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Flowering response to photoperiod combines the effect of the daylength with the effects of the daily changes in sunrise and sunset times and of temperature acclimation

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Sorghum in the 21st Century
Montpellier, France, 5 to 9 June 2023

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Good afternoon.

I am going to explain new hypotheses about the flowering time of sorghum in the field.
I will use results from experiments carried out since 1990 with partners in Mali, Nicaragua, Colombia, and France.

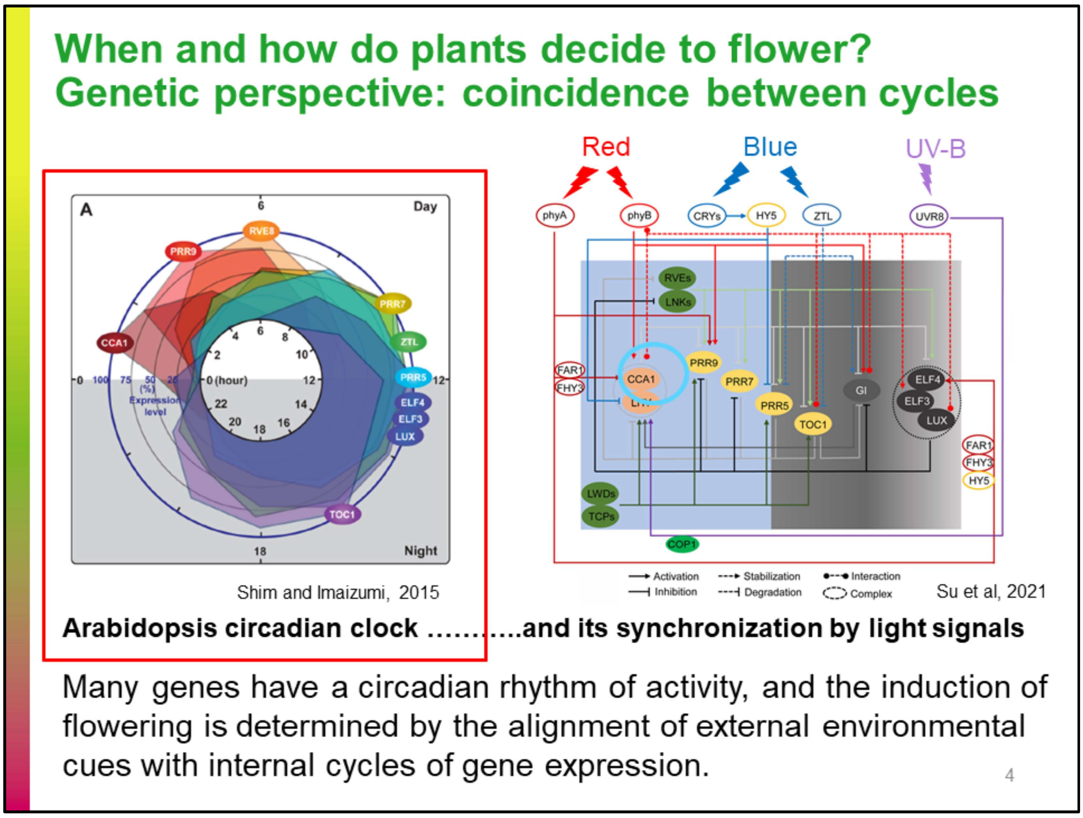
CIRAD scientists studied photoperiod sensitivity in sorghum because of the failure of the green revolution in sorghum in Africa.

The main principle of the green revolution was to create short and early varieties that better use fertilisers to produce higher yields.

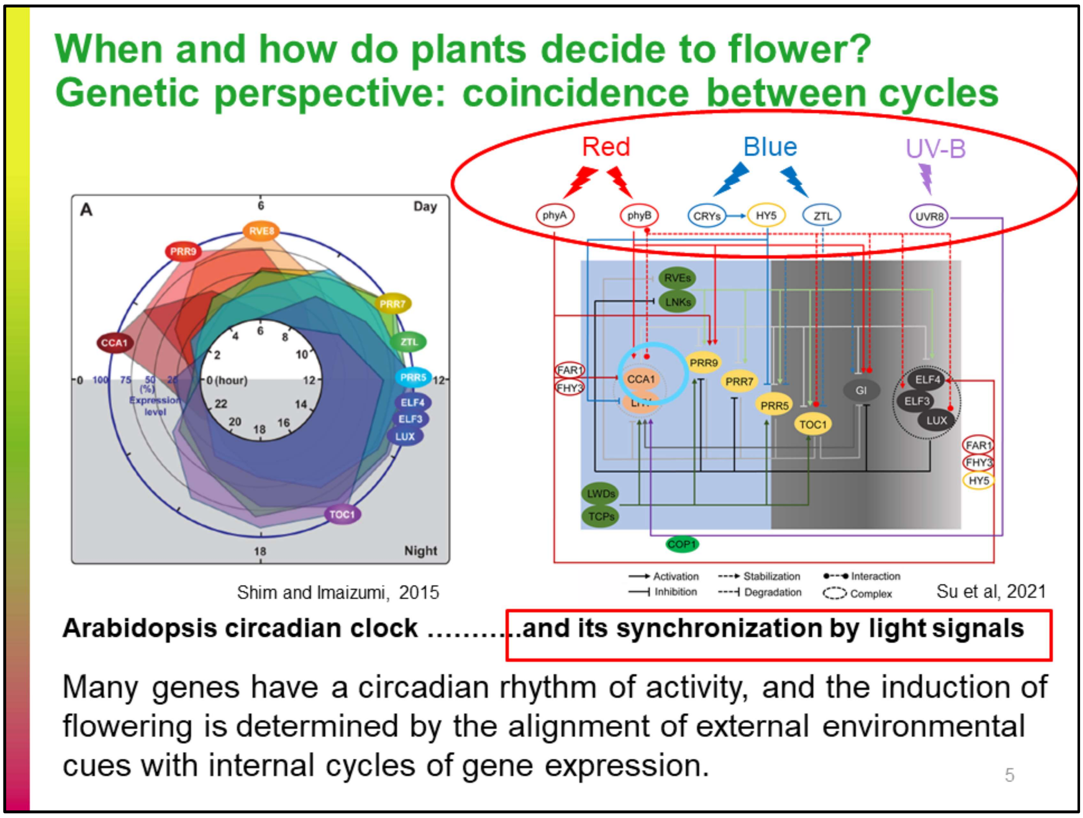
It was very successful in Asia, but not in Africa because the markets were not ready and because of strong abiotic and biotic constraints on sorghum crops.

In the 1970s and 80s, it was recognised that photoperiod sensitivity was a key trait to ensure that sorghum varieties flowered within a narrow window of favourable dates that varied with the length of the rainy season of the year.

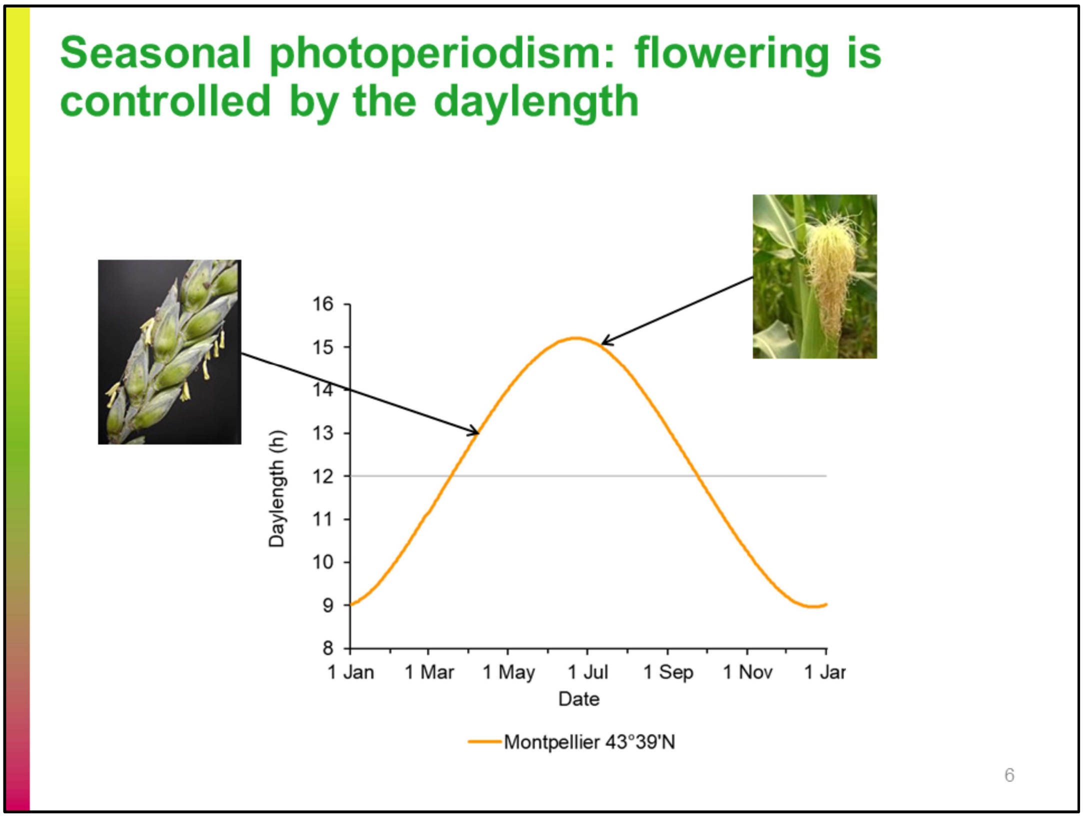
That is why breeding and plant physiology programmes were planned to consider this trait since 1990.



