QUANTIFICATION OF FOG INPUT AND USE BY QUERCUS PACIFICA ON SANTA CATALINA ISLAND

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ABSTRACT: The proportion of water input resulting from fog, and the impact of canopy dieback on fog-water input, was measured throughout 2005 in a Quercus pacifica-dominated woodland of Santa Catalina Island. Stable isotopes of oxygen were measured in water samples from fog, rain and soils and compared to those found in stem-water from trees in order to identify the extent to which oak trees use different water sources, including fog drip, in their transpirational stream. In summer 2005, fog drip contributed up to 29% of water found in the upper soil layers of the oak woodland but oxygen isotope ratios in stem water suggest that oak trees are using little if any of this water, instead depending primarily on water from a deeper source. Fog drip measurements indicate that the oak canopy in this system actually inhibits fog from reaching soil underneath the trees; however, fog may contribute additional water in areas with no canopy. Recent observations on Santa Catalina show a significant decline in oak woodlands, with replacement by non-native grasslands. The results of this study indicate that as canopy dieback and oak mortality continue additional water may become available for these invasive grasses.

KEYWORDS: Fog drip, oak woodland, Quercus pacifica, Santa Catalina Island, stable isotopes, water use.

INTRODUCTION

Fog is a ubiquitous feature of most coastal regions that have a Mediterranean climate. Periods of fog can occur year-round in these regions, but the presence of fog is most notable during the otherwise hot and dry summer season. Such summer fog has drawn much attention from ecologists because of its potential role in reducing water stress and facilitating plant activity during the most water-limited period of the year. Indeed, a number of studies have demonstrated that fog can have a significant influence on hydrological, nutritional and biotic processes in coastal Mediterranean ecosystems (Azevedo and Morgan 1974; Ingraham and Matthews 1990; Dawson 1998; Burgess and Dawson 2004; del-Val et al. 2006), and for the most part, these influences are viewed as positive.

The benefit of fog to vegetation results from several possible factors. Overall, it decreases evapotranspiration of a community by reducing solar radiation and temperature, and increasing relative humidity. Directly, it will also relieve water stress by increasing ambient vapor pressure, thereby reducing the vapor pressure deficit (VPD) between plants and the atmosphere. This lower VPD reduces transpiration demand, resulting in less plant water loss.

Fog may also serve as a water source for plants. Although it is rare, water that collects on the leaves of some species can be directly absorbed through the foliage (e.g., Stone 1957; Boucher, Munson, and Bernier 1995; Yates and Hutley 1995; Hutley et al. 1997). Burgess and Dawson (2004), for example, showed in redwoods that xylem-sap transport reversed direction (flowing back into the stem from the leaves) during periods of heavy fog, and demonstrated through the use of stable isotopes that up to 6% of water in leaves originated from fog water.

More commonly, fog serves as a water source to plants through fog drip to the soil. A considerable amount of fog water can remain temporarily on the leaves, reducing leaf temperatures until increased mid-day temperatures cause it to evaporate (Juvik and Nullet 1995). However, if the amount of water that accumulates on a leaf surface exceeds its water holding capacity, water will drip to the ground and infiltrate the soil, increasing total water availability to the plant through the soil. Azevedo and Morgan (1974), for example, collected as much as 425 mm of fog drip under a Douglas fir-dominated forest crown during the fog season in northern California. Other studies along the California coast have demonstrated that certain vegetation types are capable of “stripping” fog from the atmosphere via leaf interception – after which the fog water drips to the soil and can then be acquired through root uptake (Ingraham and Matthews 1995; Dawson 1998; Corbin et al. 2005).

The most studied and best example of fog drip utilization within an ecosystem comes from the coastal redwood forests of California where it has been shown that during summer 8-42 % of water obtained by redwood trees (Sequia sempervirens) and 6-100 % of the water obtained by understory species is derived from fog drip (Dawson 1998). Even low-statured grassland communities have shown important interactions with fog. Corbin et al. (2005), for example, found that access to surface soil water stemming from fog interception may explain how native-dominated coastal grasslands are able to suppress exotic invasive species, since exotic species complete their life cycles by spring and have died before the onset of the summer fog season.

