

## Microclimatic Protection of Overwintering Monarchs Provided by Mexico's High-Elevation Oyamel Fir Forests

*A Review*

**Ernest H. Williams and Lincoln P. Brower**

Monarchs survive the winter by taking advantage of microclimatic features of the high-elevation fir forest in central Mexico. The forest canopy serves as an insulating layer that moderates temperature extremes and shields the overwintering colonies from excessive solar radiation, rain, hail, snow, and wind; in these ways, the canopy protects the butterflies from freezing and from exhaustion of their lipid reserves. Monarchs attain additional temperature and humidity benefits in their dense bough and trunk clusters. Furthermore, the warmest part of the forest is at an intermediate height above the ground, which is where monarchs form most clusters. In combination, these microclimatic features provide protection for overwintering monarchs: blanket-like thermal insulation, umbrella-like shield against precipitation, windbreak against disruptive winds, hot-water bottle-like buffering by tree trunks against thermal extremes, and a vertical location that reduces the likelihood of freezing. All these features illustrate the importance of a dense, undisturbed forest for overwintering monarchs and show that thinning the forest increases risks for their overwinter survival.

### LOCATION OF OVERWINTERING COLONIES

Images of the spectacular overwintering clusters in Mexico emphasize the extraordinary character of the monarch's migratory phenomenon (Plate 6). Each fall, monarchs from central and eastern North America leave their summer breeding range because, having evolved from tropical ancestors, they cannot survive the deep freezes of temperate-zone winters (Ackery and Vane-Wright 1984; Larsen and Lee 1994; Brower 1996a). They migrate to volcanic highlands in central Mexico where they find a narrow range of specific climatic requirements and cluster in precise locations where they benefit from microclimatic features of the surrounding forest. Microclimate refers to small-scale patterns of temperature and humidity that are affected by vegetation, solar radiation, wind direction and velocity, precipitation, evapotranspiration, and radiation (Geiger et al. 2009). The response of the butterflies to the combined effects of these

microclimate determinants is key to understanding their overwintering survival.

Monarch overwintering sites have been reported on 12 separate mountain ranges between 19° and 20° north latitude and between 100°50' and 99°40' west longitude in the Transverse Neovolcanic Belt of central Mexico. Most are found from 2900 to 3300 m elevation (Bojórquez-Tapia et al. 2003; Slayback and Brower 2007; Slayback et al. 2007). Recent aerial surveys found no other mountain ranges supporting colonies, although a small colony was reported on the western slope of Popocatepetl, just southeast of Mexico City, during the 1978–1979 (W. Calvert, pers. comm. 1979) and 2001–2002 overwintering seasons (Cevallos 2002).

It is cold at high elevations on these mountains; the lapse rate, the decline in minimum daily temperature with elevation, has been measured in the Monarch Butterfly Biosphere Reserve as  $-4.4\text{ }^{\circ}\text{C}/500\text{ m}$  (Weiss 2005). Monarch overwintering colonies form

characteristically below ridge crests, most likely to escape high-elevation winds, and near arroyos with streams or seeps (small springs) as sources to which the butterflies periodically fly to drink (Calvert and Brower 1986; Calvert et al. 1989; Bojórquez-Tapia et al. 2003). The southwesterly aspect provides more afternoon sun, enabling them to fly to water and also to re-form their clusters after being blown down by storms. Adiabatic cooling of rising air masses that have come over the Pacific Ocean provides periodic moisture to these slopes (Calvert and Brower 1986; Calvert et al. 1989). Although the mountains lie in a summer wet season fog belt, the winters are dry (Manzanilla 1974; Brower 1995), so availability of water becomes critical as the dry season advances. Steep slopes also allow cold air to drain from ridge crests down to cold pockets below, leaving the mid-slope slightly warmer (Weiss 2005).

The boreal-like forests at these elevations are dominated by the oyamel fir, *Abies religiosa*, although other species are also present, including the Mexican cypress *Cupressus lindleyi* (= *C. lusitanica*) (Earle 2011), the Mexican pine *Pinus pseudostrobus*, and some broadleaf trees, especially oaks and alders (Manzanilla 1974; Brower et al. 1977; Calvert et al. 1989). This high-altitude area is a relict ecosystem that had a wider distribution during glacial times (Manzanilla 1974; Snook 1993; Brower 1999). A diverse understory includes numerous herbaceous species, including shrubs of *Senecio* and *Eupatorium* spp., with mosses and lichens on the forest floor (Brower et al. 1977; Calvert and Brower 1986; Núñez and Garcia 1993; Snook 1993; García-Serrano et al. 2004; Cornejo-Tenorio and Ibarra-Manríquez 2008). Increased vegetation, both canopy and understory, leads to greater moderation of environmental conditions (Geiger et al. 2009). The mosaic of vegetation creates microclimatic variation by absorbing and reradiating heat energy.

