Title

The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: a tree-ring study

Journal

Oecologia, 156(3)

ISSN

0029-8549

Authors

Williams, A Park
Still, Christopher J
Fischer, Douglas T
et al.

Publication Date

2008-06-01

DOI

10.1007/s00442-008-1025-y

Peer reviewed

Oecologia (2008) 156:601–611
DOI 10.1007/s00442-008-1025-y

ECOSYSTEM ECOLOGY - ORIGINAL PAPER

The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: a tree-ring study

**A. Park Williams · Christopher J. Still ·
Douglas T. Fischer · Steven W. Leavitt**

Received: 31 May 2007 / Accepted: 29 February 2008 / Published online: 27 March 2008

Abstract The coast of California is home to numerous rare, endemic conifers and other plants that are limited in distribution by drought sensitivity and the summer-dry climate that prevails across most of the state. Ecologists have long assumed that some coastal plant populations survived the early Pleistocene transition to a warmer and drier environment because they benefit from frequent fog and stratus clouds that provide water and shade during the rainless summer. One such population is that of Torrey pine (*Pinus torreyana* ssp. *Insularis*) on Santa Rosa Island in Channel Islands National Park. Here we report that the tree-ring width record from this population indicates strong growth sensitivities to summer fog drip and cloud shading. We quantified the effects of summer cloud cover by comparing ring-width indices to coastal airport cloud-frequency records (1944–2004). For the first time observed, summertime cloud frequency correlated positively with ring-width indices, regardless of whether the effect of rainfall was first removed from the ring-width record. The effect of ground-level fog was strongest in July early mornings (03:00 PST, $R^2 = 0.262$, $P < 0.0002$). The effect of clouds high enough to provide shade but not fog water was also strongest in July, but climbed steadily throughout the day before becoming strongest in late afternoon (16:00–18:00 PST, $R^2 = 0.148$, $P < 0.004$). Correlations were substantially stronger in years with higher soil moisture, suggesting that growth response to summer clouds is strongly affected by pre-summer rainfall. A change in the height and/or timing of coastal cloud formation with climate change would likely affect this and other populations of California's coastal vegetation.

Keywords Fog · Cloud · *Pinus torreyana* · Channel Islands · Tree rings

Introduction

Over 100 plant species are endemic to California's coastal fogbelt (Raven and Axelrod 1978). Many of these species are relicts of environments that were colder and wetter long ago. One important relict conifer species is Torrey pine (*Pinus torreyana* ssp. *insularis* Haller), which survived in isolation on Santa Rosa Island (SRI), one of the northern California Channel Islands, through the late Pleistocene and Holocene, while stands of other coastal conifers suffered widespread die-off (Heusser 1995; Millar 1999). This die-off was presumably due to the emergence of a warmer and drier climate following the last glacial maximum, and is evidenced by a dramatic shift in the types of pollen deposited in ocean and lake sediments near California's coast 11–15 kya (Millar 1999).

While no paleoecological evidence exists to confirm that *P. torreyana* once grew beyond the ranges of its present-day populations on SRI and near San Diego, CA, USA, experts infer that these populations are all that remain of a

Communicated by Todd Dawson.

A. P. Williams (✉) · C. J. Still
Geography Department, UC Santa Barbara,
1832 Ellison Hall, Santa Barbara, CA 93106-4060, USA
e-mail: williams@geog.ucsb.edu

D. T. Fischer
Department of Geography, CSU Northridge,
18111 Nordhoff Street, Northridge, CA 91330-8249, USA
e-mail: doug.fischer@csun.edu

S. W. Leavitt
Laboratory of Tree-Ring Research, University of Arizona,
105 W. Stadium Building 51, Tucson, AZ 85721, USA

more widespread distribution that flourished during a time when wetter climates favored their growth and reproduction (Axelrod 1967; J.R. Haller, personal communication, 2006). As California's central and southern coast has become warmer and drier since the last glacial maximum (and probably during previous de-glaciations as well), the distributions of several other conifer species have changed dramatically. For example, coast redwood (*Sequoia sempervirens*), which does not currently grow south of Monterey County, likely grew near Santa Barbara, CA in the late Pleistocene (Chaney and Mason 1933; Raven and Axelrod 1978). And Douglas fir (*Pseudotsuga menziesii* ssp. *menziesii*) and Gowen cypress (*Cupressus goveniana*) grew as recently 16,500 years ago on Santa Cruz Island (SCI) (Chaney and Mason 1930; Anderson et al. 2006). In the present day, Bishop pine (*Pinus muricata* D. Don) is the only native conifer growing on SCI.

Drought is a primary factor threatening the survival of the populations of *P. muricata* and *P. torreyana* growing on the northern Channel Islands. This is illustrated by their discontinuous distribution—these trees grow almost exclusively on steep north-facing slopes, and their populations thin markedly at inland sites where summertime cloud cover is lowest and evapotranspiration is highest. What allows these species to survive the long rainless summers in this region?

Scientists have long presumed that summer stratus clouds are important for plant growth and persistence during the rain-free summers of coastal Mediterranean climates, because clouds can provide direct fog-water deposition (Leyton and Armitage 1968; Azevedo and Morgan 1974; Fischer 2007). To establish the importance of fog water inputs for one coastal tree that lives in the northern Californian fogbelt, *Sequoia sempervirens*, Dawson (1998) used isotopic techniques to show that almost all water in the xylem was derived from fog during the summer dry season.

In addition to direct water inputs from fog drip, clouds within California's fogbelt also provide shade from intense summer solar radiation. The dual impacts of summer cloud cover on water budgets are apparent in the northern Channel Islands when comparing summertime meteorological data from western SCI to cloud-height data collected at nearby Santa Barbara Airport (SBA, Fig. 1). Most fog drip on SCI occurs during the early morning when clouds at SBA are observed at or near ground level (fog). During afternoon hours, clouds produce little fog drip, but higher clouds reduce photosynthetically active radiation (PAR) by approximately 30% during afternoon hours. Summertime fog and overcast, therefore, may extend the length of the growing season by reducing drought-induced stomatal closure and photosynthetic shutdown. If this is true, then interannual variability in summertime cloudiness should cause measurable variability in the year-to-year growth of many coastal species.

