

## Plant root systems and water uptake

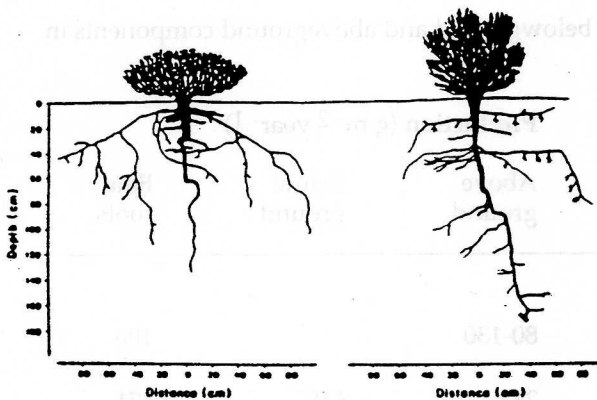
### I. Functions and specifications of roots

- A. **General functions** - capture of water, capture of nutrients, storage of carbohydrates, and anchorage
- B. **Root diameters** of plants vary from 20-55,000  $\mu\text{m}$ ; **root hair diameters** are 1-10  $\mu\text{m}$
- C. What factors of the environment influence root shapes? - an engineering analogy:

soil condition	engineering specification	plant response
physical impedance to penetration because of presence	thin probe and armored tip	thin, cylindrical shape with root cap
physical & chemical heterogeneity	movement to favorable zones	indeterminate growth habit; phenotypic plasticity
low concentrations low mobility of nutrients	progressive exploration	growth; branching root hairs, and mycorrhizae

- D. A diversity of **root types** exist reflecting general functions as well as specifics of precipitation patterns, water availability, and soil stability, etc. (see Candell et al., 1996; and Jackson et al., 1996, 2000).
- E.

1. **tap roots** - mostly unbranched with conduction and storage functions (figure).



Root-system sketches of *Haplopappus* (left) and *Chrysothamnus* (right) plants (drawn by C. Weber-Johnson). Late in the dry season, soil moisture changes most dramatically at 25 cm. This depth corresponds to a separation point for root biomass of the two species: *Haplopappus* lateral roots are concentrated in the upper, driest soil; *Chrysothamnus* laterals in the wetter soil. The thick taproots of *Chrysothamnus* can reach below 600 cm.

(from Manning & Barbour, 1988)

2. **surface roots** - may be the only root type in succulents and grasses; good for rapid response to resource availability in upper soil layers (figure)
  3. **rhizomes** - function as an underground stem, for stability and resource capture
  4. heterogeneity in **root structures** and depths in similar habitats representing diverse evolutionary patterns.
    - a. prairie (grassland) plants of North America (figure).
- F. burl-formers (stump sprouters) and non-burl formers (seed sprouters) of chaparral zones (figure).
  - G. winter and summer desert ephemerals (figure)  $\rightarrow$  winter rains are infrequent, last several days, and charge entire profile; roots are unbranched and relatively deep VS. summer rains which are more frequent, last several hours, and may charge only upper soil layers; roots are dimorphic (upper and penetrating) and often fibrous.
    - d. soil type can influence root structure.

E. Aerial roots

1. serve as anchorage devices and gas transport system (soils are often anaerobic)  
soils can be anaerobic because of high water content in porous soils or moderate water content and fine, silty or clay soils (both of which reduce oxygen diffusivity)
2. properties of mangrove root system - system of supporting aerial roots

	<u>air</u>	<u>mud</u>
lateral roots		+
chlorophyll	+	
lenticels	+	
% volume gas space	0-6	42-51

3. Comparison of mature root system of mangrove and red maple

<u>Trait</u>	<u>Rhizophora mangle</u>	<u>Acer rubrum</u>
root crown	absent	large
major roots	aerial	subterranean
gas capacity	very high	very low
mycorrhizae	absent	common

a large number of intertidal and flood plain species exhibit lacunae for gas transport (e.g., hollow stems of intertidal grasses, "knees" of swamp trees such as bald cypress)

II. *Standing biomass and annual productivity in different ecosystems*

Standing biomass and production of fine roots: total belowground and aboveground components in vegetation of different ecosystems (table below)

Ecosystem	Standing Biomass (g m <sup>-2</sup> )			Production (g m <sup>-2</sup> year <sup>-1</sup> )		
	Above ground	Below ground	Fine roots	Above ground	Below ground	Fine roots
Arctic tundra <sup>a</sup>	80-130	534-620	375-432	80-130		100
Shortgrass prairie <sup>b</sup>	218	1,173	725	218	618	471
Shrub steppe <sup>c</sup>	416	1,886	1,818	131	435	427
Deciduous forest <sup>d</sup>	14,720	3,742	1,679	609	977	930
<i>Pinus sylvestris</i> <sup>e</sup>	3,102		310	1,126		1,920

<sup>a</sup>Shaver and Billings (1975); <sup>b</sup>Sims and Singh (1978) (ungrazed shortgrass prairie, Pawnee site, 1971); <sup>c</sup>Caldwell et al. (1977) (*Atriplex confertifolia* stand); <sup>d</sup>Reichle et al. (1973) (*Liriodendron tulipifera* forest with stump and large root biomass as part of belowground); <sup>e</sup>Persson (1983), Agren et al. (1980); plantation.

**III. Phenology of root growth**

- A. in a well studied ecological system (Utah shrubs; figure), growth can occur throughout year, but peak growth period varies with species
- B. for species that grow in cold soils (arctic, alpine, montane), root growth lags well behind (10-25 d) leaf growth and only begins when the soil warms-up over the season
- C. productivity and turnover of root systems can be 2-3 times that of above ground components

**IV. Root to shoot ratios**

- A. root/shoot ratios (R/S) are used as indicators of plant effort to capture resources or measure of storage capacities
- B. at global level, R/S increases with aridity

<u>community</u>	<u>R/S; range and (maximum)</u>
moist tropical forest	.18-.29 (.48)
temperate beech forest	.26-.37 (.84)
savanna	.42-.60 (.91)
steppe	.82-1.55 (4.7)
warm desert	.85-4.1 (11.3)

- C. warm desert R/S is approximately 1, whereas cold desert R/S is higher and more variable, generally between 3-8 (see table 2; next page)
- D. R/S ratios of C<sub>3</sub> grasses (= 0.59-1.35, n = 11) is greater than that of C<sub>4</sub> grasses (= 0.41-0.82, n = 10); C<sub>4</sub> plants are more **water use efficient** = less water demand = less root allocation
- E. R/S ratio in C<sub>3</sub> plant, especially grasses, is a **very plastic trait** and a function of above ground demand (transpirational surface area) and soil temperature (figure)

**Table 2.** Root/Shoot ratios (weight/weight) for perennial desert shrubs from cool-winter and cold-winter desert habitats (Ehleringer and Mooney, 1983).

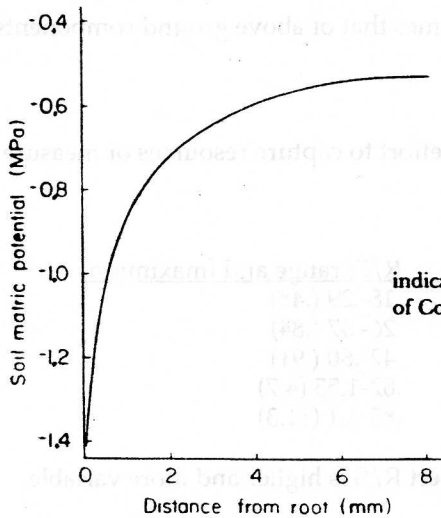
<u>species</u>	<u>reference</u>	<u>location</u>	<u>root/shoot</u>
<b>cool-winter</b>			
<i>Atriplex vesicaria</i>	4	Australia	0.41
<i>Brickellia incana</i>	6	California	0.55
<i>Eremophila gilesii</i>	2	Australia	0.36
<i>Ephedra nevadensis</i>	5	California	0.84
<i>Franseria dumosa</i>	6	California	0.64
<i>Grayia spinosa</i>	10	Nevada	0.64
<i>Hymenoclea salsola</i>	6	California	0.72
<i>Krameria grayi</i>	6	California	0.37
<i>Larrea divaricata</i>	6	California	0.33
<i>Lycium andersonii</i>	10	Nevada	0.73
<b>cold-winter</b>			
<i>Artemisia badhysi</i>	9	USSR	3.31
<i>Artemisia rhodantha</i> and <i>Acantholimon diapensioides</i>	8	USSR	6.58
<i>Artemisia rhodantha</i> and <i>Ceratoides papposa</i>	8	USSR	7.94
<i>Atriplex confertifolia</i>	3	Utah	4.09
<i>Ceratoides lanata</i>	3	Utah	6.77
<i>Eurotia lanata</i>	1	Utah	6.67
<i>Eurotia ceratoides</i> and <i>Artemisia terrae-alba</i>	7	USSR	6.30

references: 1) Bjerregaard (1971), 2) Burrows (1972), 3) Caldwell et al. (1977b), 4) Charlie and Cowling (1968), 5)

Evenari et al. (1972), 6) Garcia-Moya and McKell (1970), 7) Kurochkina et al. (1972), 8) Litvinova (1972), 9) Rustanov (1972), 10) Wallace et al. (1974).

## V. Resource depletion adjacent to roots

- A. Roots are able to reduce soil water to within very short distance (figure)



Localized depletion of soil moisture near the root surface as indicated by the predicted soil-matrix water-potential gradient using the model of Cowan (1965) (adapted from Caldwell 1976).

- B. Ability to extract nutrients is very much affected by rooting distribution, where nutrients are being taken up within root axis, and nutrient diffusivity (figure)
- C. Roots commonly proliferate in fertile-soil microsites and can adjust the rate of nutrient/ water uptake accordingly (figures)

## VI. Nocturnal water transport by plants: "Hydraulic lift" or "Redistribution"

- A. There is evidence that substantial amounts of water are transported through roots at night from deep, well-hydrated soils, to roots in the upper soil layers and released where plants will use it the next day (figures - Dawson 1993b, Dawson 1996, Emerman and Dawson 1996; Burgess et al. 2000; Ludwig et al. 2003, 2004, Brooks et al. 2003; Oliveira et al. 2005)
- B. A large fraction of the daily water that is used by the grass *Agropyron desertorum* was thought to be obtained from water hydraulically lifted to upper soil layers by its neighbor, the sagebrush species *Artemisia tridentata* ssp. *vaseyana* (Richards and Caldwell 1987, Caldwell and Richards 1989).
- C. Water can also be "redistributed" downwards in some plant species (Burgess et al., 1998; Oliveira et al. 2005); may play a role in the establishment of deep roots as they grow through dry soils.
- D. The consequences of water redistribution by plant root systems can be seen at the whole-plant, community, landscape and regional climate scales (see Caldwell et al., 1998; Horton and Hart, 1998; de Rosnay and Polcher 1998; Kleidon and Heimann, 1998, 2000; Feddes et al., 2002, 2001; Lee et al. 2005).

## VII. Water sources -- stable isotopes of hydrogen

- A. The D/H ratio of water extracted from plant roots, stems or trunks can act as a tracer to the source of water that plants are using (figures from Dawson, 1993a, Dawson and Ehleringer 1998, Dawson et al. 1998, 2002).
- B. Soil water is commonly more enriched in the heavier isotope (D) relative to hydrogen (H). This can be caused by evaporation from the soil surface (making the  $\delta D$  less negative). This is also seen in warmer (summer) precipitation versus colder precipitation (snow). These different D/H ratios can be used to trace to source of the water that influenced the D/H ratio of water extracted from stems (figures - after Dawson, 1993b, Dawson and Ehleringer 1998).

C. Using this method several investigations have shown that different size plants or different species can use different proportions of water from different sources (figures).

