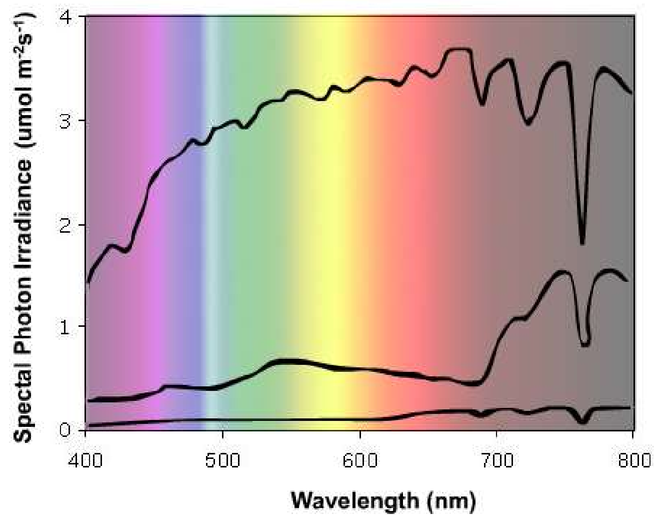


blood cells. Bilibrubin gives the brown color to feces and is converted to urobilin (r) that gives urine its yellow color.

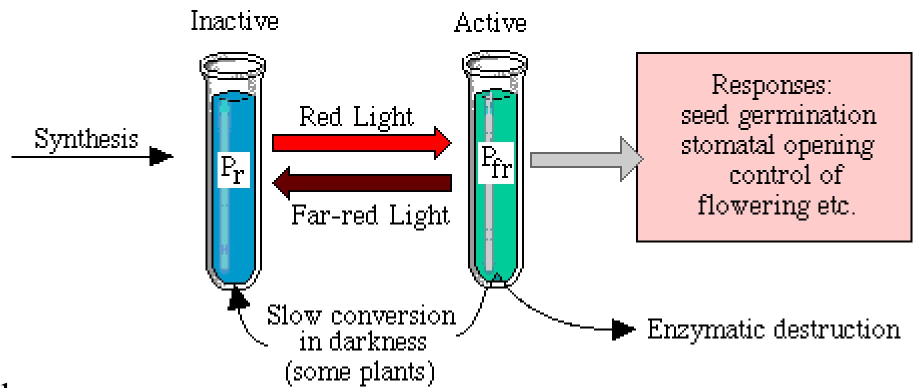


Isolated phytochrome is red-far red reversible and has **absorption spectra** that match the **action spectra** of the red light inhibition of flowering and the far red light nullification of the red light inhibition.

Phytochrome is involved in many other **photoresponses** in the **life cycle of plants** besides photoperiodism. These **photoresponses** include **seed germination**, the **de-etiolation response**, and the **shade-avoidance response**. The upper curve shows the spectral energy distribution of solar radiation at noon on a clear day. The ratio of red light to far red light is greater than unity. The middle curve shows the spectral energy distribution of solar radiation at noon after being filter through a canopy of mustard seedlings. In this case the ratio of red light to far red light is less than unity. The ratio of red to far red light inverses after the solar radiation is filtered through a canopy.



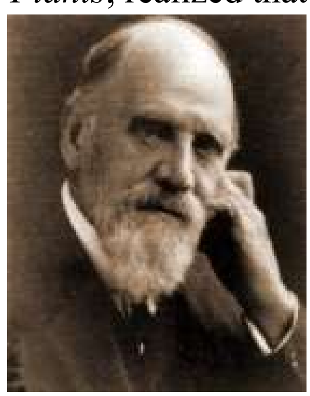
The participation of **phytochrome** in various **photoresponses** has been determined by **comparing** the **photoreversible action spectra** of these responses with the **photoreversible absorption spectra** of phytochrome. The participation of phytochrome in these responses is also determined by comparing the **photoresponses** of **phytochrome mutants** with the **wild type**.

