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# Moderating Night Radiative Cooling Reduces Frost Damage to *Metrosideros polymorpha* Seedlings Used for Forest Restoration in Hawaii

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## Abstract

Winter frosts caused by radiative cooling were hypothesized to limit successful reintroduction of Hawaiian plants other than *Acacia koa* to alien-dominated grasslands above 1700 m elevation. We determined, in the laboratory, the temperature at which irreversible tissue damage occurred to *Metrosideros polymorpha* leaves. We also conducted a field study of this species to determine if (1) leaf damage was correlated with sub-zero leaf temperatures, (2) radiative cooling could be moderated by canopies of *A. koa*, and (3) low soil temperatures contributed to seedling damage. The

last was evaluated by thermally buffering seedlings with water-filled bladders placed at their base to keep roots warm, or by installing a radiation shield to reduce early morning transpiration when water uptake from cold soils would be least. Leaf temperatures were monitored between midnight and 7:00 a.m. using fine-wire thermocouples, and leaf damage was recorded monthly. In the laboratory, supercooling protected leaves from mild sub-zero temperatures; irreversible tissue damage occurred at about  $-8^{\circ}\text{C}$ . In the field, leaf damage was strongly correlated with degree-hours below freezing. Unprotected seedlings suffered the greatest leaf damage. Those sheltered under *A. koa* trees rarely experienced temperatures below  $-3^{\circ}\text{C}$ , and damage was minimal. Shaded and thermally buffered seedlings suffered less damage than unprotected plants, probably due to elevated leaf temperatures rather than improved water relations. Using *A. koa* or artificial devices to reduce radiative cooling during winter nights should enhance establishment of *M. polymorpha* in high-elevation rangeland.

**Key words:** *Acacia koa*, El Niño, reforestation, frost injury, nurse tree, tropical islands.

## Introduction

Restoration of mixed-species native forest to high elevation rangeland in Hawaii is believed to be an essential step for long-term survival of several endangered forest birds, including *Hemignathus monroi* ('aki-apolau), *Oreomystis mana* (Hawaiian creeper), and *Loxops coccineus* (akepa). Over 100 years of human encroachment through logging, burning, and grazing destroyed thousands of hectares of *Acacia koa* (koa)-*Metrosideros polymorpha* ('ohi'a) and *A. koa*-*Sophora chrysophylla* (mamane) forests and resulted in conversion to savannah (Cuddihy & Stone 1990). This loss of habitat above and the pressure of avian diseases below (C. Atkinson, personal communication) have squeezed endangered and common forest birds into a narrow band of relatively intact forest habitat (Scott et al. 1986). Transmission of mosquito-borne (*Culex quinquefasciatus*) avian malaria cannot occur in this refuge habitat because temperatures are too cool, but global warming of only  $2^{\circ}\text{C}$  would allow its transmission (Tracy Benning, personal communication). Widening the band by converting grassland back to forest potentially would mitigate the adverse effect of global warming.

In a previous study, it was reported that *A. koa* seedlings planted in grasslands above 1900 m elevation on the eastern flank of Mauna Kea, Island of Hawaii, experienced moderate to severe mortality during the winter months of some years (Scowcroft & Jeffrey 1999). Sub-

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zero temperatures at these elevations were associated with strong night radiative cooling, and the greatest mortality occurred in drainages where freezing temperatures were most severe. *Metrosideros polymorpha* and *S. chrysophylla* planted in the open at the same elevation suffered nearly 100% mortality (unpublished data), and frost damage was suspected as the cause.

Frost protection devices of various designs were tested on *A. koa* seedlings during the winter of 1993–1994 (Scowcroft & Jeffrey 1999). A single layer of vertically oriented shade cloth placed on the east side of seedlings offered considerable protection from damage, increasing survival from 15% to 100%. The improvement was as good as the best frost protection device tested, the Wall-O-Water (<http://www.wallowater.com>), which encircled seedlings with an open-topped conical cylinder of water held by stacked plastic tubes. Why were both devices so effective? Although we were skeptical that the east-side shade cloth influenced night leaf temperatures, we had no difficulty believing that the Wall-O-Water would keep leaf temperatures above freezing by radiating heat stored in the water reservoir surrounding the seedling.

One explanation for the effect of the east-side frost protection device is that it prevented water stress by delaying the onset of rapid transpiration at sunrise until such time as soil and stem temperatures had warmed enough to meet transpiration demands of leaves in full sun. First year seedlings have small root systems and mycorrhizal associations have not fully developed (M. Habte, personal communications).

There are alternative explanations for the beneficial effect of east-side shading. Night radiative cooling occurs when the soil and vegetation surfaces radiate long-wave radiation to the sky. Reducing the rate of radiative heat loss by partially blocking the expanse of sky visible to a seedling moderates leaf temperatures (Groot & Carlson 1995; Teitel et al. 1996). Another explanation for the beneficial influence of shading involves damage to photosystem II caused by the interaction of freezing night temperatures and exposure to direct sunlight the next day. Lundmark and Hällgren (1987), and Örlander (1993) reported that *Picea abies* (Norway spruce) seedlings suffered significantly more damage when exposed to direct sunlight than when shaded after a night of freezing temperatures. Örlander (1993) also noted that injury can occur at warmer temperatures if seedlings are exposed to high light the day after the frost.