D. Hydraulic lift is **not** restricted to arid environments. *Acer saccharum* (sugar maple; Dawson 1993b, 1996) and several Amazonian trees (Oliveira et al. 2005) also conducts HL/HR (figures). Using the D/H method we see that neighboring plants around maple trees of many growth form use this water source (table/figure). This water source has a significant impact on performance, including growth (figures) and it can differ between small and large trees.

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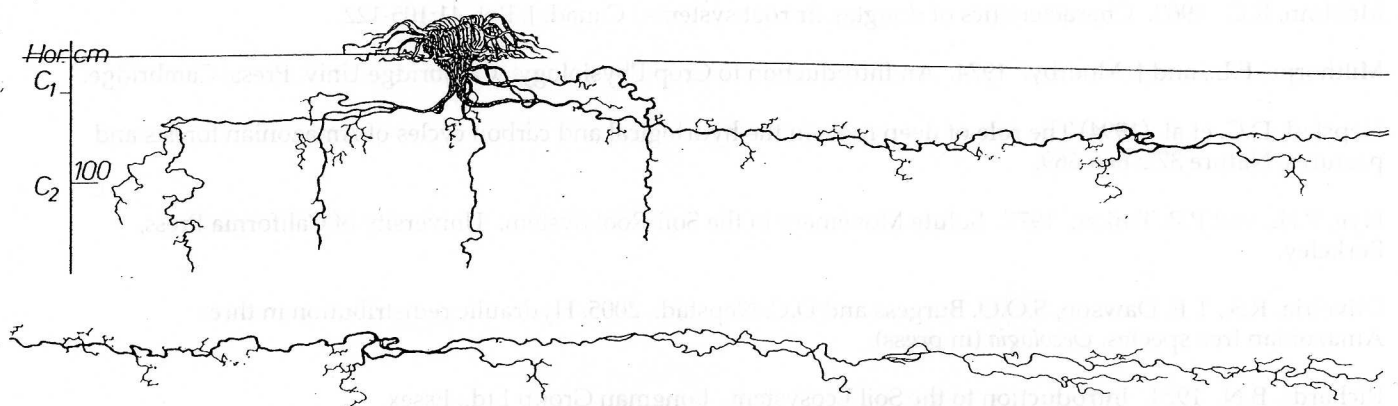


Fig. 17: *Welwitschia mirabilis*. H/T/S = 40/-/1728 cm, seichte Erosionsrinne im Damaraland, mächtige Feinsedimentdecke aus Grus und schluffigem Sand, Rohboden, Bodenprofil: Hor. C<sub>1</sub> 0-24 cm angeschwemmter grobsandiger Feingrus, lose, darunter C<sub>2</sub> grobsandiger Grus und Feinschutt, sehr dicht verbacken, hart, braun, salzbeeinflusst, pH 8,3. Am 19. 3. um 7.30 Uhr rel. Luftfeuchte 94,3 %, Temperatur 1 m hoch 14,4 °C, Bodenoberfläche 31,8 °C, Blattgrund 27,1 °C. Um 12.15 Uhr rel. Luftfeuchte 27,4 %, Temperatur 1 m hoch 30,5 °C, Bodenoberfläche 62,1 °C, Blattgrund 43,1 °C. Wurzeldarstellung weitgehend unvollständig.



Figures for Lecture topic 11

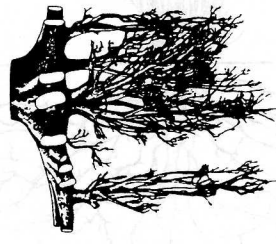
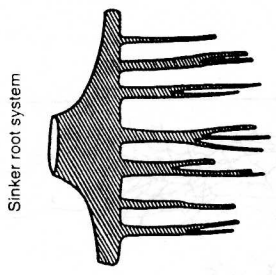
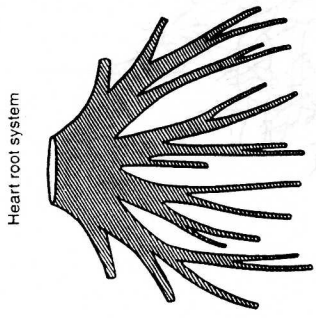
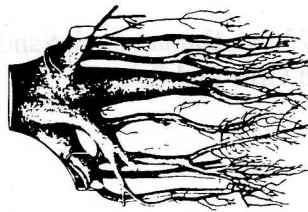
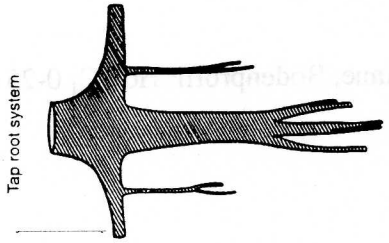
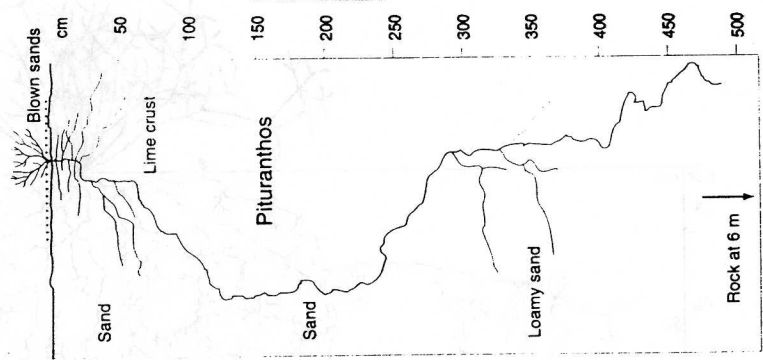
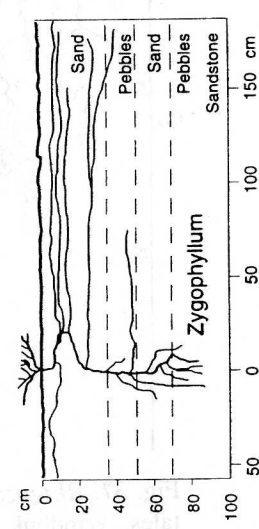
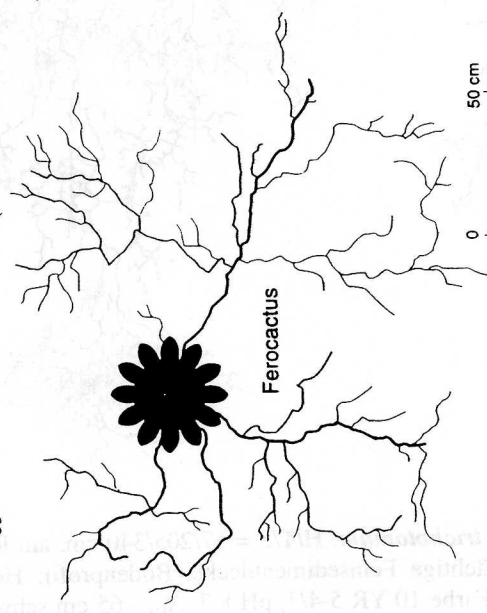
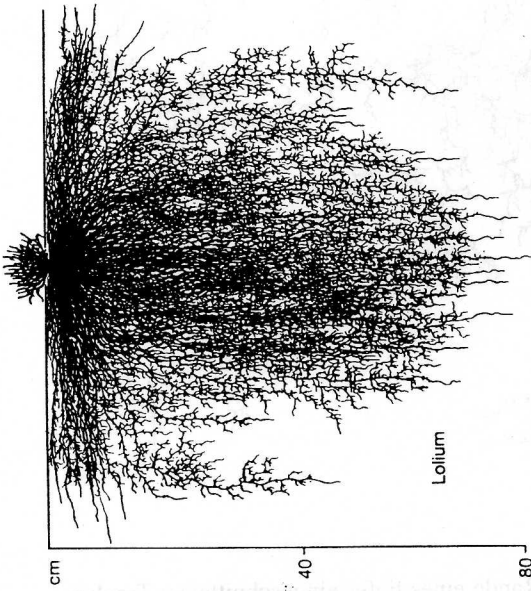


Fig. 1.8. Root systems of conifer trees of the temperate zone. *Abies alba* has a tap root system, *Larix decidua* a heart root system, *Picea abies* a sinker root system. (After Köstler et al. 1968). In tropical forests and on oxygen-deficient soils, trees may develop special types of roots, such as stilt roots, tabular roots and buttress roots. (Richards 1979; Longman and Jenik 1987)

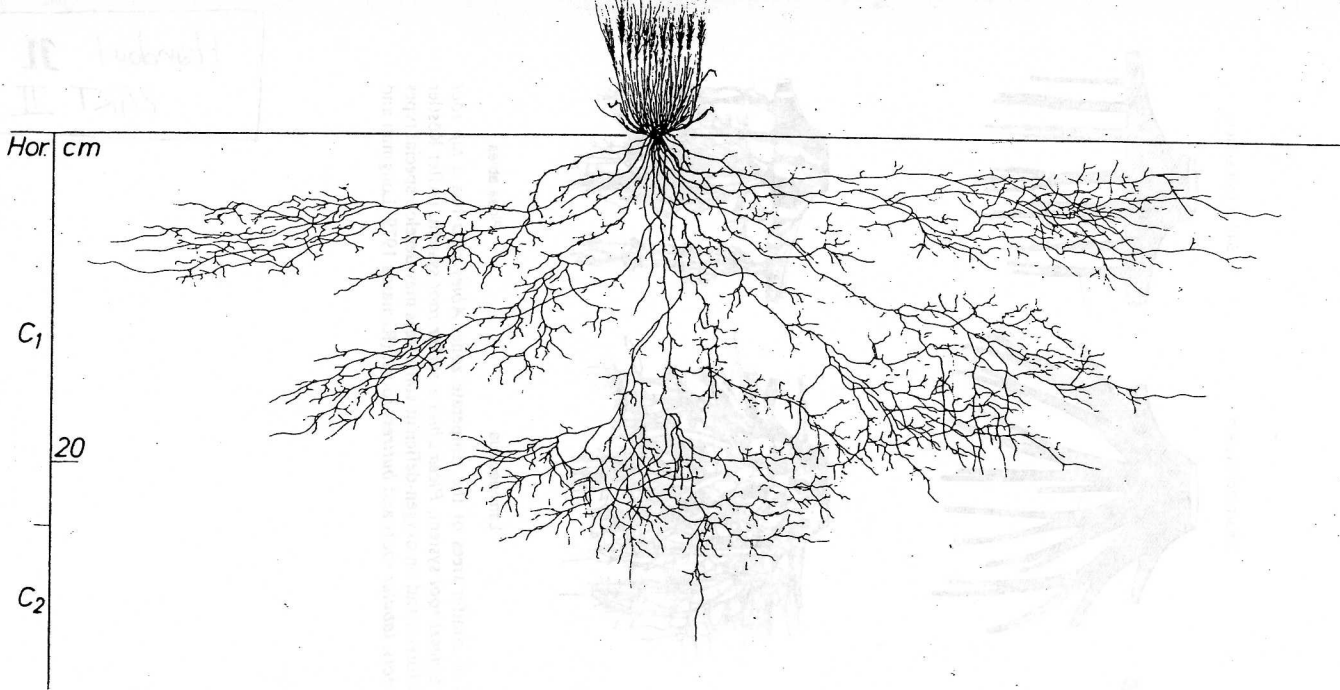


Fig. 18: *Stipagrostis obtusa*. H/T/S = 9/29/73 cm, Damaraland, Sandrinne, Bodenprofil: Hor. C<sub>1</sub> 0-25 cm griffiger Sand, lose, darunter C<sub>2</sub> Sand zwischen Grus und Schutt.