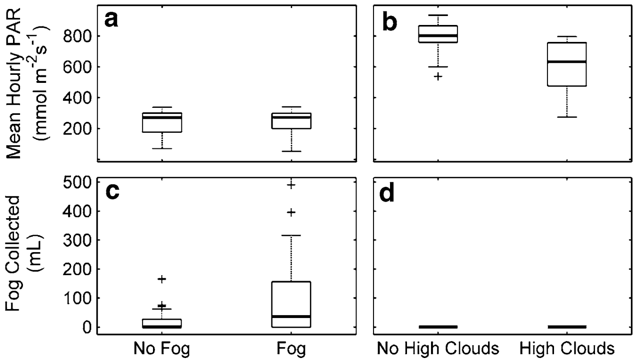

Fig. 1 **a** Western SCI hourly PAR on July mornings (01:00–09:00 PST) when clouds were and were not observed at SBA below 60 m (fog clouds; $P = 0.774$); **b** western SCI hourly PAR on July afternoons (15:00–18:00 PST) when clouds were and were not observed at SBA above 80 m (high clouds; $P < 0.0001$); **c** western SCI fog collected on July mornings (01:00–09:00 PST) when clouds were and were not observed at SBA below 60 m (fog clouds; $P = 0.001$); **d** western SCI fog collected on July afternoons (15:00–18:00 PST) when clouds were and were not observed at SBA above 80 m (high clouds). In **d**, no fog was collected in either case ($P = 1$), consistent with there being no cloud base at the surface

A good proxy for year-to-year variation in tree growth is tree-ring width. Annual ring widths are typically dictated by a suite of environmental variables such as solar radiation, air temperature, relative humidity, disturbance, and the availability of water (Fritts 1976). In temperate regions, one or more of these limiting factors generally causes growth to slow and eventually cease each year, creating a band of dense "latewood" cells with thick walls that form a visible ring. In the only published tree-ring study focusing on *P. torreyana*, which was conducted on the coastal population immediately north of San Diego, Biondi et al. (1997) found that ring width correlated positively ($R^2 = 0.14$) with an index of summer fog-frequency data derived from 49 years of visibility observations made by ships and at weather stations on the coast and nearby islands (Filonczuk et al. 1995). This correlation, however, became insignificant when the much stronger effect of fall through spring rainfall ($R^2 = 0.59$) was removed from the ring-width record. This may be because the fog dataset covered a large geographic area, did not account for cloud height variations and the impact of shading by higher clouds, and did not distinguish among fog events at various times of the day (Filonczuk et al. 1995). Summer fog may therefore more strongly affect the growth of mainland *P. torreyana* than was reported in this study.

Here, we test the general hypothesis that SRI *P. torreyana* ring-width index values correlate significantly with a proxy cloud frequency record that we derived from two nearby mainland airport climate records. Because tree growth is most strongly affected by winter and spring rainfall in this region, we assessed whether any apparent relationships between ring-width index and cloud frequency retain statistical significance after the influence of "rainwater availability" is removed from the ring-width record. We hypothesized that a stronger cloud frequency signal would be retained in the ring-width record when "rainwater availability" is defined as modeled actual evapotranspiration (AET), which has been shown to be a useful proxy for tree growth (Stephenson 1998), rather than as measured rainfall.

Further, cloud bases during summer months are nearly exclusively below 300 m. We therefore hypothesized that ring-width index values would correlate most strongly with summertime frequency of cloud cover below 300 m. Additionally, fog clouds, which are low enough to inundate the entire stand of trees and provide both direct water inputs and shade, should reach peak importance to tree growth at a different time of day than higher clouds that only provide shade. Finally, we tested whether variations in soil moisture during the months leading up to summer affect the degree to which tree growth responds to summer fog and stratus-cloud cover.

Materials and methods

Sampling and site description

We collected tree cores for ring-width analysis in May 2005 from *P. torreyana* ssp. *insularis* (Haller) individuals growing between 64 and 164 m above sea level on the east side of SRI in Channel Islands National Park, California, USA. This species has one of the most limited ranges of any extant conifer: subspecies *insularis* grows only in one stand on SRI, and the other subspecies grows in two small mainland stands 280 km to the southeast near San Diego (Critchfield 1966; Haller 1986; Wells and Getis 1999). Trees are generally 5–15 m tall and occupy ridgelines, slopes, and gullies (Biondi et al. 1997). Grazing by cattle, elk, and deer has kept the SRI stand relatively free of understory vegetation for the duration of the ring-width record. Although current grazing on pine seedlings by elk affects seedling mortality and recruitment (S. Chaney, personal communication, 2005), it does not appear to disturb interannual growth variation nearly as much as does variation in climatic conditions. Annual rainfall is roughly 500 mm (~20 in) and varies considerably in both annual totals and interannual timing. Winter temperatures are moderate (~11°C) and summers are warm (~20°C). Relative humidity is consistently high, averaging 76% in winter and 80% in summer (RAWS/NDBC 2007; Laughrin 2006).

Low rainfall and warm temperatures cause interannual growth variation to be primarily driven by drought. We preferentially sampled trees growing on steep slopes because that is where water storage is minimized and drought sensitivity is maximized (Fritts 1976). We also selected for larger trees to maximize the length of the tree-ring chronology. In total, we collected two 4.3-mm-wide increment cores from either side of 17 trees at a height of ~1 m, parallel to the contour of the slope.

All cores were transported to the Laboratory of Tree-Ring Research at the University of Arizona, where they were air dried and sanded until all rings were visible at 10× magnification. We visually cross-dated tree rings using the skeleton plot method (Douglass 1941; Stokes and Smiley 1968) and measured them to the nearest 0.001 mm using a dissection microscope and a sliding-stage electronically connected to a computer interface. We verified the dating accuracy by making sure that all ring-width chronologies were in general agreement using the computer program, COFECHA (Holmes 1983; Grissino-Mayer et al. 1996).

Ring-width series were de-trended for each core to minimize trends related to stand dynamics, size, age, and fluctuations in health unique to individuals (Cook and Kairiukstis 1990). To do this, we fit each series with a negative exponential curve, calculated a residual value for each tree ring, and normalized the residuals to produce index values. The resultant tree-ring index chronology was calculated using the average index value across all the cores for each year. Other de-trending techniques were tested and did not produce significant differences among the resultant chronologies. The full chronology extends from 1897 to 2004, but this study used only ring-width data from 1920 through 2004 because index values prior to 1920 were derived from so few cores that correlation with annual rainfall values decreased substantially.