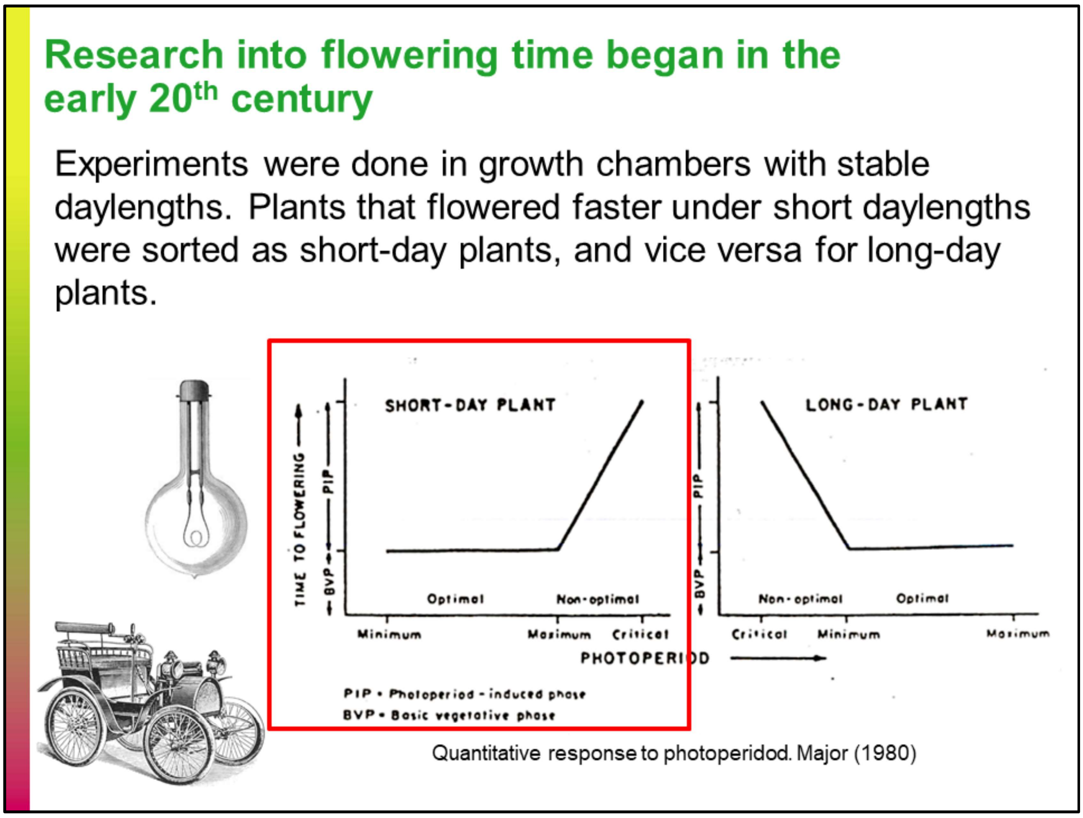
Since 2000, knowledge of the cellular machinery that controls flowering time has increased dramatically. The cell clock now consists of many circadian genes, each having a specific peak time of expression during the day or the night.



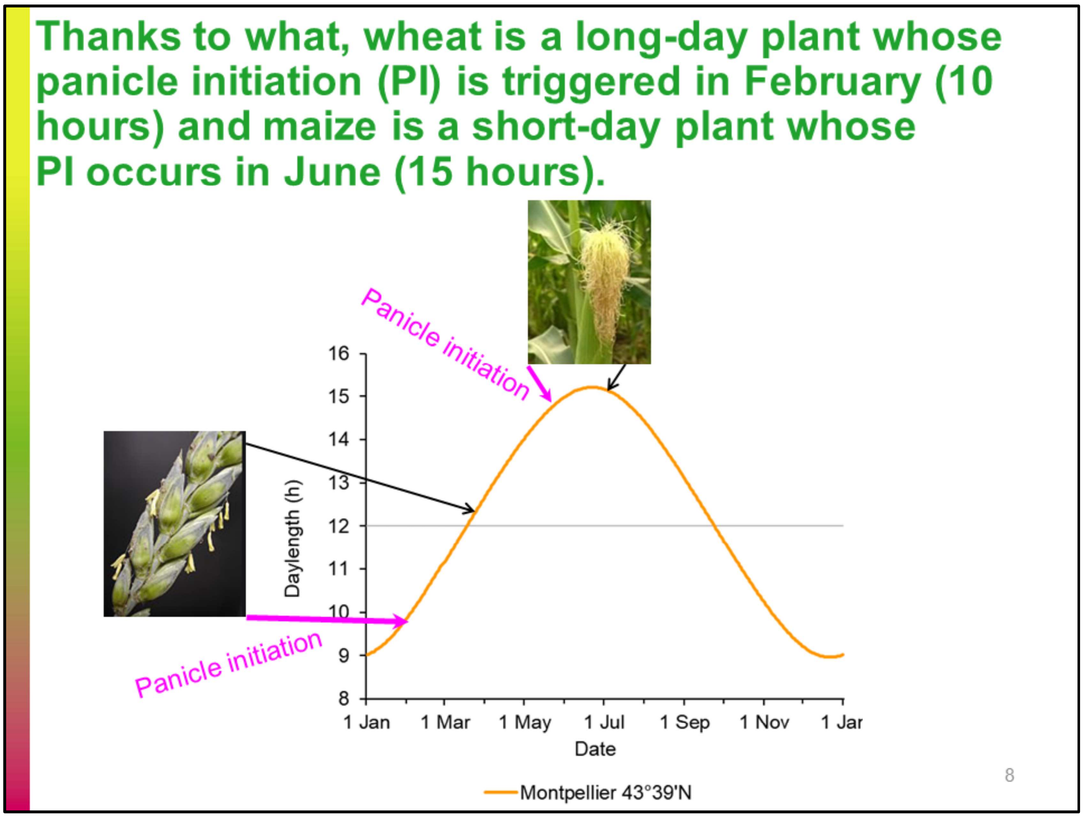
And this complex clock is set every day at dawn and dusk, which are now perceived by five pigments in the red, blue and UV-B lights.
All this cyclical machinery supports the coincidence theory: flowering is triggered by a favourable alignment of external cues and internal cycles.



Flowering time is related to daylength.
In France, for example, wheat flowers in spring when daylength is close to 12 hours and maize flowers in summer when daylength is about 15 hours.

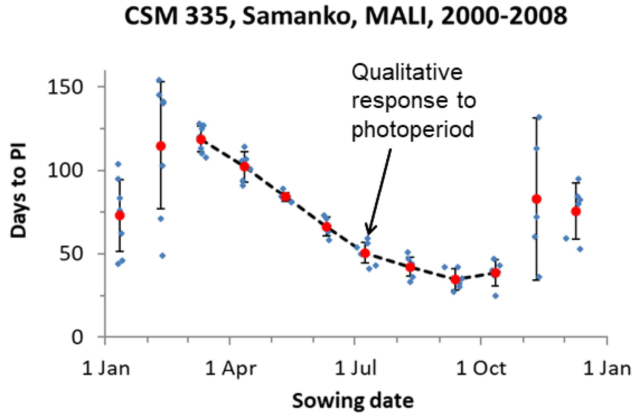


Research into flowering time began in the early 20th century.
The experiments were carried out in growth chambers with series of stable daylengths.
Plants that flowered earlier (on the Y axis) under shorter daylengths (on the X axis) were sorted as short-day plants, and vice versa for long-day plants.



Thanks to what, wheat is a long-day plant whose panicle initiation occurs when the day length is 10 hours, and maize and sorghum are short-day plants whose panicle initiation occurs when the day length is 15 hours.
Indeed, the important event to relate to environmental cues is the time of the transition from the vegetative to the reproductive phase, when the apical meristem begins to produce a panicle in grasses.

Alternative method in field : seven complete years of monthly sowing of a photoperiod-sensitive sorghum variety in Mali

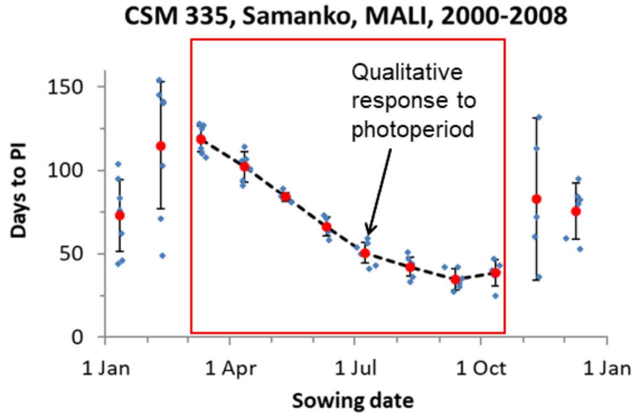


9 months old IS 15401 plot
12 October 2004

- *March to October sowings:*
  - Level of precision: 95% mean confidence interval = 13 days (or ± 6.5 d)
  - Qualitative response to photoperiod
- *November to February sowings:*
  - PI is variable and late when daylenght is short and it is not a temperature effect.

