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Fog in the California redwood forest: ecosystem inputs and use by plants

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Abstract Fog has been viewed as an important source of moisture in many coastal ecosystems, yet its importance for the plants which inhabit these ecosystems is virtually unknown. Here, I report the results of a 3-year investigation of fog inputs and the use of fog water by plants inhabiting the heavily fog inundated coastal redwood (*Sequoia sempervirens*) forests of northern California. During the study period, 34%, on average, of the annual hydrologic input was from fog drip off the redwood trees themselves (interception input). When trees were absent, the average annual input from fog was only 17%, demonstrating that the trees significantly influence the magnitude of fog water input to the ecosystem. Stable hydrogen and oxygen isotope analyses of water from fog, rain, soil water, and xylem water extracted from the dominant plant species were used to characterize the water sources used by the plants. An isotopic mixing model was employed to then quantify how much fog water each plant used each month during the 3-year study. In summer, when fog was most frequent, ~19% of the water within *S. sempervirens*, and ~66% of the water within the understory plants came from fog after it had dripped from tree foliage into the soil; for *S. sempervirens*, this fog water input comprised 13–45% of its annual transpiration. For all plants, there was a significant reliance on fog as a water source, especially in summer when rainfall was absent. Dependence on fog as a moisture source was highest in the year when rainfall was lowest but fog inputs normal. Interestingly, during the mild El Niño year of 1993, when the ratio of rainfall to fog water input was significantly higher and fog inputs were lower, both the proportion and coefficient of variation in how much fog water was used by plants increased. An explanation for this is that while fog inputs were lower than normal in this El Niño year, they came at a time when plant demand for water was highest (summer). Therefore, proportional use of fog water by plants increased. The results presented suggest that fog, as a meteorological factor, plays an important role in the water relations of the plants and in the hydrology of the forest. These results demonstrate the importance of understanding the impacts of climatic factors and their oscillations on the biota. The results have important implications for ecologists, hydrologists, and forest managers interested in fog-inundated ecosystems and the plants which inhabit them.

Key words Fog · Stable isotopes · Redwood forests · Hydrology · Plant water relations

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Introduction

Fog inundates many of the ecosystems of the world and can constitute a significant fraction of the total hydrologic input, particularly in some coastal regions which receive little or no rainfall each year (Myers 1968; Peace 1969; Goodman 1977; Schemenauer and Cereceda 1991) or during particular periods (e.g., the growing season) when plant demand for water is high (Oberlander 1956). Past investigations have shown that water input and/or soil moisture is measurably higher around tree canopies or in forest stands where the fog is "stripped" from the air mass (Kittredge 1948; Oberlander 1956; Parsons 1960; Vogelmann et al. 1968; Azevedo and Morgan 1974; Harr 1982; Ingwersen 1985; Schemenauer et al. 1988; Dawson 1996) and that when large-canopy trees, such as Douglas fir (*Pseudotsuga menziesii*), are lost or removed from the watershed both the water input from fog drip and the streamflow decline significantly (Ingwersen 1985). Went (1955) even suggested that some plant leaf shapes may have evolved to facilitate the interception or collection of fog. Other studies have suggested (Dawson 1996) or demonstrated (Vitousek et al. 1989; Bruijnzeel and Proctor 1995;

Weathers and Likens 1997; Bruijnzeel and Veneklass 1998) that ecosystem nutrient balance or other aspects of ecosystem biogeochemistry could be influenced by fog and/or cloud water inputs. Fog may help ameliorate plant moisture stress by reducing canopy transpiration (Byers 1953; Monteith 1963; Azevedo and Morgan 1974; Huntley et al. 1997) or evaporation from the habitat (Cannon 1901; Parsons 1960; Harris 1987) and/or by improving plant water status by direct absorption through the foliage (Stone 1957; Kerfoot 1968; Menges 1994; Boucher et al. 1995; Yates and Huntley 1995; Huntley et al. 1997).

Within the coastal redwood (*Sequoia sempervirens*) forests of northern California, annual water use by large redwood trees is high (Fujimori 1977 and below), on the order of 600 ± 145 l/day for a 45-m-tall tree (unpublished data) and the demand for water occurs during the summer months when rain is sparse. Past studies have claimed that fog may be an important source of water for *S. sempervirens* (e.g., Cannon 1901; Cooper 1911; Oberlander 1956; Azevedo and Morgan 1974; Libby 1996). Moreover, in summer and at sites where deep soil water is unavailable, fog may be the only source of water input, particularly for shallow rooted species, like most understory herbs which grow beneath the redwoods. While it seems reasonable to expect that plants inhabiting the coastal redwood forests might use fog water, no investigation had explicitly demonstrated if this was true nor had previous studies quantified the extent to which fog is used by different plant species.

