

AN ABSTRACT OF THE THESIS OF

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Title: Development and Morphology of Juvenile Western
Juniper (*Juniperus occidentalis* Hook.)

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Whole tree excavation of 41 western juniper (*Juniperus occidentalis* Hook.), ranging in age from 2 to 34 years old, was used to assess the development and structure of root systems, to determine biomass allocation patterns, and to develop mathematical relationships for estimating biomass and root system dimensions in seedling and young western juniper. Both aboveground and belowground developmental patterns, including structural components and vertical and horizontal root spread, were described relative to plant age. Tree age and height were evaluated as predictors of biomass, root length, and root system dimensions of juvenile western juniper.

Seedling root systems consisted of a relatively short tap root and a few weak laterals. With advancing age, root

systems expanded in depth and lateral spread. Maximum observed rooting depth and horizontal extension were 1.20 m and 5.70 m, respectively. Root biomass and length allocation shifted from tap to lateral roots with increasing plant age. Lateral root growth dominated in trees older than 10 years. The majority of lateral roots emerged from the tap root between 5 and 20 cm from the soil surface.

The relative proportions of accumulated weight in shoot components changed with progressing age. Foliage biomass accounted for the largest fraction of total standing weight throughout the developmental period examined. Adult foliage was first initiated at 17 years of age. Structural tissue increased and dead biomass decreased in relative proportion as the trees grew.

Western juniper root/shoot biomass ratios ranged from 0.50 to 1.75 and showed little correlation with age. Fine root/foliage ratios varied between 0.85 and 4.38, and exhibited a significant decline with age.

Tree age and height were consistently strong predictors for biomass of root and shoot components, root system length, and extension. Coefficients of determination from regressions on log-log transformed data ranged from 0.70 to 0.92 for tree age and from 0.84 to 0.96 for tree height.

Development and Morphology of Juvenile Western Juniper
(*Juniperus occidentalis* Hook.)

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INTRODUCTION

Plants resist the possible damaging effects of physical and biotic factors of their environment by either avoiding or tolerating the stresses they are exposed to. A set of traits, ranging from population characteristics and life history to morphological and physiological attributes, determines the overall success of a species in its particular habitat (Grime 1977).

In semiarid ecosystems, where shortage of water and nutrients and extreme fluctuations in temperature and rainfall prevail, evergreen woody perennials are the most common and apparently well adapted life form (Solbrig 1982). Seedling establishment and juvenile growth are critical periods in the life cycle of perennial species. The plants' morphological and physiological constitutions during these periods are significant factors determining ecological relationships such as succession, competition, invasion, and dominance.

Western juniper has replaced and encroached on historically shrub-grass dominated plant communities of the Intermountain Northwest (Burkhardt and Tisdale 1969, 1976). Successful establishment and growth of western juniper in

the harsh environment of these semidesert rangelands suggest adaptive morphological and physiological features, such as extensive root systems (Caldwell et al. 1977) , high root/shoot ratios (Monk 1966), and slow growth rates (Chapin 1980) that allow the species to cope with the demands and constraints of its habitat.

This study was undertaken to assess growth dynamics and morphology of young western juniper in central Oregon. Investigations focused on the belowground growth pattern as a possible mechanism enabling this species to grow and compete successfully with associated plant species.

The specific objectives of the study were to:

1. describe the spatial and structural development of root systems in seedling and juvenile western juniper,
2. determine growth strategy on the basis of relative contribution of plant organs to total biomass,
3. develop mathematical relationships for estimating biomass and root system dimensions of seedling and young western juniper from plant age and height.

LITERATURE REVIEW

Ecology of Western Juniper

Large scale successional changes have occurred throughout the vegetation of the western United States since the settlement by European man (Branson 1985). Woody species have invaded extensive areas historically dominated by herbaceous communities. In the Southwest, shrubs and mesquite (*Prosopis* L.) have replaced much of the semidesert grassland. Throughout the Great Basin, juniper (*Juniperus* L.) has encroached on sagebrush-grass and bunchgrass communities. Although factors responsible for the widespread vegetational changes are much disputed, excessive livestock grazing, fire suppression, and climatic changes are most often cited as causes (Burkhardt and Tisdale 1969, 1976, Young and Evans 1981). The biological aspects of invading species that promote their successful establishment and growth in environments not inhabited during recent history have received relatively little consideration.

Western juniper (*Juniperus occidentalis* Hook. ssp. *occidentalis*) (Vasek 1966) is a successful invader of rangelands in the Intermountain Northwest (Burkhardt and Tisdale 1969, 1976, Adams 1975, Shinn 1980, Young and Evans 1981, Eddleman 1987b). The range of this species extends from southeastern Washington through most of central and eastern Oregon, into the northern parts of California and

Nevada, and reaches its eastern extremity in southwestern Idaho (Vasek 1966, Dealy et al. 1978). Western juniper stands are best developed and most extensive in the central region of Oregon where they occur as continuous woodlands (Dealy et al. 1978).

The major part of the western juniper zone is characterized by a semiarid climate with dry hot summers and cold winters. Western juniper occupies the most xeric of all coniferous forest sites in the Pacific Northwest (Franklin and Dyrness 1973) and is commonly found in habitats intermediate in moisture between ponderosa pine forest and shrub steppe or bunchgrass communities (Driscoll 1964b).

Western juniper woodlands extend over an area with a wide variety of edaphic conditions. They occur on soils including Camborthids, Haplargids, and Haploxerolls (Franklin and Dyrness 1973). Three major types of parent material are delineated in the central and eastern Oregon juniper zone; they are of aeolian, metamorphic, and sedimentary origin (Driscoll 1964b). Soil textures range from sandy to clayey. Profile development is dissimilar among soils and varies in depth from over 100 cm to less than 25 cm. Fractured bedrock, claypans, caliche layers, rocks, and pebbles modify effective rooting depth and soil moisture availability (Eckert 1957, Driscoll 1964b, Burkhardt and Tisdale 1969, Dealy et al. 1978). Moisture

requirements of western juniper are not completely met by climatic conditions; compensating factors associated with the soil environment such as fractured rock and clay layers augment water availability (Eckert 1957).

Several shrub and grass species grow in association with western juniper. Big sagebrush (*Artemisia tridentata* Nutt.), rabbitbrush (*Chrysothamnus* Nutt.), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), and Sandberg bluegrass (*Poa sandbergii* Vasey) are the most commonly observed understory species (Driscoll 1964b, Hall 1973). On more mesic sites sagebrush and bluebunch wheatgrass may be replaced by varying amounts of bitterbrush (*Purshia tridentata* (Pursh) DC.) and Idaho fescue (*Festuca idahoensis* Elmer) (Eckert 1957, Driscoll 1964b). Other understory species commonly associated with western juniper are low sagebrush (*Artemissa arbuscula* Nutt.), horsebrush (*Tetradymia canescens* DC.), wax currant (*Ribes cereum* Dougl.), spiny hopsage (*Grayia spinosa* (Hook.) Moq.), Thurber's needlegrass (*Stipa thurberiana* Piper), bottlebrush squirreltail (*Sitanion hystrix* (Nutt.) J. G. Sm.), and cheatgrass (*Bromus tectorum* L.) (Eckert 1957, Driscoll 1964a, Burkhardt and Tisdale 1969, Hall 1973, Volland 1976).

Depending upon the successional status and the level of disturbance, various forb species can be common understory components in western juniper communities (Driscoll 1964b, Burkhardt and Tisdale 1969). Western juniper occurs in

mixtures with ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) on poor pine sites with shallow and rocky soils (Sowder and Mowat 1958).

More than half of the area currently covered by western juniper is the result of a continuous downspread of historically present stands on ridges and mesas into valleys below since the late 1800's (Burkhardt and Tisdale 1969). Ridgetop climax stands differ markedly from seral stands located on valley slopes and flats. Data from western juniper stands of different successional stages in Idaho indicate that junipers of climax communities range in age from seedlings to several hundred years (Burkhardt and Tisdale 1969). In contrast, invading stands are characterized by significantly younger, uniformly small to medium sized trees, most of which established since the turn of the century (Burkhardt and Tisdale 1969, Adams 1975, Young and Evans 1981, Eddleman 1987b).

Western juniper invasion has primarily occurred in big sagebrush and, to a lesser extent, in low sagebrush communities (Burkhardt and Tisdale 1969, 1976, Young and Evans 1981, Eddleman 1987b). Once juniper is established in a community and increases in density, it greatly affects various ecosystem properties such as species and structural diversity, nutrient cycling, hydrological processes, and productivity .

Although few studies have addressed understory/overstory relationships in western juniper communities, observations suggest that species diversity declines with increasing juniper dominance; only a few hardy understory plant species can compete in established juniper stands (Bedell 1987). Understory vegetation sharply declined with increasing dominance of arboreal species in low sagebrush communities of east-central Nevada that were invaded by Utah juniper (*Juniperus osteosperma* (Torr.) Little) and singleleaf pinyon (*Pinus monophylla* Torr. & Frem.) (Blackburn and Tueller 1970). These newly invaded communities had an abundance of young trees and few large trees. Closed pinyon-juniper stands had virtually no understory but a greatly increased litter cover that was restricted to the areas beneath tree canopies.

Although diversity and cover of understory plant species decreases in developing western juniper stands, the growing trees add to structural diversity and increase wildlife habitat and cover for various birds and mammals (Maser and Gashwiler 1978).

Investigations of soil nutrient patterns in ecosystems dominated by western juniper (Doescher et al. 1987) and other juniper species (Charley and West 1975, Klopatek 1987) indicated that juniper invasion leads to significant modifications of soil chemistry. Soil chemical changes probably result from the uptake of nutrients from an

extensive soil volume and the subsequent localized deposition in juniper litter (Charley and West 1975), and mineral accumulation from stem flow (Young et al. 1984). Nutrient accumulation under tree canopies and the associated decline of minerals in interspace areas may have a marked effect on growth and regeneration of both juniper and understory vegetation. Changes in spatial nutrient dynamics may be an autogenic mechanism contributing to the competitiveness of western juniper (Doescher et al. 1987).

The evergreen nature of juniper is likely to affect temporal aspects of nutrient dynamics. Nutrients sequestered from the soil are incorporated into longlived tissues and may be recycled internally with high efficiency. Evergreen leaves counteract mineral losses through slow leaf turnover and low susceptibility to leaching (Chapin 1980). Such longterm nutrient storage and internal conservation allows only a small percentage of the total nutrient pool to circulate and to be incorporated in soil organisms and understory vegetation.

Sites occupied by seral western juniper appear to be sensitive hydrologic systems with high risks of soil loss and overland flow. Juniper dominated ecosystems had the greatest potentials for sediment production out of ten ecosystems evaluated in eastern Oregon (Gaither 1981). Infiltration rates tended to be low, but infiltration in juniper ecosystems exceeded rates in

ponderosa pine and spruce fir ecosystems. As juniper stands increase in density, surface erosion from areas between trees and rill erosion caused by stem flow become typical features of interspace areas devoid of protective herbaceous vegetation (Buckhouse 1984).

Soil moisture patterns in western juniper woodlands and corresponding cleared sites indicated that throughout the year cleared sites exhibited a consistently higher soil water content in the top part of the profile than did woodland sites (Jeppson 1978). After juniper canopy removal, increased moisture and possible increases in nutrient availability resulted in a significant increase in production of herbaceous and shrub species (Vaitkus and Eddleman 1987). Water consumption by western juniper constitutes a major moisture loss from an environment already limited by available moisture. It could act as a key factor regulating plant establishment and production in western juniper communities (Jeppson 1978, Miller et al. 1987).

Recognition of the effects of western juniper invasion on the structure and function of semiarid ecosystems has increased the need to focus research on the autecology of this species. Information is needed to understand the processes that occur on sites with western juniper expansion. Few studies have focused on the morphological and physiological adaptations of western juniper that enhance

its successful establishment and growth in historical non-juniper communities.

The association of most seedling and sapling western juniper with sagebrush and larger juniper trees suggests that seedling establishment is closely tied to relatively mesic microsites that afford some mitigation of environmental extremes (Burkhardt and Tisdale 1976, Eddleman 1987b). Increased seedling survival of Utah juniper and oneseed juniper (*Juniperus monosperma* (Engelm.) Sarg.) with artificial shade and watering provides some evidence of the importance of favorable microclimatic conditions for juniper establishment (Meagher 1943). The highest seedling survival rates occurred with a combination of both shade and watering; all untreated seedlings died either because of drought or frost. The importance of physical factors for seedling survival was also observed for oneseed juniper in its natural habitat (Johnson 1962).

Western juniper seedlings probably germinate in March and are apparently well adapted to adverse growth conditions even during dry years (Burkhardt and Tisdale 1976). Rapid root elongation, a deeply penetrating tap root, and the association with mycorrhizal fungi observed in other semiarid juniper seedlings (Phillips and Mulford 1912, Johnson 1962) may also be factors contributing to successful western juniper seedling establishment.