In tropical countries, an alternative to growth chambers is to exploit the natural changes in daylength by annual series of monthly sowings.
I used this method on sorghum for 9 years at the ICRISAT station near Bamako in Mali.
Generally, a variety was sown for 24 consecutive months. The control variety, CSM 335, completed 7 years. It is a photoperiod-sensitive variety well adapted to the Bamako area.
The date of panicle initiation was recorded by plant dissections.
The graph shows the duration in days to panicle initiation on the Y axis as a function of the month of sowing on the X axis. The X-axis will be the same in many of the following plots.
CLICK

Alternative method in field : seven complete years of monthly sowing of a photoperiod-sensitive sorghum variety in Mali

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For sowings from March to October, panicle initiation dates occurred within a rather stable 95% confidence interval of 13 days. The response to day length well fitted a qualitative model.
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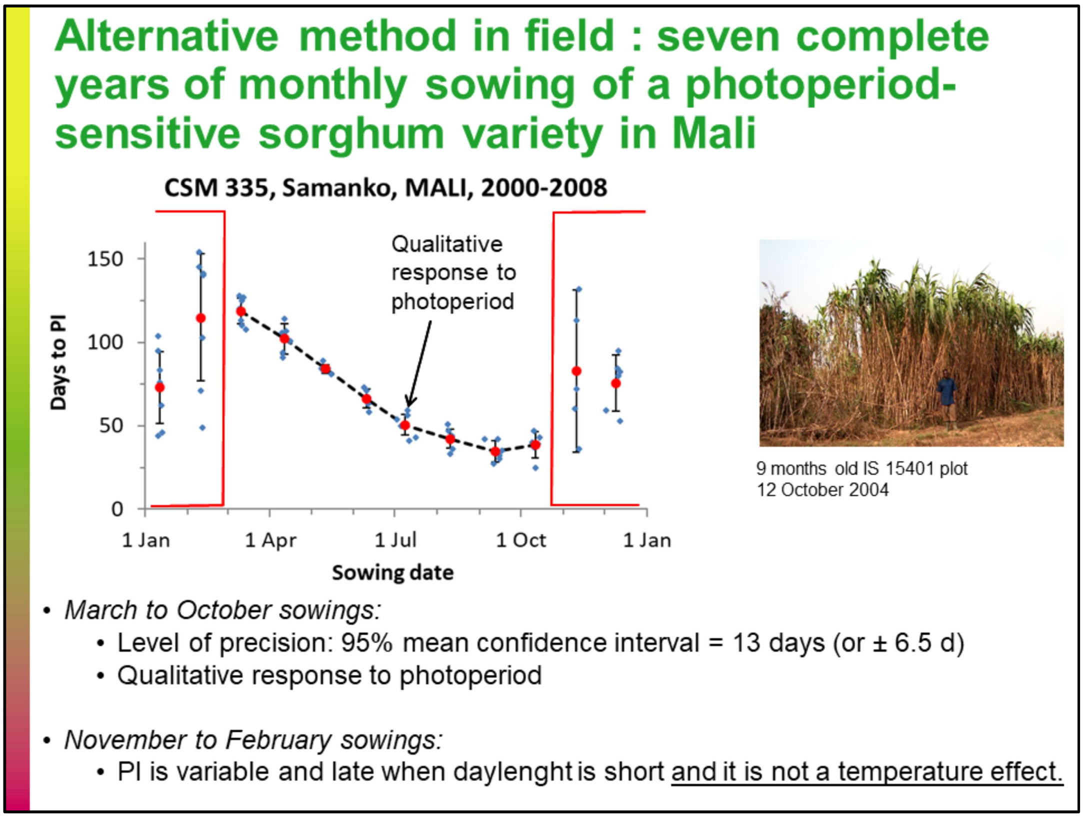
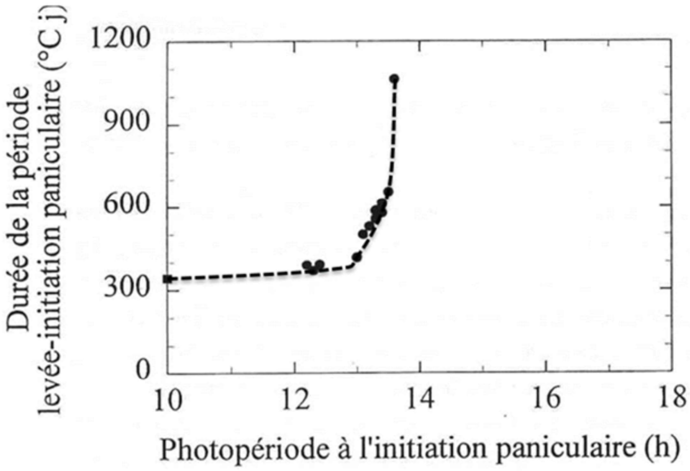


Conversely, the durations to panicle initiation for the November to February sowings varied a lot between years and were longer than for the September sowing, despite the shorter daylength.

These longer durations are not explained by the slightly cooler temperatures of the period.

Also, observations of panicle initiation at different latitudes do not fit the short-day model.

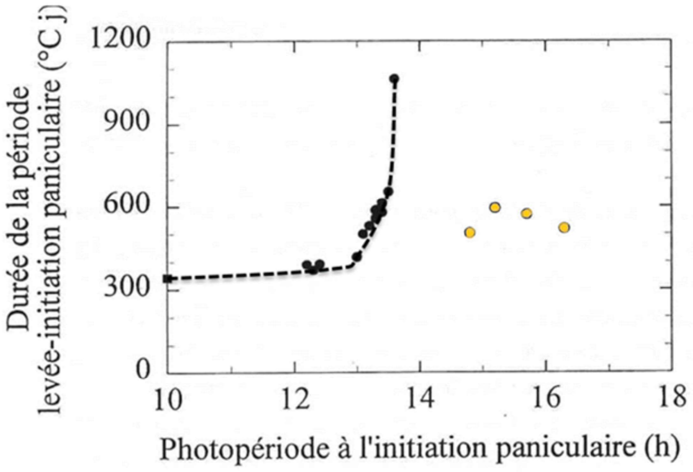


Lafarge, 1998

The sorghum variety (E 35-1) responds to the sowing date, thus to the photoperiod, in Bamako, 12°N (Mali) (●). However, this response does not apply with May-June sowings in Montpellier 43°N (●)

Also, field observations of panicle initiations at different latitudes do not fit the short-day plant model.
The graph shows the duration to panicle initiation of one sorghum variety monthly sown in an experiment in Bamako.
Here it is the daylength at the time of the panicle initiation that is shown on the X axis.
The duration to panicle initiation tripled from 13 to 13 and a half hours of daylength.
CLICK

Also, observations of panicle initiation at different latitudes do not fit the short-day model.

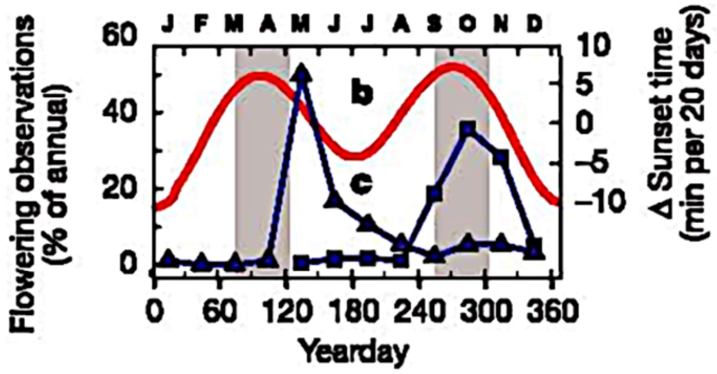


Lafarge, 1998

The sorghum variety (E 35-1) responds to the sowing date, thus to the photoperiod, in Bamako, 12°N (Mali) (●). However, this response does not apply with May-June sowings in Montpellier 43°N (●)

However, panicle initiation occurred early enough when daylength was over 15 hours for the same variety sown in May and June in Montpellier.

No published hypothesis that helps solving the growth chambers-field contradictions until Borchert et al. (2005): Flowering time in 32 tropical tree species in the tropics and equatorial regions.

