Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species

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ABSTRACT

Aim Fog drip is a crucial water source for plants in many ecosystems, including a number of global biodiversity hotspots. In California, dozens of rare, drought-sensitive plant species are endemic to coastal areas where the dominant summer moisture source is fog. Low clouds that provide water to these semi-arid ecosystems through fog drip can also sharply reduce evaporative water losses by providing shade. We quantified the relative hydrological importance of cloud shading vs. fog drip. We then examined how both factors influence the range dynamics of an apparently fog-dependent plant species spanning a small-scale cloud gradient.

Location The study area is on Santa Cruz Island off the coast of southern California. It is near the southern range limit of bishop pine (Pinus muricata D. Don), a tree endemic to the coasts of California and Baja, Mexico.

Methods We measured climate across a pine stand along a 7 km, coastal–inland elevation transect. Short-term (1–5 years) monitoring and remote sensing data revealed strong climatic gradients driven primarily by cloud cover. Long-term (102 years) effects of these gradients were estimated using a water balance model.

Results We found that shade from persistent low clouds near the coast reduced annual drought stress by 22–40% compared with clearer conditions further inland. Fog drip at higher elevations provided sufficient extra water to reduce annual drought stress by 20–36%. Sites located at both high elevation and nearer the coast were subject to both effects. Together, these effects reduced average annual drought stress by 56% and dramatically reduced the frequency of severe drought over the last century. At lower elevation (without appreciable fog drip) and also near the inland edge of the stand (with less cloud shading) severe droughts episodically kill most pine recruits, thereby limiting the local range of this species.

Main conclusions Persistent cloud shading can influence hydrology as much as fog drip in cloud-affected ecosystems. Understanding the patterns of both cloud shading and fog drip and their respective impacts on ecosystem water budgets is necessary to fully understand past species range shifts and to anticipate future climate change-induced range shifts in fog-dependent ecosystems.

Keywords California, Channel Islands, cloud shading, drought stress, evapotranspiration, fog, Pinus muricata, range limits, Santa Cruz Island, water balance.
Coastal fog and overcast conditions both result from low stratus cloud formation. The distinction is that ‘overcast’ is a cloud layer above the surface that obscures all (or most of) the sky, while ‘fog’ is in contact with the surface and reduces visibility to below 1 km (National Weather Service, 2007). Crucially, the same stratus cloud that is fog at one site on a coastal mountain can manifest as an overcast layer for sites at lower elevations (Fig. 1). Both fog and overcast can reduce the severity of plant drought stress during the summer rainless season, though via different mechanisms. Previous studies in the California fog belt have shown that stratus clouds can enhance the availability of water to the ecosystem during the rainless summer through fog drip, and some have demonstrated uptake of fog water by endemic plants (Azevedo & Morgan, 1974; Jacobs et al., 1985; Ingraham & Matthews, 1995; Dawson, 1998; Burgess & Dawson, 2004; Cole, 2005; Corbin et al., 2005; Kennedy & Sousa, 2006). In areas of frequent fog and favourable canopy structure, such as coast redwood forests, fog drip has been shown to contribute hundreds of millimetres of water to the soil surface annually (e.g., Jacobs et al., 1985; Dawson, 1998).

The other mechanism by which stratus clouds can potentially ameliorate plant water stress is by reducing ecosystem water loss. This effect has received less attention from researchers (but see Burgess & Dawson, 2004). Stratus clouds can retard water loss by absorbing and reflecting large amounts of solar radiation, thus greatly reducing net radiation at the surface. This cloud shading leads to lower air and leaf temperatures, increased relative humidities and smaller vapour pressure deficits. The overall effect of these changes in microclimate is to substantially reduce atmospheric evaporative demand and potentially decrease ecosystem water losses during the dry season. These reductions in water stress are even thought to have been consistent enough over long time periods to have allowed the evolution of larger leaf sizes in insular species within the fog belt (Hochberg, 1980). Many of the relict and endemic species throughout California’s fog belt are quite sensitive to drought (Raven & Axelrod, 1978), and so any change in summer water stress, whether from rainfall, fog drip or cloud shading, is likely to affect species range limits and long-term population viability.

**Fog climatology**

Like most of California, the coastal fog belt is characterized by a mediterranean climate, with cool, rainy winters and warm, rain-free summers. The annual summer drought ranges from 3 to 7 months, with a longer duration further south. Summer cloud cover is most common along the immediate coast, with both frequency and duration decreasing further inland. The tops of the summertime marine stratus clouds along the coast of California are most commonly below 400–500 m, which roughly corresponds to the base of the coastal inversion (Leipper, 1994). As a result of summertime inversion base height dynamics, coastal sites above 400 m or so experience a decreasing frequency of fog, sites below c. 200 m experience an increasing percentage of stratus cloud events as overcast rather than as fog, and sites at elevations of roughly 200–400 m experience the most frequent fog. Coastal mountains generally restrict the inland movement of the marine stratus layer to areas within a few km of the immediate coast (with the exception of some larger drainages). During stratus cloud events, these clouds tend to form and/or intensify overnight and then ‘burn off’ during the next day, usually evaporating progressively from inland areas towards the coast (Marotz & Lahey, 1975; Filonczuk et al., 1995; Fischer & Still, 2007).

**Fog belt biogeography**

Dozens of plant species are endemic to the fog belt. An accepted explanation for these narrow, coastal distributions is that widespread drought-sensitive species suffered range collapse as the interior of California became drier and more climatically variable following uplift of the Coast Ranges during the Pliocene and Quaternary (Raven & Axelrod, 1978).
During this transition, summer rainfall was also eliminated across most of California, with tremendous implications for drought-sensitive species. One well-documented example of a drought-sensitive species with such a relict distribution is the coast redwood (Sequoia sempervirens D. Don). Many studies have investigated the role of fog drip in maintaining stands of coast redwood and other coastal species, particularly by ameliorating the annual drought resulting from rainless summers (Leyton & Armitage, 1968; Azevedo & Morgan, 1974; Ingraham & Matthews, 1995; Dawson, 1998; Burgess & Dawson, 2004; Cole, 2005; Corbin et al., 2005). More recently arrived or evolved species, such as Monterey pine (Pinus radiata D. Don), may have spread in small pockets of equable habitat along the coast during the Pliocene (Millar, 1986, 1999), expanding and contracting in response to repeated large climate shifts throughout the Quaternary (Heusser, 1995). After the Last Glacial Maximum, the southern range limits of many California coastal species retreated tens to hundreds of kilometres north as climate warmed (Chaney & Mason, 1930, 1933; Mason, 1934; Raven & Axelrod, 1978; Millar, 1999). All of these fog-belt endemic species appear variously threatened by the projected warming and drying of the climate in the coming decades (IPCC, 2007). Also, regional climate model simulations project changes to the upwelling regime along California’s coast with climate warming (Snyder et al., 2003), a phenomenon that has already been documented in other eastern boundary coastal upwelling systems (Bakun, 1990; Schwinger & Mendelssohn, 1997; Mendelssohn & Schwinger, 2002; Snyder et al., 2003). Because fog formation is closely linked to upwelling, these projections suggest alterations in coastal fog dynamics. Changes in fog patterns, in addition to overall drying and warming, may lead to large changes in the location of suitable habitat for coastal endemic species.

