

Vulnerability to cavitation of central California *Arctostaphylos* (Ericaceae): a new analysis

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Received: 25 June 2012 / Accepted: 1 July 2012
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Abstract A recent study, ‘Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*: Ericaceae) in the chaparral of central California’ by M. Vasey, M.E. Loik, and V.T. Parker (2012, *Oecologia*, in press), presented data on the vulnerability to cavitation of eight *Arctostaphylos* species. We reanalyzed the vulnerability data presented in this manuscript using a different statistical model and have arrived at different conclusions than those reported previously. We suggest that regional differences have not lead to differentiation in cavitation resistance among populations of an *Arctostaphylos* species and, contrary to the conclusions of Vasey et al., the xylem of maritime species appears to be “overbuilt” for their current environment and do not appear to be especially vulnerable to water stress. Importantly, data on vulnerability to cavitation are limited for *Arctostaphylos* species from these sites. More specifically, treatment factors of site and region were not replicated and therefore conclusions drawn from these data are necessarily limited.

Keywords Cavitation resistance · Embolism · Mediterranean-type climate · Vulnerability curve · Vulnerability to xylem cavitation · Water relations

Introduction

A recent study analyzed the water relationships of *Arctostaphylos* spp. in central California. This study compared maritime species that experience summer marine fog to species that occurred inland and do not experience fog (Vasey et al. 2012). This included data collected at maritime (fog), transition (some fog), and interior sites (no fog) and among two different life history types (sprouting and non-sprouting). As part of this study, vulnerability to cavitation was measured on stems of eight species that each represents one of two different life history types: non-sprouters (also termed post-fire seeders) and post-fire sprouters (this group also seeds after fire).

Vasey et al. (2012) concluded that maritime non-sprouting species were more vulnerable to drought-induced cavitation than inland non-sprouting species and from sprouting species. These conclusions were based on a one-way ANOVA that considered each stem sample as a replicate of region and life history type and did not include species or site as treatment factors in a classic case of pseudoreplication (Hurlbert 1984).

Here, we combined previously published vulnerability curve data from Vasey et al. (2012) with previously unpublished data to reanalyze and reevaluate several of the conclusions of Vasey et al. (2012). In the present paper, we evaluated: (1) the difference in cavitation resistance and hydraulic efficiency between shrubs of the same species occurring at a maritime compared to a transition site; (2) the difference in cavitation resistance and hydraulic

Communicated by Russell Monson.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2414-9) contains supplementary material, which is available to authorized users.

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efficiency among species that occur in maritime compared to non-maritime sites; and (3) if maritime species are especially at risk of hydraulic failure.

Materials and methods

We reexamined eight species of *Arctostaphylos* from four different sites within central California. These included *A. tomentosa* and *A. pumila* (Ford Ord site; maritime), *A. crustacea*, *A. hookeri*, and *A. pajaroensis* (Pajaro Hills site; maritime), *A. crustacea* and *A. gabilaensis* (Gabilan Ranch site; transition), and *A. glandulosa* and *A. glauca* (Indians Station site; interior) (see Vasey et al. 2012 for site and species descriptions). At least one sprouting and one non-sprouting species were sampled from each site. Additionally, one sprouting species, *A. crustacea*, was sampled from two sites (one maritime and one transition). Minimum seasonal predawn water potentials were measured on ten individuals of each species per site in fall (2007) (Ψ_{\min}). Although water potential data were presented from multiple years in Vasey et al. (2012), 2007 was the only year in which water potentials were measured from all of the sites sampled for vulnerability to cavitation.

Vulnerability curve methods were described in Vasey et al. (2012) and thus are not reported in full here. Rather, here, we clarify some of the details of the vulnerability curve methods that were not fully reported. Vulnerability to xylem cavitation curves were constructed in October–December 2007. Vulnerability curves were measured for five to six stem samples per species per site following the methods described in Pratt et al. (2012). These data were used to evaluate the decline in hydraulic conductivity with increasingly negative water potentials for each species (Fig. S1). The water potential at 50 % loss in hydraulic conductivity (Ψ_{50}) was calculated for each species based on fatigue-corrected curves using an initial pressure of -0.25 MPa (Hacke et al. 2001). The maximum xylem-specific hydraulic conductivity (K_s) of each measured stem sample was also determined by dividing the maximum hydraulic conductivity (K_{\max}), following a 1-h flush, by the cross-sectional xylem area of each sample (see Jacobsen et al. 2007b for a detailed description of this method).