Western juniper is a slow-growing and long-lived species. Established seedlings average 1.4 to 3.4 cm height increase annually (Burkhardt and Tisdale 1976). Dominant mature trees may grow in excess of 15 cm in one growing season (Eddleman 1987b) and attain maximum heights of about 12 m (Vasek 1966). Juniper trees may produce minor seed crops at ages less than 50 years and start to become senescent at about 400 years (Young and Evans 1981).

Western juniper is capable of producing two different types of leaves. Heterophylly is a common phenomenon among juniper species and is often associated with a phase change in the life cycle (Brink 1962). The juvenile form of western juniper bears needle-shaped or acicular leaves, whereas mature leaves of western juniper are reduced to small scales that are tightly appressed to the branches (Young and Evans 1981, Miller and Shulz 1987).

The xeromorphic structure of mature western juniper leaves allows for maximum drought avoidance through minimal leaf area, low surface-to-volume ratios, thick cuticles, and the absence of stomates on exposed leaf surfaces (Miller and Shulz 1987). The relatively thick bark covering juniper stems could be a further mechanism for reducing water loss under conditions of high evaporative demand (Gholz 1980). Such structural adaptations to a semiarid environment, coupled with the evergreen character of western juniper, may increase the competitive advantage of mature trees by

allowing them to take maximum advantage of favorable growing conditions and maintain a relatively large leaf area for carbon fixation compared to associated species (Miller and Shulz 1987).

Although most of the adaptations observed in mature trees are lacking in seedling and juvenile western junipers, there is no evidence that competition from other vegetation will either prevent the establishment of juniper seedlings or suppress and crowd out small juniper plants already established (Burkhardt and Tisdale 1976). Juvenile western juniper must have evolved various kinds of adaptive strategies that allow them to tolerate or avoid adverse physical and biotic conditions in their environment during the critical early period of their life cycle. One of these strategies may be related to the development of the plants' root system.

Adaptions of Root Systems in Semiarid Ecosystems

Successful adaptation of woody plants to particular environments requires economical partitioning of resources to aboveground tissues that fix carbon and to belowground tissues that absorb water and nutrients. In arid and semiarid ecosystems, plants have evolved in response to the major environmental constraints of water and nutrients. In such xeric and nutrient-deficient habitats, the aboveground parts of plants may constitute a minor fraction of the total

biomass. More than 80 % of the net assimilates may be allocated to deep and extensive root systems to moderate the effects of an adverse belowground environment (Caldwell et al. 1977).

High root/shoot ratios have often been cited as an adaptive strategy of woody and other perennial species to infertile and water-limited environments (Daubenmire 1959, Walter 1963, Monk 1966, Mooney 1972, Chapin 1980). Barbour (1973) challenged this generalization and presented extensive data showing that perennial plants in arid areas rarely possess root/shoot ratios above 1. He concluded that xerophyte root/shoot ratios vary over a wide range and in the majority of cases are lower than values of more mesic species. Root/shoot biomass ratios for several shrub species in the transition zone of the Mojave and Great Basin Desert are between 0.5 and 4.0 (Wallace and Romney 1972). Rodin and Bazilevich (1967) reported root/shoot ratios of 4-5 for semiarid and 6-10 for arid steppe communities in Russia. These values are consistent with observations in saltbush (*Atriplex* ssp.) and winterfat (*Ceratoides* ssp.) dominated cold desert communities in the Great Basin (Fernandez and Caldwell 1975, Caldwell et al. 1977). Root/shoot biomass ratios may be more closely related to plant life forms or temperature regimes than to aridity (Noy-Meir 1973).

Although information on root/shoot ratios of xerophytic species is scant and somewhat controversial, it appears that high belowground biomass allocation is not crucial for species that inhabit water and nutrient-limited environments. However, many perennial woody species of cold desert environments exhibit higher root/shoot biomass values than most warm desert species (Rodin and Bazilevich 1967, Wallace and Romney 1972, Barbour 1973, Fernandez and Caldwell 1975, Caldwell et al. 1977).

Comparisons of published data on root/shoot ratios are problematical since reported values depict observations at various stages of phenological development and varying plant ages (Kummerow 1980). Furthermore, root sampling methods and edaphic conditions vary considerably between studies, and reported ratios are likely to be underestimates of the true values due to the difficulty of completely recovering root systems from the soil.

The importance of studying root/shoot biomass ratios for carbon allocation in plants is unquestionable. However, the physiological relevance of root/shoot ratios for growth processes of desert perennials is doubtful. Root/shoot ratios do not discriminate between living and dead biomass fractions and different functional components of aboveground and belowground biomass. A more process-oriented approach is to relate absorbing root surface area to leaf area, or the use of dry weight ratios of roots and leaves as a first

approximation (Anderson et al. 1972). The logistic difficulties of making a reasonable estimate of absorbing root area are considerable. The average diameter of absorbing roots varies with species (Kummerow et al. 1978), and only a small and seasonally changing fraction of absorbing roots is active at one point in time (Fernandez and Caldwell 1975, Kummerow 1980). Numerous plant species have associated mycorrhizal fungi. Fungal hyphae act as highly efficient extensions of the absorbing part of root systems and contribute considerably to mineral nutrition and water uptake of plants (Trappe and Fogel 1977). Further studies on fine roots and water and nutrient absorption dynamics are needed before absorbing root area can be determined. Leaf area estimates are easier to obtain for most species, but plants with photosynthesizing stems or acicular or imbricated leaves may cause some complications.

Analysis of the effectiveness of root systems for efficacious acquisition of belowground resources cannot be made in terms of root phytomass only, but must also take into account the structure of root systems. The first major efforts to study growth habit of root systems of perennial species in their native habitats were conducted by Cannon (1911) in the Sonoran Desert and Weaver (1915a, 1915b, 1919, 1920) in the prairie regions of the United States. Cannon (1949) classified root systems of perennial species according to the development of prominent tap roots and

lateral roots. He considered a root system as generalized if both a well developed tap root and lateral root system existed. Root systems with dominant tap roots or lateral roots were classified as specialized tap and specialized lateral, respectively. Cannon's system was refined by establishing limits for the proportions of phytomass allocated to the different root types (Ludwig 1977). Root systems with more than 75 % of the biomass partitioned to the main tap root were classified as specialized tap root systems. Generalized root systems had equal amounts of dry weight in the tap root and lateral roots. Neither Cannon's nor Ludwig's classification system includes a characterization of the physiologically important fine root component.

Only a small fraction of plant species have specialized types of root systems e.g. cacti, *Yucca* L., and *Ephedra* L.; these species tend to be limited in their local distributions (Cannon 1911). The high constancy in root system structure suggests that the belowground growth habit of species with specialized root systems is under tight genetic control (Ludwig 1977).

Intraspecific variability in rooting habit of species with generalized root systems is associated with differences in the soil environment to which the individual plants are exposed during their development. On shallow soils with caliche layers or impermeable horizons, tap root growth is

reduced whereas surface laterals are well developed and extensive. However, the same species growing in a deep soil may have a deeply penetrating tap root and a restricted lateral root system (Kearny et al. 1914, Hellmers et al. 1955, Kausch 1959, Frischknecht 1963, Tabler 1964, Chew and Chew 1965, Hermann and Peterson 1969, Wallace and Romney 1972, Kummerow et al. 1977, Sturges 1977). The high degree of morphological plasticity of belowground structures of species with generalized root systems could be an adaptive mechanism that permits successful growth in a wide range of environments that differ strikingly in edaphic conditions.

The flexibility of root systems may be of particular importance for understanding the basic relationships between competing or coexisting plant species (Caldwell 1987). Soil moisture and nutrients are distributed heterogeneously in space and time and availability is curtailed by the presence of root systems of other plants. The ability of plants to adjust their belowground growth pattern and relocate zones of absorption may contribute to their competitive advantage (Eissenstadt and Caldwell 1988a), or allow them to coexist side by side with other species by filling available belowground niches (Manning and Barbour 1988).

Maximum rooting depth and lateral spread attained by woody species can be quite impressive; e.g. 61 m depth for oneseed juniper (Cannon 1960) and 53 m depth for mesquite (Phillips 1963) may be extremes. The effective depth of

tree root penetration in various parts of the Colorado Plateau was determined as 9 to 21 m (Cannon 1960). The majority of plants, including many deep rooted species, do not exceed a 3 to 5 m rooting depth (Richards 1986). Maximum horizontal spread of root systems may be more than 10 m (Cannon 1911, Weaver 1920, Hellmers et al. 1955) but again, these values should be interpreted as representing individual plants in particular environments. Lateral root extension almost always extends well beyond the canopy projection of trees and shrubs. Individuals of the same species can be highly variable in rooting depth and horizontal spread when growing in different habitats.

Although some woody plant species may have very deep-reaching root systems, the bulk of root biomass occurs in the upper soil horizons (Branson et al. 1976, Sturges 1977, Sturges and Trlica 1978, Wallace et al. 1980, Heitschmidt et al. 1988, Manning and Barbour 1988). Water and nutrient availability are the main ecological factors that influence the zone where large proportions of root biomass are found. Most biologically-important minerals show some degree of accumulation towards the soil surface (Garcia-Moya and McKell 1970, Charley and West 1975, Charley 1977, Doescher et al. 1984, West et al. 1984). Biological activity and mineralization processes are highest in the top zone of the profile where soil moisture recharge is most frequent (Charley and West 1977). Localization of root biomass in

soil layers with elevated nutrient levels and high mineralization rates allows the limited amount of nutrients to be tapped by plants when soil moisture conditions are favorable. A dense root system near the soil surface permits plants to take advantage of small summer precipitation events whereas deeper penetrating tap roots have access to soil horizons where water is not limiting most of the year (Sturges 1977, Hodgkinson et al. 1978, Manning and Barbour 1988).

Root systems undergo considerable change during the initial years of the life of a plant. Root penetration and habit of growth during seedling establishment and the juvenile phase have been considered as major factors determining survival and successful growth in moisture-deficient habitats. To compensate for water loss by transpiring surfaces, the developing seedling root must reach a soil horizon where it can absorb enough moisture to sustain transpiration and growth during periods of drought (Daubenmire 1959).

Toumey (1929) examined the initial root habit of tree seedlings from a wide range of habitats and concluded that species of water-deficient regions have rapidly growing, deeply penetrating tap roots with few weak laterals. Numerous studies of seedlings of various dry-land shrubs and trees have confirmed Toumey's observations (Spalding 1904, Haasis 1921, Weaver and Kramer 1932, Muller 1946, McKell

1956, Kausch 1959, Stanton 1959, Wallace and Romney 1972). As seedlings become established, the developing root systems show great variation in form and extension (Haasis 1921, Goodwin 1956). Initial form and distribution of roots appear to be primarily genetically controlled; the influence of environmental factors becomes more pronounced as plants get older (Toumey 1929). The great morphological adaptability of seedling root systems beyond the initial tap root phase is attributed to the necessity for prompt response to changing external conditions during establishment (Haasis 1921).

Besides changes in form and biomass increment, the most prominent alterations during ontogenetic development of root systems of woody species appear to be in the proportions of functional and structural root types formed (Hermann 1977). Except for the data of Chew and Chew (1965) on creosotebush (*Larrea tridentata* (DC.) Cov.), virtually no information exists on growth dynamics of various components of xerophytic shrub and tree root systems or changes of root/shoot ratios beyond the seedling stage. Measurement of 61 creosotebush individuals, ranging in age from 1 to 65 years, indicated 3 major periods in root system development. Tap root growth dominated over lateral root growth at ages below 15 years; increased growth of laterals occurred until biomass allocated in tap and lateral root systems was approximately equal at about 45 years; shrubs beyond 45

years maintained a stable ratio of tap root:lateral root biomass of about 1.2 to 1.0.

Chew and Chew (1965) found in a field study of creosotebush that root/shoot ratios were highly variable and showed no apparent pattern with age. However, another study of creosotebush seedlings demonstrated a definite age relationship for root/shoot ratios; root growth was most pronounced early in the development of seedlings and then declined in relation to shoot growth (Walters and Freeman 1983). A similar growth pattern and a high correlation between age and root/shoot ratios were also observed in *Atriplex nummularia* Lindl. seedlings (Jones and Hodgkinson 1970).

Root growth appears to have priority during the early development of seedlings and is probably regulated by the genetic make-up of the species (Jones and Hodgkinson 1970, Walters and Freeman 1983). The inherent tendency towards uniformity in root/shoot values becomes weaker as the plants age. With age, variations in external conditions act as more or less modifying agents on allocation patterns to aboveground and belowground tissues, and age may be a weak indicator of root/shoot ratios (Chew and Chew 1965).

METHODS AND PROCEDURES

Study Site

The study was conducted 12.8 km west of Redmond in Deschutes County, central Oregon (Fig. 1). The research site was located near Barr Road ($44^{\circ} 16' 48''$ latitude north and $121^{\circ} 20' 30''$ longitude west; T14S, R12E, Sec. 18), on a gentle westfacing slope at an elevation of 1050 m. Longterm annual precipitation at Redmond, the nearest recording station, averages 217 mm, mostly occurring as snow from November to January and rain in May and June (NOAA, 1982). Summers are dry, with somewhat infrequent thunderstorms.

