

Influence of night temperature on photoperiod response of a West African guinea sorghum landrace

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Abstract — The vegetative phase of a West African landrace (Is 7680) was studied by using different sowing dates during three years at the Samanko station (Mali). During the rainy seasons, Is 7680 has shown the photoperiod response of a short-day plant. During the off-seasons, though the photoperiods were optimal for a quick panicle initiation, its vegetative phase during the off-seasons was extended. On the basis of field data, photoperiod effect on the thermal duration of the vegetative phase was modeled by two different methods: i) by using the mean daily temperatures following the Ceres procedure ii) by using a summation of the daily minimum night temperatures. The first method did not succeed in establishing the genetic parameters of Major's photoperiod response pattern (Bvp: base vegetative phase, Mop : maximum/minimum optimal photoperiod, slope of photoperiod sensitivity). The second method satisfactorily fitted the field data to Major's pattern. The results show that Is 7680 is a very photoperiod cultivar whose panicle initiation needs high night temperatures. Due to the fact that the night temperatures are low during the off-season at Samanko, the flowering of Is 7680 is delayed at that time. This kind of photoperiod reaction could be shared by the majority of the West African guinea landraces.

Résumé — Influence de la température nocturne sur la réponse photopériodique d'un écotype guinea ouest-africain. La phase végétative d'un écotype guinea burkinabé (Is 7680) a été étudiée durant trois années à la station de Samanko (Mali) à partir de semis réalisés à différentes périodes de l'année. En saison des pluies, Is 7680 a réagi comme une plante photopériodique de jours courts. En revanche, il a allongé son cycle en contre-saison froide alors qu'il poussait sous les photopériodes les plus favorables à une rapide induction florale. A partir de données expérimentales, l'effet de la photopériode sur la durée thermique de la phase végétative de Is 7680 a été modélisé de deux façons différentes : 1) selon la procédure Ceres à partir d'une sommation des températures moyennes quotidiennes ; 2) selon une sommation des températures minimum nocturnes quotidiennes. La première méthode n'a pas permis d'établir, pour Is 7680, les paramètres génétiques du développement

phénologique des plantes photopériodiques tels que Major et Vergera les ont définis (Bvp : Base vegetative phase, Mop : maximum/minimum optimal photoperiod, pente de photosensibilité). La seconde méthode a ajusté de façon satisfaisante les données expérimentales au schéma de Major et Vergera. Les résultats montrent que Is 7680 est un cultivar très photopériodique dont l'induction florale a besoin de températures nocturnes élevées. C'est la non-obtention de telles températures à Samanko en contre-saison froide qui explique l'allongement du cycle végétatif de Is 7680. Ce type de réaction à la photopériode et aux températures nocturnes serait commun à la plupart des sorghos guinea d'Afrique de l'Ouest.

In order to understand the flowering of field crops, Vergara and Chang (1976) and Major (1980) modeled the effects of photoperiod on the duration of the vegetative phase. This model involves three important genetic constants: base vegetative phase (Bvp), maximum/minimum optimal photoperiod (Mop) and photoperiod sensitivity. For a given cultivar, the Bvp is defined as the shortest possible time from seedling emergence to floral initiation under optimal photoperiods. The Mop is defined as the threshold photoperiod above or below which the time to floral initiation will be influenced by photoperiod in short- and long-day species, respectively. Under non optimal photoperiods, there are delays in flowering with photoperiod change. The photoperiod sensitivity is quantified as the slope of the response of flowering to change of photoperiod. Thus, the photoperiod sensitivity has units of vegetative delay in floral initiation per hour increase in photoperiod.

Major's response patterns of crop to photoperiod has been used as the phenological component in the Ceres maize model which expresses the time to

panicle initiation in thermal units by accumulating a value representative of mean daily temperature. This approach has been successfully applied to selected lines of sorghum by Ritchie and Alagarswamy (1989) who presented a Ceres version for sorghum (Alagarswamy and Ritchie, 1991).