The Ψ_{50} and K_s of *A. crustacea* from a maritime site and a transition site were compared using the model described below. The Ψ_{\min} of *A. crustacea* from a maritime site and a transition site were compared using a *t* test (Release 16.1.0, Minitab, State College, PA, USA). For all species, species mean Ψ_{50} was plotted against Ψ_{\min} to evaluate the relative susceptibility of species from maritime, transition, and interior regions to hydraulic failure and to compare their hydraulic efficiency.

The analysis of Ψ_{50} and K_s between sites and life histories was limited by the lack of replication of life histories within sites and sites within regions. The sampling design of Vasey et al. (2012) was a hierarchical mixed model with

the fixed factor being region, and site and species as random factors. An additional fixed factor was life history type. The independent replicates for region were sites and region was not replicated ($n = 2$ sites for coast and $n = 1$ site each for transition and interior). The independent replicates for site were species, which were also not replicated for all sites ($n = 2$ species for Ford Ord, Gabilan Ranch, and Indians Station sites and $n = 3$ for Pajaro Hills). For life history type, the replicate was species and life history type was not replicated within each site ($n = 1$ for life history for each site; only one sprouting and one non-sprouting species were sampled at each site). Because of the lack of replication on many levels, we chose to pool the data and use a model that combined the data from the coastal sites into a maritime group, and we combined data from the transition and interior sites as a non-maritime group. This is further justified by examination of the data, which are not widely divergent across pooled sites for Ψ_{50} ; however, for K_s the interior site appears lower than the others so lumping transition and interior in this case is only justified to avoid pseudoreplication.

The new model included site (maritime vs. non-maritime), life history type (sprouting vs. non-sprouting), and species as a random factor nested within site and life history type. In this pooled model, we achieved $n = 5$ species for the maritime group and $n = 4$ species for the non-maritime (inland) group. We caution that, although the site treatments were lumped into maritime and non-maritime groups, sites were not replicated within a given region (only two maritime and two non-maritime sites were sampled), thus we have not analyzed regional differences. Additional limitations to the analysis of these data are discussed in the “Results”. This model included all of the vulnerability curve data that were analyzed and reported in Vasey et al. (2012) and also included K_s data which were not previously reported. Additionally, no data were previously shown for *A. crustacea* individually nor were data previously reported for any individual species. The mixed model was analyzed using a restricted maximum likelihood approach and the degrees of freedom were calculated following Kenward and Roger (1997) (JMP 9.0.0; SAS Institute, Cary, NC, USA). We did not run an interaction between site and life history type because life history type was not replicated at each site. We also acknowledge that one species, *A. crustacea*, was sampled at two sites and thus was not independent. Residuals from models were tested for normality and constant variance.

Results

Hydraulics of *A. crustacea* did not differ between a maritime and transition site. The cavitation resistance and

hydraulic efficiency of *A. crustacea* from the Pajaro Hills (maritime) and Gabilan Ranch (transition) were not different (Fig. 1). The Ψ_{50} was not different between these sites ($F_{1,47.54} = 0.04$, $P = 0.831$), nor was K_s ($F_{1,11.47} = 0.12$, $P = 0.731$). However, the Ψ_{\min} of *A. crustacea* from these two different sites was different ($T = 5.89$, $P < 0.001$, $n = 10$ per site). At the maritime site, *A. crustacea* experienced less water stress, i.e. less negative water potentials ($\Psi_{\min} = -1.03 \pm 0.06$ MPa) than the transition site ($\Psi_{\min} = -2.71 \pm 0.28$ MPa).

In an analysis that included all species, cavitation resistance was not significantly different between maritime and non-maritime species ($F_{1,5.98} = 3.90$, $P = 0.095$; Fig. 2c) nor between life history types ($F_{1,5.98} = 0.11$, $P = 0.742$; Fig. 2b). This analysis was conducted without an interaction term due to lack of replication; however, it appears that at the inland and transition sites the non-sprouters tend to be more resistant to cavitation, whereas at

the coast the non-sprouters and sprouters are more similar (Fig. 2a), i.e. there may be a life history type and site interaction that could not be evaluated.