Study goal

The goal of the current study was to investigate the separate impacts of fog drip and cloud shading in maintaining the ranges of coastal endemic species. Our first challenge in meeting this goal was to quantify the degree to which shading by clouds, independent of any fog drip, significantly reduced summer ecosystem drought stress. We also quantified the addition of water from fog drip and the resulting spatial patterns in water availability. The second challenge was to quantify the long-term effects of both cloud shading and fog drip on the range dynamics of a fog-belt endemic species. We utilized a combination of intensive field sampling, water balance modelling and remote sensing to quantify these effects in one part of the fog belt, on Santa Cruz Island off the coast of southern California. Our study focused on a stand of the drought-sensitive, fog-belt endemic species bishop pine (Pinus radiata D. Don). This tree grows in a number of scattered groves along the coast of central California, never more than c. 30 km from the coast (Fig. 2a; Griffin & Critchfield, 1972; Lanner, 1999). In the northern part of the range of bishop pine, where rain and fog are greater and evapotranspiration is generally lower, stands are larger and more numerous, and trees are generally taller and grow more densely. Fossil records of this and related species are likewise limited to the coast (Axelrod, 1967; Raven & Axelrod, 1978; Millar, 1986). Our study site on Santa Cruz Island focused on the southern-most large stand of bishop pine.

Both the Materials and Methods and the Results sections are organized by time-scale. We first discuss short-term monitoring of water availability across our transect. These short-term efforts to characterize spatial patterns combine both remote sensing and extensive field measurements over 1–5 years. We then describe the water balance modelling experiments we conducted using 102 years of weather data to assess likely long-term biogeographical impacts of these spatial patterns.

MATERIALS AND METHODS

Site description

Santa Cruz Island (SCI), the largest of the California Channel Islands, is located c. 40 km south of Santa Barbara (Fig. 2a). The island is 38 km long and is bisected by the rift valley of the SCI fault. Steep east–west ridges rise both north and south of the fault (Fig. 2b). Bishop pines grow in three stands on the island, with approximate stand boundaries shown by white polygons in Fig. 2c. These stands form the southern end of the main distribution for this species and each stand is surrounded by more xeric shrubland. (There is one small outlying stand in northern Baja; Lanner, 1999). Within the SCI stand boundaries, pine densities are far from uniform. Our study was confined to the large western stand. In this stand, the highest pine densities occur near the centre (50–80% canopy cover). Towards the eastern and western edges of the stand, pine coverage decreases until there are only a few scattered trees in a matrix of chaparral shrubs.

We installed a network of 12 weather stations spanning and bracketing the western stand (Fig. 2b). The pines and the weather stations are located primarily on north-facing slopes, and site elevations range from 80–400 m. The stations are numbered 1–12 from coast to inland and span a 7-km gradient from the western-most to eastern-most pines within this stand (Fig. 2b). Sites 1 and 10 were installed in the late 1990s, while the remaining sites were installed between December 2003 and April 2004.

Rainfall on SCI is highly variable (Fig. 3). Rainfall is also highly seasonal, averaging more than 80 mm during each month of the December–March rainy season (79% of the average annual total of 509 mm falls during this period). Rainfall averages <10 mm during each month of the May–September dry season (4% of the average annual total falls during these months). Rainfall is also highly variable for any given month from year to year. On SCI, the standard deviation of rainfall for a given month approximately equals the mean rainfall for that month (except for February, which has a mean rainfall of 116 mm and a standard deviation of 98 mm). The interannual variability of annual rainfall is exceptionally high,
similar to that of arctic and desert ecosystems that have much lower total mean annual rainfall (Knapp & Smith, 2001).

Patterns in cloud cover

We evaluated the degree of cloud shading from fog and overcast by analysing shortwave radiometer (pyranometer) data from the weather stations along our transect (Licor Li-200X, Li-190SB and Hobo S-LIA; LI-COR Environmental, Lincoln, NE, USA and Onset Computer Corp., Bourne, MA, USA). We then used remote sensing data to spatially extend cloud cover information across SCI. Quarter-hourly and average daily radiometer data from each station were used to generate idealized ‘clear sky’ curves for each station. These ‘clear-sky’ radiation curves were manually generated as the sum of two to three annual sine curves to fit the seasonal pattern of observed clear days for each site (Fig. 4a). The difference between modelled clear sky radiation and observed radiation could then be attributed largely to cloud shading. (While aerosols other than cloud droplets could affect surface irradiance, their role is deemed insignificant in this area compared with the frequent, thick stratus cloud layers.) We calculated a daily ‘sunniness index’ for each station as 0–100% of the expected clear-sky radiation for that station for that date. On clear days, the sunniness index was 100% while on cloudy days it frequently dipped below 30%.

Evapotranspiration modelling

Irrigation managers have standardized methods for calculating evaporative demand as potential evapotranspiration (PET). The PET is the amount of water that would evaporate from

Figure 2  Maps of Santa Cruz Island (SCI). (a) Location map has stars showing areas with stands of bishop pines (Pinus muricata D. Don; data from Griffin & Critchfield, 1972). Note large gaps in range. (b) Elevation map of Santa Cruz Island (low elevations are dark, high elevations light) shows our weather stations deployed on an east–west transect throughout the island’s main, western stand of bishop pines. Stations are numbered 1–12, west to east. The island lies 30 km off the coast of southern California, is 38 km long, and reaches 753 m a.s.l. just north of site 11. Site 10 is 437 m a.s.l. (c) Shading shows spatial variability in summer cloud cover, which is represented here as the average percentage of summer mornings (3 July–30 September at 10:30 AM Pacific Standard Time) that are cloudy for 5 years (2000–04) (from MODIS satellite images; data from Williams, 2006). White polygons indicate approximate stand boundaries of bishop pine. In the western stand, pine density is highest in the centre of the stand, with only a few scattered trees towards the eastern and western edges.
plants and soils under given conditions of temperature, humidity, radiation and wind assuming unlimited water availability. Many different PET formulae of varying complexity have been developed over several decades. The most rigorously tested are derivatives of Penman–Monteith (P-M), which take into account temperature, relative humidity, solar radiation, wind speed impacts on aerodynamic conductance and vegetation properties that influence surface conductance (McKenney & Rosenberg, 1993). These models are meant to be run at hourly or daily time steps. The preferred model, when high-quality weather data are available, is the latest P-M derivative (Snyder & Eching, 2004; Allen et al., 2005). This model (see also the Appendix) has been coded into a downloadable, user-friendly spreadsheet (Snyder & Eching, 2004). We used this spreadsheet to estimate hourly reference evapotranspiration from static site parameters and hourly wind speed, solar radiation, temperature and dew point data.

