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OVERWINTERING CLUSTERS OF THE MONARCH BUTTERFLY COINCIDE WITH THE LEAST HAZARDOUS VERTICAL TEMPERATURES IN THE OYAMEL FOREST

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ABSTRACT. During winter, monarch butterflies form dense colonies in oyamel fir forests on high mountains in central Mexico, where the forest canopy serves both as a blanket, moderating temperature, and an umbrella, shielding the butterflies from rain. In this study we investigated the vertical dimension of the butterflies' use of the oyamel forest: we predicted that clusters form at the heights above ground that provide the greatest protection from freezing. By suspending temperature recorders at eight heights, from ground level up to 22m, we established two vertical transects in the forest. We set one transect in a densely forested area and the other in a thinned area, and we recorded hourly temperatures from Jan 13 through Feb 5, 2006. Intermediate heights in the forest, from 10 to 15m above ground, remained the warmest during the cold night and early morning. We also determined that this temperature distribution matched available records of the vertical distribution of butterflies roosting in branch and trunk clusters. The vertical temperature profiles became uniform during mid-day. Temperature extremes were moderated more during clear than during cloudy periods and more in the denser than in the thinned forest. Our results illustrate how the monarch butterfly is behaviorally adapted to the three-dimensional complexity of microclimate in the oyamel forest. A denser forest provides better protection for the overwintering survival of monarch butterflies than a thinned forest. This research bolsters our other microclimatic studies, all of which point to the urgency of prohibiting logging within the oyamel forest used as wintering habitat by monarch butterflies.

Additional key words: *Danaus plexippus*; conservation; Monarch Butterfly Biosphere Reserve; forest management; microclimate; trunk and bough clustering behavior; vertical temperature distribution; negative effects of forest thinning

Fall migrant monarch butterflies (*Danaus plexippus* L., Lepidoptera, Danainae) overwinter in the oyamel (*Abies religiosa* H.B.K., Pinaceae) forest ecosystem on 12 mountain ranges in the Transverse Neovolcanic Belt in central Mexico (Slayback *et al*. 2007; Slayback & Brower 2007). The current archipelago-like distribution of the oyamel ecosystem is a remnant of a much wider forest that retreated up onto the taller volcanic mountains as the environment warmed at the end of the Pleistocene (Manzanilla 1974; Rzedowski 1978; Snook 1993; review in Brower 1995). In this forest, from November through March the butterflies form colonies at elevations of 2,700 to 3,300 m, with extremely dense clusters on both the branches and trunks. Although the butterfly area is south of the Tropic of Cancer, because of its high elevation it is subjected to freezing temperatures on cold nights during much of the winter (Calvert & Brower 1986). Moreover, because the N–S running Sierra Madre mountain systems north of the volcanic highlands do not block northern polar air incursions (Hill 1969), the overwintering area can be strongly affected by cold fronts that interact with Pacific Ocean moisture and generate winter storms with rain, hail, snow, and rime ice (Lauer 1973; Garcia 1997).

Given that the monarch belongs to the tropical butterfly subfamily Danainae and has only moderate freeze resistance (Larsen & Lee 1994; Anderson & Brower 1996), it is a seeming paradox that the eastern North American population migrates to and spends the winter at such high elevations. The reason the butterflies do so is that the cool temperature and moisture inside the oyamel forest maintain the butterflies in a state of reproductive diapause (James, 1993) and allow them to conserve their lipid energy reserves that fuel their five month wintering period and their April remigration to the Gulf Coast states (Masters *et al*. 1988; Brower *et al*. 2006).

Anderson & Brower (1996) determined that 50% of monarchs die at -8ºC if they are dry, whereas if they are wet, 50% die at -4ºC, 80% are killed at -5ºC, and 100% are killed at -7ºC. The lethal combination for the overwintering butterflies is to be wetted by a winter storm and then subjected to freezing temperatures caused by the intense radiant heat loss when the sky clears. The effects of three killer storms on the butterflies have been documented by Calvert *et al.* (1983) for January 1981, by Brower *et al.* (2009) for February 1992, and by Brower *et al*. (2004) for January 2002. The 2002 storm killed an estimated 80% of all overwintering monarchs in Mexico.

An intact oyamel canopy moderates the microclimate within the forest in three ways. The canopy operates as a blanket that helps to hold heat inside the forest (Calvert *et al*. 1982, 1984, 1986; Anderson & Brower 1996). From 5–7 Jan 2008, for example, the minimum temperature beneath the forest canopy was +3.3º C, whereas in a nearby clearing it was –3.2ºC, i.e., 6.5º C colder (Brower *et al*. 2008b; see also Brower *et al*. 2009, Fig. 5). The canopy also serves as an umbrella sheltering the butterflies from rain (Anderson & Brower 1996) and from heavy dew formation. Several of our field studies have documented the presence of heavy dew and severe frosting in open areas ("llanos") and their absence within forests immediately adjacent to overwintering colonies (Calvert & Brower 1981; Calvert *et al*. 1982, 1986; Calvert & Cohen 1983; Alonso-Meija *et al*. 1992, 1993). Finally, oyamel tree trunks retain heat during the night, maintaining the butterflies' temperatures when they rest on the trunks (Brower *et al*. 2009). Thus, the oyamel forest contributes blanket, umbrella, and hot-water bottle effects, microclimatic factors that can be critically important during extreme freezes that follow winter storms.

Monarch butterflies do not distribute themselves evenly at all heights within the oyamel forest. In initial descriptions of the Sierra Chincua overwintering colony, Urquhart & Urquhart (1976), Brower (1977), and Brower *et al*. (1977) noted that the oyamel tree crowns were devoid of monarchs. This crown avoidance was confirmed during extensive aerial reconnaissance of the butterfly colonies (Slayback *et al*. 2007; see Fig. 1 in Brower *et al*. 2008b). At the lowest forest stratum, Calvert *et al*. (1982) and Calvert & Brower (1986) observed that mid-winter branch and trunk clusters rarely occur close to the ground.

Geiger (1950) and Geiger *et al.*'s (2003) summaries of forest microclimate led us to embrace a hypothesis that the butterflies avoid both the tree tops and the ground to reduce their probability of freezing. As Geiger pointed out, the tops of forest trees are colder at night than the branches beneath the canopy because tree tops lose heat through radiation to the open sky. Geiger *et al*. (2003) also noted that tree tops are subject to heavy dew condensation and rime ice deposition. We witnessed the latter during storms in January 1981 and 2002 (Calvert & Brower 1986; Brower *et al*. 2004). Finally, nighttime temperatures near the ground are often colder than at mid-forest levels due to radiant heat loss through openings in the canopy, cold air drainage (especially in mountainous terrains), and loss to the soil, which can serve as a heat sink.

The current study, spurred by our growing awareness of the spatial and temporal complexity of microclimates within oyamel forests, addresses the relationship of the butterflies' clustering behavior to the forest's vertical temperature profile. We first quantify the vertical

FIG. 1. Monarchs that have been dislodged from their clusters on the tree boughs and trunks are subject to lower and possibly lethal freezing temperatures. By shivering and crawling upwards as on this oyamel fir trunk, they are able to reestablish their clusters. Sierra Chincua colony, 11 Jan 1979 (photo, L.P. Brower.)

distribution of the trunk and bough clusters on the oyamel trees. We next compare temperatures recorded in an open area with those recorded beneath the forest canopy to demonstrate how the forest moderates the temperatures during mid-winter. We then compare the forest temperature moderation over 24 hours on clear versus cloudy days. Finally, we present the vertical temperature profiles within the oyamel forest at different times of day, for both clear and cloudy conditions, and for two trees differing in their degree of canopy cover.

We ask six questions: (1) What is the vertical distribution of monarchs? (2) How does air temperature vary with height within the forest? (3) Is vertical variation in temperature different during clear and cloudy periods? (4) How does the vertical temperature profile change over 24 hours? (5) Is the vertical temperature profile different in a closed versus an open forest? (6) Could the vertical distribution of the monarch clusters provide thermal benefits for the butterflies?

Answers to these questions amplify our knowledge of the microclimatic consequences for monarchs because of their association with the oyamel forests. They also have implications for how oyamel forests should be managed for the long-term conservation of the monarch butterfly.

MATERIALS AND METHODS

Measuring the vertical distributions of monarch clusters on oyamel trees. On 1 Mar 1979, W. Calvert and W. Zuchowski used a Spiegel Relaskop (Forestry Suppliers, Jackson, MS) to measure the vertical distributions of monarch trunk clusters on ten oyamels and the heights of nine of the ten trees (Table 1). These data were gathered in the Sierra Chincua 4 colony, located in Arroyo Zapatero, as described in Calvert & Brower (1986). On 5–6 Feb 2008 we measured the vertical distribution of branch clusters on 18 oyamel trees in the Arroyo Hondo colony, also on the Sierra Chincua, as described in Brower *et al*. (2008b). For the 2008 measurements, we used a stick method as follows: we first marked the 2 m height on a tree trunk; then, from approximately 30 m away, we held a short stick at arm's length that by eye matched the 2 m height on the tree; finally, we estimated the number of multiples of the 2 m length required to reach the cluster bottom, the cluster top, and the tree top. This method (Ontario Woodlot Assoc. 2003) provides estimates with an accuracy of approximately ±10%. Both the 1979 and 2008 measurements were taken in colonies that had not been affected by winter storms. The vertical extents of trunk and branch clusters generally coincide except after storms or other disturbances when the dislodged butterflies crawl back up the trunks as shown in Fig. 1.

