*Acta Œcologica*
*Œcol. Plant.*, 1983, Vol. 4 (18), n° 2, p. 153-164.

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

Charles T. Ball [1], Jon Keeley [2], Harold Mooney [3], Jeffrey Seemann [4], and William Winner [5]

[1] *Department of Biological Sciences, Stanford University and Division of Plant Biology, Carnegie Institution of Washington, Stanford, California, U. S. A.*

[2] *Department of Biology, Occidental College, Los Angeles, California, U. S. A.*

[3] *Department of Biological Sciences, Stanford University, Stanford, California, U. S. A.*

[4] *Department of Environmental Biology, Research School of Biological Sciences, Australian National University, Canberra, Australia.*

[5] *Department of Plant Pathology and Physiology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, U. S. A.*

## 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.*

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.

## 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).

Absorptivity of mature leaves to solar radiation between 400 to 700 nm was measured with an Ulbricht integrating sphere. In addition, we included an estimate of the total leaf area of the shrub. This was determinated as the ratio of the light impinging on top of the shrub canopy to that measured at the ground below the canopy. Higher ratios indicate the lowest leaf areas and were taken to represent the most xeric conditions. We calculated an index of "ecomorphology" by the same techniques used to calculate the species identity index scores.

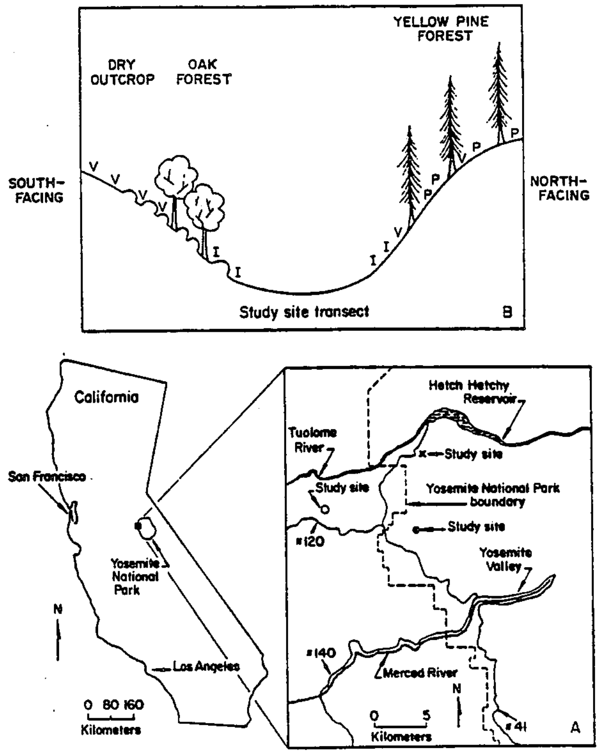

FIG. 1. — A map (*A*) showing the location of three study sites where either *A. viscida* occurred (○), *A. patula* occurred (●), or both species and plants of intermediate morphology occurred (*X*). A transect (*B*) shows the distribution of *A. viscida* (V.), *A. patula* (P.), and plants with intermediate characteristics (I) at the Inspiration Point site where both *Arctostaphylos* species co-occur (*X*).

### *Analysis of microhabitat*

At the Inspiration Point site where *A. patula*, *A. viscida*, and intermediate type plants co-occur, microhabitats near each *Arctostaphylos* study plant was defined by measuring soil water availability, slope angle and aspect, incoming radiation, and soil volume.

Dawn xylem water measured, measured with a Scholander pressure chamber (SCHO- LANDER *et al.*, 1965), was used as an approximation of the quantity of soil water available to the plant. Three replicates were taken on each of the 81 shrubs.

The angle and azimuth of the slope on which each individual was growing were measured, and the cosine of the angle of incidence of incoming radiation was calculated as:

$$\cos I = [(\cos \text{slope}) (\cos \text{zenith})] + [(\sin \text{slope}) (\sin \text{zenith}) (\cos (0\text{-azimuth}))]$$

where $I$ = angle of incoming evident radiation,
slope = topographic angle,
zenith = mean midday solar angle = 55°,
azimuth = compass heading of slope.