Mean annual temperature is 8.4° C, but the extremes in temperature are wide. Diurnal fluctuations of 15 to 20° C are typical. Although temperatures may drop below 0° C in any month of the year, late frosts generally do not occur after June 15th and early frosts not before September 7th (NOAA 1982).

A climate diagram (Walter 1955) summarizes the seasonal course of temperature and precipitation for Redmond (Fig. 2). Total annual precipitation is likely to be slightly higher at the study site, since the amount of precipitation increases to the west of Redmond due to topography and prevailing wind patterns.

Soils were loamy-skeletal, mixed, mesic, aridic Haploxerolls developed from volcanic ash and tuff. They averaged 70 cm deep. Pumice particles constituted 15 to 25 % of the soil material. The pH ranged from 6.4 in the top horizon to 7.6 in the lower layers (Appendix 1).

The study site was similar to the *Juniperus/Artemisia/Agropyron-Chaenactis* association described by Driscoll (1964b). The principal plant species were western juniper and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle). Other shrubs characteristic of the understory were bitterbrush, gray rabbitbrush (*Chrysothamnus naseousus* (Pall.) Brit.), horsebrush, and green rabbitbrush (*Chrysothamnus viscidiflorus* (Hook.) Nutt.).

Native perennial grasses, generally found close to juniper and sagebrush plants, included Idaho fescue, bluebunch wheatgrass, and scattered individuals of bottlebrush squirreltail and Sandberg bluegrass. Annual grasses and annual and perennial forbs constituted only a minor component of the community.

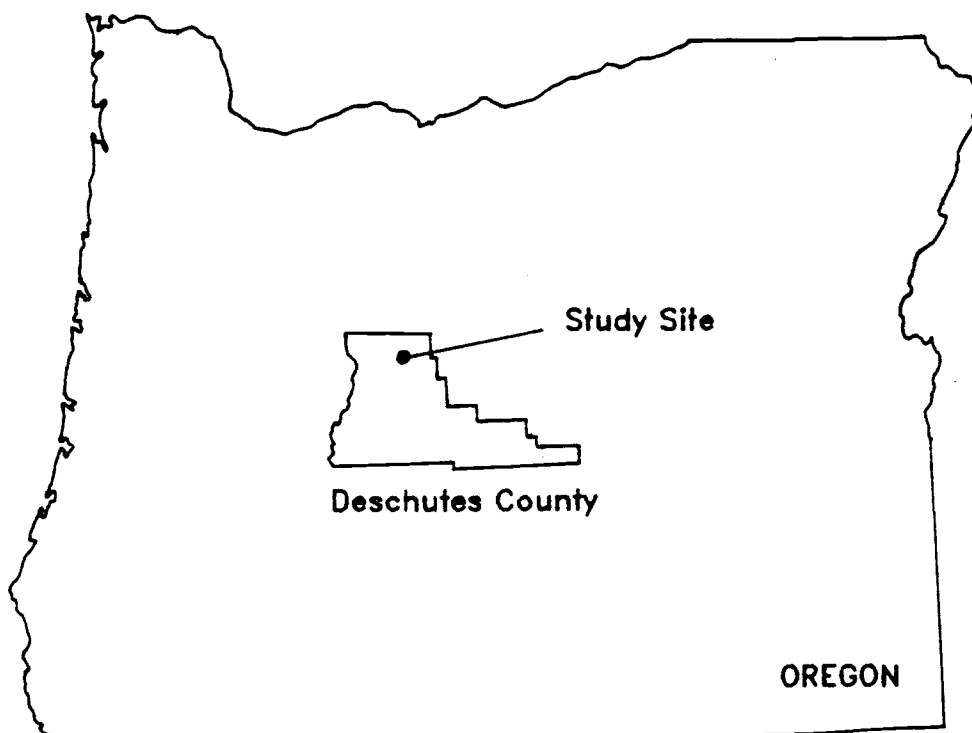


Figure 1. Location of study site.

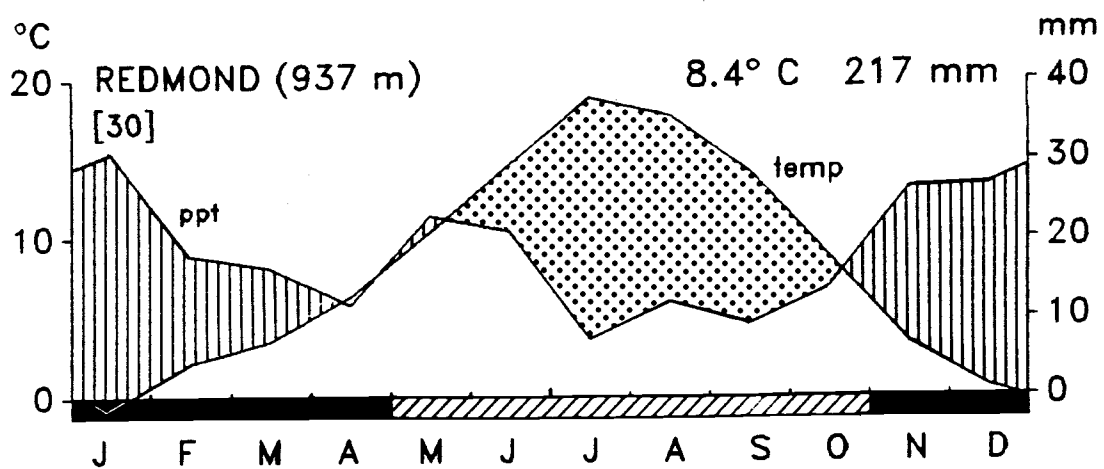


Figure 2. Climate diagram for Redmond, Oregon.

Tree Harvesting

To study the dynamic morphology and quantitative characters of juvenile and young western juniper in their natural environment, 41 individuals grown under sagebrush plants were collected in August and September 1987. Trees were selected as a stratified random sample from 7 height classes to cover the range of plants with juvenile foliage only and with both juvenile and adult foliage. Tree height classes were 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, 40-50 cm, and 50-75 cm. Ideally, plants should have been harvested on the basis of age, since a high plasticity in growth patterns may result in a loose size to age relationship (Harper 1977). However, no age estimates were possible prior to tree collection. A minimum of five plants per height class were randomly selected for the study of aboveground and belowground biomass allocation.

Individual root systems were manually exposed with the help of small garden tools. Roots were followed as far as possible within the limits of prevailing soil conditions. In most cases lateral roots and fine roots could be extracted completely. However, the tips of tap roots of several large plants were lost as they disappeared into cracks of the underlying volcanic tuff. Trees were marked at ground level and divided into shoot and root system. To remove obvious soil contamination from the roots, root systems were repeatedly washed in water. Plants were

separately stored in paper bags at room temperature for further analyses.

Root System Structure

During the process of excavation the main characteristics of each root system and atypical growth patterns such as upward curvature of roots were noted.

Maximum rooting depth and horizontal extension of the root system were determined for each tree. Rooting depth was measured as the vertical distance from ground level to the tip of the deepest penetrating root. Lateral extension was recorded as the average horizontal distance between the tips of the 5 to 6 longest lateral roots' and the central root trunk.

Photos were taken of each plant placed against a grid system. The root systems were arranged on the horizontal surface as close as possible to their natural arrangement to show their position within the horizons of the soil profile.

Biomass

Aboveground components of each plant were divided into juvenile foliage, adult foliage, branches, trunk, and dead tissue. Dead tissue was determined on the basis of color and included all grey, brown, and yellow foliage. Branches were considered dead if they did not bear any green foliage.

Belowground structures were separated into tap roots and lateral roots. Roots were further divided into fine roots (< 1 mm), medium roots (1-5 mm), and coarse roots (> 5 mm). The diameter of each lateral root and its location on the tap root were recorded during the separation process. No attempt was made to distinguish between dead and live roots.

All plant material was dried to a constant weight at 80° C, and biomass of each component was determined with an analytical balance.

Root Length

Root system length was calculated from length/weight ratios and from direct measurements. Average length/weight ratios were developed for each of the two smaller root categories. Samples were composed of a random number of 5 cm long root sections which were counted and weighed. Sample size varied with the amount of available root material. The length of 1 gram of root biomass was 833.8 cm for fine roots (< 1 mm diam.) and 136.6 cm for roots with a diameter of 1-5 mm, respectively. The length of roots > 5 mm diam. was measured directly.

Tree Age

The age of each tree was determined from a polished cross section from the base of the stem. Growth rings were counted independently under a microscope by two persons. Since ring counts varied little for individual trees, age was considered to equal the maximum number of growth rings counted.

Data Analysis

For the description of root system development, trees were grouped into 7 age classes with class intervals of 5 years. Summary statistics were calculated for each class to represent the observations.

Relative biomass of tree components, relative root length, and biomass ratios were computed from dry weight and root length measurements for each individual. To describe the relationships of the observed variables with age, least squares regression techniques were used to evaluate different mathematical curves for each data set (Landsberg 1977). The best model was selected on the basis of goodness of fit as indicated by the coefficients of determination (r^2), the standard errors of the estimate ($s_{y,x}$), and the graphical form of the curve that was most likely to represent the biological relationship of the observed variables.

Prediction equations for biomass and extension of various tree components were developed by relating each variable to tree age and height. To comply with the basic assumptions of parametric regression analysis, log-log transformed data (base-e values) were used for computing regression constants if residual analysis indicated the necessity for transformation (Sokal and Rohlf 1981). Computations were based on two models: the linearized form of the allometric function $y = a + x^b$, and the linear model $y = a + bx$. The linearized form of the allometric model, $\ln y = a + b \ln x$, proved to be the best mathematical relationship for all but one variable. Significance tests for the regression model were carried out at a probability level of $\alpha < 0.05$ (Sokal and Rohlf 1981).

Coefficients of determination can be relatively ineffective for expressing the closeness of fit and reliability of estimates for data that differ greatly in their relative magnitude (Whittaker and Woodwell 1968). To express the relative spread of points from the regression lines more effectively, estimates of relative errors (E , e) were calculated according to Whittaker and Woodwell (1968). For logarithmic regressions, E is the antilog of the standard error of the estimate. It is the factor by which a given value of y is multiplied or divided to calculate the error range. For linear regressions, e was calculated by dividing the standard error of the estimate by the mean

value of y . The error range for a given estimate of y in linear regressions is $y \pm e$. The coefficients of determination from the analyses are given as computed.

To eliminate the systematic bias introduced in the predicted values by logarithmic transformation of the variables (Baskerville 1972, Sprugel 1983), correction factors (*C.F.*) were calculated for each variable. The correction factor $s^2/2$ accounts for the bias in the predicted value y in arithmetic units as $y = e^{(\ln y + s^2/2)}$ (Baskerville 1972), where s^2 is the estimated residual variance of the regression.

RESULTS

Height Distribution

Sampling included a higher percentage of trees in the 0-5 and 5-10 cm height class than in any of the other height classes. Sampled trees ranged in height from 3.9 cm to 75.0 cm (Table 1).

Age Distribution

Individual plants ranged from 2-34 years old (Fig. 3). Approximately one third of all trees excavated were below 5 years of age; 3 year old junipers were sampled most frequently and contributed almost one fourth to the total sample.

Spatial Patterns of Root Systems

The course of root system development of seedling and young western juniper progressed through roughly three different phases (Fig. 4a, 4b, 4c).

During the first phase (tree age \leq 10 years), western juniper root systems were dominated by a long slender tap root that grew more or less straight downwards, with few laterals which were much shorter than the tap root (Fig. 4a). Average rooting depth ranged from approximately 20 cm for individuals less than 6 years of age to 34 cm for 6-10 year old trees. Minimum root penetration observed was 17 cm

Table 1. Tree height classes, number of individuals within each class, and range of tree heights at Barr Road

Tree height class cm	Number of trees	Range of tree height cm
0 - 5	7	3.9 - 4.8
5 - 10	9	5.5 - 9.4
10 - 20	5	10.6 - 19.0
20 - 30	5	21.5 - 28.5
30 - 40	5	33.5 - 39.0
40 - 50	5	41.0 - 47.0
50 - 75	5	56.0 - 75.0

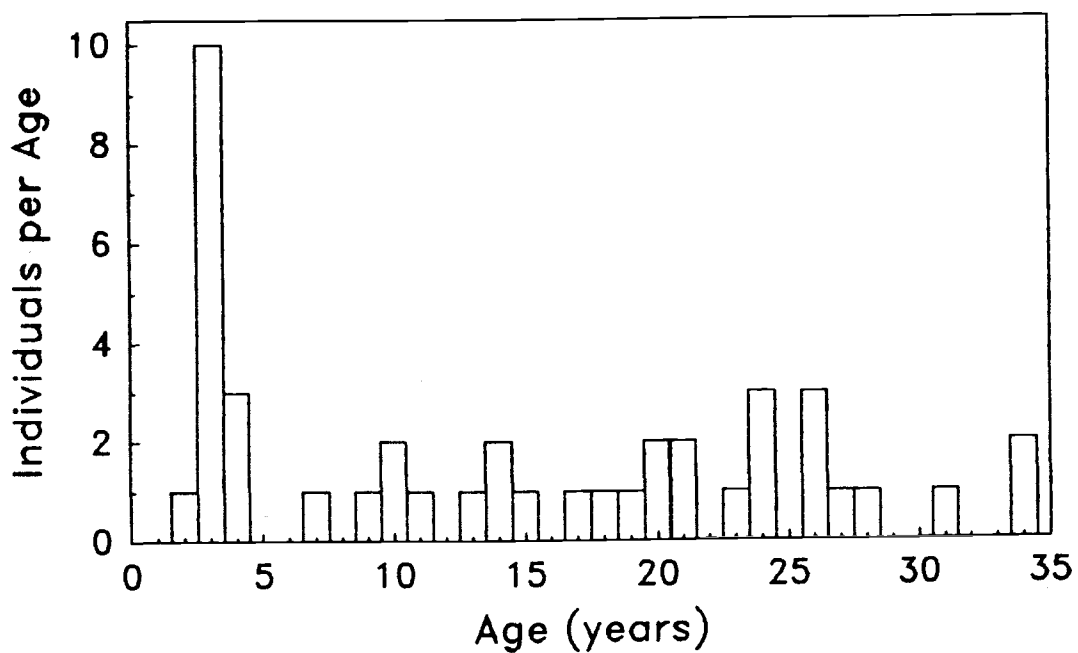


Figure 3. Age distribution of sampled trees.