The vertical transect study area. We conducted our vertical transect study in an oyamel forest on a ridge behind Chincua Station located in the Ejido los Remedios (Fig. 2). As described in Brower *et al*. (2009), the forest is within the elevational range of the known monarch overwintering areas on the Sierra Chincua and is 2–4 km ESE of where butterfly colonies have formed every year since the first Chincua colony was discovered in 1975. Even though monarch colonies have never been reported in this specific location, the forest characteristics (species composition, tree density, size distribution, slope, elevation, and southern exposure) are similar to the areas where monarchs do form colonies on the Sierra Chincua massif. The study area includes one of the sites used in Brower *et al*. (2009).

TABLE 1. Vertical distribution of monarch clusters on oyamel trees on the Sierra Chincua. Data shown are mean ± s.d. and (range).

	1979 trunk clusters	2008 branch clusters	diff
Clusters			
top of clusters	15.7 ± 3.0 m (10.0 to 19.8)	15.4 ± 2.4 m (11.0 to 20.7)	n.s.
bottom of clusters	7.2 ± 1.1 m (4.8 to 8.9)	5.9 ± 2.5 m (1.5 to 10. 4)	n.s.
vertical extent	8.5 ± 2.9 m (3.5 to 12.0)	9.5 ± 2.9 m (5.5 to 17.1)	n.s.
Trees with these clusters			
height	26.6 ± 4.8 m (15.5 to 30.5)	20 to 30 m **	
dbh	37.1 ± 14.5 cm (20.3 to 66.2)	14.9 ± 4.4 cm (6.8 to 20.8)	p<.001
Sample size	10 *	18	

*N = 9 for tree height measureiments

**estimated

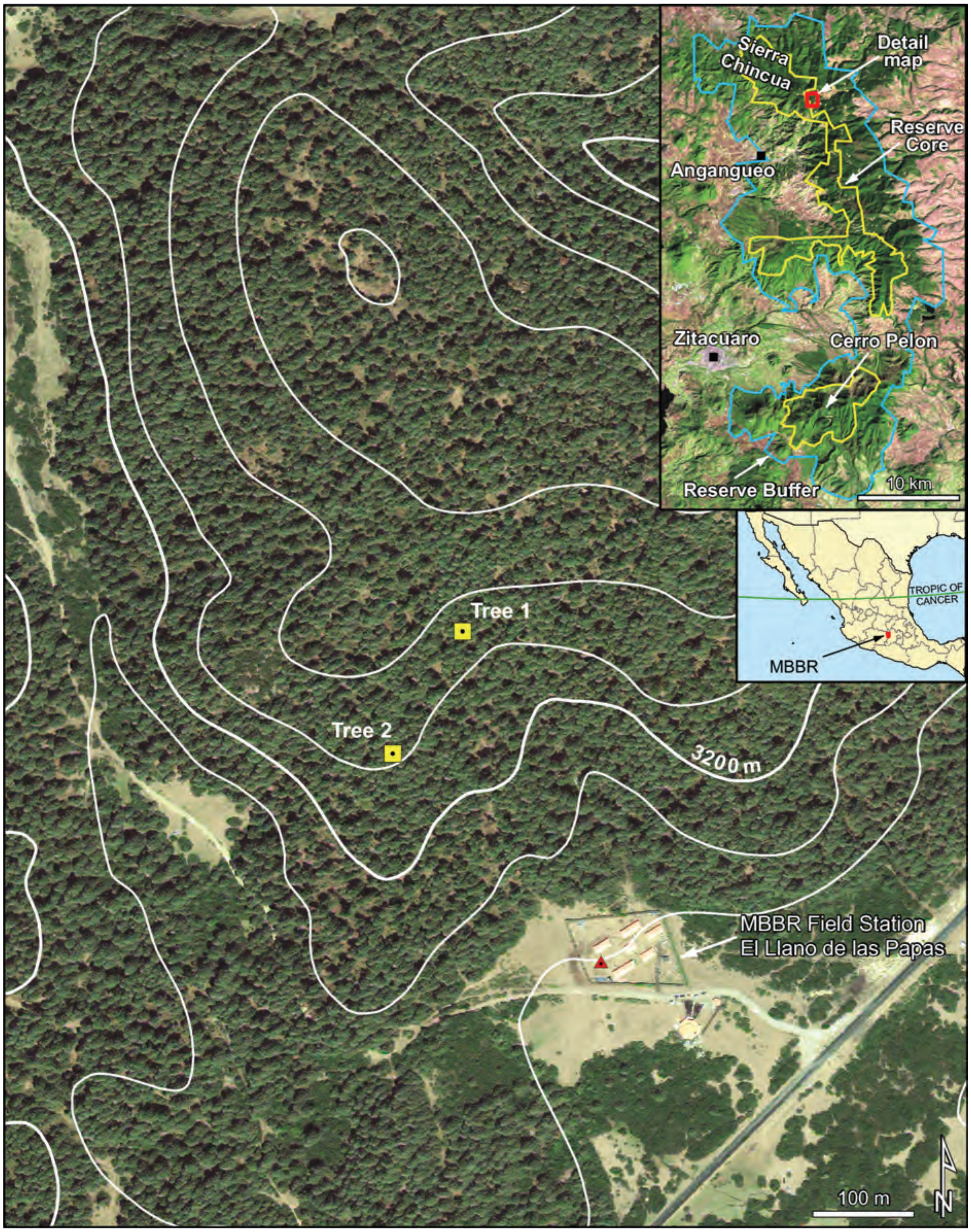

FIG. 2. The main map shows the location of our weather station as a red triangle, the Monarch Butterfly Biosphere Reserve (MBBR) Field Station (on el Llano de las Papas), the locations of Trees 1 and 2, and elevation contours at 20 m intervals, on top of a GeoEye-1 satellite image (© GeoEye) made on 11 April 2009. The distance from the weather station to Tree 1 is 350 m and to Tree 2 is 290 m. Tree 1 and 2 are 140 m apart. The down-slope facing aspects were 150º for Tree 1 and 160º for Tree 2. The inset map shows the location of this site within the MBBR and the location of the Sierra Chincua on top of a Landsat 7 satellite image made on 16 Jan 2003.

FIG. 3. The experimental trees. (A) view of the vertical transect at Tree 1; (B) same, Tree 2. Four of the eight cylinders in which the Thermochrons were mounted are visible in A, while two are visible in B; two cylinders in each photo are marked by arrows. The canopy above Tree 1 is 34% open to the sky, and Tree 2 is 13% open. (Photos, L. P. Brower, from the same facing angles as the transects.)

Small-scale timber removal has taken place in this site periodically, and all trees are relatively young, similar to those in the Chincua colony when studied during the 2007–2008 overwintering season (Brower *et al*. 2009).

Two trees were selected within the forest that differed in the immediately surrounding forest cover. The images in Fig. 3 were taken from the ground looking straight up at each tree's canopy with a Canon D-20 camera and an EF-S 17–40 mm lens set at 17 mm. Adobe Photoshop pixel analysis (Hein 2006) indicated that 34% of the open sky showed above Tree 1 and 13% above Tree 2; that is, Tree 1 was in a relatively open area of the forest whereas Tree 2 was in a more closed area. Both trees were approximately 40 cm in diameter and 30 m tall. The slopes at Trees 1 and 2, measured with a clinometer, were both approximately 15 degrees, and their aspects were 140º and 150º, respectively. For reasons of security and equipment, our data acquisition was limited to two trees.

We used a Garmin GPS MAP60CSx unit to locate the positions of the two oyamel trees and plotted them on an orthorectified, pan-sharpened GeoEye-1 satellite image (© GeoEye) with 0.50 m resolution, taken on 11 April 2009. The location of our weather station and the two oyamel fir trees are shown in Fig. 2. The coordinates for the weather station were: 19º 39' 41.9" N and 100º 16' 6.2"W, at an elevation of 3160 m. The tree coordinates were: Tree 1: 19º39' 52" N and 100º16' 10'' W; Tree 2: 19º39' 48" N and 100º16' 13'' W.

