Xylem root and shoot hydraulics is linked to life history type in chaparral seedlings

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Summary

1. Shrubs in fire prone chaparral communities have evolved different life history types in response to fire. A key to understanding the evolution of life history type differences is to understand how physiological traits are linked to differences in life history type. Vascular adaptations are important for delivering an efficient and stable water supply to evergreen chaparral shrub leaves. This study tested for a link between vascular physiology and life history type in chaparral shrubs.

2. Chaparral shrub species along the south-western coast of North America survive wildfire by three different life histories. Non-sprouters are killed by fire and re-establish exclusively through germination of fire-stimulated seeds, facultative sprouters re-establish by a combination of vegetative sprouting and fire-stimulated seeds, and obligate sprouters re-establish exclusively by vegetative sprouting because their seeds do not survive fire. Non-sprouters and facultative sprouters establish seedlings in the open canopy post fire environment, whereas obligate sprouters establish seedlings in the shady understory of the mature chaparral canopy.

3. Seedlings of nine species (Rhamnaceae) representing three each of the different life history types were grown in deep containers in a common garden under treatments of sun and shade. Hydraulic conductance was measured using a high-pressure flow meter for all organs, and a vacuum technique was used to measure conductance of fine and woody roots. We predicted that non-sprouters would exhibit greater hydraulic efficiency than the sprouting species, and that facultative sprouters would be more efficient than the shade tolerant obligate sprouters.

4. Non-sprouters had the greatest hydraulic conductance per unit leaf and sapwood area at the whole seedling level, whereas facultative and obligate sprouters were not different. Comparing hydraulic conductance across major organs (from fine roots to leaves) showed that the hydraulic system was well coordinated. At the whole seedling level, the root system was more of a bottleneck than the shoot system. This pattern was consistent with high resistance extraxylary pathways in roots and differences in root architecture.

5. The greater hydraulic efficiency of the non-sprouter life history type is attributed to its post-fire pioneering habit and may partially explain the relatively high speciation in the non-sprouters. Lower hydraulic efficiency is associated with a sprouting life history and greater shade tolerance. The seedling root systems represent a hydraulic bottleneck that may place roots under especially intense selection.

Key-words: *Ceanothus*, drought, fire, hydraulic conductance, non-sprouting, *Rhamnus*, roots, sprouting

Introduction

The Mediterranean-type ecosystems of California, South Africa, south-western Australia, and the Mediterranean Basin are hotspots of vascular plant biodiversity (Cowling *et al*. 1996; Myers *et al*. 2000; Latimer, Silander & Cowling 2005). One factor contributing to the high biodiversity of shrubs is the evolution of life history differences (Ojeda, Brun & Vergara 2005; Verdú *et al*. 2007). In the fire-prone Mediterranean-type shrublands, many woody plant lineages

have evolved from a post-fire sprouting ancestral life history type to a non-sprouting post-fire seeder life history (Wells 1969; Hardig, Soltis & Soltis 2000), whereas other lineages appear to have repeatedly lost or gained sprouting ability (Bond & Midgley 2003). A key to understanding the evolution of life history type differences is to understand how physiological traits are linked to life history type differences.

The present study examines hydraulic transport of chaparral shrub seedlings representing three life history types. The first is a shade intolerant non-sprouter (NS; also called a seeder) that recruits seedlings in open canopy post-fire environments from a dormant seed bank cued to germinate by fire. The second is a facultative sprouter (FS; also called facultative seeder) that regenerates by post-fire sprouting and seed germination. The third is an obligate sprouter (OS) that exclusively regenerates by resprouting after fire, and recruits seedlings from short-lived, non-refractory seeds in the mature and shaded chaparral understory between fire events. The seedling microclimate differs widely between the life history types. Seedlings of NS and FS recruit exclusively post-fire, in nutrient-rich charred soils, devoid of leaf litter, experiencing high radiation and thermal loads but reduced competition with adults after canopy removal by fire. In contrast, seedlings of OS recruit exclusively in deep shade of pre-fire adults, in soils having substantial leaf litter, where seedlings are in competition with closed-canopy adults but where solar radiation, wind, and thermal loads are greatly reduced. In the present study, we sought to test the hypothesis that seedling hydraulics is linked to life history type. We predicted that NS and FS species would display more efficient xylem than the OS species consistent with the post-fire pioneering habit of the NS and FS species and the higher degree of shade tolerance of the OS species (the OS have greater survival in the shade than the FS and NS; Pratt *et al.* 2008). The NS species were predicted to have the most efficient water transport system to facilitate the rapid establishment of seedlings in post-fire open canopy sites prior to the onset of the protracted summer rainless period characteristic of southern California Mediterranean-type climate regions (Cowling *et al.* 2005).

The focus on vascular physiology is justified because water uptake, transport, and use are key physiological processes in the survival and function of evergreen chaparral shrubs (Davis & Mooney 1986; Jacobsen *et al.* 2007a,b; Pratt *et al.* 2007). Xylem hydraulic traits are thought to exhibit key adaptations that allow chaparral species to endure 6 to 8 rainless months each growing season (Kolb & Davis 1994; Davis *et al.* 2002; McDowell *et al.* 2008; Pratt *et al.* 2008). This is especially true for newly germinated seedlings that, with only limited time for root development, must survive a protracted summer dry season aggravated by high radiation and thermal loads in charred post-fire soils (Thomas & Davis 1989). The seedling stage often suffers high mortality and is a critical bottleneck, yet less is known about seedling transport systems than those of adults (but see Williams, Davis & Portwood 1997, Kavanagh *et al.* 1999; Tyree *et al.* 2002; Kursar *et al.* 2009). Hydraulic traits may differ more widely at the seedling stage than at any other time during the life cycle of chaparral species due to dramatic differences in seedling microclimate for the three divergent NS, FS, and OS life history types. By contrast, post-fire resprouts experience less frequent mortality than seedlings and selective pressures and competition for limited resources are relaxed in the post-fire environment (Frazer & Davis 1988; Saruwatari & Davis 1989; Thomas & Davis 1989).