The proportion of canopy coverage obstructing incoming radiation (viewfactor) was quantified by visual estimates through a fisheye lens as viewed at the top of the shrub.

A rough evaluation of the soil volume available for each plant was made by estimating the percentage of rock cover in the immediate vicinity (within 1 meter from the canopy edge) of each plant. Presumably, more soil water is available in microhabitats with large soil volume compared to microhabitats with small soil volume.

Each microhabitat measure (dawn water potential, cos $I$, view factor and percentage rock cover) was calculated as follows:

$$I = (x - x_{\text{min}})(x_{\text{max}} - x_{\text{min}})^{-1}$$

where $I$ = microhabitat index,
$x$ = value of measure parameter,
$x_{\text{min}}$ = minimum parameter value,
$x_{\text{max}}$ = maximum parameter value.

All parameters were arranged so that the low end of the scale was that related to greatest potential aridity, *i. e.*, lowest water potential, highest cos $I$, greatest view factor and rock cover. The normalized habitat values for each parameter were summed and represent a microhabitat index value for each shrub.

### *Analysis of leaf water conductance*

Measurements of leaf water conductance were made on two cloudless days (June 25 and June 27). Three individuals of each species and of an intermediate-type plant, as defined by the species identity index, were studied in their most typical microhabitats. These measurements characterize the patterns of changing conductance for each species. On June 27, three additional sets of individuals were studied. Each set was composed of three adjacent individuals representative of both species and an intermediate type. All sets occurred on the north-facing slope.

Leaf conductances to water vapor were determinated for *Arctostaphylos* plants at Inspiration Point with a null balance porometer based on a modification of the design of BEARDSELL *et al.* (1972). Triplicate readings were determined for *A. patula*, *A. viscida*, and intermediate type plants at hourly intervals for a full day.

### *Energy balance calculations*

Plant microclimate measurements were made during the June study period on two or three *Arctostaphylos viscida*, *A. patula*, or intermediate-type plants. Leaf temperatures and adjacent air temperatures were measured using 36 gauge copper-constantan thermocouples on ten randomly chosen sunlit leaves for each plant. Five replicated measurements of wind speed were made above the shrub canopy using a hot wire anemometer. Relative humidity and water vapor density of the air were determined from measurements of dry and wet thermocouples. Quantum flux density was measured above the shrub canopy, using a Licor quantum sensor (400-700 nm). Measurements were also made of solar radiation, including both total and diffuse solar radiation. The infra-red radiation from the sky was calculated from evening measurements of net radiation and soil temperature. Soil temperatures at the soil surface were measured, using 36 gauge copper-constantan thermocouples.

Leaf absorptances to solar radiation in the 400 to 700 nanometer wave band were measured using an Ulbrecht integrating sphere (EHLERINGER, 1981). All absorptances were measured on mature leaves.

Additional leaf conductance measurements to be used in the energy budget calculations were made on two separate days. On June 25th we measured conductance and energy balance for each of three *A. viscida*, *A. patula*, and intermediate type plants growing in their most commonly occupied microhabitats, that is, south-facing slopes for *A. viscida*, north-facing slopes for *A. patula*, and bases of slopes for intermediate-type plants. On June 27th similar measurements were made on two each of *A. viscida*, *A. patula* and an intermediate type plants all found growing on a common, north-facing slope.

## RESULTS AND DISCUSSION

### *Classification of three* Arctostaphylos *types*

The species identity scores (fig. 2 A) for all *Arctostaphylos* plants at the 3 study sites were calculated from the 12 characters listed in table I. This index separated the *Arctostaphylos viscida* and *A. patula* plants which were sampled in the allopatric stands. *A. viscida* plants from the low elevation *Arctostaphylos* stand had species identity scores of less than 0.35 and *A. patula* plants from the allopatric high elevation stand had scores greater than 0.80 (fig. 2 A). *A. viscida* plants were characterized by glaucous branchlets, leaves, pedicels, and calyces. *A. patula* plants were glabrous. *A. viscida* leaves were whitish-gray in color, had acute apices and were generally smaller than the green, rounded *A. patula* leaves.