Figure 4. Roots system of 3 year old (Fig. 4a), 18 year old (Fig. 4b), and 34 year old western juniper (Fig. 4c).

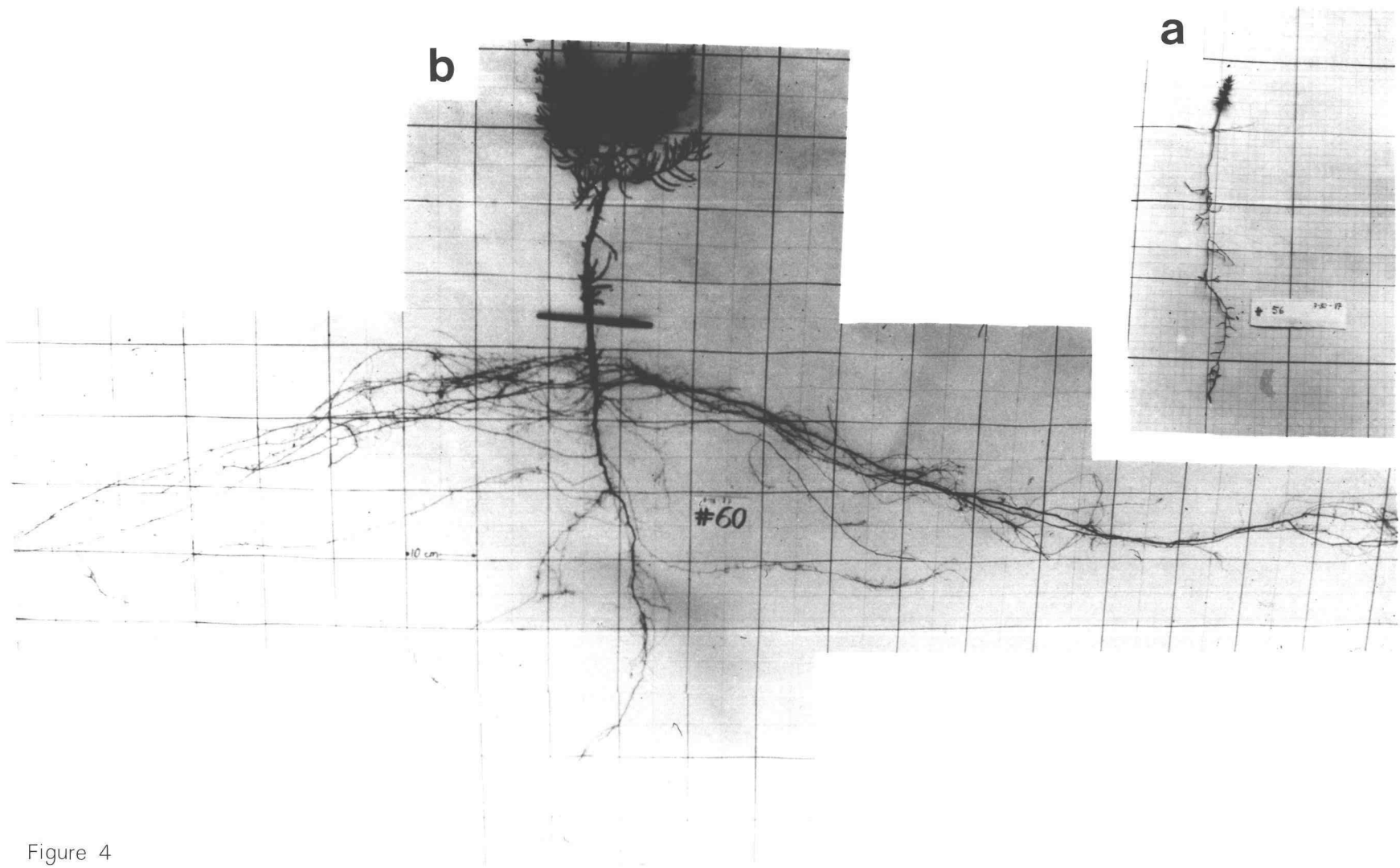


Figure 4

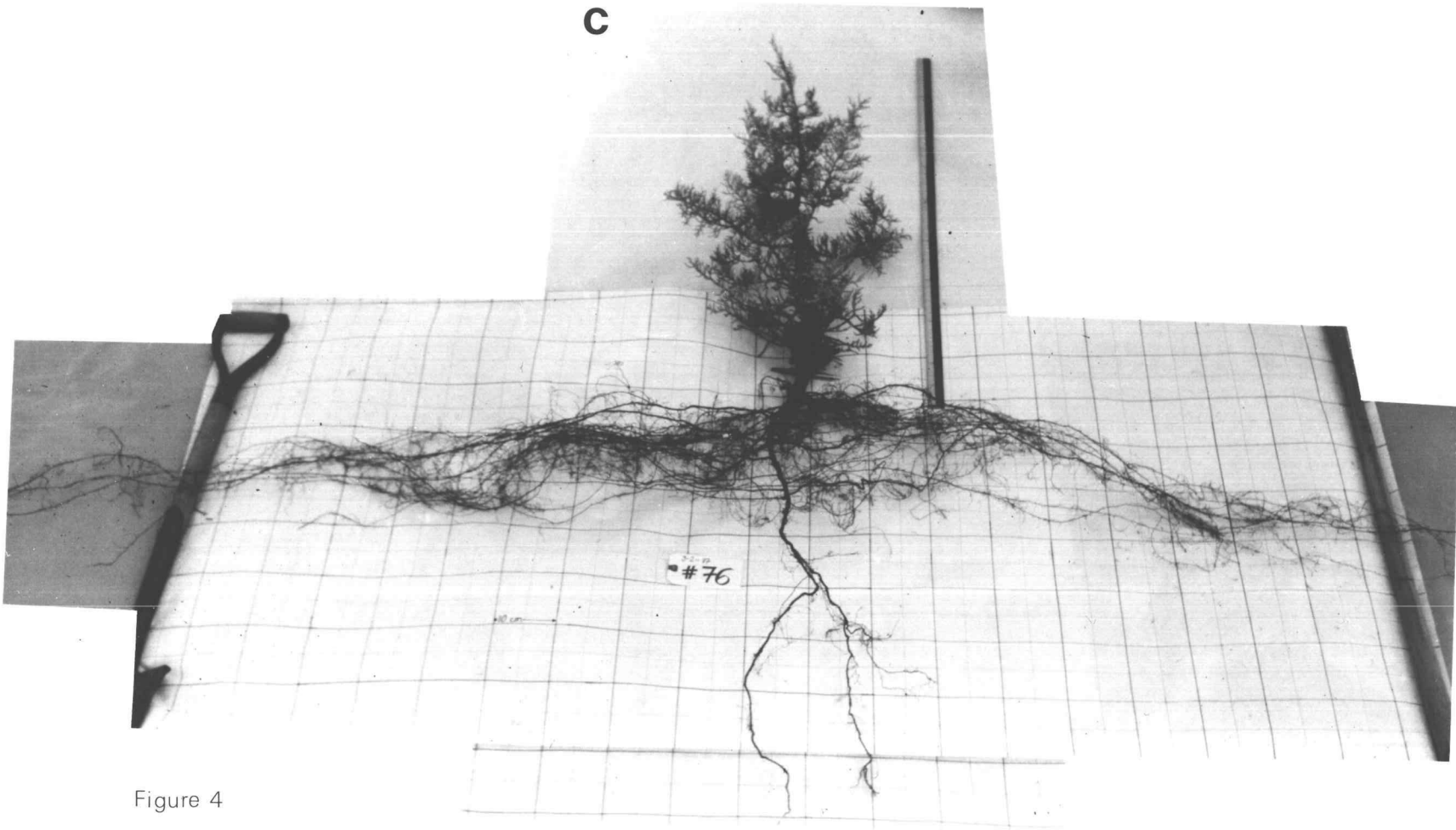


Figure 4

for 3 and 4 year old individuals (Appendix 2). Mean lateral root extension was near 3 and 13 cm for trees less than 6 and 6-10 years old (Fig. 5a).

In the second phase (age 11-25 years) the general character of the root system changed (Fig. 4b). Root penetration of older individuals in this phase had advanced to over 100 cm (Appendix 2). While some plants still possessed a dominant tap root, the tap root of others had branched and the deepest roots were branches originating from the tap root. Root systems of 11-25 year old trees showed a pronounced expansion in lateral spread compared to younger trees (Fig. 5a). A total root system width of 4.50 m was measured in two individuals. The majority of lateral roots (64-70 %) emerged from the root trunk between 5 and 20 cm depth (Fig 5b). Laterals > 5 mm in diameter at their origin accounted for an increasing percentage of all lateral roots (14-43 %) with advancing age (Fig. 5b). Most of these large roots tapered rapidly near the stem and then continued out more or less horizontally with little or no taper. Smaller, secondary and tertiary laterals grew at many angles to the vertical and some grew upward towards the root crowns of Idaho fescue plants, where they proliferated and branched into many short fine roots. Very few woody laterals grew vertically and formed sinker roots.

During the third phase (age > 25 years), root systems basically resembled the shape and gross morphology of those

Figure 5. Development of tap root depth and lateral spread of western juniper for age classes < 6 years to > 30 years (Fig. 5a), and distribution of lateral roots along tap root (Fig. 5b).

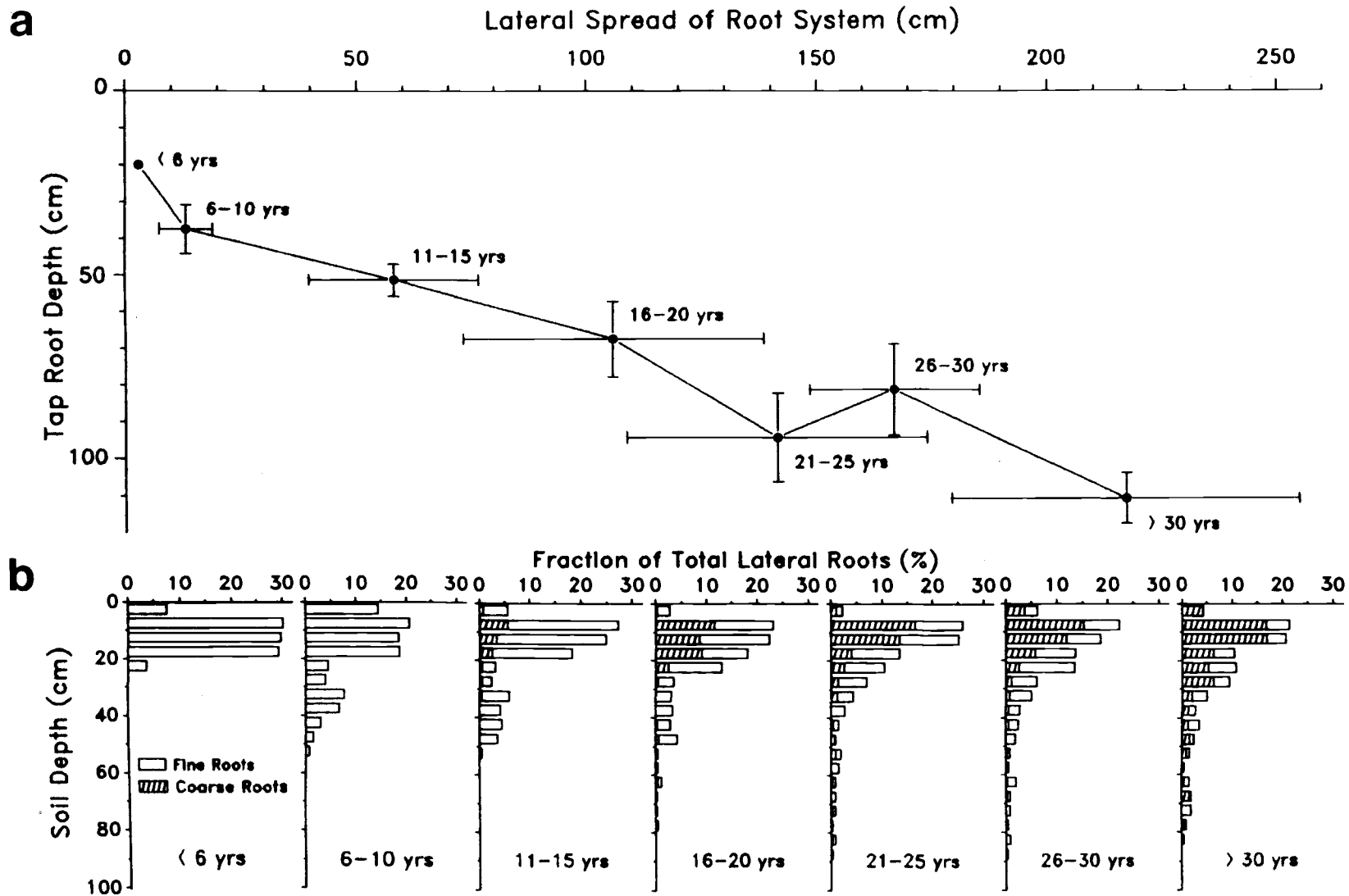


Figure 5.

in the second phase (11-25 years) (Fig. 4c). However, root system dimensions increased as a result of both lateral and tap root growth. Lateral root expansion was more pronounced (Fig. 5a) and reached a maximum diameter of 5.70 m (Appendix 2). Fine lateral roots (< 1 mm diam.) branched repeatedly over a short distance, thus forming a dense mat of roots in a volume of soil approximately one third of the diameter of the root system and about 20 cm deep (Fig. 4c). As in younger trees (\leq 25 years), more than 50 % of the lateral roots originated between 5 and 20 cm depth. However, the percentage of laterals originating beyond this depth had increased (39-43 %) in comparison to root systems in phase II (24-33 %) and phase I (4-28 %) (Fig. 5b).