Actual evapotranspiration as a proxy for available soil moisture

It was necessary to remove the effect of rain-derived soil moisture on the ring-width record before isolating a summer fog signal because the availability of rainwater strongly affects tree growth at our site (Williams 2006). However, rainfall may not be the optimal proxy for the amount of water available to plants. Actual evapotranspiration (AET), which is driven by soil moisture and potential evapotranspiration (PET), should be a better proxy for a site's actual water balance because calculations of AET account for both runoff during times of heavy rainfall and the increased potential for storage in dry soils. We estimated monthly soil moisture using a bucket-type soil–water balance model, driven by measured rainfall from SCI (Laughrin 2006), and modeled potential evapotranspiration (PET) (Thornthwaite and Mather 1955; Thornthwaite and Mather 1957; Dunne and Leopold 1978).

The only water input in the soil–water balance model was monthly rainfall data collected on SCI (i.e., fog drip was not included). The rain gauge is located in SCI's central valley, 29 km east of the stand on SRI. SCI rainfall data were chosen over the RAWS (2007) SRI data due to the unique length and completeness of the SCI record (1904 to present, Laughrin 2006). Mean annual rainfall is comparable at both sites.

Water exits the soil in our model through evapotranspiration. We first estimated monthly PET for a subset of the entire record by applying a modified Penman–Monteith (PM) model (Monteith 1965; Granier and Loustau 1994; Snyder and Eching 2004; Allen et al. 2005) to hourly weather data (air temperature, solar radiation, wind speed, and relative humidity) collected from 1997 through 2005 on the west end of SCI. The site on western SCI has a similar elevation and cloud-shading patterns to the study site on SRI, only 16 km to the west.

Fortunately, this short, data-intensive record of modeled PM PET correlated well ($R^2 = 0.84$) with monthly Blaney–Criddle (BC) model (Brouwer and Heibloem 1986; McKenney and Rosenberg 1993) calculations that required only latitude and mean monthly air temperature as inputs. Therefore, we used monthly air temperature data from Santa Barbara (~60 km northeast of SRI) to extend the PET record for SRI back to 1904 (the first year of the SCI rainfall record). We calibrated this long-term PET record to the more accurately modeled short-term (1997–2005) PM PET record from SCI (Fischer et al. 2008). We then combined this PET record with the measured rain record to calculate monthly soil moisture and monthly AET over the entire record. When the amount of precipitation available for AET exceeds PET demand in any month, AET is equal to PET. Conversely, when monthly precipitation is less than PET, AET equals precipitation plus withdrawn soil moisture. Figure 2 shows average monthly values of the water-balance parameters for the period 1904–2005.

We recognize that using AET as a proxy for soil–water availability may appear problematic for two reasons. First, if field capacity is underestimated, too much water is removed from the soil-moisture record as runoff when precipitation exceeds PET demand, potentially attributing ring growth that was actually caused by rain-derived soil moisture to fog or cloud cover. We therefore chose a field capacity of 500 mm, which is more likely an overestimate than an underestimate (Fischer et al. 2008). Second, there are often anomalously cool months with high moisture availability and high growth. However, the cool temperatures lead to low short-term estimates of AET (i.e., McKenney and Rosenberg 1993). Importantly though, soil moisture is drawn down to virtually inaccessible levels nearly every summer or fall at our study site, eventually causing annual termination of growth. Therefore, temporarily reduced AET due to a cool spell translates to increased AET later in the year, such as the summer when fog is most common. This means that averaged over a year, AET is sure to be a function of the amount of precipitation available to plants, even if AET during some individual months is driven by temperature.

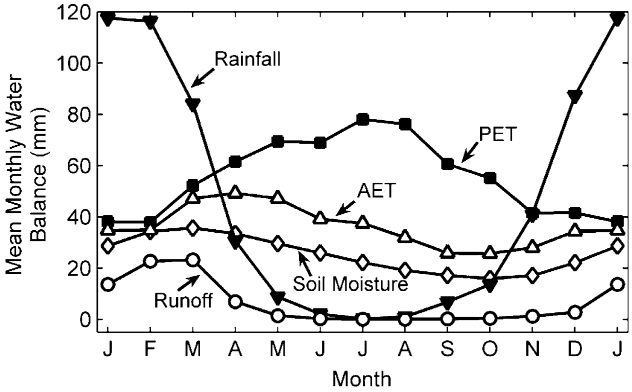

Fig. 2 Mean monthly water balance over the course of the average year (1904–2005)

Developing cloud-frequency records from hourly airport observations

We used airport records of hourly cloud presence and base heights to construct an annual record of cloud frequency for the region. "Cloud frequency" is the fraction of hours during which cloudy conditions were observed. Cloud-height data were collected at Oxnard Airport (OXR, 82 km east of the study site, 19.8 m above sea level) and Santa Barbara Airport (SBA, 33 km north, 3.7 m above sea level) from 1944 through 2005. While SBA and OXR are a fair distance from the study site, cloud observation data from both airports agree well with two years of daily and monthly observations of fog collection and solar radiation data collected at a weather station on western SCI, 22 km east of the study site (i.e., Fig. 1). This suggests that cloud frequency on the mainland coast is a reliable proxy for cloud frequency where the tree-ring samples were collected on SRI.

Importantly, the effect of cloud cover on tree growth, and thus ring width, may vary depending on the type of cloud, the time of day, and the time of year. For example, high clouds never provide fog drip, but they can provide shade during the day, and shade may only be important during a portion of the growth year. To account for the potentially varying functionality of cloud cover on growth, we split the annual cloud-frequency record into many unique records that represent ten classes of cloud-base heights (listed in Table 1) at various times of the day and year.