Under all of these scenarios, we would expect greatest seedling damage during winters with below normal rainfall, above normal proportion of sunny days, dry air masses, and frequent clear, calm nights, the latter two conditions being conducive to high radiative heat losses and lower freezing temperatures (Sakai & Larcher 1987). Such conditions typically occur in Hawaii during

El Niño years (Chu 1989). The severe El Niño of 1997–1998 provided a good opportunity to examine the relationship between freezing temperatures and survival of *M. polymorpha* seedlings.

One objective of this study was to determine under laboratory conditions the temperature at which irreversible leaf tissue damage occurs. Other objectives focused on the response of planted seedlings to sub-zero temperatures under field conditions, and included determining (1) if leaf damage is correlated with sub-zero leaf temperatures, (2) if canopies of established *A. koa* moderate radiative cooling and thus reduce seedling damage, and (3) if low-soil temperature, with its attendant low soil water and root conductivity, contributes to seedling damage.

## Materials and Methods

### Study Area

The study area is at 1840 m elevation within the U.S. Fish and Wildlife Service's Hakalau Forest National Wildlife Refuge located on the windward, northeast side of Mauna Kea, Island of Hawaii. Mean annual rainfall is about 2,000 mm and daily movement of the inversion layer frequently results in foggy, misty afternoons. Mean daily air temperature at 2 m above the surface is about 10°C. The vegetation is dominated by non-native grasses, including *Pennisetum clandestinum* (kikuyu grass), *Ehrharta stipoides* (meadow rice grass), *Anthoxanthum odoratum* (sweet vernal), and *Holcus lanatus* (velvet grass). Native forest species are scarce in the grassland.

Cattle were removed from the study area in 1987, and 11,000 *A. koa* seedlings were planted in 1989. The seedlings were planted in corridors three rows wide with about 4 m spacing between trees.

### Location and Origin of Sample Seedlings

*M. polymorpha* seedlings were obtained by transplanting wildlings from moss-covered logs located at about 1700 to 1800 m elevation in a *Metrosideros*-dominated woodland inside Hakalau Refuge. For the laboratory study, seedlings were grown for 6 months at the University of Hawaii greenhouse located at 1220 m elevation near Hawaii Volcanoes National Park. Before leaves were exposed to sub-zero temperatures, seedlings were put in a growth chamber for 1 month to acclimate them to the cool growing conditions typical of the uppermost sections of the Refuge, i.e., 15°C during the day and 5°C during the night. The light level was 600  $\mu\text{mole}/\text{m}^2 \text{ sec}$ .

For the field study, *M. polymorpha* transplants were grown for 1 year in a greenhouse located at 1980 m elevation on the Refuge. During April–May 1997, about 1,500 seedlings were planted in spots that were pre-

pared by mechanically removing a 1 × 2-m piece of sod with a miniblade mounted on a bulldozer. Some seedlings were planted within a corridor of 8-year-old, 4-m-tall *A. koa*, but most were planted in the open and up to 40 m outside and to the southeast of the corridor. Each seedling received 28 g of granular fertilizer containing 8% by weight of nitrogen, phosphorus, and potassium, which was placed in the bottom of its planting hole at time of planting.

#### Laboratory Freezing Injury

Freezing injury was determined by the electrolyte leakage technique (Wilner 1960). Eight leaves of the same age, size, and condition were selected from each of 10 seedlings. Each leaf was placed into a small plastic bag; the air was removed to avoid tissue dehydration and the bag sealed. The bags were immersed in a water-solution bath and the temperature was decreased at a rate of 10°C/hr from ambient to -13.5°C. The temperature was held constant for 15–20 minutes at 0, -2.5, -5.0, -7.5, -9.0, -10.5, -12.0, and -13.5°C. One set of bags was removed at each temperature step and allowed to equilibrate to room temperature. The leaves were then removed from the bags and placed in small scintillation vials, which were filled with 10 ml of deionized water and shaken at ambient temperature for 14 hr. Bagged reference leaves were used to determine minimum electrolyte leakage at ambient temperature and maximum leakage at -70°C. These were kept at the reference temperature for 2 hr before adding deionized water and shaking. After 14 hr the leaves were removed from the vials and the electrical conductivity of each solution was measured with a conductance meter (Yellow Springs Instruments Model 32, Yellow Springs, OH).

#### Field Sampling Design and Instrumentation

We used the following four seedling treatments: (1) open grown and without any protection, (2) open grown and shaded by a 57 × 84-cm piece of vertically oriented black, 90% shade cloth staked 30 cm east of a seedling, (3) open grown and thermally buffered by three clear plastic bags, each filled with 1.5–2 L of black-tinted water and laid flat on the soil surface concentrically around each seedling, and (4) sheltered within the corridor of *A. koa* trees. During the study, the shade treatment shielded seedlings from direct early morning sunlight for periods ranging from 1.3 hr in January to 2.8 hr in March.