Gas exchange and growth can be limited by hydraulic efficiency (Mencuccini and Comstock 1999, Sobrado 2000, Salleo *et al.* 2001). Liquid phase hydraulic efficiency of flowering plants is determined by many factors. In the roots and leaves there are extraxlary pathways where water traverses lipid membranes to enter or exit the xylem, respectively that can be largely controlled by aquaporins (North, Martre & Nobel 2004, Nardini, Salleo & Andri 2005). There are also extraxylary paths between cells. Once water enters the xylem, transport efficiency is determined by vessel dimensions (diameter and length) and the connectivity of the vessel network (Loepfe *et al.* 2007), as well as by pit conductance (Wheeler *et al.* 2005; Choat, Cobb & Jansen 2008). Finally, vapour phase conductance is controlled by guard cells. All of the variables affecting hydraulic efficiency can be adjusted to maintain a high degree of efficiency and to minimize the risk of hydraulic failure. Few studies have examined all the organ components of the hydraulic pathway to evaluate how they scale with whole plant conductance. Most work on hydraulic transport of woody plants has been conducted on lateral stems or branches.

In the present study, we examine hydraulic conductance at multiple points along the transport pathway to evaluate the degree of coordination throughout the pathway and to identify possible bottlenecks. We investigated the hydraulics of different life history types by growing even-aged seedlings of all three life history types in a common garden in uniform soil, without competition from other plant species, in shade and in full sun. Such experiments would be impossible to conduct on field plants because NS and FS seedlings only recruit post-fire whereas OS seedlings only recruit during fire free intervals. In addition to the hypothesis linking hydraulics and life history types, we hypothesized that roots and leaves, with their symplastic and extraxylary pathways, would be the chief bottlenecks in the plant hydraulic network regardless of life history.

Materials and methods

SITE AND PLANTS

Seeds were collected from naturally occurring populations of nine shrub species in the family Rhamnaceae (Table 1; Hickman 1993) at three sites in the Santa Monica Mountains in Los Angeles County, California, USA (described in Pratt *et al.* 2007). Approximately 1500 seedlings were grown in custom-crafted deep containers (1·2 m tall and 250 mm wide; Blue-X Enterprises Inc., Elk Grove, CA, USA) in a common garden located at Pepperdine University, Malibu, California, USA, in a randomized complete block design either in full sun or under shade cloth (25% of full sun). Plants were irrigated to keep their

Table 1. Species studied, abbreviations, xylem specific hydraulic conductance (k_s), and hydraulic mean vessel diameter at the stem/root junction for seedlings grown in sun (white columns) and shade (grey columns) treatments

Life history type and species	Abbreviations	Sun k_s roots (kg s^{-1} MPa^{-1} m^{-2})	Shade k_s roots (kg s^{-1} MPa^{-1} m^{-2})	Sun k_s shoot (kg s^{-1} MPa^{-1} m^{-2})	Shade k_s shoot (kg s^{-1} MPa^{-1} m^{-2})	Sun k_s stems (kg s^{-1} MPa^{-1} m^{-2})	Shade k_s stems (kg s^{-1} MPa^{-1} m^{-2})	Sun Vessel Diameter (µm)	Shade Vessel Diameter (µm)
Non-sprouter average	NS	0·87^A (0·05)	1·83^{A*} (0·08)	1·02^A (0·08)	2·72^{A**} (0·26)	1·77^A (0·16)	4·40^{A*} (0·36)	23·41^{AB} (1·14)	22·82^A (1·28)
Subgenus *Cerastes*									
Ceanothus megacarpus Nutt.	Cm	0·80^a (0·12)	1·95^{a*} (0·45)	0·88^{ab} (0·21)	2·40^{ac} (0·39)	1·79^a (0·37)	3·88^{ab*} (0·43)	25·69^{ab} (1·28)	25·25^{ab} (0·60)
C. crassifolius Torrey	Ccr	0·84^a (0·21)	1·85^{a*} (0·33)	1·17^a (0·17)	3·24^a (0·53)	2·03^a (0·31)	5·10^{a*} (0·94)	22·27^{ac} (1·12)	20·94^{ac} (1·50)
C. cuneatus (Hook.) Nutt.	Ccu	0·98^a (0·18)	1·68^a (0·30)	1·00^{ab} (0·16)	2·51^{ac} (0·73)	1·48^a (0·11)	4·24^{ab*} (1·28)	22·27^{ac} (0·63)	22·27^{ab} (0·76)
Facultative sprouter average	FS	0·51^A (0·13)	0·89^B (0·26)	0·63^{AB} (0·08)	1·19^B (0·19)	1·08^A (0·13)	1·49^B (0·34)	28·36^A (2·05)	27·75^A (0·92)
Subgenus *Ceanothus*									
C. spinosus Nutt.	Cs	0·44^a (0·10)	0·57^b (0·17)	0·48^{ab} (0·13)	0·98^b (0·35)	0·82^{ab} (0·19)	1·13^c (0·41)	26·26^{ab} (1·33)	29·08^b (1·60)
C. oliganthus Nutt.	Co	0·32^a (0·07)	0·67^{ab*} (0·13)	0·75^{ab} (0·09)	1·01^{bc} (0·19)	1·22^{ab} (0·22)	1·16^{bc} (0·23)	32·47^b (3·05)	28·20^b (2·73)
C. leucodermis E. Greene	Cl	0·78^a (0·20)	1·42^{ab} (0·50)	0·65^{ab} (0·07)	1·59^{ab} (0·42)	1·19^{ab} (0·08)	2·18^{abc} (0·66)	26·36^{ab} (1·44)	25·98^{ab} (1·50)
Obligate sprouter average	OS	0·61^A (0·03)	0·92^B (0·21)	0·62^B (0·13)	1·42^{B**} (0·14)	1·08^A (0·32)	2·53^{AB*} (0·55)	19·66^B (2·27)	21·17^A (3·33)
Rhamnus ilicifolia Kellog	Ri	0·69^a (0·12)	0·81^{ab} (0·27)	0·84^{ab} (0·18)	1·69^{ab} (0·45)	1·64^a (0·27)	3·63^{ab*} (0·73)	18·81^{cd} (1·32)	19·72^a (0·41)
R. californica Eschsch	Rca	0·58^a (0·16)	1·33^{ab**} (0·30)	0·36^b (0·06)	1·36^{ab} (0·37)	0·53^b (0·17)	2·14^{abc***} (0·82)	23·95^a (1·93)	27·52^{ab*} (0·52)
R. crocea Nutt.	Rcr	0·56^a (0·23)	0·62^{ab} (0·14)	0·64^{ab} (0·12)	1·20^{ab} (0·29)	1·08^{ab} (0·19)	1·81^{abc} (0·44)	16·23^d (0·49)	16·25^c (0·66)