No such study has so far involved West African guinea landraces. These are of the short-day plant type during the rainy season. During the off-season, in their area of origin, they show a particular phenological behaviour of prolonged vegetative phase despite short days which are optimal for panicle initiation. Simultaneously, night temperatures significantly decrease with a daily thermal range much wider than in the rainy season. Cochemé and Franquin (1967) argued that these cool night temperatures accounted for the prolonged vegetative phase of guinea landraces. In our study, we considered a typical guinea sorghum landrace that was cultivated under natural conditions in Mali at different periods of the year and we undertook to model the duration of its vegetative thermal time according to Major's pattern. For this objective, we followed two different methods and compared their efficiency: the Ceres sorghum model method using mean daily temperatures and another method relating development to minimum night temperatures.

Materials and methods

The guinea landrace used in this study was Is 7680 (Ssm 249 in the Cirad collection) a local variety from Burkina Faso named Pelogo. During three years (1994-1996), Is 7680 was sown on 18 different dates in the field at the Samanko research station in Mali (8°70' W, 12°33' N, altitude 345 m).

Plots consisted of one 6 m row with hills spaced at 0.30 m in the row and thinned to one plant per hill at about 10 days after seedling emergence. The plots received a standard level of fertilization and were irrigated when necessary.

For each sowing date, six random plants were observed for the number of leaves produced during the vegetative phase and the time to flag leaf emergence.

Maximum and minimum daily air temperatures under shade were measured in a meteorological shelter at the Samanko station.

In order to evaluate the date of panicle initiation, we considered the thermal time from sowing to flag leaf emergence. This thermal time was calculated by using the mean daily temperatures (Dtt) applied in the

Ceres sorghum model (Alagarswamy and Ritchie, 1991) :

$$Dtt = (T_{max} + T_{min})/2 - 8^{\circ}\text{C} \text{ if } T_{max} < 34^{\circ}\text{C} \text{ and } T_{min} > 8^{\circ}\text{C}$$

$$T_{tmp} = T_{min} + T_{mfac}(l) * (T_{max} - T_{min}) \text{ if } T_{max} > 34^{\circ}\text{C} \text{ or } T_{min} < 8^{\circ}\text{C}$$

$$Dtt = Dtt + (T_{tmp} - 8^{\circ}\text{C})/8 \text{ if } 8^{\circ}\text{C} < T_{tmp} < 34^{\circ}\text{C}$$

$$Dtt = Dtt + [(34^{\circ}\text{C} - 8^{\circ}\text{C}) * (1 - (T_{tmp} - 34^{\circ}\text{C})/18)]/8 \text{ if } 34^{\circ}\text{C} < T_{tmp} < 52^{\circ}\text{C}$$

with :

T_{max} = maximum daily temperature

T_{min} = minimum daily temperature

$T_{mfac}(l) = 0.931 + 0.114 * l - 0.0703 * l^2 + 0.053 * l^3$ with l varying from 1 to 8 following each 3 h period through the day.

The daily summation of Dtt from sowing to flag leaf emergence gave the thermal time to flag leaf (Dttfl).

According to Muchow and Carberry (1990) who found a ratio of 0.6 between plastochron and phyllochron in sorghum, the calendar date of panicle initiation was established at the day situated at 0.6 x the Ceres thermal time Dttfl.

For each sowing, the effective photoperiod used to model the photoperiod response of Is 7680 was assumed to be the length of the day at the estimated date of panicle initiation. The length of this day was calculated for Samanko following the model of Forsythe *et al.* (1995) for a solar elevation > -6 degrees which determines the duration of biological active day for photosensitive plants according to Aitken (1974).

To evaluate the effects of photoperiod on duration of the vegetative phase according (to Major's photoperiod response pattern), two methods were used for computing the vegetative thermal time from sowing to panicle initiation.

The first method calculated this time as 0.6 x Dttfl (the Ceres thermal time calculated from sowing to flag leaf). The result was the Dttini.

The second method took into account night temperatures only, through a summation of daily minimum temperatures:

$$Nttini = \sum_{i=1}^n (T_{i,min} - T_{base})$$

where Nttini was the thermal time accumulated over n days from sowing to the estimated day of panicle initiation, $T_{i,min}$ = daily minimum temperature. When $T_{min} < T_{base}$ the daily contribution was null. The T_{base} was estimated by means of least coefficient of variation (Cv) when T_{base} was changing by 1° from 0 to 10°C.

Table I. Environment and response parameters pertaining to the vegetative phase of Is 7680 sown at different dates at Samanko from 1994-1996.