Variation in the stable hydrogen and/or oxygen isotope composition of meteoric waters can be used to identify ('fingerprint') different water sources that might be used by the vegetation (reviewed by White 1988; Ehleringer and Dawson 1992; Dawson 1993a; Gat 1996; Dawson and Ehleringer 1998). Fog is isotopically enriched in the heavier isotopes ^{2}H and ^{18}O relative to rainfall that occurs within the same region (Gonfiantini and Longinelli 1962; Aravena et al. 1989; Ingraham and Matthews 1988, 1990, 1995). Fog can also be isotopically distinguished from water in the surface soil layers that comes from convective (colder) storm systems or has been subjected to marked evaporation (Allison et al. 1983; Dawson and Ehleringer 1998; Dawson et al. 1998). While there are a large number of factors which can influence the isotopic composition of water sources that might be used by plants, if the water sources are characterized along with the isotope values of water within the xylem tissues of plants, one can determine which and how much of each water source is being used by any plant species at a particular site (White et al. 1985, Dawson and Ehleringer 1991; Dawson 1993a; Thorburn and Walker 1993; Brunel et al. 1995; Cramer et al., in press). Therefore, for the present investigation, the stable isotope composition of fog, rainfall, shallow and deep soil water, and xylem water was determined and this information used to calculate how much of these water sources were used by plants inhabiting coastal redwood forests over a 3-year period. In addition, the amounts of fog water input to forested and deforested areas was determined using artificial fog collectors as well as the fog inputs which came directly off the redwood tree canopies using collectors placed beneath the trees themselves. These data were used to examine the relationships between fog water *inputs* to the coastal redwood ecosystem and water *use* by some of the dominant plant species.

Materials and methods

Background: fog formation and its isotopic composition

Fog can occur nearly every day from June to November along the coast of northern California and at my study site is heaviest from midnight until early or mid-morning (0700–1100 hours) and lightest in mid-afternoon (~1500 hours). This pattern is similar to other coastal regions of California (Peace 1969; Goodman 1977; Harris 1987). Within the northern California coastal zone, fog formation results from an interaction between a summer subsidence inversion of warm air which is forced coastward by the Central Pacific high-pressure cell and cold water up-welling and/or the incursion of cold oceanic currents of sub-Arctic origin. The interaction of the warm air moving over a colder ocean surface causes the air to reach its dew point and condensation occurs (Myers 1968; Harris 1987; McIlveen 1992). This condensate is composed of very small droplets and therefore remains within the air mass rather than falling out like rain. Vertical mixing lifts these moisture-laden eddies off the Pacific Ocean and they are advected onshore late in the day by a strong thermal gradient caused by the heating of land surfaces to the east (i.e., within the central valley of California; Goodman 1977). The thermally produced low-pressure area which develops landward draws these maritime fog banks up to 40 km onto land where they bathe the plants which inhabit the coastal plains and foothills (Oberlander 1956; Kerfoot 1968). The formation of fog and its movement onshore is therefore a thermodynamic process (advection) and differs from other atmospheric aerosol formation (e.g., cloud formation) because it does not require condensation nuclei (sea salts or atmospheric dust) to catalyze its formation, while cloud water seeding does (McIlveen 1992). Fog water and cloud water inputs can therefore be very different in origin, duration, chemical and isotopic composition (see Kimball et al. 1988; Fuzzi et al. 1996; Vermeulen et al. 1997 and references therein), yet they are frequently confused as being the same thing: they are not. At my site, fog was only collected, on average, during 47 ± 6% of all the fog events which occurred during the study. The remaining fog events were relatively 'light' and when tree foliage intercepted the fog, no measurable fog drip occurred.

Fog is usually isotopically enriched in the heavier (^{2}H and ^{18}O) isotopes relative to the water source from which it is formed (in this case the ocean, which by definition has an isotope ratio for both H and O of zero) because it is the first-stage condensate off the ocean and forms within the warmer air near the surface of the earth (see above and discussions in Gonfiantini and Longinelli 1962; Aravena et al. 1989; and Ingraham and Matthews 1995). Fog is also isotopically enriched relative to the rainfall which occurs along the California coast because these rains generally come from frontal (convective) storm systems whose origins are in colder regions or which have moved great distances, in the process becoming progressively more depleted in ^{2}H and ^{18}O as water continuously condenses out of the clouds while they move towards the coast where, in winter, they deposit their rain (the so-called "rain-out" effect – see Dawson 1993a; Ingraham and Matthews 1995). Depending on the temperature and vapor pressure of the air mass within which the fog forms, the $\delta^{2}H$ and $\delta^{18}O$ of fog can have either a positive or negative isotopic value (Gonfiantini and Longinelli 1962; Ingraham and Matthews 1988, 1990, 1995; Aravena et al. 1989 and below). Fog and rainfall samples collected over the course of this investigation were used to construct a local meteoric water line (LMWL) described by the equation: $\delta^2H = 7.7 \cdot \delta^{18}O + 9.6$. This description differs slightly, but significantly ($P < 0.05$), from the global meteoric water line (GMWL, $\delta^2H = 8 \cdot \delta^{18}O + 10$; Craig 1961) and was therefore more useful for interpreting local variation in the δ^2H and $\delta^{18}O$ of meteoric waters. Most importantly, the LMWL provided a mixing line that explained more of the variation ($r^2 = 0.973$) than the GMWL ($r^2 = 0.927$) and therefore permitted a more statistically robust description with which to qualitatively evaluate the plant isotope data (see below). This was especially true when water samples were isotopically enriched, like fog. The enriched fog samples collected at the study site plotted directly on the LMWL, yet always plotted off (below) the GMWL, therefore limiting its usefulness in this study. Ingraham and Matthews (1995) also reported that the fog samples they collected at Point Reyes, California did not lie on the GMWL. Using the LMWL therefore made an evaluation of the plant water samples easier and less subjective and also provided a more useful way of determining the contribution of fog water inputs to local groundwater recharge in this region (T.E. Dawson, unpublished data).