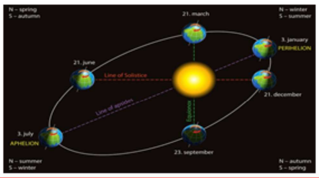


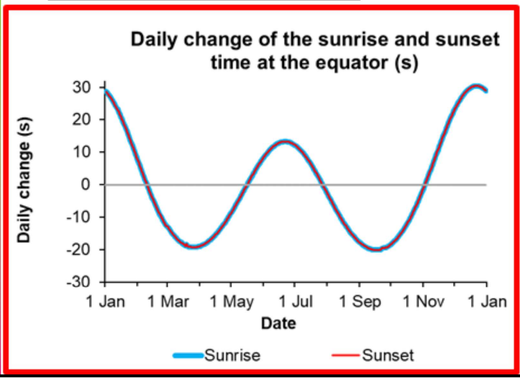
Blooming peaks are correlated with maximum daily variation of the sunset time

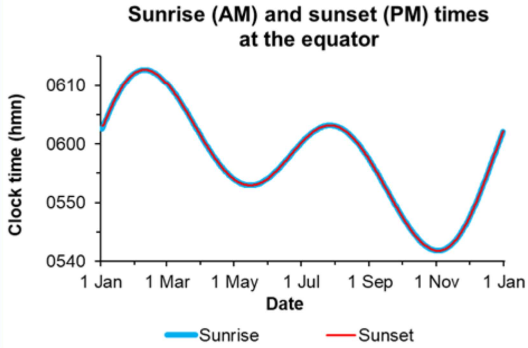
No published hypothesis could help to interpret these unexplained field observations until the 2005 paper of Borchert, a tropical tree specialist from the University of Kansas.
He collected observations of the flowering time of forest tree species in the tropics and equatorial regions and found two peaks of flowering (in blue) in March-April and September-October.
These two peaks were synchronised with the two annual maximum daily variations in sunset time (in red).

What are these daily changes in sunrise/sunset times at the equator?

The ellipsoidal orbit of the earth creates small variations in the daily sunrise and sunset times, which are equal at the equator. Thus, the photoperiod has a stable length of 12 hours.







What are these daily changes in sunrise and sunset times at the equator?
Because the Earth's orbit around the Sun is an ellipse, the time between two sunrises at the equator is never exactly 24 hours.
The difference in duration is between + 30 s and - 20 s over the year. However, the daily difference is similar for sunrise and sunset times, so the length of the day has a stable duration of 12 hours.
CLICK

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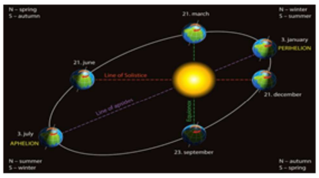
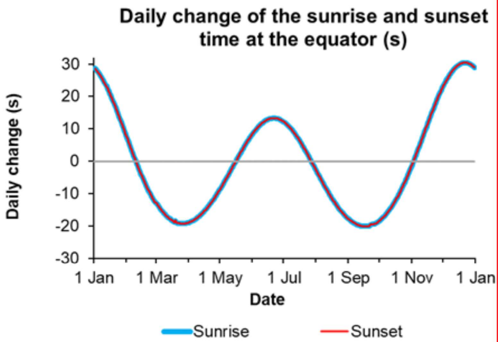
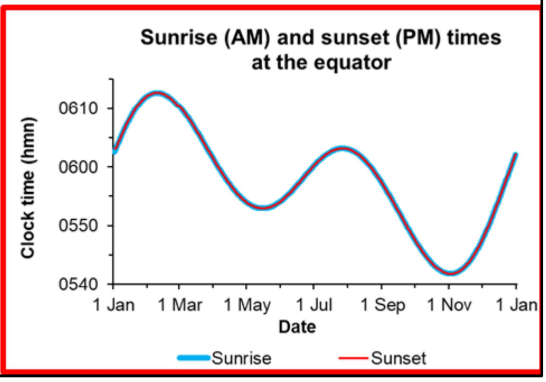


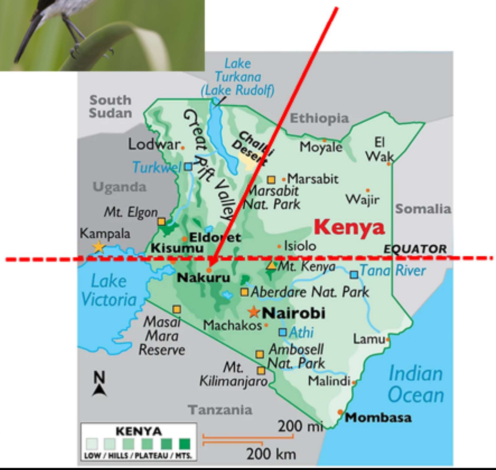


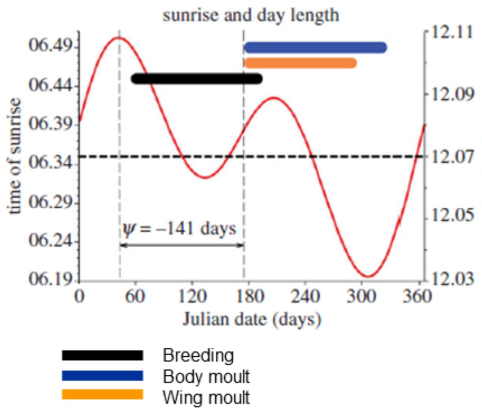


These differences accumulate daily, so that the clock time of sunrise and sunset vary by 35 minutes around six, throughout the year.

More:
Goymann et al. (2012). Breeding and moults of stonechats are synchronized in Nakuru at 26 km from the equator

→ Daily changes in sunrise time might be the cue





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Photoperiodism in animals living at the equator raises the same questions. Goymann and a team from the Max Plank Institute in Germany studied small birds, stonechats, living in Nakuru, in Kenya, 26 km from the equator.
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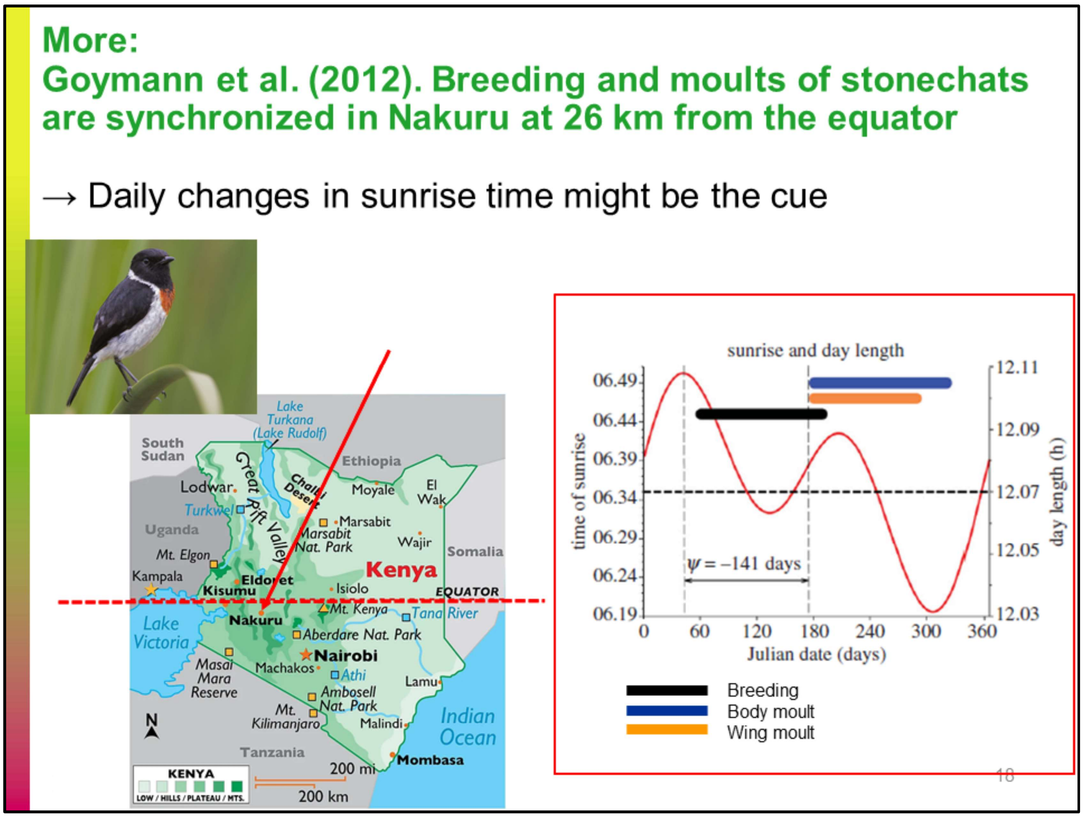
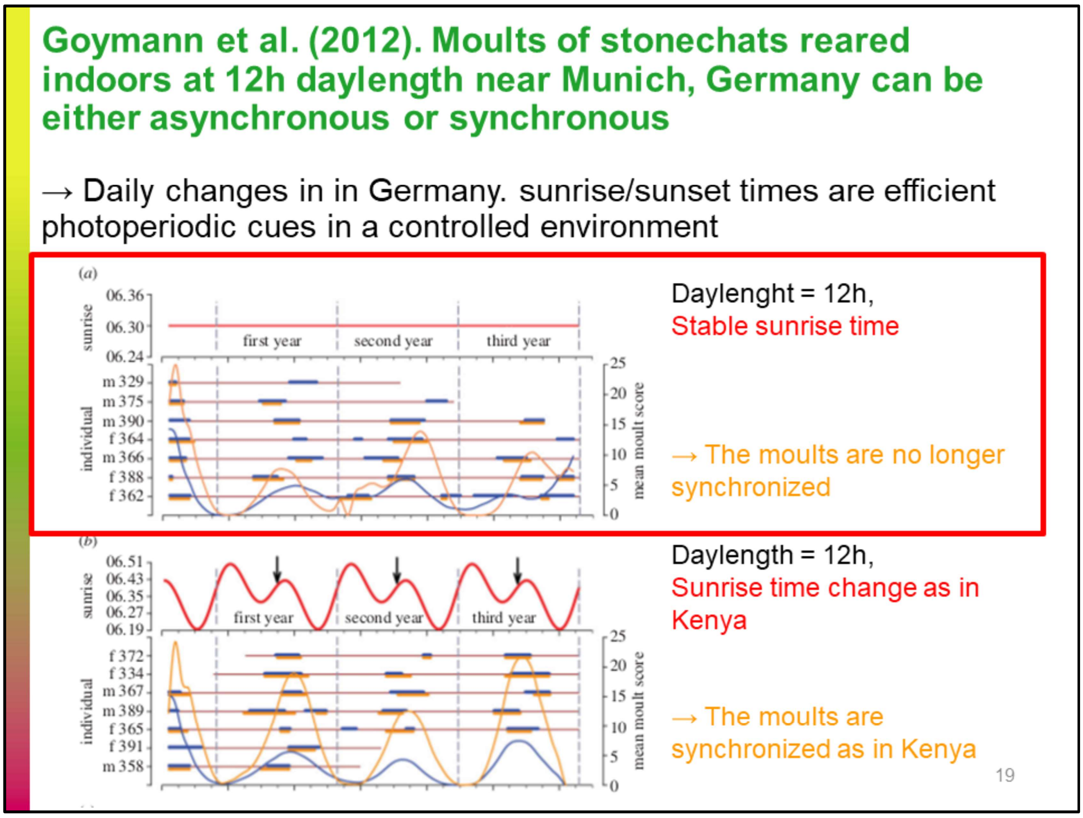