Some important general features about juniper root systems observed during excavation were as follows:

(1) Juniper root systems overlapped and intermingled with root systems of various sized neighboring junipers, sagebrush, and other plant species. (2) Root systems were not dormant during the period of excavation. Numerous succulent white and pink roots indicated active growth. (3) Coarse lateral roots frequently exhibited increasing diameter growth with distance from the root trunk.

Root Biomass Allocation and Length

Expressed as percentages of total root weight and root system length of each tree, the relative proportions of tap root and lateral roots differed considerably within similar aged individuals and between young and old trees (Fig. 6 and 7). The most obvious change that occurred with increasing age was the gradually increasing dominance of the lateral root system. Initially, the tap root represented the major part of belowground structures in terms of both biomass and length. With progressing age, the root systems of juniper trees were composed mainly of lateral roots.

The change of dominance from tap to lateral roots was more pronounced for root length than for biomass development. Lateral root biomass increased from approximately 45-55 % of the total root system in young trees to almost 70 % in the oldest trees (Fig. 6). Root length associated with the lateral root system grew from 40-60 % to over 90 % of total root system length (Fig. 7). Concurrent with the increase in age was a decrease in the variability of relative root length and biomass values.

The range of values recorded for the whole data set were 0.02-110.72 g for total belowground biomass (Appendix 3) and 0.17-291.54 m for total root length (Appendix 2).

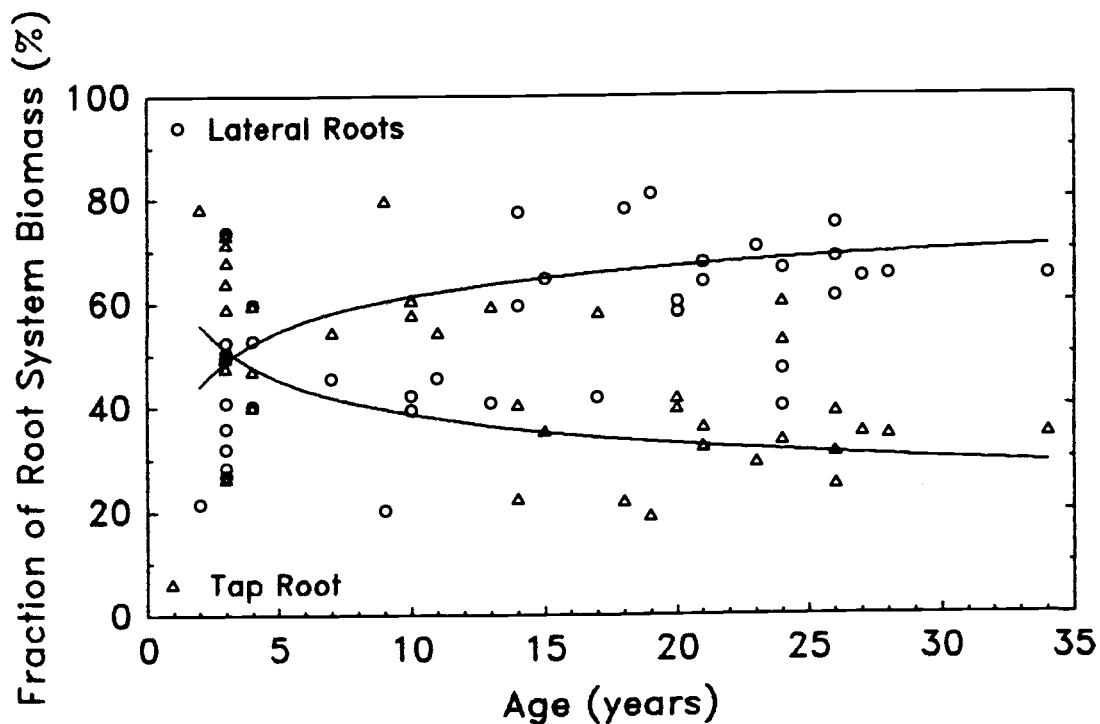


Figure 6. Biomass allocation between tap root and lateral roots in western juniper age 2 to 34 years with lines of best fit from least squares regressions.

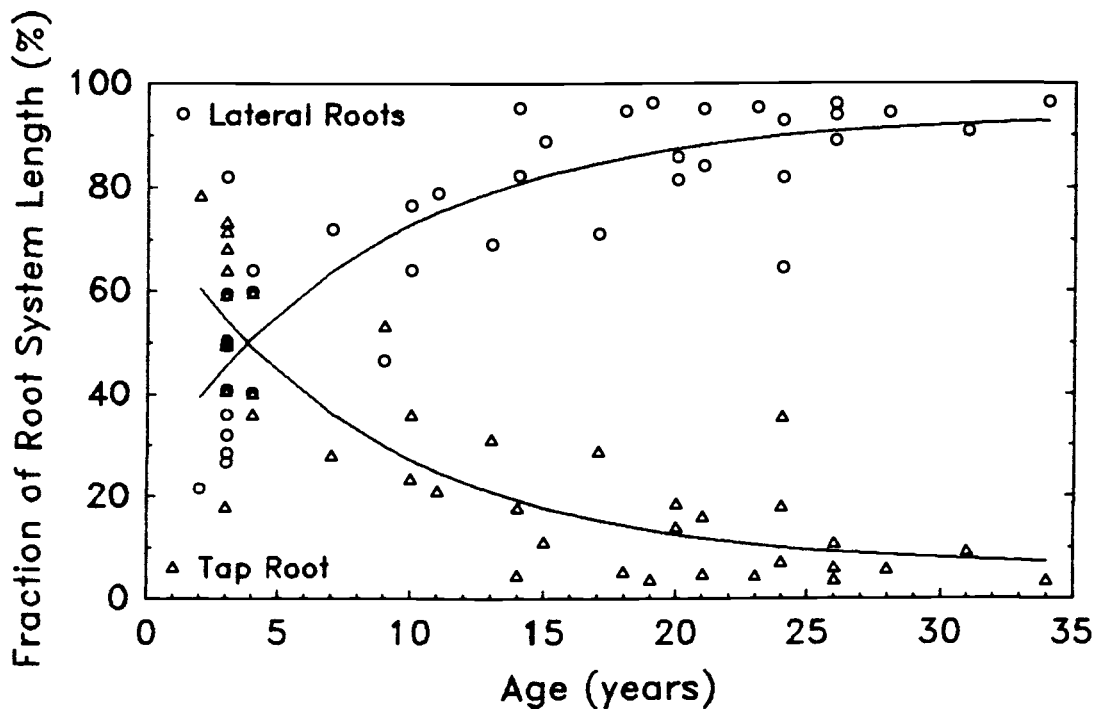


Figure 7. Root length allocation between tap root and lateral root systems in western juniper age 2 to 34 years with lines of best fit from least squares regressions.

Whole Tree Dry Weight Distribution

Trends of relative proportions of accumulated weight of foliage, branches and stems, dead biomass, tap root, and lateral roots of the sampled individuals changed with progressing age (Fig. 8). Shoot biomass formed an increasing fraction of total tree weight with greater age. Foliage biomass development paralleled that of the shoot at a fairly constant rate, increasing from 26 % in the youngest trees to 31 % in the oldest individuals. Foliage biomass accounted for the largest fraction of total standing weight at all ages. Branches and stems contributed a relatively small proportion to the total in the smallest trees (about 10 %), but increased rapidly with greater age to 29 % at 34 years. Conversely, dead biomass formed a progressively smaller percentage of total tree weight, decreasing from 9 to 2 % as age increased from 2 to 34 years.

Root weight, expressed as a percentage of total tree biomass, was highest in young trees and gradually decreased to less than 40 % in the oldest individuals. Up to about age 10, tap root biomass contributed relatively more to total biomass than lateral roots. However, the lateral roots fraction increased gradually to over 25 % of total tree dry weight as the plants aged.

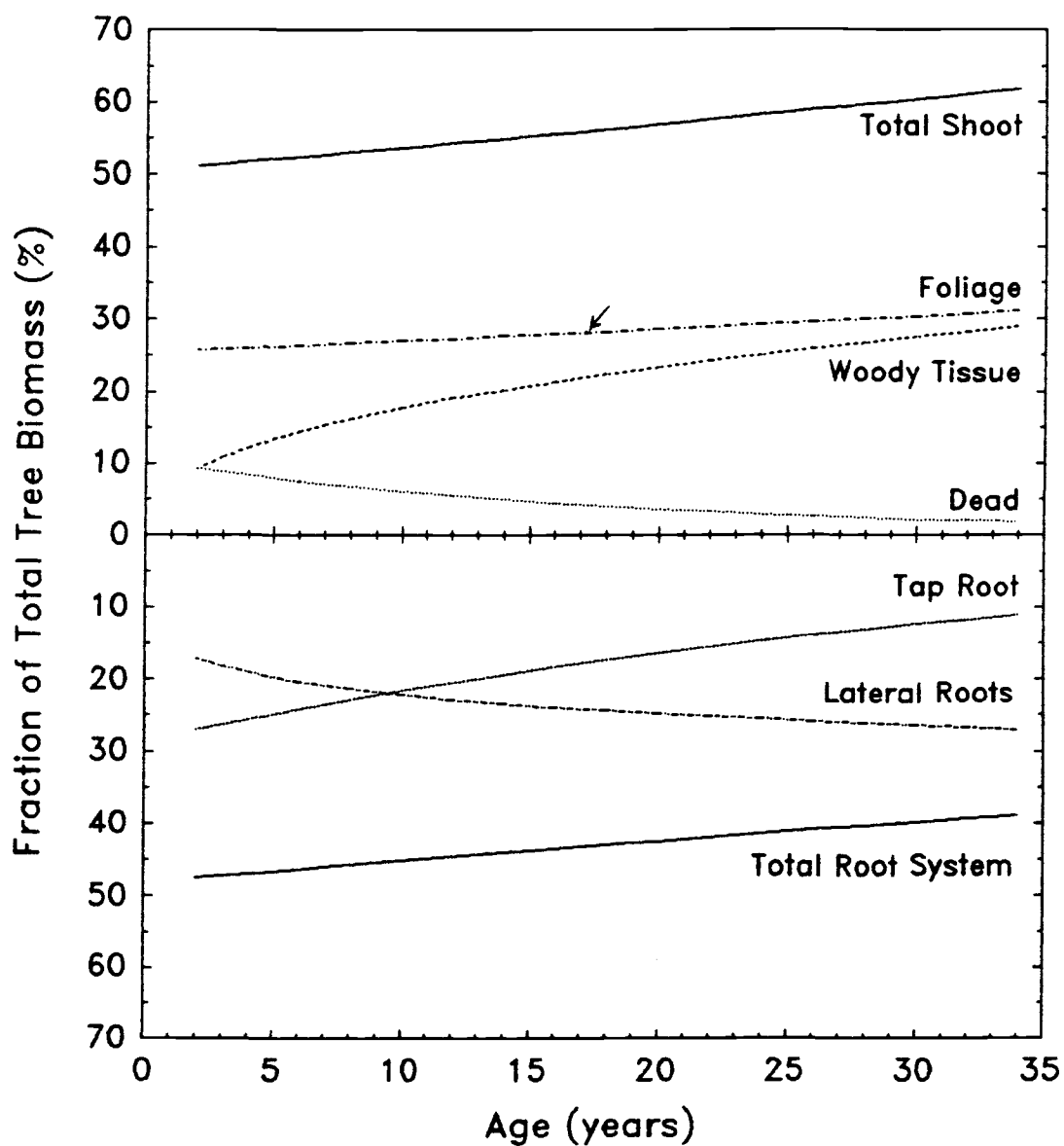


Figure 8. Biomass allocation in shoot and root system of western juniper age 2 to 34 years (lines of best fit from least squares regressions). The arrow indicates the age of the youngest tree with adult foliage.

