Streamside trees that do not use stream water

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A LONG-STANDING axiom is that plant distribution is strongly influenced by soil moisture content[1,2]. While it has been shown that plant taxa inhabiting streamside communities receive or use more water[3], it is assumed that this water is obtained from the stream adjacent to where they are found growing. Here we show, using hydrogen isotope ratio analyses at natural abundance levels, that mature streamside trees growing in or directly next to a perennial stream used little or none of the surface stream water. The deuterium to hydrogen content of both source and xylem waters indicated that mature trees were using waters from deeper strata. Although adult trees may have roots distributed continuously throughout a soil profile, it seemed that the most active sites of water absorbtion were limited to deeper soil layers. In contrast, small streamside individuals appeared to use stream water, whereas small non-streamside individuals used recent precipitation as their primary water source. Our analyses provide both a relatively non-destructive method for assessing water sources of plants and a means of assessing potential competitive interactions among co-occurring taxa. In addition, the method may aid in resolving the role of water in determining plant distributions in areas characterized by sharp soil moisture gradients.

The use of stable isotopes at natural abundance levels in ecological, physiological and environmental research has greatly increased over the past decade[4-6]. Whereas previous ecological work has emphasized the usefulness of carbon, nitrogen and sulphur isotopes, hydrogen and/or oxygen isotope analyses have proved to be useful for understanding the dynamics of water in atmospheric and geochemical studies[6,7]. There is no fractionation of isotopes by plant roots during water uptake[8-10]. Therefore, hydrogen isotope analysis of xylem sap, which has not been exposed to evaporative enrichment, should reflect the water sources in use by that plant. Such analyses have made it possible to distinguish quantitatively between recent precipitation and groundwater as water sources for white pines[10] and between fresh- and salt-waters as the water sources for mangrove species[11]. In both studies, the hydrogen isotope ratio of the possible water sources was significantly different and the percentage of water used from either source was determined by interpolation between the two end members.

In temperate, continental zones, the isotopic composition of precipitation varies both seasonally and with elevation[12,13]. Precipitation falling in the summer months as rain has a higher deuterium content than winter snows; precipitation falling at higher elevations is depleted in deuterium relative to that at lower elevations[7,12]. The deuterium to hydrogen content of groundwaters and soil water in deeper layers not exposed to evapotranspiration reflect a weighted average of annual precipitation inputs. However, fossil groundwaters reflect the precipitation inputs of earlier time periods[6,7].

In the Intermountain West of the United States, most of the annual precipitation comes in winter as snow, especially at higher elevations[14,15]. Soil moisture is recharged by this winter precipitation, but then declines quickly to low values by late spring[15]. Snow melt from higher elevations supports perennial streams and the development of an extensive streamside riparian vegetation in an otherwise semi-arid region. Although infrequent summer convection storms can occur, they contribute little to the annual water balance of perennials in these regions[15]. Along the Wasatch Mountains of Utah, a scrub oak-maple (*Quercus-Acer*) vegetation type surrounds the streamside (riparian) zone. Both the streamside and adjacent scrub oak-maple vegetation are active in the spring and summer but it is not clear which water sources these plants have available to support metabolic activity during the driest summer months (July–September). Based on precipitation patterns, we hypothesized that streamside trees would use surface stream water while non-streamside plants would be limited to recent precipitation as their primary water sources. Therefore, we examined dominant streamside and non-streamside tree species in the Red Butte Canyon Research Natural Area in the Wasatch Mountains immediately east of Salt Lake City (40° 46′ N, 111° 55′ E, 1,820–1,890 m elevation). Streamside trees were growing in or within 2 m of a perennial stream. Non-streamside trees were growing 25–45 m from and 2–6.5 m above the stream.

Hydrogen in water was reduced to its diatomic form using zinc[16] and the deuterium content measured on a Finnigan MAT, model delta E, isotope ratio mass spectrometer early in the study, and on a delta S later on. Deuterium content is expressed in delta notation (δD in ‰) relative to the Standard Mean Ocean Water standard[17]

$$\delta D = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000\,‰$$

where R_{sample} and $R_{standard}$ represent the molar deuterium/hydrogen ratios of sample and standard, respectively. Overall precision of the preparation and analysis is ±1.4‰ for the delta E and ±1.0‰ for the delta S.