Data shown are means ($N = 6$) with 1 standard error in parentheses. Within a column, means followed by the same letter are not different, whereas those with unique letters are different. Upper case letters are comparisons among life history type, lower case letters are among species within each life history category. Asterisks in the shade columns denote instances where sun and shade treatments were different for life history type comparisons (* = $P < 0.10$; ** = $P < 0.05$) and for species comparisons (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

water potential in a range typical of field conditions during the wet winter months (Pratt *et al.* 2008). The climate in the study area is Mediterranean-type with hot and dry summers and cool wet winters. For full growing information on the common garden see Pratt *et al.* (2008).

PLANT HYDRAULIC CONDUCTANCE AND SIZE

Hydraulic conductance of seedlings ($N = 6$ per species and treatment) was measured using a high-pressure flow meter (HPFM, Dynamax, Houston, TX, USA). Seedlings were watered at least one day prior to measurements to reduce complications due to embolism (Tyree *et al.* 1995). Based on predawn water potential measurements, we determined that one day sufficed for the seedlings to rehydrate fully. Measurements were made in the field starting at about 09:00 h. Shoots were cut underwater and placed in a large sealed bag with a moistened paper towel. The HPFM was immediately attached to the root stump at the soil level to measure root system conductance. Measurements were made rapidly in the transient mode to minimize errors associated with protracted measurements of roots (Tyree *et al.* 1995). Briefly, a water-filled tube was connected to a stump, pressure was applied at a rate of about 5–10 kPa s^{-1}, and the flow rate through a calibrated tube was plotted against the applied pressure. From 0–100 kPa, the plot tended to be non-linear, and at higher pressures the response was linear. Hydraulic conductance was calculated from the slope of the linear region. At least three measurements were made in < 8 minutes, and measurements were averaged. The temperature of the perfusion solution was monitored to correct for viscosity effects and the equipment was shaded to minimize thermal effects. Shoots were transported to a climate-controlled laboratory adjacent to the common garden study site for sampling. Shoots were measured in the same fashion as roots except they were measured initially with leaves, and subsequently after leaf removal. This allowed us to assess the hydraulic conductance of the root system, shoot system, leaves, and stems separately. Hydraulic conductance was measured on 2–6 plants per day.

Prior to sampling, maximum plant height (h) and crown diameter (d) and main stem diameter at the soil surface were measured. The crown volume was calculated for plants using the equation for the volume of a cone for all NS and *R. ilicifolia*.

$$\text{Volume} = (\pi d^2 h)/12 \tag{1}$$

The equation for a parabolic cone was used as a closer approximation for all FS and *R. californica* and *R. crocea*.

$$\text{Volume} = (\pi d^2 h)/8 \tag{2}$$

Whole plant hydraulic conductance (k_h plant) was calculated from the inverse of the sum of the root and shoot hydraulic resistance. Xylem cross-sectional area, at the point where the HPFM was attached, was used as a denominator in k_h measurements to yield xylem specific hydraulic conductance (k_s). After measurements, a portion of the leaf area was measured (Li-3000, Li-Cor, Lincoln, NB, USA) and then oven-dried along with the rest of the plants. The leaf biomass was measured separately, which allowed us to convert from biomass to leaf area of the whole plant. Leaf area was used to divide whole plant, shoot, and leaf k_h to give leaf specific hydraulic conductance (k_l).