The mixed Inspiration Point population, however, had scores which spanned the entire range of the species identity index. Some of these plants were clearly similar to *A. viscida* and others were similar to *A. patula*. However, some of the *Arctostaphylos* plants at the Inspiration Point site had species identity scores between those of the two allopatric species. We refer to plants with species identity scores between 0.35 and 0.80 as intermediate type plants.

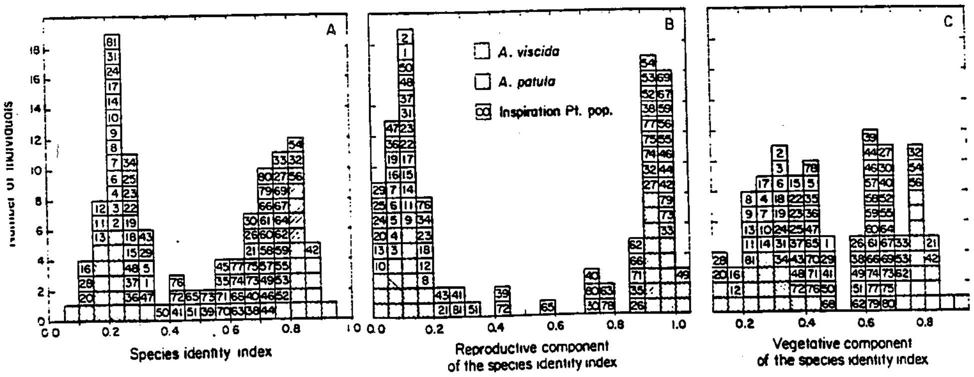

FIG. 2. — The species identity index (*A*) is a composite index consisting of a reproductive component (*B*) and a vegetative component (*C*). These indicies were calculated from characteristics listed in table I for specimens of *A. viscida* (o) and *A. patula* (●) from the allopatric sites and for the mixed population (*X*) at Inspiration Point.

TABLE I. — *Characters comprising the indices used for analyzing* Arctostaphylos *species at sites where* A. viscida *and* A. patula *are either segregated or co-occur. All characters were normalized from 0-1.*

1. *Species identity index* (1)

Vegetative component
A. Petiole length
B. Leaf length
C. Leaf width
D. Leaf thickness
E. Leaf margin
F. Leaf color
G. Leaf indument
H. Branch indument

Reproductive component
I. Pedical length
J. Calyx apex
K. Calyx indument
L. Fruit indument

2. *Ecomorphological index* (2)
M. Leaf angle
N. Leaf area
O. Leaf absorptivity (radiation from 400-700 nm)

3. *Microhabitat index* (3)
P. Soil water availability
Q. Slope and aspect
R. Solar radiation
S. Soil volume

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(1) Low values = *A. viscida* and high values = *A. patula.*
(2) Low values = xeromorphic and high values = mesomorphic.
(3) Low values = xeric microhabitat and high values = mesic microhabitat.

Similar histograms were constructed which distinguished between the reproductive characters (table I, characters *I-L*) (fig. 2 B) and the vegetative character (table I, characters *A-H*) (fig. 2 C). These figures showed that a greater separation of allopatric population members and a more complete segregation of intermediate-type plants was achieved when reproductive characters rather than vegetative ones were used in calculating species identity scores.

In order to determine how the *A. viscida* and *A. patula* type plants differed in their morphological features associated with drought adaptation, we plotted the reproductive component of the species identity index against scores calculated for the ecomorphology index (fig. 3). The ecomorphology index reflects adaptation to aridity with low scores indicating plants with xerophytic characteristics. *A. viscida* leaves were characterized by features which reduced absorption of solar irradiation; compared to *A. patula*, *A. viscida* leaves were positioned to reduce light interception, were smaller, and reflected more light.

The high correlation ($r = .80$, $p < .05$) between the ecomorphological and reproductive indicies 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*.

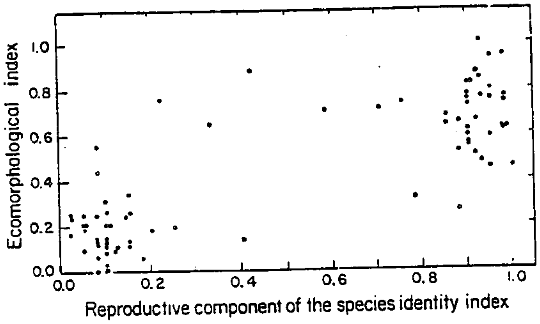

FIG. 3. — Reproductive component of the species identity index correlated with the ecomorphology index ($r = 0.80$, $p < .05$) for the sympatric *Arctostaphylos* population at Inspiration Point. Plant characters used in three indicies are given in table I.

