FREEZING TOLERANCE IMPACTS CHAPARRAL SPECIES DISTRIBUTION IN THE SANTA MONICA MOUNTAINS

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ABSTRACT: A shift in chaparral species composition occurs from coastal to inland sites of the Santa Monica Mountains of southern California. Past studies have attributed this pattern to differential adaptations of chaparral species to gradients in moisture and solar radiation. We examined an alternate hypothesis, that shifts in species composition from coastal to inland sites is a result of differential response to freezing and the interactions of freezing with drought. Coastal sites rarely experience air temperatures below 0 °C whereas just 5 to 6 km inland, cold valleys experience temperatures as low as -12 °C. Seasonal drought can last 6 to 8 months and may extend, on rare occasions, into the month of December, coincidental with the onset of winter freeze. Either water stress or freezing, by independent mechanisms, can induce embolism in stem xylem and block water transport from soil to leaves, leading to branchlet dieback or whole shoot death. Water stress in combination with freezing may enhance xylem embolism formation. Post-fire seedlings are especially vulnerable because of greater tissue sensitivity to freezing injury, diminutive roots that preclude access to deep soil moisture or resprout success, and greater exposure to nighttime radiation freezes after canopy removal by fire. *Ceanothus megacarpus*, *C. spinosus,* and *Malosma laurina* dominate the non-freezing landscape of coastal exposures, whereas *C. crassifolius* and *Rhus ovata* dominate inland cold air drainages. Because *C. spinosus* and *M. laurina* form lignotubers they can persist immediately upslope of cold valleys through vegetative resprouting after periodic freeze-induced death of shoots. Because *C. megacarpus* and *C. crassifolius* are not capable of vegetative resprouting (non-sprouters after shoot death by freezing), they are either eliminated from cold inland sites (*C. megacarpus*) or are adapted to freezing in combination with drought (*C. crassifolius*). In some cases, stems are more susceptible to freezing induced dysfunction than leaves (*R. ovata*) whereas in other species, both stems and leaves are extremely resistant to freezing-induced dysfunction, even when partially dehydrated

(*C. crassifolius*). In the case of *M. laurina*, both stems and leaves are susceptible to freezing with total shoot dieback at -6 °C. However, stunted individuals of *M. laurina* may persist at -9 °C sites in the Santa Monica Mountains through repeated resprout success. We conclude that a suite of factors, such as resprout success, the susceptibility of leaves and stem xylem to freezing injury, and the interactions of drought and freezing, contribute to the final distribution patterns of chaparral species in the Santa Monica Mountains.

KEYWORDS: Freezing, xylem, cavitation, LT_{50}, Chaparral, *Malosma, Rhus, Ceanothus*

INTRODUCTION

Chaparral is a dominant vegetation type in the Santa Monica Mountains of southern California. Differential distribution of chaparral species along elevational gradients and in response to slope, aspect, and hill-valley effects in the Santa Monica Mountains and associated Transverse Mountain Ranges has primarily been attributed to differences in moisture availability and exposure to solar radiation (Harrison et al. 1971, Nicholson 1993, Davis et al. 1999a, Meentemeyer et al. 2001, Moody and Meentemeyer 2001). Here we focus on the neglected topic of freezing air temperatures as a possible determinant of chaparral species distribution in the Santa Monica Mountains (cf. Ewers et al. 2003, Davis et al. 2005).

CHAPARRAL DISTRIBUTION AND FREEZING TEMPERATURES

Differences in daily minimum air temperatures from coastal to inland regions of the Santa Monica Mountains often exceed 10 ºC (Figure 1A). Shrub species that dominate coastal exposures (*Malosma laurina, Ceanothus megacarpus, C. spinosus*) are rare to infrequent just a few kilometers inland, especially in low-lying valleys (Figure 1B). Surprisingly, species that typically occur at higher elevations of the Transverse Mountain Ranges (e.g. *C. crassifolius, C. oliganthus, Rhus ovata*) are found in the Santa Monica Mountains to occupy lower elevations (cf. Nicholson 1993, Meentemeyer et al. 2001, Moody and Meentemeyer 2001). These same valleys experience cold air drainages and nighttime temperatures that may dip below -11 ºC (Figure 1B).