The P-M equation we used calculates ‘reference ET’ (ETref) for a ‘tall canopy’, similar to alfalfa (Snyder & Eching, 2004). Since most vegetation transpires at different rates from fields of alfalfa, a ‘crop coefficient’ is used to scale ETref up or down to estimate PET for a specific vegetation type (Dunne & Leopold, 1978; Costello et al., 2000). Pines transpire significantly less water than alfalfa, even if they are well watered (due to lower hydraulic and stomatal conductivity and lower leaf-level photosynthetic capacity; Larcher, 2003). Careful measurements...
of another maritime pine species (*Pinus pinaster* Ait.), when well watered, showed transpiration rates to be 60% of P-M ETref (Granier & Loustau, 1994). We have adopted this value to estimate PET for bishop pines (and the other plants in the surrounding chapparal community, all of which have similar or lower water requirements; Costello et al., 2000). In the remainder of this paper, we will use ETref to refer to the values predicted by the P-M equations and PET to mean ETref values that have been scaled down to 60% to estimate evaporapotranspiration for bishop pine stands. (The precise value used to scale PET affects patterns of water availability across the transect in absolute but not relative terms).

The dense network of weather stations across our transect allowed us to quantify the gradient in evaporative demand. We calculated hourly PET for each of the sites that had a functional datalogger for the warm season (March–October) of 2005. We chose this time period because it brackets the period of maximum drought stress. It also includes the period of maximum tree growth rates as observed by dendrometers installed across the transect; in 2005 and 2006, the maximum growth rates occurred between March and July, with variations related to the timing of final rainfall events of the preceding rainy season (Williams, 2006).

**Water balance modelling**

In order to extend our analysis across more years than those for which we had weather data with high spatial and temporal resolution, we used 102 years of monthly temperature and rainfall records to drive a simple water balance model. This model accounts for interactions among rainfall, PET and soil moisture storage, and it estimates both actual evaporapotranspiration (AET) and Deficit, which is a measure of drought stress. Running this water balance model for the last century provided insights into how cloud patterns may have driven spatio-temporal differences in water availability and drought stress.

The water balance model we used was modified from Thornthwaite & Mather (1955, 1957), and was driven by monthly precipitation and estimated monthly PET. All other terms were calculated from these two quantities as follows (in units of mm of water per unit area; see the Appendix). Incoming precipitation left the system via run-off or evapotranspiration for bishop pines. On a monthly basis, a small percentage (3%) of precipitation was diverted immediately to run-off as storm flow (Dunne & Leopold, 1978; Fig. 5b). This negative exponential roughly captured the increasingly negative soil water potential that occurs as soil water content is decreased. If there was not sufficient plant-available soil moisture, the shortfall between PET and AET was termed Deficit. Note that in the water balance model we initially made no allowance for additions of water to the soil by fog drip, so that the only water input was from rainfall.

Many water balance studies include additional terms that we omitted. In particular, canopy interception is generally less important in this ecosystem than in many others as the rain comes in a relatively few, intense storms. Groundwater flow and delayed run-off were deemed unimportant for determining plant-available water on the relatively steep slopes that typify SCI and the Californian coast ranges.

**Constructing long-term time-series data**

The water balance model required monthly inputs of precipitation and PET. Rainfall at the main ranch on SCI has been measured continuously since 1904 (Fig. 2, Laughrin, 2005). However, rainfall can vary significantly over short distances in the coast ranges of California due to the rugged topography. To account for this spatial variation in rainfall, we regressed monthly totals at sites 1 and 10 against the long-term record from the main ranch (*n* = 76 for the period from 1998 to 2005, with gaps). Site 10 received the same amount of rainfall as the ranch (100.4%, *R*² = 0.92). Site 1 received 70% as much rainfall as the ranch (*R*² = 0.93). For Site 12, we regressed daily rainfall totals at Site 12 to daily totals at Site 10 (as a proxy for the ranch). Site 12 received 92% as much rainfall as Site 10 (*n* = 99 rainy days, 6 April 2004 to 11 November 2005, *R*² = 0.96). For the model runs below we used rainfall estimated for each site (i.e. ranch rainfall multiplied by 0.70, 1.0 or 0.92 for Sites 1, 10 and 12, respectively).

There are no long-term records of ETref for our site, and we estimated PET from soil moisture storage, which is a measure of drought stress. To calculate ETref, we used the Blaney–Criddle (B-C) formulation, which requires 0.70 to 1.0 or 0.70 to 0.92 for Sites 1, 10 and 12, respectively. The water balance model required monthly inputs of precipitation and PET. Rainfall at the main ranch on SCI has been measured continuously since 1904 (Fig. 2, Laughrin, 2005). However, rainfall can vary significantly over short distances in the coast ranges of California due to the rugged topography. To account for this spatial variation in rainfall, we regressed monthly totals at sites 1 and 10 against the long-term record from the main ranch (*n* = 76 for the period from 1998 to 2005, with gaps). Site 10 received the same amount of rainfall as the ranch (100.4%, *R*² = 0.92). Site 1 received 70% as much rainfall as the ranch (*R*² = 0.93). For Site 12, we regressed daily rainfall totals at Site 12 to daily totals at Site 10 (as a proxy for the ranch). Site 12 received 92% as much rainfall as Site 10 (*n* = 99 rainy days, 6 April 2004 to 11 November 2005, *R*² = 0.96). For the model runs below we used rainfall estimated for each site (i.e. ranch rainfall multiplied by 0.70, 1.0 or 0.92 for Sites 1, 10 and 12, respectively).
We also calculated hourly P-M ETref from 1998 through 2005 (with some gaps) for sites 1 and 10 and for 2005 at site 12. When we regressed monthly B-C ETref against the monthly sum of hourly P-M ETref, the agreement was very good (Fig. 5c). We then used these regressions to hindcast monthly ETref (and PET) time series for sites 1, 10 and 12 back to 1904.