Root/Shoot Biomass Ratios

Root/shoot ratios for the 41 juniper trees analyzed showed little correlation with age ($r = -0.37$) and ranged from 0.52 to 1.74 (Fig. 9). Ratios varied most for individuals from 2-7 years old and converged with increasing age. With one exception, all root/shoot ratios of individuals exceeding 7 years of age fell between 0.53 and 0.87. The overall mean root/shoot ratio was 0.84 with a standard error of 0.05.

Fine Root/Foliage Biomass Ratios

Ratios of fine root to foliage biomass exhibited a significant decline with age (Fig. 10). Values for trees up to 7 years were highly variable, ranging from a minimum of 0.85 to a maximum of 4.38. Values for trees older than 7 years varied between 0.16 and 1.11, but were mostly below 1.

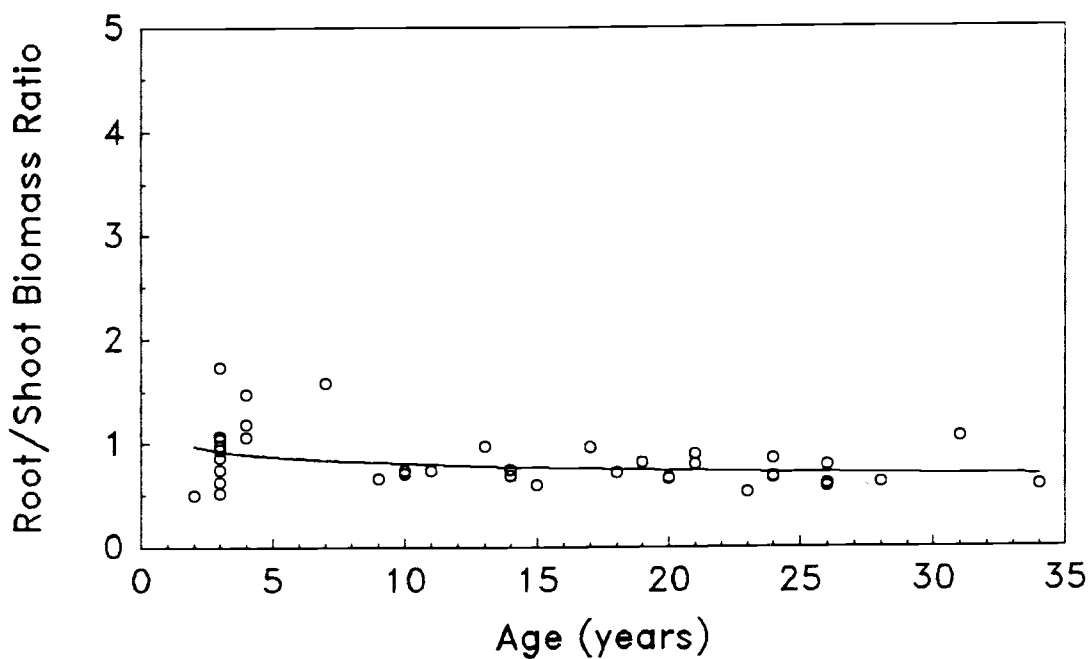


Figure 9. Root/shoot biomass ratios for western juniper, age 2 to 34 years, with line of best fit from least squares regression.

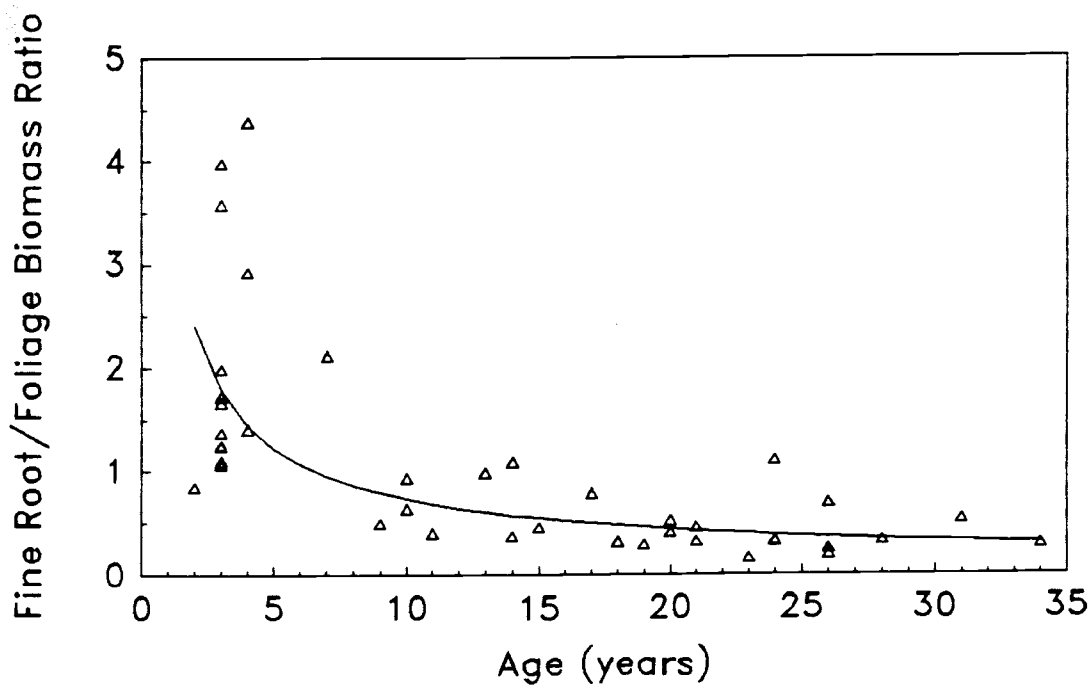


Figure 10. Fine root/foliage ratios for western juniper, age 2 to 34 years, with line of best fit from least squares regression.

Regressions

Regression constants were determined using both plant age and height as the independent variable (Table 2 and 3). Coefficients of determination, using log-log transformed data, ranged from 0.70 (coarse root length) to 0.92 (tap root biomass) for regressions on age (Table 2). The allometric relationships of age with root system depth and lateral extension showed a smaller relative error (1.33 and 1.96) than the more dynamic components of root system biomass (2.14-3.11), root system length (1.77-3.02), and shoot biomass (2.75-3.13). Within the root system, larger errors were associated with estimates of coarse roots (> 1 mm diam.) and lateral roots than of tap root and fine root characteristics, both in terms of biomass and length (Table 2). Within the canopy, the dynamic components of total foliage and juvenile foliage had the lowest accuracy (3.13 and 2.91). Regressions of adult foliage versus age, estimated from untransformed data, exhibited the lowest relative error (0.94) and the lowest coefficient of determination (0.46).

Relative errors of estimates and coefficients of determination for regressions with tree height as the independent variable indicate a better closeness of fit of observed versus estimated values (Table 3), compared to regressions against age (Table 2). Coefficients of determination for logarithmic height regressions mostly

Table 2. Relationships between tree components (y) and tree age (x).

Tree component y	N	Intercept a	Slope b	r ²	E, e	C.F.
Tap root depth (cm)	41	2.19	0.87	0.84	1.33	0.04
Lateral spread (cm)	41	-1.33	1.93	0.88	1.96	0.23
Tap root biomass (g)	40	-6.79	2.68	0.92	2.14	0.29
Lateral root biomass (g)	40	-7.70	3.14	0.88	2.99	0.60
Fine root biomass (g)	40	-5.85	2.30	0.87	2.25	0.33
Coarse root biomass (g), x ≥ 7	27	-10.47	4.12	0.71	3.11	0.64
Total belowground biomass (g)	40	-6.49	2.91	0.90	2.50	0.42
Tap root length (cm)	40	1.14	1.55	0.87	1.77	0.16
Lateral root length (cm)	40	-0.56	2.82	0.89	2.50	0.42
Fine root length (cm)	40	0.88	2.30	0.87	2.25	0.33
Coarse root length (cm), x ≥ 7	27	-4.91	3.87	0.70	3.02	0.61
Total root system length (cm)	40	0.73	2.44	0.88	2.28	0.34
Juvenile foliage biomass (g)	41	-6.77	2.70	0.85	2.91	0.57
Adult foliage biomass (g), x ≥ 17	18	-77.39	3.98	0.46	0.87	
Total foliage biomass (g)	41	-7.31	3.08	0.86	3.13	0.65
Structural biomass (g)	41	-8.53	3.41	0.91	2.77	0.52
Dead biomass (g)	41	-7.67	2.49	0.84	2.76	0.52
Total aboveground biomass (g)	41	-6.62	3.08	0.89	2.75	0.51
Total plant biomass (g)	40	-5.81	2.97	0.89	2.60	0.46
Height (cm)	41	-0.50	0.99	0.88	1.40	0.06

The regression model used was $\ln y = a + b \ln x$ for all variables except adult foliage biomass, which was analyzed with $y = a + bx$. Regression constants (a, b) and coefficients of determination (r²) are given as computed; estimates of relative errors (E for logarithmic regressions, e for linear regression) are listed in arithmetic units. Correction factors (C.F.) are given for each logarithmic regression.

Table 3. Relationships between tree components (y) and tree height (x).

Tree component y	N	Intercept a	Slope b	r ²	E, e	C.F.
Tap root depth (cm)	41	1.87	0.68	0.92	1.22	0.02
Lateral spread (cm)	41	-2.17	1.90	0.94	1.59	0.11
Tap root biomass (g)	40	-7.89	2.62	0.95	0.57	0.16
Lateral root biomass (g)	40	-9.16	3.13	0.95	1.20	0.24
Fine root biomass (g)	40	-6.92	2.29	0.95	1.68	0.14
Coarse root biomass (g), x ≥ 8.7	27	-9.31	3.21	0.90	1.93	0.22
Total belowground biomass (g)	40	-7.80	2.89	0.96	1.77	0.16
Tap root length (cm)	40	0.55	1.50	0.88	1.72	0.15
Lateral root length (cm)	40	-1.82	2.79	0.95	1.86	0.19
Fine root length (cm)	40	-0.20	2.29	0.95	1.68	0.14
Coarse root length (cm), x ≥ 8.7	27	-3.45	2.90	0.82	2.34	0.36
Total root system length (cm)	40	-0.40	2.43	0.95	1.67	0.13
Juvenile foliage biomass (g)	41	-8.09	2.70	0.95	1.85	0.19
Adult foliage biomass (g), x ≥ 14	18	-40.83	1.42	0.67	0.46	
Total foliage biomass (g)	41	-8.80	3.08	0.96	1.81	0.18
Structural biomass (g)	41	-9.90	3.31	0.95	2.10	0.27
Dead biomass (g)	41	-8.51	2.36	0.84	2.75	0.51
Total aboveground biomass (g)	41	-7.99	3.03	0.96	1.80	0.17
Total plant biomass (g)	40	-7.18	2.96	0.96	1.76	0.16
Age (years)	41	-0.18	0.89	0.88	1.38	0.05

The regression model used was $\ln y = a + b \ln x$ for all variables except adult foliage biomass, which was analyzed with $y = a + bx$. Regression constants (a, b) and coefficients of determination (r²) are given as computed; estimates of relative errors (E for logarithmic regressions, e for linear regression) are listed in arithmetic units. Correction factors (C.F.) are given for each logarithmic regression.

exceeded 0.90. Relative errors of estimates fell between 0.57 and 2.75, with most of the calculated values between 1.0 and 2.0. Allometric regression equations for root extension and biomass showed a higher relative accuracy (1.22-1.59 and 0.57-1.93) than equations for root length (1.67-2.34) and shoot biomass (1.79-2.75). Errors associated with estimates of root components were lowest for tap root biomass (0.57) and lateral root biomass (1.20), whereas those for coarse root dimensions were highest (1.93 and 2.34). Within the shoot, dead and structural biomass exhibited the least closeness of fit with relative errors of 2.75 and 2.1, respectively. Adult foliage had the lowest relative error (0.46), although the coefficient of determination was only 0.67.

Variation in the data set was closely related to the magnitude of the independent variables tree age and height. This type of variation was not evident from the generally high values of the coefficients of determination.

DISCUSSION AND CONCLUSIONS

In natural plant communities, competition is one of the most important influences on the growth of individual plants (Evans 1972). In semiarid environments, competition between plants of different species or between individuals of the same species is likely to involve some aspect of root competition. Root system structure and extension are major factors contributing to competitive withdrawal of water and mineral nutrients from the soil (Caldwell and Richards 1986).