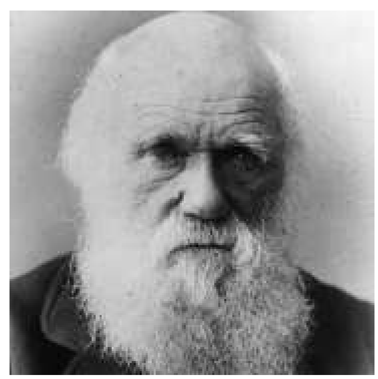


While the **photoperiodic response** helps plants to **orient in time**, the **phototropic response,** which is the **lateral bending of plants in the direction of light,** helps plants **orient in space**. Unlike the photoperiodic response, which is a response to **red light**, the phototropic response is a response to **blue light**.

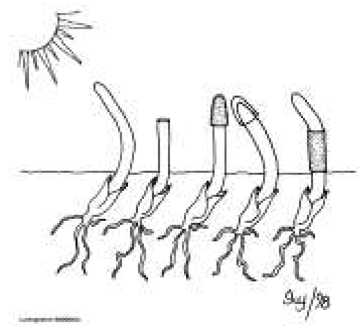
Julius von Sachs (1864) determined that phototropism is a **blue light** response by passing light through **various colored filters** and seeing which colored light caused the plants to bend.

Charles Darwin (1880) and his son **Francis**, who studied *The Power of Movement in Plants*, realized that the **light acted catalytically and not as a substrate** since the light produced by the gas light, which was twelve feet from the seedlings, "*was so obscure that we could not see the seedlings themselves, nor read the large Roman figures*

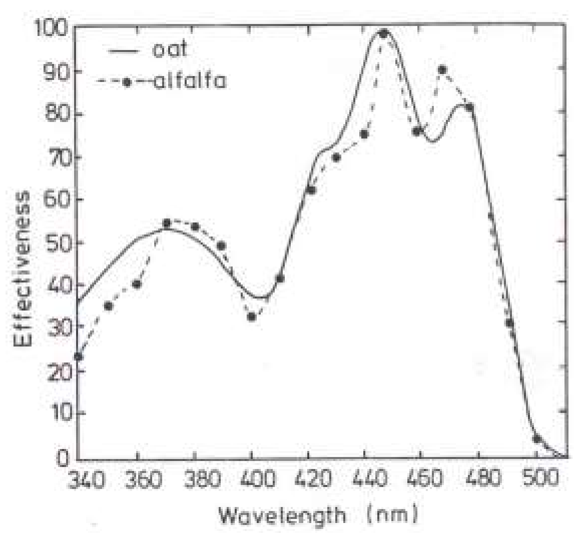




on the white face of a watch, nor see a pencil line on paper, but could just distinguish a line made with Indian ink." Even when the light was so dim, the seedlings bent towards the light in three hours and the curvature occurred about an inch below the tip. Remember that in photoperiodism, light also acted **catalytically** and a one minute pulse of light was sufficient to determine if the plant was to be vegetative or reproductive.

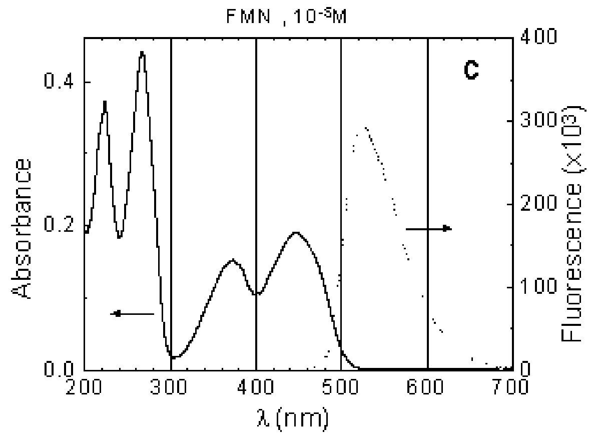


Charles and Francis Darwin determined the **site of light perception** for phototropism, by cutting off the tip, covering the tip with an opaque cap or transparent cap, or covering the middle with an opaque or transparent tube. As long as the tip was present or accessible to light, the seedling bent, indicating that the **tip of the seedling was the site of perception for phototropism**. The tip is the site of perception; it transmits a message to the middle of the seedling where the bending takes place. Remember that for photoperiodism, the leaves are the **site of perception**; they transmit a message to the buds of the plant which are the parts of the plant that flower.

