

Relationship between form, function, and distribution of two *Arctostaphylos* species (Ericaceae) and their putative hybrids

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SUMMARY

Plants of *Arctostaphylos viscida* occur in xeric, low elevation habitats in the Sierra Nevada. *A. patula* occurs in more mesic, high elevation sites. Where the distributions of these two species overlap, putative hybrids are formed. At a site of co-occurrence of these species we analyzed vegetative characters, reproductive characters, water relations, energy balances, and microhabitat quality for each of 81 *Arctostaphylos* plants which were randomly selected across a local environmental gradient. These plants represented not only an apparent genetic cline but also a cline of xerophytism. The plants with mesic characteristics were excluded from xeric habitats but those with xeric features were found to be relatively insensitive to microhabitat aridity.

KEY-WORDS: *Arctostaphylos* - Hybrids - Genetic cline - Water relations - Energy balance.

RÉSUMÉ

Arctostaphylos viscida est une espèce qui se rencontre dans des habitats xériques de basse altitude de la Sierra Nevada, tandis que *A. patula* se trouve dans des habitats plus mésiques, situés à des altitudes plus élevées. Là où les aires de répartition des deux espèces se recouvrent, des hybrides putatifs se sont formés. Dans une station où les deux espèces cohabitent, nous avons analysé les caractéristiques de la végétation, le mode de reproduction, le régime hydrique, le bilan énergétique et les caractéristiques du micromilieu pour chacun des 81 individus sélectionnés par tirage au sort le long d'un gradient environnemental local. L'ensemble de ces plantes représente non seulement un cline génétique évident, mais également un cline de xérophytisme. Les plantes à caractéristiques mésiques sont exclues des habitats xériques, alors que celles qui présentent des caractères de xéricité se sont avérées comme étant relativement insensibles à l'aridité du microhabitat.

MOTS-CLÉS : *Arctostaphylos* - Hybrides - Cline génétique - Régime hydrique - Bilan énergétique.

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INTRODUCTION

Arctostaphylos is a large genus of evergreen shrubs which occurs in many communities in California ranging from coastal to subalpine sites. This broad range of distribution is likely related to the diversity of growth forms and morphological characteristics exhibited by *Arctostaphylos* species. For example, coastal and subalpine species are often prostrate mats while chaparral species may be small trees over 10 m in height.

The diverse topography of these regions, with their complex mosaic of habitats, led JEPSON (1939) and others (GANKIN & MAJOR, 1964; VASEK & CLOVIS, 1976) to suggest that much of the variation in the genus was associated with minor climatic differences. SHAVER (1978) provided evidence of this by showing that leaf characteristics of size, angle, and absorptance may differ between species in an apparently adaptive manner to habitat conditions. Thus morphological forms of *Arctostaphylos* appear related to environmental factors. To date, though, no studies have attempted to link morphological forms of *Arctostaphylos* to specific physiological adaptations for environmental stresses.

Two co-occurring Sierra Nevada taxa of *Arctostaphylos*, *A. viscida* Parry ssp. *mariposa* (Dudley) Wells and *A. patula* Greene, provide an excellent opportunity for testing hypotheses of form-function relationships in natural plant populations. *A. viscida*, a glandular, glaucous, gray-leaved shrub is characteristic of the chaparral zone, while *A. patula*, a glabrous green-leaved shrub is an associate of the montane forest zone at higher elevations. These two taxa have overlapping distributions at about 1,400 m elevation in the Californian Sierra Nevada and populations may include individuals which either combine characteristics of both taxa and/or have characteristics intermediate between them. Early studies of *Arctostaphylos* morphology in the Sierra Nevada Mountains have implicated hybridization and introgression between *A. viscida* and *A. patula* as the source of variation in leaf structure and plant growth form (EPLING, 1947; DOBZHANSKY, 1952). On the other hand, controlled crosspollination experiments or electrophoretic analyses have not been made to support claims of either hybridization or introgression. Whether plants with growth forms intermediate between *A. viscida* and *A. patula* are due to hybridization or to morphological plasticity of these 2 species at their range limits is not central to this ecological analysis of relationships between plant form, function, and habitat.