For K_s , species from maritime and non-maritime sites were not significantly different ($F_{1,6.05} = 2.54$, $P = 0.161$; Fig. 2f) and neither were life history types ($F_{1,6.05} = 0.13$, $P = 0.730$; Fig. 2e). It appeared that species at the inland site had lower K_s than the other two sites, but this could not be analyzed statistically due to lack of replication at the inland site (Fig. 2d).

When Ψ_{50} for species and site were plotted by species Ψ_{\min} , species from the three sampled regions separated (Fig. 3). Of the three sampled regions, species from the interior region fell closest to the 1:1 line and therefore were experiencing the greatest amount of hydraulic stress (the great percentage loss in hydraulic conductivity). In contrast, species from the transition and maritime sites were relatively well hydrated for their level of cavitation resistance and had lower levels of declines in hydraulic conductivity.

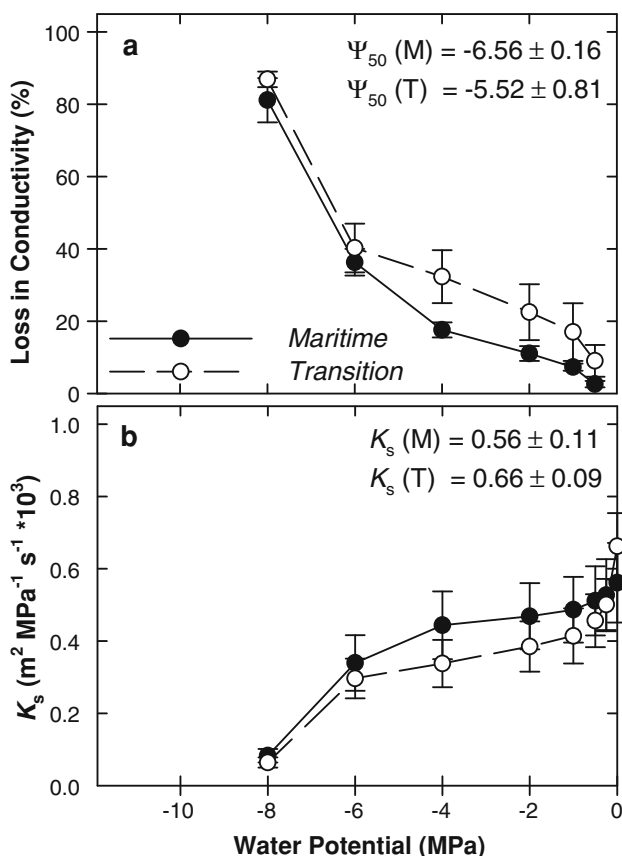


Fig. 1 Vulnerability to cavitation curves showing both the percentage loss in hydraulic conductivity (a) and the decline in xylem specific conductivity (b; K_s) for populations of *Arctostaphylos crustacea* sampled at a maritime (M, closed circles) and a transition site (T, open circles). Each point represents a mean \pm 1 SE and $n = 6$ for each population. Values shown within each panel for Ψ_{50} and K_s are means \pm 1 SE. The vulnerability curves shown in a and the Ψ_{50} values both represent fatigue-corrected data (see “Materials and methods”)

Discussion

Fog in maritime regions did not appear to have significantly impacted the hydraulics of *Arctostaphylos*. Within *A. crustacea*, the only sampled species that occurred both in a summer fog site and also in a less foggy transitional site, cavitation resistance and hydraulic efficiency were not different between maritime and non-maritime populations even though they experienced significantly different levels of water stress. This suggests that, within this *Arctostaphylos* species, differences in microclimate and marine influence did not significantly affect cavitation resistance. This conclusion was also supported by an interspecific analysis including all the sampled species; maritime species did not differ from non-maritime species in cavitation resistance or hydraulic efficiency.

Sprouting and non-sprouting *Arctostaphylos* did not vary in their cavitation resistance among the eight measured taxa. This finding contrasts from the conclusions of a different analysis of these data reported in Vasey et al. (2012). It also differs from previous studies of Mediterranean-type climate region shrubs that found that cavitation resistance varied among life history types (Jacobsen et al. 2007a; Pratt et al. 2007, 2008; however, see Pratt et al. 2012). However, it should be noted that there may be an interaction between region and life history type that could not be analyzed, and the inclusion of additional species in future studies may be required before the influence of life history type on cavitation resistance in *Arctostaphylos* can be determined.