Setting the vertical transects. The vertical line and cylinders for Tree 1 were set on 11 Jan 2006 with the line facing 340º; those for Tree 2 were set on 12 Jan 2006 with the line facing 255º. Both Fig. 3 A & B were taken on 12 Jan 2006, an overcast day. We used a Big Shot slingshot (Sherrill Arborist Supply, Greensboro, N.C.) to throw a nylon string over an upper bough on each oyamel. For each height, one temperature data logger (see below) was mounted on a lateral wall inside a white plastic PVC cylinder (12.5 cm long, inside diameter 5.2 cm, outside diameter 6.0 cm). The cylinders were suspended horizontally from nylon strings tied through small holes bored 1.25 cm from each end. The cylinder strings were attached to the suspended vertical line, which was pulled up so that the cylinders were suspended at eight heights (0, 3, 6, 9, 13, 16, 19, and 22 m above the ground). The cylinders were free to rotate. The temperature recorders were shielded from direct sunlight by the PVC cylinder and by the forest canopy. The main string was secured near the base of the tree so that the transect hung 0.5 to 1 m away from the tree trunk (Fig. 3A & B).

Temperature measurements. Each hour the weather station (WeatherHawk, Model 232, Logan, UT) recorded the previous hour's average, minimum, and maximum temperatures, with an accuracy of 0.01ºC. Vertical transect temperatures were measured with iButton Thermochrons (Model DS1921G, Maxim Integrated Products, Dallas Semiconductor). These small (1.6 cm by 0.7 cm) digital recorders measure temperature in 0.5ºC increments, with a range of -40º to 85ºC and a rated accuracy of ±1.0ºC (Dallas Semiconductor); we have previously determined that under our experimental conditions their accuracy is better than ±0.5ºC (Brower *et al*. 2008b). We programmed the Thermochrons to record one instantaneous reading each hour. They were in place by mid-afternoon on 12 Jan 2006 and were retrieved on 6 Feb 2006. We used the data for 24 days, from 13 Jan through 5 Feb 2006. For a comparison of temperature profiles during different weather conditions, we selected five cloudy days (Jan 25, 26, 28, 29, and 31) and five clear days (Jan 13, 18, 19, and Feb 4, 5) for analysis of mid-morning, mid-day, and afternoon temperature profiles. Similar choices were made for nighttime comparisons (19:00 through 07:00 hrs) under cloudy conditions on Jan 24–25, 25–26, 26–27, 27–28, 28–29) and under clear conditions (Jan 13–14, 18–19, 19–20, Feb 3–4, 4–5). The difference between the cloudy and clear days (Duchon & O'Malley 1999) is illustrated by comparing the highest recorded solar output for each day (recorded hourly); the averages of the daily high readings (mean ± 95% C.I.) were 519.2 ± 56.0 watts/sq-meter for the five cloudy days and 814.8 ± 22.2 watts/sq-meter for the five clear days (t-test, $p < 0.001$). The only precipitation recorded during the 24-day study was on cloudy days, 6 mm on Jan 26 and 9 mm on Jan 27.

Analysis. All data were analyzed using SPSS versions 16 and 17 (SPSS, 2008). We analyzed patterns in the vertical profiles using regression analysis, both linear and polynomial, with tree incorporated as a fixed effect and day as a random effect in a mixed effects model. All regressions used height and height squared as explanatory variables. The daily temperature ranges of the two trees were compared by paired t-tests, with a strict Bonferroni correction (Walsh, 2004) applied to the comparisons at all heights.

To examine temporal autocorrelation of the data, we developed a correlogram based on time lags $j = 1$ to 9 hr (Diggle 1990). The results revealed significant autocorrelation for time lags up to four hours but negligible effects for longer lags. Thus, measurements close in time on the same day are not independent, while records from different days provide independent measures. To ensure correctness of the patterns we're reporting, we assessed the validity of these patterns by comparing them to the same analyses using only those data that were separated by five or more hours.

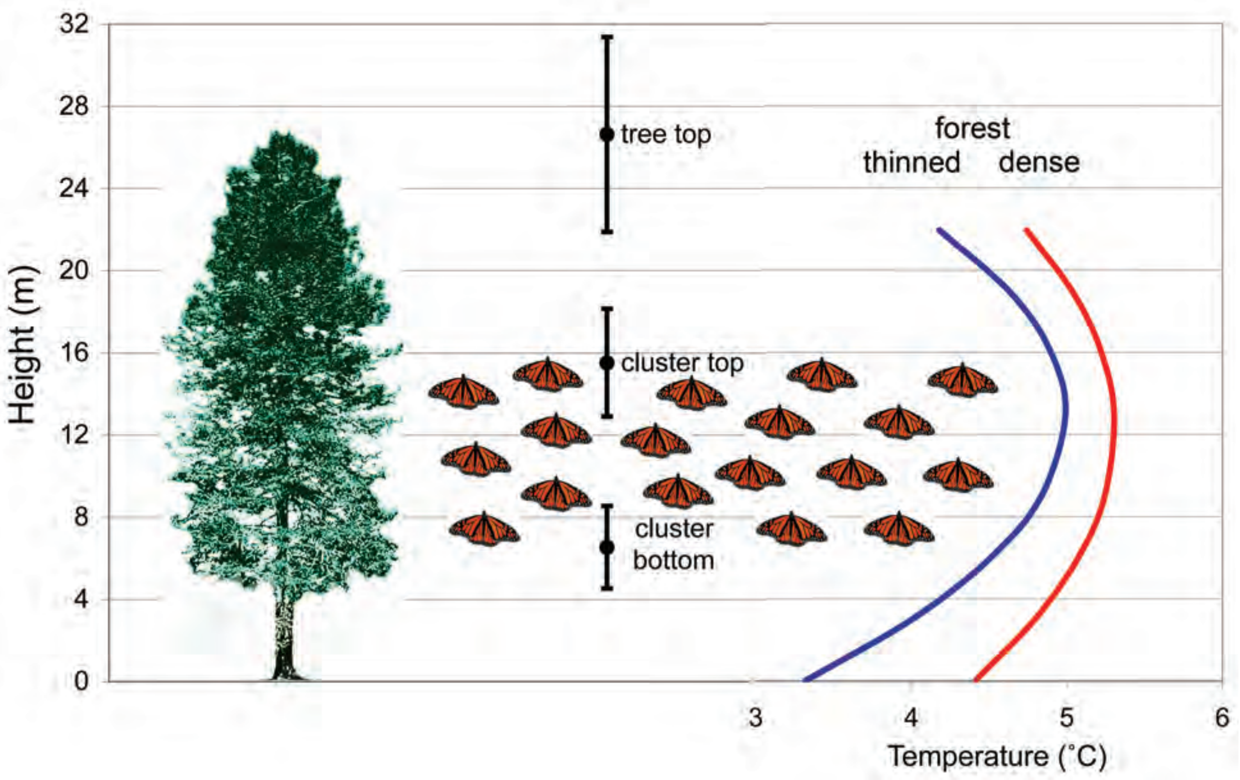

FIG. 4. The relationship of nighttime vertical temperatures (right) and monarch cluster heights (center) on an oyamel fir of average height (27 m, left). The black height bars are mean m above the ground ± 1 s.d. (data from Table 1). The blue and red lines show the fitted nighttime vertical temperature profiles from measurements made from the ground to 22 m on two oyamels; the blue line is from Tree 1 in the thinned forest, while the red line is from Tree 2 in the denser forest (data from Fig. 7; regressions given in the text). The height of the lowest branches varies. The clusters averaged 6.4 m above the ground and extended on average upwards to 15.5 m, which is more than 10 m below the canopy (Table 1), with most monarchs concentrated at middle levels. The mid section of both trees is about 1–2° warmer than both the ground and the upper canopy temperatures. The data thus indicate that the butterflies behaviorally select the safest microclimate by avoiding the ground and the treetop, where they would be subjected to more severe cold temperatures, and (in the treetop) to wetting by dew. The vertical temperature profile for the tree in the thinned forest is up to 1°C colder at all heights. The tree image is based on Earle (2009).

RESULTS

Vertical distribution of the trunk and bough clusters on oyamels. The trunk clusters in 1979 extended, on average, between 7.2 m and 15.7 m above the forest floor, with an average vertical extent of 8.5 m (Table 1). The average tree height was 26.6 m, that is, 11 m above the top of the clusters. The branch clusters in 2008 showed a similar pattern: the clusters were between 5.9 m and 15.4 m above the ground, with an average vertical extent of 9.5 m (Table 1). Although we did not measure tree heights in 2008, we estimated them to be between 20 and 30 m; thus, the canopy extended 5 to 15 m above the topmost clusters. Fig. 4 summarizes these vertical distributions of the clusters on a 27 m oyamel.

Moderation of daily temperature extremes by the forest canopy. The moderating effect of the canopy on temperatures is evident from a comparison of the ambient temperatures at the 3m height at our two study trees with those at the nearby weather station (Fig. 5). The temperatures inside the forest beneath the canopy are always cooler during the day and almost always warmer at night than they are in the open area. Through the 24 days, the temperature range at the weather station was 23.8°C (from –4.9° to +18.9°C), while the temperature range for the two forest trees was 15.6°C (from –0.3° to +15.3°C). Thus, the temperature varied in the open area 8.2°C more than beneath the forest canopy, and freezing temperatures occurred only once in the forest compared to most nights in the open.