Overall, monarchs encounter a protective microclimatic envelope produced by the interplay of the physical features of elevation, slope, exposure, and water, and the biological features created by the fir forest ecosystem (Brower 1996a). Temperature and precipitation are key features. The sites must be cold enough to lower the consumption of the monarchs' lipid reserves and keep them in reproductive diapause (Barker and Herman 1976; Tauber et al. 1986; James 1993), but not so cold that they freeze to death. At the same time, the surrounding environ-

ment must stay warm enough to allow butterflies to fly when needed, as when clusters are disrupted by storms, and wet enough to provide nearby drinking sources and to reduce the likelihood of fires (Brower 1985a; Calvert and Brower 1986; Brower and Missrie 1998). In the pages that follow, we examine these effects in detail. The importance of microclimate is shown by the butterflies themselves in the locations where they aggregate. We know that the colonies move downslope as spring approaches and re-form where they are partially exposed to sun and where water is available nearby (Calvert and Brower 1986), but we do not know the environmental cues that cause them to move.

## PROTECTIVE EFFECTS OF FOREST CANOPY

### Thermal insulation

The insulating effect of the forest, with temperatures moderated under the canopy, has long been emphasized (Calvert and Brower 1981; Calvert et al. 1982; Alonso-Mejía et al. 1997; Brower 1999; Geiger et al. 2009). The butterflies avoid clearings, where radiational heat loss leads to nocturnal temperatures dropping as low as  $-11^{\circ}\text{C}$  (Manzanilla 1974); instead, they aggregate under the protective canopy of dense forests (Plate 6), where the temperature rarely falls to freezing. The denser the forest, the stronger the insulating effect. By comparing forests of different densities, Calvert et al. (1982, 1984) reported that a decrease in density of 100 trees/ha correlated with a lowering of minimum temperatures by 0.37 to 0.53  $^{\circ}\text{C}$ . A similar conclusion was reached by Brower et al. (2011), who found that a thinned forest (34% open canopy) was colder on average by 0.33  $^{\circ}\text{C}$  than a denser part of the same forest (13% open canopy). Although monarchs do become somewhat cold hardened (Larsen and Lee 1994), they succumb to hard freezes, especially when wet (Anderson and Brower 1996), so protection from extreme cold is necessary.

Not only must the butterflies be protected from freezing at nighttime, but they must also remain cool enough during the day to slow the usage of their energy reserves. Stored lipids made from nectar consumed during the fall migration (Brower et al. 2006; this volume, Chapter 10) provide the butterflies with energy to maintain their basal

metabolism and allow flights to drink water during the long winter, as well as to fuel the beginning of the spring remigration. Although monarchs attempt to feed from both *Senecio* and *Eupatorium* spp. that flower at the overwintering sites, these resources are not sufficient to replenish lipid reserves prior to migration (Brower 1985a). Like all biochemical processes, the metabolic rate of monarchs depends on body temperature, and as ectotherms, whose body temperature is influenced by the surrounding environment, they burn lipids at a rate influenced by ambient temperatures. In the heat of the open sun during the day, they would use up their energy supply too quickly; estimates are that active butterflies at 25 °C would exhaust all lipids in less than 40 days of the 150-day winter (Masters et al. 1988). As Weiss (2005) noted, higher temperatures also increase water deficits by reducing relative humidity, so the butterflies would have to fly more to rehydrate, thus burning even more of their limited fuel reserves. Furthermore, reproductive diapause can be broken by high temperatures (Barker and Herman 1976; Tauber et al. 1986; James 1993), and spring migration may begin too early. These factors all point to the need to avoid excessive warmth.

In summary, a dense canopy provides thermal stability (Brower et al. 1985a; Geiger et al. 2009), with a balance of cold to reduce lipid loss and maintain reproductive torpor but with sufficient warmth to avoid freezing and allow flight to water. Thus, overwintering survival is facilitated by the blanket-like insulating capacity of the vegetative cover.

