

Warmer springs disrupt the synchrony of oak and winter moth phenology

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Spring temperatures have increased over the past 25 years, to which a wide variety of organisms have responded. The outstanding question is whether these responses match the temperature-induced shift of the selection pressures acting on these organisms. Organisms have evolved response mechanisms that are only adaptive given the existing relationship between the cues organisms use and the selection pressures acting on them. Global warming may disrupt ecosystem interactions because it alters these relationships and micro-evolution may be slow in tracking these changes. In particular, such shifts have serious consequences for ecosystem functioning for the tight multitrophic interactions involved in the timing of reproduction and growth. We determined the response of winter moth (*Operophtera brumata*) egg hatching and oak (*Quercus robur*) bud burst to temperature, a system with strong selection on synchronization. We show that there has been poor synchrony in recent warm springs, which is due to an increase in spring temperatures without a decrease in the incidence of freezing spells in winter. This is a clear warning that such changes in temperature patterns may affect ecosystem interactions more strongly than changes in mean temperature.

Keywords: timing; phenotypic plasticity; *Operophtera brumata*; *Quercus robur*; climate change; multitrophic interaction

1. INTRODUCTION

The timing of reproduction and growth is under strong natural selection as there is often only a short period of favourable conditions in the annual cycle (Murton & Westwood 1977). In many multitrophic systems, the period in which these favourable conditions occur is to a large extent determined by the timing of growth or reproduction of species at the underlying level of the multitrophic interaction. We may therefore expect that timing in the dependent species responds to abiotic variables (such as temperature) in such a way that synchronization under the normal range of conditions is maintained. However, these response mechanisms are the result of selection under the range of conditions experienced in the past (Van Noordwijk & Müller 1994), in which there are certain relationships between the selection pressures and cues organisms use to anticipate them. There is no reason to suppose that the response mechanisms will lead to synchrony under novel environmental conditions.

Due to the increased spring temperatures over the past 25 years (Houghton *et al.* 1996), conditions in spring have changed, perhaps altering the existing relationship between the cues organisms use and the selection pressures acting on them. This could mean that the response mechanisms evolved are no longer adaptive and that synchronization between the different trophic levels breaks down. A wide variety of organisms have responded to the increase in spring temperature (Hughes 2000; Wuethrich 2000), including species that have advanced their timing of reproduction or growth (Beebee 1995; Crick *et al.* 1997; Winkel 1997; McCleery & Perrins 1998; Brown *et al.* 1999; Crick & Sparks 1999). However, what remains to be shown is that these responses match the

temperature-induced shift of the selection pressures acting on these organisms (Visser *et al.* 1998). Merely showing advancement in timing does not ensure that synchronization is maintained. Our aim is to study whether the synchronization between different trophic levels has been disrupted by the recent climate change. We will do this by determining whether the degree of synchronization in a well-studied trophic interaction, that is, winter moth (*Operophtera brumata*) egg hatching and oak (*Quercus robur*) bud burst (Embree 1970; Feeny 1970; Buse & Good 1996; Van Dongen *et al.* 1997; Buse *et al.* 1998, 1999), has altered over the last 25 years.

Adult winter moths emerge in early winter and the wingless females mate at the base of tree trunks before crawling up into the canopy where they lay their eggs. The eggs have a diapause and start developing from late February onwards. The timing of egg hatching in relation to bud burst has major fitness consequences for the caterpillars. If the eggs hatch prior to bud burst the caterpillars will starve, whereas if hatching occurs after bud burst the caterpillars will have to eat less digestible leaves due to increased tannin concentrations (Feeny 1970). This may lead to a lower weight at pupation (Feeny 1970; Zandt 1994) or to a longer larval period resulting in a higher probability of being predated or parasitized. As a result, there is strong selection on close synchrony between egg hatching and bud burst (Feeny 1970; Van Dongen *et al.* 1997).

There is large annual variation in the date of bud burst of the preferred host tree, the oak (Wint 1983; Van Dongen *et al.* 1997) and, thereby, also in the optimal time of egg hatching for winter moth eggs. Thus, the eggs need to use environmental cues in order to time their hatching and achieve synchrony with bud burst. There is no direct effect of bud burst itself on egg hatching (Buse & Good 1996; M. E. Visser and L. J. M. Holleman, unpublished results) and, as there is no

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annual variation in photoperiod patterns, temperature is likely to be a primary cue. We expect the response mechanism relating the timing of egg hatching to temperature to be selected so that egg hatching varies in the same way with temperature as bud burst.