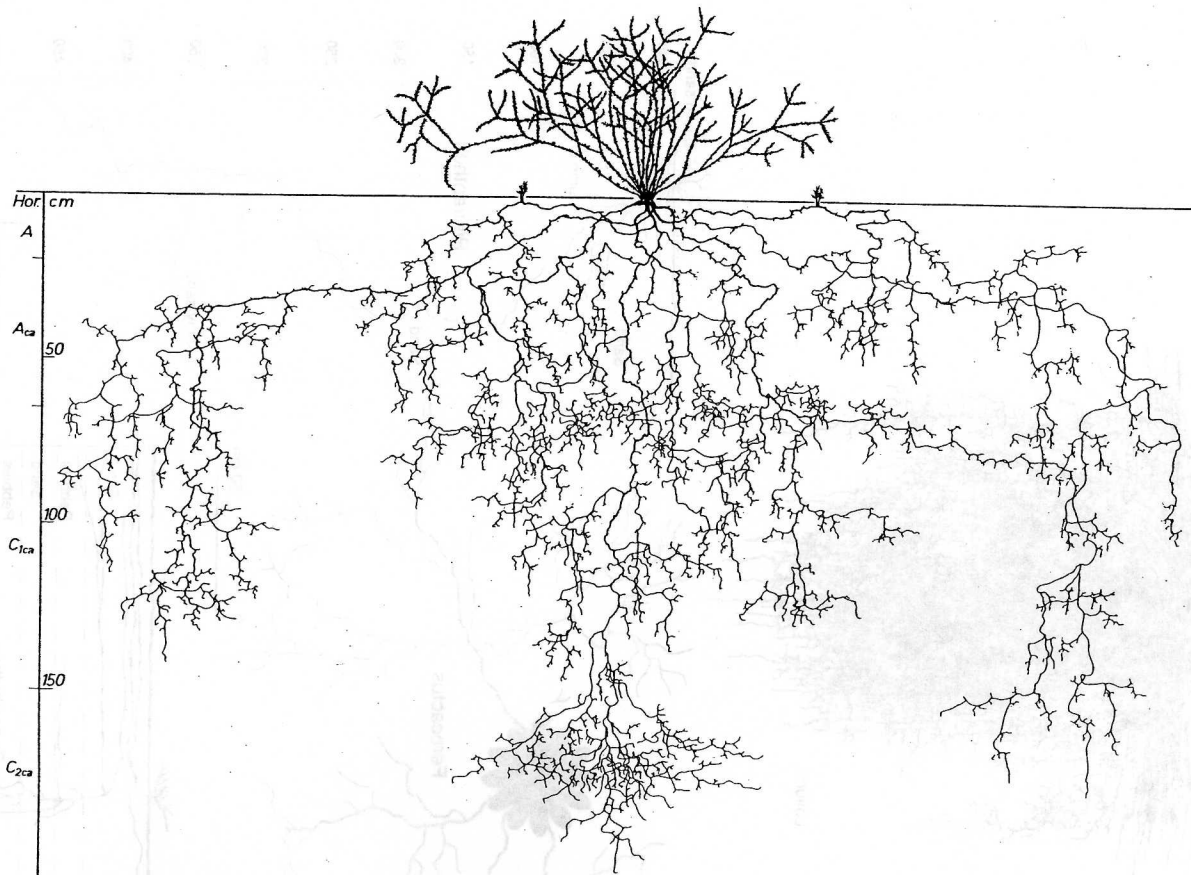


Fig. 37: *Rhigozum trichotomum*. H/T/S = 57/205/340 cm, am Rande eines tiefer eingeschnittenen Trockentales, Windhuk, mächtige Feinsedimentdecke, Bodenprofil: Hor. A 0-20 cm schwach humoser lehmiger Schluff, krümelig, Farbe 10 YR 5-4/3, pH 8,7, A<sub>ca</sub> - 65 cm schwach humoser lehmiger Schluff, durch Kalkausscheidungen verkrustet, aber nicht hart, Struktur prismatisch, C<sub>1ca</sub> - 150 cm lehmiger Schluff, durch Kalkausscheidung steinhart verkrustet, Farbe gelbbraun-gelblichweiß, pH 8,3, darunter C<sub>2ca</sub> lehmiger Schluff, durch Kalkausscheidungen verbacken, aber nicht so hart wie C<sub>1ca</sub>.

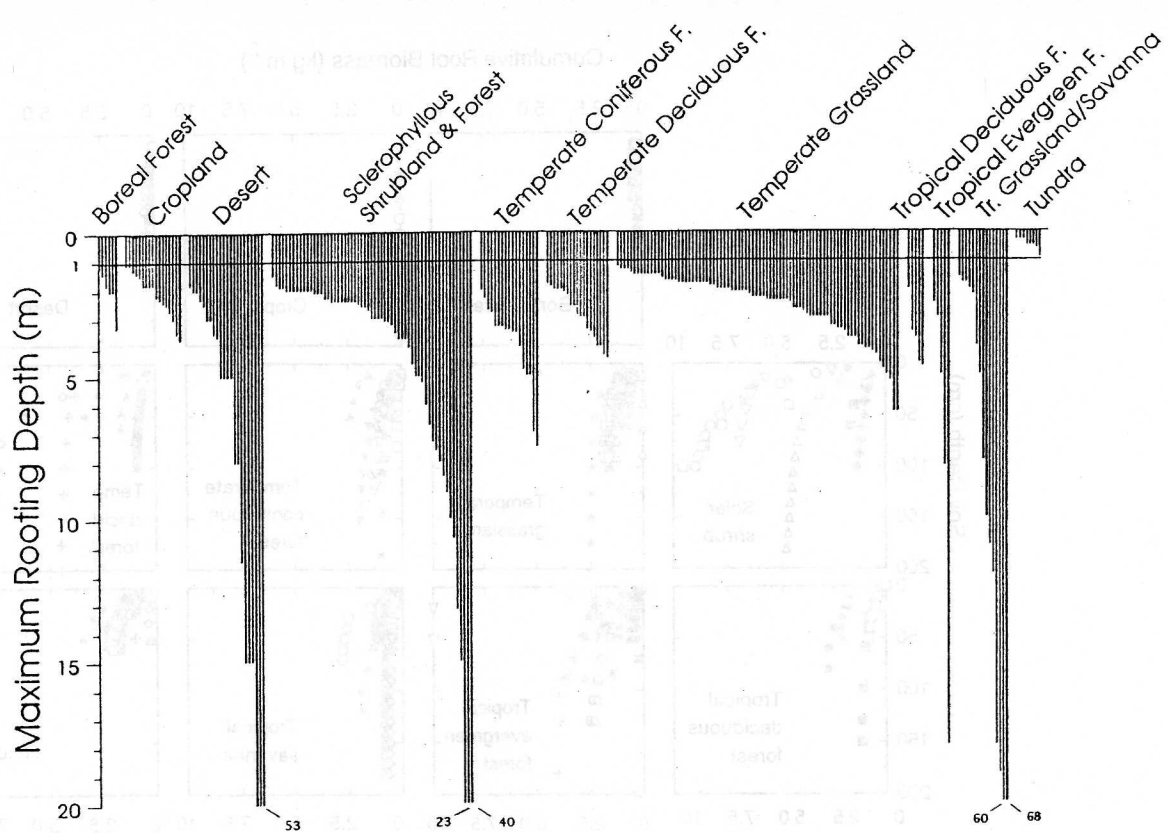


Fig. 1 Reported species maximum rooting depth (m) grouped by terrestrial biome. When there are more than one observations for a given species, only the maximum value is plotted

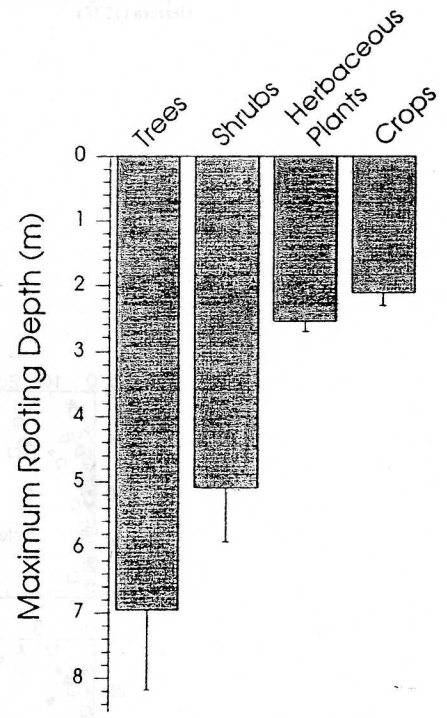


Fig. 2 Mean and SE of reported maximum rooting depth (m) by three major functional groups (trees, shrubs, and herbaceous plants) and crops

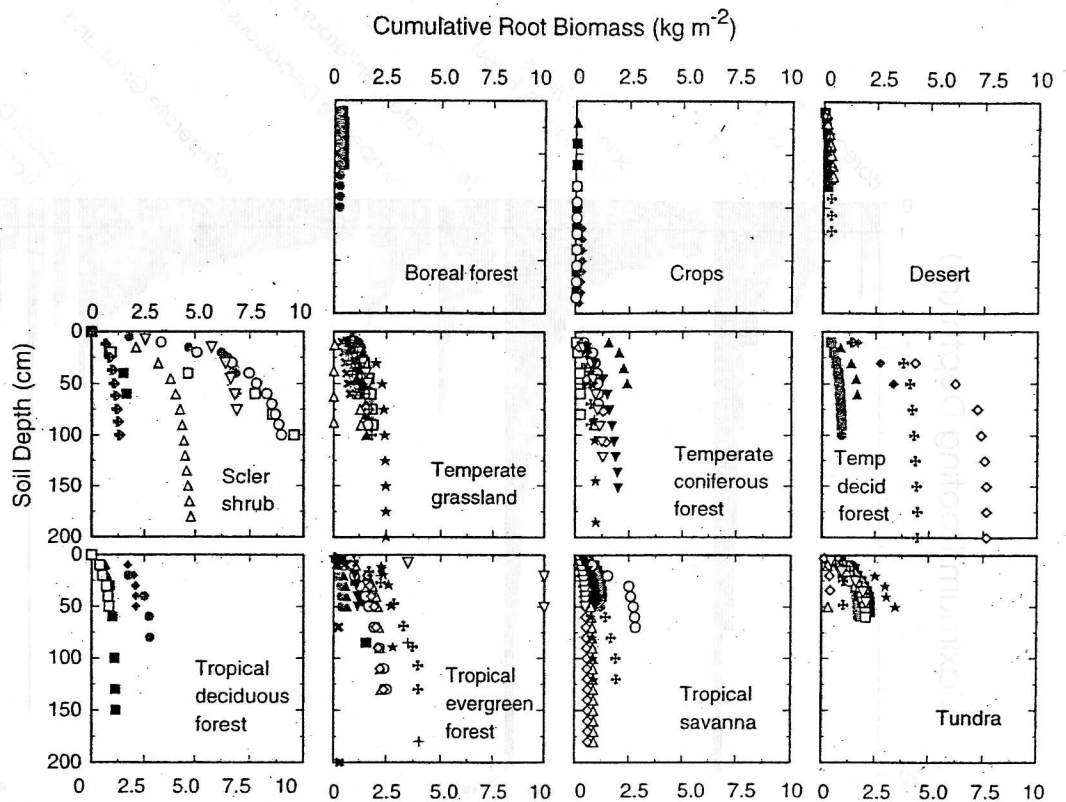


Fig. 3 Cumulative root biomass ( $\text{kg m}^{-2}$ ) for 11 terrestrial biomes. The key to the symbols in each panel can be found in Table 2. Actual values for the two points shown at the upper right corner of tropical evergreen forest are 11.2 and 13.2  $\text{kg m}^{-2}$  from Klinge and Herrera (1978)