Fifteen sample seedlings were selected outside of the *A. koa* corridor and five were selected inside the corridor at 1900 m elevation. Selected plants were of similar size, vigor, and topographic exposure. All vegetation within a 0.5 m radius of each sample seedling was removed to minimize the influence of herbaceous compe-

tion. Five of the 15 seedlings outside the koa corridor were randomly assigned to the open-grown treatment, 5 to the shaded, and 5 to the thermally buffered treatment. All sample seedlings were within a 0.2 ha area that faced east-northeast.

Two leaves of each sample seedling were instrumented with fine-wire (0.5106 mm diameter) copper-constantan thermocouples wired in parallel. Each thermocouple was attached with porous paper surgical tape to the underside of a fully mature leaf located on the outer surface of the crown 10–15 cm above ground. One sensor was on the east and the other on the west side of the plant. We also used shielded fine-wire thermocouples to measure air temperatures at 10 and 50 cm above ground and soil temperatures at 1 mm and 5 cm directly under each seedling. The air temperature sensors were located on the north side and within 30 cm of seedlings. We also measured daily solar radiation (LiCor model LI200S pyranometer; Li Cor, Lincoln, NE) at sample leaf height for each of the four treatments, and net radiation (Q-7.1 net radiometer; Radiation and Energy Balance System, Inc., Seattle, WA) and wind speed (model 03101-5 anemometer; R. M. Young, Traverse City, MI) in the open at 2.0 m above grass-covered ground.

Leaf, air, and soil temperature sensors were interrogated with two Campbell Scientific (Logan, UT) CR10 data loggers each connected to two multiplexers. The sampling interval for leaf sensors was 10 sec, and means were recorded every 30 sec between 0000 and 0700 hr, the time when sub-zero temperatures were most likely to occur. Air and soil sensors in the vicinity of seedlings were sampled at 30 sec intervals and means were recorded (on Campbell Scientific storage modules) every 30 minutes around the clock. The remaining sensors were sampled with a separate CR10 data logger, and means were recorded every 30 minutes around the clock.

Degree hours below 0°C were calculated as follows:

$$\text{DegreeHours} = \sum_{i=1}^{840} [T_i \times (30 / 3600)]$$

where  $T_i$  is leaf temperature below 0°C for each 30-sec measurement interval  $i$  between midnight and 0700 hr. Mean degree-hours below freezing were calculated for each day and each treatment. Freezing leaf temperatures occasionally occurred before midnight, possibly as early as 2100 hr, so our data, although adequate for comparative purposes, did not reflect total degree-hours below freezing.

#### Initial Seedling Characteristics and Damage Assessment

The sample seedlings were measured in December before and 3 days after the first frost, and approximately

monthly thereafter through March. Initial data included maximum plant height, average crown diameter, number of live shoots per plant, length of each live shoot, and number of leaves per shoot. Initial leaf area of each seedling was estimated from allometric equations relating leaf area to shoot length, which we developed from destructive harvest of shoots from non-measured seedlings. Separate equations were used for koa-sheltered seedlings ( $\ln$  leaf area =  $0.869 + 1.087 \times \ln$  shoot length;  $r^2 = 0.81$ ;  $p \leq 0.0001$ ) and those not under a koa canopy ( $\ln$  leaf area =  $0.052 + 1.326 \times \ln$  shoot length;  $r^2 = 0.90$ ;  $p \leq 0.0001$ ).

There were no significant differences in seedling characteristics among treatments at the start of the study (data not shown). Means computed using all 20 sample seedlings were as follows: height, 34.2 cm ( $\pm 8.6$  SD); crown diameter, 38.0 cm ( $\pm 7.2$  SD); number of shoots, 28 ( $\pm 13$  SD); number of leaves, 415 ( $\pm 165$  SD); total shoot length, 322 cm ( $\pm 127$  SD); and estimated leaf area, 891 cm<sup>2</sup> ( $\pm 350$  SD). Branching was highly bifurcate with second-order shoots comprising from 13 to 93% of the shoots per plant. Seedlings were still actively growing in December 1997, and one-fourth to one-third of the total shoot length and total number of leaves for each seedling were succulent new growth.

Post-frost measurements consisted of counting the number of leaves that were dead or had visible necrosis. Frost damage for each measurement was calculated by taking the ratio of number of visibly damaged leaves to the number of pre-frost leaves.

We also determined percent survival and height growth between September 3, 1997 and March 19, 1998, for the larger population of koa-sheltered, shaded, and open-grown seedlings that were scattered throughout the study area. Refuge managers had imposed these treatments as part of a separate study. Their treatments were identical to ours except that they did not use the thermally buffered treatment nor did they remove grasses and other herbaceous vegetation from around the base of seedlings. Consequently ground cover ranged from less than 5 to 100%, and several seedlings were well beneath the general height of the overtopping grasses.