Plant, soil, and water sampling

Plant and soil samples were collected at ten sites between 26 km north of Arcata and 14 km south of Crescent City, California, USA. One site was instrumented for fog and rain water collection along the north side of the Klamath River, west of the town of Requa (41°33′N, 124°4′W) near the boundary between Redwood National Park and the Yurok tribal lands and approximately 0.75 km from the coast (between 47–191 m above sea level). Fog input to the site was determined with two types of fog collectors. (1) artificial collectors, based on the designs of Falconer and Falconer (1980), Goodman (1985) and Weathers and Likens (1997); each collector was constructed of vertically oriented Teflon lines (0.8 mm thick) strung between two Plexiglas plates (total surface area of 0.25 m^2) that directed the water which was collected into a funnel and then into a water-tight container. Each collector was cylindrical in shape which permitted the collection of fog from all directions, and had a 'roof' which extended 20 cm in all directions beyond the collection surfaces to prevent rainfall from entering the collectors. (2) Foliar interception collectors were large and saucer shaped and were placed directly beneath the live crown of seven mature redwood trees between 34.7 and 37.8 m tall. This collector type was designed to gather all of the 'fog drip' which occurred off each tree into a water-tight vessel. Each saucer therefore extended beyond the drip line around the entire circumference of each tree crown for which the interception (leaf) area had been estimated (see Bowers 1942; Fujimori 1977). Collection trees were at least 3 m away from any other trees in the stand. These collectors were only used to quantify fog drip when there were no rain events. Artificial collectors placed within intact forest stands were affixed to tethered poles near target trees at the mid-point of the live crown (~20 m off the ground). Collectors placed in the open were on poles 1.5 m off the ground; the site was a 115 × 85 m area adjacent to the forest site. Five collectors were placed at each location. It is important to note that only fog and rainfall input information was collected for the purposes of this investigation. Throughfall, canopy interception losses, drainage, and runoff were not determined, but would needed to construct a complete hydrologic balance (see Dawson 1993b; Huntley et al. 1997).

Plant water use

Whole-tree transpiration was estimated using the heat-pulse velocity method outlined by Hatton and Vertessy (1990; see also Hatton et al. 1995 for a full discussion of the assumptions and calculations). Two sapflow sensors (Greenspan Technology, Queensland, Australia) per tree were used; they measured sap velocity at 10 and 35 mm depths within the sapwood. Values from both depths were averaged to arrive at the sap velocities reported here. The thick outer bark of the trees was removed and the sensors placed in the bole of the trees 1.5 m above the ground. Active sapwood was estimated by injecting 1% acid fuchsin dye across the sapwood with a needle and then coring the trees 24 h later and visually determining the sapwood-heartwood boundary. This boundary was generally within 150–200 mm from the cambium for the trees measured. Therefore, the sapflow sensors only sampled the outer 17–23% of the active sapwood and the data should only be used here as a relative estimate of water use among the different size classes of trees. A more complete analysis will be required before robust quantitative measures of whole-tree transpiration can be provided. The sap velocity data collected was converted to mm day^{-1} following Jolly and Walker (1996) and then used in conjunction with fog and rainfall input information as well as water source information from isotope analyses to arrive at the fraction of water used by plants which was derived from fog.

Isotope methods

Sampling

Stable hydrogen and oxygen isotope analyses were performed on water collected from fog, rainfall, soil water (two depths; see below), and the xylem water that was extracted from the dominant plant species. The stable H and O isotope composition was determined from a gas sample generated from pure liquid introduced into an isotope ratio mass spectrometer (delta S, Finnigan MAT, Germany or SIRA 9, VG Instruments, UK). The stable H isotope composition of all water samples was determined using the zinc-reduction method outlined by Coleman et al. (1982). The stable O isotope composition of these same water samples was determined using the CO_2-water equilibration method outlined by Dugan et al. (1985). Values are expressed in the internationally accepted delta notation (‰ or "per mil") where the ratio of the heavy to light isotopes in the sample (e.g., $^2H/H$ or $^{18}O/^{16}O$) is determined relative to an accepted standard (V-SMOW; see Dawson 1993a); these are denoted as δ^2H and $\delta^{18}O$, for the H and O isotope ratios, respectively. Fog drip was collected into an airtight container affixed to the outlet of a single tipping-bucket rain gauge (model TE525, Texas Electronics, USA) placed in the open. Rainfall and other meteorological data were collected with a computerized data acquisition system (model CR10, Campbell Scientific, USA).

Shallow/upper soil water was obtained from cores collected to a depth of 20 cm beneath redwood trees ($n = 12$). Deep soil/groundwater was obtained from soil samples taken at a depth of 1.5–1.6 m. Six root cores/species at three sites were also taken to see if any of the plants formed root platforms at several depths in the soil profile and not just at shallow (0–20 cm deep) and deep (>1.5 m deep) layers. No platforms were found in any of the plants I sampled. Non-photosynthetic tissue samples (tree cores, twigs, or rhizomes) were collected from each plant species ($n = 15$) following the methods of Dawson and Ehleringer (1993). Water was extracted from soil cores and plant samples by cryogenic vacuum distillation. Isotopic analysis was performed on fog water taken from both types of fog collectors at pre-dawn, at or near the peak of a fog drip event, but before isotopic fractionation had occurred from re-evaporation or modification from the mixing of isotopically lighter transpiration water (unpublished data).