Representing fog drip at each site was more difficult. We collected fog drip at each site along the transect 2004–05 and found consistent spatial patterns related to local topography, generally increasing with elevation (Fischer & Still, 2007). Temporal patterns were more difficult, as the summer of 2005 had much more fog drip than 2004. To put these 2 years of spatially explicit data into a longer temporal context, we employed nearby airport weather records. Williams (2006) developed an index of summer fogginess based on the number of hours per day (between midnight and 10 AM) when weather observers at Oxnard and Santa Barbara airports reported cloud bases of different heights. These airports are 59 km east-north-east and 46 km north of site 10, respectively, across the Santa Barbara Channel and within 11 m of sea level. Summer stratus cloud layers tend to be relatively level across the Santa Barbara Channel so that months with many hours of low cloud on the mainland generally also have many hours of low cloud on SCI. The frequency with which cloud bases are observed below the altitude of a given site is related to the amount of fog drip, because fog drip can only occur at sites higher than the local cloud base. The fogginess index based on these airports is not a perfect proxy for fog drip at our sites on SCI for several reasons, but it does allow at least some insight into how our recent fog drip records fit into the long-term picture for the local region. Further, fog collection and solar radiation data collected at site 7, as well as tree-ring widths on Santa Rosa Island, are significantly and positively correlated with this fogginess index (Williams et al., 2008). The fogginess index is available for 49 years during which sufficient observations were recorded (1944–2005 with some gaps). For cloud bases of 400 m and lower, the fogginess index varied from 3.3 to 8.3 h per day. The summers of 2005 and 2004 were 32% and 10% foggier than average, respectively. To estimate ‘typical’ fog drip inputs, we adjusted downward the cumulative 2005 and 2004 summer fog collection values at each site by 32% and 10%, respectively. The results from both years were nearly identical (± 10 mm) at each site (data from Fischer & Still, 2007; typical values are listed in Table 1).

There was no strong correlation between the fog index and either of our long-term data sets (rainfall and PET), so building a continuous fog time series was problematic. Instead, we added the same ‘typical’ fog drip values to the water balance in every year. We added that annual fog drip in the model as extra monthly precipitation from June to September (distributed as 10%, 40%, 40%, 10%, respectively) to match observed seasonal patterns of fog drip (Goodman, 1985; Estberg, 2001; Ruiz, 2005; Fischer & Still, 2007). Given the limited data...
Table 1 Site characteristics and model results. Model run (a) takes into account differences in rainfall between the sites and serves as a reference point for subsequent model runs. Deficit is the difference between potential evapotranspiration (PET) and actual evapotranspiration (AET). Model run (b) shows that reduced coastal PET decreases both average and maximum drought stress by about a third compared to just 7 km further inland. Run (c) shows that the average amount of fog drip received at higher-elevation sites is sufficient to reduce drought severity by 19–36% (compared to run a). Run (d) includes both fog drip and PET reduction. The combined effect is a 36–56% reduction in average deficit. At site 10 (which receives both persistent cloud and significant fog drip) only 1989–90 had deficits > 400 mm, while such severe droughts were common at site 1 (little fog drip) and site 12 (little fog drip and little cloud cover).

<table>
<thead>
<tr>
<th>Site characteristics</th>
<th>Site 1</th>
<th>Site 10</th>
<th>Site 12</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance inland (km)</td>
<td>2.1</td>
<td>7.1</td>
<td>9.2</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>61</td>
<td>437</td>
<td>387</td>
</tr>
<tr>
<td>Avg. annual PET (mm)</td>
<td>681</td>
<td>766</td>
<td>916</td>
</tr>
<tr>
<td>Avg. annual rain (mm)</td>
<td>356</td>
<td>509</td>
<td>468</td>
</tr>
<tr>
<td>(as % of Ranch rain)</td>
<td>70%</td>
<td>100%</td>
<td>92%</td>
</tr>
<tr>
<td>Est. typical fog drip (mm)</td>
<td>10</td>
<td>139</td>
<td>178</td>
</tr>
</tbody>
</table>

(a) Reference case (holding PET constant, without fog drip)

| Avg. AET (mm) | 344 | 468 | 439 |
| Avg. deficit (mm) | 572 | 448 | 477 |
| Max. deficit (mm) | 809 | 753 | 768 |

(b) Effect of ΔPET only (without fog drip)

| Avg. AET (mm) | 339 | 449 | 439 |
| Avg. deficit (mm) | 342 | 318 | 477 |
| Max. deficit (mm) | 561 | 593 | 768 |
| Reduction of Avg. deficit by ΔPET | 40% | 29% | –% |
| Reduction of Max. deficit by ΔPET | 31% | 21% | –% |

(c) Effect of fog drip only (holding PET constant)

| Avg. AET (mm) | 354 | 597 | 609 |
| Avg. deficit (mm) | 562 | 319 | 307 |
| Max. deficit (mm) | 798 | 607 | 582 |
| Reduction of Avg. deficit by fog drip | 2% | 29% | 36% |
| Reduction of Max. deficit by fog drip | 1% | 19% | 24% |

(d) Effects of ΔPET and typical fog drip

| Avg. AET (with fog drip) (mm) | 349 | 570 | 609 |
| Avg. deficit (with fog drip) (mm) | 332 | 197 | 307 |
| max deficit (with fog drip) (mm) | 551 | 441 | 582 |
| Reduction of Avg. deficit by ΔPET plus fog drip | 42% | 56% | 36% |
| Reduction of Max. deficit by ΔPET plus fog drip | 32% | 41% | 24% |
| No. annual deficits > 400 mm (1904–2005) | 21 | 2 | 20 |
| years | years | years |

available and large uncertainties involved, more complex modelling of temporal variability in fog drip did not seem justified and would be likely to introduce additional errors in our analysis.

Long-term modelling experiments

We ran the water balance model for the three sites (sites 1, 10 and 12 from Fig. 2a) for the period 1904–2005 to look for temporal and spatial patterns in cumulative annual Deficit. All runs used the observed spatial patterns in rainfall and PET from site 12 (inland) at each site but also included ‘typical’ summer fog drip amounts at each site. Run C used PET from site 12 (inland) at each site but also included ‘typical’ summer fog drip and PET variations to simulate their combined impacts on water balance. Specifically, run B incorporated reduced PET at sites 1 and 10 as observed in the weather record (due to increased relative humidity and cloud shading at these more coastal sites) but did not incorporate fog drip at any site. Run C used PET from site 7 (near the centre of the stand) but did not incorporate fog drip at any site. Run D incorporated both fog drip and PET variations separately to quantify their individual impacts, while run D incorporated both fog drip and PET variations to simulate their combined impacts on water balance. Specifically, run B incorporated reduced PET at sites 1 and 10 as observed in the weather record (due to increased relative humidity and cloud shading at these more coastal sites) but did not incorporate fog drip at any site. Run C used PET from site 12 (inland) at each site but also included ‘typical’ summer fog drip amounts at each site. Run D included both fog drip and PET variations across the three sites (results are summarized in Table 1).

RESULTS

Spatial and temporal patterns of cloud cover

We wanted to know whether differences in frequency and intensity (opacity) of cloud shading across the transect were significant, and if so whether they appreciably reduced water loss through evapotranspiration. Cloud cover varies seasonally. The radiation record from site 7 (near the centre of the stand and having the most complete record) shows that the frequency and thickness of fog and cloud cover varied substantially over time (Fig. 4a). There were periods of pronounced reductions in mean daily solar radiation (W m⁻²), particularly around the June solstice (locally referred to as the ‘June gloom’). These radiation reductions were large and persistent, even when viewed over a 14-day running average.