To distinguish between two possible water sources, differences in δD must exist between summer precipitation and stream water. Over a two-year period, significant differences were maintained between stream water and precipitation δD values (Fig. 1). As expected[12,13], stream water, derived primarily from snow melt at higher elevations, was lighter (more depleted in deuterium) than summer precipitation. Stream water δD values remained essentially constant at −121.4 ± 0.7‰ (mean and standard error) over the entire sampling period, whereas individual precipitation events varied between −11‰ in summer and −213‰ in winter, respectively. Over the growing season, soil water adjacent to the stream (−122.1‰) was indistinguishable from that of the stream water (Student's t-test, $t = 0.51$, d.f. = 10, $P = 0.621$), demonstrating that no evaporative enrichment occurred as water may have diffused from the stream through

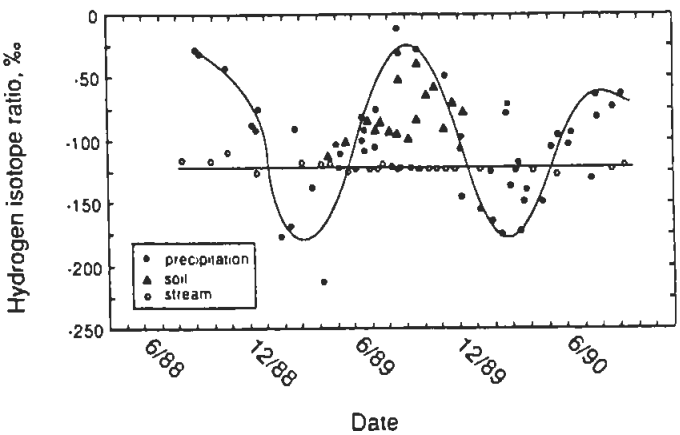

FIG. 1 The hydrogen isotope ratio (δD in ‰) of precipitation, surface stream water and soil moisture at a non-streamside location in the Red Butte Canyon Research Natural Area between July 1988 and September 1990. Soil water δD was obtained by a cryogenic vacuum-distillation extraction from cores collected in the field to a depth of 50 cm. The upper 10 cm of soil was not included to avoid biasing the δD values as a result of evaporative enrichment.

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the soil. In contrast, soil moisture at non-streamside locations had substantially higher δD values, reflecting both spring and summer precipitation input (Fig. 1).

The most common tree species at both streamside and non-streamside sites (*Acer grandidentatum* Nutt., *A. negundo* L. and *Quercus gambelii* Nutt.) were sampled during the peak of the growing season in July. Xylem sap was obtained by cryogenic vacuum distillation of only mature, suberized stem tissues. Younger, partially suberized tissues were isotopically enriched (10–55‰) owing to cuticular water loss and so were not used. Figure 2 shows that the δD values of xylem sap differed among trees, depending both on tree size (based on diameter at breast height; DBH) and location. For all species, δD values of streamside trees with a diameter of less than 20 cm (-125.5 ± 9.2‰) were significantly lighter (Student's t-test, $t = 3.54$, d.f. = 31, $P = 0.001$) than equivalent-sized trees at non-streamside locations (-89.6 ± 4.3‰). Larger individuals, regardless of the site, showed no significant difference in xylem water δD values (streamside = -133.3 ± 0.8‰, non-streamside = -132.8 ± 0.9‰, $t = 0.47$, d.f. = 44, $P = 0.643$).

As anticipated from Figs 1 and 2, small and large trees had significantly different δD values at non-streamside ($t = 7.37$, d.f. = 46, $P = 0.000$) sites. Unexpectedly, different sized trees at the streamside sites also had significantly different δD values ($t = 4.78$, d.f. = 31, $P = 0.000$). Smaller-diameter streamside trees δD values (-125.5‰) were similar to that of the adjacent stream (-123‰ for this sample date). In contrast, larger streamside trees gave δD values significantly lighter than that of the stream ($t = -13.13$, d.f. = 25, $P = 0.0001$). Thus, whereas young streamside trees were using stream water (because they exhibited equivalent δD values), larger mature trees were not using this same water source. Instead, they either used a lighter water source (more negative δD) or there was isotopic fractionation during water uptake.