The observed temperature extremes between coastal and inland sites may impact distribution patterns of chaparral species. Figure 2 displays two photographs taken of the same interior, Northeast-facing slope of the Santa Monica Mountains on two different dates, 4 March 2003 and 29 April 2003. These two photographs correspond to the vegetation gradient diagramed in Figure 1B. Peak floral display on the upper slope in March is *C. megacarpus* (Figure 2A). Peak flowering seen on the lower slope in April is *C. crassifolius* (Figure 2B). On close inspection of Figure 2B, lavender colored flowers, restricted to upper slopes, indicate the location of *C. spinosus* (Figure 2B)*.* Why is *C. megacarpus* absent from lower elevations, where it is replaced by *C. crassifolius*, a species that typically occupies high elevations in the Transverse Mountain Range (Nicholson 1993, Meentemeyer et al. 2001)? Why is *C. spinosus*, which typically occupies moist ravines (Schlesinger et al. 1982) and low elevations, absent from the valley floor where it is replaced by what is normally higher elevational *C. oliganthus* (Nicholson 1993, Meentemeyer et al. 2001)? Why is *M. laurina* excluded from the valley floor and apparently displaced by a morphologically similar member of the Anacardiaceae family, *Rhus ovata*? One possibility is that inverted freezing gradients, due to cold air drainage, regulate this pattern (Figure 1A, B).
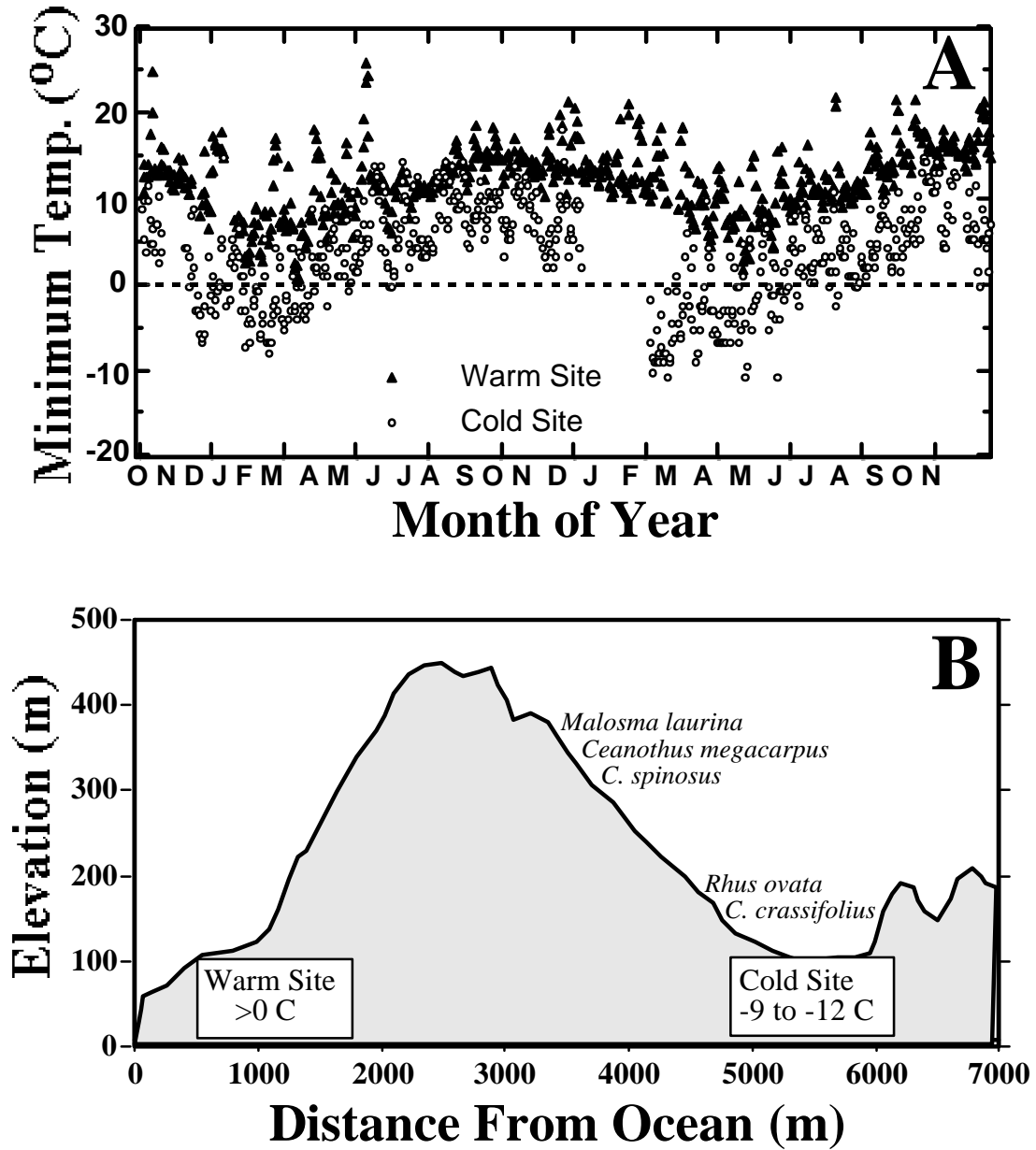
Figure 1. A) Minimum daily temperatures measured at a "Warm Site", coastal exposure, of the Santa Monica Mountains (modified from Boorse et al. 1998b). The site was located in a mixed chaparral stand on the Pepperdine University campus in Malibu at an elevation of 165 m. The "Cold Site" was located about 6 km inland, at the Malibu Forestry Unit of Los Angeles County Fire Department, just off Malibu Canyon Road, at an elevation of 195 m. **B)** Diagram illustrating approximate distance, topography, elevation, and species distribution of plants shown in Figure 2 and relative position of the warm and cold study sites (modified from Davis et al. 2005).
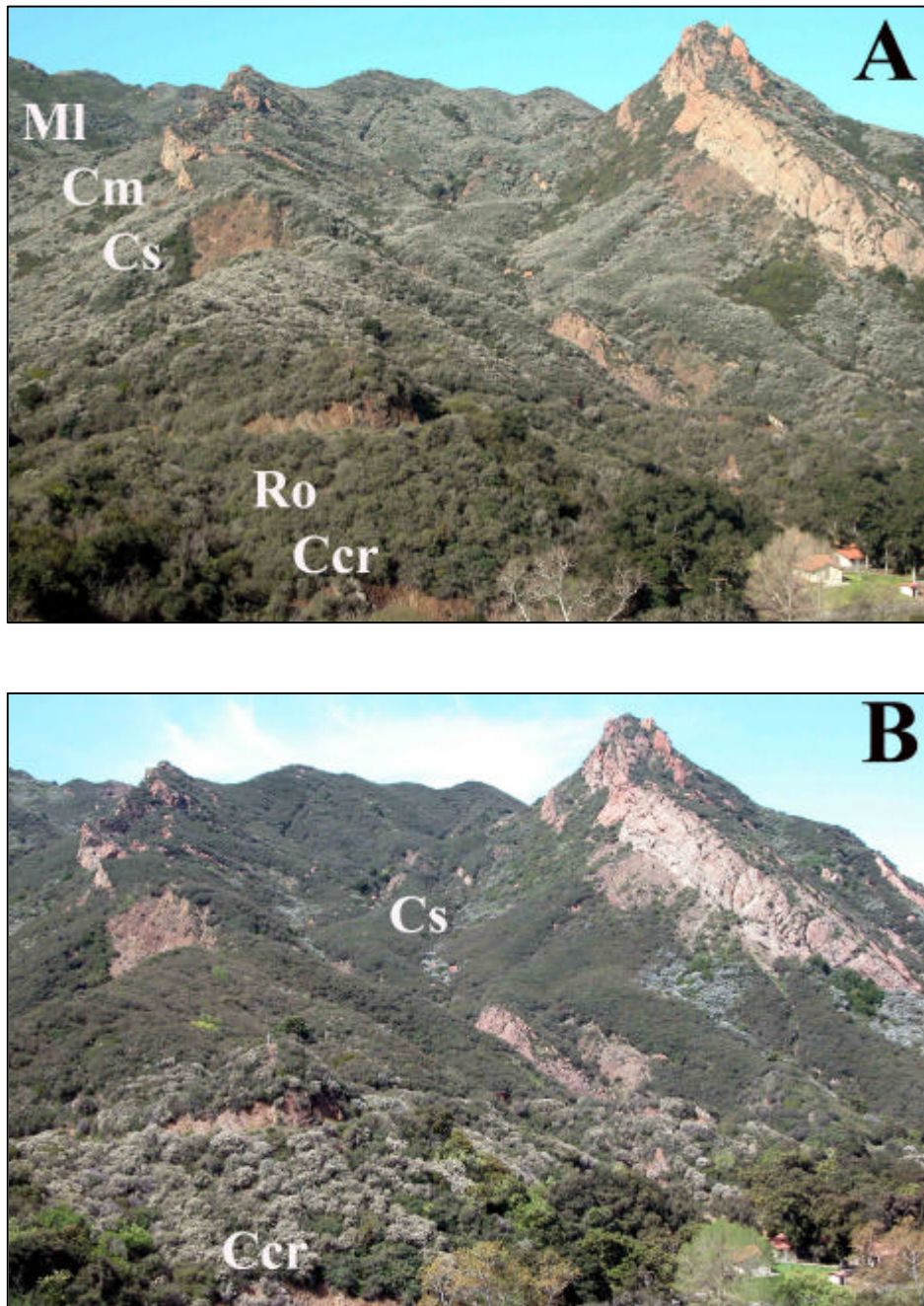
Figure 2. **A)** Photograph taken 4 March 2003 of the Northeast-facing slope of the Santa Monica Mountains, about 5 km inland from the coastline. Photograph taken from Tapia Park with the Salvation Army Camp in the foreground. *Ceanothus megacarpus* is in peak bloom on the upper slope (white inflorescence). *C. crassifolius* and *C. spinosus* are not yet in bloom. Letters stand for Ml = *Malosma laurina*, Cm = *C. megacarpus*, Cs = *C. spinosus*, Ccr = *C. crassifolius*, and Ro = *Rhus ovata*. **B)** Same photograph as in "A" above, but taken 29 April 2003. Note that *C. crassifolius* is in peak bloom on lower slopes (white inflorescence) and *C. spinosus* is in peak bloom, in moist ravines on upper slopes (lavender inflorescence).