HYDRAULIC CONDUCTANCE OF ROOT AND STEM SEGMENTS

Root hydraulic conductance (L_p; m s^{-1} MPa^{-1}) and its radial (L_r; m s^{-1} MPa^{-1}) and axial (through the xylem; k_h; m^4 s^{-1} MPa^{-1}) components were investigated for fine roots, both young and woody, from sun- and shade-grown plants of three species, *C. crassifolius* (NS), *C. spinosus* (FS), and *R. californica* (OS). For 4–6 plants from each species and light level, intact root systems were accessed by laying the plants while still in their containers on their sides and opening the containers along their longitudinal seams. Individual roots were removed from the loosened soil, wrapped in moist paper towels, and transported in sealed plastic bags to the laboratory. Two regions were sampled for each root: the white, unbranched segment including the root tip, identified as a young root, and the older woody segment approximately 20–30 cm proximal to the tip, identified as a woody root. Segments were immersed in distilled water and trimmed to 8-cm lengths, with the tip left intact on young roots. At the proximal end of a root segment, tissues external to the stele were removed to expose ca. 8 mm of stele which was then inserted into a piece of flexible tubing connected by a compression fitting to glass microcapillary tubes half-filled with distilled water. For woody roots, the distal end of the root segment was sealed with dental impression material to prevent water uptake directly into the xylem. Root segments were immersed in distilled water and a partial vacuum was applied to the open end of the microcapillary. The volumetric flow rate through the root segment (Q_v, m^3 s^{-1}) was measured at three pressures, −40, −30 and −20 kPa, and used to calculate L_p (North & Nobel 1991).

Axial (xylem) hydraulic conductance (k_h; m^4 s^{-1} MPa^{-1}) was measured on the same root segments as for L_p, with the distal seal removed and the end re-trimmed under water. About 1 mm of the cut end was immersed in distilled water, and Q_v was measured as above and used to calculate k_h:

$$k_h = Q_v/\Delta P/\Delta x \tag{3}$$

where the pressure difference ΔP (MPa) was applied across the length Δx (m) of the root segment.

The radial hydraulic conductance (L_r; m s^{-1} MPa^{-1}) along a root was calculated using values of L_p, k_h, and the length l (m) and the radius r_{root} (m) of the root segment:

$$L_r = L_p \, \alpha/\tanh(\alpha l) \tag{4}$$

where α (m^{-1}) equals $(2\pi \, r_{root} \, L_r/k_h)^{1/2}$ which represents the length along the xylem where the pressure decreases by half (Landsberg & Fowkes 1978).

To scale up L_p from root segments to root systems, root systems of representative sun- and shade-grown plants of the three species were photographed and WinRhizo software (Regent Instruments Inc., Quebec City, QC, Canada) was used to measure the surface area of young and woody roots. The proportional surface area of young and woody roots, along with mean values of L_P for each root type, was used to calculate k_{roots} (kg m^{-2} s^{-1} MPa^{-1}) and this value was divided by leaf area to yield leaf specific hydraulic conductance (k_l). Proportional surface areas were also used with mean values of L_r and k_h to calculate radial and axial resistances, respectively.

Hydraulic conductivity (K_h; kg m MPa^{-1} s^{-1}) was measured on main stems and roots ($N = 6$ for each species and organ) that had been previously flushed to remove emboli. Stems were measured using a tubing apparatus connected to a low-pressure head ($\sim$4 kPa) at the basal end and a 0·1 mg resolution analytical balance (AE163,
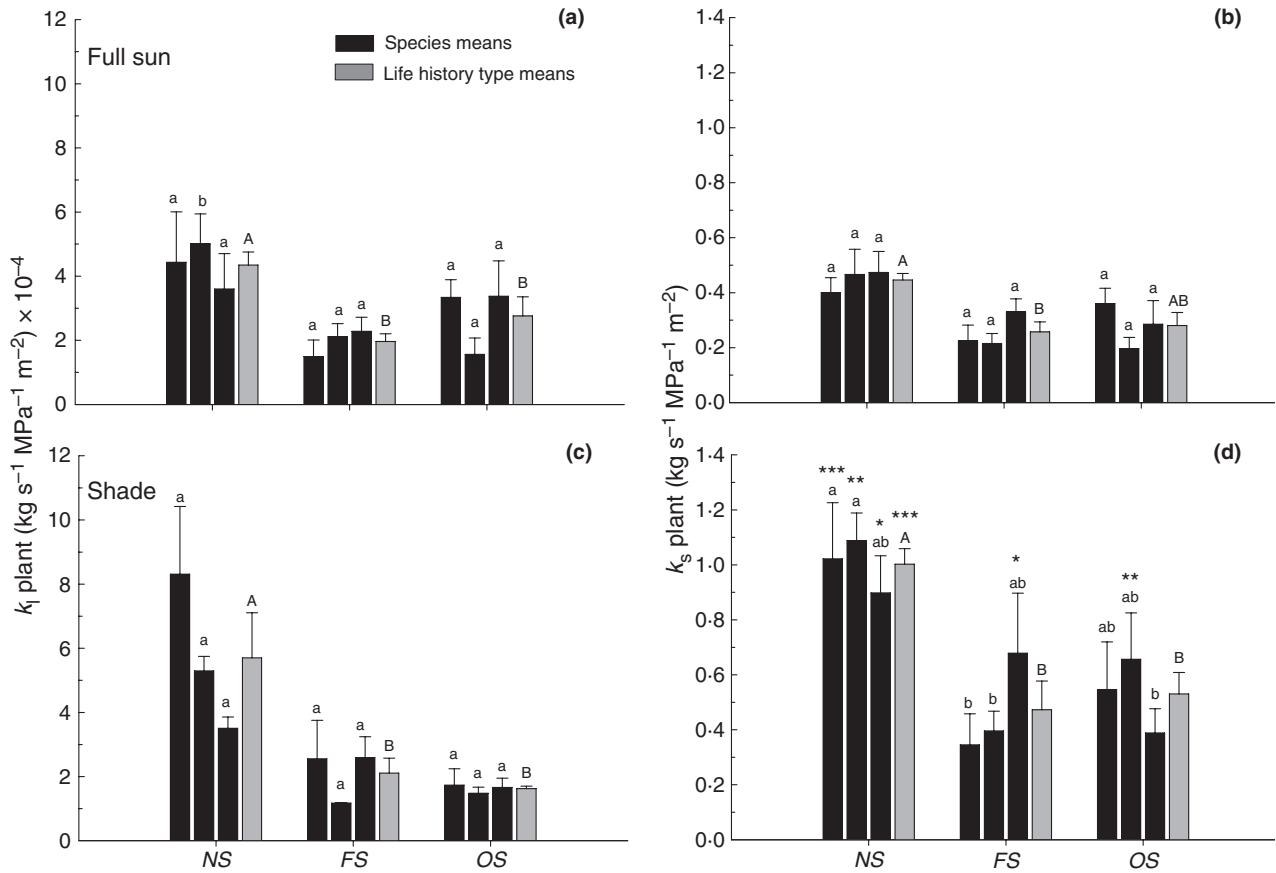
Fig. 1. Seedling leaf specific conductance (k_1) and xylem specific conductance (k_s) grown in full sun (a, b) and shade (c, d; 25% of full sun). Data are means $\pm$ 1SE ($N = 6$) for species (coloured bars) and life history type (grey bars). The order of species are as follows: *Cm, Ccr, Ccu, Cs, Co, Cl, Ri, Rca, Rcr* (see Table 1 for species abbreviations). Bars within each panel labelled with unique letters indicate significant differences (lowercase for species means and uppercase for life history type means). Asterisks in panel (d) denote differences between sun and shade (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