#### Shield from precipitation

A second important feature of an intact canopy is that it provides an umbrella-like cover that deflects precipitation from falling directly on the butterfly clusters (Anderson and Brower 1996). The canopy also protects the butterflies from dislodgement by snow. Butterflies wetted by rain, dew, or snow are killed at higher subfreezing temperatures than dry butterflies (Larsen and Lee 1994; Anderson and Brower 1996): 50% of wetted butterflies froze at -4.2 °C whereas 50% of dry butterflies remained alive down to -7.7 °C (Anderson and Brower 1996). Temperatures of a few degrees below zero are regularly encountered in the overwintering colonies, so shielding from precipitation is a critical protective feature of a full canopy.

#### Windbreak

The forest canopy also serves as a windbreak, lessening the frequency with which butterflies are blown off branches and onto the ground. High winds can dislodge tens of thousands of butterflies (Calvert and Brower 1986), and on the ground, they are more susceptible to wetting from dew and subsequent freezing (Brower 1999), as well as to predation by mice (Brower et al. 1985a; Glendinning et al. 1988; Glendinning and Brower 1990). When cold and stranded on the forest floor, monarchs may crawl onto the understory vegetation to escape the ground; they can crawl at 4.6 °C, shiver at 8.0 °C to elevate thoracic temperature, and fly at 13.0 °C (Alonso-Mejía et al. 1993). If blown to the forest floor into shady areas without direct insolation, they may not escape the cold zone next to the ground, where the probability of freezing is higher. Furthermore, winds can be drying and thus increase the need for drinking, which requires energetically expensive flights to find water (Brower 1999). Firs are effective windbreaks, however, and coniferous forests in general provide even more resistance to wind than do deciduous forests (Geiger et al. 2009).

### MICROCLIMATIC EFFECTS UNDER THE FOREST CANOPY

#### Bough clusters

Classic images of overwintering monarchs show conifer branches draped in dense layers of butterflies, with only a few twigs and needles apparent through a nearly continuous layer of orange and black wings (Plate 6). An immediate question is, why do monarchs cluster in such large numbers; is there an advantage to being part of dense clusters on tree boughs?

Most bough clusters are found on oyamel fir, the most abundant tree species in the high-elevation overwintering colonies, but clusters also form on smooth-bark Mexican pine and Mexican white cedar or cypress. While fir branches are needle-dense and drape in a way that may facilitate the formation of dense aggregations, we do not know if the architecture of firs actually provides the best substrate for clustering (Brower 1999). Oyamel firs appear to form the climax community at these elevations, but abundant cedars, upon which monarchs also densely

cluster, are found on the south slope of Cerro Pelón and appear to represent a fire-induced subclimax community.

Studies of microclimate inside and immediately outside bough clusters by Brower et al. (2008) showed slight microclimatic moderation for those butterflies inside each cluster. This conclusion was drawn from gently lowering dowels with attached temperature/humidity loggers (hygrochron iButtons, Maxim Integrated Products) into clusters. For each cluster, one iButton was located inside and another remained just outside the cluster. During the day, based on hourly measurements from 1200 to 1700 hours, the inside of the clusters averaged from 0.2 to 0.6 °C cooler, with relative humidity 1–2% higher than the air just outside the cluster. The difference at night was minimal, with the average of hourly temperatures inside the clusters only 0–0.2 °C warmer from midnight to 0800 hours. These measurements were taken during moderate weather, and the differentials between the inside and outside may be greater during occasional temperature drops and more extreme conditions. Whether these differences are enough to affect monarch lipid usage or survival is uncertain. Another effect is that butterflies inside and on the bottom of the bough clusters are better protected from wetting than those on the outside (Anderson and Brower 1996).

#### Trunk clusters

Monarchs cluster densely in the overwintering colonies not only on boughs but also on tree trunks, where they sometimes aggregate so tightly that the trees themselves are no longer visible (Plate 6). When clusters start forming in November, the butterflies first settle on the outer branches of the trees, but by January they have also packed onto the trunks (Calvert and Brower 1986). Trunk clusters are generally 5–15 m above the ground (Brower et al. 2011), but sometimes extend to the base of the tree, as happens after a storm when butterflies have been knocked down to the forest floor and begun to crawl back up (Brower et al. 2011). The presence of dense aggregations on tree trunks raises the question of whether roosting on trunks gives the butterflies any microclimatic advantages.