Summer cloud shading decreases from the coast inland. This gradient of decreasing cloud shading from the coast is illustrated in Fig. 2c by a composite of morning MODIS satellite images across five summers (averaged across 2000–04). The resulting image shows the percentage of days that are cloudy at 10:30 AM Pacific Standard Time (PST) (Williams, 2006). At the western coast, c. 50% of days were cloudy at 10:30 AM, while in the centre of the stand the figure decreased to 35% and to <30% near the last few pines at the eastern (inland) edge of the stand (Fig. 2c). This metric serves as a proxy for overall cloud shading because clouds and fog tend to form or intensify overnight, burn off towards the coast the next morning, so that the spatial cloud patterns captured by morning MODIS images are representative of mean daily cloud patterns (Fischer & Still, 2007). The radiometer records for summers 2004–05 from our weather stations across the western stand show the same pattern of a steady decrease in...
cloud frequency and opacity from west to east for all hours of the day (not shown).

**Spatial and temporal patterns of evapotranspiration**

Calculated values of ETref across the transect showed that, with small exceptions related to local aspect, ETref increased consistently from the coast to inland. Throughout the 2005 warm season (March–October), hourly calculations of ETref at each site showed that seasonal mean ETref was 25–30% lower at the coastal sites than at the inland sites.

We tested the role of clouds in reducing ETref at individual weather stations. For example, clouds significantly reduced ETref at site 7 for three adjacent days in June 2005 (Fig. 4b). Hourly shortwave radiation observations show that 7 June was clear all day, while 8 June was cloudy in the afternoon, and 9 June was cloudy for most of the day. Temperature varied diurnally by 5°C on 7 June and early on 8 June, but then temperature dropped sharply as the cloud layer arrived in the late afternoon. Temperature variation was much more muted for the rest of the period. Similarly, relative humidity showed a moderate daily cycle until the arrival of the cloud layer, at which point relative humidity rose to 100% and remained unchanged for the rest of the period. These three variables, plus wind speed, are used in the P-M ETref formulation (Snyder & Eching, 2004; Allen et al., 2005).

The reduction in daily total ETref from 7 June (4.5 mm) to 9 June (1.5 mm) was 66%. This was due to the combined effects of reduced solar radiation, reduced midday temperatures and increased relative humidity, all of which were driven by increased clouds (wind speeds averaged c. 3 m s⁻¹ on both days). Reduced short-wave radiation not only limits the energy required for vaporization of water inside the leaf and at the soil surface, but it reduces surrounding air temperature and vapour pressure deficit. To test the relative impact of each weather component on ETref, we substituted hourly 9 June variables into the 7 June calculations one at a time. Low solar radiation (from 9 June) reduced ETref by 40% (holding all other variables at 7 June values). Increased relative humidity reduced ETref by 22%. Substituting temperature from 9 June (lower at midday, but higher at night) reduced ETref by 2%. Therefore, the primary driver of changes in ETref at a given site, under the relatively narrow ranges of temperature and relative humidity that typify our sites and the fog belt in general, is variation in solar radiation. Aerosols other than cloud droplets also reduce incoming solar radiation, but in this area of frequent thick stratus cloud cover their effects are comparatively small.

The spatial gradient in ETref across the transect is also driven primarily by variations in radiation. Across a landscape, radiation variations are strongly driven by aspect, but among our sites, primarily on north-facing slopes, we hypothesized that the strongest driver of radiation differences (and therefore differences in ETref) was the observed gradient in cloud shading. To test this hypothesis, we compared the daily coastal/inland gradient in ETref with the daily cloud-driven gradient in solar radiation (comparing sites 1 and 12, at opposite ends of the transect). We used the longest period of continuous hourly data, 17 March–12 July 2005 (which also generally coincided with the period of maximum tree growth, mid-March to mid-July; Williams, 2006). We calculated a daily cloud shading gradient as the sunniness index (0–100%) at site 12 (inland) minus site 1 (coastal). We also calculated a daily ETref gradient as the percentage difference between ETref at site 12 minus site 1 (Fig. 4c). The cloud shading gradient explained most of the difference in daily ETref. Mean daily ETref over this period was 4.9 mm at site 12, and 4.0 mm at site 1. Departures from the linear regression (of cloud shading gradient vs. ETref difference) are primarily on days with unusual altitude effects (e.g. a strong temperature inversion between Site 1 at 61 m and Site 12 at 387 m, or rain only at the higher site). The small positive intercept of the regression indicates a slightly higher ETref at site 12 even when cloud shading is equal, resulting from the slightly greater continentality of this site. In summary, ETref is significantly lower near the coast than just a short distance inland. Despite differences in elevation and continentality, most of that difference can be attributed to the observed differences in solar radiation resulting from increases in frequency and intensity of cloud shading near the coast.

**Spatial and temporal patterns of fog drip**

Fog water was collected and volumes were logged at each site with harp-style passive fog collectors (Fischer & Still, 2007). There were large spatial differences in the amounts of fog water collected during the 2005 dry season (10 May to 16 October; Fig. 6a). Site 1, at the lowest elevation, received a negligible amount, while sites 10 and 12 received substantial fog water inputs (Fig. 1). At site 10 we calibrated the fog collector against a throughfall collector placed immediately under a mature pine canopy. The regression estimated 30 mm of throughfall per litre of collected fog water, $R^2 = 0.74$ (Fischer & Still, 2007). This calibration allowed us to estimate how much fog drip a mature pine might collect at each site, irrespective of current pine abundance at each site. Under areas of similarly dense pine canopy, the fog water collected at site 10 could generate of the order of 175 mm of throughfall, or 34% of the mean annual rainfall at this site, using the above calibration. Assuming a similar relationship between throughfall and the fog collector at site 12 (which collected more fog water in fewer, larger events in 2004 and 2005; Fischer & Still, 2007), throughfall from fog drip might approach 225 mm. It should be noted that the long narrow leaves of conifers are more effective at collecting fog drip than the leaves of many other plants (Goodman, 1985).

Previous work has shown that fog drip can penetrate into the soil and increase soil water potential (Cole, 2005). We installed paired sets of soil water potential sensors from depths of 2–15 cm both inside and outside the tree canopy at site 7 (Fig. 6b). The two soil profiles are c. 10 m apart. The soil sensors outside the canopy had gone off scale as the soil dried (i.e. below −1.5 MPa) within 2 weeks after the last rain of the
season on 9 May 2005. By contrast, under the tree canopy, repeated fog drip events throughout the summer kept the upper soil moist into mid-August. We dug a soil pit under a canopy on an adjacent slope on 2 September 2005, and found the soil quite wet to the touch at the bottom of the soil profile (50 cm depth). This was 4 months after the last rain.