As a consequence of the increase in temperature in winter and early spring over the past 25 years (Houghton *et al.* 1996), oak bud burst has advanced (Visser *et al.* 1998). The outstanding question is whether egg hatching of the winter moth has advanced at the same rate, i.e. whether synchrony has been preserved. The response mechanisms of the winter moth to temperature will have evolved under a range of conditions as they occurred in the past. If during the recent climate change the relationships between various abiotic variables have changed it may well be that the response mechanism of the winter moth is no longer adaptive. It may lead to a weaker or stronger advancement of egg hatching with increasing spring temperatures compared to the advancement in oak bud burst, leading to mis-timing. We will show that this is the case and that this mis-timing is due to changes in the relationship between abiotic variables. It is therefore not so much the increase in spring temperature that leads to mis-timing but rather the change in the 'pattern' of the weather.

In the absence of long time-series on both bud burst and egg hatching, our approach will be first to develop and validate descriptive models relating oak bud burst and winter moth egg hatching to winter and spring temperatures and then to use these models to calculate the degree of synchrony (the timing difference = date of egg hatching – date of bud burst) for the last 25 years (1975–1999). We use actual observed daily minimum and maximum temperatures, thereby preserving the temperature pattern. This enables us to look for trends in the degree of synchrony over the years and, thus, at the effect of the recent climate change (Houghton *et al.* 1996).

2. METHODS

(a) *Descriptive model of oak bud burst*

In Kramer's (1994) sequential model on oak bud burst, trees first have to build up a 'chilling sum' (onset date set to 1 November) and, after a threshold value is reached, they start building up a 'warmth sum' (or day degree accumulation). This also has a threshold value after which bud burst occurs. This model explained 82% of the variance in bud burst in a 58-year-long time-series from The Netherlands (Kramer 1994).

In order to validate the model independently we collected data on the bud burst of 102 oaks on the Hoge Veluwe, The Netherlands (05°50' E, 52°05' N) from 1988 to 2000 (excluding 1991, 12 years). Trees were visited two to three times a week and the stages of the buds (0, fully closed; 0.5, swollen buds just opening; 1, young leaves protruding partly from buds; 2, young leaves free of bud scales; and 3, fully leaved) were scored, both averaged over the entire tree and over the crown only (the buds in the crown develop earlier). As Kramer's (1994) model predicts the timing of the young leaves partly protruding from buds (1) for the crown of the tree, we validated his model using the dates at which the crown of the trees reached this stage.

(b) *Descriptive model of the timing of winter moth egg hatching*

We developed a model inspired by the work of Embree (1970), who developed a warmth sum threshold model with a base temperature of 3.9 °C (only that part of the temperature which is above 3.9 °C contributes to the build up of the warmth sum) and Kimberling & Miller (1988), who described the effect of the number of frost days (days with a minimum temperature below 0 °C, from 1 December onwards) on egg hatching. We calculated the relationship between the warmth sum from 1 January to the date at which 50% of the winter moth eggs hatched (D_{50}) and the number of frost days (days with a minimum temperature below 0 °C) from 1 December onwards. The warmth sum was calculated using the daily maximum and minimum temperatures using a sine-wave model (Baskerville & Emin 1969) and a base temperature of 3.9 °C. Data were collected from eggs of female winter moths that were caught at various locations in The Netherlands (Oosterhout (05°50' E, 51°55' N), Warnsborn (05°50' E, 52°05' N) and Doorwerth (05°48' E, 51°59' N) around Arnhem) in November 1995–1999 using traps attached to mature oak trees. The eggs were kept in an outdoor insectarium and checked three times a week for hatching. We determined the D_{50} for each clutch (range 25–200 eggs) and the mean across clutches was used in order to calculate the threshold warmth sum. Temperatures were obtained from the KNMI (Royal Dutch Meteorological Institute) in De Bilt, The Netherlands.

In order to check whether the D_{50} observed in the outdoor insectarium was representative of the date of egg hatching in the field we carried out a split-brood design experiment using 15 females caught in Oosterhout in November 1999. One part of the clutch was kept in the insectarium while another part was attached to the bark of a tree (at 3 m) in Oosterhout (one brood per tree). Clutches were checked three times a week for hatching.