Trunks do provide protection against freezing. Calvert et al. (1983) found that following a severe 1981 winter storm in the Sierra Chincua colony,

78% of monarchs on the tree trunks remained alive, versus 56% in boughs. Brower et al. (2009) reported a similar result after a 1992 storm in the Herrada colony, with 43% survival on tree trunks and only 5% survival on boughs. Thermal buffering by living tree trunks is expected because their high heat capacity leads to slower warming up and cooling down than the surrounding air (Brower et al. 2009; Geiger et al. 2009). The difference can be seen by examining measurements of specific heat, which is the amount of heat needed to raise a unit of mass 1°C. The specific heat of a living tree, which is essentially wet wood, falls between that of dried wood at 1.2 J/g-K (Simpson and TenWolde 1999) and that of water at 4.2 J/g-K (CRC 1992). Analysis of five species of firs (Simpson and TenWolde 1999) showed that the average moisture content ranged from 25% to 49% for heartwood and 53% to 63% for sapwood. When our research team bored into trees in the Sierra Chincua colony, water squirted out of 12 of 60 oyamels, confirming how wet they are. The above data indicate that the specific heat of a living tree is at least 2.0 J/g-K, about 1000 times greater than the specific heat of an equivalent volume of air, which is 0.0013 J/cm<sup>3</sup>-K (1 g of wood is approximately 1 cm<sup>3</sup>). Thus, trunk surfaces cool and warm slowly compared with the surrounding air. The small size of insects leads to rapid heat conformity with their surroundings (Casey 1992), so those clustered on tree trunks of high thermal mass should receive significant thermal moderation through both conduction and convection.

To compare the temperature of tree trunks and the immediately surrounding air, Brower et al. (2009) placed paired iButtons on oyamel fir trunks, with one of each pair directly on the bark and the other near the first iButton but on a dowel extending 3 cm away from the trunk. The experiment was replicated in two different colonies with a total of 22 trees for at least 27 days. The results showed not only significant moderation of temperature variation by the trunks, but also that larger trunks had a greater buffering effect. At night, smaller trees (mean = 38.7 cm dbh, diameter at breast height) were 0.8–1.5 °C warmer than ambient, while larger trees (mean = 72.0 cm dbh) remained 1.1–2.2 °C warmer. During the day, smaller trees were 0.8–0.9 °C cooler than ambient, while the large trees were 1.0–2.0 °C cooler. All measurements of trunks and surrounding air were significantly different, and three of four comparisons

of smaller and larger trees yielded significant differences. As would be expected from temperature changes within masses of wet wood, larger trees provide greater microclimatic buffering. In addition, relative humidity remains higher in the surrounding air near the trunks during the day because of the cooler temperatures (Geiger et al. 2009).

The greater protection provided by larger trees raises the question of what these forests must have looked like centuries ago, before the beginning of logging. The overwintering forests currently comprise trees smaller on average than they used to be. Calvert (2004b) described the average dbh of trees in the Sierra Chincua colony in 1979 to be 31 cm, and Brower et al. (2009) reported a similar mean of 32.8 cm in 1985. In the early 2000s, Keiman and Franco (2004) measured trees from 13 plots in the Sierra Chincua, with mean dbh values ranging from 1.9 to 39.2 cm, and only 2 plots had means above 30 cm. Recently, Brower et al. (2009) chose 11 of the largest oyamel firs available for an analysis of trunk microclimate, and the largest tree had a dbh of 91.8 cm. In contrast, oyamel fir diameters of up to 2 m (and heights of 50 m) have been reported in the past (Loock 1950; Earle 2011), and one of us (LPB) has found large stumps up to 1.8 m diameter on the south face of Cerro Pelón. Furthermore, Manzanilla (1974) reported that in an old-growth oyamel fir forest west of the overwintering colonies, 15% of 331 trees had a diameter greater than 80 cm, with the largest at 2 m, and some trees were at least 272 yrs old. Logging over the years has reduced the average size of trees in the colonies, and the largest are gone completely.

