



Cambridge University

Botanic Garden

Rhythms in Plants Trail

The earth rotates on its axis every 24 hours, resulting in day and night cycles. It also orbits around the sun, causing annual seasonal shifts in day length, light levels, temperature, rainfall and other climatic conditions.

Plants develop rhythms in response to these cyclical changes. These rhythms can be as a result of direct responses to environmental cues, or the presence of an inbuilt clock. The latter gives them the innate ability to measure time and anticipate rhythmic changes in the environment, such as day and night. 'Circadian rhythms' are biological cycles completed in 24 hours, allowing plants to tell the time of day.

This trail takes a closer look at rhythms in plants, including cyclic changes in growth rates, flowering times, opening and closing of stomata, production of scent and leaf loss.

**See an online version of this trail
at www.botanic.cam.ac.uk/plant-rhythms**

Rhythms in Plants

The natural world is full of rhythms. The day/night cycle results in changes in light levels and temperature, while the yearly cycle gives alternation of wet and dry seasons at the equator, and progressions of temperature and day length with the seasons at latitudes further towards the poles. Responding to these rhythms is crucial to the survival of animals and plants. Animals can move, allowing them to shelter in the shade of a tree during the hot noon day sun, or migrate to a warmer climate for winter, while plants remain literally rooted to the spot, and must physiologically adapt to be able to cope.

These adaptations fall into two categories: direct responses to an environmental cue, or anticipatory responses controlled by an internal 24-hour circadian clock. An example of a direct response is when sensors in the leaf detect the light of dawn and cause leaf pores called stomata to open, allowing the intake of air for use in photosynthesis. Another is when cooling temperatures in autumn trigger leaf fall in deciduous trees. Relying solely on direct responses is inefficient and potentially dangerous: opening pores is slow and, if only triggered by an increase in light, part of the day where photosynthesis could occur would be wasted. Likewise, an unseasonably cool summer could cause trees to lose their leaves too early, resulting in months of lost photosynthesis and a smaller reserve of sugars for the tree to use as food the following spring. For these reasons, many responses are regulated both directly and by an internal clock to provide anticipation.

Plants supplement environmental cues with their own internal circadian clock, which anticipates the 24-hour cycle of light and dark and associated temperature changes. The clock

takes the form of rising and falling levels of certain proteins within the plants' cells. Production of one set of proteins causes the levels of a second set to fall, which turns off the production of the first set; levels of the second set then rise, allowing the first set to be produced again. This sets up an oscillating loop of protein levels: the basis of the circadian clock in plants. (For a fuller explanation of the mechanism, see the panels in the Circadian Beds at point 13 on the map.)

Using these cycles, the plant can keep track of when dawn is approaching, opening its leaf pores in anticipation of light levels rising. The appearance of light at dawn is also how the plant keeps its clock 'in sync' with the 24-hour days: light resets the clock at the start of every day.

The clock can also inform the plant about seasons, because it can be used to measure the length of the day. By combining information from light sensors in the leaves with protein levels which build up during the day, the plant can tell if it has been sunny for more than a certain number of hours: if so, then it must be spring and time to start growing. Likewise, shortening days indicate that it is approaching autumn and therefore the plant should start shedding leaves.

Circadian rhythms in plants are studied by Prof. Alex Webb and his research group in the Department of Plant Sciences. By growing plants in day/night cycles which are longer or shorter than the normal 24 hours, and by using plants defective in particular elements of the circadian clock, the scientists are looking at what keeps the clock ticking with its daily regularity. Changing the clock's timing can mean plants grow slower or faster, so this research will help increase crop yields for food and bioenergy production.
www.plantsci.cam.ac.uk/research/alexwebb



1

Persian Silk Tree (*Albizia julibrissin*)

Many plants display sleep movements (known as nyctinasty), folding their leaves closed at night, thought by some to be a defense against nocturnal herbivory.

This can be seen in French bean, wood sorrel, clover, sensitive plant (*Mimosa pudica*) and in the Persian silk tree here and in the Brookside bike park nearby. Such movements of leaves are caused by changes in turgor pressure – the swelling of plant cells with water – at the base of the stalks of the leaves of these species. The opening movement requires an increase of turgor in the top part of the leaf stalk, and the closing movement requires an increase of turgor in the bottom part. These movements have been shown to be under control of the circadian clock.

An understanding of the complex cellular physiological mechanisms resulting in these turgor movements was obtained using this species. Look out for its pink, fluffy-headed flowers in the summer.

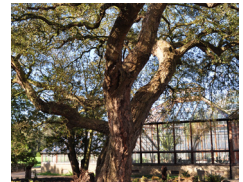


2

Cork Oak (*Quercus suber*)

Quercus suber is found growing in drought-prone regions around the Mediterranean basin. In hot, dry areas such as these, some species exhibit a daily suppression in photosynthesis around noon, at the hottest part of the day. This is known as the 'midday depression', when the plant closes its stomata to reduce water loss.