All eight sampled species were relatively cavitation resistant, and there was less variation among species and

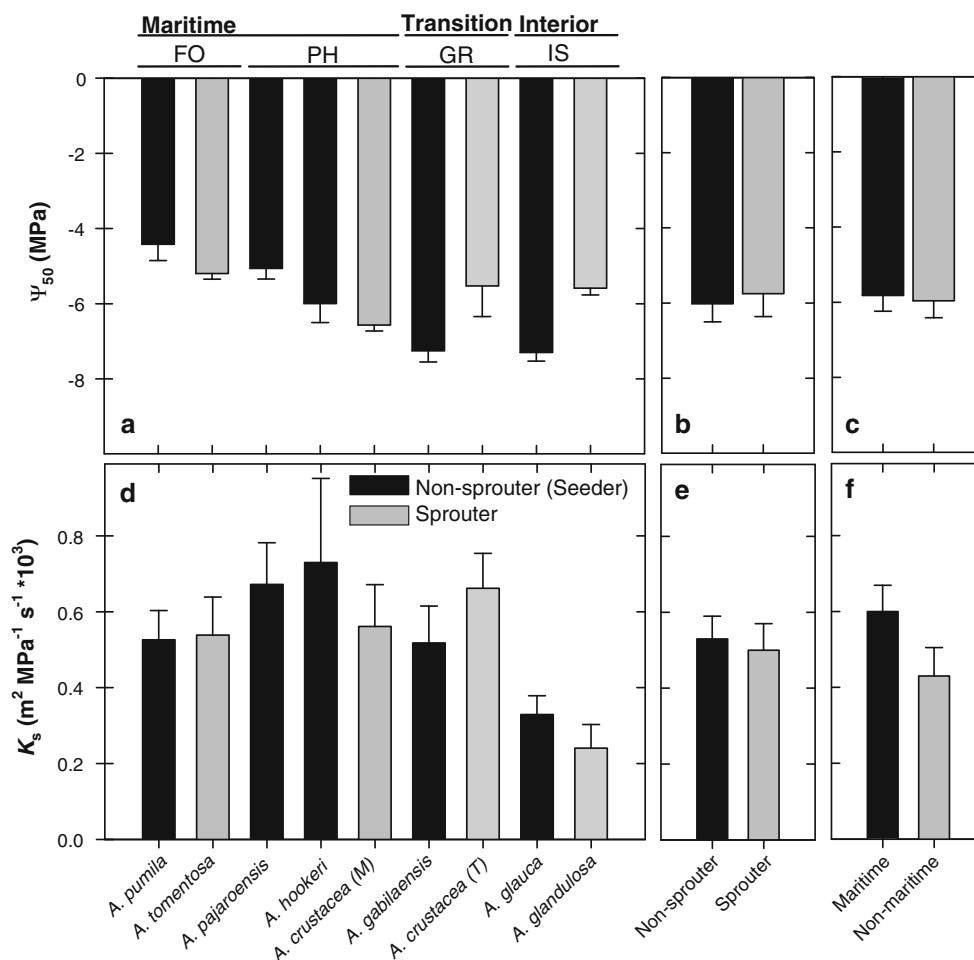


Fig. 2 Cavitation resistance (Ψ_{50}) and xylem specific hydraulic conductivity (K_s) for eight species of *Arctostaphylos* measured at four different sites (*FO*, *PH*, *GR*, and *IS*; see Vasey et al. 2012 for site descriptions) from three different regions (maritime, transition, and interior). **a** and **d** show species means \pm 1 SE. One species,

A. crustacea, was measured from two regions and data from these regions are shown as separate columns. **b** and **e** show LS means \pm 1 SE for non-sprouting and sprouting species. **c** and **f** show LS means \pm 1 SE for maritime compared to non-maritime (transition and interior pooled) species

sites than has been reported previously interspecifically at single sites among diverse chaparral shrub communities (Jacobsen et al. 2005, 2007a, b). Indeed, shrub species from some chaparral sites have varied as much as 10 MPa in Ψ_{50} , while in the present case all species varied by only 2.9 MPa. This is surprising, especially considering the widely divergent climatic conditions of the sites from which these *Arctostaphylos* species were sampled. Additionally, most species in the present study were more resistant than the median Ψ_{50} reported for Mediterranean shrubs and evergreen angiosperm shrubs globally (Maherali et al. 2004), suggesting that they generally have greater levels of cavitation resistance than other Mediterranean-type shrub species.