Despite living at the equator, the breeding (in black) and moulting dates (in blue and yellow) within the population are highly synchronised.
As suggested by Borchert, the daily variation in sunrise time (the red curve) may be the cue for this synchronisation.



This team proved the hypothesis.
They transported birds from Kenya to Germany. First in natural light then in growth chambers with 12 hours of daylength during three years.
When sunrise time was stable at 6 30, the moults of the 7 tested birds (one per line) were not synchronized.
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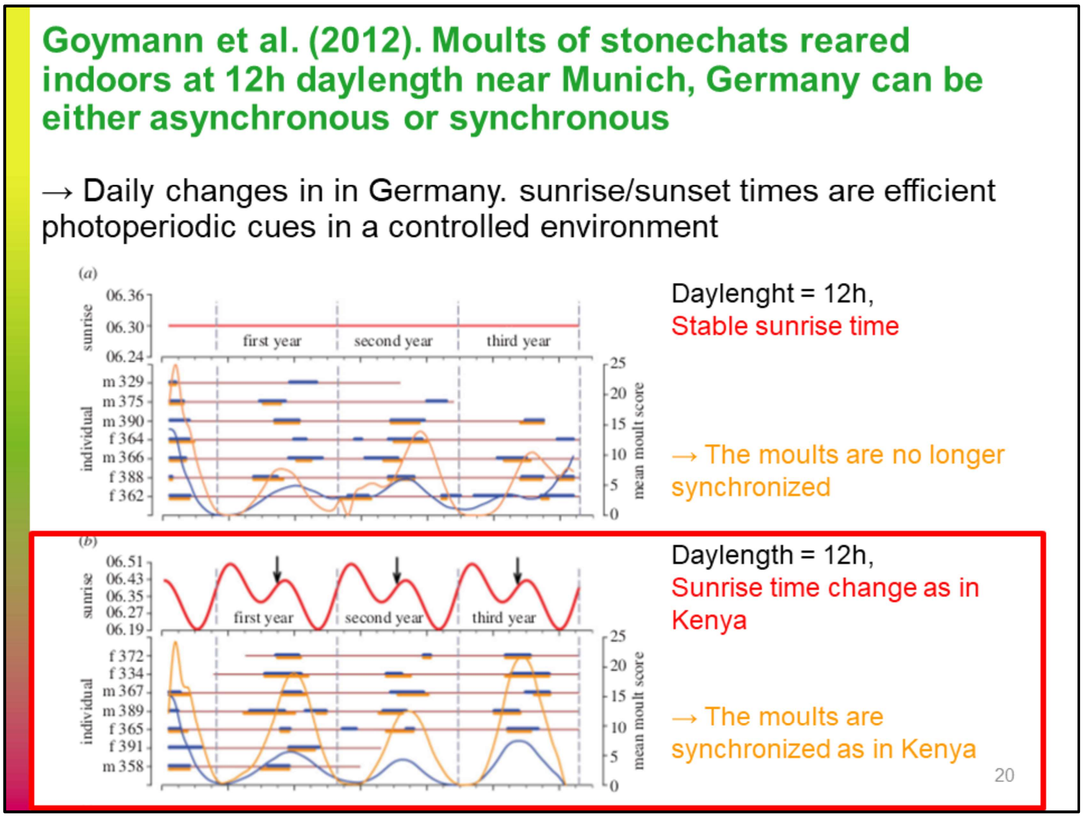
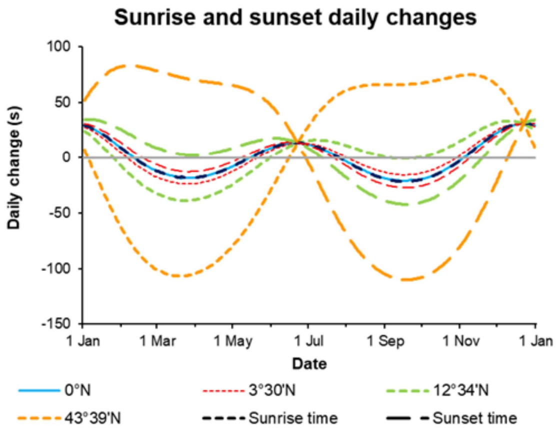


Conversely, when sunrise time varied as in Kenya (in red), still with 12 hours daylength, the moults of the 7 birds were synchronous and synchronized with the moults in Kenya.

Thus, the daily change in sunrise and sunset times is the photoperiodic cue that synchronises the sexual cycle of stonechats, other things being equal.

Everywhere: daily variations in sunrise and sunset times from the equator to temperate latitudes



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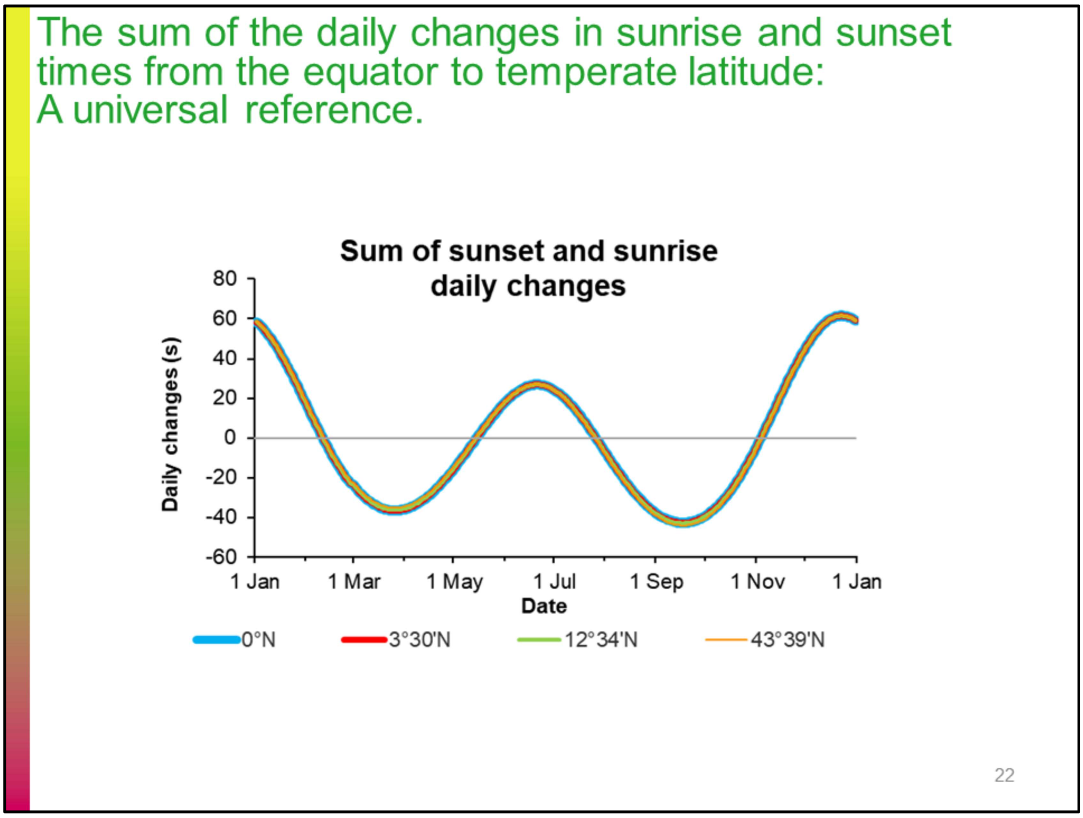
The range of the daily change in sunrise and sunset times increases with the latitude and the annual symmetry is different.
Here from the equator in blue, to Cali in red, Bamako in green and Montpellier in yellow.