This closure can cause other short-term effects to the plant. Gas exchange through stomata is important for cooling, so leaves with closed stomata can overheat. Additionally, the suppression of photosynthesis means the light energy cannot be used as normal, and the energy surplus can damage cells within the plant. However, water loss would be more catastrophic to the plant than either overheating or problems caused by high light, and there are rhythmic repair processes which deal with the damage.



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3

Barrel Cactus (*Echinocactus grusonii*)

Plants harvest the sun's energy using photosynthesis, turning carbon dioxide and water into sugars. In most plants, pores called stomata on the underside of the leaf open during the day to allow carbon dioxide to flow in, and close at night. When healthy plants are moved to artificial, constant 24-hour light, the pores still open and close over what would naturally be day and night, showing that the opening and closing is regulated by the circadian clock.



'CAM plants' (including cacti, agave and pineapple) have evolved a version of photosynthesis where the stomata open at night, instead of during the day. They then store the carbon dioxide for when it is light. They shut their stomata during the day, when it is hotter, meaning less water can escape. The control of opening and closing is still under circadian control, but is also affected by levels of accumulation of various products of photosynthesis.

4

Tar Gum Tree (*Clusia minor*)

Almost all plants photosynthesise, but not all in the same way: there are three pathways through which plants can convert carbon dioxide into the sugars that fuel plant growth and development.



About 90% of plant species use 'C3' photosynthesis, absorbing carbon dioxide during the day; about 7% use 'C4', which operates in a similar way but has different biochemistry behind it. The remaining 3% of plant species use CAM photosynthesis, and the tar gum tree is the only tree which does so. Surprisingly, it also utilizes C3 and C4 photosynthesis, and can swap between photosynthesis types depending on environmental conditions. It can even use different pathways in different parts of the same leaf at the same time.

Integral to CAM photosynthesis are daily rhythms where the stomata remain closed during the day and open at night when it is cooler. C3, C4 and CAM photosynthesis are all governed by the circadian clock.

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Rhythms in Plants





5

Sensitive Plant (*Mimosa pudica*)

The sensitive plant is well known for its response to touch, but less known for its sleep movement similar to *Albizia* and the French bean. It was originally thought that this was a response to an external environmental cue, perhaps light.

This nightly leaf folding in *Mimosa pudica* was the subject of the first-ever experiment in the field of chronobiology, undertaken in 1729 by Jean-Jacques de Mairan, a French astronomer. He put the plant in his cupboard, and found that it would open and close its leaves on a daily cycle even when it was kept in the dark. In 1758, researchers repeated the experiment, placing the plant in a suitcase wrapped in a blanket, inside a wardrobe in a cave, eliminating all light; it still moved, showing that the plant was indeed responding to an internal rhythm. Some were still not convinced, arguing that it could potentially be driven by some subtle and undetected geophysical cue associated with the rotation of the earth on its axis. The role for an internal circadian clock was definitively proven by the field of molecular genetics, which identified the timekeeping components.



6

Tulips (*Tulipa* spp.)

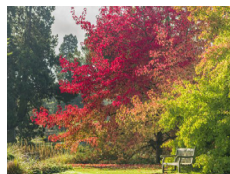
Many tulip species originate from Southwest and Central Asia, where summer temperatures can be extremely high. As a survival mechanism, these plants become dormant in the hot summer months, moving below ground as bulbs. Plants that produce underground storage organs as a way of storing food for the next growing season or to escape adverse environmental conditions are known as 'geophytes'. After flowering in the cooler spring months, their leaves wither and die off, meaning no parts of the plant remain above ground during the dormant period. Consequently, the remaining underground bulb cannot detect the length of the day by sensing light, so instead it relies on its ability to sense changes in temperature, starting to grow only once a set period of cold (i.e., winter) has passed. Sensing seasonal rhythms often requires environmental cues as well as activity of the circadian clock.



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7 Sweetgum (*Liquidambar styraciflua*)

Visitors to the Botanic Garden in autumn are treated to a spectacular display of colour from the *Liquidambar* tree by the Lake, when the foliage floods deep wine-red in early autumn.

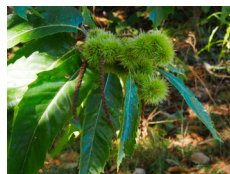


This colour change marks the start of the process of leaf death. Allowing green leaves to fall would waste the nitrogen contained in the chlorophyll used to harvest the sun's light. Instead, the plant stops making new chlorophyll and breaks down and reabsorbs any that exists. The red of the *Liquidambar* leaves is a result of the breakdown of sugars within the ageing leaf.

The process of leaf ageing is regulated by some of the elements of the circadian clock that regulate flower production. One part of this, the 'evening complex', maintains circadian rhythms and brings together signals from day length and temperature. As well as helping trigger flowering in spring as days lengthen and temperatures increase, it plays a part in triggering leaf death as autumn approaches.

8 Sweet Chestnut (*Castanea sativa*)

Trees and other plants that live for several years must cope with conditions ranging from drought and high heat in summer to freezing cold in winter. To cope with cold weather, many become dormant in winter, stopping growth and slowing down their metabolism and energy consumption. This results in the formation of annual tree rings in their woody stem, providing a direct record of rhythmicity.