## Results

### Laboratory Freezing Injury

Although there was little evidence of damage at mild sub-zero temperatures, electrolyte leakage increased sharply once *M. polymorpha* leaves were exposed to temperatures colder than  $-7.5^\circ\text{C}$  (Fig. 1). This was consistent with previous work that showed that ice nucleation occurred at about  $-6^\circ\text{C}$  (G. Goldstein, unpublished data).

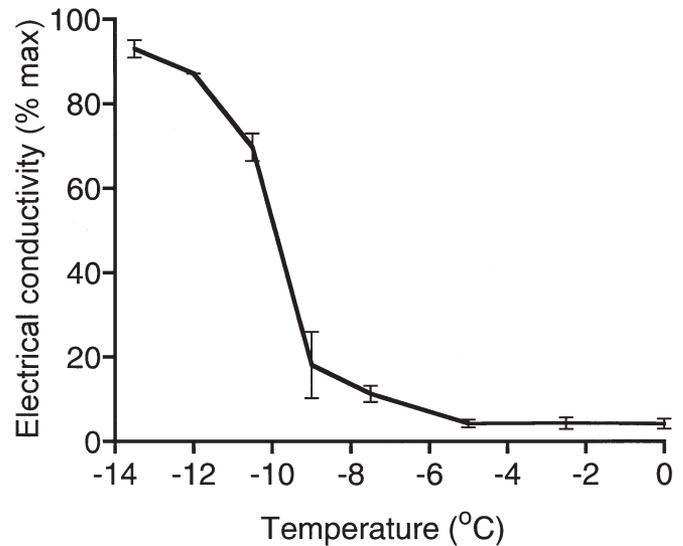


Figure 1. Electrical conductivity, as percentage of maximum conductivity, of the bathing solution resulting from electrolyte leakage of leaves of *Metrosideros polymorpha* seedlings exposed to different sub-zero temperatures in the laboratory. Seedlings were transplants from moss-covered logs in a *Metrosideros*-dominated woodland located at 1980 m elevation. Before exposure, seedlings were grown for several months under cool conditions,  $15^\circ\text{C}$  during daylight hours and  $5^\circ\text{C}$  during the night. Vertical bars denote  $\pm 1$  SEM;  $n = 10$ .

### Solar and Net Radiation

The amount of daily incoming short-wave solar radiation varied predictably among treatments (Fig. 2a). Koa-sheltered seedlings consistently received the least solar radiation, although on overcast days the differences were not as large as on clear days. Shaded seedlings received less direct sunlight than open-grown (and by implication, thermally buffered) plants because of the shade cloth on the east side, which reduced light levels for 1.3 to 2.8 hr after sunrise, depending on the time of year. Net radiation during the day (Fig. 2b) closely tracked solar radiation. The preponderance of dry air and cloudless nights during the study resulted in net radiation losses and, on some nights, losses were large enough to produce radiative frosts. Cumulative degree-hours below freezing during the night for air at 10 cm above ground were highly correlated with cumulative net radiation at night (data not shown), suggesting that the radiation balance was the main factor controlling near-ground air temperatures.

### Freezing Events

Leaf temperatures for open-grown *M. polymorpha* seedlings fell below freezing in 60 out of 90 sample nights. Shaded and thermally buffered seedlings encountered freezing temperatures 48 and 51 nights, respectively.

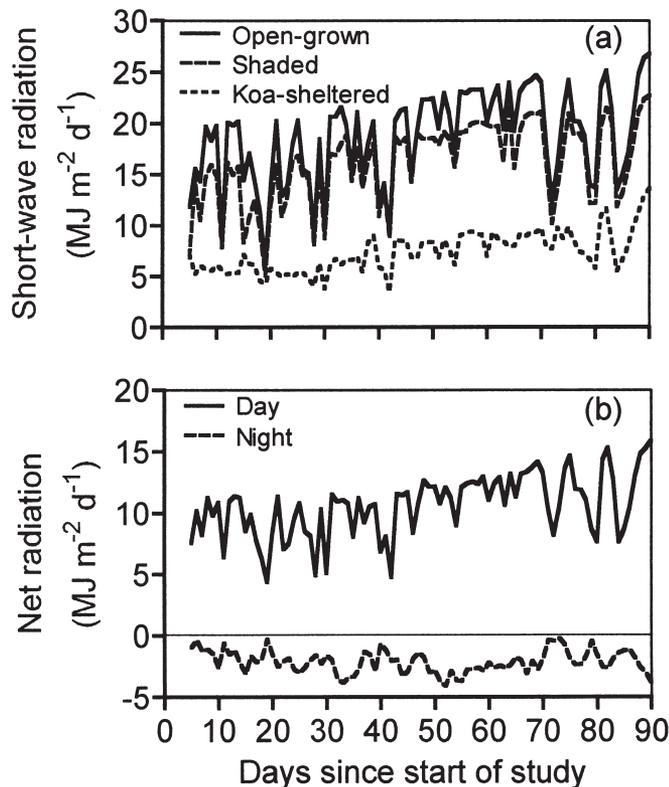


Figure 2. Variation in (a) total daily short-wave radiation at 10 cm above ground for three treatments and (b) net radiation in the open at 2 m for day and night periods over the course of the study, 12 December 1997 to 10 March 1998. Solar energy density values for the open-grown treatment were assumed to also represent those for the thermally buffered treatment.