At a finer scale than shown in Figure 1, very near the site pictured in Figure 2, we installed thermocouples, spring loaded to place them in physical contact with leaves in the upper and lower canopy of *M. laurina* and *R. ovata* and recorded daily changes in temperature between hillcrest and valley floor (Figure 3B; Langan et al. 1997). Lowest temperatures were observed just prior to dawn on calm, clear nights, consistent with the occurrence of radiation freeze and cold air drainage, and were 4 to 5 ℃ lower in the valley than on the hillcrest (Figure 3A, B). Adult *M. laurina* experienced freezing dieback, especially in upper canopy leaves, whereas *R. ovata* did not (Figure 3A, C). Adult *M. laurina* resprouted vigorously from root crowns and thus were not eliminated from the hillcrest but persisted, albeit stunted in growth (Figure 3C). This was not the case for seedlings of *M. laurina* that experienced 100% mortality after a -7 ℃-freezing event on 28 December 1997 (Figure 4). Presumably, *M. laurina* on the hillcrests produced seeds that were carried downhill into the valley by surface erosion and were promoted to germinate by the effects of wildfire in the fall of 1996 (Pratt et al. 2005). However, in the subsequent fall of 1997, newly germinated seedlings of *M. laurina* experienced increasing freezing injury to leaves as temperatures declined (estimated by dark adapted chlorophyll fluorescence, Fv/Fm; Figure 4B). Eventually, after experiencing leaf temperatures of -7.2 ℃ on Julian Day 362 (28 December), there was 100% mortality of seedlings on the valley floor (Figure 4B, C, D). Presumably, post-fire seedlings did not have sufficient time to develop root crowns to facilitate resprouting after freezing injury, which is typical for adults. Thus none of the seedlings that initially germinated on the valley floor survived (Pratt et al. 2005). Adjacent seedlings of *R. ovata* were uninjured by the -7 ℃ freezing event and unlike *M. laurina* recruited new individuals into the valley population after the wildfire of 1996 (Figure 4B; Pratt et al. 2005).

These results for the Santa Monica Mountains are consistent with previous observations on a broad geographical scale for southern California. Misquez (1990) found *M. laurina* to experience greater freezing damage when located in valley bottoms than upper slopes. She reported 95% canopy damage at valley bottoms, 72% on lower slopes, and 18% on upper slopes. She found *M. laurina* to be entirely absent from low altitude basins near Campo and Elsinor California and in the Perris Plain south of Riverside she reported that "*M. laurina* is found only on summits and flanking slopes of hills above the level of ground inversions that normally overlie the basin" (Misquez 1990, page 29). This hill versus valley displacement is also consistent with the restricted distribution of *M. laurina* to warm microsites and coastal exposures from Baja California to its northernmost extension in San Luis Obispo County, California (cf. Mooney 1977, Keil et al. 1985, Misquez 1990).