Researchers investigating the molecular and genetic basis of dormancy took samples from dormant trees at midday, and analysed which genes were active. They were surprised to find high levels of a circadian clock component which is usually turned off during the daytime. Further analysis of dormant chestnut trees showed that the circadian clock is disrupted during dormancy, and restarts when the plant is exposed to warmer temperatures. This disruption could control changes in the tree's processes to help it survive winter.

9

Tobacco (*Nicotiana tabacum*)

'Photoperiodism' is the physiological and behavioural reaction of organisms to changes in the length of the daylight period throughout the year. It was discovered in *Nicotiana tabacum*, a 'short-day' plant, which only flowers when the daily period of light is shorter than some critical length. By contrast, long-day plants such as *Nicotiana sylvestris* only flower when the period of darkness is shorter than some critical length. The plant measures the length of the dark period by coordinating its circadian clock with the action of a pigment called phytochrome (a photoreceptor found in plant cells which is sensitive to red and far red light). Phytochromes provide plants with time signals, making sure the plant's internal time matches environmental time.

Tricking plants into believing it is the right time to flower is key to several industries, including the production of cut flowers. Chrysanthemums are a short-day plant, so will not naturally flower in summer. Chrysanthemum growers artificially darken their glasshouses for part of the day in summer to trigger flowering.



10

Tomato (*Solanum lycopersicum*)

Tomato was domesticated from the wild plant *Solanum pimpinellifolium*, which grows in equatorial countries including Ecuador and Peru. In these countries, the number of sunlight hours in a day remains relatively constant throughout the year, so the plant cannot use the relative lengths of day and night to detect the changing seasons.

Researchers in Germany found that the circadian clock in the domestic tomato runs on a cycle which is around two hours longer than that of its wild relative. Detailed analysis showed that this longer cycle is driven by a regulatory gene. Experiments which replace this longer-cycle gene in the domestic tomato with the shorter-cycle copy from its wild relative show that plants carrying the longer-cycle gene are shorter, flower later, and have more chlorophyll. All of these changes may in turn improve crop performance.



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11 Cabbage (*Brassica* spp.)

When faced with a predator, plants cannot get up and run away as an animal would do. Instead, they protect themselves with an arsenal of chemicals. One such chemical is a plant hormone called jasmonate. Increasing jasmonate levels drive the production of chemicals which deter herbivores, and also trigger the production of cellular machinery to repair damaged tissue.



The cabbage looper caterpillar is a common pest of cabbages. It has its own circadian rhythm, with the peak of its feeding behaviour happening in late afternoon. Remarkably, it has been shown that jasmonate production in plants is also under the control of the circadian clock. The plants synchronise their jasmonate production with the feeding behaviour, producing more deterrent chemicals when the caterpillars are more likely to be active.

12 Sunflower (*Helianthus annuus*)

It has long been known that young sunflowers bend their growing shoots to follow the sun's movement from east to west during the day, bending back to the east again to be ready for the new day. It was thought that this was simply the plants following the light, but careful experimentation has shown that this is not the case. When outdoor-grown sunflowers were moved into an indoor growth chamber with a fixed overhead light, the plants still bent back and forth to track an imaginary sun for several days, indicating that the movement was driven by an internal clock. To find out how movement affected the growth of plants, the researchers staked sunflowers so they were unable to move. These immobile plants grew to be smaller overall, indicating that tracking the sun gives them a growth boost.



Fully grown sunflowers do not track the sun, but instead always face east to catch its morning rays. This helps the flowers heat up more quickly, attracting many more pollinating insects.

13 Circadian Beds

This display explains how plants regulate the time of day at which they flower, as determined by their circadian clock. Three key external factors regulate the plant's clock and ensure it keeps to a 24-hour rhythm: sugars made during photosynthesis, light levels, and temperature.

The two beds in this display represent a clock. One bed contains plants which open in the morning and which attract familiar pollinators such as bees; the other contains evening-flowering species which attract evening pollinators such as moths. These flowers are often scented.

Some plants open their flowers at sunrise and close at sunset (such as morning glory), while others open at dawn but close just after noon (Jack-go-to-bed-at-noon). The four-o'clock plant opens its flowers in late afternoon and shuts them before dawn.



14 Angel's Trumpet (*Brugmansia suaveolens*)

As its name suggests, the angel's trumpet has enormous flared flowers, which are pollinated by night-flying moths. To attract these moths, the plant produces an intense fragrance. Both scent production and flower opening are under circadian control: the flowers are closed and lack fragrance during the day, but open and emit scent in the evening.

For most animals, the plant is highly poisonous. Interestingly, some caterpillars that eat the plant are unaffected by the poison, instead storing it until they metamorphose into a butterfly. The stored poison is still active against other animals, and deters predators. The nectar contains scopolamine, an alkaloid which is somewhat poisonous to bees (and less poisonous to moths), which is another way in which the plant limits the range of pollinators which visit it.

The angel's trumpet is native to Brazil, but is now extinct in the wild.



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