Comparison of the temperature patterns during cloudy versus clear conditions. The temperature regimes on cloudy and clear days at the 3 m height under the forest canopy and in the nearby open area reveal an interaction between the effects of canopy and cloud cover (Fig. 6A and B). Each hourly temperature inside the forest is based on the average of Trees 1 and

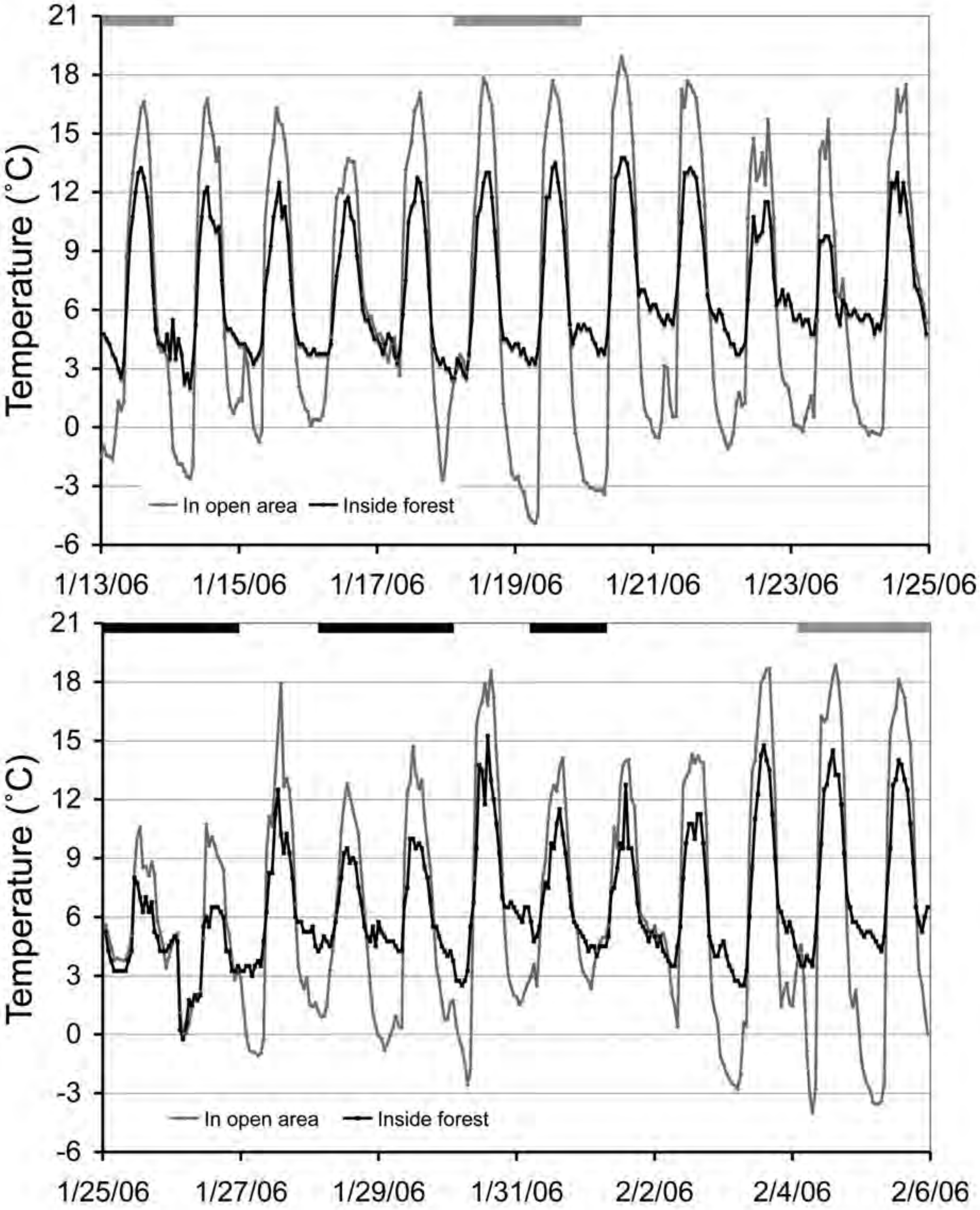

FIG. 5. Hourly temperatures from 13 Jan to 5 Feb 2006. The temperatures in the open area (gray line) are from the WeatherHawk weather station located in the open area on El Llano las Papas (Fig. 2); the inside-forest readings (black line) are the ambient temperatures at the 3m height beneath the nearby oyamel forest, averaged for Tree 1 and Tree 2. Marked by the labelled tick marks, each day begins at 0:00. Dark bars along the top designate the five cloudy periods analyzed and the gray bars designate the five clear periods. The data show that the forest substantially moderates the microclimate: freezing temperatures occur almost nightly in the open but rarely beneath the canopy, and the temperatures inside the forest are always cooler during the day than in the open area and almost always warmer at night.

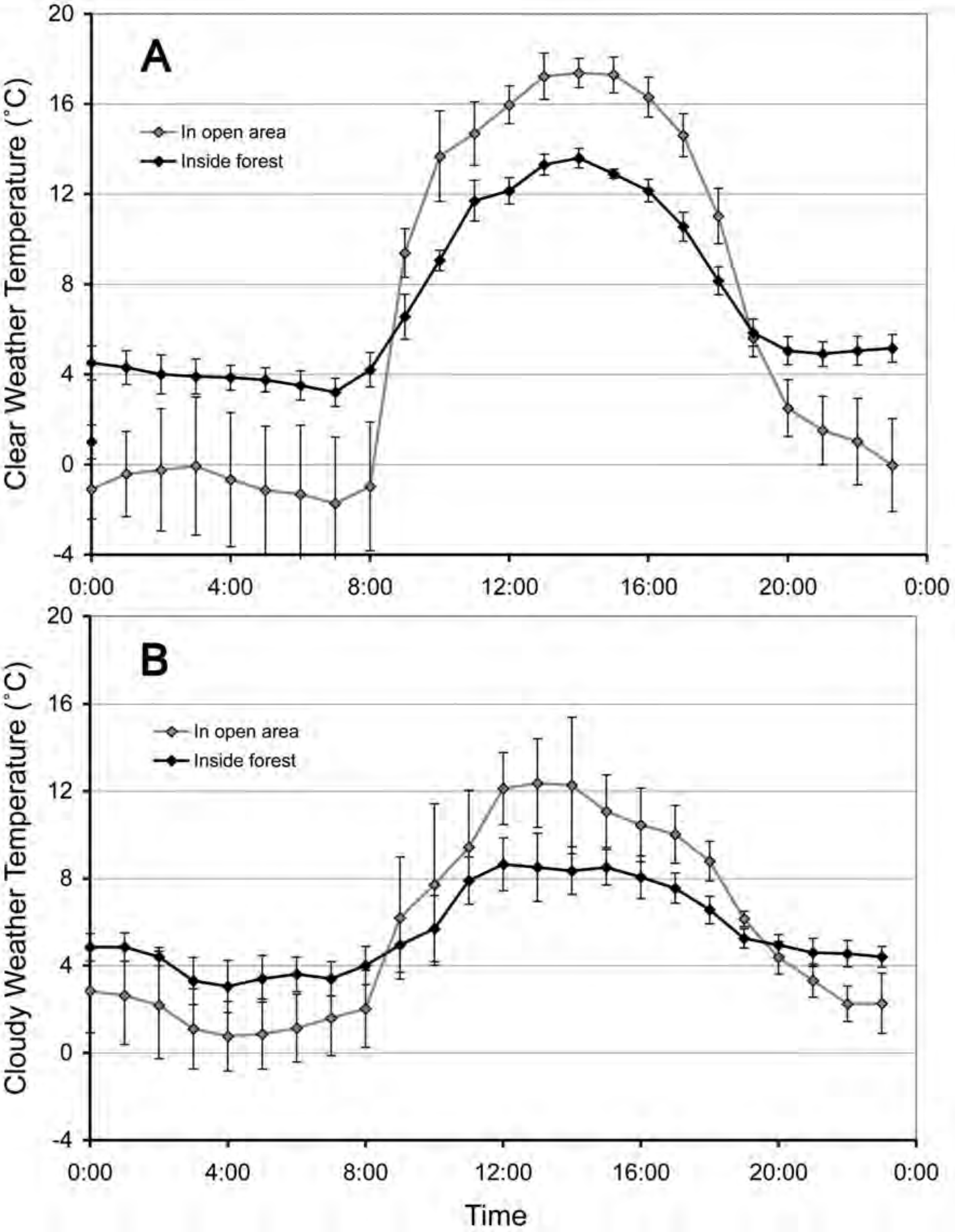

FIG. 6. Daily temperature patterns during (A) clear and (B) cloudy conditions comparing temperatures that occur at 3m elevation inside the forest (black line) with temperatures in the nearby open area (gray line) as recorded at the weather station. Each hourly temperature inside the forest is based on the average of Trees 1 and 2 for five clear days (Jan 13, Jan 18–19, Feb 4–5) or five cloudy days (Jan 25–27, Jan 27–29, Jan 31). The error bars show 95% C.I. Under all conditions, the open area is warmer during the day and colder at night. The data illustrate that: (1) the freezing risk is highest during nighttime (from 19:00 to 7:00); (2) during both weather conditions the canopy holds heat inside the forest during the nighttime and reduces the probability of the butterflies' freezing; and (3) clouds have little effect on forest temperatures at night but they substantially reduce daytime temperatures in both the forest and the open area.