This hill versus valley displacement is somewhat paradoxical because newly germinated seedlings of *M. laurina* typically demonstrate low survivorship in response to water stress and would normally benefit from increased soil moisture in valley bottoms. In two separate studies at warm coastal sites shown in Figure 1B, we found seedling survivorship to range between 0.6 and 1.1 % during the first summer drought after wildfire (Frazer and Davis 1988, Thomas and Davis 1989). After the summer drought of 1997 at our inland cold site (Figure 1B), *M. laurina* seedlings shown in Figure 4A had a survivorship of 7.5% (unpublished data), significantly higher than typical, presumable due to greater moisture availability in the valley floor. However, by the end of December 1997, these same *M. laurina* seedlings had 0% survivorship on the valley floor because of the additive effects of freezing-induced mortality (Figure 4B). It is also paradoxical that resprout success after freezing is probably more significant for persistence than resprout success after wildfire. This is because freezing-induced dieback occurs every 3 or 4 years whereas fire events occur on average about once every 21 years (Radkte et al.1982). A third underappreciated paradox is that decreasing air temperature with elevation, based on a typical lapse rate of -5 ℃ per 1000 m (Nobel 1999) is much lower in magnitude and in the reverse
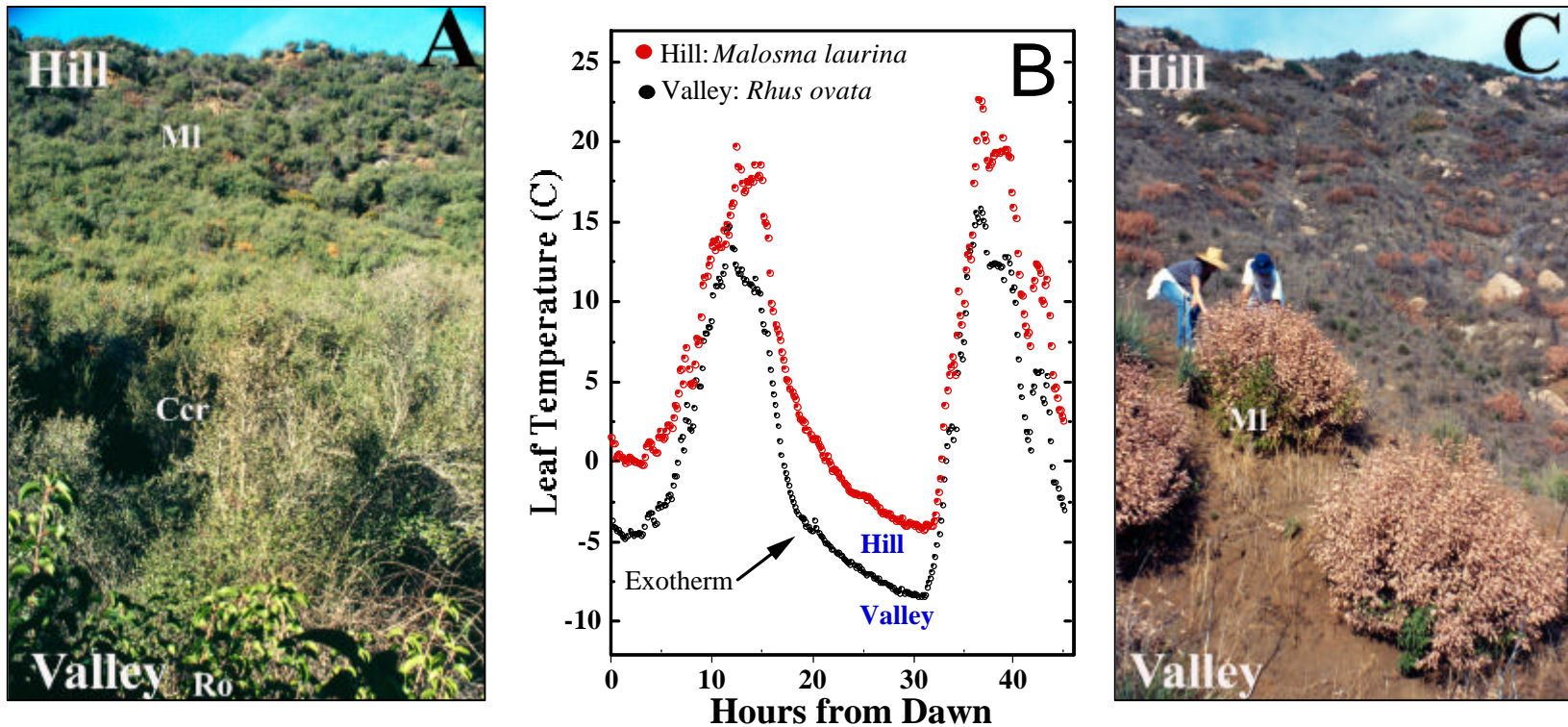
Figure 3. A) Photograph taken of "hill and valley effects" at the Malibu Forestry Unit of Los Angeles County Fire Department, just off Malibu Canyon Road, in January of 1993, about one month after a nighttime freezing event of 19 and 20 December 1992 (shown in Figure 3 B). Letters stand for Ml = *Malosma laurina*, Ccr = *C. crassifolius*, and Ro = *Rhus ovata*. Red plants near the hillcrest represent shoot dieback among *M. laurina* after the nighttime freezing event (modified from Langan et al. 1997) **B)** Thermocouples placed on leaves of *M. laurina* (hill: in red symbols) and *R. ovata* (valley: in black symbols) indicated 4 to 5 ºC lower minimum temperature in the valley. Note the exotherm that indicates freezing of plant tissues occurred in the valley at about –5 ºC but did not occur on the hillcrest. Data shown for 19 and 20 December 1992, modified from Langan et al. 1997. **C)** Hill and valley gradient at Tapia Park, adjacent the Malibu Forestry Unit shown in Figure 3A. Note stunted form of *M. laurina*, leaf dieback due to freezing, and evidence of resprout success near the base of dead shoots (Label "Ml" = *Malosma laurina*).
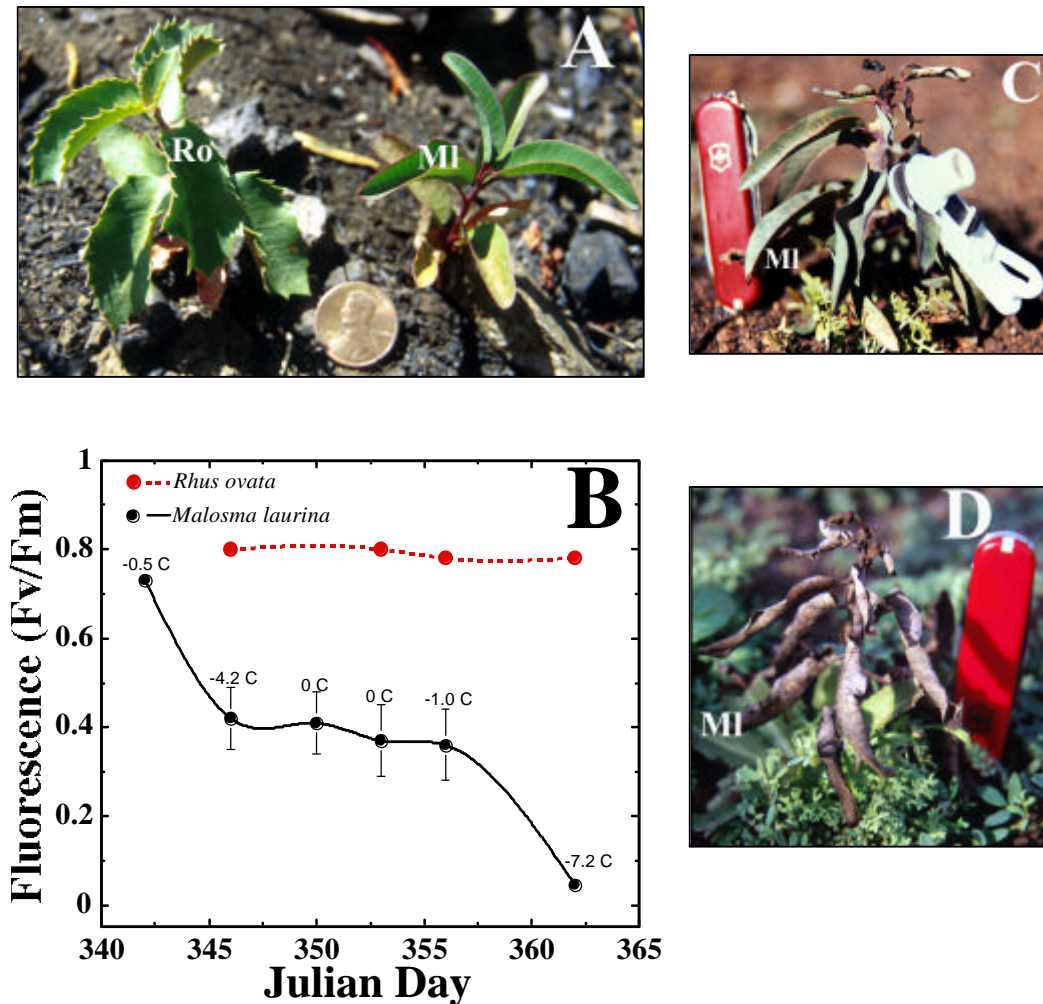
Figure 4. A) Seedlings of *Rhus ovata* (labeled Ro) and *Malosma laurina* (labeled Ml) that germinated adjacent each other, in the valley floor near Tapia Park, after the wildfire of 1996. *Malosma laurina* seedlings persisted in the valley until the first freezing event occurred in December 1997 (cf. Figure 4B). **B)** Dark adapted chlorophyll fluorescence on leaves of *Rhus ovata* and *Malosma laurina* seedlings growing in the valley floor at the Malibu Forestry Unity in late fall of 1997. Temperatures by black symbols indicate minimum leaf temperatures measured the night before each Fv/Fm determination. None of 12 *M. laurina* seedlings survived the freezing exposure of -7.2 ℃ whereas all 10 *R. ovata* seedlings survived (modified from Pratt et al. 2005). **C)** Photograph of a *M. laurina* seedling (labeled Ml) taken the day after a -4.2 ℃ freezing event showing partial injury assessed by a dark-adapted cuvette for Fv/Fm determination. **D)** Same seedling one month after a freezing event of -7.2 ℃. Like all 12 seedlings measured, the seedling shown did not resprout or survive. There was 100% mortality of seedlings in the valley floor.