We tested for isotopic fractionation during water uptake through roots by growing *Acer negundo* in pots and watering with a known water source. The δD for the water source was -120.5 ± 0.5‰. The δD from suberized stems of ten individually grown trees was -120.7 ± 0.5‰, which is not significantly different from the source water value. This result confirmed earlier studies indicating that there was no isotopic fractionation during water uptake[8–10], and suggests that larger trees in the field are using a non-surface stream water source.

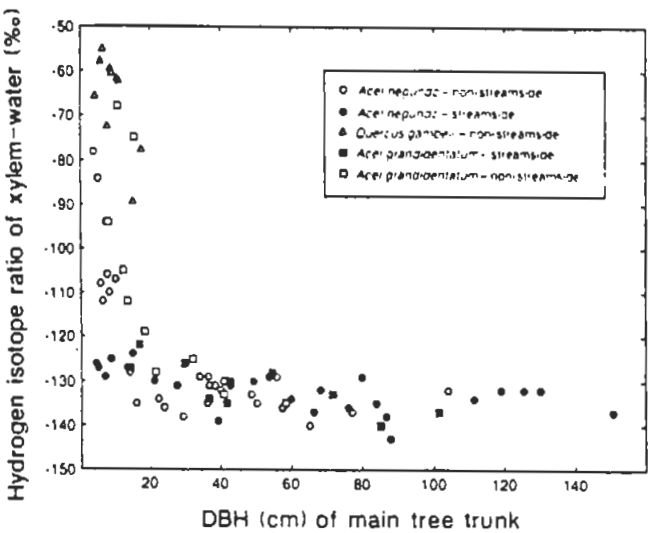

FIG. 2 The hydrogen isotope ratio (δD in ‰) obtained from xylem sap of three common streamside (closed symbols) and adjacent non-streamside (open symbols) tree species in the Red Butte Canyon Research Natural Area in 1989 as a function of the diameter at breast height (DBH) of the main trunk. Mean δD values of stream water (from Fig. 1) and local well water (see text) were -121.4 ± 0.7‰ and -132.3 ± 2.6‰ respectively. Methods are outlined in the text and in ref. 10.

TABLE 1 Hydrogen isotope ratios (δD in ‰) from xylem sap of mature tree species

Species	δD
Betula occidentalis Hook	-129.8 ± 3.2 (5)
Populus angustifolia James	-131.0 ± 3.0 (2)
Prunus virginiana L.	-132.3 ± 4.1 (3)

Data from tree species not shown in Fig. 2. Data are given as means and standard deviation, with the sample size in parentheses. For well water δD was -132.3 ± 2.6‰. The trees stood in or next to Red Butte Creek in the Red Butte Canyon Research Natural Area, Utah.

The most likely alternative water sources are subsurface flows below the stream, coming from higher elevations, or possibly deeper bedrock layers with waters derived from higher elevations. We sampled two springs and one well less than 2.5 km from our study site and an additional well near the head of the drainage basin; the mean δD value of these deeper waters was -130.7 ± 1.8‰. For another two springs and a well within 15 km of the study site, the mean δD for these deeper water layers was -132 ± 1.1‰. The subsurface water samples were collected during three different months and in two different years, suggesting that δD of subsurface water remains relatively stable over the course of time. All subsurface water δD values were similar to that of the largest streamside trees, strongly suggesting that mature trees utilize waters from deeper bedrock layers. We sampled a limited number of mature individuals (>50 cm DBH) of other common riparian zone trees at the streamside site (Table 2). As before, for each of these species, the xylem sap δD values suggested that the primary source of water was deeper soil layers and not stream water.