There are 78 possible combinations of consecutive months in a year (i.e., January, January–February, January–March, February–March, February–April, and so on), and

Table 1 For each range of cloud-base heights analyzed (column 1), the range of optimal months and times for which cloud frequency has the strongest correlation (highest R^2)

Cloud-base height range (m)	a				b				c	
	Unadjusted ring widths				Adjusted by		December–September AET		June–April rain	
	Optimal		R^2	P	Optimal		R^2	P	R^2	P
	Month range	Time range			Month range	Time range				
0–50	Jun.–Jul.	3:00	0.280	0.0001	Jul.	2:00–3:00	0.251	0.0002	0.127	0.0121
0–200	Dec.–Feb.	18:00–23:00	0.394	<0.0001	Jul.	17:00–19:00	0.167	0.0020	0.037	0.1617
100–300	Dec.–Mar.	1:00–2:00	0.428	<0.0001	Jul.–Aug.	15:00–16:00	0.191	0.0009	0.129	0.0076
200–400	Dec.–Mar.	1:00–3:00	0.332	<0.0001	Feb.	19:00	0.122	0.0010	0.086	0.0312
300–500	Dec.–Jun.	15:00–19:00	0.250	0.0002	Dec.–Mar.	3:00–11:00	0.172	0.0040	0.096	0.0361
400–600	Dec.–Feb.	15:00–16:00	0.264	<0.0001	May	5:00–7:00	0.108	0.0141	0.069	0.0519
500–700	Dec.–Mar.	8:00–14:00	0.251	0.0001	Dec.–Feb.	16:00–17:00	0.146	0.0047	0.060	0.0783
600–800	Dec.–May.	9:00–23:00	0.290	<0.0001	Dec.–May	7:00–20:00	0.200	0.0008	0.013	0.4132
700–900	Mar.	15:00–17:00	0.200	0.0007	Mar.	15:00–18:00	0.188	0.0011	0.039	0.1525
800–1,000	Dec.	6:00–12:00	0.256	0.0001	Dec.	16:00–17:00	0.310	<0.0001	0.129	0.0084

(a) Unadjusted ring-width index and (b) ring-width index absent of the influence of December–September AET are shown. Column (c) shows R^2 values for the correlation between cloud frequency and ring-width index when June–April rainfall influence is removed during the month and hour ranges listed in (b)

300 combinations of consecutive hours in a day (i.e., 12:00, 12:00–01:00, 12:00–2:00, 01:00–2:00, and so on). For each cloud-base height class, and for each airport, we calculated a unique annual cloud-frequency record that represents a unique combination of months and hours within a growth year (23,400 combinations of months and hours). We defined the growth year as December through November based on data showing that growth in a nearby stand of *P. muricata* on SCI initiates in December (A. P. Williams, C. J. Still, and D. T. Fischer, unpublished data). All statistical calculations were performed using MATLAB 7.0.1.

There were temporal gaps in the cloud-height data from each airport, ranging from one hour to several years. For each of the many cloud-frequency records produced, we dismissed any year for which more than 5% of the scheduled hourly observations were missing. To fill data gaps, we combined the records from OXR and SBA to create general records for the region. Correlations between airport cloud-frequency records were generally high ($R^2 = 0.55$–0.85) for specific combinations of cloud height, month, and hour. Those records that did not correlate between airports at a 95% confidence level were assumed be unrepresentative of the region and were discarded from the analysis. Among the records that were significantly correlated, data gaps in the OXR record were filled with calibrated SBA data. Data from the two airports were never averaged. We gave priority to the OXR record because it correlated more closely with the *P. torreyana* ring-width index in an exploratory analysis.

Data analysis

We first identified the months and hours of the day when cloud cover in each of the ten height classes correlated most strongly with the ring-width index. We considered the best linear relationship to be the one described by the largest positive correlation coefficient (r value). While excessive cloud cover could conceivably inhibit growth and produce a negative or nonlinear relationship, we only inspected for linear relationships because preliminary analyses yielded no evidence for other relationships between summer cloud frequency and *P. torreyana* ring-width index.

We next determined whether the correlations between cloud cover and ring widths held when the effect of rainwater availability (i.e., AET) was already accounted for. To do this, we removed the influence of December through September average AET on the ring-width index record, because that is the range of months during which AET has the most positive correlation with ring-width index. This produced an annual time series of ring-width index residuals that represented ring-width variations not associated with variations in AET. These residuals are hereafter referred to as adjusted ring-width indices.

Before repeating the correlation analysis between cloud frequency and the adjusted ring-width index record, we also adjusted cloud frequency records, because most cloud frequency records also correlated positively with December through September AET. This is probably because some of the atmospheric processes that cause variations in AET, such as rainfall and temperature, also influence variations in cloud frequency. We calculated adjusted cloud frequencies for all cloud-frequency records that correlated significantly with previous December through September AET. We then tested the correlations between the adjusted ring-width and adjusted cloud-frequency records and identified the times of year and day when cloud frequency in each height class correlated most strongly with radial growth.

A major difference between this study and that of Biondi et al. (1997), conducted on the mainland stand of *P. torreyana*, was that Biondi et al. removed the influence of raw rainfall, rather than AET, from the ring-width index record. These authors found that the positive correlation between cloud frequency and ring width lost significance when rainfall was accounted for. We believe, however, that AET, which incorporates rainfall, represents the record of water available to plants more accurately than does rainfall alone. It follows that a ring-width record adjusted to eliminate the influence of AET should be more representative of non-rainfall parameters such as cloud cover. It was important, then, to conduct a comparative study in which we account for the influence of rainfall rather than AET on ring width, and then compare the adjusted ring width records to cloud frequency records.

In this comparative study, we removed the association with June (previous year) through April (growth year) rainfall from ring-width and cloud-frequency records because that is the range of months during which cumulative rainfall is most positively associated with annual ring-width index. We then reevaluated the correlation between the "rain-free" ring widths and "rain-free" cloud frequencies for the same months and hours during which cloud frequency for each of the ten height classes was previously found to be most influential on "AET-free" ring width. We compared correlation coefficients to evaluate how significantly the association between cloud cover and tree growth was altered by simply changing how we accounted for the influence of rainfall, hypothesizing that correlation coefficients would be higher when the influence of AET was removed compared to when the influence of rainfall was removed.

We then refined our analysis to focus on (1) clouds low enough to inundate the *P. torreyana* stand entirely and potentially provide water inputs via fog drip (cloud base < 60 m) and (2) clouds that provide shade but are too high to provide direct water input for the entire stand (cloud base > 80 m). For simplicity, clouds below 60 m will be referred to as "fog clouds" and clouds above 80 m will be referred to as "high clouds." To test our hypothesis that these two cloud types mitigate summer drought stress in very different ways at very different times of the day, we determined the range of summertime hours during which the adjusted frequency of each cloud type reaches peak correlation with adjusted ring widths. We then compared the slopes of the regressions to evaluate the relative importance of the drought-mitigating services provided by each cloud type, assuming that the higher the slope, the greater the positive effect that a given hour of cloudy conditions has on growth.