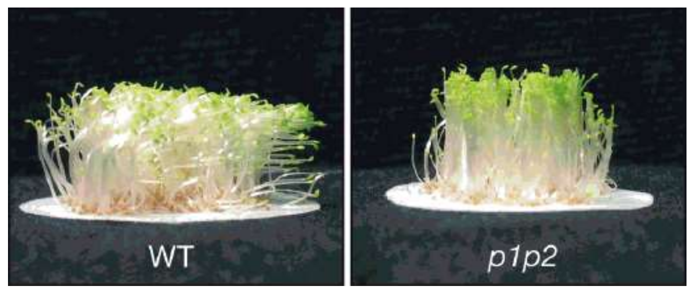


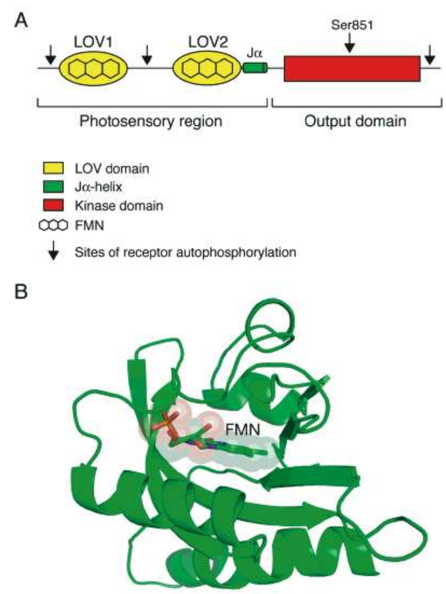
The **action spectrum** for phototropism, obtained by Kenneth Thimann and Curry (1960) shows a peak in the blue and another smaller peak in the ultraviolet region of the spectrum.

The **action spectrum** for phototropism is consistent with the **absorption spectrum** of an FMN (flavin mononucleotide)-containing flavoprotein.



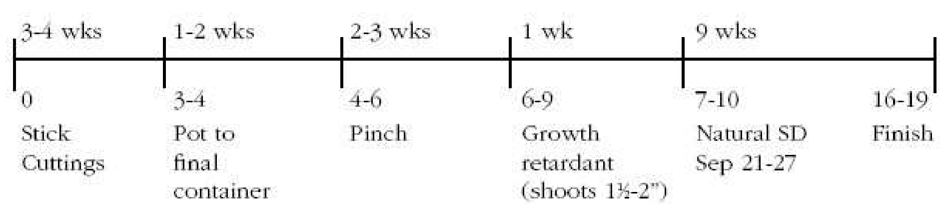
Genetic studies showed that a certain **mutant** (p1p2) that lacks a **FMN-containing flavoprotein** is unable to sense blue light whereas the wild type is phototropic and bends towards the blue light. This is strong evidence that the FMN-containing flavoprotein, now known as **phototropin**, is the photoreceptor pigment that permits plants to **orient in space**. Remember that **phytochrome** is the photoreceptor pigment that permits plants to **orient in time** with the photoperiodic response.





Photobiology is the study of the effect of light on living organisms. It is fascinating from a theoretical, experimental and applied point of view. For example, an understanding of photoperiodism has made it possible to **force plants** to flower out of season or for a specific holiday.

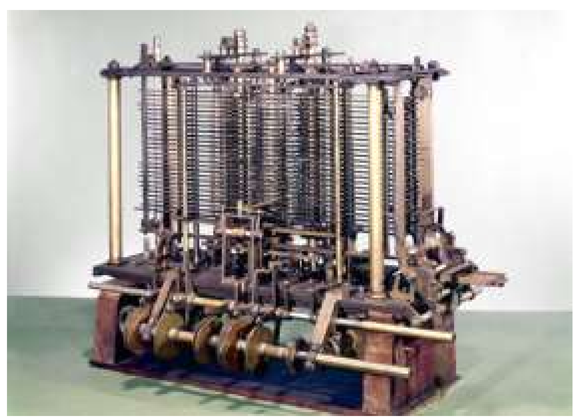
Figure 1. Scheduling Time Line for 6-inch Pinched Poinsettia



Moreover, the discovery of photoperiodism in plants has led to the understanding of the effect of seasons on reproduction and migration in animals.