Mettler-Toledo, Columbus, Ohio, USA) at the distal end (see full methods in Pratt *et al.* 2008). The xylem area was measured with calipers to calculate xylem specific conductivity (K_s; kg s^{-1} m^{-1} MPa^{-1}). Due to time constraints, only three species, one representative of each life history type, was measured in the shade treatment.

STATISTICS

Differences among treatments were analyzed using ANOVA (SAS v.9.1, SAS Institute Inc., Cary, NC, USA). The terms in all the models included life history type (NS, FS, and OS), sun and shade, block, species as a random factor nested within life history type, and all possible interactions. Life history type differences were analyzed as pre-planned comparisons using species nested in life history type as the error term (SAS, CONTRAST statement). In the Results section, reported *P*-values are from ANOVA output. It was not a chief objective of this study to compare differences among species, but nonetheless these comparisons are reported in Tables and Figures. For the species comparisons we used a Tukey's correction to control the experiment-wise type I error rate. Comparison among species should be viewed cautiously because they have little power and thus have elevated risk for type II error due to the relatively large number of post-hoc comparisons and the associated Tukey's correction. In cases where the

design was unbalanced, a Satterthwaite correction was used (Potvin 2001). Data were transformed as necessary to satisfy assumptions of statistical models. When comparing treatments, differences were considered significantly different at an $\alpha \leq 0.05$, except for differences across life history types, for which we adjusted α to 0.10 to avoid committing type II errors on account of small sample size ($N = 3$).

Results

Leaf specific hydraulic conductance (k_1) of whole plants differed among life history types ($P = 0.007$; Fig. 1a,c). The NS life history type had the greatest k_1 (NS vs. FS $P = 0.005$ NS vs. OS $P = 0.005$) and the FS and OS life history types were not different ($P = 0.94$).

Sun and shade treatments did not differ in k_1 ($P = 0.55$) and this result was consistent across all life history types and species (Fig. 1).

Xylem specific hydraulic conductance (k_s) of whole seedlings differed among life history types ($P = 0.003$; Fig. 1b,d). As with k_1, the NS life history type had the greatest k_s (NS vs. FS $P = 0.001$ NS vs. OS $P = 0.003$) and the FS and OS life history types were not different (FS vs. OS $P = 0.57$).

Table 2. Leaf hydraulic conductance (k_h), and leaf specific hydraulic conductance (k_l) for seedlings grown in sun (white columns) and shade (grey columns) treatments