Finally, we determined whether the amount of rainwater available leading up to summer affects how strongly tree growth responds to cloud cover during summer. To do this, we divided the annual records of cloud frequency and ring-width indices into "wet" and "dry" years using monthly AET calculations, where high AET indicates wet and low AET indicates dry. However, there were many years that experienced high AET for part of the year and low AET at another part. We therefore created 78 separate sets of wet and dry years; one for each possible combination of months in a water year (October–September). This was repeated several times, varying the AET thresholds used to distinguish between wet and dry years, and requiring wet and dry years to each be represented by at least 20 years of data. Then, keeping wet and dry yeas separate, we re-evaluated the correlation between adjusted cloud frequency and adjusted ring-width index to determine whether the correlation between adjusted ring-width index and summertime cloud cover is stronger following either unusually wet or dry conditions. We also evaluated the effect of fog clouds versus high clouds separately.

Results

Just as was shown by Biondi et al. (1997), we found that unadjusted cloud frequency correlated positively and significantly with the unadjusted ring-width index series. This was the case for all ten classes of cloud-base heights. The time of day and year when unadjusted cloud frequency correlated best with unadjusted ring widths varied among cloud-height classes (Table 1, column a). Ring-width index values correlated most strongly with the frequency of clouds below 50 m during the pre-dawn hours of summer months (03:00 PST in June–July). Among the nine higher cloud-height classes, wet-season (December–April) cloud frequencies correlated best with the unadjusted ring-width record. This likely reflects clouds associated with rainfall, as December through April rainfall accounts for 86% of the annual average rainfall in the region and contributed to 59% of the variation in ring widths from 1920 to 2004.

Unlike the high storm clouds of the winter months, 85% of summer cloud bases fall within the three lowest cloud-base height classes analyzed here (0–300 m) due to a persistent and low summertime temperature inversion in the atmosphere (Leipper 1994). After removing the effect of December through September AET from ring-width and cloud-frequency records, cloud frequency within these three height classes became most strongly correlated with ring-width indices during summer months, rather than winter (Table 1, column b). Interestingly, the time of day at which low clouds (i.e., below 300 m) are most associated with adjusted ring widths varied strongly with cloud height. Adjusted ring widths were most strongly correlated with the frequency of 0–50 m cloud cover in the early morning hours (02:00–03:00 PST July), while summertime afternoon and evening cloud frequency correlated better for the 0–200 and 100–300 m cloud-height ranges. At higher altitudes (i.e., above the height of typical summer cloud cover), winter and spring cloud frequency remained most influential on the adjusted ring-width record. There was no particular time of day at which these clouds are most associated with tree growth, unlike low clouds.

When we removed the effect of rainfall (previous June–April), rather than AET (December–September), from the ring-width and cloud-frequency records, the effect of cloud frequency during the optimal range of hours and months (listed in Table 1, column b) was consistently weaker. Results hereafter are reported for ring-width indices and cloud frequencies are adjusted for AET, not rainfall.

Using adjusted ring-width and cloud-frequency records, we tested whether tree-ring widths are sensitive enough to differentiate between the dual drought-mitigating effects of summer fog inundation versus summer shading by higher clouds. July and August are the least rainy months on the northern Channel Islands (Fig. 2). Figure 3a shows relative frequencies of cloud presence throughout an average day during these months for (1) fog clouds (below 60 m), which are low enough to inundate all trees sampled, and (2) high clouds (above 80 m), which are too high for cloud-water deposition within the entire tree stand (though lower bases may impact some trees in the upper portion of the stand). As observed in the analysis of the 10 cloud-height classes, fog clouds and high clouds experience maximum and minimum correlation with tree growth at different times of the day during summer (Fig. 3b). Fog frequency reached peak correlation with ring-width at 03:00 PST in July ($R^2 = 0.262$, $P < 0.0001$). The frequency of high clouds reached peak correlation from 16:00 through 18:00 PST in July ($R^2 = 0.148$, $P = 0.0037$). The slopes of the best-fit lines for these two regressions are approximately equal (Fig. 4).

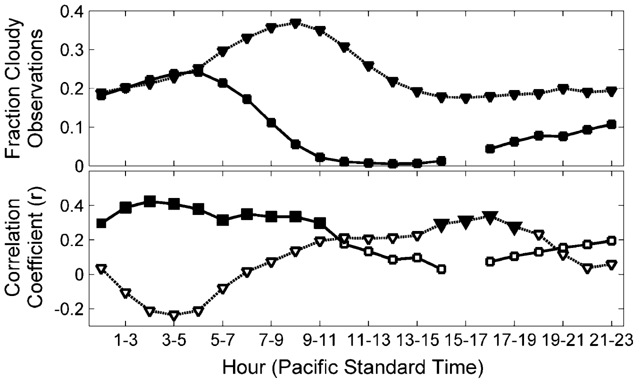

Fig. 3 **a** Cloud frequency and **b** correlation with adjusted ring-width indices for fog <60 m (*solid lines, square markers*) and high clouds >80 m (*dashed lines, triangle markers*) throughout an average (3-h running windows) July–August day. *Solid markers* in **b** indicate significant ($P < 0.05$) correlation

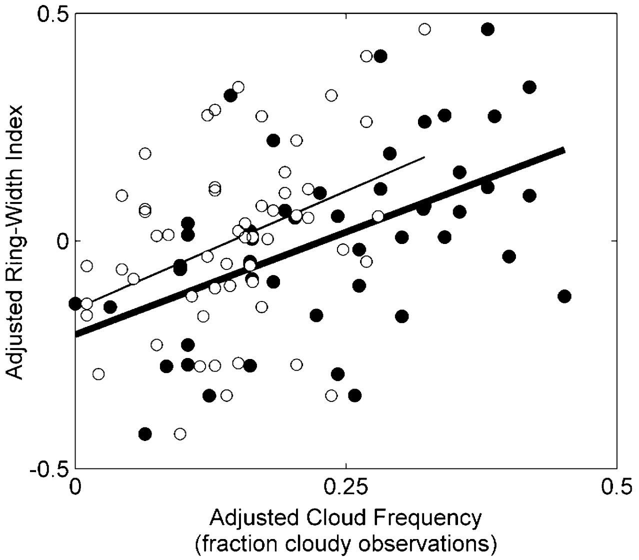

Fig. 4 Regression of annual adjusted ring-width index values on July 0–60 m fog frequency at 03:00 PST (*solid circles and bold trend line*; $R^2 = 0.262$, $P < 0.0001$, slope = 0.899) and July 80+ m hourly high-cloud frequency at 16:00–18:00 PST (*open circles and skinny trend line*; $R^2 = 0.148$, $P = 0.0037$, slope = 1.032)