In this lecture I have been discussing the consciousness of plants in terms of how they sense the external world and respond in space and time appropriately to it. I started this lecture discussing the origin of consciousness in single-celled organisms such as *Euglena*. There are similarities and differences among all taxa. However, our consciousness, used in our attempt to understand truth and the **Laws of Nature** by which the universe is governed, is so much greater than the consciousness of *Euglena*, plants and chimpanzees.

William Whewell (1837) ended his *History of the Inductive Sciences* like so "*The real philosopher, who knows that all the kinds of truth are intimately connected, and that all the best hopes and encouragements which are granted to our nature must be consistent with truth, will be satisfied and confirmed, rather than surprised and disturbed, thus to find the natural sciences leading him to the borders of a higher region. To him it will appear natural and reasonable, that, after journeying so long among the beautiful and orderly laws by which the universe is governed we find ourselves at last approaching to a source of order and law, and intellectual beauty:--that, after venturing into the region of life and feeling and will, we are led to believe the fountain of life and will, not to be itself unintelligent and dead, but to be a living mind, a power which aims as well as acts. To us this doctrine appears like the natural cadence of the tones to which we have so long been listening; and without such a final strain our* *ears would have been left craving and unsatisfied. We have been lingering long amid the harmonies of law and symmetry, constancy and development; and these notes, through their music was sweet and deep, must too often have sounded to the ear of our moral nature, as vague and unmeaning melodies, floating in the air around us, but conveying no definite thought, moulded into no intelligible announcement. But one passage which we have again and again caught by snatches, though sometimes interrupted and lost, at last swells in our ears full, clear, and decided; and the religious 'Hymm in honour of the Creator,' to which Galen so gladly lent his voice, and in which the best physiologists of succeeding times have ever joined, is filled into a richer and deeper harmony by the greatest philosophers of these later days, and will roll on hereafter, the 'perpetual song' of the temple of science."*



Charles Babbage (1838), inventor of the mechanical computer, responded to Whewell's claim that "*We may thus, with the greatest propriety, deny to the mechanical philosophers and mathematicians of recent times any authority with regard to their views of the administration of the universe; we have no reason whatever to expect from their speculations any help, when we ascend to the first cause and supreme ruler of the universe. But we might perhaps go farther, and assert that they are in some respects less likely than men employed in other pursuits, to make any clear advance towards such a subject of speculation*" by producing *A Fragment*, the Ninth and unauthorized Bridgewater

Treatise. In the second edition, Babbage described the power of mathematics in understanding the Creator:

"*First, The truths of pure mathematics are necessary truths; they are of such a nature, that to suppose the reverse, involves a contradiction.*