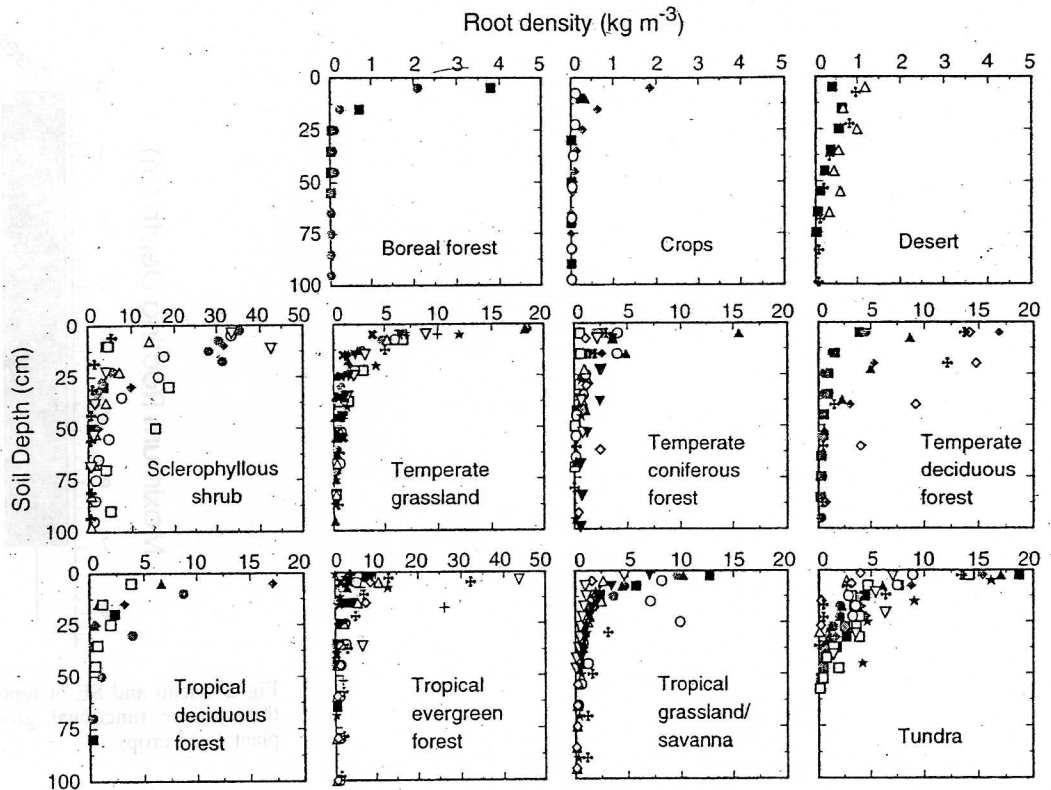
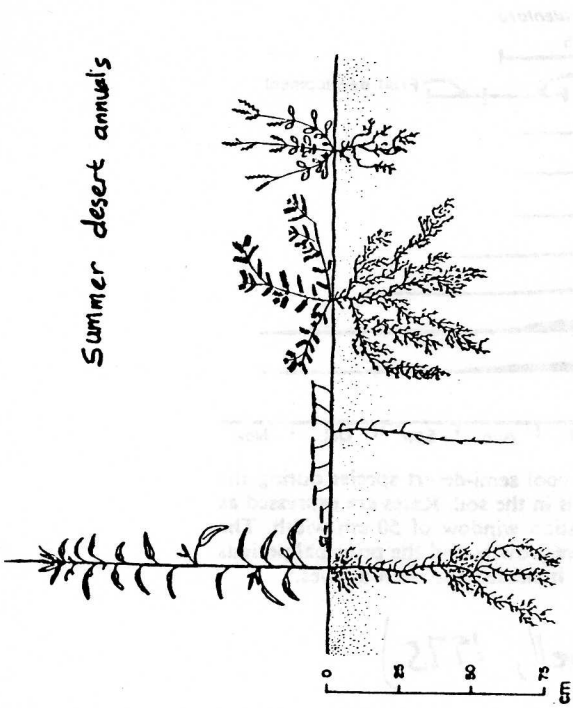
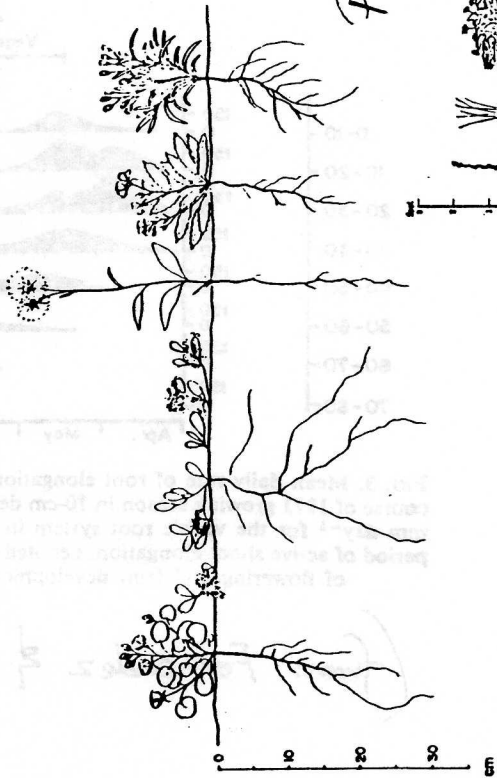


Fig. 4 Root density ( $\text{kg m}^{-3}$ ) for eleven terrestrial biomes. The key to the symbols in each panel is in Table 2

Summer desert annuals



Winter desert annuals



from Hellmers et al. 1955

Chaparral (sprouters)

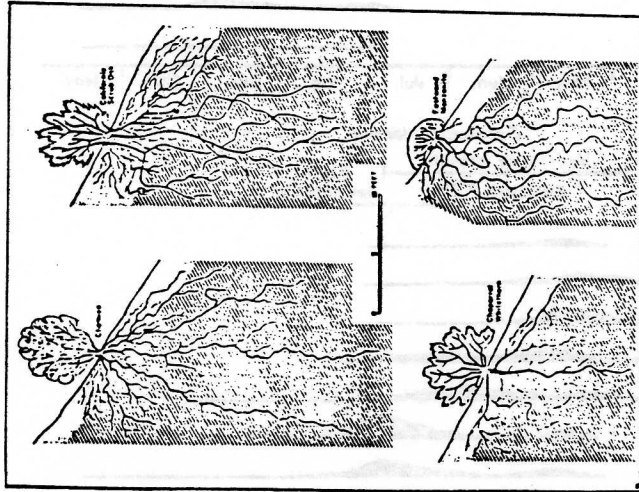


FIG. 1. Diagrammatic sketch of typical root systems of woody shrubs with deeply penetrating roots.

Chaparral (non-sprouters)

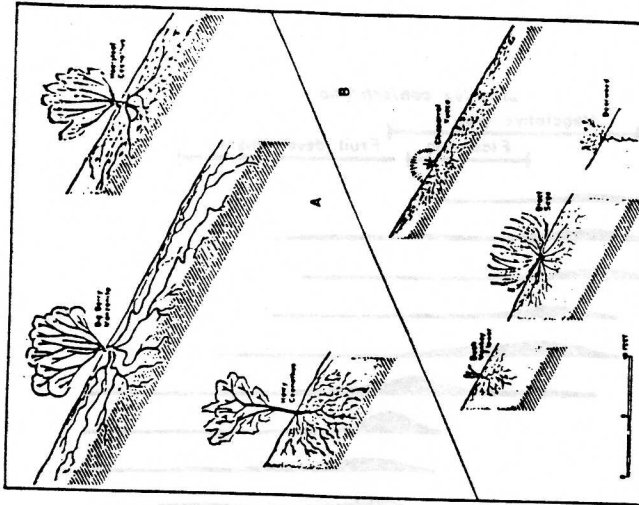


FIG. 2. Diagrammatic sketch of the root systems of woody shrubs with shallow roots and a scale from 0 to 100 cm.

Prairie Plants

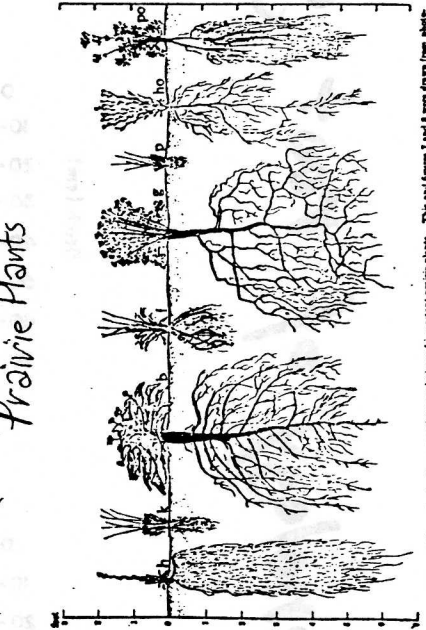


FIG. 3. Diagrammatic sketch of the root systems of prairie plants. This and figures 1 and 2 were drawn from photographs of plants in the field and data obtained by the gravimetric and anatomical methods of Hellmers and Hellmers (1955). A, *Andropogon scoparius*; B, *Andropogon scoparius*; C, *Andropogon scoparius*; D, *Andropogon scoparius*; E, *Andropogon scoparius*; F, *Andropogon scoparius*.

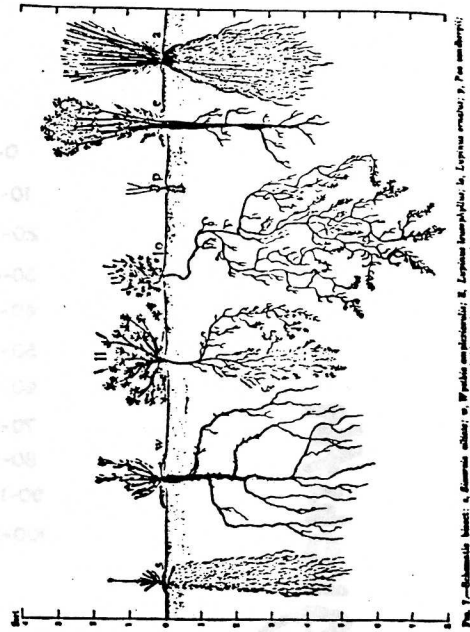


FIG. 4. Diagrammatic sketch of the root systems of prairie plants. This and figures 1 and 2 were drawn from photographs of plants in the field and data obtained by the gravimetric and anatomical methods of Hellmers and Hellmers (1955). A, *Andropogon scoparius*; B, *Andropogon scoparius*; C, *Andropogon scoparius*; D, *Andropogon scoparius*; E, *Andropogon scoparius*; F, *Andropogon scoparius*.