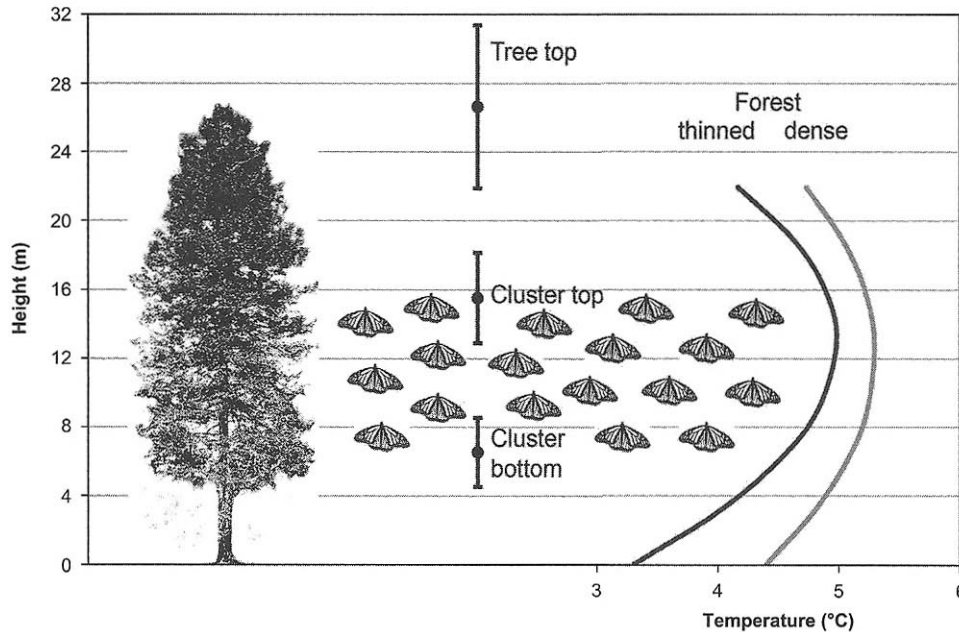
Calvert (2004b) estimated that in the Sierra Chincua colony during the winter of 1985–1986, approximately 10% of the butterflies were in trunk clusters and 90% in bough clusters. Would a higher percentage of butterflies have aggregated on trunks rather than boughs centuries ago in uncut old-growth forest with large trees? Large trunks provide more space for clustering, and the buffering of temperature changes would be greater. Compared with trees with an average diameter of 55 cm, which was the average diameter of the 22 large trees studied by Brower et al. (2009), trees of 2 m diameter would provide 3.6 times as much surface area for roosting and 13 times as much volume for thermal buffering. This increase results from changes in diameter only, but larger trees would also have been taller and pro-

vided an even more expanded surface and buffering capacity. Strong microclimatic buffering provided by the trunks of such large trees would enhance protection from large fluctuations in temperature, i.e., an increased hot-water bottle effect. We hypothesize that, in pre-Columbian forests, a higher percentage of overwintering monarchs would have been in trunk clusters than is the case currently, and the butterflies would have therefore benefited from enhanced protection against freezing as well as reduced consumption of lipid reserves.

#### Vertical profile

Whether on boughs or on trunks, most clusters occur at heights intermediate between the forest floor and the canopy (Brower et al. 1977; Keiman and Franco 2004). Measurements in 2008 of 18 bough clusters in the Sierra Chincua, where the canopy ranged from 20 to 30 m high, showed that clusters ranged in height above the ground from a lower average of  $5.9 \pm 2.5$  m to an upper average of  $15.4 \pm 2.4$  m (Brower et al. 2011). Similar height measurements had been found some years earlier for trunk clusters (Calvert and Brower 1986). This persistent pattern of clusters forming at intermediate heights is determined to some degree by the architecture of the trees but suggests that the butterflies benefit from avoiding both the ground and the canopy.

There is good reason for the butterflies to avoid the forest floor and the tree crowns. The temperature in a montane forest remains coldest near the ground, which is a deep heat sink, and dew formation is also more likely there (Geiger et al. 2009); in addition, radiational cooling in the tree crowns leads to rapid cooling at night, as well as greater exposure to wind, rain, hail, snow, and dew. Measurements through the vertical profile of the oyamel forest have shown that the nightly minimum temperature remains higher at intermediate heights than at the ground or in the canopy (Figure 9.1). The strongly curved thermal profile at night becomes uniform during the day as both air and ground surface warm (Geiger et al. 2009; Brower et al. 2011). With reduced insolation, cloudy periods produce lower daytime temperatures but higher nighttime minimum temperatures throughout the vertical profile. In all conditions, however, intermediate heights are warmer at night than those near the ground or in the canopy.