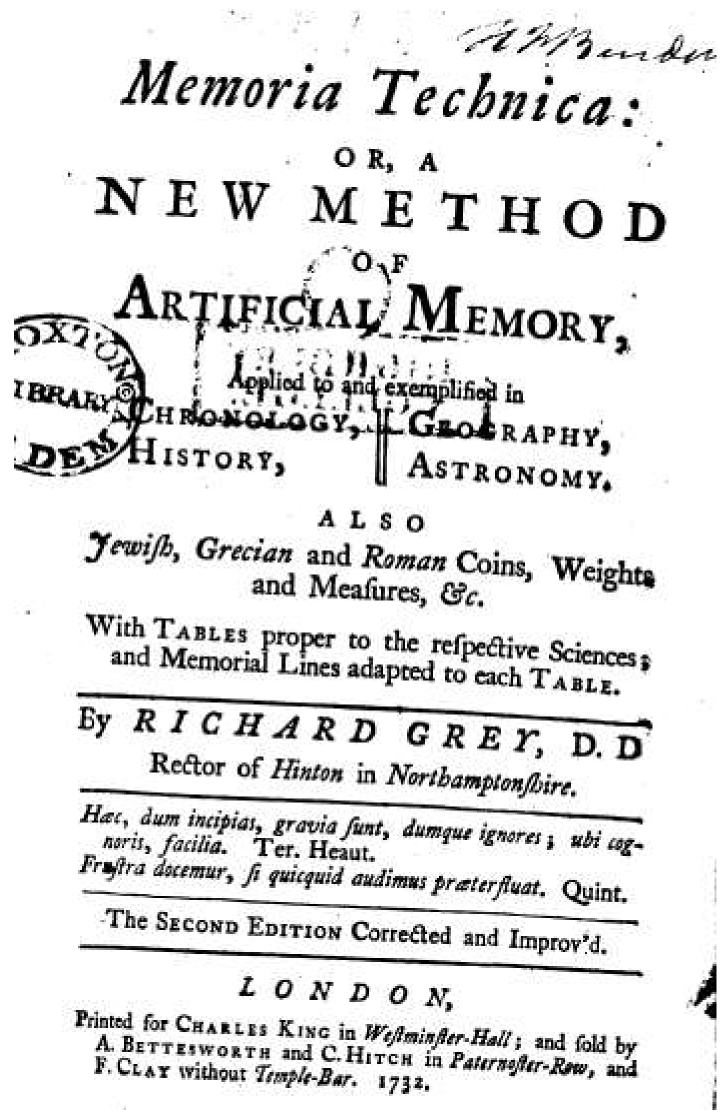
Secondly, The laws of nature, on which physical reasonings are founded, although some of them are considered as necessary truths, depend, in many instances, on the testimony of our senses. These derive their highest confirmation from the aid of pure mathematics, by which innumerable consequences, previously unobserved, are proved to result from them.

Thirdly, The truths of natural religion rest also on the testimony of our external senses, but united with that internal consciousness of intention or design which we experience in our own breast, and from which we infer similar powers in other beings. Many of the facts on which the conclusions of natural religion are founded, derive their chief importance from the aid supplied by the united power of the two former classes, and the amount and value of this support will be enlarged with the advance of those sciences.

Fourthly, Revealed religion rests on human testimony; and on that alone. Its first and greatest support arises from natural religion. I have endeavoured in one chapter of the present volume to show, that, notwithstanding the weakening effect of transmission upon testimony, a time may arrive when, by the progress of knowledge, internal evidence of the truth of revelation may start into existence with all the force that can be derived from the testimony of the senses.

The first class of truths then (those of Pure Mathematics) appears to rest on necessity. The second, (the Laws of Nature,) on necessity and our external senses. The third, (those of Natural Religion,) on our external senses and internal consciousness. The last, (those of Revelation,) on human testimony. If they admit of *any classification, as subjects having a common resemblance, or as possessing different degrees of evidence, I have placed them in the only order which, in my opinion, is consistent with truth; convinced that it is more injurious to religion to overrate, than to undervalue the cogency of the evidence on which it rests.*"

Having trouble with remembering things? We can learn from the plants. In this lecture I have shown you that plants have a real notion of time and place. Richard Grey (1732) wrote in the second edition of *Memoria Technica: or, a New Method of Artificial Memory, Applied to and exemplified in Chronology, Geography, History, Astronomy, Also Jewish, Grecian and Roman Coins, Weights and Measures, &c.*, "*I believe it will be agreed on all Hands, that, to instance in History only, a Man who has an exact Notion of Time and Place, finds incomparably more Pleasure, and make a speedier Progress in that Study, than he who has not.*"



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Jewish, Grecian and *Roman* Coins, Weights and Measures, *&c.*

With TABLES proper to the respective Sciences; and Memorial Lines adapted to each TABLE.

By *RICHARD GREY*, D. D

Rector of *Hinton* in *Northamptonshire.*

Hæc, dum incipias, gravia sunt, dumque ignores; ubi cognoris, facilia. Ter. Heaut.
Frustra docemur, si quicquid audimus præterfluat. Quint.

The SECOND EDITION Corrected and Improv'd.

LONDON,

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