Beyond providing an additional water source, fog can also influence productivity in other ways, including raising photosynthetic efficiency due to increased CO₂ concentrations that are trapped within fog layers (Dawson 1998) or by diffusing intense summer radiation. However, most evidence suggests that the greatest benefit of fog is through enhanced water status of plants and soils, and such influences may be especially important during periods of drought when water availability is low and evaporative demand is high (Dawson 1998; Corbin et al. 2005).

The island of Santa Catalina, 40 km west of coastal Los Angeles, experiences fog events throughout the year and, as in other Mediterranean regions, late spring and early summer fog events may play a particularly important role in maintaining plant activity and health. A severe decline has recently been noted in the oak cover on the island (Figure 1), but the cause of this decline is unclear. Prior to 2005, the island experienced a five-year drought and throughout this period water availability may have been reduced to a critical threshold that led to the death of many oaks.

Canopy decline due to oak death may further alter the input of fog due to a reduction of leaf and stem surface areas for fog interception and drip. Perturbations of this type have been seen in a number of fog-influenced ecosystems. For example, stream flow in logged areas of the western Cascades was reduced by 30 % due to the reduction of fog drip (Harr 1982) with recovery occurring only after 5-6 years of canopy regrowth (Ingwersen 1985). Aboal et al. (2000) likewise found that mean total throughfall (rain and fog drip) in natural plots on the Canary Islands was double the amount of incident rainfall alone. These findings indicate that canopy cover and subsequent fog deposition is often a critical part of the hydrological balance of fog-inundated forests (see also Hamilton et al. 1995).

Currently the functional importance of fog drip in the oak woodlands of Santa Catalina Island is unknown. It is also not known if oak mortality is negatively affecting the amount of fog drip that enters these woodlands or if the dominant oak, Quercus pacifica Nixon & C. H. Muller (Channel Island scrub oak), uses fog as a water source. In this study we addressed these questions by: (1) characterizing the rainfall and fog drip input into a representative oak woodland community of Santa Catalina Island to determine if fog is a significant water source, (2) examining the effects of canopy density differences on the amount of measured fog drip, and (3) using stable isotope differences among the potential water sources.

sources for *Quercus pacifica* (fog drip, rain, soil, and ground water) to determine if there is any evidence of fog-water use by this species.

**METHODS**

**Study Site and Species**

The study took place on Santa Catalina Island, from January 2005 to December 2005, in an oak woodland site located on the northern-facing slopes of the Twin Rocks area (~ 1.6 km W of the Catalina airport; 33° 24.211’ N, 118° 23.362’ W; Figure 1). This location was selected because it is one of the primary areas of oak dieback on the island. Long-term weather records from the Santa Catalina airport were used to characterize the climate of the study site. Data from the airport included hourly relative humidity, temperature, rainfall and weather type (including fog events and visibility). For the latter, days with fog (fog-days) were defined as a day when visibility was 0.8 km or less for more than 1 hour. Monthly precipitation and number of fog-days were determined and used to calculate long-term mean precipitation and fog-day occurrence for each available year. Monthly data from each year were combined to calculate historic monthly means, standard deviations, and standard errors of rainfall (1949 - 2005) and fog days (2001 - 2005).

Climate conditions, including hourly relative humidity, temperature, and incident rainfall, were also recorded at the site from March to December 2005 using a SpecWare Basic weather station (Spectrum Technologies Inc., Plainfield, IL). Data from the weather station as well as the Catalina airport were used to determine the number of fog events at the study site and to trace weather conditions throughout the study.

The tree canopy at the study site is dominated (> 80 %) by *Quercus pacifica* with a few large shrubs interspersed, including lemonade berry (*Rhus integrifolia*) and laurel sumac (*Malosma laurina*). Interspaces between trees were filled throughout winter and spring with a mixture of non-native annual grasses and a few native annual and herbaceous perennial forbs.

*Quercus pacifica* is endemic to three of the California Channel Islands: Santa Cruz, Santa Rosa and Santa Catalina. It is normally found between sea level and 300 m in elevation, and averages 5 m in height (Nixon 1997). The root structure of *Quercus pacifica* suggests that the species may use water from a variety of soil depths; fallen trees at the field site provide evidence of a significant root biomass just under the soil surface with a taproot that likely reaches much deeper water sources (S. Evola, pers. obs.). This rooting pattern is consistent with those of closely related *Quercus* species. Roots of *Quercus douglasii* are abundant at 1.5 m below the surface (Millikin and Bledsoe 1999), however, they can exceed 24 m in depth (Lewis and Burgy 1964). Another closely related species, *Quercus dumosa*, has been observed with roots to a depth of 8.5 m (Hellmers et al. 1955).