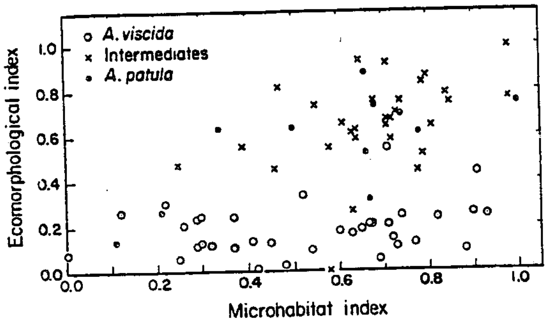

FIG. 4. — Microhabitat index plotted against the ecomorphology index for the sympatric *Arctostaphylos* population. Correlation was significant for *A. patula* (●) ($r = 0.68$, $p < .05$) and the intermediate-type plants ($X$) ($r = 0.50$, $p < .05$), but not *A. viscida* (○) ($r = 0.35$, $p > .05$).

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.

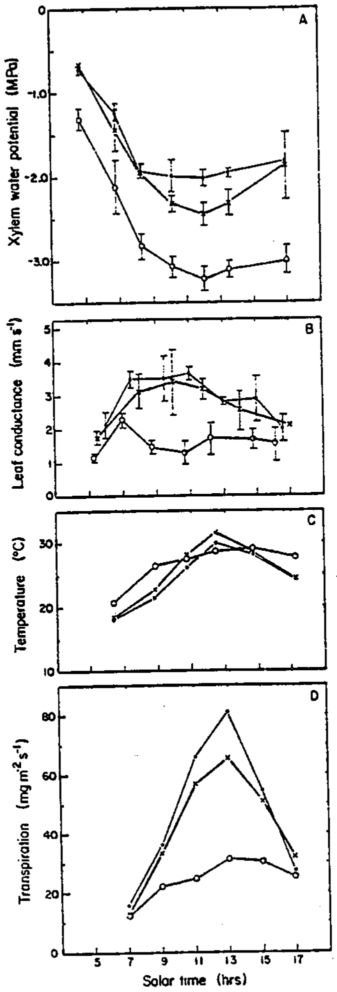

FIG. 5.

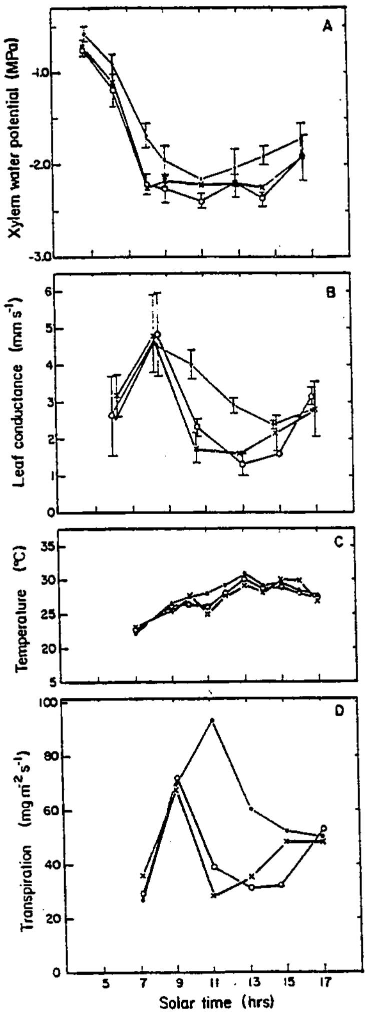

FIG. 6.

FIG. 5. — The daily course of measured xylem water potentials (*A*), leaf conductances (*B*), leaf temperatures (*C*), and calculated transpiration rates (*D*) for *Arctostaphylos* 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 ± 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 *Arctostaphylos* 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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