The positive relationship between adjusted summertime cloud frequency and adjusted ring-width index values was much stronger in years when there was substantial soil moisture remaining during the rainless summer months from the previous winter and spring rainfall (Fig. 5). This was true for morning fog and higher afternoon clouds. Among wet years when the August through September (late growing season) average monthly AET was above 28 mm ($n = 28$), the correlation between adjusted ring with and adjusted fog frequency in July at 03:00 PST (when fog was most associated with ring width) was $R^2 = 0.39$. In drier years, when the August through September average AET was below 28 mm ($n = 21$), this correlation disappeared ($R^2 = 0.04$). Ring-width index and frequency of high clouds (July 17:00–19:00 PST) correlated most strongly in years when average monthly AET was greater than 41 mm from the previous November through July ($R^2 = 0.326$; $n = 24$). The correlation disappeared ($R^2 = 0.012$) in years with lower AET during these same months ($n = 31$). The two above sets of "high AET" years (i.e., average AET from August to September AET above 28 mm and average AET

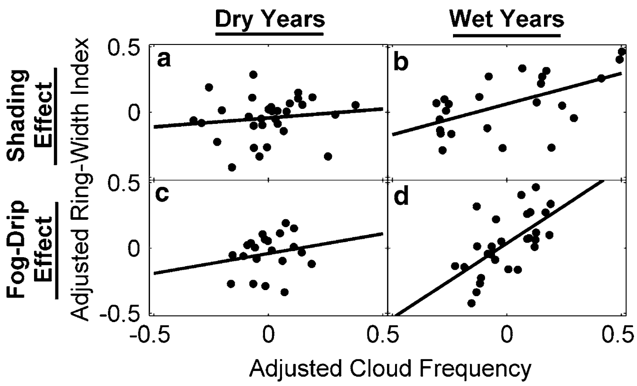

Fig. 5a–d Regressions of adjusted ring-width indices versus adjusted cloud frequency. *Top* Adjusted ring-width index versus high-altitude, afternoon cloud frequency (>80 m, July 16:00–18:00 PST) in years when November–July mean AET: **a** <41 mm ($R^2 = 0.012$, $n = 31$) and **b** >41 mm ($R^2 = 0.326$, $n = 24$). *Bottom* Adjusted ring-width index versus ground-level, pre-dawn cloud frequency (<60 m, July 03:00 PST) in dry summers when August–September mean AET: **c** <28 mm ($R^2 = 0.039$, $n = 21$) and wet summers **d** >28 mm ($R^2 = 0.391$, $n = 28$)

from the previous November–July was above 41 mm) shared 15 overlapping years. However, there was no correlation between morning fog frequency and the frequency of afternoon high clouds during these 15 years. This suggests that the relationship between tree growth and cloud cover of one altitude class is not a false artifact caused by a real relationship between ring width and cloud cover at the other altitude class.

Discussion

Interannual variation in winter and spring rainfall is by far the largest single influence on annual growth rates of *P. torreyana* on SRI. The months of cumulative rainfall that produced the strongest correlation with ring widths were the previous June through April ($R^2 = 0.592$). This correlation is approximately equal to that of the mainland *P. torreyana* stand north of San Diego, CA, USA (Biondi et al. 1997) and similar to that of *Pseudotsuga macrocarpa* (Vasey) Mayr. growing on nearby Big Pine, Pine, and San Rafael Mountains (Michaelsen et al. 1987; Haston and Michaelsen 1994).

Before removing the effect of rainfall, ring-width index values correlated positively and significantly ($P < 0.05$) with cloud frequency at all ten cloud-height classes. For the nine height classes that included cloud bases above 50 m, this correlation was strongest in the winter and spring months because tree growth is primarily driven by winter/spring storms, which are always accompanied by high clouds. For clouds below 50 m, correlation with unadjusted ring-width index values was strongest in summer. Given the dominance of winter and spring precipitation on tree growth, this correlation between unadjusted ring widths and summer cloud frequency below 50 m testifies to the importance of the additional summertime water input of these clouds.

When we removed the influence of previous December through September AET from both the ring-width and cloud-frequency records, adjusted cloud frequency still correlated positively and significantly with adjusted ring-width indices at all ten height classes (Table 1, column b). Further, cloud frequency at heights typical of summer stratiform clouds (below 300 m) became most important during summer months. Frequencies of clouds higher than 300 m should not be expected to also become dominant during summer after adjusting for AET because summer clouds very rarely have bases above 300 m.

Removing previous June through April rainfall, rather than AET, caused correlations to become less significant for all cloud-height ranges. This is likely because annual rainfall (which mostly falls in several large storms in coastal central and southern California) has a nonlinear relationship with tree growth due to much more runoff after soil is saturated. This may partially explain why Biondi et al. (1997) found that correlation between fog frequency and mainland *P. torreyana* ring width lost significance when the influence of rainfall was included in a multivariate regression. Also, the fog-frequency dataset used by Biondi et al. was derived from only three observations per day and did not include height stratifications like our cloud frequency dataset (Filonczuk et al. 1995). This probably hid the positive influence of early-morning ground-level clouds on growth. In our study, ground-level cloud frequency only retained a significant relationship with rain-adjusted ring-width index when we limited cloud observation data to morning hours, likely because afternoon evaporation rates are too high to allow substantial fog drip to occur. This corresponds well with our observation that no fog water was collected at our weather station on western SCI during the afternoon hours of summers 2005 and 2006.