**Study Design**

**Rainfall, Fog Drip and Canopy Influences**

Rainfall and fog drip were collected using custom-built fog/rain collectors consisting of a 43-cm diameter funnel draining into a collection tube housed within a 5-gallon bucket that serves as both a support and an overflow collector (Figure 2). Mineral oil (10 ml) was placed in the collection tube before every
Figure 1. Map of Santa Catalina Island portraying healthy and dieback areas of island scrub oak (Quercus pacifica). The research site was located in the Twin Rocks area approximately 1.6 km from the Catalina airport (33° 24.211’ N, 118° 23.362’ W). (Map courtesy of the Catalina Island Conservancy)
Fog Input and Use by *Quercus pacifica*  

**Figure 2.** Diagram of custom fog-drip/rain collector. Water collected by the funnel drains into a collection tube containing 10 ml mineral oil. If the amount of water collected exceeds the collection tube capacity, water spills into the overflow bucket.

collection period creating a 23 mm oil layer to prevent evaporation of the water sample that is amassed within the collection tube.

Six plots (~ 50 m²) were selected within the 500 m² study site. Plots were chosen with the same aspect and elevation in order to avoid potential topographic effects on temperature and water input. In each plot, one collector was placed under a tree with > 80 % foliar coverage (full canopy), one beneath a tree with < 50 % foliar coverage (partial canopy), and one beneath a tree with no foliage, but still standing (dead). (Percent canopy coverage was assessed visually by the authors.) One collector was also placed in an open area (control) within the plot.

The amount of water that accumulated in each collector was measured approximately every three weeks from January to December 2005. Average measurement accuracy based on laboratory trials showed <0.07% measurement error. If no rainfall was recorded by the weather station over a collection period, water that accumulated in the collector was assumed to be solely from fog. If no fog-days occurred during a collection period, but rain events were recorded, the water was assumed to be entirely from rain. In the event that both fog and rain events occurred between collection periods, rainfall records from the Catalina airport and the site weather station were used to determine rainfall amount, with the residual being ascribed to fog, dew or mist input. (We use the term “fog” to represent any of these three sources since their ecological effects are virtually the same with respect to the questions examined in this study.)

For each collection date, the mean amount of water collected was calculated for each canopy class. A one-way ANOVA using SAS version 9.1 (SAS Institute 2000) was used to compare differences among means for the amount of water collected. Post-hoc Tukey tests were performed to identify significant differences among canopy classes when ANOVA results indicated a significant difference was present (P < 0.05).

**Isotopic Analyses of Water Sources, Soils and Stems**

Fog (and dew) condenses from moisture in air that is normally enriched (high) isotopically. Rain, however, forms from evaporated water that is initially depleted (low) isotopically and becomes even more depleted due to continual condensation and rainfall as it travels towards the coast (Ingraham and

As such, fog and rain have distinctly different hydrogen ($\delta^2$H) and oxygen ($\delta^{18}$O) stable isotope ratios that can be used to determine input sources for the water budget of a system (Ingraham and Matthews 1990; Dawson 1998).

Fog and rain can serve as immediate sources of water for plants once they permeate the soil, but water at the soil surface changes dramatically over time, whereas deep-soil water does not (Clark and Fritz 1997). Deep-soil water forms from the accumulation of large rain events that penetrate down into soil, where it is not subject to evaporative processes. As such, the isotopic composition of deep water in most systems represents the long-term integration of the isotopic composition of precipitation that falls in an area (Clark and Fritz 1997; Hsieh 1997). In contrast, water that remains at the soil surface and within the upper layers of the soil profile is subject to fractionation during evaporation, resulting in isotopic enrichment. The variation of isotope ratios between shallow and deep soil layers can therefore be used to identify sources of water used by plants (e.g., Ehleringer et al. 1991). Importantly, isotopic fractionation does not occur during the uptake of water from the soil into roots and xylem of a plant, which means that xylem water can be used as a reliable indicator of a plant’s water source (Dawson 1993; Ehleringer, Roden, and Dawson 2000; Robertson et al. 2001).