Life history type and species	k_h leaves sun (kg s^{-1} MPa^{-1})	k_h leaves shade (kg s^{-1} MPa^{-1})	k_l leaves sun (kg s^{-1} MPa^{-1} m^{-2})	k_l leaves shade (kgs^{-1} MPa^{-1} m^{-2})
NS average	0·18^A (0·03)	0·11^A (0·02)	7·71^A (2·34)	8·17^A (1·22)
Cm	0·23^a (0·05)	0·15^a (0·03)	10·66^a (4·44)	10·24^a (1·21)
Ccr	0·19^a (0·02)	0·07^{ab*} (0·01)	9·37^a (1·90)	8·25^a (1·11)
Ccu	0·11^{ab} (0·03)	0·10^{ab} (0·02)	3·09^{ab} (0·80)	6·01^{ac} (1·43)
FS average	0·19^A (0·04)	0·08^A (0·02)	3·80^A (0·92)	1·46^{B**} (0·64)
Cs	0·11^{ab} (0·03)	0·03^{b**} (0·01)	2·19^{bc} (0·64)	0·81^b (0·10)
Co	0·27^a (0·10)	0·10^{ab*} (0·04)	5·38^{ab} (0·56)	0·83^{b***} (0·20)
Cl	0·17^{ab} (0·03)	0·12^{ab} (0·05)	3·83^{ab} (0·81)	2·74^{ab} (0·80)
OS average	0·10^A (0·03)	0·12^A (0·03)	5·02^A (1·84)	3·49^{AB} (1·28)
Ri	0·16^{ab} (0·04)	0·16^a (0·01)	8·20^a (2·19)	6·02^a (0·78)
Rca	0·05^b (0·02)	0·16^{ab**} (0·05)	1·81^b (0·78)	1·89^{bc} (0·73)
Rcr	0·09^{ab} (0·02)	0·04^{ab} (0·01)	5·03^{ac} (1·01)	2·56^{bc} (0·67)

Data shown are means ($N = 6$) and standard error in parentheses. Within a column, means followed by the same letter are not different, whereas those with unique letters are different. Upper case letters are comparisons among life history type, lower case letters are among species within each life history category. Asterisks in the shade columns denote instances where sun and shade treatments differed for life history type comparisons (* = $P < 0·10$; ** = $P < 0·05$) and for species comparisons (* = $P < 0·05$; ** = $P < 0·01$; *** = $P < 0·001$).

The sun and shade treatments differed in k_s ($P < 0·001$) with the general trend that shade plants had greater k_s than sun plants. This effect was not significant across all life history types. Only the NS group had significantly greater k_s in the shade (Fig. 1d; life history x sun/shade $P = 0·02$).

Examined separately, the k_s of the root system, the shoot, and the stems (the shoot minus the leaves) was similar to that for the whole plant. In all cases, the NS had the greatest k_s among the life history types and this effect was strongest in the shade (Table 1). For the root, shoot, and stem, shade k_s was greater than sun k_s for the NS life history type (Table 1). By contrast, the FS life history type showed no shade effect (Table 1). The OS life history type showed increased levels of k_s in the shade for shoots and stems, but no effect in the roots (Table 1).

Hydraulic conductance of leaves was analyzed by comparing unscaled hydraulic conductance (k_h) and with k_h divided by leaf area (k_l; Table 2). None of the life history types differed in leaf k_h ($P > 0·05$). There was a general pattern that individual species in the shade treatment had lower k_h than sun plants with the exception of *R. californica* (Table 2).

Leaf specific hydraulic conductance (k_l) was greatest for the NS life history type (ANOVA NS vs. FS $P = 0·05$ NS vs. OS $P = 0·14$ FS vs. OS $P = 0·45$). The shade treatment had the general effect of reducing k_l for the FS and OS life history types (Table 2). For the NS, the shade treatment did not result in a general decrease in k_l of leaves (Table 2).

Xylem specific hydraulic conductivity (K_s) of main stem and main root segments for plants grown in full sun was different among life history types ($P = 0·02$; Fig. 2a,c). The OS life history type had lower K_s than either the NS or the FS (NS vs. OS $P = 0·01$ FS vs. OS $P = 0·01$) and the NS and FS were not different ($P = 0·77$). This result was not general for stems and roots. Only the roots showed this pattern (life history type x organ $P = 0·05$; Fig. 2c). In addition, main

roots had greater K_s than stems for all species and life history types ($P < 0·001$; Fig. 2a,c).

Main stem and main root K_s was measured on a subset of three species, one each of NS, FS, and OS, in the shade. The three species differed for K_s ($P < 0·001$; Fig. 2b,d). The FS species had the greatest stem K_s (FS vs. NS $P < 0·05$ FS vs. OS $P = 0·004$) and the NS and OS species did not differ ($P = 1·0$). For root K_s, the NS and FS species were not different ($P = 1·0$) and both the NS and FS species were greater than the OS (NS vs. OS $P < 0·001$ FS vs. OS $P = 0·01$). Main roots had greater K_s than stems for all life history types and species ($P < 0·001$; Fig. 2b,d).

Species K_s differed between sun and shade ($P = 0·006$). The general trend was that K_s was greater in the shade (Fig. 2); however, this difference was only significant for the FS and OS species ($P = 0·01$ and $P = 0·05$, respectively).

Hydraulic conductance of fine roots (L_p) differed among the three species measured, representing the three life history types ($P < 0·001$). The NS species measured had the greatest L_p (NS vs. FS $P < 0·001$ NS vs. OS $P < 0·001$), whereas the FS and OS were not different ($P = 0·89$). Woody (older) roots had greater L_p than did the young (white, non-woody) roots (Fig. 3a,b; $P < 0·001$). Life history type differences were consistent across the different root age classes (Fig. 3a; life history type x age $P = 0·74$). In full sun (Fig. 3a), L_p was lower than in shade (Fig. 3b; $P < 0·001$), but only for the FS and OS life history types (life history × treatment $P = 0·028$).