direction to hill-valley temperature gradients in the Santa Monica Mountains (+5 °C per 100 m, Figure 3B). Furthermore, coastal to inland minimum temperatures, just 6 km apart, at the same elevation, may differ by as much as 12 °C in the Santa Monica Mountains (Figure 1B).

PHYSIOLOGICAL TOLERANCE TO FREEZING TEMPERATURES

To understand the physiological mechanisms driving chaparral distribution patterns in response to freezing, we employed several types of controlled laboratory experiments: 1) we assessed the lethal temperature that caused 50% mortality (LT_{50}) of leaf cells by four different methods (Boorse et al. 1998a, 1998b); 2) we used a freezing chamber to simulate freeze thaw cycles experienced by shrubs at our field sites and measured impacts on both leaves (LT_{50}) and stems (freezing-induced xylem cavitation) (Langan et al. 1997, Ewers et al. 2003, Pratt et al. 2005); and 3) we employed a freezing-centrifuge technique to separate the effects of water stress and freezing on xylem embolism (Davis et al. 1999b, Davis et al. 2005).

Consistent with field observations and chaparral distribution patterns, results of our LT_{50} experiments showed that leaves of *M. laurina* were more susceptible to freezing injury (LT_{50} -6 °C) than *C. megacarpus* (-10 °C) and *C. spinosus* (-9 °C) and dramatically more susceptible than *Rhus ovata* (-16 °C) and *C. crassifolius* (-18 °C) (Figure 5A, Boorse et al. 1998a, Boorse et al. 1998b, Ewers et al. 2003, Davis et al. 2005). Leaf level results were consistent with observed distribution patterns from coastal to inland sites (Figure 1A, B), inverted freezing gradients into cold air drainages (Figure 1B; Figure 2A, B; Figure 3A, C), and differential mortality of seedlings (Figure 4B). When leaf-freezing injury was compared between warm coastal sites and cold inland sites (Figure 6A), leaves at cold sites had lower LT_{50} suggesting ecotypic variation between coastal and inland populations (Boorse et al. 1998b). When leaf-freezing injury was compared between summer and winter, winter leaves were most resistant, indicating seasonal hardening (Figure 6B). When leaf-freezing injury was compared between seedlings and adults (Figure 6C), adult leaves were found to be more resistant (lower LT_{50}), suggesting that freezing effects on seedlings during establishment may be a primary determinant of final chaparral distribution patterns in the Santa Monica Mountains (cf. Figure 3A, 4B).