Given this relationship, it is important to know the isotope ratio from each possible source—such as precipitation, fog, shallow soil water, and deep soil water. The $\delta^{18}$O values of water from the fog/rain collectors were periodically analyzed to determine $\delta^{18}$O of these seasonal inputs. For these evaluations, water from each collection tube was separated from the oil and immediately transferred into 15 ml storage vials. Vials were sealed with screw-top lids and Parafilm. $\delta^{18}$O values of shallow soil water were also measured seasonally. Soil samples (~ 15 g) were collected from a depth of 20 cm using a 10 cm diameter soil auger. Samples were taken from beneath partial-canopy trees within each plot, transferred to 10 ml storage vials and sealed with screw-top lids and Parafilm. All water and soil samples were stored at 4 °C until water could be extracted for isotopic analyses (described below).

To estimate which water sources were being used by Quercus pacifica at the study site, stem samples were periodically collected from mature trees, from which xylem water was extracted and measured for $\delta^{18}$O (described below). Two to three stem samples were collected from one full-canopy and one partial-canopy tree in each plot (n = 6). Only woody stems that were > 1-year old were sampled. All stems from an individual tree were immediately placed in 10 ml glass vials, sealed with screw top lids and Parafilm, and stored at 4 °C prior to extraction.

Water was extracted from stem and soil samples using a cryogenic vacuum distillation extraction method (Ehleringer, Roden, and Dawson 2000). The distillation process was carried out for 90 min to ensure all water was removed from the sample. Upon completion, the liquid water was transferred to a 3 ml storage vial, covered with a screw top and sealed with Parafilm then stored at 4 °C until shipped for analyses of $\delta^{18}$O.

$\delta^{18}$O values of extracted water from soil and stems, and of water from fog/rainfall collectors were determined on a Delta Plus isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany) at the University of California Irvine, Department of Earth System Sciences. Results are reported using standard stable isotope delta notation ($\delta$) as the ratio of $^{18}$O to $^{16}$O relative to the Vienna Standard Mean Ocean Water (VSMOW) standard in per mil (‰) units (Ehleringer and Rundel 1989).

Mean $\delta^{18}$O values and standard errors were calculated for each collection period for soils, stems and all fog/rain collectors (across all treatments). One-way ANOVA was used to test for seasonal differences of stem $\delta^{18}$O means, with post-hoc Tukey tests performed to identify significant differences between each pair of dates (P < 0.05). Comparisons between stem $\delta^{18}$O values versus fog/rain or shallow soil water
were performed using Students t-tests. Statistical comparisons to deep-soil water δ^{18}O values could not be performed since this source could not be sampled directly and only a single deep-soil δ^{18}O value with no associated variance could be estimated. This estimate was based on the cumulative δ^{18}O values of rainwater samples, weighted for amount of each sample (Clark and Fritz, 1997), a method that provides a reliable representation of deep-soil δ^{18}O, especially in wet years as seen during this study.

RESULTS

Climate Variation

Average annual rainfall at the Catalina airport over the past 57 years (1949 to 2005) was 298 mm. Most rain falls between October and April with a mean of 66.0 mm (± 42.5) per month during this period (Figure 3A); February is the wettest month, receiving 145 mm on average. There is very little summer rain compared to winter amounts; rainfall from May to September averages 9.8 mm per month (± 5.4) with the driest month being July (3.4 mm ± 0.2).

![Figure 3](image-url)

**Figure 3.** Climate data from Catalina airport, approximately 1.6 km from the oak woodland study site. (A) Average monthly rainfall (1949-2005), and (B) average number of fog-days (2001-2005). Error bars are ± 1 SE.

In contrast to rainfall, fog events occur most frequently during the summer period (Figure 3B), accounting for 52% of the annual number of fog days (74 d ± 9, 2001 to 2005). On average, 15 (± 2) days per month are classified as fog-days between May and September with June being the peak month for fog (17 d ± 3).

The mean number of fog days per month between October and April is 10 d (± 1) with January having the least (7 d ± 2).

During the 2005 study period, total rainfall recorded at the Catalina airport was 555.8 mm, almost double the annual average. Although this qualified as the sixth wettest calendar year since 1949, the pattern of monthly precipitation closely followed historical trends (Figure 4A). February was the wettest month (236.0 mm) with no measurable rain during June and July. Fog events during 2005 also corresponded to longer-term patterns (Figure 4B). May and June experienced the most frequent number of fog days (16 and 17, respectively) while most winter months had fewer than 7 days of fog.