Koa-sheltered plants experienced freezing temperatures only 19 nights.

Treatments had marked effects not only on frequency of nights with sub-zero leaf temperatures, but also on how cold it got. During cloudless periods, mean leaf temperatures were consistently coldest for the open-grown treatment, followed in order of warmer temperatures by thermally buffered, shaded, and koa-sheltered treatments. For example, the coldest night of the study occurred on 20–21 February 1998 (Fig. 3). That night, the coldest leaf temperature for open-grown seedlings was below  $-8^{\circ}\text{C}$ , whereas the coldest leaf temperature for koa-sheltered seedlings was  $-3^{\circ}\text{C}$ . The seemingly small differences in sub-zero temperature among treatments other than koa sheltering were biologically important as further analysis showed.

Degree-hours below  $0^{\circ}\text{C}$ , which combines intensity and duration of sub-zero conditions, differed among treatments. Open-grown seedlings exceeded 10 degree-hr below freezing on four separate nights (Fig. 4, vertical bars). Shaded and thermally buffered plants only had two such nights, and koa-sheltered seedlings had none.

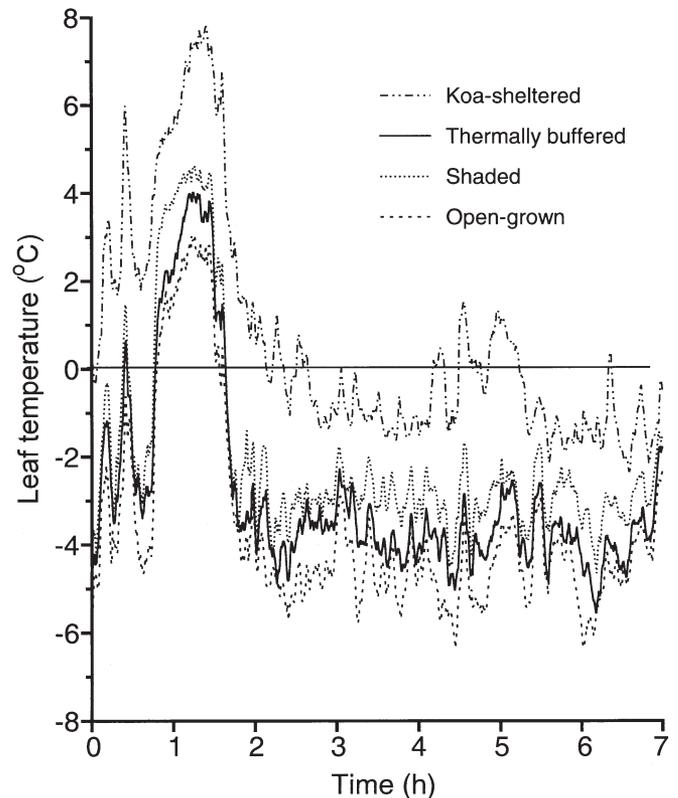


Figure 3. Mean temperature of *M. polymorpha* leaves at 10 to 15 cm above ground between midnight and 0700 hr on the night of 20–21 February 1998, the coldest night of the study, by treatment. Temperatures for all four treatments were significantly different ( $\alpha \leq 0.05$ , Bonferroni pairwise comparisons).

Cumulative degree-hours below freezing over the course of the study differed greatly among treatments (Fig. 4). After 90 days, open-grown *M. polymorpha* had accumulated almost 180 degree-hr, while thermally buffered, shaded, and koa-sheltered seedlings had accumulated 110, 85, and 10 degree-hr, respectively.

Air and soil temperatures in the immediate vicinity of seedlings were affected by treatments (data not shown). At 50 cm above ground, air temperatures among the three non-koa treatments were not significantly different ( $\alpha \leq 0.05$ , Bonferroni pairwise comparisons), but temperatures for the koa-sheltered treatment were significantly warmer (as much as  $1\text{--}2^{\circ}\text{C}$ ) than the non-koa treatments. The same pattern was observed at 10 cm above ground, although there appeared to be a slight elevation of air temperature above the water-filled bags, and temperatures were as much as  $3^{\circ}\text{C}$  warmer under koa trees.