Modeling proportional fog water use by plants

For presentation purposes, only the δ^2H data are shown. However, both the δ^2H and $\delta^{18}O$ data were used in determining the proportion of fog water (P_f) used by plants. P_f was determined using a minimum residual isotopic mass balance model developed by Brunel et al. (1995). This model assumes that water obtained by plants comes from two compartments (e.g., fog or rain water vs deep soil/groundwater). For my purposes, I weighted the source water isotopic values by the amount of each source present at each sampling date. The amount of each source was determined from fog collector and rain gauge data and from soil water content data determined gravimetrically from the cores. Weighting the isotope values in this manner explicitly incorporates the fact that not all sources of water were equally available and acknowledges the widely known fact that plants use water where it is most easily obtained (most available or at its highest water potential). The final P_f value that was calculated for each plant species each month during the course of the study is therefore not a simple proportion based on fog or rainfall versus deep soil water isotope data (see Fig. 2a); P_f is a weighted proportion. Similar procedures have been outlined by White et al. (1985) and Dawson (1993a). The δ^2H and δ^{18}O data obtained from any two water sources are then compared to the δ^2H and δ^{18}O data obtained from plant water and the P_f calculated using the two-compartment mixing model procedure outlined in Brunel et al. (1995). This procedure successfully predicted the proportion of fog and rain water used by all plants in 94% of the cases by comparing the δ^2H and δ^{18}O of either summer fog in summer and winter rain in winter to deep soil/groundwater samples (>150 cm in depth) because I could not detect any significant isotopic differences between summer fog and winter rain water samples and the water present in the upper soil layer (0–20 cm in depth) surrounding the plants. While isotopic profiles are commonly observed in soils (see Dawson et al. 1998), the lack of a detectable profile in these redwood forest soils was likely due to several factors: (a) that evaporation from the soil surface in these forests is extremely low due to a dense cover of vegetation; (b) there was a "closed" canopy above the soils which prevented solar radiation from reaching the forest floor and causing isotopic enrichment from the surface layers, and (c) because samples were always collected at pre-dawn before any evaporative gradients might develop. In 6% of the cases, the simple two-compartment calculations could not be used because (1) fog or rainfall differed isotopically from upper soil water and deep soil/groundwater, or (2) rainfall and fog water inputs had occurred simultaneously at the site and differed isotopically from upper soil water and deep soil/groundwater. In these cases, there were three (case 1) or four (case 2) potential water sources (compartments) that plants might be using. Resolving the proportional water use of each source by plants in these cases requires the use of a multi-compartment model. Such a model was recently developed by Cramer and her colleagues (in press), permitting these sorts of analyses in the future. However, here I do not use a multi-comparment model. Instead, I assumed that fog water (in summer) or rain water (in winter) was as equally available to plants as the water in the upper soil layer. This allowed me to combine the summer fog or winter rain isotope values with the isotope value from the upper soil layer, divide this value by 2 (sources) to then arrive at a single end member value which could be compared to the deep soil/groundwater isotope value (the other end member) and then to the plant isotope value so that P_f in these cases could be estimated.

Results and discussion

General findings

Rainfall and "fog-day" information was obtained from long-term records for the coastal redwood forest between Arcata and Crescent City, California (see Fig. 1 caption for other details). A fog-day is defined as a day where visibility was 0.8 km (1/2 mile) or less for more than 8 h. During the growing season ('summer'; June–November), rainfall is at its lowest and fog-days are at their highest for the year (precipitation = 55 ± 65 mm/month; fog-days/month = 10 ± 3.3) (Fig. 1). In contrast, during the 'winter' (December–May), rainfall was highest and the number of fog-days were at their lowest (precipitation = 156 ± 75 mm/month; fog-days/month = 3.8 ± 1.1).

Data obtained from the artificial fog collectors showed an average input within the forest of 59 ± 18 mm for a 12-h fog-day, while interception input off the tree foliage itself was 98 ± 23 mm (Table 1). Input to the artificial fog collectors placed in the open (without trees) averaged only 46 ± 13 mm for the same periods (Table 1). These data show that during heavy fog events, water input off trees was always higher than input from the artificial fog collectors by 18–40%. The difference existed because tree foliage is more effective at 'strip-