# Phenology of root growth

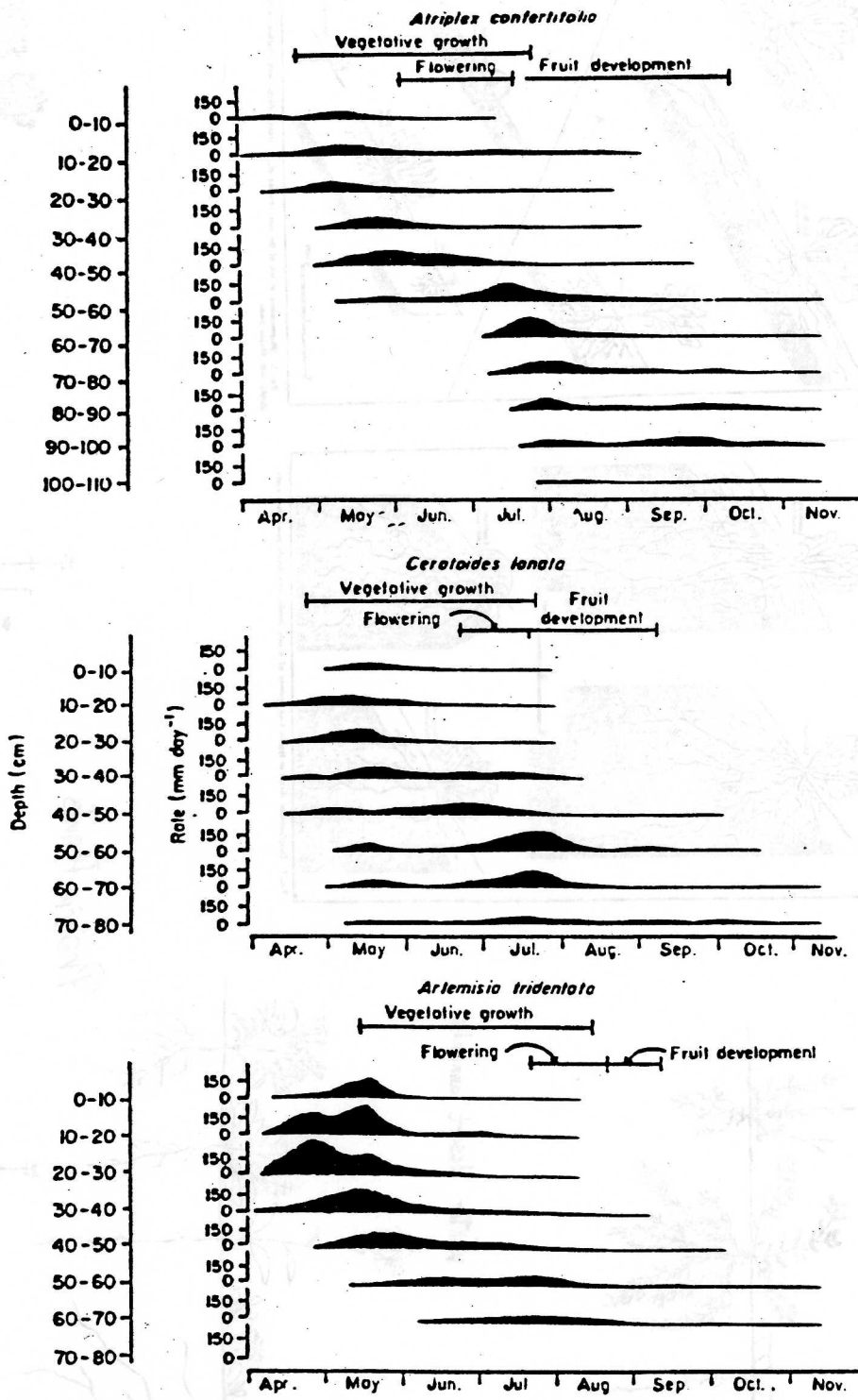
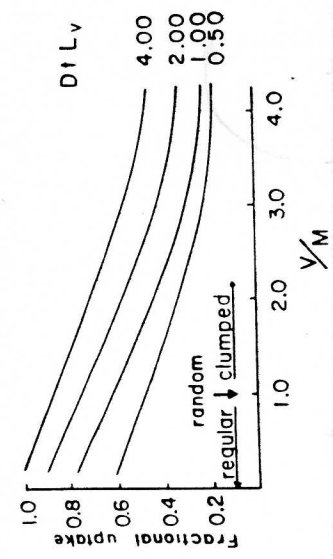


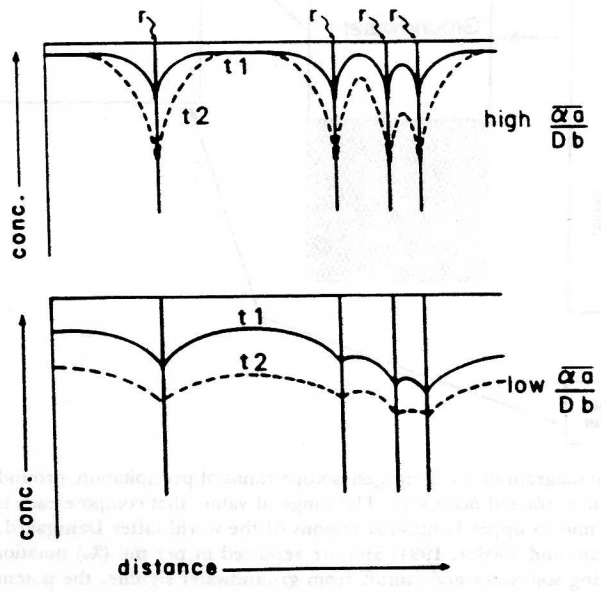
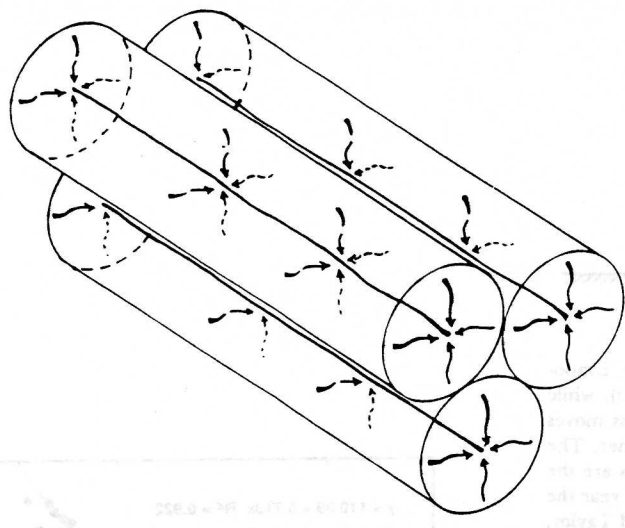
FIG. 3. Mean daily rate of root elongation for three cool semi-desert species during the course of 1973 growing season in 10-cm depth intervals in the soil. Rates are expressed as mm day<sup>-1</sup> for the visible root system in an observation window of 50 cm width. The period of active shoot elongation, denoted as vegetative growth, and the principal periods of flowering and fruit development are also indicated for each species.

(from: Fernandez & Caldwell, 1975)



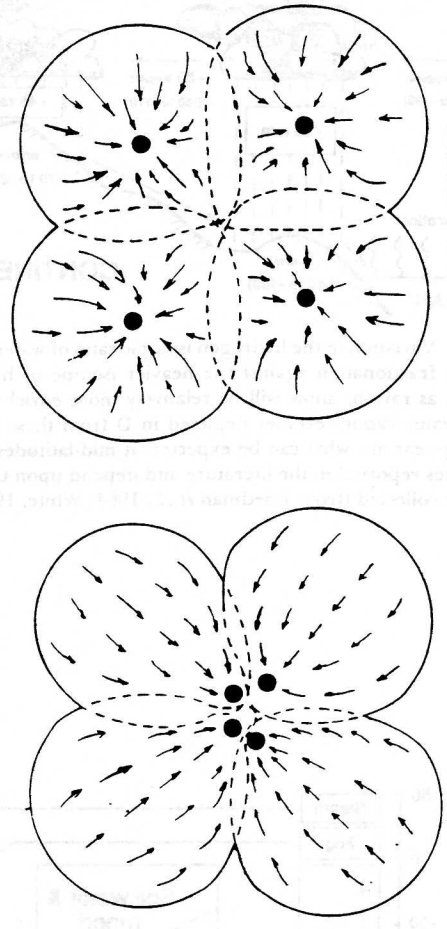
Nutrient uptake for root systems with distribution patterns ranging from regular to very clumped. The distribution pattern is expressed as the ratio of the variance,  $V$ , to the mean,  $M$ , of interroot distance. The magnitude of uptake is also influenced by the product of diffusivity,  $D$ , time,  $t$ , and rooting density,  $\alpha L_v$ , (adapted from Baldwin et al. 1972).

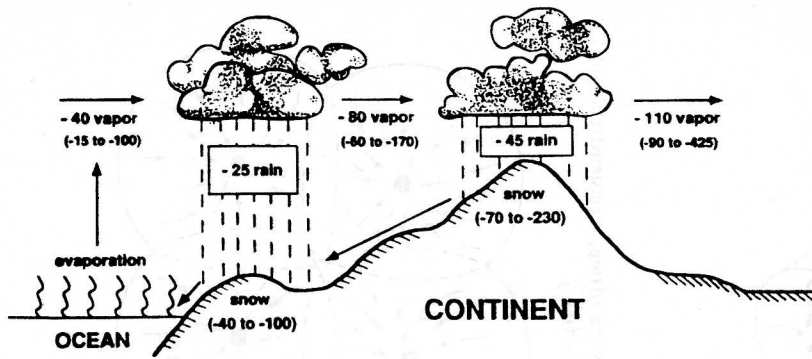
Patterns of water and nutrient flow toward individual roots following assumptions of single-root uptake models. The roots are parallel, absorbing uniformly along their length, and each root has exclusive access to resources in a soil cylinder surrounding the root. The radii of the soil cylinder represent half the distance between roots.



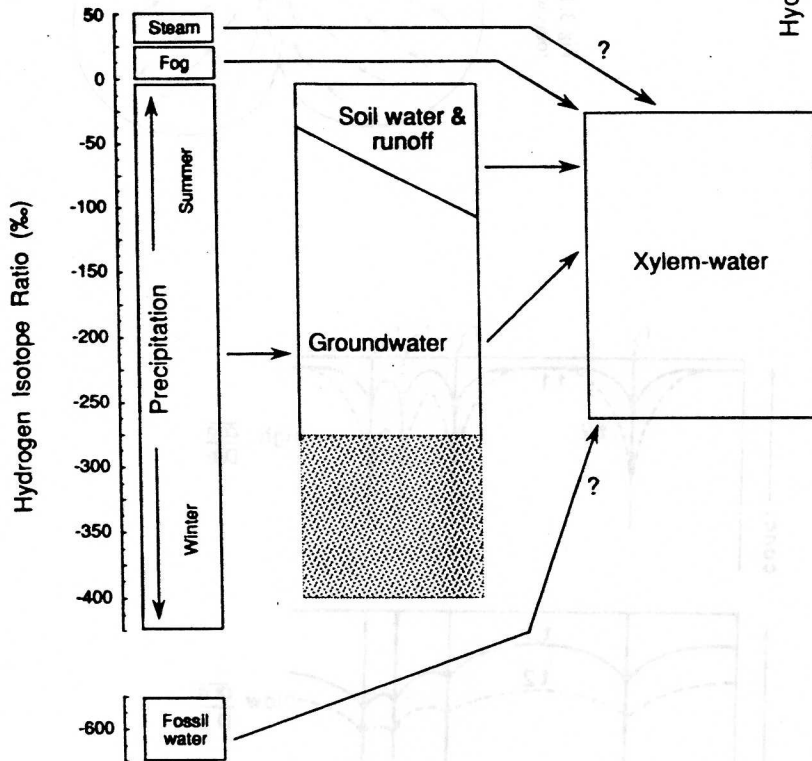
Localized depletion zones around parallel roots spaced at irregular intervals. These roots have the same root demand coefficient,  $\alpha a$  (i.e., they have the same uptake capacity). Concentration profiles are represented for two times. The soil is assumed initially to be uniform, and the roots are not growing. Changes in concentration through time are the result of root absorption and diffusion. For a case of high  $\alpha a / Db$ , there are few effects of neighboring roots on one another until time  $t_2$ . Concentration profiles shown are based on the behavior of nutrient absorption models and portrayal of neighboring root interactions in Nye and Tinker (1977).