Several important ecological implications arise from these results. First, during establishment, these tree species depend on waters in the upper soil layers. Because the isotopic signatures of summer precipitation (non-streamside sites) and surface stream waters (streamside sites) are different, we can distinguish between these two water sources. Second, once established, trees from streamside sites as well as from adjacent non-streamside sites use a deeper and possibly more constant water source, abandoning the water sources on which they were dependent during establishment. By no longer using upper-soil-layer water sources, these species may be able to avoid interspecific competition with more shallow-rooted shrub and herb species that inhabit the same sites. This might ensure a greater probability of survival during droughts common to these semi-arid regions. Studies of plant interaction and competition for water should include the possibility that some trees might use deeper water sources. Such a conclusion may not be evident when looking at comparative leaf water potential values, but requires knowledge of the exact water source used by the plant, which can best be obtained through hydrogen isotope analysis. □

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1 de Candolle, A. L. *Géographique Botanique Raisonée* (Masson, Paris, 1855)
2 Schimper, A. F. W. *Pflanzengeographie auf Physiologischer Grundlage* (Fisher, Jena, 1898)
3 Woodward, F. I. *Climate and Plant Distribution* (Cambridge University Press, 1987)
4 Peterson, B. J. & Fry, B. *A. Rev. Ecol. Syst.* **18**, 293–320 (1987)
5 Rundel, P. W., Ehleringer, J. R. & Nagy, K. A. *Stable Isotopes in Ecological Research* (Springer, New York, 1988)
6 Fritz, P. & Fontes, J. C. *Handbook of Environmental Isotope Geochemistry* (Elsevier, Amsterdam, 1980)
7 Gat, J. R. & Confiantini, R. *Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle* (International Atomic Energy Agency, Vienna, 1981)
8 Confiantini, R., Gratziu, S. & Tongiorgi, E. in *Isotope and Radiation in Soil–Plant–Nutrition Studies* 405–410 (International Atomic Energy Agency, Vienna, 1965)
9 Wershaw, R. L., Friedman, I. & Heller, S. J. in *Advances in Organic Geochemistry*, 55–67 (Pergamon, New York, 1966)

10. White, J. W. C., Cook, E. R., Lawrence, J. R. & Broecker, W. S. *Geochim. cosmochim. Acta* **49**, 237–246 (1985).
11. Sternberg, L. S. L. & Swart, P. K. *Ecology* **68**, 1898–1905 (1987).
12. Dansgaard, W. *Tellus* **16**, 436–468 (1964).
13. Siegenthaler, U. & Oeschger, H. *Nature* **285**, 314–317 (1980).
14. *Climate of the States, Utah* (US Weather Bureau, Washington DC, 1960).
15. Caldwell, M. M. in *Physiological Ecology of North American Plant Communities* (eds Mooney, H. A. & Chabot, B. F.) 198–212 (Chapman & Hall, London, 1985).
16. Coleman, M. C., Shepherd, T. J., Durham, J. J., Rouse, J. D. & Moore, G. R. *Analyt. Chem.* **54**, 993–995 (1988).
17. Craig, H. *Science* **133**, 1833–1834 (1961).

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Plumage coloration is a sexually selected indicator of male quality

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FEMALE choice of mates based on the expression of characters that correlate with male quality remains a controversial and largely untested idea[1]. By choosing quality males, females stand to gain resources[2], genetic benefits for their offspring[3–5], or both. In the house finch (*Carpodacus mexicanus*), male plumage coloration is a function of dietary intake of carotenoids[6,7]. Here I present results of field studies that indicate that females prefer to mate with colourful males and that plumage brightness correlates with a male's capacity for parental care and perhaps its genotypic quality. Artificially brightened males paired more quickly and frequently than sham control or lightened males. Among unmanipulated males, plumage coloration was correlated with nest attentiveness and overwinter survival. In addition, there was a positive correlation between the coloration of fathers and sons.

The house finch is a small, sexually dichromatic passerine that is socially monogamous[8,9]. Unlike many passerine species, house finches do not defend territories during the breeding season[9,10], although both males and females defend mates from rivals. Pairing begins several weeks before the start of nestbuilding and, once paired, house finches form tight associations. Paired individuals are rarely seen alone until the female begins to incubate, so the pairing status of individuals can be determined unambiguously before nesting. Within populations, males display continuous variation in plumage coloration, ranging from pale yellow to bright red[9,11]. Captive feeding experiments indicate that all male house finches have the same potential to display bright or drab plumage[7] and that variation in plumage coloration reflects the type and quantity of carotenoids ingested by individuals at the time of their annual moult[6,7]. In laboratory mate-choice experiments with wild-caught house finches, females display a significant preference for the reddest male available[9].