**Figure 4.** Monthly rainfall (A) and number of fog-days (B) in each month during the 2005 study period. Data are from the Catalina airport located 1.6 km from the oak woodland study site.

**Canopy Influence on Rain and Fog Input**

For eight out of 12 collection periods, the amount of water that accumulated in the fog/rain collectors was significantly different between at least two of the four canopy cover classes (P < 0.005; Table 1). Regardless of water input type (rain or fog), collectors under a healthy canopy usually accumulated less water than those under all other canopy classes (Table 1).
In January and early March, collectors under full canopies had significantly less water than those in the open and under partial or dead canopies. It also appeared that a full canopy inhibited fog drip during several summer collection periods. On four of the six summer collection dates, full canopy collectors had virtually no water (< 0.1 mm) and for three of these periods, they had significantly (P < 0.05) less water than collectors in the open (Table 1). It was only during the highest rainfall periods (14 March – 6 April; 23 April – 24 May; and 31 September – 25 October) that the full canopy did not hinder throughfall of water (Table 1).

### Table 1. Amount of water collected (mean ± 1SE) by fog/rain collectors for each canopy class during sampling periods of 2005. Within each date, canopy classes having different letters are significantly different at P < 0.05 (Tukey post-hoc test).

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>No Canopy</th>
<th>Dead Canopy</th>
<th>Partial Canopy</th>
<th>Full Canopy</th>
</tr>
</thead>
<tbody>
<tr>
<td>12-Jan</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>31-Jan</td>
<td>15.1 ± 2.80</td>
<td>12.7 ± 2.58</td>
<td>14.5 ± 2.71</td>
<td>11.9 ± 1.83</td>
</tr>
<tr>
<td>27-Feb</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>7-Mar</td>
<td>7.5 ± 0.24</td>
<td>8.2 ± 0.78</td>
<td>8.0 ± 0.70</td>
<td>4.6 ± 0.35</td>
</tr>
<tr>
<td>13-Mar</td>
<td>0.2 ± 0.03</td>
<td>0.4 ± 0.07</td>
<td>0.7 ± 0.23</td>
<td>0.1 ± 0.04</td>
</tr>
<tr>
<td>6-Apr</td>
<td>29.6 ± 1.63</td>
<td>29.1 ± 2.21</td>
<td>31.0 ± 2.76</td>
<td>20.8 ± 3.05</td>
</tr>
<tr>
<td>22-Apr</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>24-May</td>
<td>29.4 ± 2.51</td>
<td>25.8 ± 2.07</td>
<td>32.4 ± 3.52</td>
<td>24.2 ± 2.19</td>
</tr>
<tr>
<td>20-Jun</td>
<td>1.6 ± 0.11</td>
<td>0.9 ± 0.19</td>
<td>0.6 ± 0.09</td>
<td>0.1 ± 0.07</td>
</tr>
<tr>
<td>15-Jul</td>
<td>0.1 ± 0.04</td>
<td>0.1 ± 0.03</td>
<td>0.1 ± 0.03</td>
<td>&lt; 0.1 ± 0.03</td>
</tr>
<tr>
<td>3-Aug</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>25-Aug</td>
<td>0.8 ± 0.10</td>
<td>0.1 ± 0.07</td>
<td>0</td>
<td>&lt; 0.1 ± 0.01</td>
</tr>
<tr>
<td>10-Sep</td>
<td>0.4 ± 0.07</td>
<td>0.1 ± 0.07</td>
<td>&lt; 0.1 ± 0.01</td>
<td>0 ± 0.00</td>
</tr>
<tr>
<td>30-Sep</td>
<td>6.9 ± 0.35</td>
<td>2.7 ± 0.36</td>
<td>2.9 ± 0.28</td>
<td>2.3 ± 0.89</td>
</tr>
<tr>
<td>25-Oct</td>
<td>54.8 ± 1.06</td>
<td>44.3 ± 1.91</td>
<td>49.7 ± 2.03</td>
<td>50.7 ± 2.76</td>
</tr>
<tr>
<td>13-Dec</td>
<td>22.0 ± 2.20</td>
<td>16.8 ± 1.98</td>
<td>23.3 ± 3.06</td>
<td>15.7 ± 1.81</td>
</tr>
<tr>
<td>Totals</td>
<td>168.4</td>
<td>141.2</td>
<td>163.2</td>
<td>130.4</td>
</tr>
</tbody>
</table>

* Amount of water exceeded collector capacity and was not measured on these dates
Fog/rain collectors under partial canopy trees also accumulated less water in general than collectors in the open (Table 1). This difference was statistically significant (P < 0.05) for five of the collection periods, all of which occurred during very low (< 7 mm) water input periods.