Fig. 3. Patterns of water and nutrient movement toward evenly spaced (top) or clustered (bottom) roots which have the same available soil volume. (X-section)

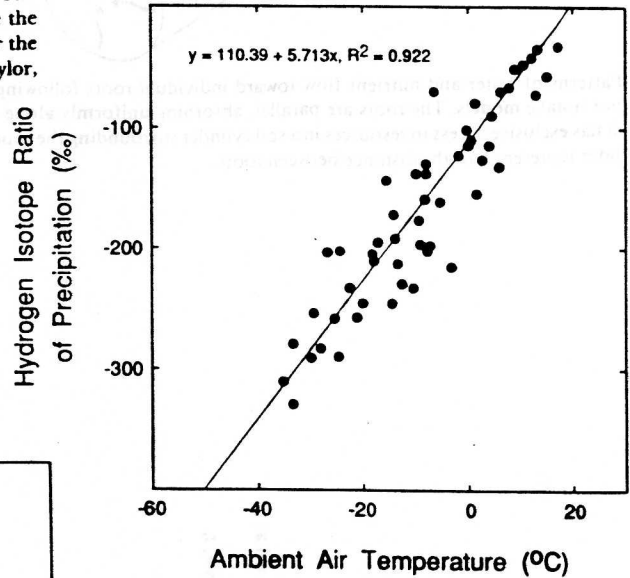




**Figure 1.** Variation in the hydrogen isotopic ratio of water in the hydrologic cycle. Evaporation causes fractionation against the heavier isotope of hydrogen (deuterium, D), while condensation as rain or snow will be relatively more enriched in D. As an air mass moves inland, the water vapor becomes depleted in D from these processes acting together. The values that appear are what can be expected at mid-latitudes; values in parentheses are the range of values reported in the literature and depend upon the latitude and time of year the samples were collected (from Friedman *et al.*, 1964; White, 1988; and Ingraham and Taylor, 1991).

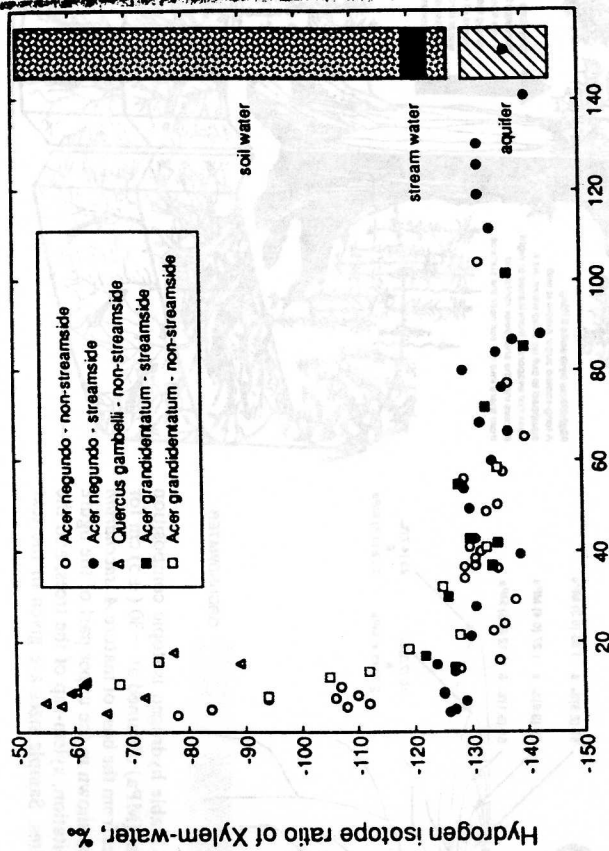


**Figure 3.** General diagram of the hydrogen isotope ratios of precipitation, groundwater, and xylem water (from extracted plant sap). The range of values that compose each box are those reported from mid to upper latitudinal regions of the world (after Dansgaard, 1964; White, 1988; Ingraham and Taylor, 1991) and are reported in per mil (‰) notation. The diagonal line separating soil water and runoff from groundwater signifies the potential for these two water sources to overlap significantly. The stippled area at the most negative end of the groundwater box signifies a range of possible isotopic values that could occur for groundwater based on precipitation (snow) inputs but are rarely reported in the literature. The data for fog water use are for the California Coastal Redwood, *Sequoia sempervirens* (Dawson, unpublished). The question marks on the lines connecting steam and fossil water to xylem water of plants appear because these sources exist and could potentially be used by plants; however, to date no such reports exist.

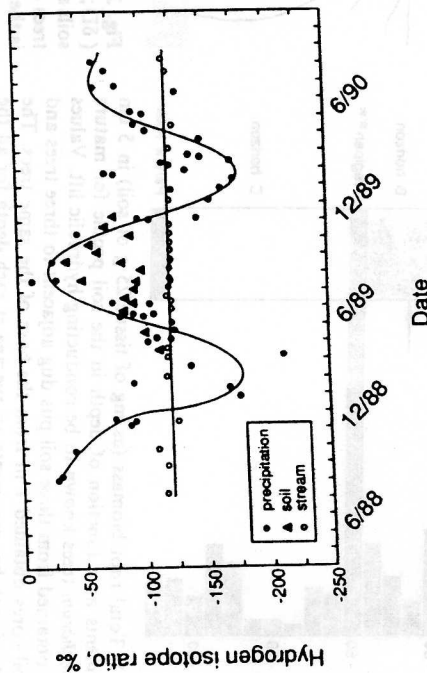


**Figure 2.** The relationship between the hydrogen isotopic ratio in precipitation and the ambient air temperature at the time of the rainfall (after Craig, 1961; Dansgaard, 1964; Dawson and Ehleringer, 1991; Dawson, unpublished data). Values are reported in per mil, ‰ notation.

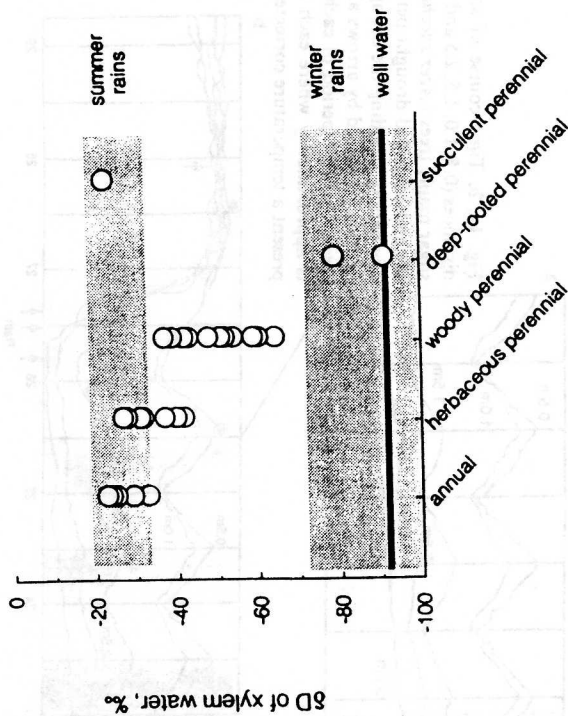




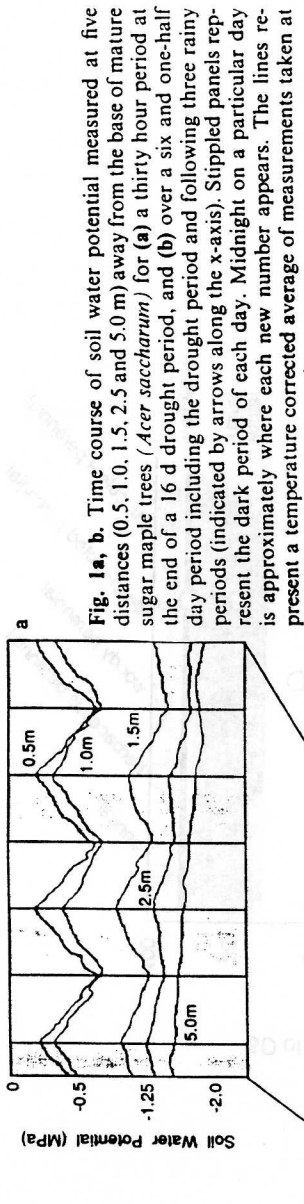
**Figure 7.** The hydrogen isotope ratio (%) obtained from xylem water (sap) of three common streamside (closed symbols) and adjacent nonstreamside (open symbols) tree species in the Red Butte Canyon Research Natural Area in 1989 as a function of tree size (circumference in centimeters of the main trunk). Mean  $\delta D$  values of stream water (from Fig. 6) and local well (ground) water were  $-121.4 \pm 0.7\%$  and  $-132.3 \pm 2.6\%$  respectively; the range of values for each of three water sources is shown by the bars on the right hand side of the figure (from Dawson and Ehleringer, 1991; reprinted by permission from *Nature* 350: 335-337, copyright © 1991 Macmillan Magazines Ltd.).



**Figure 6.** The hydrogen isotopic composition (‰) of precipitation (●), soil water (at -50 cm; ▲), and surface stream water (○) measured over a 2-year period in Red Butte Canyon Research Natural Area, east of Salt Lake City, Utah. Precipitation values vary with the seasonal temperature regime. Soil water values reflect precipitation inputs. Values for the stream water were essentially unaffected by seasonal variation due to the fact that the catchment basin that contributes to stream runoff is very large, spanning over 350 m in elevation (from Dawson and Ehleringer, 1991; reprinted by permission from *Nature*, 350: 335-337, copyright © 1991 Macmillan Magazines Ltd.).

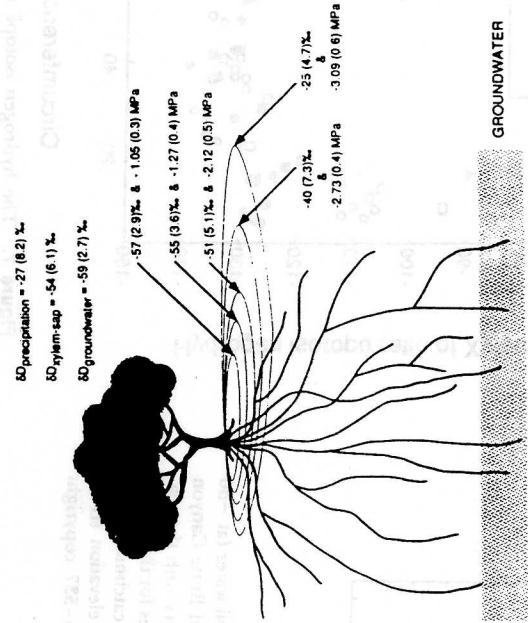


**Figure 9.** Hydrogen isotope ratios ( $\delta D$ ) of xylem water (‰) during the summer from an array of plants in a desert scrub community in southern Utah. The mean winter precipitation  $\delta D$  value was  $-88.3\%$ , well water was  $-91\%$ , summer precipitation values ranged between  $-22$  and  $-80\%$  (from Ehleringer *et al.*, 1991; reproduced with permission).