Our study is divided into several sections. First, we examine the morphological variability of *A. viscida* and *A. patula* in allopatric populations. This analysis of *Arctostaphylos* morphology provides the basis for understanding the morphological variability of these 2 species. Secondly, we examine the morphological features of a large group of plants at a site where the two *Arctostaphylos* species co-occur. At this site we assess the functional relations of the various leaf morphologies in terms of plant water relations and leaf energy balance. Thus our approach for studying form and function in *Arctostaphylos* is based on ecophysiological analysis of plants with morphological variability which are growing in a habitat with diverse microclimates.

STUDY AREA DESCRIPTION

Our analysis of *Arctostaphylos* involved studies at 3 sites located near the western edge of Yosemite National Park (fig. 1 A). Plants of *A. viscida* were found in an area located 6.2 km west of Camp Mather at an elevation of 1,150 m. *A. patula* plants were studied growing at an elevation

of 1,550 m in an area 4.2 km east of Yosemite National Park west entrance. The site at the lower elevation contained only plants clearly ascribable to *A. patula* whereas the high elevation site had only *A. viscida* plants. *Arctostaphylos* populations at these two sites had different and distinctive phenotypes and no putative hybrids could be found. Thus at the low and high elevation sites the two *Arctostaphylos* species appeared to be isolated.

A third study site at an altitude of about 1,350 m was located near Inspiration Point, about 2.5 km south of Hetch Hetchy Reservoir (fig. 1 A). Both *A. viscida* and *A. patula* were found at this site. In addition, some plants with morphological and reproductive characters intermediate between those of *A. patula* and *A. viscida* could also be found.

Arctostaphylos species were distributed at the Inspiration Point site in a pattern consistent with their geographic distribution (fig. 1 B). *A. patula*, the more mesic species found at high elevations, was predominately found on north-facing slopes. *A. viscida* the low elevation species, was most commonly found on the more arid south-facing slopes but could also be found on north facing slopes. Finally, *Arctostaphylos* plants with characteristics of both *A. patula* and *A. viscida* were found at the base of both north-facing and south-facing slopes.

METHODS

Analysis of Arctostaphylos morphology

At the Inspiration Point study site (fig. 1 A) 81 individuals were selected and a branch, to be scored for the species identity index, was collected. Vouchers have been deposited at Occidental College Herbarium (LOC). The selection of individuals was random except that only individuals of reproductive age were included. Plants were sampled from the full range of microhabitats that was available. Only fruiting individuals were selected because of the important role reproductive characters play in *Arctostaphylos* taxonomy. Potentially this could bias against inclusion of sterile hybrids. However, there is abundant evidence that some putative *Arctostaphylos* hybrids from parents of similar ploidy level may be vigorous seed producers (*A. viscida* and *A. patula* are both diploid with $n = 13$, WELLS, 1968). For comparison of morphological differences between *A. viscida* and *A. patula*, 15 specimens of both species were collected from the low and high elevation sites where the two species appeared to be isolated (fig. 1 A).

Initially, twenty or more characters were used to characterize *Arctostaphylos* plants from the high and low elevation sites. However, for plants at Inspiration Point, where the two *Arctostaphylos* species co-occur fewer characters were used. Here we used five quantitative and seven qualitative characters which appeared not to be linked closely and which were not biased by differences in plant or fruit age (table I). The species identity index was modified from ANDERSON'S (1949) hybrid index as follows. All quantitative characters were normalized on a scale from 0 to 1. For all traits the *A. patula* types had the highest values and *A. viscida* the lowest. Similarly, qualitative characters of *A. patula* and *A. viscida* were measured on a meristic scale from 0 to 1. The species identity score for each individual was computed by summing the normalized scores and dividing by the number of characters included. In a very few cases, because of missing data, not all characters were included. Use of the species identity index in this study was limited to providing a morphological scale against which ecological and physiological parameters could be compared and is not intended to suggest any genetic basis to account for the wide range of *Arctostaphylos* morphology which we observed.

Analysis of morphological adaptation to aridity

Since it appeared that habitat aridity played an important role in the distribution of these two species, we devised a plant classification scheme which was based upon foliar characteristics that are likely to vary in relation to water availability. These characteristics included leaf angle, leaf area, and leaf absorptivity. Leaf angles were measured with an inclinometer, and readings for 25 leaves per shrub were averaged. Leaf area was calculated with the formula:

$$LA = L.(W.0.786)$$

where LA = leaf area (cm^2), W = leaf width (cm), L = leaf length (cm).