**Figure 9.1.** The relationship between nighttime vertical temperatures (right) and monarch cluster heights (center) compared with an oyamel fir 27 m tall (left). The clusters averaged from 6.4 m above the ground up to 15.5 m, more than 10 m below the canopy, with most monarchs concentrated at middle levels (black height bars show mean  $\pm$  SD). The curved lines on the right show nighttime vertical temperature profiles from the ground to 22 m on two oyamel firs, one in a thinned forest area and the other in a denser area. The midsections of the vertical profiles are about 1–2 °C warmer than both the ground and the upper canopy. Reprinted from Brower et al. 2011 by permission of The Lepidopterists' Society.

Calvert and Brower (1981) found monarchs crawling up available foliage when they had been blown or knocked to the cold ground. Butterflies caught on the ground at night are more likely to freeze, so getting onto vegetation is important; in experimental studies, those butterflies that crawled at least 30–40 cm above the forest floor escaped freezing mortality even at very low ambient temperatures (Calvert and Cohen 1983; Alonso-Mejía and Arellano-Guillermo 1992; Alonso-Mejía et al. 1997). This means that the presence of understory vegetation is a component of the complex microclimate environment to which monarchs respond. The understory remains warmer and drier than surrounding open areas, and even monarchs that do not get off the ground are better off in understory vegetation than being more exposed (Calvert et al. 1986); nevertheless, they are more subject to freezing if they remain within 1 m of the ground.

Important microclimatic differences occur across vertical transects of the forest. At the warmest height (12 m) above the ground, nighttime temperatures

were approximately 0.5 °C colder in areas where the forest had been thinned than in the denser forest, and the thinned forest was even colder at both lower and higher heights (Brower et al. 2011). The effect of forest density is also apparent in the daily variation in temperature at each height, with the denser forest providing greater buffering capacity and experiencing less variability. In all these cases, however, the best protection from freezing is found at intermediate heights beneath the canopy, and this is the height at which dense butterfly clusters form on boughs and trunks.

Although primordial forests with trees up to 60 m in height no longer exist in the Monarch Butterfly Biosphere Reserve, they would have provided an expanded zone of modified microclimate under the canopy. In the Sierra Chincua, where the majority of our research has been done, most of the oyamel trees do not exceed 30 m in height (Brower et al. 2011); among 62 trees measured during the 1984–1985 overwintering season, the maximum trunk diameter in the colony area was 65 cm, and the oldest tree was 84 years old (Brower et al. 2009). In contrast, in

mostly undisturbed forests in the states of Mexico, Morelos, and Puebla (east of Michoacán), Manzanilla (1974) determined that some oyamel were more than 140 cm in diameter, more than 61 m in height, and more than 200 years old. Manzanilla's forests were also nearly pure (323 of 327) oyamel stands. Thus, the maximum heights, diameters, and ages of the oyamels in the undisturbed forest were more than twice those in the current Chincua forests. We do not know how the primordial monarch overwintering phenomenon differed from that in the current largely degraded forests.

### Behavior

In addition to their choices of where to cluster, monarchs can respond to microclimatic conditions with thermoregulatory behaviors. When cold and stranded on the ground, they can shiver to increase thoracic temperatures enough to enable flight (Kammer 1970), but this succeeds only when they can raise their temperatures above 13 °C. When too warm in the intense sun of high elevations, monarchs may move to shade or take sun-minimizing postures (Masters et al. 1988). Another thermoregulatory behavior is that of flying up from the clusters to glide in cold air. While flight may seem energetically expensive, this behavior costs less energy than remaining flightless and overheated in a warm cluster; in flight, the thorax is warm from muscular usage, but the abdomen cools to ambient (Masters et al. 1988).

### IMPORTANCE OF FOREST QUALITY

A protective layer of dense forest serves to shield overwintering monarchs from freezing cold, excessive warmth, precipitation, and wind. Forest cover is destroyed by clear-cut logging and degraded by moderate tree thinning, forest fragmentation, and fires set to clear the land for agriculture (Manzanilla 1974; Williams et al. 2007; Ramírez et al., this volume, Chapter 13). Where the forest has been degraded, the butterflies are exposed to greater climatic variation. A thinned forest has reduced insulative capacity, allowing greater radiational cooling at night (Calvert et al. 1982; Brower et al. 2011), which leads to lower minimum temperatures. In addition, greater daytime warming, higher

wind speeds, and reduced buffering in the absence of large trees threaten microclimatic integrity. In response, the butterflies may experience increased desiccation, greater burning of stored lipids leading to starvation, insufficient fuel for spring migration, and early departure from overwintering colonies (Brower 1999; Brower et al. 2009). Partial thinning can also degrade habitat quality of a larger area because of subcanopy air circulation (Weiss 2005; Geiger et al. 2009). Additional threats to the fir forest are climate change (Oberhauser and Peterson 2003; Sáenz-Romero et al. 2012) and bark beetle and mistletoe infestations that may lead to an increase in forest thinning (Vázquez 2009).