But… the sum of the daily changes in sunrise and sunset times gives a universal reference.
If they can perform this sum, cells are at home everywhere in the world.

A crop-photoperiodism model 2.0 that combines additive effects of the daylength and of the daily change in sunrise and sunset times.

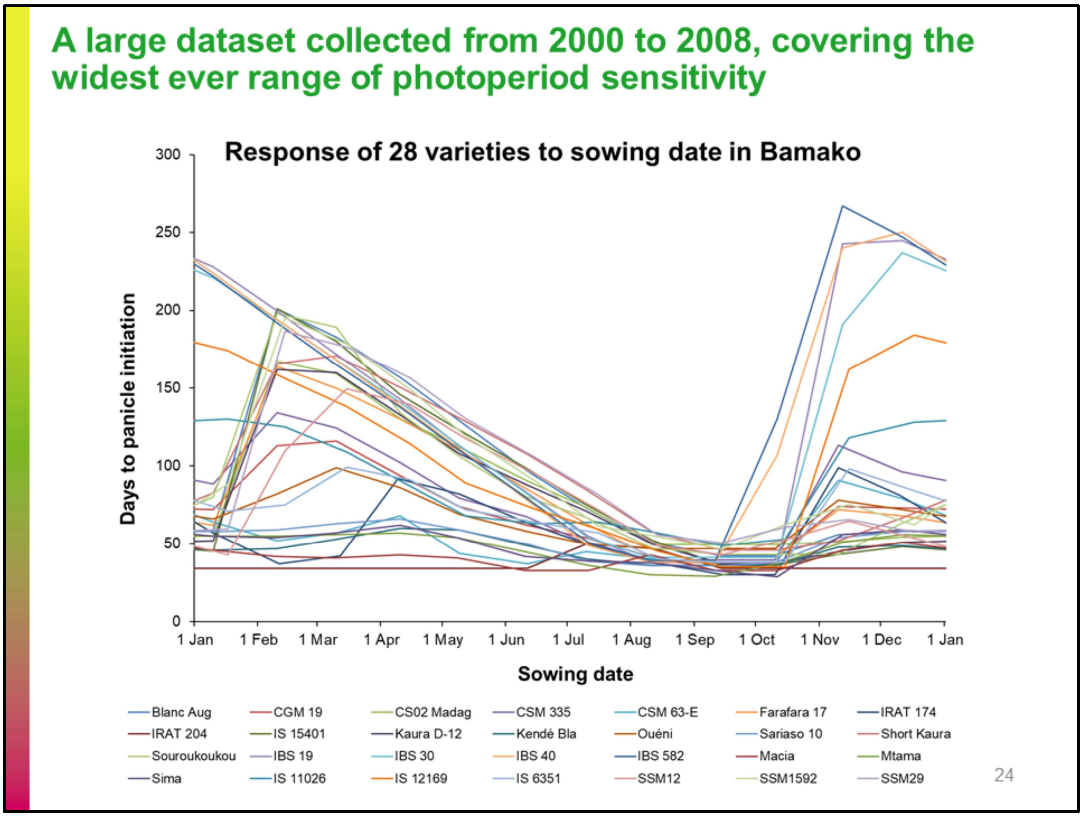
$$PSP(day) = Ps \times \max(0, PP - Pb) + SRs \times dSR + SSs \times dSS$$

Daily progress towards panicle initiation = 1/ PSP(day)

As in previous models, the photoperiodic conditions of the day determine a daily progress towards triggering panicle initiation. Daily progress is accumulated until the panicle initiation threshold is reached.

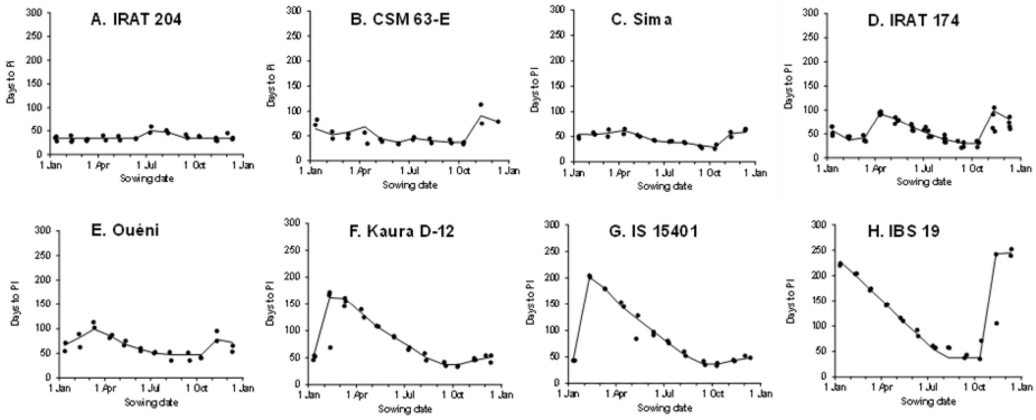
Details in Annals of Botany **128**: 97–113, 2021

I tested a simple additive model combining three photoperiodic components: the daylength and the two daily changes in sunrise and sunset times.
We will call it Model 2.0.
Otherwise, the model is based on the usual concept of the accumulation of a daily progress towards panicle initiation, that is inversely proportional to the total duration that would be required under the photoperiod of the day.



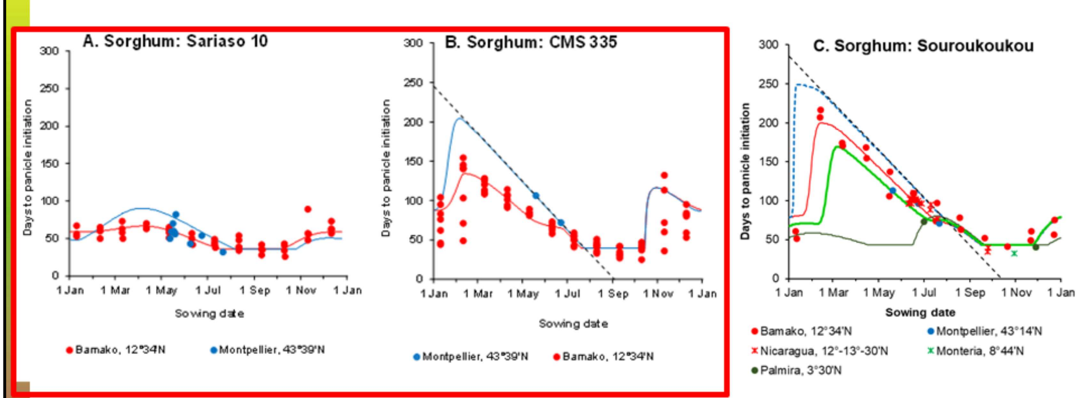
Model 2.0 was tested on the panicle initiation dates of 28 varieties with the largest ever range of photoperiod sensitivity recorded in Bamako from 2000 to 2008.

Model 2.0 could tightly fit all the patterns of response to sowing date of sorghum varieties grown in Bamako, especially for November to February sowings.



As shown in this sample, Model 2.0 could always be calibrated to fit the observed data tightly, especially for November to February sowings, which was not feasible with the previous models.

Even better: once calibrated in Bamako, the Model 2.0 accurately predicted the duration to PI of two varieties in Montpellier, and across latitudes from the equator to Montpellier for Souroukoukou



These results strongly support the hypothesis of combined effects of the daylength and of the daily changes in sunrise and sunset times on the flowering time