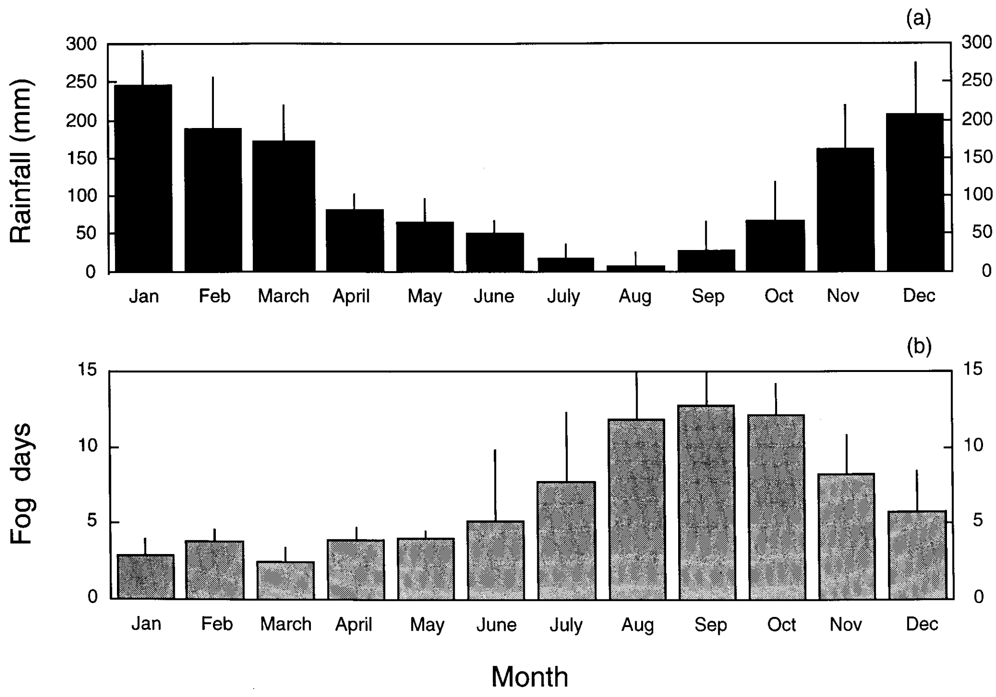

Fig. 1 Rainfall (mm) (**a**) and the number of fog-days (**b**) each month for the coastal redwood forest between Arcata and Crescent City, California. Each bar represents an average ($\pm$SD) for that month calculated from records obtained from the Arcata and Crescent City airports (35-year record for Arcata, 17-year record for Crescent City). A fog-day is defined as a day when visibility is 0.8 km (0.5 mile) or less for at least 8 h (an average fog-day is generally between 12–17 h)

Table 1 The average and range of fog water input (mm) during a 12-h fog-day by different 'collectors', the average rainfall, fog drip and total moisture inputs to the sites occupied by different collectors, and the average percentage (and range) of the annual hydrologic inputs as fog. All data were obtained during 1992–1994 at a redwood forest site along the Klamath River near Requa, California. Fog input values are based on millimeters of fog collected for collectors of a known interception area. Input values from different collector types can therefore be compared directly. Values for fog water input are means (SD) from seven interception or ten artificial fog collectors and the same number of 12-h 'fog-days'. Other values are means with either SDs or ranges shown in parentheses. Values within a row with different supercripts are significantly different from one another ($P < 0.05$; Students t-test). Differences between years were not tested (but see Table 3)

	Year		Off trees (interception)	Fog collector in the forest	Fog collector in the open
Fog water input	1992	Average	93 (21)[a]	55 (17)[b]	42 (13)[c]
		Range	63–128	37–73	25–71
	1993	Average	104 (26)[a]	62 (20)[b]	40 (22)[c]
		Range	55–132	39–70	33–69
	1994	Average	93 (21)[a]	60 (18)[b]	51 (21)[c]
		Range	59–130	38–66	29–60
	3-Year average		**98 (23)[a]**	**59 (18)[b]**	**46 (19)[c]**
	3-Year range		55–132	37–73	25–71
Rainfall (mm)			1315 (340)	1315 (340)	1315 (340)
Fog-drip (mm)			447 (289–605)	303 (17–434)	224 (79–368)
Total (mm)			1762 (413)[a]	1618 (292)[a,b]	1540 (325)[b]
Annual fog input		%	**34 (8)[a]**	**23 (7)[b]**	**17 (10)[b]**
		Range	22–46	13–33	6–28

ping' fog from the air mass (see also Joslin et al. 1990) and because in deforested (open) areas, solar radiation and wind velocities were greater and the evaporative conditions increased fog dissipation (Parsons 1960; Monteith 1963; Harr 1982; Ingwerson 1985; McIlveen 1992) and therefore less fog was collected. Annually, forested sites receive a greater total input of water (Table 1); on average 34 ± 8% of this total was due to fog drip off the redwood trees themselves (Table 1). These data are consistent with other fog input information collected in other regions inhabited by coast redwood (Cooper 1917; Byers 1953; Oberlander 1956; Azevedo and Morgan 1974; Harris 1987), Douglas fir (Harr 1982; Ingwerson 1985) and other tree species or fog-inundated-forest types (Stone 1957; Pook et al. 1991; Menges 1994: Bruijnzeel and Proctor 1995; Juvik and Nullet 1995; Cavelier et al. 1996). In fact, in a recent study by Huntley et al. (1997), in a subtropical forest in Australia, fog deposition comprised nearly 40% of all the water which reached the forest floor. It is striking how similar these findings are to the ones reported here for a north temperate climatic zone. The findings from Huntley et al. (1997) and those presented here reinforce the notion that fog deposition may be a critical, yet often unaccounted for, part of the hydrological balance of fog-inundated forests (see also Bruijnzeel and Proctor 1995; Juvik and Nullet 1995).