(c) *Split-brood design experiment on the effect of temperature*

Two series of experiments were carried out: winter moth females were collected in November 1998 for series 1 and in November 1999 for series 2. Clutches of 40 female winter moths (20 from Oosterhout and 20 from Warnsborn) were divided over three treatments (25 eggs per treatment) for each series. We mimicked a specific year in temperature-controlled cabinets for each treatment, i.e. years with a cold (series 1 1986 and series 2 1973), a normal (series 1 1988 and series 2 1983) or a warm (series 1 1998 and series 2 1999) winter and early spring. Components of winter and spring temperatures are correlated in a particular way resulting in 'temperature patterns'. As we do not know exactly how egg hatching is affected by these temperature patterns we aimed at keeping these patterns intact rather than creating warm and cold years by just adding or subtracting a fixed temperature from the average pattern. The cabinets were restricted to at most a three-phase cycle and the temperature was set to 6 h at the daily minimum temperature as observed in the specific year, 12 h at the mean of the daily maximum and the daily average temperature and 6 h at the daily average temperature. This pattern gives the same daily minimum and mean temperatures that were observed. Eggs were checked three times a week for hatching and the D_{50} determined.

3. RESULTS

We additionally validated the sequential model of Kramer (1994) for oak bud burst with our own data set of

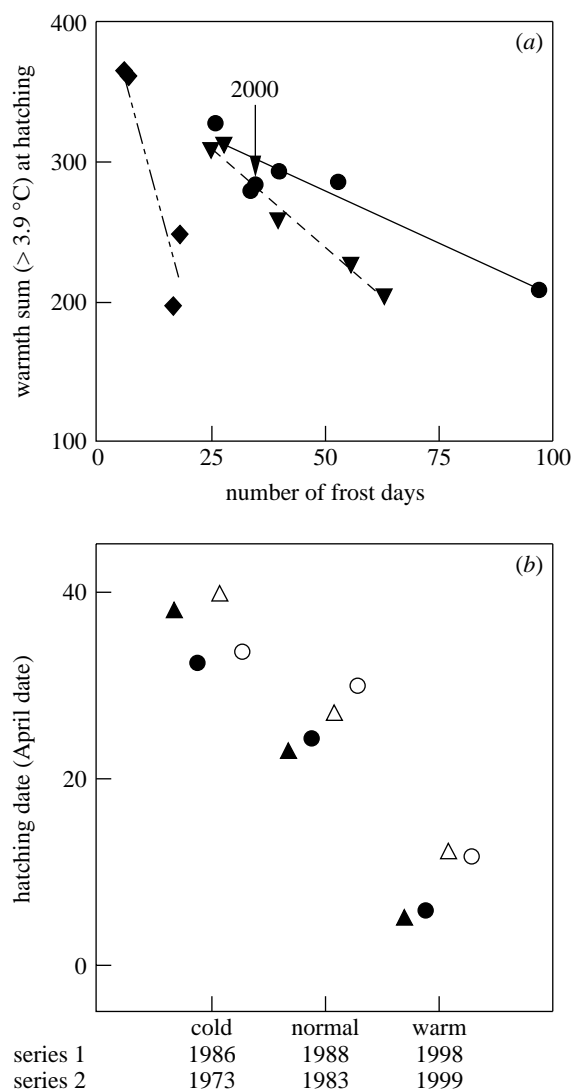


Figure 1. Descriptive model of the timing of winter moth egg hatching. (a) The relationship between the warmth sum to the date at which 50% of the winter moth eggs hatched and the number of frost days. Solid circles represent data from The Netherlands (see § 2). The solid line was fitted using the 1995–1999 data only. Solid triangles represent data taken from a study in Scotland using females collected on Sitka spruce (Watt & McFarlane 1991). Solid diamonds represent data taken from a study in the USA (Kimberling & Miller 1988). (b) Data from the two series of the split-brood design experiment (see § 2). The observed D_{50} value (\pm s.e.) (too small to be visible) (solid circles, series 1; open circles, series 2) and the D_{50} value predicted by the descriptive model (solid triangles, series 1; open triangles, series 2 in (a)) are presented for specific years.