To determine whether female house finches use male plumage coloration as a criterion for mate choice in the wild and to investigate whether male plumage coloration might be an indicator of male quality, I studied a breeding population of house finches at Ann Arbor, Michigan. Between 10 February and 21 March in 1989 and 1990, I used hair dyes to brighten 40 males and hair lighteners to lighten 40 males. I also assigned 20 males as sham controls by treating them with colour developer which did not alter plumage coloration. There were no significant differences among treatment groups in the size or pre-manipulation plumage scores of males, but all three groups differed significantly in post-manipulation plumage scores (Table 1). The range of plumage scores of manipulated males (96–177) fell within the range of natural plumage coloration in the Ann Arbor population (87–177).

There were no significant differences in dispersal or mortality between manipulated and unmanipulated males ($\chi^2 = 0.12$, d.f. = 1, $P > 0.25$) or among manipulated males used in different treatments (Table 1). Brightened males were significantly more likely to attain a mate than lightened or sham-control males, and sham-control males were more successful than lightened males (Table 1). Of the males that paired, brightened males paired earlier than lightened or sham-control males (Table 1), but the differences were not significant. Thus, field experiments indicate that female house finches prefer to pair with brightly plumaged males.

Male house finches feed their mates during incubation as well as their offspring[8,12]. To test whether male coloration reflects a male's ability to provide food for its mate and offspring, I recorded the time between feeding visits by males at 32 nests. I found a significant correlation between male attentiveness

TABLE 1 Results of plumage coloration manipulation experiments

Male characteristics	Brightened ($N = 40$) $\bar{x}$ (s.d.)	Sham control ($N = 20$) $\bar{x}$ (s.d.)	Lightened ($N = 40$) $\bar{x}$ (s.d.)	Test statistic	P
Weight (g)	21.9 (1.3)	22.3 (1.4)	21.8 (1.3)	0.87*	0.42
Wing length (mm)	80.2 (1.8)	79.3 (1.6)	80.3 (2.3)	1.83*	0.17
Original plumage score	140.7 (12.5)	139.9 (14.3)	141.0 (11.4)	0.05*	0.95
Manipulated plumage score	161.6 (7.9)	139.9 (14.3)	129.4 (10.3)	98.7*	0.0001
Number resighted (proportion resighted)	23 (0.58)	10 (0.50)	26 (0.65)	1.30†	>0.25
Number paired (proportion paired)	22 (1.00)	6 (0.60)	7 (0.27)	24.75†	0.0001
Time to pair (days)‡	12.1 (12.5)	20.2 (17.8)	27.8 (22.4)	2.82*	0.07

Higher plumage scores correspond to brighter plumage; see ref. 9 for details of scoring technique. I captured house finches at feeding stations and individually marked them with one aluminium and three coloured plastic leg bands. Males used in the experiment had dye, lightener, or colour developer applied to pigmented regions of their plumage[9] at times between 13:00 and 15:00 on the day they were trapped. After excess colourant was rinsed from their feathers, males were placed in front of a heat lamp for 2 h to dry, held overnight with food and water *ad lib*, and released at 10:00 the next morning. All manipulations were completed before the onset of nestbuilding in the study population. Only previously unbanded males were included in the manipulation. They were assigned to treatment groups so that each group received approximately the same number of males each day and so that males in each treatment were similar in size and pre-manipulation plumage score. Males were counted as 'resighted' if they were seen at least 48 h after release and 'paired' if they were seen in exclusive association with a female. In 1990, one brightened male was trapped 3 weeks after release but was otherwise not seen, so this male was counted as resighted but was excluded from pairing data. There were no significant differences between years in the pre-manipulation plumage scores or sizes of males or in the effects of the manipulations, so data were pooled for 1989 and 1990.

* F, One-way analysis of variance (ANOVA).

† χ^2, One-tailed test.

‡ Only males that paired were counted in the time to pair comparison, as measured by the interval between release following manipulation and exclusive association with a female.