The resistance of plants to desiccation is often a function of root penetration depth (Oppenheimer 1960). Rooting depth in western juniper averaged 20 cm during the initial years of development and increased to over 100 cm in trees older than 30 years. Western juniper appears to have a shallower root system than similar-aged woody species from moisture-limited environments (Table 4). The differences in rooting depth of the commonly associated western juniper, rabbitbrush, bitterbrush, and sagebrush are especially pronounced during the seedling stage. One year old rabbitbrush seedlings, excavated at a site with soils and climatic conditions similar to this study, had roots penetrating more than 76 cm deep (McKell 1956). A rooting depth of over 100 cm was reported for 1 year old bitterbrush plants (Hubbard 1957, Stanton 1959). Sagebrush roots from

Table 4. Rooting depth of shrubs and trees from moisture-limited environments.

Species	Age (yrs)	Rooting Depth (cm)	Reference
<i>Artemisia tridentata</i>	0.4	85	McKell 1956
	21-32	122-183	Tabler 1964
	28-42	122-213	Sturges and Trlica 1978
<i>Chrysothamnus naseousus</i>	0.4	105	McKell 1956
	1	>76	McKell 1956
<i>Chrysothamnus viscidiflorus</i>	0.4	56	McKell 1956
	1	>76	McKell 1956
<i>Juniperus osteosperma</i>	1-7	27-66	Phillips and Mulford 1912
<i>Pinus edulis</i>	1	15-22	Harrington 1987
<i>Pinus lambertiana</i>	1	36-61	Toumey 1926
<i>Pinus ponderosa</i>	1-4	15-66	Haasis 1921
<i>Purshia tridentata</i>	1	51-107	Hubbard 1957
	1	>100	Stanton 1959
	25-30	305-351	McConnell 1961

seedlings grown in a greenhouse attained 85 cm depth within 12 weeks (McKell 1956).

The difference in seedling rooting depth of semiarid species apparently does not account for their contrasting response to competition from herbaceous vegetation. Even though sagebrush, rabbitbrush, and bitterbrush have seedling root systems that penetrate beyond the zone where grass roots are most concentrated (Weaver 1915b), they experience high seedling mortality and suppressed growth rates in competition with annual and perennial grasses (Blaisdell 1949, Holmgren 1956, McKell 1956, Hubbard 1957, Eissenstat and Caldwell 1988b). In contrast, western juniper seedlings seem to be little or not at all affected by associated herbaceous species (Burkhard and Tisdale 1976) although their comparatively shallow roots must derive soil resources from the same level as native grasses. Factors other than rooting depth must be critical for survival and growth during the initial years of juniper establishment.

Western juniper developed both tap and lateral roots. Although the tap root was usually the most deeply penetrating root, lateral roots predominantly contributed to total root biomass and length once the seedlings were beyond their initial tap root phase (Fig. 6, Fig. 7). Most lateral roots originated from the upper 5-20 cm of the tap root (Fig. 3b) and were heavily concentrated in the area close to the crown (Fig. 4c). A dense lateral root system, largely

confined to the upper soil horizons, in combination with a deeper penetrating tap root appears to be useful for the exploration of an extensive soil volume. Fine lateral roots are likely to function primarily for nutrient and water uptake during periods of moisture availability in the topsoil. In addition, they could absorb moisture from light rains and thundershowers which only penetrates into the surface horizons of the soil. The tap root may serve primarily for water absorption from deeper soil layers, especially after moisture in the upper parts of the profile is depleted and during winter months, when the topsoil is frozen (Caldwell and Richards 1989).

Access to soil resources throughout the year in combination with the evergreen nature of juniper foliage could allow the species to grow and transpire year-round, once it is established on a site. Preemption of shared resource pools while herbaceous species are dormant, and the ability to use spatially unavailable moisture and nutrients, could explain the competitive advantage of western juniper over associated herbaceous species.

The structure of western juniper root systems beyond the tap root phase was similar to that described for mature big sagebrush from different habitats (Kearny et al. 1914, Robertson 1943, Tabler 1964, Sturges and Trlica 1978). Both species occupy approximately the same volume of soil and probably draw moisture and nutrients from the same soil

horizons. The similarities in sagebrush and juniper root systems suggest considerable belowground interference between closely spaced shrubs and trees. The increase in dead sagebrush on sites with abundant juniper saplings indicates significant belowground competition and a definite competitive advantage of western juniper. However, the positive and negative aspects of this relationship need to be tested.

Western juniper takes 20-30 years to develop root system extensions comparable to mature sagebrush plants (Fig. 3a, Tabler 1964, Sturges and Trlica 1978). During this period, seedling and sapling juniper appear to be little influenced by competition from sagebrush and are able to eventually gain dominance in established sagebrush stands.

The positive spatial association of most seedling and sapling western juniper with sagebrush (Burkhardt and Tisdale 1976, Eddleman 1987b) indicates that sagebrush may act as a nurse plant for juniper. A similar relationship is implied by enhanced survival of bitterbrush, shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.), and winterfat (*Eurotia lanata* (Pursh) Moq.) seedlings in the proximity of large individual shrubs (Nord 1965, Gasto 1969). The influence of nurse plants on seedling survival was extensively studied for the saguaro cactus (*Carnegiea gigantea* (Engelm.) Britt. & Rose) in Arizona (e.g. Turner et

al. 1966, Brum 1973, Steenbergh and Lowe 1977, Nobel 1980, Gibson and Nobel 1986). Saguaro seedlings commonly grow under the protective influence of palo verde trees (*Cercidium microphyllum* (Torr.) Rose & Johnston) or other perennial species. The positive effects of nurse plants on saguaro establishment mainly relate to the amelioration of temperature extremes in the seedling microenvironment.

The importance of favorable microclimatic conditions has been demonstrated for Utah juniper and oneseed juniper establishment (Meagher 1943, Johnson 1962). Recent research on nocturnal hydraulic lift in big sagebrush (Richards and Caldwell 1987, Caldwell and Richards 1989) indicates that associated western juniper seedlings might experience an improvement of the belowground microenvironment. Water absorbed by deeply penetrating sagebrush roots moves through the root system and is released in the upper soil horizon at night. Additional soil moisture available from hydraulic lift, in combination with decreased transpirational losses due to shading from sagebrush canopies, may be sufficient to sustain transpiration and growth in juniper seedlings during long drying cycles. A relatively short tap root with few weak laterals, as observed in this study, could be sufficient to secure enough moisture for the growing seedling. The juniper root system is located in the zone of highest sagebrush root concentration (Sturges and Trlica 1978, Richards and Caldwell 1987) and therefore in the zone

where moisture from hydraulic lift is likely to be most abundant.

During the tap root phase, juniper seedlings probably exert little influence on associated sagebrush. However, the decreasing vigor of sagebrush individuals adjacent to juniper saplings is an indication of mounting competition for limited resources between the two species as western juniper grows.

The continuous expansion of juniper roots and shoots results in an increasing demand for water, mineral nutrients, and energy. To maximize the uptake of water and minerals, the investment of a high proportion of biomass into roots appears advantageous. However, in young western juniper low root/shoot ratios (Fig. 9) and the consistently high contribution of foliage to total tree biomass with age (Fig. 8) suggest that other strategies operate.

As juniper seedlings grow, the relative amount of biomass allocated to the root system and shoot appears to decline (Fig. 9). However, the dominant allocation pattern in the root system shifted from the tap root to fine lateral roots once root systems entered their second phase of development (Fig. 6 and Fig. 7). An extensive fine lateral root system located in the upper soil layers probably represents a minimal cost both in terms of construction and maintenance while providing maximum nutrient and water absorbing capacity for western juniper.

In contrast to other evergreen species of the same age range (Chew and Chew 1965, Ovington 1957), western juniper is capable of maintaining foliage biomass as the largest fraction of total standing weight throughout its seedling and juvenile growth periods. With age, newly initiated juniper foliage gradually changes from juvenile to more xeromorphic, adult characteristics. High relative foliar biomass of increasingly xeromorphic nature probably allows a gradual enhancement of photosynthate production with minimal water loss.

The period of major changes in root system structure and foliage morphology coincided with a significant decrease in the fine root/foliage biomass ratio (Fig. 10). This decrease may be a reflection of an improvement of the overall resource use efficiency and performance of the developing plant. The improvement is likely to result from changes in morphological, structural, and physiological characteristics and their interactions in western juniper seedlings and saplings as they progress through their first two phases of development. This initial period of change was followed by a phase where major structural and functional patterns were maintained (Fig. 6, Fig. 7, Fig 10). The relatively constant root/shoot ratio throughout the observation period did not reflect the dynamic nature of western juniper growth and development.

During the period of development beyond the tap root phase, the association with sagebrush may have further implications for successful growth. If in fact hydraulic lift by sagebrush results in available moisture for juniper seedlings and if the amount of water proves to be significant, water supplied from hydraulic lift for juniper water status can be expected to decrease. However, the additional moisture may allow western juniper to maintain an extensive fine root system during short-term droughts, and resume belowground activities with the onset of favorable growing conditions. Improved survival of fine roots during short drought periods probably increases the overall efficiency of young western juniper by reducing root replacement costs. Hydraulic lift promotes soil nutrient mineralization and absorption by roots (Richards and Caldwell 1987) and is therefore likely to improve the nutrient status of western juniper seedlings and saplings.

Sagebrush concentrates nutrients from a large soil volume in the upper soil horizons under the crown (Doescher et al. 1984). Western juniper growing in the proximity of sagebrush probably absorbs and incorporates large amounts of these nutrients into long lived tissues. This continuous mining and immobilization of nutrients otherwise available may deprive sagebrush of a critical resource base and probably results in reduced nutrient turnover and acquisition costs for western juniper.

Structural changes of western juniper observed in this study, in combination with possible functional changes and environmental modifications due to sagebrush, may improve the competitive ability of western juniper and eventually exclude sagebrush from the site. However, the adaptive significance of structural development and biomass allocation patterns in young western juniper cannot be fully explained by the analysis of a limited data set from one study site. Growth patterns of juniper must be examined relative to its whole autecology, the nature of associated species, abiotic factors of the environment, and the interactions and changes of all these factors through time. Additional research is necessary to identify how and to what degree individual factors affect the observed overall trend and variability in growth and allocation patterns.

The regression equations developed in this study can be used to estimate age, total biomass, and biomass of aboveground and belowground components of western juniper from simple height measurements. The use of regression equations results in a reduction of effort and expense to sample and predict biomass, productivity, and age of individual plants and whole communities.

The study of competition and nutrient cycling in natural vegetation requires information on biomass and the structure and extension of root systems. The results of root biomass and length analysis show that it is possible to

predict the extension, length, and total biomass of the component parts of western juniper root systems from height measurements and age.

The description of growth patterns in combination with the developed regression relationships offer a generalized working model for western juniper seedling growth and development. A full extrapolation of the results of this study to other western juniper communities of the same age range in central Oregon or elsewhere will require verification with similar data sets from other sites. However, even without such information, the described growth patterns and relationships can be used as a preliminary model for the study of western juniper. Hopefully, future research will help to elucidate and explain more aspects of western juniper growth and help to develop a more complete picture of the ecology of this species in its natural environment.

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APPENDICES

Appendix 1. Soil profile descriptions.

Profile 1.

Classification: Aridic Haploxeroll, coarse-loamy, mixed, mesic.

Soil type: Redcliff

Location: Deschutes County, Oregon. 44° 16' 48" latitude north, 121° 20' 30" longitude west; T14S, R12E, Sec. 18.

Topography: Sloping.

Drainage: Well drained.

Vegetation: Western juniper woodland.

Parent material: Mazama ash over older ash over non-welded tuff.

Described by: Soil Conservation Service, Bend, Oregon. 1987.

Horizon	Depth (cm)	Description
A1	0 - 5	brown (10YR 5/3) dry; dark brown (10YR 3/3) wet; sandy loam; moderate thin platy structure; soft, very friable, nonsticky and nonplastic; many very fine and fine roots; many very fine irregular pores; pH 6.4; abrupt smooth boundary.
A2	5 - 40	brown (10YR 5/3) dry; dark brown (10YR 3/3) wet; sandy loam; weak fine subangular blocky structure; soft, very friable, nonsticky and nonplastic; common fine and medium roots, few very fine roots; many very fine irregular pores; pH 7.5; clear wavy boundary.
Bw	40 - 84	light yellowish brown (10YR 6/4) dry; dark yellowish brown (10YR 3/4) wet; sandy loam; moderate fine and medium subangular blocky structure; slightly hard, friable, nonsticky and nonplastic; few very fine, fine, and medium roots; many very fine irregular and few fine tubular pores; pH 7.5; clear wavy boundary.
Cr	84+	nonwelded tuff, paralithic contact, discontinuous opal capping and pediments on underside, roots between layers in tuff.

Appendix 1. continued.

Profile 2.

Classification: Aridic Haploxeroll, loamy-skeletal, mixed, mesic.

Soil type: Redcliff

Location: Deschutes County, Oregon. 44° 16' 48" latitude north, 121° 20' 30" longitude west; T14S, R12E, Sec. 18.

Topography: Sloping.

Drainage: Well drained.

Vegetation: Western juniper woodland.