Water balance for an ‘average’ year

Modelling plant water availability during the growing season is more complicated than just assessing annual rainfall and PET. Other important factors include the timing of rainfall and seasonal changes in soil moisture storage. For areas with highly variable rainfall, year-to-year changes in soil moisture must also be considered. Given the extreme variability of rainfall throughout southern California both within and among years (Fig. 3), it is important to consider a broad suite of both wet and dry years in order to estimate how observed differences in quantities like PET actually affect availability of water to plants. Years with very high rainfall in a few storms may not provide as much summer moisture as years with moderate rainfall that occurs more evenly, or that falls later in the season. Water availability in low-rainfall years is strongly dependent on how wet the previous year was. Also, in very wet years, changes in PET have less of an impact on plant drought stress. Tracking this temporal variability required a running water balance in which monthly soil moisture carried over from 1 month to the next across years.

To calculate long-term effects of the observed spatial pattern of cloud shading and fog drip, we used a running water balance driven with monthly rainfall and PET time-series data from 1904 to 2005. Figure 5a shows the water balance for an ‘average’ year at site 10. Rainfall and PET are long-term site averages from these time series. Rainfall averages 509 mm year$^{-1}$ and is concentrated during the winter months, with almost no rain from May to October. Rainfall surplus (beyond evaporative demand) allows for recharge of soil moisture from December to March. Run-off is a minor part of the water balance in the ‘average’ year. PET averages 766 mm year$^{-1}$; it is low during the winter and peaks in late summer. AET peaks in spring as temperature and insolation are rising, but before soil moisture becomes limiting. AET is higher than rainfall from April to October, by an amount that equals the drawdown of soil moisture for that month. Still, the available soil moisture is not sufficient to match the evaporative demand (Fig. 5b). Deficit is greatest in August, but remains large from June to October.

Both cumulative annual AET and cumulative annual Deficit have been shown to be ecologically meaningful predictors of plant distributions for species, including other Californian conifers (Stephenson, 1998). We tested AET from this running water balance model as a predictor of tree growth based on a tree-ring chronology developed on torrey pines (Pinus torreyana ssp. insularis Haller) on adjacent Santa Rosa Island, and found AET to be a better predictor of tree growth than rainfall (Williams, 2006; Williams et al., 2008). Annual Deficit appears to correlate with mortality risk for bishop pines as well (see Discussion).

We compared site 10, near the heart of the stand where pine density is highest, with sites 1 and 12, which bracket the coastal and inland ends of the stand as described previously. We compared ‘average’ water balances for the three sites, holding...
Fog and overcast conditions in coastal California

Long-term running water balance

Figure 7 shows 10 years of running water balance estimates for site 10, spanning two of the most extreme years of the century. Water year 1983 (WY 1983, 1 October 1982 to 30 September 1983), associated with a very large El Niño–Southern Oscillation (ENSO) event, was the fifth wettest year of the century. Soil moisture reached the estimated rooting zone capacity of 500 mm, and AET remained high throughout the summer. In contrast, WY 1989 and WY 1990 had the fifth lowest and second lowest rainfall totals of the century, respectively. Further, each water year during the period 1987–1991 experienced <80% of the long-term average of 510 mm rainfall, resulting in a prolonged drought that was unprecedented in the historic record. (It should be noted that the historic record up to the mid-1980s shows substantially fewer and less intense droughts than inferred for the previous 300–500 years based on tree-ring analyses; Michaelsen et al., 1987; Haston & Michaelsen, 1994, 1997). The largest annual Deficits of the century were in 1989 and 1990 (Fig. 7). (Water year rainfall was analysed using water years ending 30 September so as to keep entire rainy seasons together. Annual Deficit was analysed using calendar years, as monthly Deficits often continue from summer through the autumn.) Stored soil moisture was extremely low in these years, especially WY 1990, so that AET was essentially the same as monthly rainfall. Modelled PET did not vary substantially over the 10-year period (Fig. 7).

We also examined the long-term (1904–2005) running water balance for three sites (1, 10 and 12) to quantify interactions among rainfall, fog drip and PET in determining annual Deficit, which we took as a proxy for drought stress and mortality risk. As described previously, run A was the reference case (no fog drip and cloud shading/PET held constant across sites); run B included variations in cloud shading/PET but did not include fog drip; run C included ‘typical’ amounts of summer fog drip at each site but held cloud shading/PET constant across sites; and run D included both fog drip and variations in cloud shading/PET.

In run B (effects of cloud shading on PET only), average Deficits decreased by 29% at site 10 and 40% at site 1 relative to run A (control case; Table 1). At site 1, the reduction in PET compared with site 10 was sufficient to make up for the 30% lower rainfall received at the low elevation of site 1. Average Deficit at site 1 across the entire record was 572 mm under run A; reduction in Deficit from cloud shading under run B regularly exceeded 200 mm at this site. This made Deficits at site 1 comparable to site 10, even though the low elevation of site 1 reduces rainfall by 30%. The reduction in Deficit at both sites was greater in dry years than wet years, reducing overall climatic variability. Another measure of variability we examined is the recurrence interval of severe droughts. At site 1, the 1987–91 drought resulted in the highest modelled Deficit of 561 mm. At site 12, this extreme Deficit was exceeded in 30 years out of 102, and by as much as 207 mm. This comparison shows that observed changes in PET over a short distance can have large impacts on climatic variability and consistency of habitat suitability over time.

In run C (effects of typical fog drip only), the low elevation of site 1 resulted in negligible fog drip, while sites 10 and 12 both received large amounts (139 and 178 mm, respectively) resulting in reductions in Deficit of 29% and 36% at sites 10 and 12, respectively (Table 1, Fig. 8). The reductions in average Deficit from fog drip are similar in magnitude to those from reduced PET, but occur primarily at the}

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**Figure 7** Running water balance for site 10, Santa Cruz Island 1983–92. This decade started with one of the rainier years on record during the 1982–83 El Niño event. The most severe multi-year drought of the century began in 1987, culminating in the driest year of the century in 1990. Potential evapotranspiration (PET) is relatively consistent from year to year. Actual evapotranspiration (AET) varies much more, depending on both monthly rainfall (R) and soil moisture (SM). Deficit (Def) is the difference between PET (black squares) and AET (grey circles). Annual Def is also shown in grey bars plotted against the right axis; it varies greatly from year to year.
higher-elevation stations (sites 10 and 12) rather than at the more coastal ones. Including fog drip in the water balance shifts the prediction of the most drought-prone habitat to low-elevation coastal habitat, with both high-elevation sites being more mesic.

In run D (combined effects of fog drip and cloud shading), the impacts of fog drip and cloud shading were essentially additive (despite minor differences related to timing and interactions among variables). Annual Deficits were reduced by about a third at higher elevation (sites 10 and 12) as a result of higher fog drip. Annual Deficits were reduced by about a third near the coast (sites 1 and 10) by reduced PET from increased cloud cover. Sites 1 and 12 showed similar levels of deficit for most years. Site 10 (with both abundant fog drip and low PET) had the lowest mean Deficit (a 56% reduction in mean Deficit from run A), and the lowest frequency of droughts exceeding any given threshold (Fig. 8; Table 1).