The amount of water that accumulated in fog/rain collectors under trees with dead canopies was usually not significantly different than that in the open (Table 1). However, on the three dates that there was a significant difference (P < 0.05), the amount of water found in the open collectors did not exceed 1.6 mm.

**Oxygen Isotope Ratios of Water Sources and Plants**

The mean oxygen isotope ratio of winter water input (January through mid-March) was -7.09‰, with February having the most negative δ¹⁸O (-9.10‰ ± 0.27; Figure 5). During this period, rain dominated the water input, however, as the season progressed the δ¹⁸O of late spring and early summer water samples became increasingly enriched, potentially due to increased fog contributions (Figs. 4B and 5). In mid-summer, δ¹⁸O values for water inputs ranged from 0.26‰ (± 0.99) in June, to -4.77‰ (± 0.01) in August (Figure 5). These enriched values are a characteristic of California fog and small summer precipitation events (Ingraham and Matthews 1990; Clark and Fritz 1997).

Heavy rainfall between mid-January and May saturated soils, leading to mean soil δ¹⁸O values at 20 cm of -6.41‰ (± 0.80) for these months. In summer (June-August) these soil values increased to -2.46‰ (±1.00), as expected due to evaporation and summer fog/rain input (Figure 5). In contrast, mean δ¹⁸O of stem water remained relatively constant throughout the year, although there was significant variation across seasons (F = 11.1, P < 0.001). In January and March, mean δ¹⁸O of stem water (-5.25‰ ± 1.19 and -7.18‰ ± 0.65, respectively) was low and closely matched winter input values (-5.55 to -9.10‰; Figure 5). Stem-water values increased significantly between March and May (to -5.48‰, ± 1.01; P < 0.05) but summer stem-water δ¹⁸O values, including August (-6.07‰, ± 0.65), were always significantly lower than water input values during this season (P < 0.001 for all comparisons; Figure 5).
**Figure 5.** Oxygen isotope ratios of water from fog/rain collectors (solid circles, averaged for all treatments), soil (solid triangles) and plants (oaks, open squares) throughout 2005 at the Twin Rocks oak woodland site. Values shown are means ± SE.

**DISCUSSION**

**Quantification of Fog Input**

Evaluation of climate, stable isotope and fog/rain collector data indicate that very little of the annual water input into the oak woodland ecosystem in the Twin Rocks area of Santa Catalina Island comes from fog. However, this small input may be important during the very dry summer months. Indeed, between 24 May and 30 September 2005 there were 58 fog days, and over this period, 9.8 mm of water accumulated in the fog/rain collectors versus only 7.6 mm being recorded by the rain gauge tip bucket (Table 2), a difference of 29% (2.2 mm). In addition, our fog input calculations may be slightly underestimated since it is assumed that the rain gauge (tip bucket) records only rainfall events, but it is possible that fog events are occasionally misclassified as rain events when the tip threshold of the tip bucket (0.25 mm) is achieved quickly, as might occur during very dense fog events. Unfortunately, there is no means to determine if, and how often, such misclassifications occur. Our study was limited to a single year and one of the wettest on record, but even in very dry years, this small amount of fog input is probably not enough to contribute directly to plant water uptake, especially when spread out over more than a few days. Such input may have important consequences for other ecosystem processes, such as soil microbial activity, however (Schwinning and Sala 2004; Potts et al. 2006).

Such low fog input was not expected for this woodland given that studies on other Channel Islands have found relatively large amounts of water input from fog and clouds (Estberg 2001; Fischer and Still 2007). However, across a topographically diverse landscape, such as that found on Catalina Island, fog density can be highly variable in space and time (Fischer and Still 2007). Indeed, satellite data showing cloud cover for summer months over Catalina (2000–2006; A. P. Williams, unpublished) suggest that the low fog input measured at the Twin Rocks study site is probably representative of most of the northeast-facing areas of the Island, but that much higher input is likely on the west and southwest-facing portions. Interestingly, these parts of the island have yet to show any evidence of oak mortality, as found in the Twin Rocks area (Figure 1).