Sowing date	Sowing date in julian day	Number of days from sowing to flag leaf	Number of leaves	Phyllochron (day/leaf)	Mean daily temperature with mean daily maximum and minimum in brackets (sowing to flag leaf) (°C)
17/06/94	168	78.3	26.5	3.0	26.6 ° (31.1°-21.1°)
01/07/94	182	68.0	23.5	2.9	26.3 ° (30.6°-22.0°)
15/07/94	196	58.3	21.2	2.8	26.3 ° (30.5°-22.1°)
29/07/94	210	52.2	19.4	2.7	26.2 ° (30.3°-22.1°)
09/09/94	252	44.4	14.8	3.0	26.5 ° (31.0°-22.0°)
16/12/94	350	118.0	27.0	4.4	25.0 ° (34.9°-15.1°)
03/02/95	34	71.5	23.5	3.0	28.1 ° (37.9°-18.3°)
23/06/95	174	75.5	27.1	2.8	27.1 ° (31.9°-22.3°)
01/07/95	182	72.1	24.0	3.0	27.1 ° (32.0°-22.2°)
09/07/95	190	66.0	23.8	2.8	26.9 ° (31.8°-22.0°)
20/07/95	201	60.6	21.0	2.9	27.0 ° (31.9°-22.1°)
11/09/95	254	44.2	15.8	2.8	27.5 ° (33.4°-21.6°)
30/11/95	334	112.5	26.0	4.3	25.4 ° (35.1°-15.7°)
01/02/96	32	71.2	20.7	3.4	28.3 ° (37.7°-18.9°)
13/06/96	165	80.2	28.0	2.9	27.2 ° (31.5°-22.8°)
01/07/96	183	65.6	23.2	2.8	27.0 ° (32.2°-21.8°)
22/07/96	204	61.5	20.0	3.1	26.2 ° (30.8°-21.6°)
18/10/96	292	58.0	16.2	3.6	24.5 ° (34.8°-14.2°)

Results and discussion

The annual variations of the daily photoperiod and minimum/maximum temperatures averaged for the 1995 and 1996 years at Samanko are presented in figure 1. The transition from the rainy season to the off-season is marked by the increase of the thermal range associated with decreasing of the daily minimum temperatures.

The sowing dates of Is 7680 at Samanko ranged from 17 June 1994 to 18 October 1996 (table I). Some of these dates occurred in the off-season. Sowings done in November or December when the temperatures were the coolest corresponded to the longest vegetative phase duration. When still in the off-season but under warmer temperatures as in February, the vegetative phase was shortened. The shortest vegetative

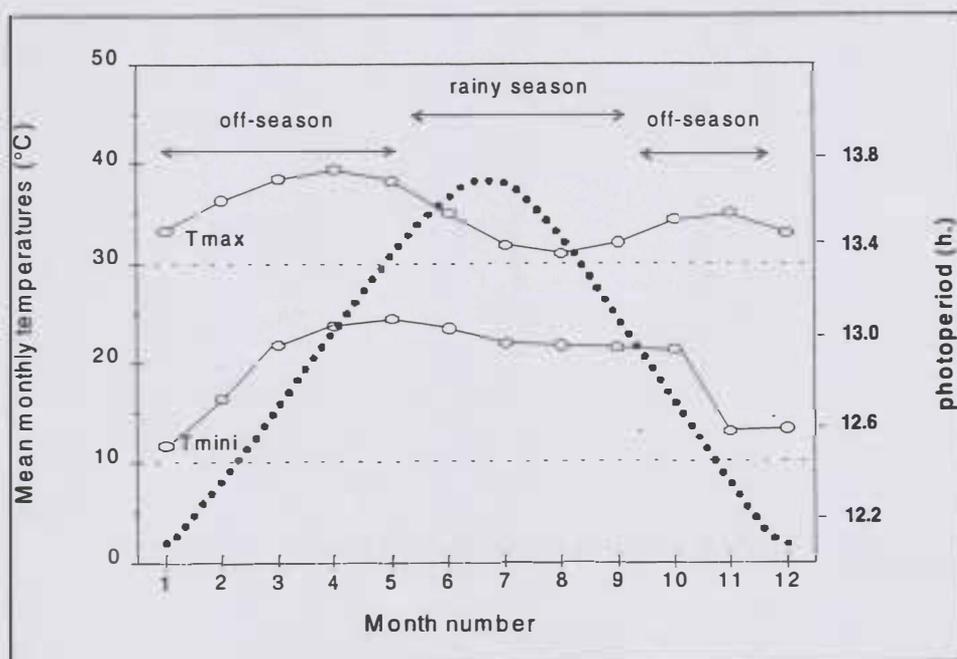


Figure 1. Annual variation of daylength and maximum - minimum temperatures (averaged during each month at Samanko from 1995-1996).

phase occurred in September sowings when photoperiods were already short and temperatures still high .