12 years on the bud burst of the 102 oaks on the Hoge Veluwe. The model described the observed bud burst very well (paired t -test, observed versus predicted $t = -0.65$ and $p = 0.53$). Kramer's model (1994) explained the variation in bud burst on the Hoge Veluwe much better than the photothermal model of Nizinski & Saugier (1988) ($t = 3.22$ and $p = 0.008$) (see also Hunter & Lechowicz 1992).

We parameterized the model on egg hatching of the winter moth using four years of data on egg hatching from female winter moths collected at three sites in The Netherlands (figure 1a). These egg hatching dates were

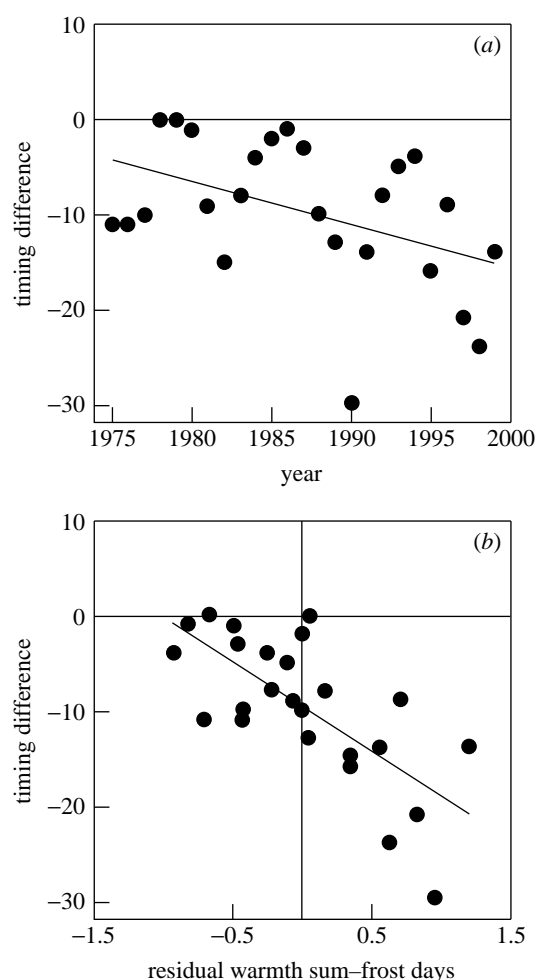


Figure 2. The annual degree of synchrony (timing difference = date of egg hatching – date of bud burst) between oak bud burst and winter moth egg hatching (a) plotted against year (1975–1999) and (b) plotted against the residuals of the relationship between the mean daily warmth sum above 3.9 °C (1 January to 15 April) and the number of frost days (1 December to 1 March) for the years 1975–1999.

obtained from clutches kept in an insectarium. They are representative of egg hatching in the field as there was no difference between the egg hatching dates in the split-brood design experiment for eggs attached to trees in the field and eggs kept in the insectarium (mean D_{50} , field 13.9 April and insectarium 12.4 April) (paired t -test, $n = 15$, $t = 1.31$ and $p = 0.22$).

We validated the model in three ways. The data point for 2000 was collected after the model was constructed and parameterized and fell close to the predicted line (figure 1a). Furthermore, for the two data sets we found in the literature on egg hatching of winter moths (Kimberling & Miller 1988; Watt & McFarlane 1991) we again found a clear linear relationship between the warmth sum threshold and the number of frost days (figure 1a). Finally, we specifically tested whether the difference in the annual mean date of egg hatching was solely due to differences in temperature and not to other correlated weather variables in a split-brood design experiment in controlled temperature cabinets. The observed hatching dates were close to the values predicted from the descriptive model, with the possible exception of