Even better, data collected by breeders from Cali at 3°N to Montpellier at 43°N were available to validate the model at other latitudes.
Once calibrated on the Bamako results (in red), Model 2.0 fitted well the results of some varieties sown in May and June in Montpellier (in blue).
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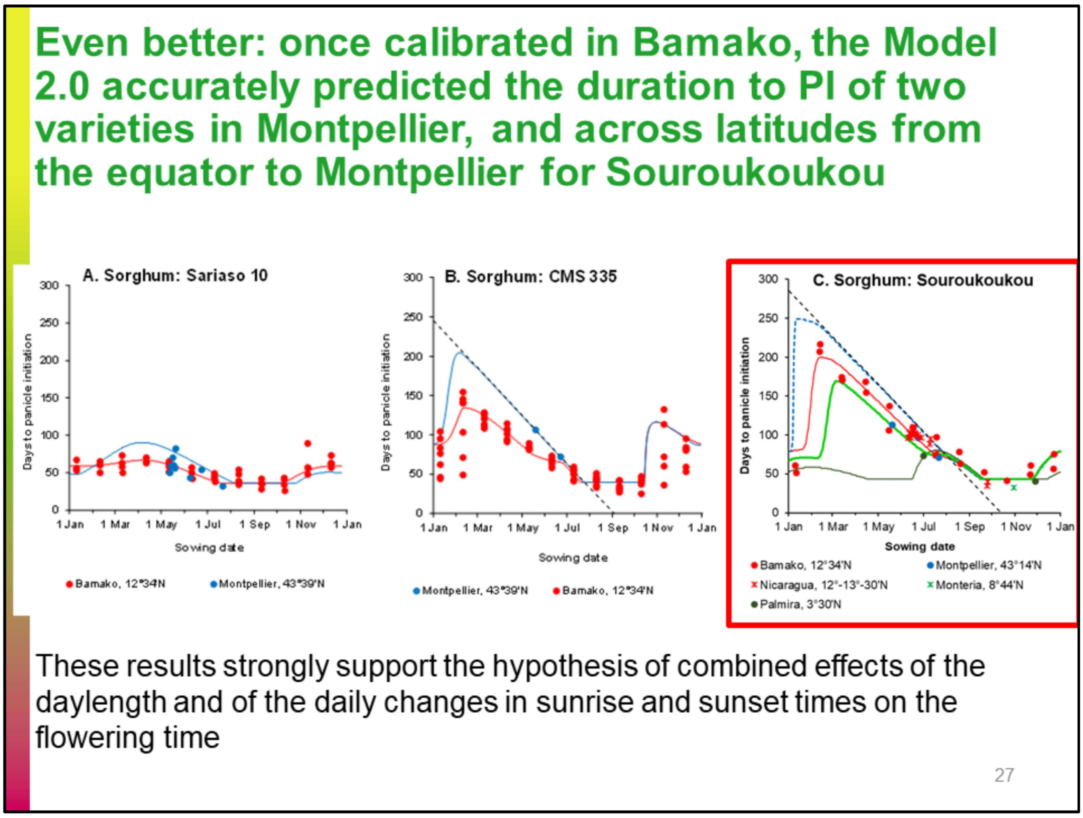
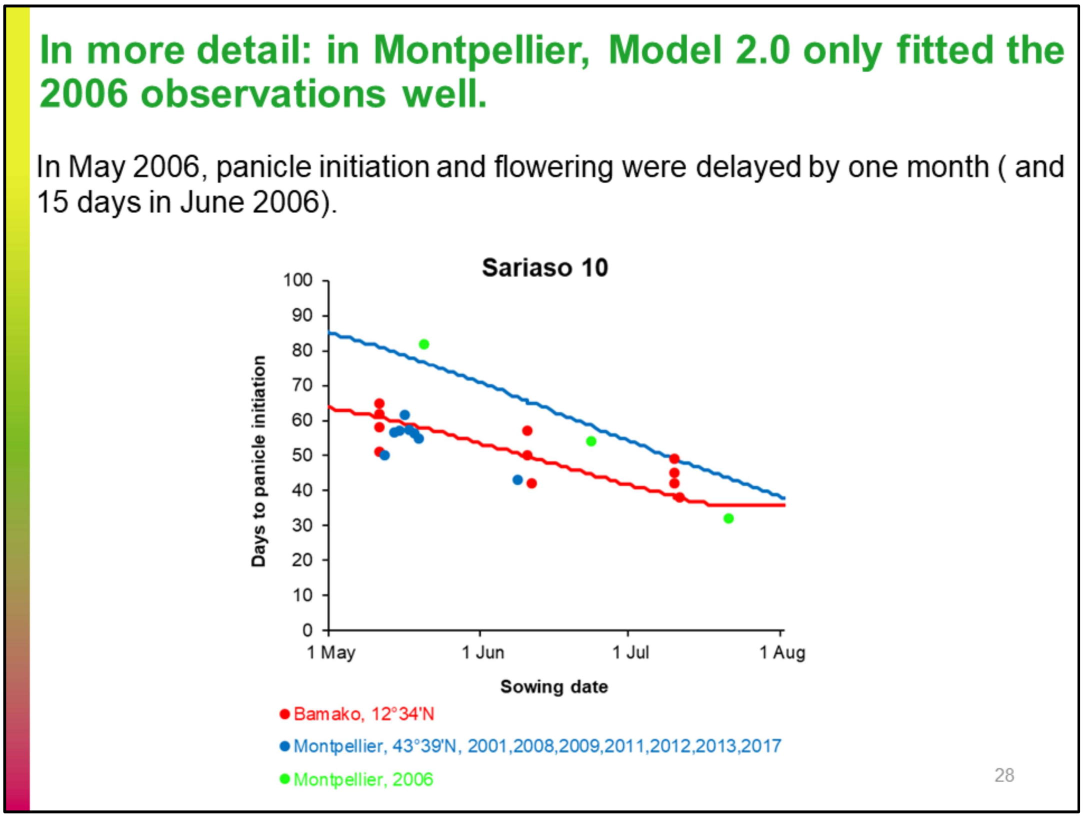


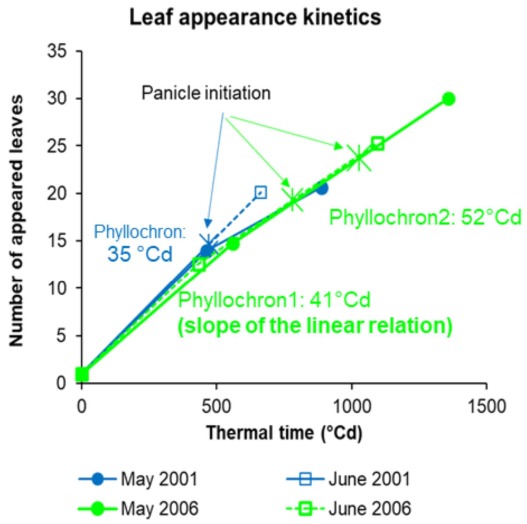
For the Malian variety Souroukoukou, Model 2.0 fitted data from Cali (in dark green) to Montpellier well.
This successful result across all latitudes strongly supports the hypothesis of combined effects of the daylength and of the changes in sunrise and sunset times on the flowering date.



However, model 2.0 only fitted really well the 2006 observations in Montpellier (green points).
In fact, 2006 was a special year and sorghum flowering was delayed by one month for different varieties in Montpellier and in the South of France, as shown by the difference between the green points and the blue points for the other years.

Correlation between the acclimation of the rate of leaf appearance and the duration to panicle initiation

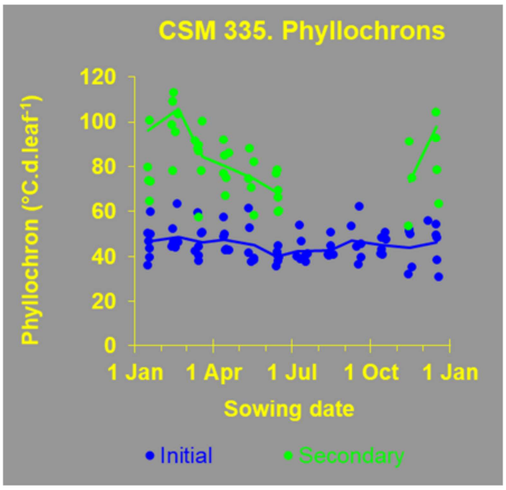
Leaf appearance kinetics was slower in 2006 than in 2001, in response to the higher mean temperature at seedling emergence in 2006 (an acclimation already reported in maize = adaptation to high latitudes)



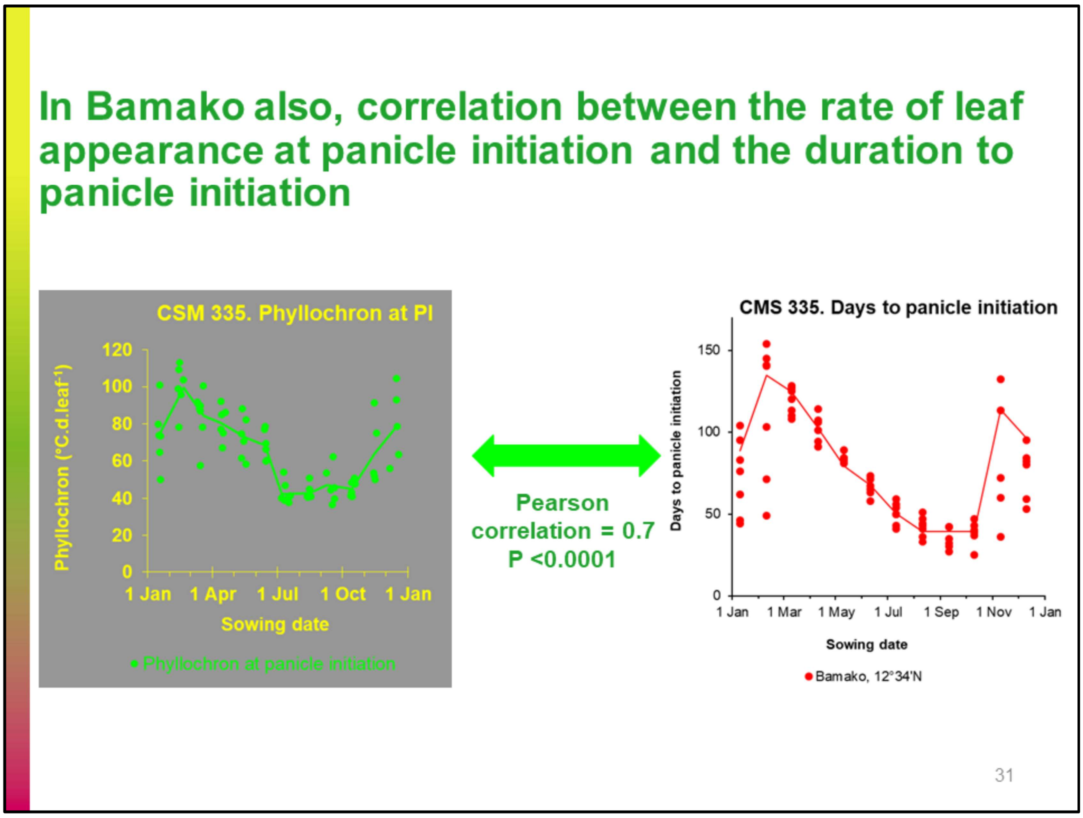
At panicle initiation (✱) :
Phyllochron x thermal time
Pearson correlation = 0.94,
P = 0.06