Leaf number responds to change in sowing date in the same way as vegetative phase duration (table I). Nevertheless, the increase in leaf number observed during the off-season is comparatively less important than the increase observed in the duration of the vegetative phase.

The phyllochron calculated by the number of days to produce one leaf is negatively related to temperature. It tends to increase when mean daily temperature decreases as in the off-season (table I).

The pattern of response of the vegetative phase of Is 7680 to sowing dates is shown by figure 2. According to the sowing dates expressed in julian day of year, the duration of the vegetative phase measured by the number of days from sowing to flag leaf emergence ranges more than twofold (44 days at 254th julian day in September vs 118 days at 350th julian day in December). During the rainy season (150-210th julian day), the photoperiod response of Is 7680 is clearly exhibited by the shortening of its vegetative stage. The substantial increase in the duration of the vegetative phase at the end of the year cannot be due to the photoperiods which are the shortest of the year.

For each sowing date, table II presents the steps to estimate the date of panicle initiation and the variables used to model the photoperiod response of Is 7860 with two methods of calculating vegetative thermal time.

The vegetative thermal time (Dttini) calculated following Ceres model do not fit the scheme of photoperiod response developed by Major (1990) (figure 3). The scattering of off-season points with short photoperiods does not correspond to the short Bhv expected for the guinea landrace Is 7680 under short-day conditions.

The vegetative thermal time calculated with the daily minimum temperatures (Nttini) gives different results. To compute the sum of the night temperatures, the tests of different Tbase (base temperature) consider the cv attached to off-season data from September to February. The thermal times to panicle initiation calculated for these data are supposed to define the Bvp. We used the Tbase of 6° which gives the smallest Cv value (table III).

With Tbase = 6°, the vegetative thermal times calculated with daily minimum temperatures are nearly in accordance with short-day plant reaction to photoperiod all year long. The fitting of data to Major's pat-

Table II. Estimation of dates, photoperiods and thermal times (following two methods) at panicle initiation of Is 7860 sown at different dates in Samanko from 1994-1996. The thermal time using minimum temperatures (Nttini) is presented calculated with two different Tbases.

Sowing date	Dttini (1)	Date to achieve Dttini (2)	Photoperiod at date to achieve Dttini (hours) (3)	Nttini Tbase = 0° (4)	Nttini Tbase = 6° (5)
17/06/94	883 °	02/08/94	13.41	1023°	747°
01/07/94	759 °	11/08/94	13.32	902 °	656 °
15/07/94	651 °	19/08/94	13.23	779 °	569 °
29/07/94	584 °	30/08/94	13.10	709 °	517 °
09/09/94	505 °	06/10/94	12.67	594 °	432 °
16/12/94	1104 °	04/03/95	12.63	908 °	442 °
03/02/95	753 °	21/03/95	12.83	735 °	459 °
23/06/95	871 °	07/08/95	13.36	1016 °	746 °
01/07/95	834 °	13/08/95	13.30	964 °	706 °
09/07/95	760 °	18/08/95	13.24	893 °	653 °
20/07/95	701 °	26/08/95	13.15	818 °	596 °
11/09/95	520 °	08/10/95	12.65	595 °	433 °
30/11/95	1118 °	10/02/96	12.41	981 °	549 °
01/02/96	762 °	14/03/96	12.74	783 °	537 °
13/06/96	929 °	30/07/96	13.44	1044 °	762 °
01/07/96	753 °	09/08/96	13.34	852 °	618 °
22/07/96	686 °	28/08/96	13.12	805 °	583 °
18/10/96	575 °	21/11/96	12.25	528 °	324 °

(1) Ceres sum of temperatures from sowing to estimated panicle initiation (0.6 x Dttfl) (°C).

(2) Estimated date of panicle initiation.

(3) In hours and decimals.