Parent material: Mazama ash over older ash over non-welded tuff.

Described by: Soil Conservation Service, Bend, Oregon. 1987.

Horizon	Depth (cm)	Description
A1	0 - 8	brown (10YR 5/3) dry; very dark grayish brown (10YR 3/2) wet; sandy loam; weak very fine granular structure; loose, nonsticky and nonplastic; many very fine roots; many very fine irregular pores; pH 6.4; clear smooth boundary.
A2	8 - 33	brown (10YR 5/3) dry; very dark grayish brown (10YR 3/2) wet; sandy loam; weak medium and coarse subangular blocky structure; soft, very friable, nonsticky and nonplastic; few very fine and fine roots, many medium roots; common very fine irregular pores; pH 7.2; clear wavy boundary.
Bw	33 - 64	light yellowish brown (10YR 6/4) dry; dark yellowish brown (10YR 3/4) wet; very cobbly sandy loam; moderate medium and coarse subangular blocky structure; slightly hard, very friable, nonsticky and nonplastic; few very fine and fine roots; many very fine tubular pores; pH 7.6; clear wavy boundary.
Cr	64+	highly fractured tuff to 81 cm, then unweathered tuff.

Appendix 1. continued.

Profile 3.

Classification: Aridic Haploxeroll, loamy-skeletal, mixed, mesic.

Soil type: Redcliff

Location: Deschutes County, Oregon. 44° 16' 48" latitude north, 121° 20' 30" longitude west; T14S, R12E, Sec. 18.

Topography: Sloping.

Drainage: Well drained.

Vegetation: Western juniper woodland.

Parent material: Mazama ash over older ash over non-welded tuff.

Described by: Soil Conservation Service, Bend, Oregon. 1987.

Horizon	Depth (cm)	Description
A1	0 - 5	brown (10YR 5/3) dry; dark brown (7.5YR 3/2) wet; sandy loam; moderate very fine and fine platy subangular blocky structure; soft, very friable, nonsticky and nonplastic; few very fine roots; many very fine irregular pores; pH 6.6; clear smooth boundary.
A2	5 - 41	brown (10YR 5/3) dry; dark brown (10YR 3/3) wet; sandy loam; weak fine and medium subangular blocky; soft, very friable, nonsticky and nonplastic; common very fine and fine roots, few medium roots; many very fine irregular pores; pH 7.4; clear wavy boundary.
Bw	41 - 66	light yellowish brown (10YR 6/4) dry; dark brown (10YR 3/3) wet; very cobbly sandy loam; moderate medium coarse subangular blocky; hard, very friable, nonsticky and nonplastic; moderate very fine roots; many very fine irregular pores; pH 7.6; clear wavy boundary.
Cr	66+	highly fractured tuff to 91 cm, then unweathered tuff.

Appendix 2. Root system extensions and lengths by age classes.

		Age Class (yrs)						
		< 6	6-10	11-15	16-20	21-25	26-30	> 30
Rooting Depth (cm)	N	14	4	5	5	6	4	3
	Mean	19.9	37.4	43.3	63.8	91.8	101.5	107.7
	SEM	0.8	6.7	0.9	7.5	8.2	11.3	5.5
	min	17.0	19.6	40.0	46.0	62.0	76.0	97.0
	max	25.3	51.0	45.0	82.0	120.0	130.0	115.0
Lateral Spread (cm)	N	14	4	5	5	6	4	3
	Mean	2.9	13.1	39.6	83.0	153.8	183.4	239.0
	SEM	0.6	5.8	9.6	14.3	24.3	12.0	23.1
	min	1.0	4.0	15.0	40.0	85.0	153.0	212.0
	max	10.5	29.0	72.5	124.3	225.0	210.5	285.0
Tap Root (<1 mm) (cm)	N	14	4	5	5	6	4	2
	Mean	21.0	36.5	65.6	46.0	125.1	13.7	214.9
	SEM	2.3	15.0	14.8	16.0	75.0	11.9	21.8
	min	4.0	7.1	28.5	15.1	0	0	193.1
	max	37.1	64.4	114.1	94.2	489.3	49.3	236.7
Tap Root (≥1 mm) (cm)	N	14	4	5	5	6	4	3
	Mean	0.5	25.3	145.2	262.8	375.1	563.1	679.4
	SEM	0.3	6.7	36.9	49.5	71.6	149.4	186.9
	min	0	13.4	32.6	171.4	213.5	373.0	469.2
	max	4.8	40.4	239.6	447.6	615.5	1008.3	1052.2
Lateral Roots (<1 mm) (cm)	N	14	4	5	5	6	4	2
	Mean	21.2	131.0	695.9	2101.3	4406.6	8221.0	14617.4
	SEM	5.0	52.2	147.1	504.8	706.5	3686.5	7097.3
	min	4.6	24.3	358.4	709.8	1561.2	2355.1	7520.2
	max	74.5	256.7	1113.6	3817.7	6691.4	19007.0	21714.7

Appendix 2. continued.

		Age Class (yrs)						
		< 6	6-10	11-15	16-20	21-25	26-30	> 30
Lateral Roots (≥ 1 mm) (cm)	N	14	4	5	5	6	4	3
	Mean	0	0	50.0	198.5	1289.2	3200.5	6902.7
	SEM	0	0	37.0	72.7	255.5	1318.7	2944.0
	min	0	0	0	41.6	344.0	1045.7	2195.2
	max	0	0	195.4	439.8	2220.6	6854.4	12319.2
Tap Root Total (cm)	N	14	4	5	5	6	4	2
	Mean	21.5	61.8	210.8	308.8	500.2	576.8	999.5
	SEM	2.5	21.5	37.2	55.4	133.7	144.9	245.8
	min	4.6	21.6	77.3	201.0	213.5	414.3	753.7
	max	41.9	100.5	299.8	521.7	1053.0	1010.6	1245.3
Lateral Roots Total (cm)	N	14	4	5	5	6	4	2
	Mean	21.2	131.0	745.8	2299.9	5695.8	11421.5	18811.9
	SEM	5.0	52.2	176.3	554.0	958.7	4951.1	9096.5
	min	4.6	24.3	358.4	751.4	1905.2	3400.8	9715.4
	max	74.5	256.7	1309.0	4103.9	8912.0	25861.5	27908.4
Fine Roots Total (cm)	N	14	4	5	5	6	4	2
	Mean	42.2	167.5	761.4	2147.4	4531.7	8234.6	14832.4
	SEM	6.7	65.8	141.4	519.0	658.7	3683.6	7075.5
	min	16.9	38.7	403.1	724.9	2050.4	2358.1	7756.9
	max	111.6	316.8	1173.8	3912.0	6782.7	19009.4	21907.8
Coarse Roots Total (cm)	N	14	4	5	5	6	4	3
	Mean	0.5	25.3	195.2	461.3	1664.3	3761.2	7571.5
	SEM	0.3	6.7	68.8	112.7	253.4	1450.2	2909.5
	min	0	13.4	32.6	227.5	907.7	1457.1	2712.1
	max	4.8	40.4	435.0	887.4	2585.9	7852.7	12773.4

Appendix 2. continued.

		Age Class (yrs)						
		< 6	6-10	11-15	16-20	21-25	26-30	> 30
	N	14	4	5	5	6	4	2
Root System Total (cm)	Mean	42.7	192.8	956.6	2608.7	6196.0	11998.3	19811.4
	SEM	7.0	72.5	206.0	574.7	907.2	5092.8	9342.4
	min	16.9	52.1	435.7	952.4	2958.2	3815.1	10469.0
	max	116.3	357.2	1608.8	4369.4	9368.6	26872.1	29153.8

Appendix 3. Whole tree biomass distributions by age classes.

		Age Class (yrs)						
		< 6	6-10	11-15	16-20	21-25	26-30	> 30
Age (yrs)	N	14	4	5	5	6	4	3
	Mean	3.1	9.0	13.4	18.8	22.8	26.5	33.0
	SEM	0.1	0.7	0.7	0.6	0.6	0.5	1.0
	min	2	7	11	17	21	26	31
	max	4	10	15	20	24	28	34
Height (cm)	N	14	4	5	5	6	4	3
	Mean	5.3	10.6	26.7	29.0	40.6	46.0	62.3
	SEM	0.3	1.1	4.2	4.7	6.9	5.2	10.7
	min	3.9	8.7	16.5	14.5	19.0	34.5	41.0
	max	7.7	13.5	41.5	39.0	64.0	59.5	75.0
Juvenile Foliage (g)	N	14	4	5	5	6	4	3
	Mean	0.03	0.20	4.12	4.85	9.04	13.11	11.34
	SEM	0.01	0.08	2.17	1.51	3.22	4.02	3.44
	min	0.01	0.09	0.44	0.36	0.41	6.75	4.59
	max	0.10	0.45	12.14	8.44	23.51	23.49	15.87
Adult Foliage (g)	N	14	4	5	5	6	4	3
	Mean	0	0	0	4.08	9.34	20.33	61.49
	SEM	0	0	0	2.37	3.74	15.62	27.77
	min	0	0	0	0	0	0	7.89
	max	0	0	0	10.19	18.09	66.92	100.92
Foliage Total (g)	N	14	4	5	5	6	4	3
	Mean	0.03	0.20	4.12	8.92	18.37	33.44	72.83
	SEM	0.01	0.08	2.17	3.77	6.45	19.26	30.90
	min	0.01	0.09	0.44	1.02	1.08	6.75	12.48
	max	0.10	0.45	12.14	18.15	41.33	90.41	114.48

Appendix 3. continued.

		Age Class (yrs)						
		< 6	6-10	11-15	16-20	21-25	26-30	> 30
Structural Tissue (g)	N	14	4	5	5	6	4	3
	Mean	0.01	0.16	2.61	6.14	15.27	24.05	66.33
	SEM	0	0.04	1.43	2.47	5.89	11.60	27.61
	min	0	0.08	0.44	1.07	1.50	5.01	11.12
	max	0.04	0.25	8.08	13.36	38.76	57.66	94.90
Dead Tissue (g)	N	14	4	5	5	6	4	3
	Mean	0.01	0.05	0.46	0.90	2.25	4.48	3.98
	SEM	0	0.01	0.27	0.41	0.57	2.56	2.89
	min	0	0.03	0.09	0.35	0.55	0.61	0.41
	max	0.03	0.09	1.51	2.51	3.49	11.83	9.70
Aboveground Total (g)	N	14	4	5	5	6	4	3
	Mean	0.06	0.42	7.19	15.97	35.89	61.97	143.14
	SEM	0.01	0.12	3.87	6.49	12.79	33.36	59.51
	min	0.01	0.22	0.97	2.44	3.13	12.37	25.42
	max	0.14	0.74	21.73	34.02	83.58	159.91	217.17
Fine Roots (<1 mm) (g)	N	14	4	5	5	6	4	2
	Mean	0.05	0.20	1.77	3.03	5.09	9.41	16.48
	SEM	0.01	0.08	0.75	1.00	1.37	4.56	9.79
	min	0.02	0.05	0.48	0.80	1.19	2.83	6.69
	max	0.13	0.38	4.48	5.64	9.30	22.80	26.28
Coarse Roots (≥1 mm) (g)	N	14	4	5	5	6	4	3
	Mean	0	0.19	3.13	9.04	18.40	28.71	78.88
	SEM	0	0.05	1.86	4.18	6.02	15.58	32.33
	min	0	0.10	0.24	1.56	1.48	5.02	20.31
	max	0.03	0.30	10.39	22.40	37.73	74.41	131.89

Appendix 3. continued.

		Age Class (yrs)						
		< 6	6-10	11-15	16-20	21-25	26-30	> 30
Tap Root (g)	N	14	4	5	5	6	4	3
	Mean	0.03	0.23	1.52	3.01	8.10	10.98	24.02
	SEM	0	0.07	0.52	0.80	2.05	4.63	14.67
	min	0.01	0.11	0.29	1.37	1.41	3.04	9.35
	max	0.08	0.37	3.34	5.28	13.00	24.22	38.69
Lateral Roots (g)	N	14	4	5	5	6	4	2
	Mean	0.03	0.16	3.39	9.05	15.39	27.14	44.84
	SEM	0.01	0.06	2.10	4.33	5.28	15.48	27.20
	min	0.01	0.03	0.43	0.99	1.26	6.67	17.64
	max	0.09	0.31	11.53	22.34	31.30	72.99	72.03
Belowground Total (g)	N	14	4	5	5	6	4	2
	Mean	0.05	0.39	4.91	12.07	23.49	38.12	68.86
	SEM	0.01	0.13	2.60	5.12	7.25	20.07	41.86
	min	0.02	0.14	0.72	2.36	2.68	9.71	26.99
	max	0.17	0.68	14.87	27.62	44.29	97.21	110.72
Tree Total (g)	N	14	4	5	5	6	4	2
	Mean	0.11	0.80	12.10	28.04	59.38	100.08	174.99
	SEM	0.02	0.23	6.46	11.60	19.89	53.42	122.57
	min	0.03	0.37	1.69	4.80	5.80	22.08	52.42
	max	0.28	1.27	36.60	61.64	127.87	257.12	297.56