**DISCUSSION**

**Drought sensitivity of bishop pines**

Bishop pine, like many rare and endemic species of the fog belt, is sensitive to drought. The most severe 2-year drought of the last century on SCI (and in most of CA) occurred in WY 1989–90 (Fig. 3; WY 1989 is 1 October 1988 to 30 September 1989). This drought was followed by widespread pine mortality across the island over the next few years – estimated as 70–90% of individuals (Walter & Taha, 1999). The previous large 2-year drought of WY 1976–77 was also followed by widespread
pine mortality (M. Carroll, J.R. Haller, L. Laughrin, personal communication, 2006). In both instances, the proximal cause of the die-off is reported to be bark beetle infestation. Bark beetles, fungi and other pathogens often cause mortality in pines in the years following drought because the weakened trees are unable to produce sufficient pitch and defensive chemicals (Richardson, 1998). During severe droughts, even relatively healthy pines may succumb to disease as large concentrations of weakened trees provide abundant breeding ground for pathogens (Richardson, 1998; Breshears et al., 2005; White et al., 2006).

Range limits are necessarily determined by a balance between recruitment and mortality. On the recruitment side, seedlings are abundant throughout the stand in most years, even following drought when mature trees are dying en masse (Wehtje, 1991; Walter & Taha, 1999). Prior to the removal of feral sheep in the 1990s, pine recruitment was somewhat limited as most seedlings were eaten (Hobbs, 1980). However, despite intensive sheep grazing, starting in the 1850s, a 1929 aerial photograph suggests that overall range limits of the western stand that we studied (Fig. 2) were similar to the present day (J. Howarth, personal communication). This suggests that range limits are less influenced by recruitment than mortality.

On the mortality side, the die-off of the early 1990s appears to have been spatially selective. A 1983 photograph shows large numbers of mature pines between sites 11 and 12 prior to the 1987–91 drought (M. Carroll, personal communication). In 2006, none of those trees remained alive, or even standing dead, and all of the pines east (inland) of site 11 appear to have established since 1990. Also, the entire area west (coastward) of site 4 contains few, if any, pines that pre-date the last drought. Around sites 7 and 10 older pines are fairly common, although the oldest pines we could find to core at both sites date back to just 1952. This suggests another die-off and recruitment pulse following the severe drought of the late 1940s (Fig. 3). Drought-mediated mortality appears to be the main driver of range limits at least in the western stand, with some range expansion in wet years, and range reduction (or density reduction, especially near the edges) following droughts.

**Direct effects of fog drip and cloud shading**

Fog drip is taken up by coastal pines and contributes to tree growth. Uptake of fog water has been demonstrated using isotopic techniques (Fischer, 2007). Increased growth is apparent in a tree-ring chronology developed from torrey pines 15 km west of site 1 on adjacent Santa Rosa Island (Williams et al., 2008). This chronology (1920–2004) was compared with a rainfall-based water balance model that explained most of the variability in tree growth ($R^2 = 0.60$). However, more than half of the remaining variability could be explained using proxies for fog drip and cloud shading (derived from nearby airport weather observations, 1944–2005). Importantly, cloud shading was shown to significantly increase growth even when looking only at clouds too high to provide fog drip. In addition to statistical correlation, the increased growth from fog drip can also be observed directly in the form of numerous ‘false bands’ in tree cores from both Santa Rosa Island and SCI. These bands occur when a tree whose summer growth has slowed reverts to rapid growth in the same season (Schulman, 1947). Since growth is so tightly linked to water availability in these systems, and no rainfall was recorded during these summers, we interpret these false bands as indicating additions of fog water to the ecosystem. The presence of numerous false bands within the tree ring record from SCI, combined with the strong correlation of annual growth and a fog proxy, suggest that fog drip relieves drought stress significantly across individual years and multiple decades (Williams, 2006; Fischer, 2007; Williams et al., 2008).

**Long-term effects**

Higher PET due to reduced cloud shading at the inland edge of the stand (site 12) is potentially significant as a range-limiting factor for this drought-sensitive species. Given similar amounts of soil water at the beginning of a drought, trees growing under a higher PET regime will run out of water before trees growing where PET is lower (see Results: ‘Water balance for an “average” year’).

Lower rainfall at the coastal end of the stand where elevation decreases (Site 1) is also potentially range-limiting. However, the results of run B show that reduced coastal PET (attributable largely to increased cloud shading) essentially compensated for the 30% lower rainfall (compared with site 10) leaving no large differences in deficits between those two sites.

Both fog drip and cloud shading can sharply reduce drought frequency and drought severity. Run B shows that lowered PET from cloud shading not only reduced mean Deficit, but also reduced climatic variability. Run C suggests the same is true of fog drip, although more rigorously assessing the strength of that effect will require more long-term data on fog drip. Run D shows that cloud shading and fog drip were somewhat spatially independent, and, importantly, that their effects may be additive in only limited locations.

We have used Deficit as a proxy for drought stress, and, by extension, as a proxy for mortality risk. Deficit is a useful proxy for mortality risk, but the relationship is nonlinear. Mortality in most years is very low, with only a few trees succumbing to insects or disease. As drought becomes more severe, more and more pines weaken and become susceptible to disease. As a result, host/pathogen population dynamics and stand connectivity patterns become important factors in the spread of epidemic disease (Richardson, 1998; White et al., 2006). To better assess mortality risk, then, it makes less sense to examine average Deficit than to look at the return interval of extreme events. The two most extreme annual Deficits at site 10 were just over 400 mm (1989–90). This level of Deficit, associated with the severe pine die-off of the early 1990s, seems an appropriate threshold for analysis. At site 10, near the middle of the stand, this level of Deficit was modelled in just those 2 of
the last 102 years. By contrast, at sites 1 and 12, modelled Deficits of this severity (> 400 mm) occurred in 20 or more years out of 102 (Table 1, Fig. 8d). This same pattern of reduced drought severity at site 10 also holds when comparing the frequency of severe 2-year droughts (measured as summed monthly Deficit for two calendar years). There were at least 13 2-year droughts at both sites 1 and 12 that exceeded the driest 2-year drought at site 10. There were at least 23 3-year droughts at both sites 1 and 12 that exceeded the driest 3-year drought at site 10. The greatly reduced frequency of severe drought at site 10 suggests that the middle of the stand provides suitable habitat much more consistently over time than do areas near the edges. This habitat consistency, or reduced frequency of severe droughts, due to the combined effects of fog drip and cloud shading, is a critical habitat feature for long-term population viability.