Freezing-chamber experiments on whole branches of *M. laurina* showed that stem xylem was as susceptible as leaves to freezing injury (Figure 5A, B). Freezing stems below -6 °C resulted in nearly 100% embolism, indicating total blockage of water transport to leaves. Thus both freezing injury to leaves and freezing-induced embolism of stem xylem contributed to the shoot dieback of *M. laurina* observed at field sites after freezing events (cf. Figure 3C). This was not the case for *C. megacarpus*, *C. spinosus,* and *C. crassifolius*. Under hydrated conditions, leaves were more susceptible to freezing injury (LT_{50} = -9 °C for *C. megacarpus* and *C. spinosus* and -18 °C for *C. crassifolius*) than stems (resistant to -20 °C; cf. Langan et al. 1997, Ewers et al. 2003). However, if stems were dehydrated to -5 MPa and then frozen, which is not uncommon in late fall when late seasonal drought coincides with the onset of winter freezing, *C. megacarpus* and *C. spinosus* became highly susceptible to freezing-induced embolism (Figure 5B). This was not the case for *C. crassifolius*, which remained the most resistant to freeze-induced cavitation of stem xylem in addition to having the lowest LT_{50} of leaves (Figure 5B; Davis et al. 2005). This pattern is consistent with the dominance of *C. crassifolius* in cold air drainages in the Santa Monica Mountains and its occurrence at higher elevations in the Santa Ynez and San Gabriel Mountains (Nicholson 1993, Meentemeyer et al. 2001). The only apparent inconsistency in our data comparing freezing tolerance to chaparral species distribution is for *Rhus ovata*. Although leaves of *R. ovata* tolerate temperatures well below -12 °C (LT_{50} = -16 °C; Figure 5A), stem xylem undergoes > 95% embolism after a single freezing event of -6 °C (Figure 5B; Pratt et al. 2005). How can this species flourish in cold air drainages shown in Figures 1 and 2 and displace its
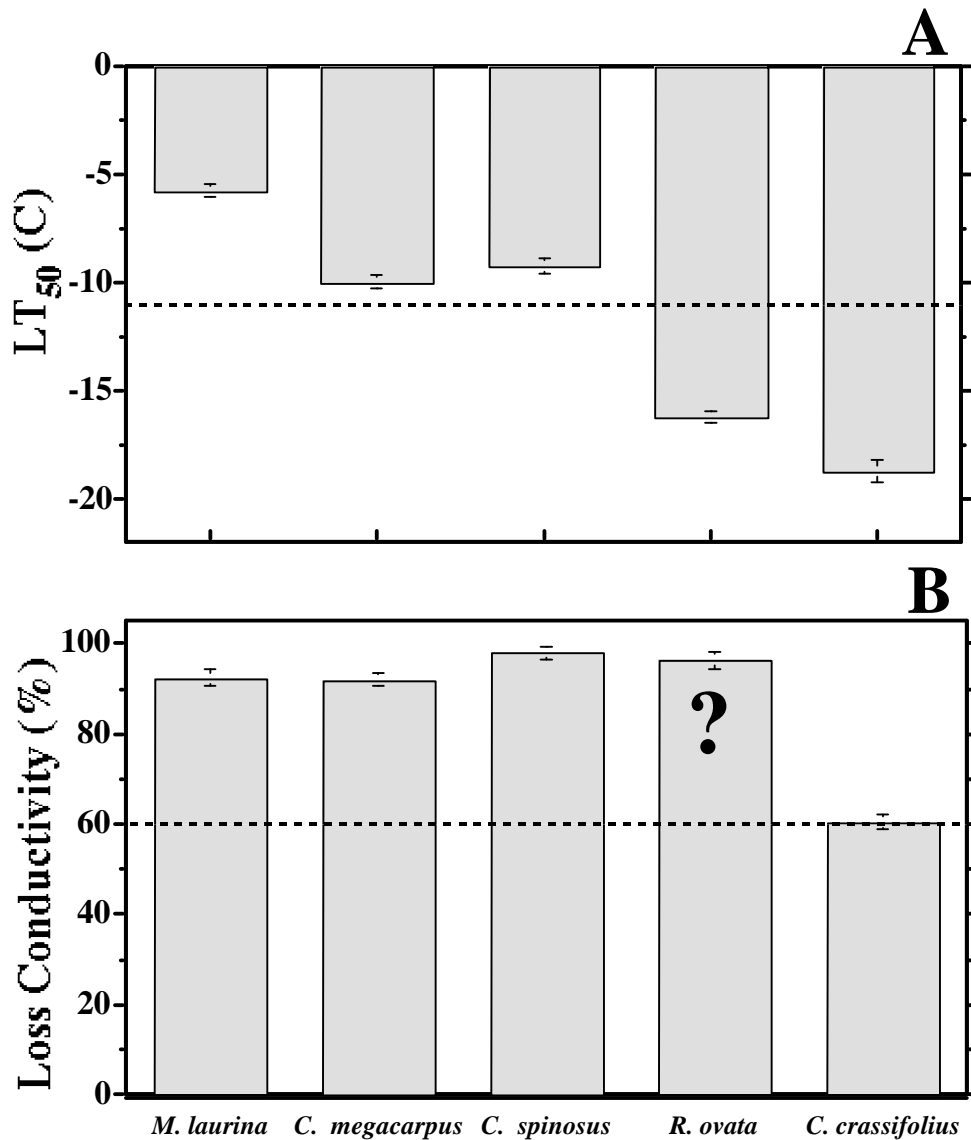