**Table 2.** Climate data for summer 2005: Fog-days were measured at the Catalina airport. Rain was measured by a tip-bucket at the field site, and fog/rain amounts are shown for the Open and Full-Canopy collectors at the field site.

<table>
<thead>
<tr>
<th>Collection period (Summer 2005)</th>
<th>Fog-days at airport (d)</th>
<th>Rain at Field Site tip-bucket (mm)</th>
<th>Fog/rain in open collectors (mm)</th>
<th>Fog/rain in full-canopy collectors (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5/25 - 6/20</td>
<td>22</td>
<td>1.00</td>
<td>1.62</td>
<td>0.11</td>
</tr>
<tr>
<td>6/20 - 7/15</td>
<td>14</td>
<td>0.00</td>
<td>0.11</td>
<td>0.04</td>
</tr>
<tr>
<td>7/15 - 8/03</td>
<td>4</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>8/03 - 8/25</td>
<td>6</td>
<td>0.50</td>
<td>0.76</td>
<td>0.00</td>
</tr>
<tr>
<td>8/25 - 9/10</td>
<td>4</td>
<td>0.00</td>
<td>0.41</td>
<td>0.00</td>
</tr>
<tr>
<td>9/10 - 9/30</td>
<td>8</td>
<td>6.10</td>
<td>6.94</td>
<td>2.31</td>
</tr>
<tr>
<td>Total</td>
<td>58</td>
<td>7.60</td>
<td>9.84</td>
<td>2.46</td>
</tr>
</tbody>
</table>

Impact of Canopy Density on Water Input

Canopy density did not influence the amount of water accumulation under trees during large (> 20 mm) rainfall events (Table 1). However, canopy density had a significant effect on rain through-fall and fog drip when collectors received < 20 mm of water (Table 1), especially during the low-input summer months.

On average, collectors under healthy, full canopies collected 75% less water (7.4 mm) in the summer than collectors in the open (Table 2), and 22% less water throughout the year. This is contrary to the prediction that fog drip would increase with canopy density, as found by Dawson (1998) under the canopy of coastal redwood trees of Northern California. One possible explanation for low fog drip and through-fall is that canopy storage capacity (the quantity of water that can be held on the aerial portions of a plant) may be relatively high for oaks. This capacity depends on the surface area of leaves and bark, their roughness, orientation, arrangement, and wettability (Corbin et al. 2005). Unlike redwoods and other conifers with needle-like, vertically-oriented leaves, oaks have relatively broad, randomly-oriented leaves that appear to have a high water holding capacity. With such leaves, the oak trees (especially ones with high canopy areas) likely restrict through-fall and provide a greater opportunity for accumulated fog droplets to evaporate before falling to the ground.

Thermal radiation from the oak canopy will also affect sub-canopy water input. This would be especially true for water derived from dew, since droplet formation would be reduced on a sub-canopy collector receiving the additional radiation from the canopy as compared to a collector in the open.

Although the exact cause remains unresolved, collectors in the open received higher water input than those under the oak canopy (Table 1). This result was unexpected but has important implications in the oak woodlands of Catalina. It indicates that inter-canopy species – most of which are non-native grasses – are receiving additional water that would otherwise not be available under a contiguous, healthy oak canopy. This water supplement, 29% over the entire year and 75% in summer, may contribute to the success and spread of these alien species.

Tracing Water Use by Oaks Using Stable Isotopes

Rainfall in the winter of 2005 was very high and continued late into spring (May 24th). The annual δ¹⁸O mean of -7.3‰ was strongly influenced by the low δ¹⁸O values of these winter rains, but over the entire year the δ¹⁸O of input waters varied greatly. These δ¹⁸O values became increasingly enriched (higher values) from spring into summer due to the decrease of winter rain activity and an increase of input from fog and locally generated (convective) rain storms. These summer rains have higher δ¹⁸O values than winter rains because they are formed at warmer temperatures and from a water source that is more proximal to Catalina, reducing the rain-out effect (Clark and Fritz 1997) that causes a decrease of δ¹⁸O.