Soil temperatures at 1 mm directly under seedling canopies differed significantly ( $\alpha \leq 0.05$ , Bonferroni pairwise comparisons) among treatments (data not shown). The open grown treatment had the coldest soil, followed

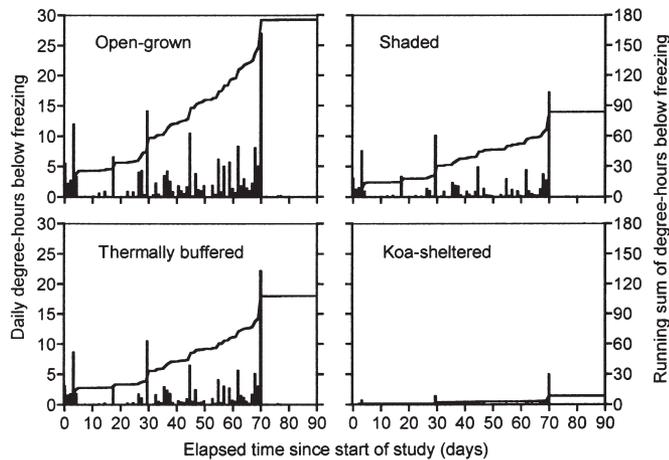


Figure 4. Daily and running sums of degree-hours below freezing between the hours of midnight and 0700 hr over the course of the study, 12 December 1997 to 10 March 1998, by treatment. Daily degree-hours below freezing for a given treatment are the average for sample seedlings in that treatment.

in order by progressively warmer soil for shaded, koa-sheltered, and thermally buffered treatments. Soil at 1 mm for the last treatment never dropped below 0°C. At 5 cm below ground, soil temperatures never fell below 6°C, and those for the thermally buffered treatment were significantly warmer (by an average of about 5°C) than the other treatments. Clearly the water-filled bags accomplished their purpose of keeping soils warm.

#### Seedling Damage

The first damaging frost occurred the night of 14–15 December 1997, just 5 days into the study, when leaf temperatures for open-grown seedlings fell to -5.2°C. Damage was light and mainly confined to open-grown individuals, including one short-stature seedling that died. Additional damage accumulated with successive frosts until, after 90 days, differences among treatments were pronounced (Fig. 5a). Open-grown *M. polymorpha* averaged 94% leaf damage, which was significantly greater than experienced by koa-sheltered seedlings (27%). Damage to shaded and thermally buffered plants was intermediate at 52% and 56%, respectively. Unfortunately, neither of these treatments could be shown to statistically differ from the open-grown or koa-sheltered treatments due to the large within-treatment variation in damage.

The degree of leaf damage over the course of the study was linearly correlated with cumulative degree-hours below freezing (Fig. 5b). Nearly 100% damage occurred after seedlings had accumulated 180 degree-hr below freezing. When data for koa-sheltered seedlings were considered separately, they appeared to diverge from the fitted regression. However, there were only

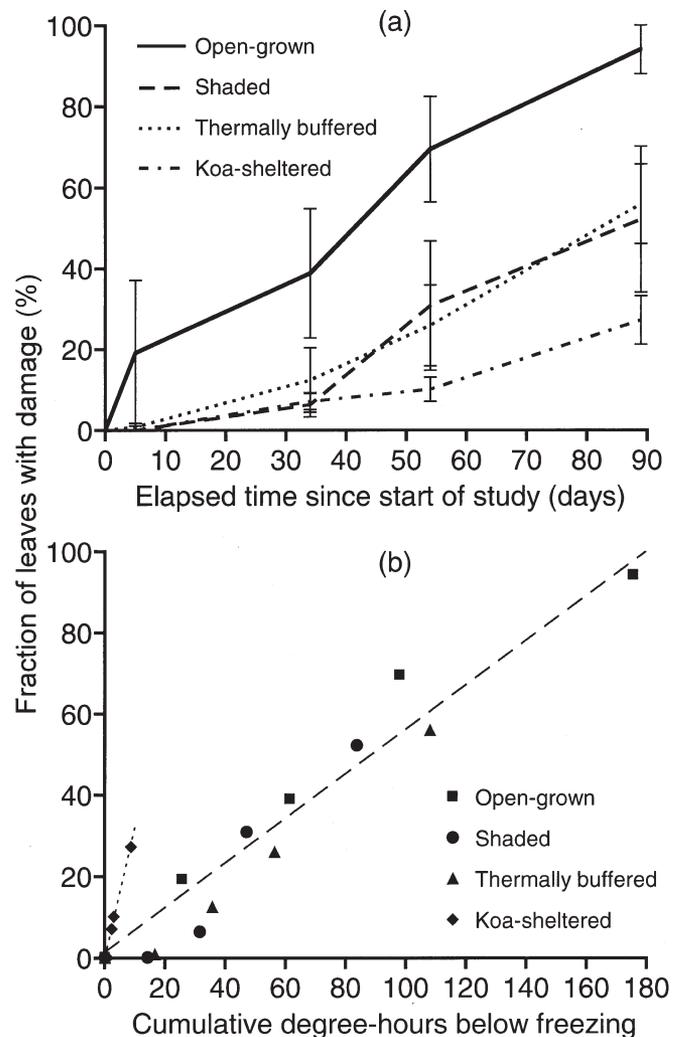


Figure 5. (a) Change in the average fraction of *M. polymorpha* leaves with visible damage over the course of study, 12 December 1997 to 10 March 1998, by treatment. Error bars are standard errors of means. (b) Relationship between cumulative degree-hours below freezing and *M. polymorpha* leaf damage. The dashed line is the least squares fitted linear regression line for all plotting points ( $r^2 = 0.90$ ). The dotted regression is for koa-sheltered data only ( $r^2 = 0.99$ ).