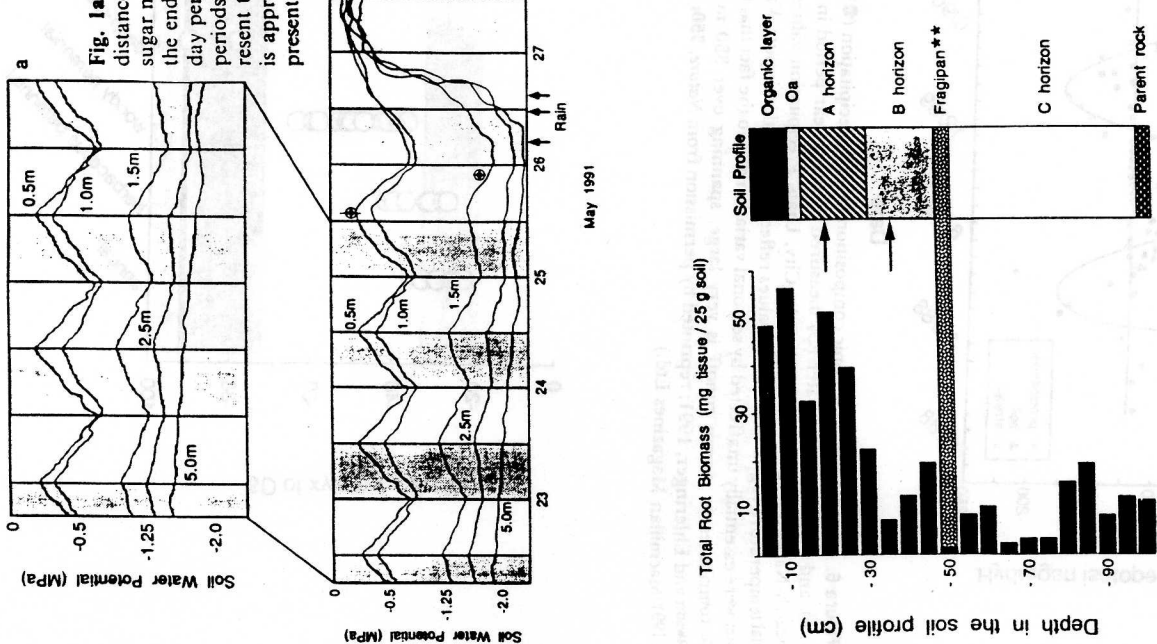


**Fig. 1a, b.** Time course of soil water potential measured at five distances (0.5, 1.0, 1.5, 2.5 and 5.0 m) away from the base of mature sugar maple trees (*Acer saccharum*) for (a) a thirty hour period at the end of a 16 d drought period, and (b) over a six and one-half day period including the drought period and following three rainy periods (indicated by arrows along the x-axis). Stippled panels represent the dark period of each day. Midnight on a particular day is approximately where each new number appears. The lines represent a temperature corrected average of measurements taken at

from:  
Dawson, PA36

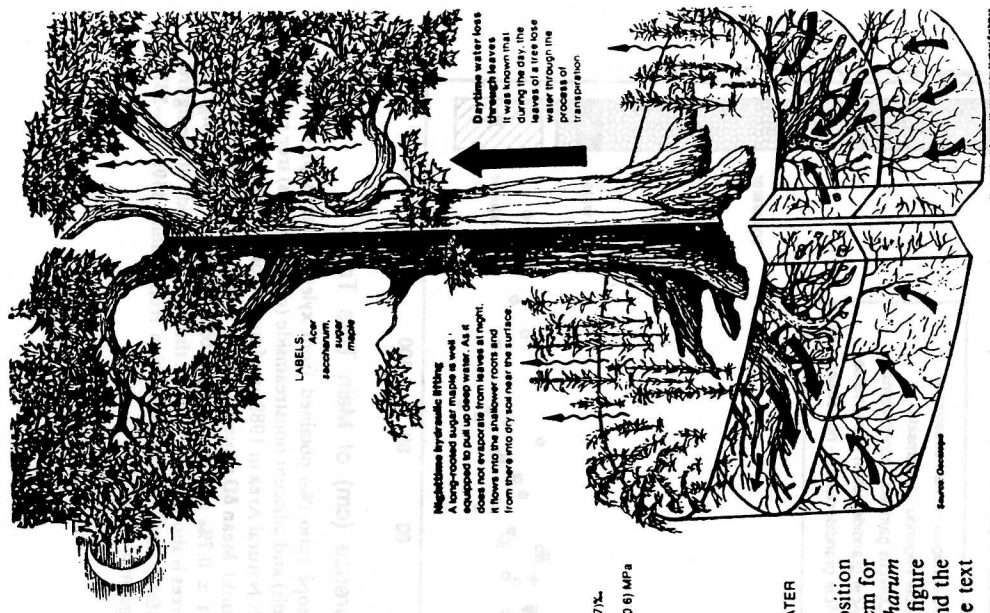


**Fig. 3.** The average ( $\pm$  SD) stable hydrogen isotopic composition ( $\delta D$ ; ‰) and water potential (MPa) obtained at  $-30 (\pm 5)$  cm for soils at the same five distances from the base of mature *A. saccharum* trees as shown in Fig. 1. Also shown in the upper part of the figure is the average  $\delta D$  for precipitation, xylem-sap of the trees, and the groundwater at the same sites. Sample sizes are given in the text



**Fig. 2.** Total root biomass (as mg of tissue/25 g of soil) in 5 cm increments as a function of depth in the soil profile for mature *A. saccharum* trees known to be conducting hydraulic lift. Values were obtained from three soil pits dug adjacent to three trees and 12 soil cores obtained 1 m from the base of the same trees. The length of each bar represents an average at each depth for all the data combined. The overall variation was  $\pm 5.7$  mg. On the right side of the figure is a diagrammatic representation of the soil structure seen in the profile. Note the hardpan (fragipan\*\*) layer at  $-50 \pm 3.9$  cm

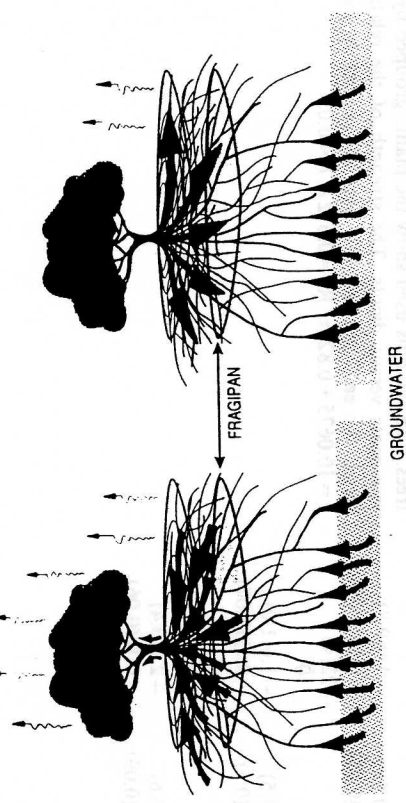
two depths in the soil profile ( $-20$  and  $-35$  cm), at the four cardinal compass directions, around three trees. The values which appear on the figure indicate the distance away from the tree base associated with a particular line; for 0.5, 1.5 and 2.5 m distances, the line below the value applies, for 1.0 and 5.0 m distances, the line above the value applies. The target symbols which appear in the daylight panels for May 25 and 27 represent the average ( $\pm$  SD) dawn (*upper symbol*) and dusk (*lower symbol*) leaf water potential for the same three trees



**A New View of How Trees Obtain and Share Water**  
Schematics are showing that plants that draw water from deep in the soil share the water with nearby plants. In a drought, the deep-rooted, well-watered, podocarp were to thirty sugar maples, the latter they did not. For the tree a root system is above the hard fragipan layer of soil, with only a few roots penetrating to tap the deep water supply.

DAY

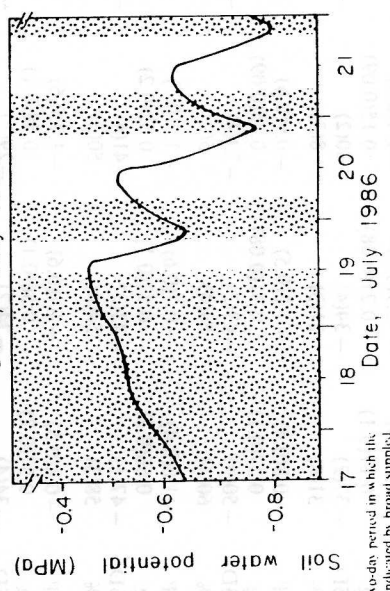
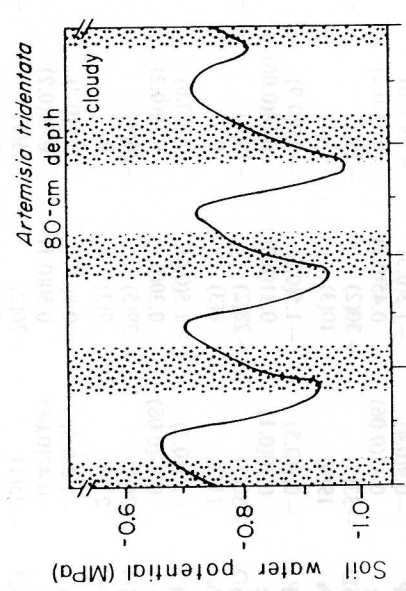
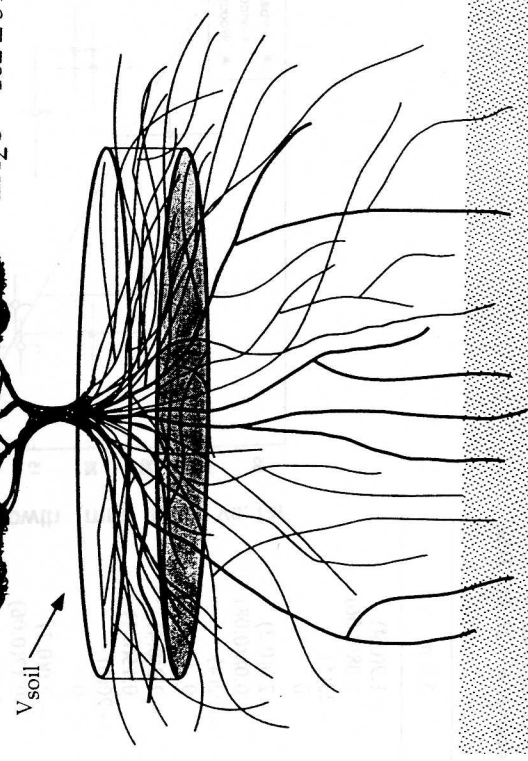
NIGHT



$$\Delta\Psi = 0.41 - 2.02 \text{ MPa}$$

$$\Delta\phi = 0.51 - 0.23$$

$$\Delta H_2O = 102 \pm 54 \text{ L}$$

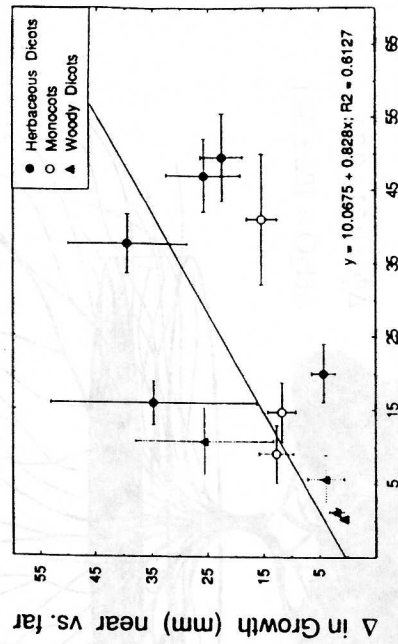


Diel fluctuations of soil water potential at 80-cm depth in an experimental plot planted with *Artemisia tridentata* shrubs. The stippled zones indicate nighttime. Adapted from Richards & Caldwell (1987).

Fluctuations in soil water potential as in fig. 9 showing a two-day period in which the shrubs were covered with opaque plastic to suppress transpiration (indicated by broad stippled zone). Overheating of the shrubs during the transpiration suppression was prevented by applying moistened layers of cloth over the plastic coverings. Adapted from Richards & Caldwell (1987).