(4) Vegetative thermal time by sum of minimum temperatures (sowing to panicle initiation) (°C).

(5) Vegetative thermal time by sum of minimum temperatures (sowing to panicle initiation) (°C).

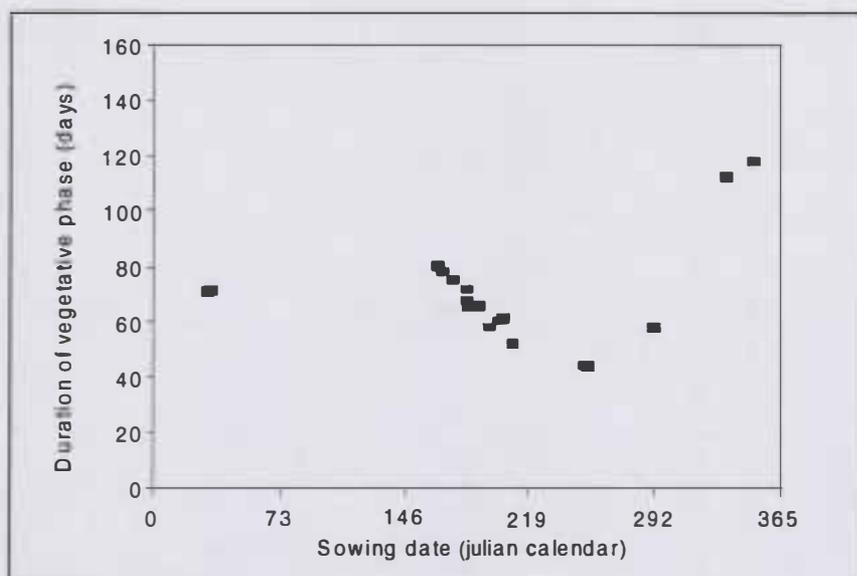


Figure 2. Duration of vegetative phase (from sowing to flag leaf emergence) of Is 7680 sown at different dates in Samanko (1994-1996).

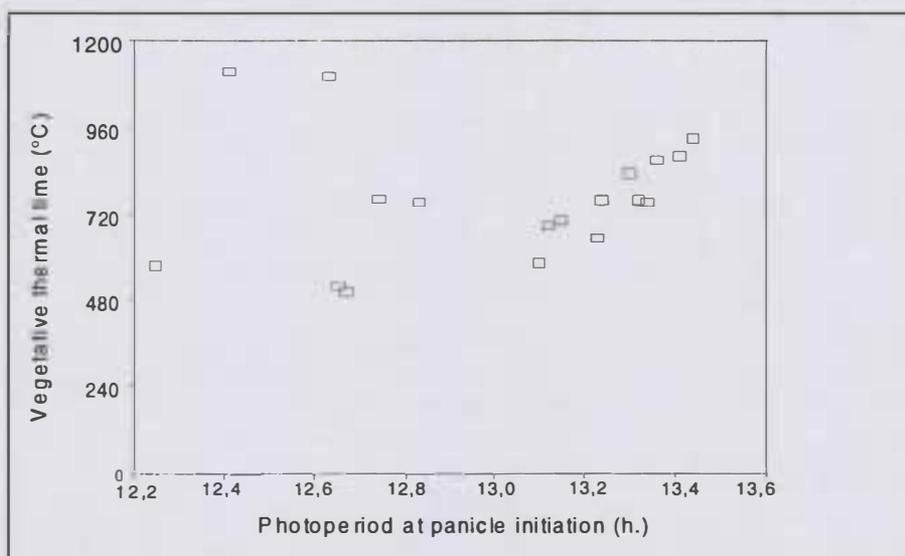


Figure 3. Thermal time to panicle initiation calculated following Ceres model (Dttini) as influenced by daylength at panicle initiation of Is 7680 cultivar sown in Samanko (1994-1996).