In spite of the abundant winter rainfall, δ¹⁸O values of water in the upper-soil layers became significantly enriched between winter and late summer. The addition of ¹⁸O-rich fog or dew may have caused some increase of δ¹⁸O in this soil layer, but evaporation, which preferentially eliminates ¹⁶O from surface soil water, probably accounted for a greater portion of this isotopic change. Regardless of the process, the fluctuation of δ¹⁸O in shallow soil layers provides a baseline to which plant stem δ¹⁸O values can be compared for the analysis of plant water-source use.

Despite fluctuations of δ¹⁸O spanning -9.1‰ to 0.3‰ for water input sources (rain or fog) and -6.4‰ to -2.5‰ for surface-soil water, the δ¹⁸O values of plant stem water remained relatively low and less variable.

Water in deep-soil layers tends to have more consistent δ¹⁸O values because it is buffered from the enriching effects of evaporation and of minor water inputs such as fog (Clark and Fritz 1997). It is also the reservoir that integrates inputs throughout the year, and is therefore most strongly influenced by deeply saturating abundant winter rains, with low δ¹⁸O values. The large rain events of late 2004 and early 2005 most likely saturated all soil layers with water of low δ¹⁸O values. As such it is no surprise that δ¹⁸O values of oaks on 12 January and 27 February were very similar to rain input values at this time (Figure 5).

Although stem water δ¹⁸O values suggest that oaks are primarily using deep-water, they may not be limited to this source. For example, in late spring and into summer, when δ¹⁸O values of water inputs and upper-soil layers increased, stem δ¹⁸O values also increased slightly (Figure 5). Indeed, stem δ¹⁸O values in May were significantly higher (P < 0.05) than those in February; however, they were still much lower than the δ¹⁸O of fog water inputs. This small increase between months suggests that some water from the upper soil layers might be present in stem water during this period of the year. Also of note is that δ¹⁸O values of stem water returned to a lower value (-6.1‰) late in the summer in spite of no new rain water input over this period and shallow soil water increasing to -2.5‰ (Figure 5). This change may indicate a shift back to deeper water sources during late summer when little to no surface soil water is available, a response also reported for Quercus havardii in the arid Colorado Plateau (Gebauer and Ehleringer 2000) and for many other trees that experience seasonal drought (e.g., Smith et al. 1991; Meinzer et al. 1999). Such shifts in water use are likely to be beneficial in systems where deep water is more reliably available throughout the year, but nutrients are found in upper soil layers.

Summary

A primary objective of this study was to determine if fog drip provided supplemental water to the oak woodlands of Santa Catalina Island during summer. It is clear that fog occurs regularly throughout the summer (58 d) and may increase the amount of summer water input by 29 %. But given the small amount of water this actually represents (2.2 mm), this input may not have a significant impact on the water budget of most plants in this system. A greater impact on water input was due to canopy effects. For all but one sampling period, the canopy of healthy oak trees reduced the input of fog drip and rainfall that reached the forest floor, at times accounting for up to a 75 % reduction in water input (7.4 mm more in open spaces vs. under the canopy in summer 2005). This amount could have significant impacts on plant growth, especially of herbaceous non-native species in the canopy interspaces.

The results of this study also suggest that Quercus pacifica trees of Santa Catalina Island are primarily using water from a deep, isotopically consistent water source which appears to be replenished by annual winter rains. However, evidence from δ¹⁸O ratios in stem water indicates that a small proportion of surface water is also used during the spring and early summer, although it is not possible at this time to determine if this isotopically enriched water is derived from fog input or residual rainwater that has become enriched due to evaporation.

Although most evidence from this study suggests that fog does not supply a substantial amount of water to the trees of this oak woodland community, the persistence of fog in summer may serve other important roles such as reducing air temperature, thereby allowing more efficient leaf-level gas exchange (higher photosynthesis rate and lower transpiration) and reducing ecosystem evapotranspiration. Understanding such effects may be important to the preservation of these woodlands and warrants further investigation, especially since a significant decline in the oak populations has been noted recently, with replacement by
non-native annual grasslands (D. Knapp, pers. comm.). As canopy thinning and oak mortality continue, more water may actually be available for these non-native grasses, due to the additional input of atmospheric water. As such, oak tree dieback could facilitate non-native grass success and the eventual conversion of these native woodlands to grasslands.

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LITERATURE CITED