**Table 2.** The leaf water potential ( $\Psi$ ; MPa), stomatal conductance to water vapor ( $g$ ;  $\text{mol m}^{-2} \text{s}^{-1}$ ), hydrogen isotopic composition of xylem-water ( $\delta D$ ; ‰), and the percentage of water derived from a source tree (%; equation  $4 \times 100$ ) measured in plants at five distances from the tree. Values are means ( $\pm$ SD);  $n = 5$  per species. The source tree was *Acer saccharum*.  $\delta D$  of groundwater =  $-59.1$  (2.7)‰.  $\delta D$  of precipitation that fell 26 days earlier =  $-26.5$  (8.2)‰.  $n = 5$

Species	0.5 m	1.0 m	1.5 m	2.5 m	5.0 m	
<i>Podophyllum peltatum</i>	$\Psi$	-0.9(0.4)	-1.0(0.3)	-0.9(0.6)	-1.6(0.6)	-1.9(0.4)
	$g$	0.24(0.2)	0.13(0.1)	0.13(0.1)	0.10(0.07)	0.08(0.06)
	$\delta D$	-49(3)	-43(2)	-41(3)	-31(4)	-23(5)
<i>Asarum canadense</i>	%	61(5)	53(6)	50(2)	9(3)	0
	$\Psi$	-0.6(0.4)	-0.9(0.5)	-1.4(0.4)	-1.7(0.5)	-2.0(0.3)
	$g$	0.17(0.1)	0.21(0.08)	0.15(0.09)	0.11(0.09)	0.08(0.08)
<i>Smilacina racemosa</i>	$\delta D$	-37(2)	-34(4)	-30(2)	-25(2)	-22(4)
	%	31(6)	21(3)	8(3)	0	0
	$\Psi$	-0.8(0.4)	-1.2(0.5)	-0.9(0.6)	-1.6(0.6)	-2.2(0.4)
<i>Fragaria virginiana</i>	$g$	0.37(0.1)	0.31(0.08)	0.35(0.09)	0.22(0.09)	0.15(0.1)
	$\delta D$	-50(4)	-47(3)	-29(4)	-24(2)	-20(5)
	%	60(4)	58(4)	5(2)	0	0
<i>Solidago flexicaulis</i>	$\Psi$	-1.0(0.4)	-0.7(0.6)	-1.7(0.7)	-1.6(0.6)	-2.0(0.3)
	$g$	0.66(0.2)	0.59(0.1)	0.52(0.2)	0.31(0.09)	0.17(0.06)
	$\delta D$	-47(1)	-43(3)	-41(4)	-32(4)	-28(2)
<i>Vaccinium vacillans</i>	%	58(3)	54(6)	50(5)	13(2)	1(1)
	$\Psi$	-0.8(0.5)	-1.1(0.6)	-1.7(0.6)	-2.3(0.8)	-2.2(0.5)
	$g$	0.57(0.2)	0.56(0.1)	0.58(0.1)	0.24(0.1)	0.20(0.2)
<i>Lindera benzoin</i>	$\delta D$	-34(4)	-34(2)	-29(3)	-25(1)	-21(3)
	%	20(3)	19(3)	6(2)	0	0
	$\Psi$	-0.9(0.4)	-1.3(0.5)	-1.9(0.6)	-2.6(0.6)	-2.7(0.4)
<i>Holcus lanatus</i>	$g$	0.41(0.06)	0.45(0.1)	0.31(0.2)	0.12(0.09)	0.09(0.04)
	$\delta D$	-33(3)	-30(2)	-28(4)	-27(2)	-20(3)
	%	19(4)	10(3)	5(2)	1(1)	0
<i>Tilia heterophylla</i>	$\Psi$	-0.9(0.5)	-1.5(0.5)	-2.0(0.9)	-2.8(0.6)	-2.7(0.3)
	$g$	0.30(0.1)	0.31(0.08)	0.18(0.06)	0.10(0.07)	0.05(0.05)
	$\delta D$	-30(3)	-28(2)	-19(3)	-21(6)	-25(2)
<i>Fagus grandifolia</i>	%	11(2)	6(3)	0	0	0
	$\Psi$	-1.1(0.3)	-1.5(0.4)	-1.3(0.6)	-1.9(0.5)	-1.9(0.8)
	$g$	0.37(0.08)	0.30(0.1)	0.30(0.2)	0.12(0.07)	0.09(0.08)
<i>Podophyllum peltatum</i>	$\delta D$	-34(2)	-29(5)	-26(3)	-26(1)	-22(4)
	%	21(3)	7(3)	0	0	0
	$\Psi$	-1.0(0.3)	-0.8(0.7)	-1.1(0.2)	-1.7(0.5)	-1.6(1.0)
<i>Asarum canadense</i>	$g$	0.47(0.06)	0.50(0.1)	0.49(0.2)	0.32(0.1)	0.19(0.07)
	$\delta D$	-25(1)	-26(2)	-25(1)	-26(3)	-24(1)
	%	0	1(1)	0	1(2)	0
<i>Smilacina racemosa</i>	$\Psi$	-1.7(0.5)	-1.4(0.9)	-1.9(0.3)	-2.2(0.6)	-2.0(0.4)
	$g$	0.25(0.07)	0.26(0.09)	0.26(0.03)	0.20(0.09)	0.14(0.06)
	$\delta D$	-25(3)	-24(2)	-23(3)	-24(2)	-22(4)
<i>Fragaria virginiana</i>	%	1(3)	0	0	0	0



**Fig. 4.** The difference ( $\Delta$ ) in aboveground growth of terminal stems or shoots (in mm) of plants growing near (within 1.5 m of the bole) or far (> 2 m from bole of tree) as a function of the difference in proportion of hydraulically-lifted water (HLW) used by these same plants. The values are means ( $\pm$ SD;  $n = 5$ ) for the twelve most common neighboring plant species (in Table 2) growing near sugar maple trees. The symbols used show the plants grouped by habit and for monots versus dicots. The strength of the relationship is different for each species, but over all species in the community,  $y = 10.0675 + 0.828x$ ,  $R^2 = 0.6127$ ,  $P < 0.05$

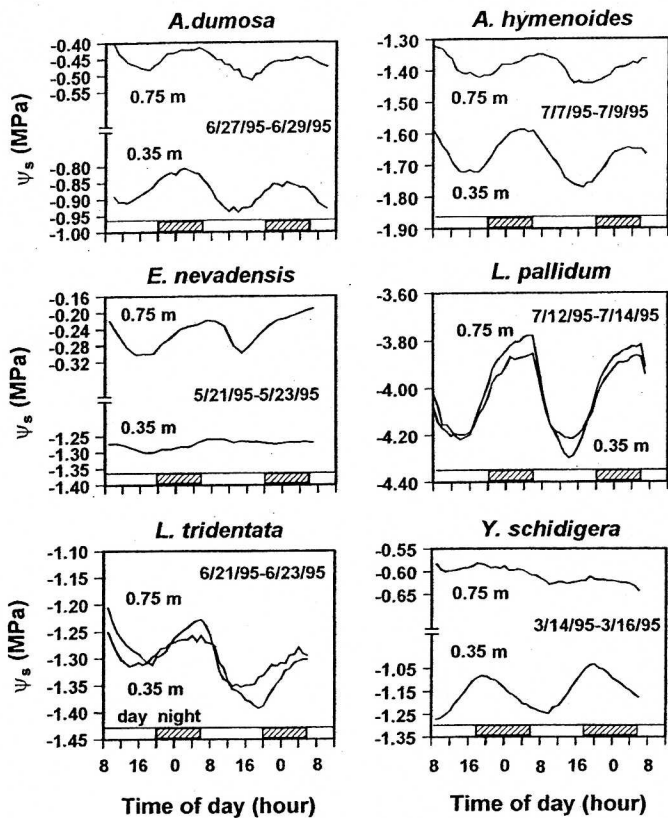


Figure 1. Examples of changes in  $\Psi_s$  at two soil depths that indicate hydraulic lift for the six study species during spring and summer 1995. Values are means of measurements collected beneath three plants of each species, except for *Lycium pallidum* where  $N=1$ . Day/night periods are indicated by open/shaded areas along the x-axis.

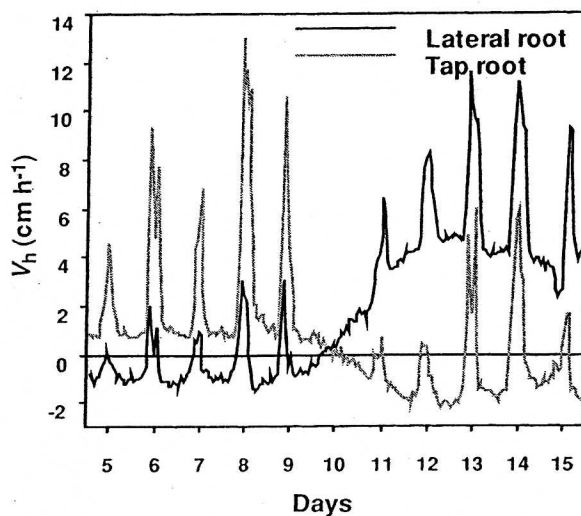
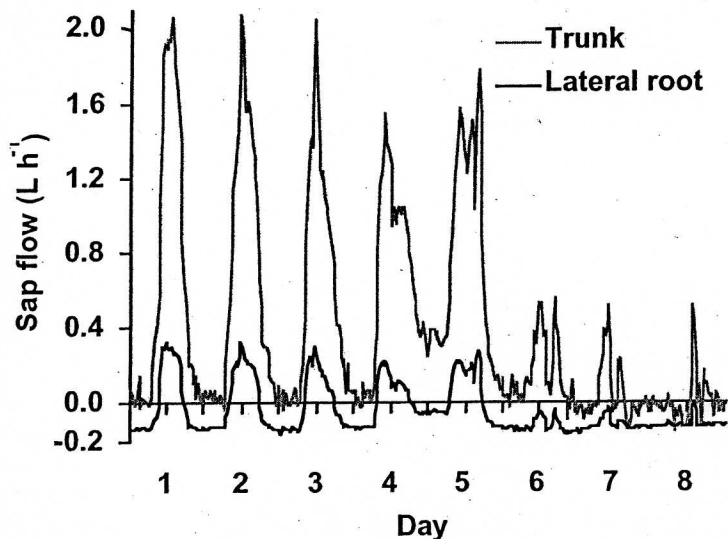


Fig. 4 Diurnal sap flow pattern in the taproot and a single representative lateral root of *Eucalyptus camaldulensis* for 5 days before and after break of season rains (14–24 May 1997) at Katanning, Australia. Day numbers correspond to the night numbers in Fig. 5, and tick marks represent midday. Data shown are hourly averages of  $V_h$ .

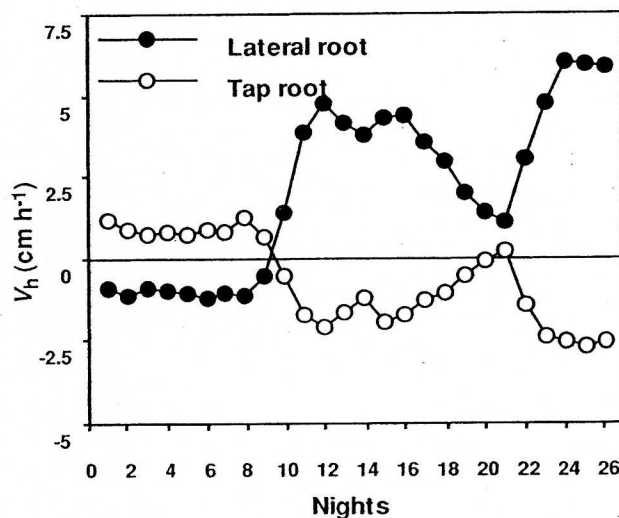


Fig. 5 Nocturnal heat pulse velocity measured by the heat ratio method in the taproot and a single lateral root of *E. camaldulensis*, 10 May–4 June 1997. Measurements of  $V_h$  between 8:30 p.m. and 5:00 a.m. were averaged. The break of season rains occurred on night 9 (19 May) and further significant rain (12 mm) occurred on night 21.