Comparing these model results with reality, we observed that pine density is much higher around site 10 (50–80% cover) than near sites 1 and 12 (a few widely scattered young trees in chaparral). Growth rates and longevity (from tree cores) are also much higher at site 10 than at sites 1 and 12 (not shown). For a drought-sensitive species like bishop pine this spatial pattern only makes sense when compared with drought frequency under run D. Each of the other model runs fails to produce a credible spatial pattern of moisture availability; it is only by incorporating both cloud shading effects (reduced PET near the coast) and fog drip (estimated typical water additions each summer) that the model matches well with the observed pattern of pine density.

CONCLUSIONS

Fog is recognized as an important component of the hydrological cycle in many ecosystems that are of great conservation concern (Olson & Dinerstein, 1998). The same low stratus clouds that produce fog drip where they intercept vegetation also influence ecosystem hydrology by cloud shading. Low clouds shade plants, both where they intercept vegetation, and at lower elevations beneath stratus clouds. This shading reduces PET and water loss by reducing net radiation, increasing relative humidity and decreasing air temperature.

We evaluated the potential ecological effects of cloud shading and the resulting spatial differences in PET using a water balance model. The model tracked monthly ecosystem water availability over the last century at three sites across a stand of endemic coastal pines. We compared tree mortality risk among these sites by analysing the frequency and severity of drought stress, and examined how cloud patterns mediate drought stress and thereby influence range dynamics. We show that for low-elevation sites within the California fog belt, the effects of cloud shading can be much greater than those of fog drip. Even high-elevation sites that receive substantial fog drip may benefit as much from shading as from fog drip – this would be particularly true for species whose leaves are less efficient than conifers at collecting fog droplets. Either effect alone can reduce annual drought stress by a third compared with adjacent less cloudy areas, and together these effects can reduce drought stress by more than half. The shading aspect of coastal fog and its potential impact on vegetation growth and range dynamics has not previously been quantified, but should be considered in future fog-vegetation research.

Inferred range dynamics of the western stand of bishop pine on SCI over the last century suggest that pines can disperse outward from the centre of the stand in favourable years, but that drought frequently kills off pines near the periphery of the stand. Further, there are micro-refugia from severe drought near the centre of the stand. This pattern was not predicted by water balance modelling until the separate spatial patterns of both fog drip and cloud shading were taken into account. While this study focused on bishop pine, the same cloud-influenced patterns of episodic drought at coastal and inland range edges presumably affect many other species endemic to the Californian fog belt. Similar large differences in moisture availability over relatively small changes in distance and altitude also exist in other semi-arid, fog-inundated ecosystems (e.g. other Mediterranean-climate coasts and the lomas of the Atacama Desert; Rundel et al., 1991). Even tropical montane cloud forests, which receive much more precipitation and are much wetter, are drying in places (Pounds et al., 1999, 2006). As global climate change and deforestation alter cloud patterns in fog-dependent ecosystems around the world (e.g. Still et al., 1999; Lawton et al., 2001), increasing attention and effort are focusing on conserving their disproportionately large share of global biodiversity and species endemism. Conservation efforts in these ecosystems will be better able to anticipate range dynamics of drought-sensitive species by considering the spatially distinct hydrological impacts of both fog drip and cloud shading.

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REFERENCES


Schulman, E. (1947) *Tree-ring hydrology in southern California*. Bulletin No. 4, Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ.


Thornthwaite, C.W. & Mather, J.R. (1957) *Instructions and tables for computing potential evapotranspiration and the water balance*. Laboratory of Climatology, Centerton, NJ.

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**APPENDIX**

The standardized reference evapotranspiration equation (Allen et al., 2005) follows:

\[
ET_{\text{ref}} = \frac{0.408(A - G) + \frac{c_s}{1 + 0.273 u_2(c_v - e_v)} \Delta + \frac{C_d}{1 + C_d u_2}}{\Delta + \gamma(1 + C_d u_2)},
\]

where \(A\) = calculated net radiation at the crop surface (MJ m\(^{-2}\) h\(^{-1}\)); \(G\) = soil heat flux density at the soil surface (MJ m\(^{-2}\) h\(^{-1}\)); \(T\) = mean hourly air temperature at 2-m height (°C); \(u_2\) = mean hourly wind speed at 2-m height (m s\(^{-1}\)); \(e_v\) = mean hourly saturation vapour pressure at 2-m height (kPa); \(e_v\) = mean hourly actual vapour pressure at 2-m height (kPa); \(\Delta\) = slope of the saturation vapour pressure–temperature curve (kPa °C\(^{-1}\)); \(\gamma\) = psychrometric constant (kPa °C\(^{-1}\)); \(C_0\) = numerator constant (66 K mm s\(^{-3}\) Mg\(^{-1}\) h\(^{-1}\)) for tall vegetation, hourly time step; \(C_d\) = denominator constant (0.25 s m\(^{-1}\) for tall vegetation, hourly time step, during the day, 1.7 at night). Units for the 0.408 coefficient are m\(^2\) mm MJ\(^{-1}\). Snyder & Eching’s (2004) spreadsheet calculates these terms (following procedures in Allen et al., 2005) using site parameters and hourly measurements of air temperature, dew point, wind speed and incoming solar radiation.

The relevant terms of the monthly water balance model are presented below (modified from Thornthwaite & Mather, 1955, 1957, and excluding terms for calculating run-off). Soil moisture storage is in mm (or mm\(^3\) mm\(^{-2}\)) and all fluxes are in mm month\(^{-1}\).

<table>
<thead>
<tr>
<th>Term</th>
<th>Symbol</th>
<th>Calculation</th>
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<tbody>
<tr>
<td>Precipitation</td>
<td>(P_t)</td>
<td>Estimated as (f(t)), after excluding stormflow</td>
</tr>
<tr>
<td>Potential evapotranspiration capacity</td>
<td>(\text{PET}_t)</td>
<td>Estimated as (f(t)), from modelled (ET_{\text{ref}})</td>
</tr>
<tr>
<td>Field soil moisture capacity</td>
<td>(\text{FSMC})</td>
<td>Estimated as 500 mm</td>
</tr>
<tr>
<td>Accumulated potential water loss</td>
<td>(\text{APWL}_t)</td>
<td>If ((P_t - \text{PET}_t) &lt; 0), (\text{APWL}<em>t = \text{APWL}</em>{t-1}); else (\text{APWL}_t = \text{FSMC} \times \ln(\text{SM}_t/\text{FSMC}))</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>(\text{SM}_t)</td>
<td>If ((P_t - \text{PET}_t) &lt; 0), (\text{SM}_t = \text{FSMC} \times \exp(\text{APWL}_t/\text{FSMC})); else (\text{SM}<em>t = \min(\text{FSMC}, \text{SM}</em>{t-1} + (P_t - \text{PET}_t)))</td>
</tr>
<tr>
<td>Actual evapotranspiration deficit</td>
<td>(\text{AET}_t)</td>
<td>(\text{AET}_t = \min(\text{PET}_t, \text{PET}_t - (\text{SM}<em>t - \text{SM}</em>{t-1})))</td>
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