Figure 2a shows the stable hydrogen isotope values (δ^2H) during 1992–1994 for fog and rainfall, and for the xylem sap of *S. sempervirens*, the dominant canopy tree, and for the four common understory plants. Results from the isotopic mixing model calculations showed that during summer, when fog was most frequent and fog drip an almost daily occurrence, *S. sempervirens*, obtained between 8–43% (mean = 18.6%) of its water from fog (Fig. 2b). In general, understory plant species used a higher proportion of fog than *S. sempervirens* and at times (e.g., the drier than normal year of 1994), some species appeared to be completely dependent upon fog (e.g., *Polysticum munitum*, sword fern; Fig. 2b). On average, the understory species obtained between 6–100% (mean = 66.5%) of their water from fog after it had dripped from the tree foliage into the soil (Fig. 2b; but see Table 3 and below). Differences in the fraction of fog water used by understory species is likely to reflect (a) their unique rooting patterns and depths, (b) their demands for water and hence the phenology of root growth and the nature by which they are able to proliferate roots to take advantage of the fog drip (Dawson 1996), (c) how well water can directly enter their leaves, and/or (d) their unique canopy architecture which can serve to 'collect' and channel water towards shallow roots at the base of the plant (e.g., *P. munitum*; Dawson 1996 and unpublished data).

The water inside shallow roots of all the plants studied was either identical to the fog water δ^2H or a mixture of fog-derived water in the shallow soil and deep soil/groundwater provided primarily by winter rainfall recharge events (Dawson 1996). Water within the xylem of aboveground stems for the three woody species (*S. sempervirens*, *Rhododendron macrophyllum*, and *Gaultheria shallon*) was never significantly different from root water δ^2H, indicating that water uptake by roots was the primary route by which they obtained most of their water (Dawson 1996). Direct fog uptake through plant foliage may be important and has been reported in other species (see Stone 1957; Monteith 1963; Kerfoot 1968; Menges 1994; Boucher et al. 1995; Yates and Huntley 1995; Huntley et al. 1997) but was not quantified here.