Figure 5. A) Leaf temperature at 50% cell death of leaf palisade parenchyma using fluorescein diacetate vital stain in conjunction with an epifluorescence microscope for *Malosma laurina, Ceanothus megacarpus, C. spinosus, Rhus ovata*, and *C. crassifolius*. Error bars on symbols are $\pm$ 1 SE, N = 6. As a reference, the dashed line represents -11 ºC air temperature shown in Figure 1A (adapted from Davis et al. 2005). **B)** Effect of freeze-thaw treatments on excised, > 2 m long branches, placed in a freezing chamber that simulated the freeze thaw cycle observed in the field at our cold study site (Figure 3B). To represent typical field conditions, *M. laurina* and *R. ovata* were hydrated (-0.5 MPa water potential) whereas *C. megacarpus, C. spinosus*, and *C. crassifolius* were partially dehydrated (-5.0 MPa water potential). As a reference, the dashed line shows a modest embolism level of 60% for *C. crassifolius* in comparison to all other species. The question mark indicates an apparent inconsistency in correlating physiological data to chaparral species distribution in the Santa Monica Mountains. That is, *R. ovata* occurs at cold sites but experiences high freezing-induced embolism (adapted from Davis et al. 2005).
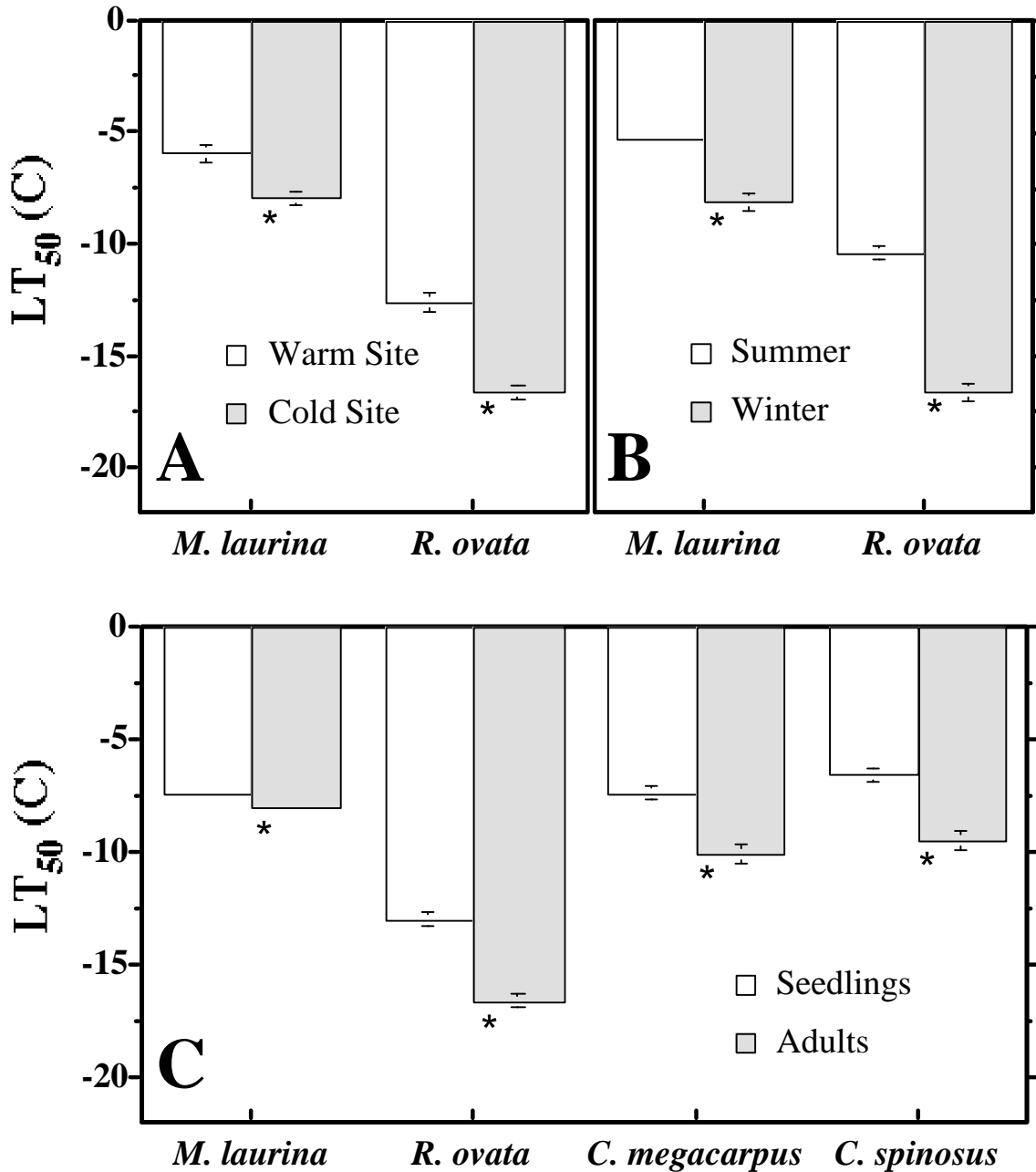
Figure 6. A) Changes in LT_{50} (leaf temperature at 50% cell death by fluorescein diacetate vital stain) between *Malosma laurina* and *Rhus ovata* adults located at our warm and cold sites shown in Figure 1B. Bars represent $\pm$ 1 SE, N = 5. Asterisks on adjacent bars represent significant difference by unpaired Student's t test at P < 0.05 (adapted from Boorse et al. 1998b). **B)** Differences in LT_{50} between *M. laurina* and *R. ovata* at our cold site during summer and winter months (adapted from Boorse et al. 1998b). **C)** Differences in LT_{50} between seedlings and adults of *M. laurina*, *R. ovata, Ceanothus megacarpus,* and *C. spinosus* in winter months (adapted from Boorse et al. 1998b).