The axial (through the xylem) component of root hydraulic conductance (k_h) differed among the life history types (Fig. 3e,f; $P = 0·003$), with significant interactions between root type and the two other factors, life history type and light. Due to such interactions, statistical comparisons were made only for woody roots, which had lower k_h in full sun than in shade (Fig. 3a vs. b; $P = 0·003$). With respect to life history type, k_h was higher for woody roots of NS than for FS and
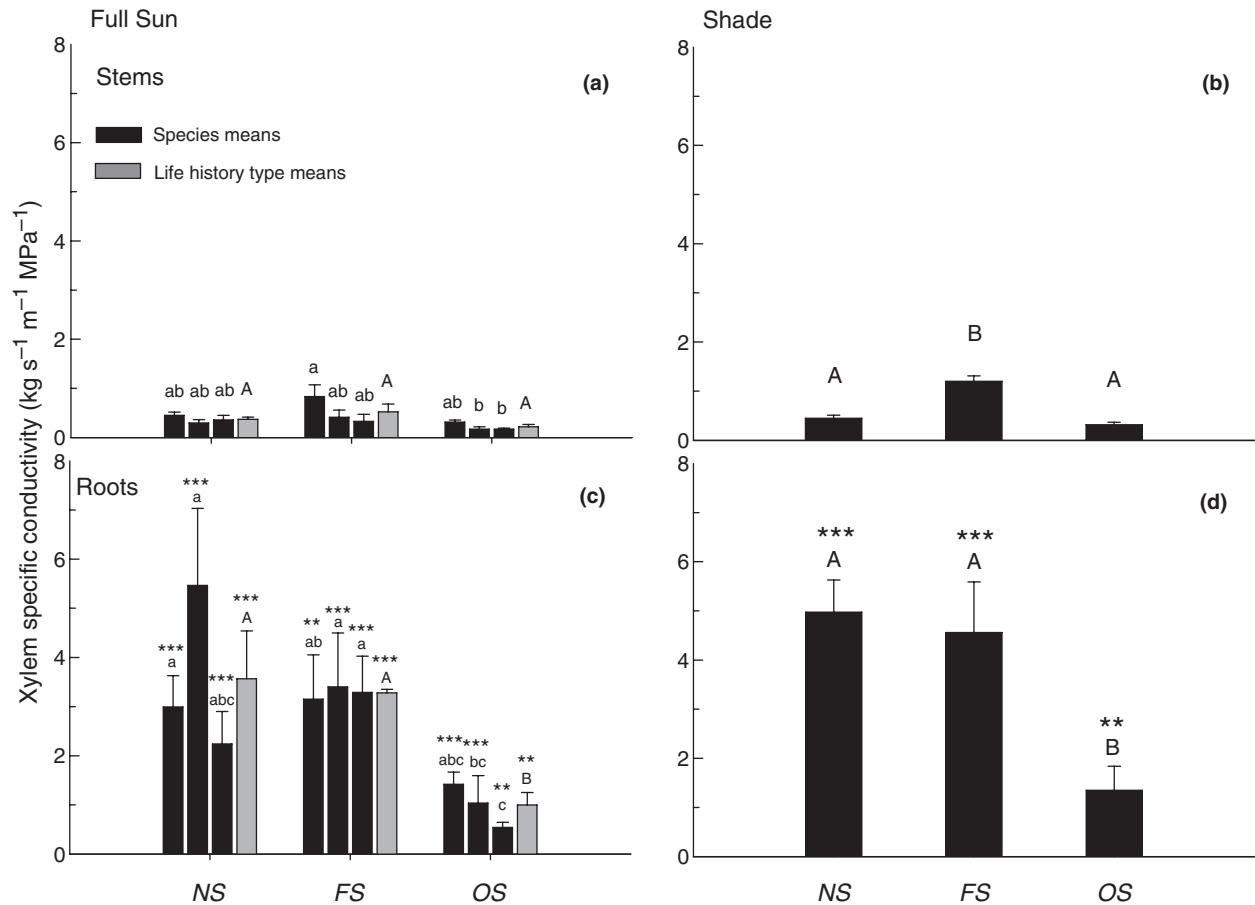
Fig. 2. Xylem specific hydraulic conductivity of main stem (a and b) and main root (c and d) segments in full sun (a and c) and shade (b and d). Data are means ± 1 SE (*N* = 6–9) for species (coloured bars) and life history type (grey bars). The order of species in full sun are *Cm, Ccr, Ccu, Cs, Co, Cl, Ri, Rca, Rcr*, and the species in the shade are *Cm, Co*, and *Rca* (see Table 1 for species abbreviations). Bars within each panel labelled with unique letters (lowercase for species means and uppercase for life history type means) are different, and asterisks in panels c and d denote differences between stems and roots (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). For comparisons between life history types **$P < 0.05$ and ***$P < 0.01$.

OS ($P = 0.006$), while the latter types did not differ ($P = 0.751$).

The radial or extraxylary component of root hydraulic conductance (L_r) differed among the life history types (Fig. 3c,d; $P < 0.001$), although differences due to light were not assessed due to its significant interaction with life history type ($P = 0.017$). For both young and woody roots, L_r was higher ($P < 0.001$) for NS than for FS and OS, which did not differ. The general pattern for L_r for woody roots was similar to that for L_p for the three life history types ($P = 0.602$), although for young roots L_r was greater than L_p across life history types in both sun and shade ($P < 0.001$).