four non-zero plotting points for the koa-sheltered treatment, and the largest value of degree-hours below freezing for the koa-sheltered treatment was below the smallest non-zero value for all of the other treatments. So at this time, we can only speculate about whether, at low cumulative degree-hours below freezing, koa-sheltered seedlings are more susceptible to frost damage than those growing in the open.

The residual effects of frost damage on sample seedling height growth and condition were still evident midway through the 1998 growing season (Table 1). All open-grown seedlings were dead, while all seedlings in the other treatments were alive. However, only the koa-

**Table 1.** Survival and mean height growth ( $\pm$  SE) of *M. polymorpha* seedlings from 12 December 1997 to 25 August 1998, and number of seedlings in each subjective residual damage class at the end of the period, by treatment.

Treatment	Survival (%)	Height Growth (cm)	Visible Residual Damage Class		
			None	Moderate	Severe
Koa-sheltered	100	7.6 (0.5)	5	0	0
Shaded	100	10.6 (3.7)	2	2	1
Thermally buffered	100	-9.6* (7.6)	1	1	3
Open-grown	0	—	0	0	5

\*Negative growth was due to a prevalence of top dieback.

sheltered treatment showed strong height growth coupled with no visible residual damage to any seedling. Shaded seedlings also showed rapid height growth, but three of them had moderate to severe residual damage. Thermally buffered plants showed considerable residual damage, including top dieback, which resulted in negative height growth.

#### Fate of the Larger Seedling Populations

On March 19, after the last frost, 93% ( $\pm$  5% SEM,  $n = 7$ ) of koa-sheltered seedlings in the larger population were alive compared with 53% ( $\pm$  10% SEM,  $n = 9$ ) of shaded seedlings and only 7% ( $\pm$  4% SEM,  $n = 7$ ) of open-grown seedlings. Thus, although survival of the shaded seedlings in this larger population averaged only one-half of that for instrumented subset of seedlings, east-side shade cloth still appeared to offer considerable advantage over no protection. Ground vegetation had not been removed around any seedling in the larger population.

Height growth of survivors between 3 September 1997, and 19 March 1998, averaged 7.3 cm ( $\pm$  1.6 cm SEM) for koa-sheltered seedlings, and only one plant lost height due to dieback. Almost without exception, shaded seedlings experienced shoot dieback resulting in negative height growth ( $-10.6$  cm  $\pm$  2.7 SEM). Surprisingly, open-grown survivors averaged 2 cm height growth ( $\pm$  5.9 cm SEM) due to one seedling that was overtopped by tall grass and, thus, insulated from frost damage.

## Discussion

#### Laboratory Freezing Injury

Our laboratory results showed that leaves of *M. polymorpha* seedlings did not tolerate tissue freezing. Instead, they underwent transient supercooling (Melcher

et al. 2000), which allowed them to cope with mild sub-zero temperatures. However, once ice nucleation occurred at about  $-6^{\circ}\text{C}$ , leaf tissues tolerated little additional cooling without suffering irreversible damage (Fig. 1). This was consistent with our field results; for unprotected seedlings, frost damage appeared to be survivable at  $-6^{\circ}\text{C}$  but not at  $-8^{\circ}\text{C}$ . Janáček and Prášil (1991) noted that the transition between no harm to plants and death takes place over a narrow temperature interval, which can be described by a logistic S-curve.

#### Freezing Under Field Conditions

We observed large variations in leaf temperature over 30-sec intervals at night when freezing would occur (Fig. 4). These rapid changes were probably due to turbulent air mixing. In addition to rapid temperature fluctuations for individual leaves, there were large differences among plants within a given treatment. Depending on the night, leaf temperatures for plants in each of the non-koa-sheltered treatments differed by as much as  $6.5^{\circ}\text{C}$ . Temperatures for plants in the koa-sheltered treatment were slightly less variable with a maximum difference of  $4.7^{\circ}\text{C}$ . Micro-site variation in surrounding vegetation, topography, and air movement most likely accounted for the within treatment variation.

Of the three alternative explanations to account for the protective effect of east-side shade—reduced radiative cooling, reduced water stress, or reduced exposure to direct sunlight—our data support the first. Leaf temperatures during clear nights were consistently warmer in the shade treatment than in the open-grown treatment. A reduction in the amount of sky visible to seedlings with east-side shade probably accounted for the elevated temperatures. Bolstering this argument, Scowcroft and Jeffrey (1999) reported improved over-winter survival of *A. koa* seedlings when protected by west-side shade cloth, although the improvement was markedly less than achieved with east-side shade. The amount of sky visible on the west side was already reduced by terrain upslope from plants, hence the reduced benefit of west-side shade cloth.