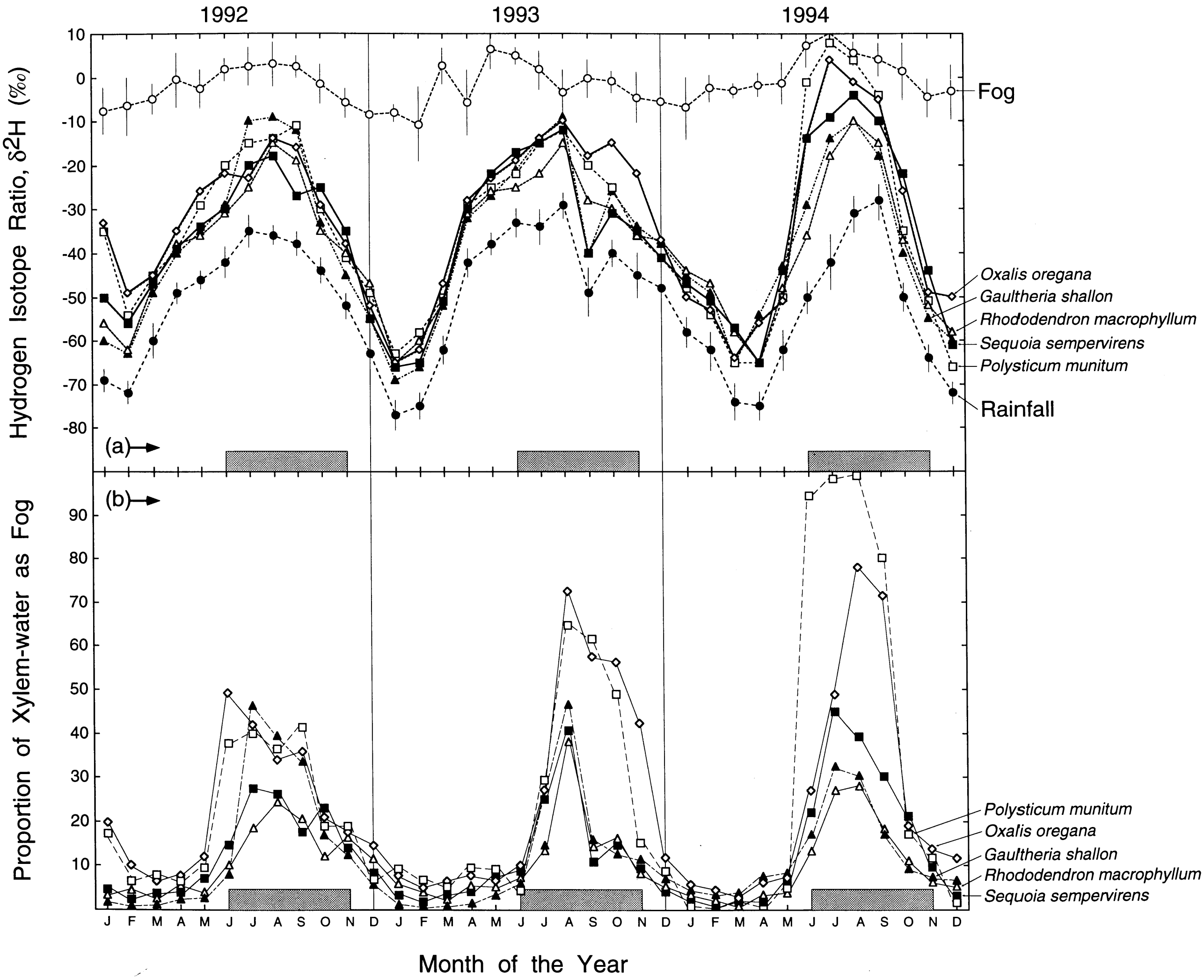

Fig. 2 The average stable hydrogen isotope ratio (δ^2H; ‰) (**a**) of rainfall (*filled circles*), fog (*open circles*), and water extracted from the xylem of plants ($n = 15$/species) from a coastal site north of Arcata, California (USA) during the period from January 1992 through December 1994, and the proportion of xylem water as fog water (**b**) calculated using an isotopic mixing model weighted by the average monthly rainfall and fog drip inputs. The plant species are the coastal redwood (*Sequoia sempervirens*; *filled squares*), redwood sorrel (*Oxalis oregana*; *open diamonds*), California rose-bay (*Rhododendron macrophyllum*; *open triangles*), sword fern (*Polysticum munitum*; *open squares*), and salal (*Gaultheria shallon*; *filled triangles*). Fog was obtained from fog-collectors ($n = 10$) and from fog drip off *S. sempervirens* foliage ($n = 7$) and pooled to obtain the mean value. Error bars on the fog and rainfall data are SDs. Error bars for the plant data are not shown because they made it difficult to see the trends for each line. However, the SDs about the mean values displayed for xylem water from all the plant species taken together were ±7.4‰ in 1992, ±8.6‰ in 1993, and ±9.1‰ in 1994. The *stippled bars* at the bottom of each section are the periods when fog was most common at the study sites

In an attempt to relate the proportion of fog water in the xylem of redwood trees to their water use patterns, I used the estimates of tree water use from my sapflow measurements (converted to millilitres of water used per day) and water input information from fog and rainfall collectors and their isotopic values to arrive at an estimate of the fraction of fog within the xylem that was used (not just stored) by trees. This preliminary analysis shows that fog can comprise between 13–45% of all of the water used (transpired) annually by a redwood tree (Table 2); data collected from four tree size classes showed that all trees used a significant fraction of fog precipitation and that smaller trees transpired more fog (39%) water than did large trees (19%; Table 2). This analysis adds to and extends the isotopic information presented in Fig. 2b by showing that while on average redwood trees obtain ~19% of their summer water from fog, this water source constitutes a major fraction of the water used by these trees annually. This is because water use is two- to fourfold higher in the summer months when trees take up and use significantly more fog water compared to the winter water sources; fog therefore constitutes a more important source of water used by redwood trees than the isotopic information alone implies. Lastly, the findings that smaller trees use more fog water than large trees is consistent with rooting depth information and other stable isotope data (not shown) demonstrating that smaller trees possess a greater fraction of shallow roots and may therefore use a greater

Table 2 The fraction of water used (%; ≈ transpiration) which is derived from fog for each of four tree size classes of *Sequoia sempervirens*. Size classes are diameter (cm) at breast height (*DBH*; ~1.4 m). Estimates are based on fog input and rainfall data (mm day^{-1}), isotope information collected from each water source and plant xylem water in or around each tree at the site, and on water use estimates from average sapflow velocity integrated across the outer 35 mm of sapwood which was converted to the same units (mm day^{-1}; see Materials and methods). Sapflow estimates were obtained over a 5-day period each month during 1994 using three trees in each size class in the same stand. Estimates shown are a relative and conservative index of water use since they are for 1 year only, do not include all of the sapwood which may be transporting water, or all of the days per month when trees would use water. Values which are significantly different from one another ($P < 0.05$; Students *t*-test) have different superscripts

	Size classes (DBH)			
	31.9 (±3.8)	38.0 (±3.2)	45.1 (±4.4)	62.3 (±6.3)
Fraction of tree water use as fog (%)	39 (±6)[a]	29 (±5)[b]	25 (±4)[b,c]	19 (±6)[c]

proportion of shallow soil water; in summer, the shallow soil water is from fog drip.

It is interesting to note that for all plants, there was a significant reliance on fog as a water source, especially in summer when there was no rainfall. As mentioned above, dependence on fog as a moisture source was highest, on average, in 1994, the year of lowest winter precipitation during the study (Fig. 2b, Table 3). Huntley et al. (1997) also pointed out the importance of fog deposition as a critical plant water source during the dry season at their subtropical site (see also below). At this redwood forest site in California it was also very interesting to note that during the mild El Niño year of 1993, when the ratio of rainfall to fog water input was significantly higher (and therefore fog inputs lower), both the proportion (P_f) and coefficient of variation in how much fog water was used by plants (CV-P_f) increased (Table 3). I believe this results from the fact that although there was more rainfall than fog input in 1993, the rainfall came mostly during the winter months when plant demand was low. In summer, however, when fog inputs did occur, plant demand for water was at its highest and was likely to be of greater importance for performance. Thus, plant dependence on fog water was higher in the El Niño and dry years of 1993 and 1994 than during an average climatic year (Table 3).