The high correlation ($r = .80$, $p < .05$) between the ecomorphological and reproductive indices indicates that *A. viscida* is more xeromorphic than *A. patula*. *Arctostaphylos* plants with reproductive characters not clearly ranked with either species (intermediate types) are more xerophytic than *A. patula* but less xerophytic than *A. viscida*.

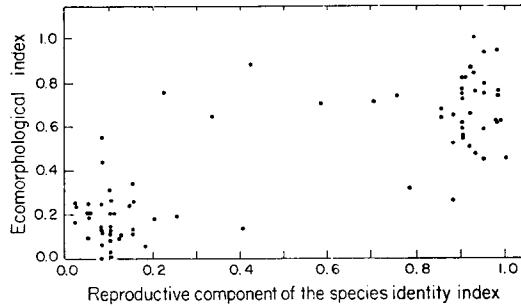


FIG. 3. — Reproductive component of the species identity index correlated with the ecomorphology index ($r = 0.80$, $p < .05$) for the sympatric *Arctostaphylos* population at Inspiration Point. Plant characters used in three indices are given in table I.

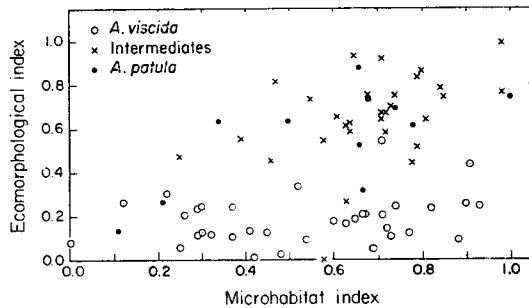


FIG. 4. — Microhabitat index plotted against the ecomorphology index for the sympatric *Arctostaphylos* population. Correlation was significant for *A. patula* (●) ($r = 0.68$, $p < .05$) and the intermediate-type plants (X) ($r = 0.50$, $p < .05$), but not *A. viscida* (○) ($r = 0.35$, $p > .05$).

Since *A. patula* and *A. viscida* plants differed with respect to xeromorphic features we assessed how such characteristics are related to plant distribution at a site where both species co-occurred. Figure 4 shows that *A. viscida*, the more xeromorphic species, showed little variability in ecomorphological values and occurred in the full range of microhabitats which were available at Inspiration Point. Apparently even though *A. viscida* is adapted to xeric microhabitats, it is not excluded from mesic ones. *A. patula* and the intermediate-type *Arctostaphylos* plants had wide ranges of ecomorphology scores and these scores were positively correlated with microhabitat index scores (*A. patula* : $r = .68$, $p < .05$ and intermediate-type plants: $r = .47$, $p < .05$). Thus the more xeric microhabitats had only plants which were morphologically adapted for aridity whereas the mesic sites had plants ranging from the most xeromorphic to the most mesomorphic.

Leaf water relations and energy balance

Leaf water balance was measured and energy balances calculated on June 25 for three representatives of *A. viscida*, *A. patula*, and the putative hybrids of the Inspiration Point study site. The *A. viscida* plants were located on a south-facing slope, while *A. patula* and intermediate type plants occurred on a north-facing slope.

Dawn and midday water potentials were -0.7 and -1.2 MPa lower, respectively, for the *A. viscida* plants than for the *A. patula* plants (fig. 5 A). Intermediate-type plants had dawn and early morning water potentials similar to *A. patula*, but had midday water potentials intermediate between the type species. Leaf conductances were lower for *A. viscida* than for either *A. patula* or the intermediate-type plants (fig. 5 B).

Diurnal measurements of leaf temperature obtained on June 25 were averaged for three representatives of each plant type (fig. 5 C). Of all the *Arctostaphylos* plant types, *A. viscida* had the highest leaf temperatures early in the morning and late in the afternoon, but the lowest temperatures during midday when solar radiation loads are maximum. The low midday leaf temperatures of *A. viscida* were presumably the result of their nearly vertical leaf angle (79°), which reduced the incident radiation during midday. *A. patula* had a daily pattern of leaf temperature change which was similar to the pattern observed for intermediate-type plants. The temperatures ranged about 12° C during the day for *A. patula* and the intermediate-type plants but only about 6° C for *A. viscida*.