We found no compelling evidence that maintaining a warm root environment contributed to reduced seedling damage. The warming of leaves by the thermally buffered treatment, although slight, resulted in a significant reduction in degree-hours below freezing, and that alone seemed sufficient to account for the reduced damage. Nevertheless, low soil-root temperatures on soil and root conductivity can not be ruled out as a factor contributing to low-temperature damage because we did not study treatment effects on plant water relations. Certainly cold soils keep root conductivity low (Running & Reid 1980; Lopez & Nobel 1991), and the viscosity of water in the soil layer near the surface also

increases sharply as the soil temperature approaches 0°C. Additional study is needed to clarify this issue.

Damage to photosystem II caused by the interaction between sub-zero temperatures and high light intensity the day after a freezing event, which was reported by Örlander (1993) and Lundmark and Hällgren (1987) for *Picea abies* (Norway spruce) and *Pinus sylvestris* (Scots pine), was probably not significant in our study. Damage to shaded and thermally buffered *M. polymorpha* seedlings was nearly identical. The former were shielded from direct sunlight for 1 to 3 hr after sunrise, but the latter were fully exposed during those same hours. The accumulation of degree-hours below freezing for these treatments was not substantially different; if anything, the thermally buffered plants experienced lower temperatures and longer exposure than did shaded plants. If freezing temperatures and high light intensity were interacting, the thermally buffered plants should have suffered greater damage than shaded plants. This was not the case, although by midsummer seedlings that had been thermally buffered showed more residual damage.

Clearing vegetation around sampled seedlings may have had a beneficial effect on leaf radiation balances. Litter and live ground vegetation insulate the soil surface, thereby inhibiting heat transfer from soil to the leaves of young seedlings and to the boundary air layer above the soil surface (Sakai & Larcher 1987). By removing the litter and vegetation we allowed more heat to be absorbed by the soil during the day and more to be transferred at night from the soil to leaves of seedlings. In other portions of the study area where ground vegetation was not removed, survival of shaded seedlings was reduced from 100% (sample seedlings with bare ground) to only 50%, and shoot dieback of survivors was extensive. One benefit of not removing herbaceous vegetation was its ability to insulate seedlings from sub-zero temperatures by overtopping and burying them within its own foliage, a situation that occurred for only 2 out of 105 seedlings. But this benefit is temporary; seedlings eventually have to grow above the herbaceous layer, at which time they will again be exposed to frost. Another potential benefit is that soil and root temperatures may be warmer under an insulating layer of vegetation. At this time, the importance of warm roots to preventing low temperature damage is questionable.

Sakai and Larcher (1987) noted that a forest canopy reduces thermal radiant loss and thus the freezing risk of the understory layer. Caramori et al. (1996) found that during nights with moderate to severe radiative frosts the minimum leaf temperatures of *Coffea arabica* (coffee) were 2 to 4°C higher under an overstory of *Mimosa scabrella* than in the open. Scowcroft and Jeffrey (1999) reported that air temperatures under a closed

canopy of *A. koa* were 2°C warmer than in the open. In the present study, we found warmer leaf temperatures even under a partial canopy of *A. koa* trees.

### Management Implications

Land owners and managers who want to re-establish native plants in high elevation pasture lands in Hawaii should consider using *A. koa* as a nurse tree. Not only is it endemic, it is a nitrogen-fixing species that is capable of rapid growth, which allows it to quickly dominate a site when planted in groves or corridors, and enhance soil nitrogen availability (H. Pearson, unpublished data). Within 2 or 3 years *A. koa* should be tall enough to be out of danger from frosts. If planted at a spacing of 4 to 5 m, crowns should close after 10 years resulting in reduced herbaceous competition in the understory (Scowcroft & Jeffrey 1999). The improved temperature, nutrient, and herbaceous competition regimes under this species may favor establishment of other native species.

The negative effects of closed canopy stands of *A. koa* as a nurse crop are that light levels are low in the understory (Fig. 1b in Scowcroft & Jeffrey 1999), and root competition from the trees themselves may be substantial, although growing evidence suggests that competition for nutrients may be moderated where plants share fungal symbionts (Perry 1998). Using individual trees or clumps of *A. koa* rather than closed canopy stands, and planting seedlings near, but not under, *A. koa* crowns may be ways of avoiding these negative effects while retaining the benefits.

Our data indicate that even without an overstory of *A. koa* trees, refuge managers can reduce damage and significantly improve first-year survival of *M. polymorpha* through the use of shade cloth screens placed on the east side of seedlings. On mountain slopes that do not face eastward, the shade cloth should be placed on the downhill side of seedlings to block as much night sky as possible. However, ultimate establishment may require control of grasses and other herbaceous vegetation in the immediate vicinity of seedlings for several years or until they are tall enough to be out of danger of being overtopped and buried by rapid regrowth of surrounding vegetation.

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