The orientation of North American mountain ranges allows arctic air masses to dip down into Mexico (Brower 1999), bringing large winter storms that can buffet the monarch colonies and drop to lethally freezing temperatures. These weather events highlight the need for a protective canopy. Storms in 1981–1982 that penetrated the forest led to 40% mortality (Calvert et al. 1983, 1984), and an even more severe storm in January 2002 was estimated to have killed 75% of the butterflies in two colonies and upward of 500 million butterflies across the overwintering region (Brower et al. 2004). In addition to their impacts on clustering monarchs, storms lead to mudslides and soil erosion, degrading the habitat (Aridjis 2004; Brower et al. 2010). Historical records suggest that storms intense enough to kill a large percentage of butterflies—those that produce wetting and are followed by severe drops in temperature—occur about once a decade. Because the impact of these storms can be so severe, and because their impacts are exacerbated by thinned forests, it is imperative that mature forests are protected and that tree regeneration, including natural reseedling, is encouraged in degraded areas (Keiman and Franco 2004).

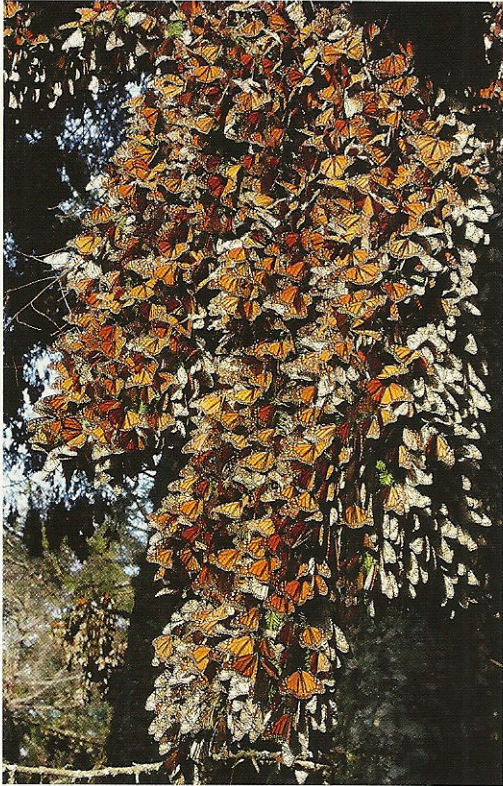
Despite the conspicuous value of the forest canopy for protecting the butterflies, degradation of the forest within the overwintering area has continued. From 1971 to 1999, 44% of conserved forest was degraded (Brower et al. 2002). Between 1999 and 2008, heavy illegal logging occurred (Simmon et al. 2008), and although the rate of illegal deforestation has decreased over the past four years (Navarrete et al. 2011; Ramírez et al., this volume, Chapter 13), salvage logging of trees downed by storms (Anon. 2011) continues to degrade the forest in the legally

protected Monarch Butterfly Biosphere Reserve (Brower, pers. observ.). In addition, rising temperatures and different precipitation patterns caused by climate change will alter the forest in ways that may severely reduce the umbrella and blanket effect of the oyamel fir forest (Allen et al. 2010; Flores-Nieves et al. 2011). The overwintering area is equal to less than 0.01% of the summer breeding area (Brower 1999), a ratio that illustrates the importance of protecting this small area of concentrated usage. Since 1995, the size of the total monarch overwintering population has declined significantly, a decline that follows both the loss and degradation of the oyamel overwintering habitat and increasing loss of breeding habitat (Brower et al. 2012a, 2012b; Pleasants and Oberhauser 2012). In our opinion, continued logging is having a devastating effect. The combined evidence from these microclimate studies indicates that an intact fir forest ecosystem is key to the survival of overwintering monarch butterflies in Mexico.

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**Plate 6.** Monarch overwintering clusters in the Sierra Chincua colony. Clockwise from top left: (a) On hanging oyamel fir branches (8 January 2007). (b) On oyamel tree trunks (5 February 2008). (c) Inside the forest (6 February 2008). Photos by Ernest Williams. (Chapter 9)