Computer simulations (EHLERINGER & MILLER, 1975) of the rate of transpirational water loss, using the leaf conductance and temperatures from figures 5 B and C, respectively, indicate that the maximum transpiration rate of *A. viscida* would be about 39 % of the value obtained for *A. patula* (fig. 5 D). Thus, even though leaf temperatures were highest for *A. viscida* over most of the day, total daily water loss was predicted to be 52 % of that for *A. patula*. Water loss was highest for *A. patula*, even though it occurs in protected north-facing slopes. Presumably this is due to its lower leaf angle, greater leaf size, greater absorptance, and high leaf conductance to water loss. The intermediate-type plants had simulated transpiration rates which were midway between *A. patula* and *A. viscida*. *A. patula* would have even higher leaf temperatures, transpiration, and water loss if it grew in the hotter, drier sites occupied by *A. viscida*.

We further monitored leaf water relations, conductance, and temperatures for *A. viscida*, *A. patula* and intermediate type plants which were growing immediately adjacent to one another. All three plants occupied the same microhabitat on a north-facing slope. This sampling strategy was designed to minimize physiological differences between plants due to the wide range of microhabitats available and to show the intrinsic physiological characteristics of the three types of *Arctostaphylos* as clearly as possible. Differences in water potential (fig. 6 A) and leaf conductances (fig. 6 B) for the three *Arctostaphylos* plants were much less than found in the previous north slope-south slope comparison (fig. 5 A-D). However, compared to *A. patula*, the *A. viscida* plant tended to have lower water potentials throughout the hottest part of the day. Leaf conductances for both *A. patula* and *A. viscida* and the intermediate type plant reached similar maximum values near 0900 and then conductance declined throughout the remainder of the day. However, *A. patula* maintained higher leaf conductances during midday than did either *A. viscida* or the hybrid.

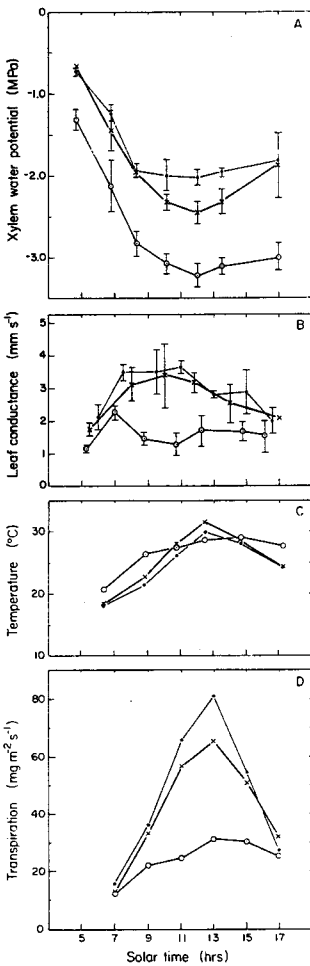


FIG. 5.

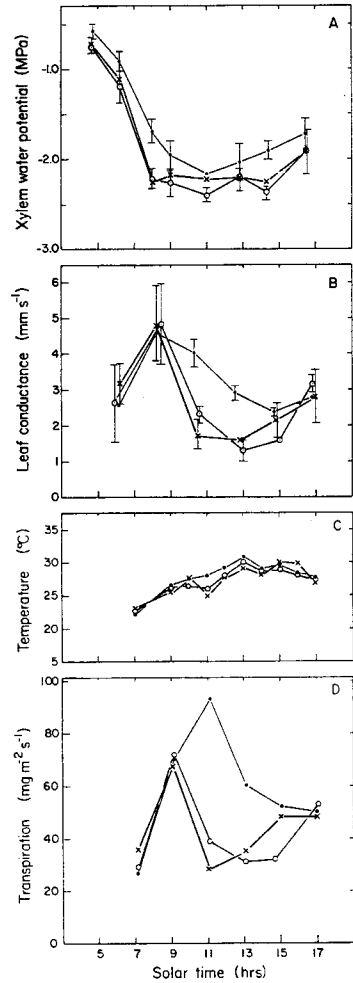


FIG. 6.

FIG. 5. — The daily course of measured xylem water potentials (A), leaf conductances (B), leaf temperatures (C), and calculated transpiration rates (D) for *Arcrostaphylos* species at the Inspiration Point study site on 6/25/79. *A. viscida* (○) was sampled on south-facing slopes, *A. patula* (●) on north-facing slopes, and intermediate type plants (X) at the bases of slopes. Each data point is the mean \pm S. E. for three replicate measurements of each of three individuals.