Implications

Fog may provide other benefits beyond additional water, which could influence the ecology of forest plants and the biogeochemistry of the forested ecosystem they compose. For example, the higher CO_2 concentrations 'trapped' within the fog inversion as well as higher relative humidities, lower evapotranspiration and/or vapor pressure deficits, and higher diffuse radiation could all enhance plant photosynthesis (Harris 1987; Dawson 1996 and unpublished data; Huntley et al. 1997). During fog events, the temperature gradients through the canopy profile and over the course of the day/night cycle also tend to be more uniform, stable, and generally cooler (Huntley et al. 1997) which could have a number of important physiological effects. Moreover, fog can contain critical nutrients, such as nitrogen derived from several sources (unpublished data) which are essential for healthy plant growth and can influence biogeochemical cycles (Vitousek et al. 1989; Weathers and Likens 1997).

Beyond the new finding presented here that plants of coastal redwood forests use a large fraction of fog water is the result that the total moisture input to the study site during the course of a hydrologic year was increased by the trees themselves (Table 1); until now, this result has not been reported for this species or ecosystem. In *P. menziesii* forests, both Harr (1982) and Ingwerson (1985) also showed that water yield from a forested catchment declined when trees were logged because fog water inputs declined. These results and those shown here suggest that the hydrology and ecology of redwood and other forests composed of tall trees which can act as effective interception surfaces could be determined by an interplay between the ecosystem and the climate system

Table 3 The ratio of rainfall to fog drip (from interception collectors beneath tree canopies, see Table 1) inputs (*R*/*F*), and the proportion (P_f) of and coefficient of variation (CV-P_f) in fog water used by different plant groups inhabiting the redwood forest between July and November (fog season) in the 3 years of this investigation. The years are categorized as an average climate year (with long-term average rainfall and number of fog days), a mild (type 2) El Niño year (when sea surface temperatures were 0–2°C above normal; rainfall was higher and fog input lower than the long-term average), and a drier than normal year (with an average number of fog days), based on the isotope (Fig. 2) and climate data (some for Table 1). P_f values for the different plant groups are reported here as ranges

	R/F	Plant group					
		Trees		Shrubs		Herbs	
		P_f (%)	CV-P_f	P_f (%)	CV-P_f	P_f (%)	CV-P_f
Average year (1992)	2.94	12–25	0.26	10–46	0.38	19–50	0.43
El Niño year (1993)	5.5	7–40	0.51	6–50	0.64	10–72	0.71
Drier year (1994)	1.68	20–51	0.37	6–33	0.46	28–100	0.55

and begs the question, does fog essentially mediate a number of critical organismal and biogeochemical processes? Hydrologically, it is clear that fog is more readily removed when forests are intact; this ameliorates the microclimate and increases the annual income of water (also see Harr 1982; Ingwerson 1985; Bruijnzeel and Proctor 1995; Juvik and Nullet 1995; Huntley et al. 1997). A decline in fog inputs due to tree removal causes more xeric site conditions and may also significantly influence the biogeochemistry of the forest because as moisture inputs decline so do nutrient inputs, decomposition, and mineral cycling in forest soils (e.g., Cannon 1901; Azevedo and Morgan 1974; Vitousek et al. 1989; Pook et al. 1991; Dawson 1996; Huntley et al. 1997; Weathers and Likens 1997).

From the management perspective, it is clear that the loss of redwood trees to natural disasters (e.g., fire, wind throw, or floods), timber harvesting, or other land use practices which convert the forests to open habitats will dramatically alter the hydrological balance and ecological integrity of these forests (Harr 1982; Ingwerson 1985; Bruijnzeel 1991; Bruijnzeel and Proctor 1995; Juvik and Nullet 1995; Huntley et al. 1997; Bruijnzeel and Veneklass 1998). Loss of the canopy tree *S. sempervirens* is not only a loss of biomass and the nutrients contained within it, but will lead to a loss of the diverse canopy "community" that is just now being studied (S. Sillett, personal communication) as well as the organic-rich forest soils to post-disturbance erosion. Tree loss will also convert a once moist, cool, closed ecosystem into a more drought prone, warmer, open ecosystem. Plants and animals which depend upon the moisture input from fog drip or other microclimatic benefits caused by the presence of fog will experience more frequent water stress when *S. sempervirens* is removed. In addition, both *S. sempervirens* seedlings and understory plant species which require moist and cool conditions to regenerate could suffer or disappear if inputs of fog decline (unpublished data). Results from this and other ongoing studies in the Mediterranean regions of California (Ingraham and Matthews 1995; Dawson 1996; Dawson and Vidiella 1998), Chile (DiCastri and Hajek 1976; Aravena et al. 1989; Cereceda and Schemenauer 1991; Weathers and Likens 1997; Dawson and Vidiella 1998), and central Italy (Fuzzi et al. 1996) as well as in both lowland and montane cloud forests (Grubb and Whitmore 1966; Cavelier and Goldstein 1989; Bruijnzeel 1991; Juvik and Nullet 1993; Bruijnzeel and Proctor 1995; Cavelier et al. 1996; Huntley et al. 1997; Bruijnzeel and Veneklass 1998; Feild and Dawson 1998) are showing that the importance of fog or low clouds as meteorological factors has been underestimated, from both the hydrological and the ecological perspectives. Incorporating the influences that fog and/or cloud water inputs have on a variety of ecosystems could benefit future efforts to conserve and manage them.

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