2 for five cloudy days or for five clear days. The open area temperatures are based on the same 5 days from the weather station.

Under clear conditions, for all hours from 10:00 through 17:00 the daytime forest temperature was significantly cooler, by 3–4ºC, than in the open. The nighttime forest temperature was significantly warmer, by 4–5ºC, between 21:00 and 08:00. In contrast, under cloudy conditions the difference between the forest and open sites was reduced, especially at night. The daytime temperature rise was smaller both in the open and in the forest; the difference between the two sites each hour was 1–4ºC, and significant during only four of the hours. On cloudy nights the difference between the forest and open sites was reduced to 2–3ºC, and was significantly different for only two nighttime hours.

These results illustrate that clouds (1) reduce the radiant energy loss at night in open areas, but (2) have little effect inside the forest. The data also indicate that the forest (3) maintains cooler daytime temperatures during both clear and cloudy daytimes and (4) also maintains warmer temperatures at night irrespective of cloud cover. Moreover, (5) the moderating effect of the canopy is greater under clear conditions than under cloud cover. Most importantly, the blanket effect of the forest during the night reduces the risk of the butterflies' freezing and during the day reduces the temperatures and therefore also the rate at which the butterflies burn lipids.

Vertical temperature profiles during the nighttime. During the night and early morning, from 19:00 through 07:00 hrs, the intermediate heights were warmer than the ground and the top of the forest for both vertical transects (Fig. 7). At each height and for each transect, the average temperature was based on 312 measurements (13 records per night for 24 days). A polynomial model yielded the best fit for each tree, and the regressions were significant (Tree 1, F=228.58, p<0.001; Tree 2, F=68.96, P<0.001). The regressions for the two trees were also significantly different (t=15.424, p<0.001). For Tree 1, $Temp = -0.010\ Ht^2 + 0.259\ Ht + 3.311$; for Tree 2: $Temp = -0.006\ Ht^2 + 0.147\ Ht + 4.405$. Equivalent results obtained when using only separated data points per night to avoid autocorrelation (three records per night, at 20:00, 01:00, and 06:00 hrs, for 24 days): Tree 1, $Temp = -0.010\ Ht^2 + 0.260\ Ht + 3.338$; for Tree 2: $Temp = -0.006\ Ht^2 + 0.151\ Ht + 4.443$; statistics in Table 2). The warmest heights given by the regressions were at 13.0 m for Tree 1 and at 12.2 m for Tree 2; based on the actual measurements, the warmest temperatures were from 6 to 16 m for Tree 1 and from 13 to 16 m for Tree 2. The regressions indicate that the ground was 1.7ºC colder than the warmest intermediate heights for Tree 1 and 0.9ºC colder for Tree 2, and that the temperature at 22m was 0.8ºC colder than the warmest intermediate height for Tree 1 and 0.6ºC colder for Tree 2. Both regressions were significant, as were the curvilinear

Table 2. Regression statistics for analyses of the nighttime temperature profiles measured at eight heights on two oyamel trees (2496 measurements for each when all data are analyzed; 576 measurements for separated, independent temperatures). For the analysis by temperature differences, the temperature at the 3 m height was subtracted from the temperature at each of the seven other heights. The regression statistics show the fit of the polynomial (curvilinear) model to the temperature data, while the quadratic coefficients show the significance of the curvilinear component. These statistical results confirm that nighttime temperatures are significantly warmer at intermediate heights.

	Tree 1	**Tree 2**
Analysis by actual temperatures		
regression	F = 228.58; p < 0.001	F = 68.96; p < 0.001
quadratic coefficient	t = 17.367; p < 0.001	t = 10.579; p < 0.001
R square	0.155	0.052
Analysis by separated temperatures		
regression	F = 55.498; p < 0.001	F = 19.624; p < 0.001
quadratic coefficient	t = 8.545; p < 0.001	t = 5.696; p < 0.001
R square	0.159	0.061
Analysis by temperature differences		
regression	F = 1584.25; p < 0.001	F = 521.25; p < 0.001
quadratic coefficient	t = 45.721; p < 0.001	t = 29.084; p < 0.001
R square	0.560	0.295

(quadratic) components of the regressions (Table 2). The temperatures were consistently lower for Tree 1, which had 34% of the canopy opened to the sky, compared to Tree 2 which had only 13% of the canopy opened to the sky (Fig. 2A and B). The curvilinear regressions of nighttime temperatures for Tree 1 and Tree 2 are summarized diagrammatically in Fig. 4 and demonstrate that the vertical distribution of monarch clusters matches the safest part of the vertical temperature profiles in the oyamel forests.

Similar patterns resulted when we ran a separate analysis of the vertical temperature profiles based on the temperature differences between the actual reading at each height and the temperature measured at the 3 m height. We ran this analysis to exclude the influence of some days being warmer than others (treating time as a random effect), and therefore to reduce the variance in day-to-day measurements. As a result, the R square values were much higher, as were the F and t statistics (Table 2). The regression equations based on the temperature differences are identical to the regression equations based on the actual temperatures, except for the axis intercepts (–0.729 for Tree 1 and –0.786 for Tree 2). Thus, the curvature of each line (the dependence of temperature on height above the ground) and the interpretation of the results were identical whether the regressions were based on actual temperatures or temperature differences.

We examined the influence of cloud cover on the nighttime temperature profiles. Our initial analyses showed that, when we separated the data for clear and cloudy nights, a polynomial regression provided a better fit than a linear regression for temperatures of both trees under both clear and cloudy conditions. This result was similar to that with all data combined (Fig. 7). Comparisons of the polynomial model to the linear model gave these measures of fit: Tree 1 clear weather, R square (polynomial) =0.656 versus R square (linear) =0.266; Tree 1 cloudy 0.326 versus 0.041; Tree 2 clear 0.412 versus 0.118; Tree 2 cloudy 0.168 versus 0.002). From the regressions, intermediate heights (12 to 14m) of Tree 1 were 3.0° warmer than the ground during clear nights but only 1.0° warmer on cloudy nights. For Tree 2, in the denser part of the forest, the differences were less, at 1.3° for clear nights but only 0.6° for cloudy nights. From the analyses for Tree 1, we found greater curvature (a greater difference between temperatures at intermediate heights and those at the top and bottom of the transect) on clear nights than on cloudy nights (t=2.971, p=0.003). For Tree 2, the differences during clear and cloudy conditions were reduced and not quite significant (greater curvature on clear nights, t=1.754, p=0.080).

Nighttime temperatures may also be viewed separately for cloudy and clear nights (Fig. 8). The same vertical pattern is apparent as in Fig. 7, with Tree 1 being colder than Tree 2 but with the cloudy nights having lower temperatures.

Temperature profiles during mid-morning hours. During morning hours (0900 and 1000; Fig. 9) of clear days, the temperature increased significantly from the ground towards the canopy (regression, effect of height: t=3.890, p<0.001 for Tree 1; t=1.991, p=0.048 for Tree 2). The averages over all heights were 8.7±0.5°C for Tree 1 and 9.0±0.5°C for Tree 2. In contrast, on cloudy days the vertical temperature profile was remarkably uniform (regression, effect of height: t=0.277, n.s. for Tree 1; t=0.312, n.s. for Tree 2) and averaged 5.3±0.5°C for both trees. This average was less than 1°C warmer than the nighttime average (Figs. 7, 8). The differences between clear and cloudy days were significant (Tree 1: t=12.198, p<0.001; Tree 2: t=11.627, p<0.001), with the average temperature being more than 3° cooler on cloudy days than on clear days.

Temperature profiles during the mid-day hours. By mid-day (12:00 and 13:00) the nighttime profile was fully erased on both clear and cloudy days, and temperatures were uniform throughout the vertical profiles (Fig. 10). There was no effect of height on temperature for either transect (Tree 1: t=0.007, n.s.; Tree 2: t=0.309, n.s.). The clear days, however, were significantly warmer than cloudy days (Tree 1: t=11.279, p<0.001; Tree 2: t=12.015, p<0.001). For Tree 1, mid-day temperatures averaged 12.7° on clear days and 8.5° on cloudy days, while for Tree 2, the averages were 12.3° and 7.9°.

Temperature profiles during the afternoon hours. On clear and cloudy days, the afternoon hours (from 1500 to 1700) continued to produce a mostly uniform vertical temperature profile (Fig. 11) as overall temperatures began to decrease. Similar to mid-day, there was no effect of height on temperature for either transect under cloudy conditions (Tree 1: t=0.153, n.s.; Tree 2: t=0.216, n.s.), and despite some variability in temperatures, there was no consistent effect of height during clear conditions either (Tree 1: t=0.883, n.s.; Tree 2: t=1.137, n.s.). On Tree 1, we suspect that the 19 m Thermochron received direct insolation on clear days, producing a temperature spike at that height. As was true during morning and at mid-day, temperatures were significantly higher on clear than on cloudy days (Tree 1: t=16.684, p<0.001; Tree 2: t=23.410, p<0.001); the averages were 12.7° on clear days and 8.1° on cloudy days for Tree 1 and 11.8° on clear days and 7.8° on cloudy days for Tree 2.