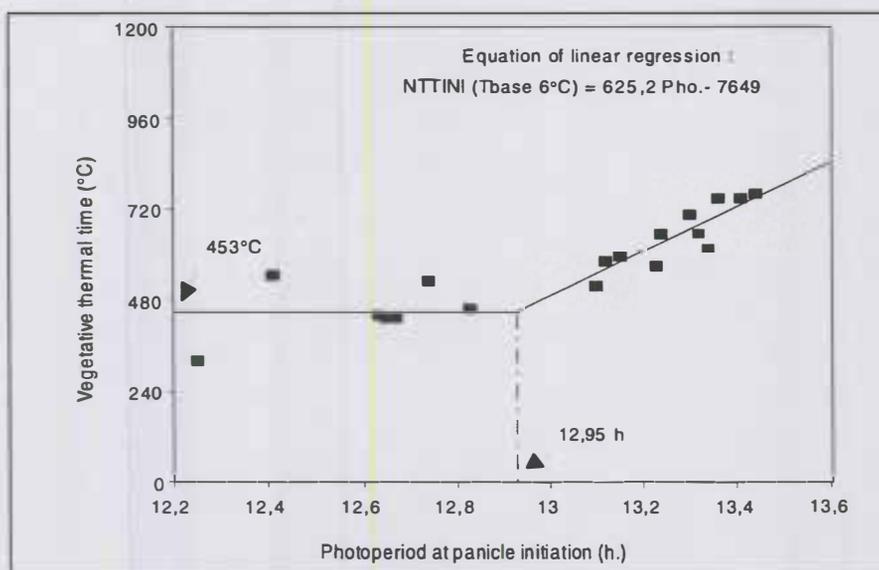
tern is much more satisfactory (figure 4). In the rainy season the vegetative thermal time of Is 7680 reacts to small differences in daylength by decreasing linearly to reductions of the photoperiod. In the off-season the vegetative thermal times is at its minimum and is roughly stable despite a high variability in calendar times from sowing to flag leaf emergence.

The improvement in modelling the photoperiod response is mainly for the off-season. Nevertheless, there is a poor adjustment of three critical points of the Bvp. One possible explanation for the observed biases stems from differences in temperature between the experimental plots used to implant Is 7680 and the meteorological shelter in Samanko station. Because the daily minimum were close to the Tbase in the off-season small temperature differences would be enough to cause marked differences in the duration of vegetative phase of Is 7680. The recording of temperatures at Samanko station might have also

Table III. Estimation of base temperature for Is 7680 cultivated during the off-season in Samanko (seven sowings from September to February in 1994-1996).

Base temperature (°C)	Thermal time average (sum of minimum temperatures) (°C)	Cv (%)
0°	732 °	21.6
1°	685 °	20.5
2°	640 °	19.4
3°	592 °	18.2
4°	546 °	16.9
5°	499 °	15.9
6°	453 °	15.2
7°	407 °	15.4
8°	362 °	16.8
9°	319 °	19.7
10°	278 °	23.8

Figure 4. Thermal time to panicle initiation calculated by using night temperatures (Nttini) as influenced by daylength at panicle initiation of Is 7680 cultivar sown in Samanko (1994-1996).



been subject to small errors. Further, the number of plants observed per plot was low.

The research carried out underlines on the importance of night temperatures. Contrary to vegetative thermal time calculated following Ceres approach, vegetative thermal time of Is 7680 calculated with daily minimum temperatures indicates a classical photoperiod short-day response similar to Major's pattern. Thus, it is possible to estimate the three genetic constants for Is 7680: $Bvp = 453^{\circ}\text{C}$, $Mop = 12,95\text{ h}$ and photoperiod sensitivity = $625^{\circ}\text{C days/h}$. T_{base} for the calculation of Bvp is 6°C .

The results obtained from a typical guinea sorghum landrace could be valid for the majority of the West African guinea landraces. On the basis of field observations, many guinea landraces appear to have a similar short-day photoperiod reaction and cold sensitivity in off season with T_{base} close to daily minimum temperatures as is the case for Is 7680.

As suggested by Cochemé and Franquin (1967), taking account of the night temperature gives encouraging results for modeling the photoperiod response of guinea sorghums. Biologically, the importance of night temperature in panicle initiation is logical because night is the active period in the diurnal cycle for flowering of short-day plants such as sorghum (Horie, 1994). Our approach differentiates temperature effects for growth and development processes, each one reacting respectively to daily and night temperatures. For more precise results it is necessary to verify if the time to panicle initiation is 60% of thermal time from sowing to flowering in photoperiod sensitive sorghum. It will also be necessary to measure temperature on the experimental plots themselves and consider mean daily night temperature rather than daily minimum temperature.

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