FIG. 6. — The daily course of measured xylem water potentials (A), stomatal conductances (B), leaf temperatures (C), and calculated transpiration rates (D), for *Arcrostaphylos* species at the Inspiration Point study site on 6/27/79. *A. viscida* (○), *A. patula* (●), and intermediate type plants (X) were sampled on north-facing slopes. Sampling and statistics as in figure 5.

Comparisons of water potential and conductances for *A. viscida* growing on the south-facing slope (fig. 5 A, B) and growing on the north-facing slope (fig. 6 A, B)

illustrate the much more favorable nature of the latter habitat. *A. viscida* growing on the south-facing slope had lower water potentials and leaf conductances presumably reflecting the greater aridity of this microhabitat.

Leaf temperatures were followed throughout the day on representatives of the three types of different *Arctostaphylos* which co-occurred in the same microsite on a north-facing slope. Daily leaf temperatures were not significantly different among the three *Arctostaphylos* types. However, calculated transpiration rates (fig. 6 D), determined from measured leaf conductances and leaf temperatures (fig. 6 C), were markedly different amongst them (fig. 6 D). These differences in transpiration rates are consistent with differences observed for the three types of *Arctostaphylos* plants growing in different microhabitats (fig. 5 D); *A. viscida* had lower transpiration rates than *A. patula* and plants with morphological characters of both species had intermediate transpiration rates.

The intermediate-type plants help clarify the link between xeromorphism and plant distribution at the site where all three *Arctostaphylos* types occur. On a large scale, *A. viscida* occupies the more arid habitats found at low elevations and *A. patula* occupies the more mesic habitats found at high elevations. The fact that the intermediate-type plants are found at the range limits of the two true species is consistent with these large scale distribution patterns.

On a smaller scale, at Inspiration Point, similar patterns emerged. In this case *Arctostaphylos* plants which represent a cline of xeromorphism occur at a site with microhabitats of differing aridity. The fact that the more mesophytic plants were excluded from the more arid microhabitats suggests aridity is a key factor in controlling plant distribution. However the more xerophytic plants did not seem limited to the more xeric habitats. Clearly then, factors other than aridity, alone, limit *A. viscida*, and the more xeromorphic intermediate-type plants from occupying sites at higher elevations. Recognition of intermediate-type plants and including them in our analysis of plant form and function played a large role in developing our understanding of factors important for influencing *Arctostaphylos* distribution.

CONCLUSIONS

Plants of *A. viscida* and *A. patula* occur at low and high elevations, respectively, on the western slope of the Sierra Nevada mountains and they co-occur at the limits of their ranges. *A. viscida* has pubescent leaves, a conservative water-use strategy, and leaves positioned at an angle which minimizes the absorptance of solar radiation at midday. *A. viscida* can be characterized as the more xeromorphic of the two species since plants of *A. patula* have glabrous and more horizontally-angled leaves.

Where *A. viscida* and *A. patula* co-occur, *Arctostaphylos* plants with vegetative and reproductive characters intermediate between those of the two species can be found. The intermediate-type, putative hybrids, are more xeromorphic than *A. patula* but less so than *A. viscida*.

The site where the two *Arctostaphylos* species co-occur has microhabitats which differ in aridity. Analysis of the range of xeromorphism for *Arctostaphylos* species there helps explain their distribution. The more xeromorphic plants occupy microhabitats which range from mesic to xeric whereas the least xerophytic plants are restricted to only the more mesic microhabitats. Thus aridity seems to limit the distribution of *A. patula* and the more mesic intermediate-type plants whereas other

factors limit the distribution of *A. viscida*, and the more xerophytic intermediate-type plants.

ACKNOWLEDGMENTS

In addition to the listed authors the following persons were involved in data collection, data analysis, and manuscript preparation: H. CALKIN, J. EHLERINGER, I. FORSETH, N. HERR, D. HOLLINGER, S. KNAPP, A. MCGEE, D. MANGIS, R. MILLER, R. PEARCY, M. ROANTREE, P. RUNDEL, N. TOFT, S. USTIN & C. WISDOM. Citation practice did not permit listing all of their names as authors and an attempt to use pseudonyms for authors was unsuccessful. We acknowledge B. LILLEY for drafting the figures. We thank Malcolm NOBS for introducing us to the problem.

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