Although species were not highly divergent in their cavitation resistance, species had significantly different dry season water potentials (Vasey et al. 2012). This resulted in maritime and transition region species appearing to have a

greater “safety margin” in their cavitation resistance than interior species. A previous study examined the relationship between Ψ_{50} and Ψ_{min} among many chaparral species and found that most species fell along the 1:1 line (Jacobsen et al. 2007a), suggesting that maritime and transition species are more “over built” than most southern California chaparral shrub species. This suggests that maritime species may be able to tolerate some future drying, at least with respect to their stem vascular function. Additionally, a previous study found that, during an extreme drought year, it was the species that already had low water potentials in normal years that experienced the greatest increase in the water stress with extreme drought (Jacobsen et al. 2007a). This may not offer a direct comparison to the present study because the loss of marine fog has the potential to rapidly alter summer conditions, but suggests that the species with the greatest likelihood of increased water stress are the interior species.

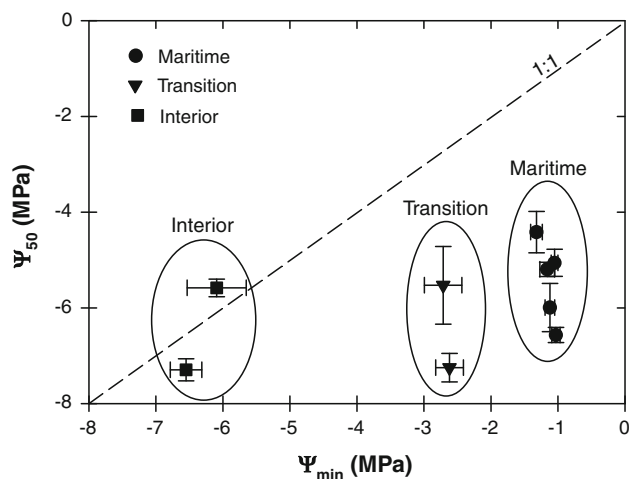


Fig. 3 Cavitation resistance (Ψ_{50}) plotted against minimum seasonal water potential (Ψ_{\min}) for 8 species of *Arctostaphylos* from three different regions (maritime, transition, and interior). The dashed line represents the 1:1 line. Each point represents a species mean \pm 1 SE

It is interesting to consider why these *Arctostaphylos* spp. are not more divergent in their cavitation resistance, and there are a number of competing hypotheses that may be relevant. It may be that cavitation resistance is conserved within *Arctostaphylos*. Cavitation resistance has been shown to be labile in some lineages, with cavitation resistance varying between ecotypes and populations (Mencuccini and Comstock 1997; Sparks and Black 1999; Kolb and Sperry 1999b). Cavitation resistance has also been shown to be plastic seasonally (Kolb and Sperry 1999a; Jacobsen et al. 2007b), and when plants were experimentally exposed to water deficit (Fichot et al. 2010). However, other lineages have been described as being relatively conserved in their cavitation resistance, both within (Lamy et al. 2011) and between species (Hao et al. 2008; Wilson et al. 2008). Alternatively, cavitation resistance has been shown to predict chaparral seedling survival (Pratt et al. 2008), and convergence in cavitation resistance may result from selection at the seedling stage when rooting depth is limited and plants experience very low water potentials and high mortality (Frazer and Davis 1988; Thomas and Davis 1989; Williams et al. 1997). Adult cavitation resistance could also be affected by selection to survive episodic drought (Pockman and Sperry 2000).

In summary, using the same vulnerability curve data as analyzed in Vasey et al. (2012), as well as previously unpublished data, we do not find support for several of the conclusions of Vasey et al. (2012). Region apparently did not influence the hydraulics of the single species for which there were data from multiple regions. Non-sprouting and sprouting species did not appear to vary in their hydraulics even though they vary in their seasonal water stress (Vasey

et al. 2012). And, based on their vulnerability to cavitation and level of water stress they experience, maritime species appear to be relatively buffered against hydraulic failure.

The ecology and water relations of diverse *Arctostaphylos* spp. are intriguing and deserve further study. Although we have commented here on the analysis of cavitation resistance in Vasey et al. (2012), many of their other conclusions are based on a range of data from more species and sites than the data which we have discussed. Future research will likely clarify many of the outstanding questions that cannot be addressed with the current data. Study of the vulnerability of coastal species to the loss of fog would benefit from transplanting studies where coastal species are grown inland and their performance evaluated. Moreover, without analysis of seedling water potential data and adult water potential during drought, it may be difficult to determine why *Arctostaphylos* spp. at maritime and transition sites appear to be hydraulically overbuilt.