While the lowest clouds (0–50 m) in our initial analysis were most important in the pre-dawn hours of summer, the two classes of clouds low enough to fall within the typical height range of summer cloud cover (below 300 m), but too high to fully inundate the *Pinus torreyana* stand, were most important during the summer afternoon hours. This suggests that these pines are not only sensitive to the presence of summer cloud cover, but are sensitive to the time of day at which different cloud types occur.

The analysis comparing clouds low enough to enshroud the entire tree stand in fog (<60 m) to clouds too high to inundate the entire stand (>80 m) strengthens this claim (Fig. 3). Correlation between summer fog frequency and adjusted ring width oscillated in a smooth sinusoidal pattern throughout the day, peaking in pre-dawn hours. Pre-dawn, being dark and cool, is an ideal time for fog water to collect on pine needles, drop to the ground, and percolate into the upper centimeters of the soil column before being subject to high daytime evaporation rates. The loss of significance in the relationship between tree growth and fog cloud frequency after 09:00 PST suggests that the ecological functionality of fog is associated more with providing water rather than shade.

Correlation between adjusted ring width and cloud frequency above 80 m also oscillated throughout the day, beginning negative but insignificant during pre-dawn hours, climbing throughout the day, before reaching and maintaining statistical significance in the afternoon and evening, and finally losing significance near sunset. The negative pre-dawn correlation makes sense because a recorded observation of pre-dawn high clouds indicates an absence of important ground-level fog clouds. The steep increase in correlation between adjusted ring width and higher-altitude cloud frequency after sunrise, and then the decrease in correlation after sunset, is consistent with the functionality of higher clouds as providers of shade rather than water. The smooth increases in correlation throughout the day give us confidence that the significant correlations reported here are not spurious.

The response of adjusted ring width to pre-dawn fog frequency in July was only significant in years when there was enough summertime soil moisture left over from that year's rainfall to allow relatively high AET in August and September (late growing season). This suggests that fog water alone is not sufficient for summertime growth, but supplements soil moisture left over from the rainy season. During years with little winter and spring rain, summer soils are left too dry for fog water alone to sustain growth, and *P. torreyana* may halt photosynthesis and radial growth early in the summer or in the spring. Such years would manifest in the tree-ring record as having a small response to summer fog frequency.

Interestingly though, the growth response to higher clouds was not dependent on whether there was enough rainfall to keep soils relatively moist into late summer (i.e., when average AET from August to September AET was above 28 mm). Instead, growth was only responsive to higher-altitude cloudiness in years when average AET from the previous November through July was high. This could conceivably happen in a year with a very wet early winter followed by a dry late winter and spring. In such a year, early rainfall may contribute to a lasting supply of water at depth even though dry conditions in late winter and spring may cause soil to be dry near the surface. While upper roots may lose access to fog water in summers with dry upper soils, deeper roots may continue to access water that could have conceivably originated during a wet early winter. In this case, cloud shading may still be important in limiting drought stress during summers when there is sufficient soil moisture at depth.

This relict stand's sensitivity to summer fog inundation and cloud shading is not unique. Preliminary data show that leaf ^{13}C concentration in Island manzanita (*Arctostaphylos insularis*) on SCI, which is a function of drought stress in the region, was dominated by summer cloud frequency more so than winter and spring rainfall in the 2007 growing season (A. P. Williams, unpublished data). Fischer et al. (2008) also showed that the boundary locations of a *P. muricata* stand on SCI are strongly dictated by summer cloudiness. Specifically, trees near the coastal, low elevation stand boundary receive plenty of cloud shading but are limited by rainfall and fog deposition, while trees near the inland, high-elevation boundary receive more rainfall and fog water but less cloud shading. Should rainfall, relative humidity, temperature, fog deposition, and/or cloud-shading change, the boundaries of this stand would adjust accordingly. On a larger spatial and temporal scale, the southern boundaries of *Pinus muricata*, *Sequoia sempervirens*, *Pseudotsuga menziesii*, *Cupressus goveniana*, and other species receded towards the cooler and moister north as temperatures warmed following the last glacial maximum (Chaney and Mason 1930, 1933; Raven and Axelrod 1978; Millar 1999). As temperatures have warmed and many stands have disappeared, the southernmost stands surviving today along the immediate coasts of California and Mexico owe their existence at least in part to anomalously high frequencies of fog deposition and cloud shading, compensating for increased PET and decreased rainfall. As the climate continues to change, we should expect the southern boundaries of these drought-prone species to continue to adjust themselves.

While the magnitude and timing of rainfall have not changed significantly along California's central coast during the past century, temperatures have risen substantially. Additionally, SBA cloud-height data indicate that spring and summer stratus clouds have increased in base height since 1948 (A. P. Williams, unpublished data). This is consistent with observations of decreasing fog observations at Los Angeles International Airport, reported by Witiw and Baars (2003). Given the sensitivity of many plant species in the region to drought and the timing and height of cloud cover, changes in temperature and/or summer stratus-cloud formation will likely alter the growth dynamics of *Pinus torreyana* and other coastal species.

Our results also have implications for the science of dendroecology. Without years of growth-monitoring data, such rich ecological detail as presented here can only be acquired from a tree-ring analysis. While the high sensitivity of *P. torreyana* to drought stress was necessary for summer cloud cover to influence ring widths significantly, partitioning airport cloud data into many height-, hour-, and year-specific subsets was the only way to differentiate between the ecological importances of clouds that provide fog drip versus shade. Thus far, however, dendroecological studies usually have not incorporated hourly climate data to infer more details about relationships between growth and climate. We suggest that, when possible, hour-specific detail be considered in future studies that identify specific climate parameters affecting tree growth by comparing ring-width index data to local climate data.

Acknowledgments This work was supported by the Andrew W. Mellon Foundation, UCSB, and a NASA Earth System Science Graduate Student Fellowship. Weather station data from 1997 through 2005 were provided by J.B. Wall at CSU Northridge and collected on the University of California Natural Reserve System's Santa Cruz Island Reserve, on property owned and managed by The Nature Conservancy. Tree cores were collected from the Channel Islands National Park. Thanks to K. McEachern, S. Chaney, C. Cowan, and CINP staff for their knowledge and assistance in conducting the field work. Thanks to D. Roberts, J. Michaelsen, J. Schimel, and R. Perroy for their helpful comments. Field work could not have been performed without the help of C. Ebert, D. Nelson, L. Merrill, and W. Amselem. Rainfall data were provided by L. Laughrin at the UC Natural Reserve System. Oxnard Airport cloud-height data were provided by J. Johnstone. All sampling and experiments complied with the current laws of the USA.