closest relative, *M. laurina*? Is it possible that *R. ovata* experiences high embolism of stem xylem yet retains evergreen leaves because of unusually high water conservation ability? We tested this possibility by comparing water loss rates and chlorophyll fluorescence (Fv/Fm) of excised leaves of *R. ovata* to *M. laurina* in controlled environmental chambers. Consistent with our water conservation hypothesis, *R. ovata* leaves conserved water and retained fluorescence viability nearly 5-fold longer than did *M. laurina* leaves (retained Fv/Fm viability for ~5 day versus ~1 day: Figure 7A, B). Thus it appears that *R. ovata* flourishes in cold inland valleys of the Santa Monica Mountains by having leaves that are not only resistant to freezing injury (LT_{50} = -16 ºC; Figure 5A) but that are also exceptional in water conservation compared to leaves of *M. laurina* and many other species we have tested (Figure 7, data shown only for *M. laurina* and *R. ovata*). Evidently, *R. ovata* undergoes high xylem embolism at cold inland sites each winter but maintains sufficient leaf hydration to insure survival until the vascular cambium lays down new xylem in late winter and restores hydraulic supply, facilitating spring growth (Pratt et al. 2005).

CONCLUSIONS

While it is true that chaparral species distributions in the Santa Monica Mountains and associated Transverse Mountain Ranges are to some extent correlated with moisture availability, solar radiation, and fire patterns, it is likely that freezing air temperatures also play a causative role in distribution patterns. Obviously there are suites of factors during the life cycle of chaparral species that determine final habitat preference and niche segregation. The regeneration niche during seedling establishment and post-disturbance reprouting may be particularly important (Davis 1991). We have established at least one incident where 100 % freezing mortality of newly germinated seedlings precluded *M. laurina* occurrence in a cold inland valley of the Santa Monica Mountains. Once seedlings establish, on warmer hillcrests, *M. laurina* persists through vigorous resprouting, about every 21 years or so after wildfires but every three or four years after freezing events. Thus freezing events may be more crucial to persistence than wildfires at such sites. Seedlings may establish at hillcrests when post-fire germination is followed by three or more years of minimum seasonal temperatures > -6 C. We suspect that three years of growth is prerequisite for adequate root crown development and resprout success after freezing. It is unlikely that post-freezing resprout success would be possible in cold valleys where minimum temperatures are 4 to 5º C colder than hillcrests.

Based on recent predictions from climate models, it should be noted that the distribution patterns in the Santa Monica Mountains presented here might change. Global warming is predicted to have a greater impact on nighttime sky temperatures, than on maximum air temperatures or average air temperatures. Thus radiation freezes on calm, clear nights are predicted to decrease in frequency and intensity, especially in western regions of the United States (Frich et al. 2002; Meehl et al. 2004). Furthermore, global warming is predicted to promote more frequent and larger wildfires, also predominantly in western regions of the United States (Westerling et al. 2006; Running 2006). Taken together, it is probable that cold sensitive species that are also vigorous resprouters after wildfire, such as *M. laurina* and *C. spinosus,* will expand their range in the Santa Monica Mountains, in response to ongoing changes in climate for California.
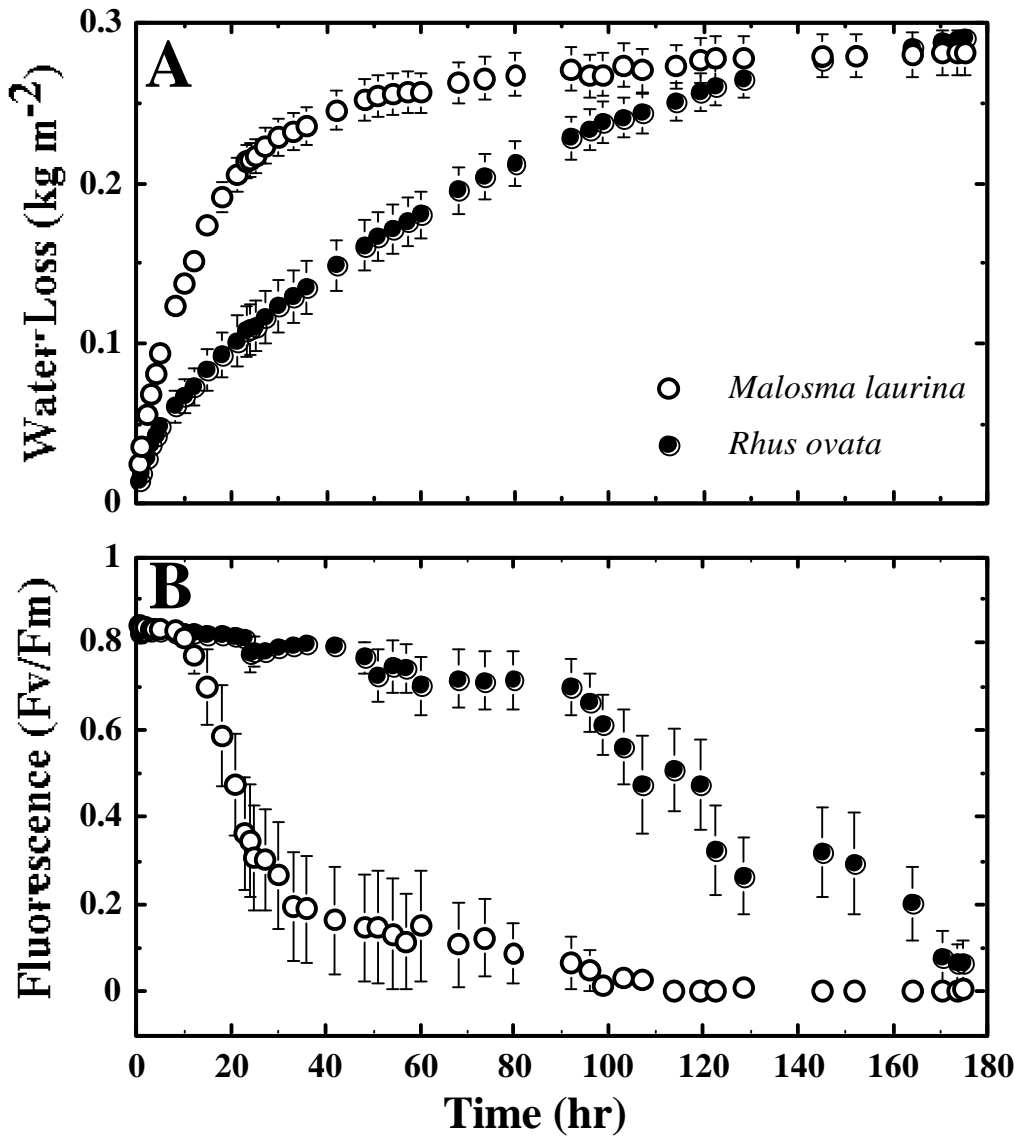
Figure 7. A) Water loss per unit leaf area and **B)** dark-adapted chlorophyll fluorescence (Fv/Fm) for *M. laurina* and *R. ovata*. Data were collected on excised leaves in which petioles were sealed with epoxy and allowed to dehydrate in growth chambers at 21.5 °C and a VPD (vapor pressure difference between the leaf and air) of 0.95 kPa for 7 days (adapted from Davis et al. 2005).

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