Acknowledgments A.L.J. and R.B.P. thank the Andrew Mellon Foundation and R.B.P. thanks NSF Career Grant IOS-0845125 for support.

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Supplemental Fig. S1

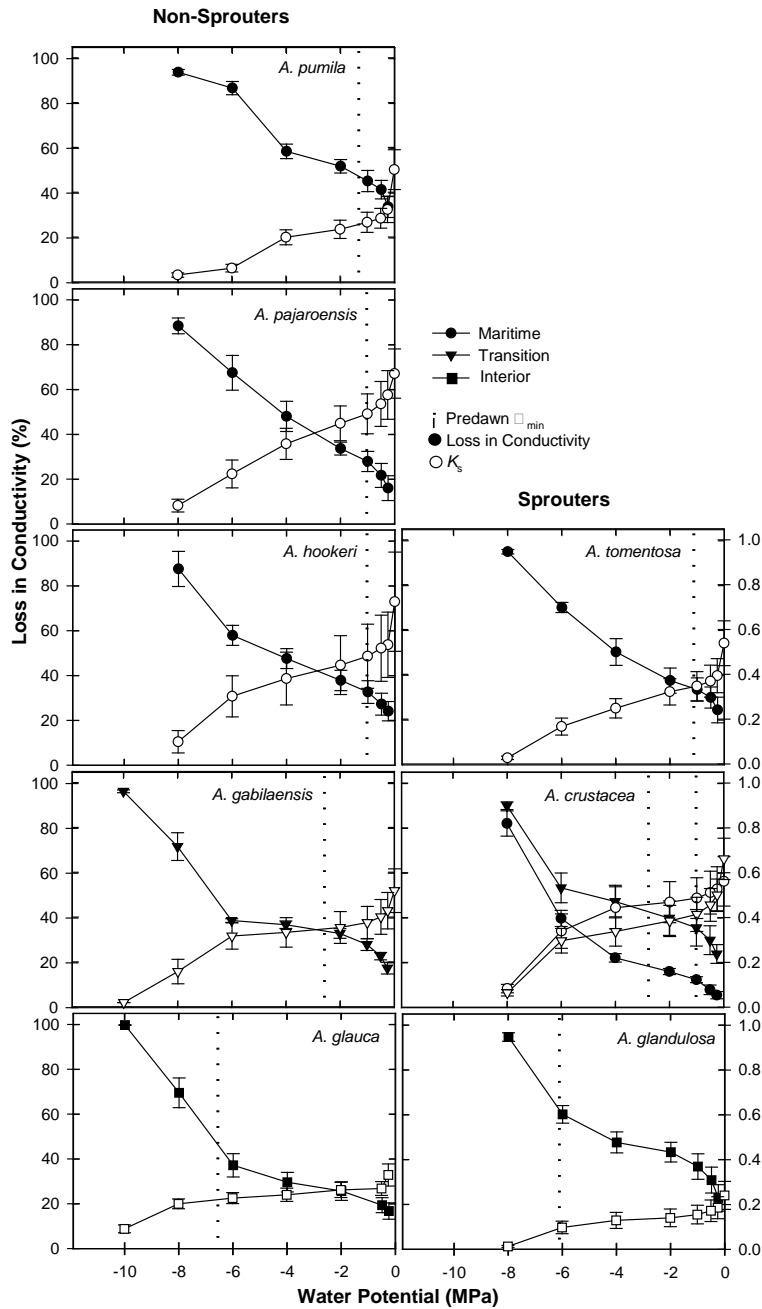


Figure S1. Vulnerability to cavitation curves of 8 *Arctostaphylos* species from three different regions, maritime (circles), transition (triangles), and interior (squares). Vulnerability curves are shown as both the increase in percentage loss in conductivity (closed symbols) and the decrease in xylem specific conductivity (open symbols) with declining water potential. Mean minimum seasonal water potential (Ψ_{min}) from Fall 2007 is shown for each species as a vertical dashed line. One species, *A. crustacea* was measured from two regions and data from these regions are shown together in the same panel. The vulnerability curve data included in this figure are not fatigue corrected and initial PLC levels therefore start at relatively high percentages even at very high water potentials for some species.