Daily pattern. Comparison of Figs. 7-10 shows that,

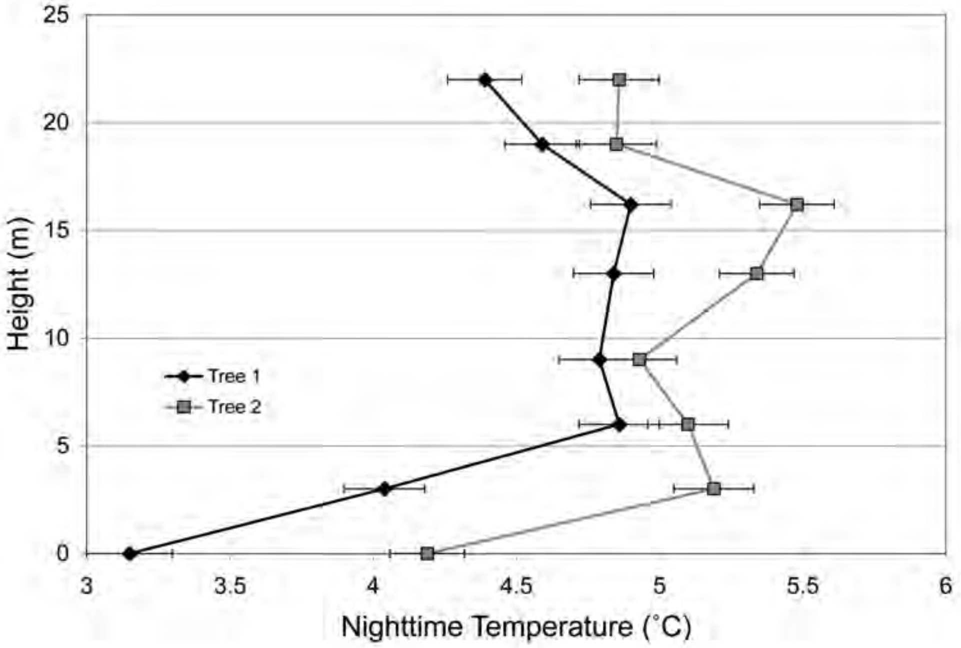

FIG. 7. Average nighttime (19:00 to 07:00 hrs) temperature measurements at eight heights above the ground for Tree 1 (black line) and Tree 2 (gray line) over 24 days (13 Jan through 5 Feb 2006). Error bars show 95% C.I.; statistics are in Table 2. These results, in combination with Table 1, indicate that the vertical distribution of monarch clusters matches the safest part of the vertical temperature profiles in the oyamel forests. At night Tree 2 averages 0.55 degrees warmer than Tree 1, which is more exposed. The curvilinear regression lines are displayed along with the monarch cluster height preferences in Fig. 4.

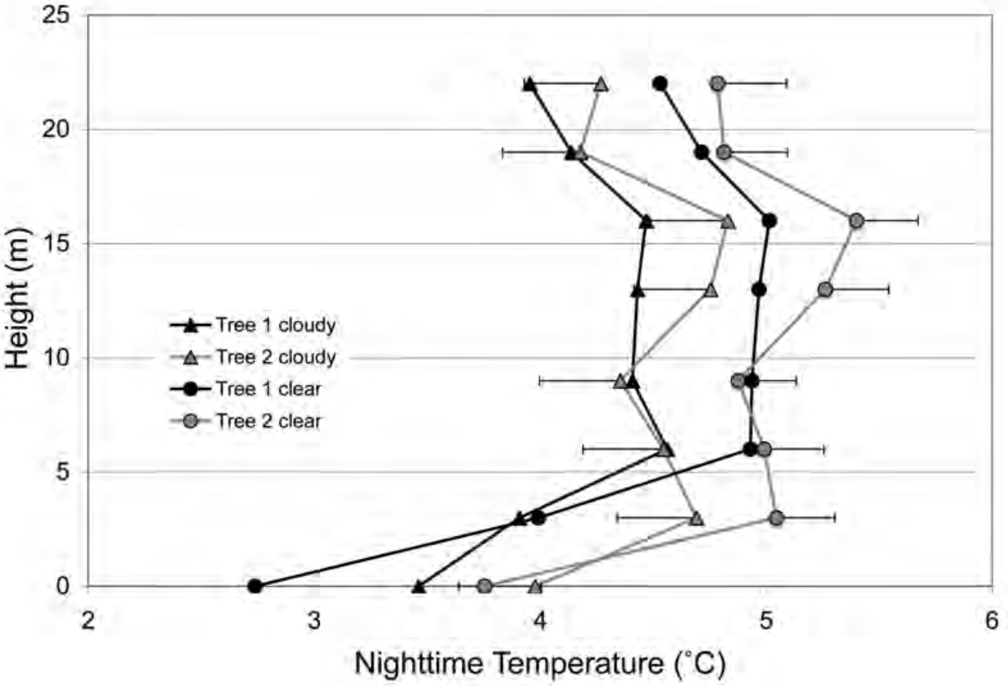

FIG. 8. Average nighttime (19:00 to 07:00 hrs) temperature measurements at eight heights above the ground for Tree 1 and Tree 2 during five cloudy nights and five clear nights. Error bars show 95% C.I. Fig. 7, in contrast, shows the overall comparison of Tree 1 and Tree 2 during all nights.

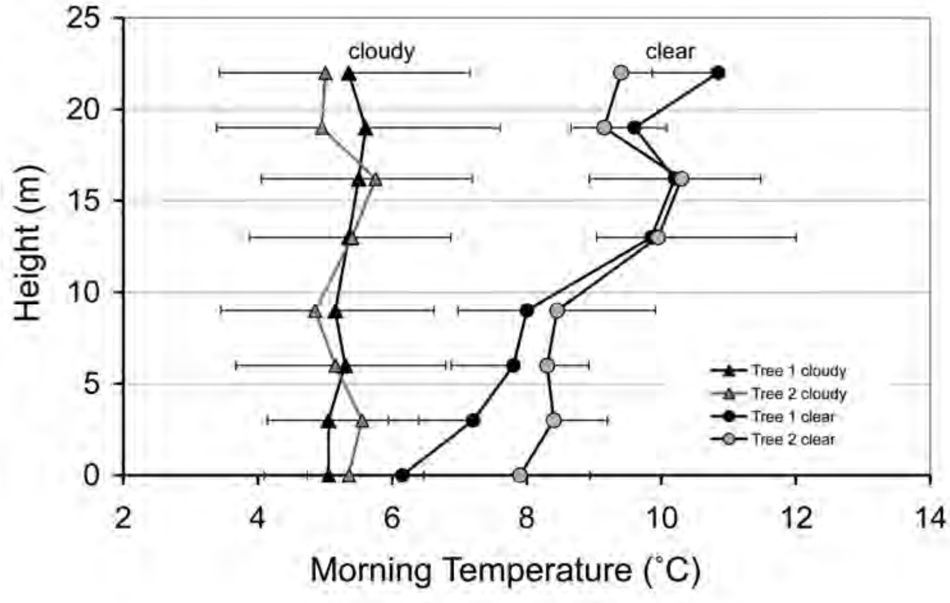

FIG. 9. Vertical temperature profiles during mornings (0900 and 1000 hr) for both Tree 1 and Tree 2, with a comparison of cloudy and clear days. Each data point is an average calculated from 10 measurements during five cloudy days and five clear days. Error bars represent 95% C.I.

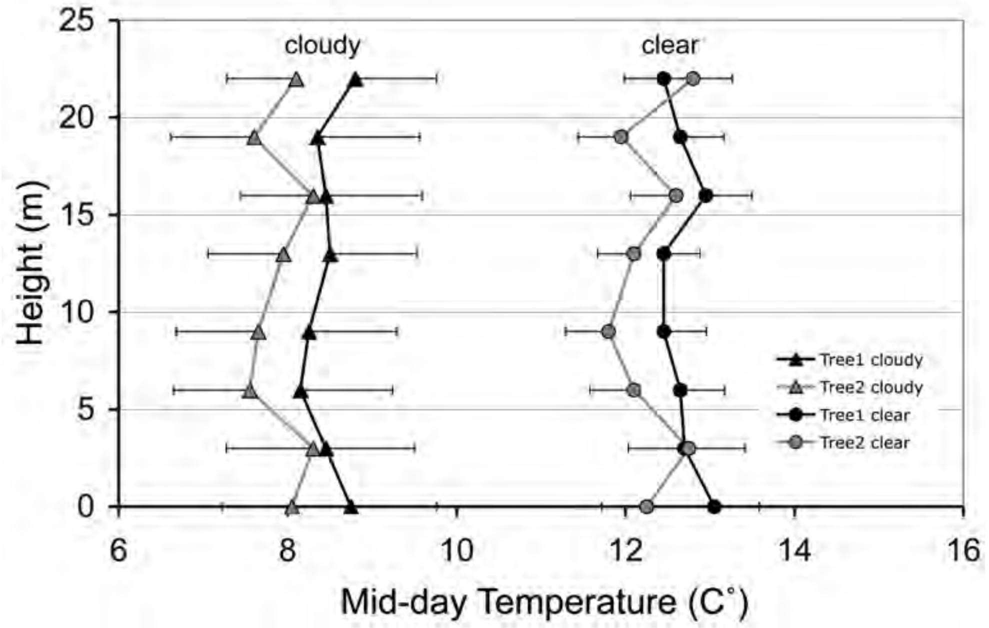

FIG 10. Vertical temperature profiles at mid-day (1200 and 1300 hrs). The temperature profiles became vertically uniform by mid-day on both cloudy and clear days, and clear days were uniformly about 4° warmer than cloudy days at all heights. Each average was calculated from 10 data points (2 hours per day over 5 days that were either cloudy or clear); error bars represent 95% C.I.