The development rate of Sariaso 10, here the leaf appearance (on the Y axis) with the thermal time (on the X axis),
was slower in 2006 (in green) than in 2001 (in blue), with a strong slowdown after the appearance of the 15th leaf, a long delay until panicle intitiation and 10 to 15 more leaves produced.
The phyllochrons are the slopes of the linear relationships.
The correlation between the phyllochron at panicle initiation and the duration to panicle initiation is 0.94.
The mean temperature at seedling emergence in 2006 was unusually high compared to other years.
Thus, the usual cool temperature at seedling emergence causes an acclimation of the phyllochron, which was lost in 2006.
This temperature acclimation was already described in maize and contributes to the adaptation of such photoperiodic varieties to temperate latitudes.

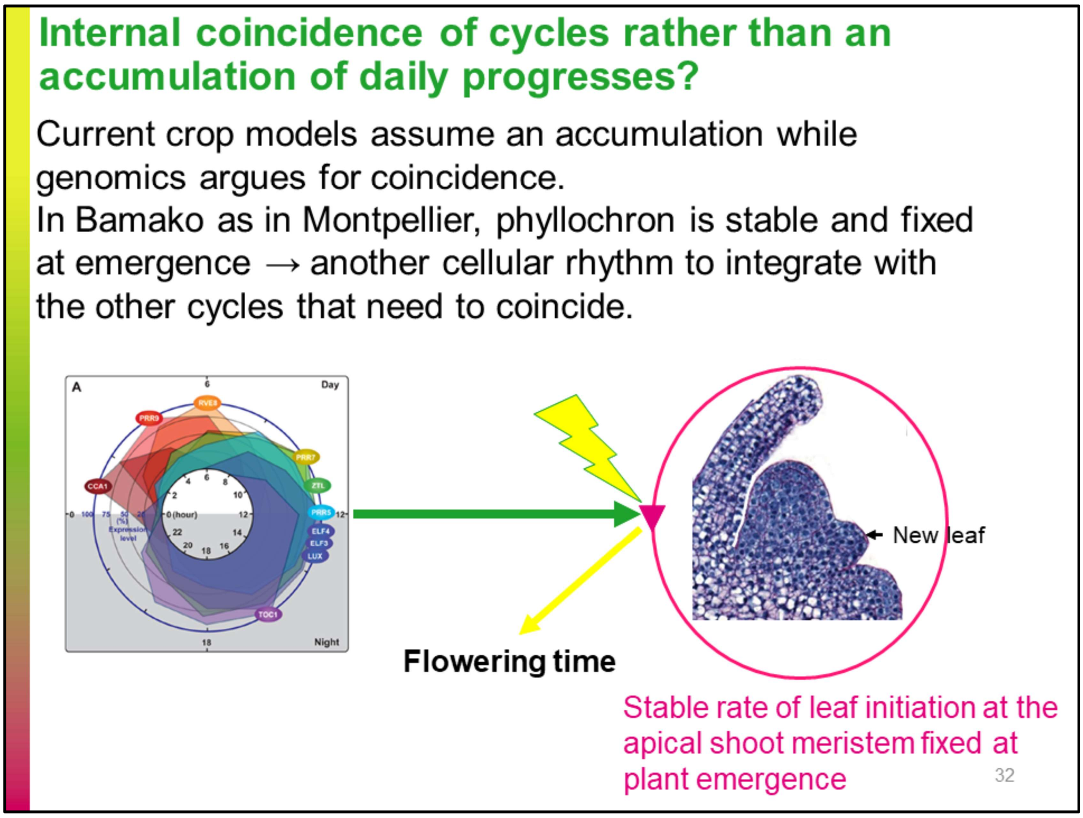
In Bamako also, phyllochron responds the environmental variations with the sowing date.



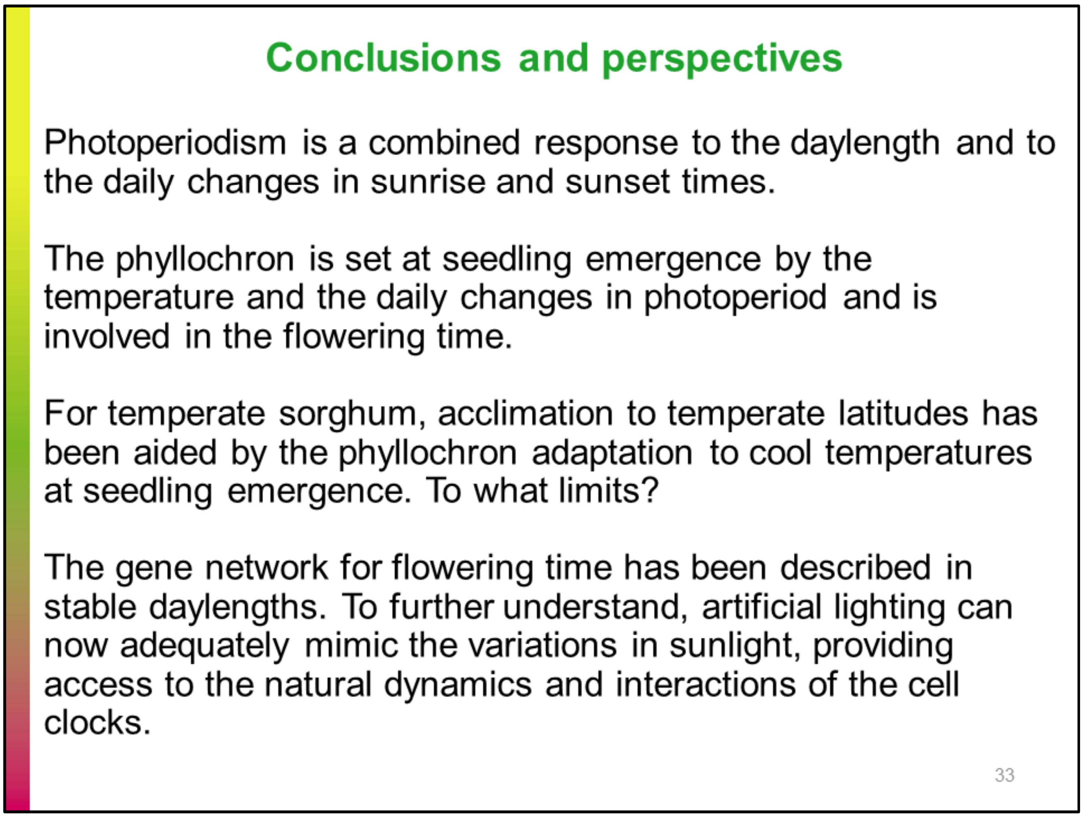
In Bamako, the phyllochron also adapts to the sowing date, probably in response to the photoperiod that correlates better than the mean temperature.
Here, the results of the seven years of monthly sowings of CSM 335.
In blue the phyllochrons at emergence (45 degree days on average) and in green the secondary phyllochrons after the appearance of the 15th leaf (between 65 and 100 degree days and not applying for the July to October sowings).



Thus, the phyllochron at panicle initiation (in green) varied with the sowing date from 40 to 100 degree days.
The correlation between the phyllochrons at panicle initiation and the durations to panicle initiation (in red) is 0.7 and highly significant.



Current models of crop flowering time assume an accumulative process but without physiological evidence, whereas genomics argues for the coincidence of cyclic gene expressions to trigger flowering time.
Sorghum phyllochrons are stable once they are set at plant emergence or at the 15th leaf.
This stability is caused by a stable rhythm in the initiation of new leaves by the shoot apex.
This internal cycle in the apex would intervene in the regulation of the flowering time.
Thus, the flowering time would depend on environmental cues **both** at the time of plant emergence and at the time of the transition to the reproductive phase, **without** the need for accumulated information.



Conclusions and perspectives

1. Photoperiodism is a combined response to the daylength and to the daily changes in sunrise and sunset times.

2. The phyllochron is set at seedling emergence by the temperature and the daily changes in photoperiod and is involved in the flowering time.

3. For temperate sorghum, acclimation to temperate latitude has been aided by the phyllochron adaptation to cool temperatures at seedling emergence. To what limits?

4. The gene network for flowering time has been described in stable daylengths. To further understand, artificial lighting can now adequately mimic the variations in sunlight, providing access to the natural dynamics and interactions of the cell clocks.

Thank you

To the audience.

To the hundreds of people, institutions, and funding agencies who have participated over 30 years.

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Thank you to the audience and to the so many people who took part.