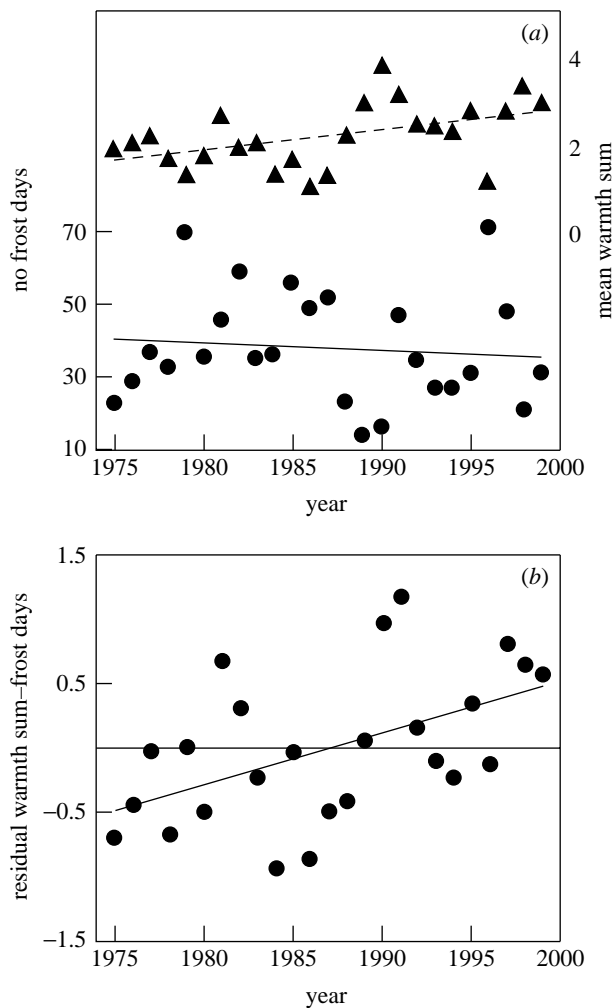


Figure 3. (a) The number of frost days (the number of days with a minimum temperature below 0 °C from 1 December to 1 March) and the mean daily warmth sum above 3.9 °C (from 1 January to 15 April) for 1975–1999 against year and (b) the residuals of the relationship between the mean daily warmth sum above 3.9 °C (from 1 January to 15 April) and the number of frost days (from 1 December to 1 March) for 1975–1999 against year. Temperatures were obtained from the KNMI (Royal Dutch Meteorological Institute) in De Bilt, The Netherlands.

the cold year in both series (figure 1b) (*t*-test for series 1, warm year $t = -0.84$ and $p = 0.41$, normal year $t = -1.73$ and $p = 0.09$, and cold year $t = -18.8$ and $p < 0.001$; and *t*-test for series 2, warm year $t = -0.87$ and $p = 0.39$, normal year $t = 5.47$ and $p < 0.001$, and cold year $t = -13.6$ and $p < 0.001$). However, even for the cold years the eggs hatched only a few days earlier than predicted. These results show that the way in which the annual variation in egg hatching date depends on temperature is adequately described by the descriptive model of egg hatching in the winter moth.

The timing difference (date of egg hatching – date of bud burst) as calculated from the descriptive models has become increasingly negative over the past 25 years (figure 2a) ($F_{1,24} = 5.50$ and $p = 0.028$) and, thus, there has been increased mis-timing of egg hatching in recent years. In addition to predicting the date of bud burst and egg hatching from the descriptive models, we also had six years of data (see figure 1a) on the actual timing of bud

burst and egg hatching. The observed timing difference does not deviate from the predicted values (paired *t*-test, $t = -0.64$ and $p = 0.55$) (Pearson's correlation between observed and predicted values = 0.92).

There has therefore been an increase in mis-timing of egg hatching in the winter moth over the past 25 years. In order to understand why this has happened we need to look at how the climate has changed over this period in more detail. The winter moth egg hatching model implies that two aspects of winter and early spring temperature affect egg hatching: the number of frost days and the mean warmth sum above the base temperature of 3.9 °C. When we plot this mean warmth sum against the number of frost days for 1975–1999, there is a clear correlation (as expected). However, the residuals from this relationship explain a large part of the variation in the predicted timing difference (figure 2b) ($F_{1,24} = 25.63$ and $p < 0.001$). In years where the mean temperature is high given the number of frost days (positive residuals) there is a strong negative predicted timing difference (egg hatching is earlier than bud burst).