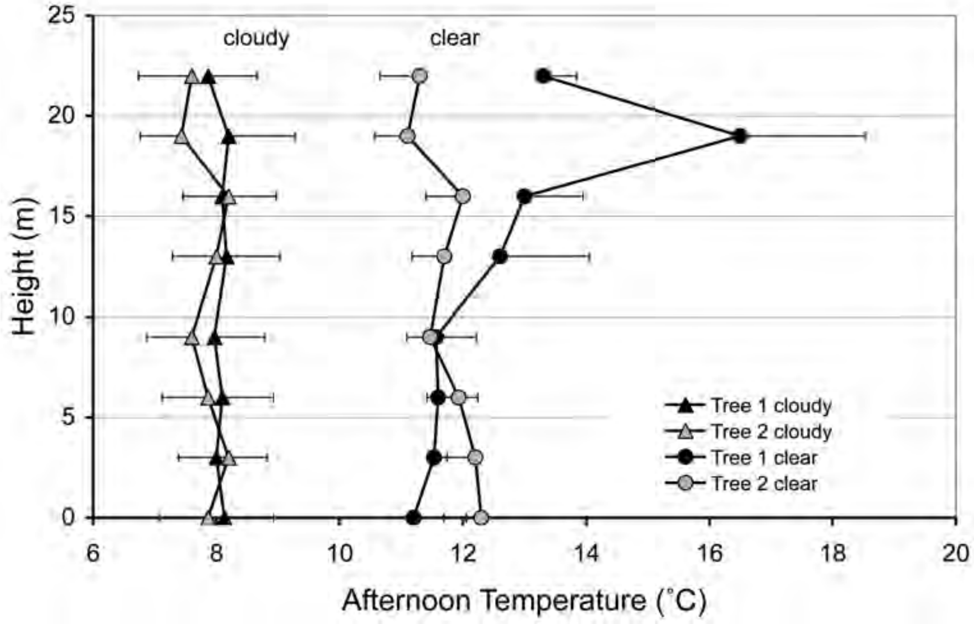

Fig. 11. Vertical temperature profiles for afternoon (1500, 1600, 1700 hr) temperatures for both transects, showing a comparison of cloudy and clear days. These afternoon temperature profiles were nearly the same as mid-day (Fig. 10) and were uniform and nearly identical for the two trees on cloudy days. On clear days, they were both about 4ºC warmer, with no vertical differences in Tree 2. The spike in temperature for Tree 1 at the 19 m level resulted from its receiving direct insolation in the late afternoon. Each average is calculated from 15 measurements (3 hours across 5 days); error bars represent 95% C.I.

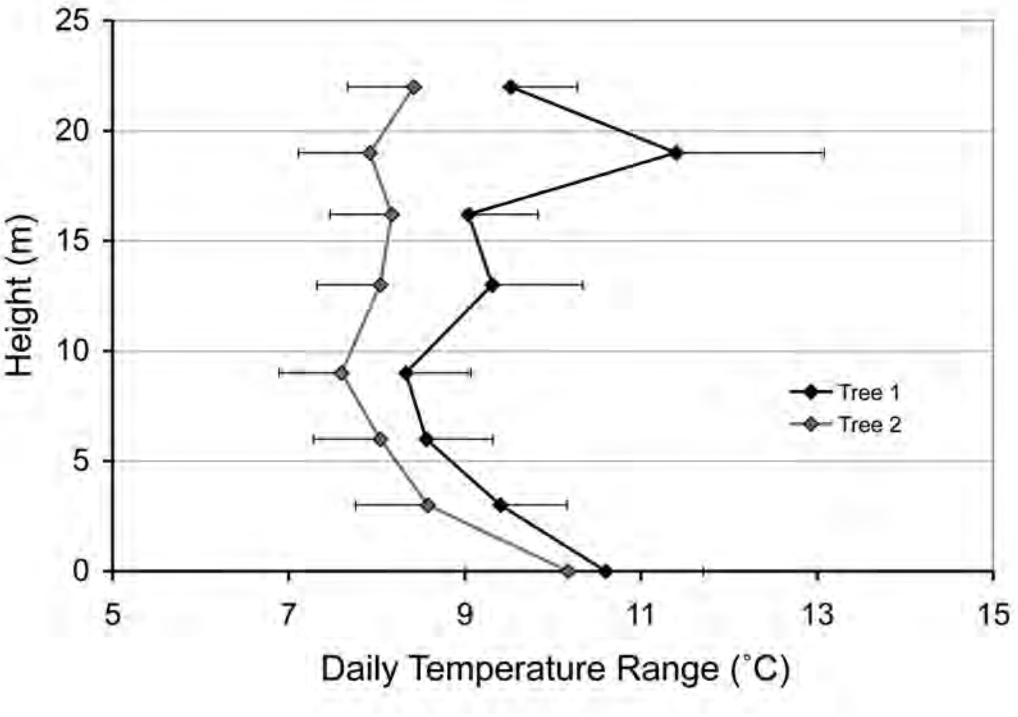

Fig. 12. The average daily range in temperatures at each height along the vertical transects of Tree 1 (black line) and Tree 2 (gray line). Tree 1, in the more open area of the forest, varies more in temperature each day than does Tree 2. The temperature spike for Tree 1 at 19 m was caused by late afternoon sunlight directly warming the Thermochron. Error bars represent 95% C.I.

during both clear and cloudy weather, the curvilinear nighttime profile (Fig. 7) becomes uniform as the day advances (Figs. 9–11), and the temperatures at all heights are about 4° warmer on clear days than on cloudy days (Figs. 9–11).

Effect of forest density. The vertical temperatures within the forest were further moderated by the extent of tree cover (Fig. 12). Each point in the graph shows the average daily range (daily maximum minus the daily minimum temperatures) for each tree at each height over the 24 days of the study. The daily range in temperature for Tree 1, in a more open part of the forest, averaged 9.6±2.7°C, whereas the daily range for Tree 2, in denser forest, averaged 8.2±2.0°C. The overall difference is significant (paired t-test, $t=9.509$, $df=183$, $p<0.001$), and the differences at each height except the ground are also significant (paired t-tests with strict Bonferroni correction [Walsh 2004], from $t=3.990$ to $t=6.633$, $df=22$, $p \leq 0.001$ for each of the seven heights above the ground; n.s. at ground level). These results illustrate that opening of the forest canopy increases the daily temperature range at all heights in the forest, a result that has conservation implications.

DISCUSSION AND CONCLUSION

Why do monarchs cluster at intermediate heights? The data presented in this paper establish that monarch butterflies form clusters on the oyamel boughs and trunks at intermediate heights beneath the forest canopy (Fig. 4) and that these heights coincide with the warmest nighttime temperatures in the forest (Fig. 7). Clustering at these slightly warmer intermediate levels during severe cold events may be critical when the temperature drops below –3°C, the temperature at which the freezing risk for wet butterflies increases dramatically (Anderson & Brower 1996). We interpret these data as indicating an adaptive behavior that reduces the probability of freezing mortality in the oyamel overwintering forests.

A behavioral response to the warmest parts of conifer forests is not unique to monarchs. For example, Wachob (1996a, b) reported that mountain chickadees seek out the warmest microclimates in a high elevation coniferous forest for nesting and foraging. The clusters may moderate their own immediate microclimate (Brower *et al*. 2008b), in part by blocking wind and reducing convection. Furthermore, there is evidence that trunk clusters attain greater thermal protection than do branch clusters (Brower *et al*. 2009).

Exceptions to the typical vertical cluster distribution have occurred after storms that dislodge millions of butterflies (Brower *et al*. 2002) and also after the clusters have been disrupted by wind or by logging. Monarch butterflies are unable to fly below a thoracic temperature of approximately 13–15°C (Masters *et al*. 1988; Alonso-Meija *et al*.1993), but they are capable of crawling when their thoracic temperatures are as low as 4°C (Alonso-Meija *et al*. 1993). The daytime temperatures we measured beneath the forest were usually high enough (Fig. 6) to enable the butterflies to crawl back up onto the tree trunks (Fig. 1) and eventually reestablish their clusters at intermediate heights (Brower & Calvert unpubl. obs.).