References

Anderson RL, Byrne R, Dawson TE (2006) Stable isotope evidence for late Pleistocene climate on Santa Cruz Island. In: California Association of American Geographers Annual Meeting, Chicago, IL, 7–11 March 2006

Allen RG, Walter IA, Elliott R, Howell TA (2005) The ASCE standardized reference evapotranspiration equation. American Society of Civil Engineers, Reston, VA

Axelrod DI (1967) Drought, diatrophism, and quantum evolution. Evolution 21(2):201–209

Azevedo J, Morgan DL (1974) Fog precipitation in coastal California Forests. Ecology 55:1135–1141

Biondi F, Cayan DR, Berger WH (1997) Dendroclimatoloty of Torrey pine (*Pinus torreyana Parry ex Carr.*). Am Midl Nat 138(2):237–251

Brouwer C, Heibloem M (1986) Irrigation water management: irrigation water needs (Training Manual 3). FAO, Rome

Chaney RW, Mason HL (1930) A Pleistocene flora from Santa Cruz Island, California. Carnegie Inst Wash Publ 415:1–24

Chaney RW, Mason HL (1933) A Pleistocene flora from the asphalt deposits at Carpinteria, California. Carnegie Inst Wash Publ 415:45–79

Cook ER, Kairiukstis LA (1990) Methods of dendrochronology: applications in the environmental sciences. Kluwer, Boston, MA

Critchfield WB (1966) Crossability and relationships of the California big-cone pines (US Dept Agric Forest Serv Res Paper NC-6). North Central Forest Experimental Station, St. Paul, MN, pp 36–44

Dawson TE (1998) Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117:476:485

Douglass AE (1941) Crossdating in dendrochronology. J Forestry 39:825–831

Dunne T, Leopold LB (1978) Water in environmental planning. WH Freeman and Co., New York

Filonczuk MK, Cayan DR, Riddle LG (1995) Variability of marine fog along the California coast. Climate Research Division, Scripps Institution of Oceanography, University of California, San Diego, CA

Fischer DT (2007) Ecological and biogeographic impacts of fog and stratus clouds on coastal vegetation, Santa Cruz Island. Dissertation, Department of Geography, University of California, Santa Barbara, CA

Fischer DT, Still CJ, Williams AP (2008) Significance of summer overcast and fog to the ecology of coastal California endemic species. J Biogeogr (in review)

Fritts HC (1976) Tree rings and climate. Academic, London

Granier A, Loustau D (1994) Measuring and modelling the transpiration of a maritime pine canopy from sap-flow data. Agric Forest Meteorol 71:61–81

Grissino-Mayer HD, Holmes RL, Fritts HC (1996) The International Tree-Ring Data Bank Program Library, version 2.0: user's manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ

Haller JR (1986) Taxonomy and relationships of the mainland and island populations of *Pinus torreyana* (*Pinaceae*). Syst Bot 11(1):39–50

Haston L, Michaelsen J (1994) Long-term central coastal California precipitation variability and relationships to El Niño-Southern Oscillation. J Clim 7:1373:1387

Heusser L (1995) Pollen stratigraphy and paleoecologic interpretation of the 160-ky record from Santa Barbara Basin, Hole 893A. In: Kennett JP, Haskins L (eds) Proceedings of the Ocean Drilling Program, scientific results, Santa Barbara Basin; covering Leg 146 of the cruises of the vessel JOIDES Resolution, Santa Barbara Channel, California, Site 893, 20 September–22 November 1992. ODP Ocean Drilling Program, Texas A & M University, College Station, TX

Holmes RL (1983) Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull 43:69–78

Laughrin L (2006) Santa Cruz Island rainfall record, 1904–2006. Santa Cruz Island Reserve, UC Natural Reserve System, Santa Barbara, CA

Leipper DF (1994) Fog on the United-States West-Coast—a review. Bull Am Meteorol Soc 75:229–240

Leyton L, Armitage IP (1968) Cuticle structure and water relations of needles of *Pinus Radiata* (D Don). New Phytol 67:31–38

McKenney MS, Rosenberg NJ (1993) Sensitivity of some potential evapotranspiration estimation methods to climate change. Agric Forest Meteorol 64:81–110

Michaelsen J, Haston L, Davis FW (1987) 400 years of central California precipitation variability reconstructed from tree-rings. Water Resour Bull 23:809–818

Millar CI (1999) Evolution and biogeography of *Pinus radiata*, with a proposed revision of its Quaternary history. NZ J Forestry Sci 29:335–365

Monteith JL (1965) Evaporation and environment. Symp Soc Exp Biol 19:205–234

Raven PH, Axelrod DI (1978) Origin and relationships of the California flora. University of California Press, Berkeley, CA

Remote Automated Weather Stations (RAWS)/National Data Buoy Center (NDBC) website (2007) Santa Rosa Island temperature and relative humidity data, 1990–2007. http://www.wrcc.dri.edu/channel_isl/, last accessed 25 May 2007

Snyder RL, Eching S (2004) EToETr: Penman-Monteith HourlyET$_{ref}$ for short and tall canopies. Univ. of California, Davis. http://www.biomet.ucdavis.edu/evapotranspiration/PMhrXLS/PM-hr.xls, last accessed 15 Jan 2006

Stephenson NL (1998) Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J Biogeogr 25:855–870

Stokes MA, Smiley TL (1968) An introduction to tree-ring dating. University of Arizona Press, Tucson, AZ

Thornthwaite CW, Mather JR (1955) The water balance. Laboratory of Climatology, Centerton, NJ

Thornthwaite CW, Mather JR (1957) Instructions and tables for computing potential evapotranspiration and the water balance. Laboratory of Climatology, Centerton, NJ

Wells ML, Getis A (1999) The spatial characteristic of stand structure in *Pinus torreyana*. Plant Ecol 143:153–170

Williams AP (2006) Teasing foggy memories out of pines on the California Channel Islands using tree-ring width and stable isotope approaches. Masters Thesis, Department of Geography, University of California, Santa Barbara, CA

Witiw M, Baars J (2003) Fog in Los Angeles. FogQuest News 9:3