The increased winter and early spring temperatures in Western Europe over the past 20 years are due to a large-scale meteorological phenomenon, the North Atlantic Oscillation (NAO) (Schiesinger & Ramankutty 1994; Hurrell 1995). Apart from this increase in mean temperature the NAO also affects the temperature pattern. While the mean daily warmth sum above 3.9 °C from 1 January to 15 April has increased over the period 1975–1999 ($F_{1,24} = 6.24$ and $p = 0.02$), there has been no change in the number of frost days from 1 December to 1 March ($F_{1,24} = 0.23$ and $p = 0.64$) (figure 3a). As a consequence, the residuals of the relationship between spring temperature and number of frost days have increased with year ($F_{1,24} = 7.74$ and $p = 0.01$) (figure 3b) and, hence, the mis-timing of winter moth egg hatching has increased over the years.

4. DISCUSSION

Natural selection will favour response mechanisms that result in adaptive decisions over the whole range of natural environments. In these environments certain relationships exist between selection pressures and the cues organisms use. In the case of the winter moth, annual shifts in oak bud burst should result in concomitant shifts in egg hatching. Climate change may disrupt these relationships and, as selection on response mechanisms may be slow (Van Tienderen & Koelewijn 1994), this results in maladaptive behaviour (Dewar & Watt 1992; Visser *et al.* 1998). We believe this is the reason for the increased mis-timing of winter moth egg hatching. Mistiming occurs because of the extreme temperature patterns that have occurred in recent years given the existing relationship between mean temperatures and the number of frost days over the past 25 years.

In the recent warm springs, winter moth eggs were predicted to hatch up to three weeks before oak bud burst. Because newly hatched caterpillars can only survive for two to three days (with a maximum of ten days) without food (Wint 1983) this will lead to either mortality or dispersal of these small caterpillars (Topp & Kirsten 1991). Hence, mis-timing may have profound effects on the

population dynamics of the winter moth as the key factor in their dynamics is the 'winter disappearance', which is primary hatchling mortality (Varley & Gradwell 1960, 1968).

It is likely that the NAO will return to less extreme values in the coming years and that mis-timing of winter moth eggs will no longer be the case. However, due to global warming it is expected that the global mean surface air temperature will have increased by *ca.* 2 °C (0.9–3.5 °C) by 2100 (mid-range Intergovernmental Panel on Climatic Change emission scenario) (Houghton *et al.* 1996). Recent studies on the oak–winter moth system have focused on this increase in temperature and assessed the consequences for timing of egg hatching. Using descriptive models, Dewar & Watt (1992) also found decreased synchrony between winter moth egg hatching and Sitka spruce bud burst when the mean temperature was increased by 2 °C. However, Buse & Good (1996) found no effect of increased temperature in their experiments on the degree of synchronization of winter moth egg hatching and oak bud burst. They kept both oak trees and winter moth eggs in solar domes that either had ambient or ambient +3 °C temperatures and registered bud burst and egg hatching. However, there may have been a methodological flaw in their experiment as their eggs were all kept at 7 °C until they were introduced to the experimental treatment on 21 January. This means that a large part of the period in which the occurrence of frost days is important was omitted from their experiment. In order to assess whether this is the reason for the difference in the results obtained by Buse & Good (1996) and the results of this study, we are planning to repeat the experiments in the solar domes together with A. Buse, but this time introducing the eggs to the treatments as soon as they are laid.

Synchronization between the different levels of the many multitrophic interactions in the temperate zone may have become disrupted because of the recent climate change. However, this may not be so much due to an increase in the mean temperature; rather, it may be because of changes in the pattern of winter and spring temperatures. Another example where a change in the temperature pattern may be the cause of mis-timing in warmer springs is the timing of reproduction in great tits (*Parus major*). The birds have not advanced their laying date in accordance with the advancement of their main selection pressure, the peak in the abundance of food for the nestlings (Visser *et al.* 1998; Stevenson & Bryant 2000). Similar to the winter moths, this is because temperatures in one period of spring have changed in a different way from the temperatures in another period.

Discussion on global warming is mainly about the effects that an increase in temperature will have. Much less attention is given to the effect of changes in temperature patterns. Such changes are not unlikely. In fact, global warming may cause the extreme values of the NAO. Furthermore, winter temperatures may be affected differently than spring temperatures (Houghton *et al.* 1996). As changes in temperature patterns may have more profound consequences than a fixed increase in temperature over the entire period, this calls for predictions of changes in temperature patterns from the meteorological models on global warming, as well as for ecological studies on how

trophic interactions are affected by changes in temperature patterns (Harrington *et al.* 1999).

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