Opportunities for butterflies to remain quiescent or fly during the day. From morning through afternoon, on both clear and cloudy days (Figs. 9–11), the temperatures at all heights in the forest were as much as 10°C below flight threshold, except when the sun hit the highest branches (Fig. 11). Under these conditions, butterflies were able to remain quiescent and minimize consumption of their lipid reserves. In contrast, in the nearby open area (Fig. 6), the flight threshold was exceeded for four or more hours on most clear days, from at least 12:00 to 16:00.

Despite the energetic benefits of remaining cool and inactive, however, on sunny days, large numbers of butterflies leave their clusters and fly to water. We hypothesize that they must drink periodically to maintain their water balance. Although butterflies shaded by the forest cannot bask, at ambient temperatures greater than 6°C they can elevate their thoracic temperature by shivering (Alonso-Meija *et al*. 1993). When ambient temperatures are 1–3° below flight threshold, shivering butterflies can reach flight threshold (Masters *et al*. 1988). On clear days, therefore, between approximately 11:00 and 16:00, the butterflies clustering at all levels within the forest could shiver, reach flight threshold, and fly to water or perform other necessary behaviors. Those that bask in direct sunlight could rapidly raise their thoracic temperatures (Masters *et al*. 1988) and fly either back into shaded areas or engage in other active behaviors. In contrast, on many cloudy days the butterflies are not able to reach flight threshold and therefore cannot leave the colony.

Effect of canopy openings on the vertical temperature profile. Previous experiments have demonstrated that for butterflies stranded at ground level, denser forests provide greater protection against freezing than do more open forests (Calvert *et al*. 1982, 1983, 1984; Calvert & Brower 1986; Brower *et al*. 2004). Comparison of the vertical transects of Tree 1 and Tree 2 (Fig. 3A & B) demonstrates that this pattern holds true above the forest floor, as well: even a slight opening in the canopy increases the daily temperature range at all heights within the forest. During the dangerous nighttime period, the temperatures beneath the more exposed tree were colder at all heights by at least 0.5º (Fig. 7). Furthermore, the variation of the daily temperature measured at all heights was 0.5º to 4º C greater beneath the more open canopy (Fig. 12). These slight temperature differences can be critical when the ambient temperature beneath the forest canopy drops below –3ºC (Anderson & Brower 1996). More generally, our results are consistent with the findings of Chen *et al.* (1999), who determined that openings in a Douglas-fir forest (*Pseudotsuga menziesii* [Mirb.] Franco) in Washington impaired the ability of the canopy to buffer the understory radiant energy exchange.

Implications for lipid conservation. An additional challenge that confronts monarchs during the overwintering season is conserving the lipid reserves upon which they depend for their winter survival and their spring migration back into the southern U.S. breeding habitat in late March and early April (Brower *et al*. 2006). Our vertical temperature data show that the temperature beneath the forest canopy during the daytime at all heights and on both clear and cloudy days was several degrees cooler than in the nearby open area (Fig. 6). Thus, the forest canopy provides substantial moderation of temperature extremes that results in the dual benefits of freezing protection during the night and lipid conservation during the day. The uniform vertical temperature profile during the daytime indicates that the butterflies' resting height does not affect their lipid use, as long as the butterflies avoid the highest canopy layer.

Future Research. The lowest temperature recorded at a weather station in an oyamel forest area (in the Valle de Mexico) was –11ºC (Madrigal-Sánchez 1967). The lowest temperatures recorded so far in an open area in the Sierra Chincua has been –8ºC (Alonso-Meija *et al*. 1992), and inside a colony, where whole branch clusters of wetted monarchs froze in situ, the low was estimated to have been -4.4ºC (Brower *et al*. 2004). Measuring the vertical temperature distribution beneath canopies during severe cold periods is imperative. We predict that the intermediate heights beneath the closed oyamel canopy remain the safest areas within which to cluster.

Collecting data from additional vertical transects, including relative humidity as well as temperature, and extending the measurements to the tops of the oyamels, would provide a more complete understanding of how the butterflies respond to the complex vertical microclimate. We predict that the microclimate of the exposed upper canopy will resemble that of the open field area by being exposed to heavy dew and frost and by being dangerously colder at night and warmer during the day.

An important variable that we have not addressed is wind, which can substantially alter the microclimatic profile in coniferous forests (Raynor 1971; Gustavsson *et al*. 1998). Based on occasional direct field observations (Brower unpubl.) as well as the aftereffects of the January 2002 storm (Brower *et al*. 2004), there can be little doubt that forest thinning increases the negative impacts of wind, both on cluster architecture and in disrupting the vertical microclimate profile.

Following the vertical microclimate profile and relating it to colony architecture from colony formation in November through the winter and into the spring may provide an adaptive explanation of why the colonies move down arroyos in February and March (Calvert & Brower 1986). Are the butterflies tracking a shifting optimal microclimatic profile as the dry season advances?

On the south side of Cerro Pelon (located in the southernmost part of the Reserve, map in Slayback *et al*. 2007), monarchs regularly form colonies in mixed forest stands of oyamel, Mexican cedar (*Cupressus lusitanica* Miller, Cupressaceae), and smooth bark Mexican pine (*Pinus pseudostrobus* Lindl., Pinaceae). In contrast to the pines and the cedars, the oyamel branch architecture allows monarchs to form very large bag-like clusters that provide them with a temperature advantage (Brower *et al*. 2008b). We predict that the vertical temperature profiles beneath both cedars and pines will be found to provide a suboptimal microclimate compared to that beneath oyamels.

Implications for conservation of the oyamel forests. The vertical temperature profiles illustrate the three-dimensional complexity of the microclimate within the oyamel forest and add to an understanding of the importance of dense, undisturbed forest in protecting overwintering monarch butterflies. The fact that the temperature in the transect of the less dense forest was lower at night and had a wider daily range at all heights means that dense forest provides greater temperature protection during winter cold events.

Observations dating back to 1977 have led us to conclude that the oyamel fir is almost certainly the preferred tree species on which monarchs cluster (Soto-Nunez & Garcia 1993; Calvert 2004; Brower unpubl. field notes) and has likely been so since pre-historical times. This conclusion is supported by fragmentary reports of the original forests in this region (*e.g.*, Leopold 1950). Based on observations made around 1938, Loock (1950, p. 32) stated: “between the altitudes of 9,500 and 11,000 feet, there is another clearly marked zone which is occupied by *Abies religiosa*. This magnificent tree occurs in pure stands of dense forest, reaching heights of up to 150 or more feet with diameters of up to 5 or 6 feet." Such large trees in the primordial overwintering forests would have provided additional temperature buffering against freezing for the butterflies that clustered on their trunks (Brower *et al*. 2009). While we may never know what the original climax oyamel forest was like, it is instructive to consider how its original forest architecture may have affected the butterflies' clustering behavior and winter survival. One approach to this question would be to compare and contrast the three dimensional complexity and the effects of disturbances in current oyamel forests with those in old growth Douglas-fir forests in the Cascades in Washington (Spies & Franklin 1991; Ishii *et al*. 2004; Nadkarni *et al*. 2004; Parker *et al*. 2004). How might the structure of such forests, including trees of variable heights and ages and the occurrence of forest gaps, snags, and complex spacing, have provided the microclimate to which monarch butterflies originally adapted?

If the oyamel forest is the safest overwintering environment, why do the butterflies also cluster on cedars and pines? The most likely explanation is that the monarchs are returning to overwintering areas that were formerly oyamel climax forests (Soto-Nunez & Garcia 1993). The current mixed forests are almost certainly successional, resulting from repeated logging and breakaway forest fires that are ignited to clear land for agriculture (Loock 1950; Leopold 1950; Perry 1991; Snook 1993; Brower & Missrie 1998).

Firmly establishing that oyamels provide the optimal overwintering microclimate is important for managing both the core and buffer zones in the Monarch Butterfly Biosphere Reserve. Extensive illegal logging has occurred in both zones, and limited logging is allowed in the buffer zone. Reforestation policy should be based on a scientific assessment of the original stand compositions on the known overwintering massifs. It is possible that the best policy within the Reserve is to restore pure oyamel stands at higher elevations and mixed oyamel/pine/cedar forests at lower elevations.

This paper provides evidence that small openings in the forest canopy cause a lessening in the temperature buffering provided by the oyamels at mid-heights of the forest, i.e., those heights at which the butterflies form their clusters. The greatest threat to maintaining these forests as safe overwintering havens is the illegal logging that has accelerated in recent years (Ramirez *et al*. 2003, 2005; Anon. 2004, 2008; Brower *et al*. 2008a, 2009; Honey-Roses 2009a, b). The accumulating microclimatic information underscores the necessity of stopping logging and overwhelmingly supports our assertion that the key to winter survival of the butterflies is the microclimate protection provided by the intact coniferous forest canopy, principally by the oyamel fir.

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