Root hydraulic conductance was used in conjunction with measurements of young and woody root surface areas of representative plants of each life history type to scale L_p to whole root conductance. This value was then divided by whole plant leaf area to get leaf specific root system conductance (k_l). This parameter is the same that was directly measured with the HPFM. Comparisons between the values of k_l from scaling up from L_p to those measured with the HPFM showed similar patterns among life history types (Fig. S1 in Supporting Information). Scaled k_l was 50–70% lower than HPFM measured k_l in the sun (Fig. S1a), but only about 25–50% lower in the shade (Fig. S1b).

Maximum height and crown diameters were different among life history types ($P = 0.06$ for height and $P = 0.03$ for diameter; Table S1 in Supporting Information). Likewise stem diameter and crown volume were also different ($P = 0.01$ for diameter and $P < 0.001$ for crown volume; Table S1). With some exceptions, the general pattern for most of the parameters was that the FS was larger than the NS, and the OS was the smallest of the three (Table S1). This pattern was affected by the shade treatment with plants generally growing taller with narrower diameter stems in the shade compared to the sun (Table S1). The FS and OS had greater crown volumes in the shade, whereas the NS had reduced crown volume (Table 2). These differences were not found significant by the ANOVA on account of a significant interaction between life history type and the light treatment ($P < 0.001$).

In order to compare how different hydraulic conductances scaled in different regions of the seedlings, data were analyzed
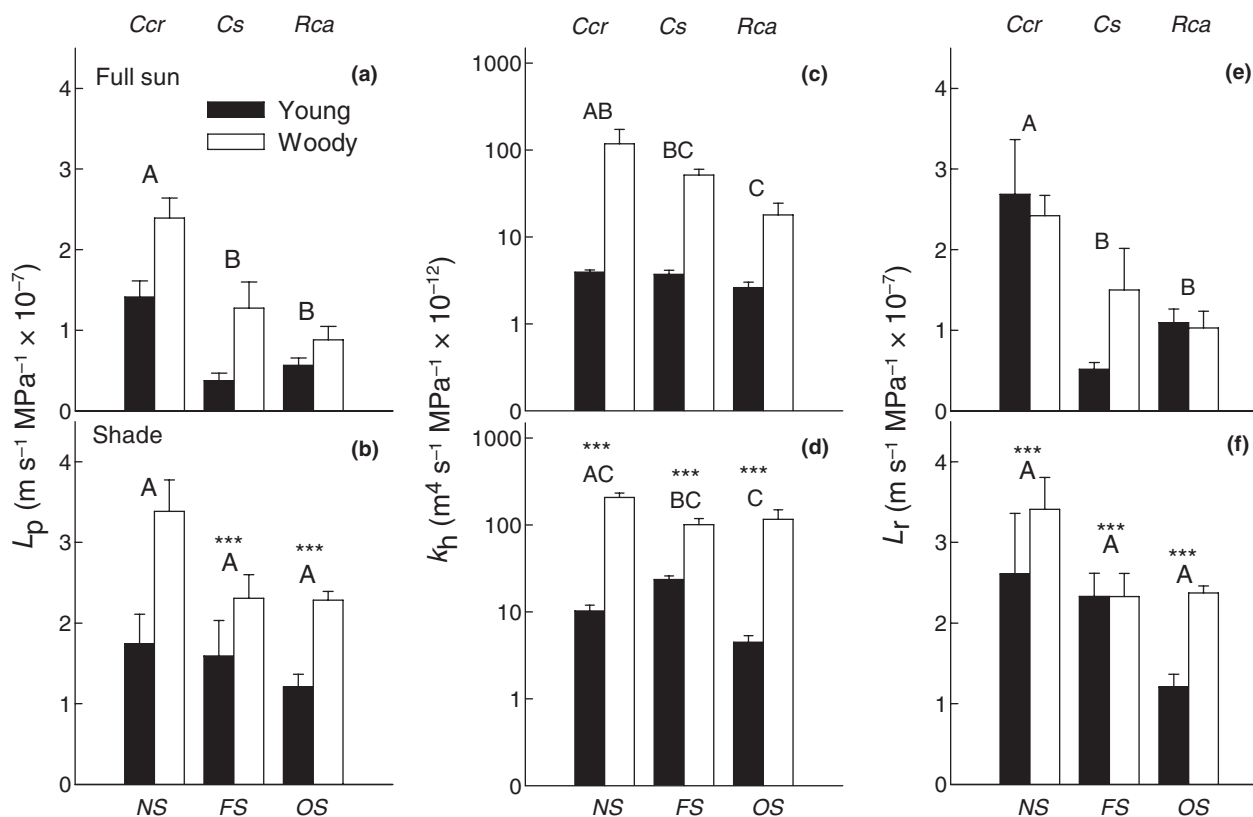
Fig. 3. Hydraulic conductance of fine roots (L_p) measured in full sun (a) and shade (b), axial hydraulic conductance (k_h) in full sun (c) and shade (d), and radial conductance (L_r) in full sun (e) and shade (f). Data are means $\pm$ 1 SE ($N = 4$) for fine roots (black bars) woody roots (white bars). Species abbreviations above panels (a), (c), and (e) are defined in Table 1. Bars within each panel labelled with unique letters are different, and asterisks in panel (b), (d), and (f) denote differences between sun and shade (***$P < 0.001$).

by comparing conductances and conductivities to the NS life history type, i.e. the NS was set at 100% (Fig. 4). The relative differences among life history types at the whole plant level were generally similar at different points in the plant hydraulic continuum (Fig. 4).

Percentage hydraulic resistance of roots and stems were similar for the life history types in the sun and shade ($P = 0.24$). In full sun for all life history types, root resistance was about 53% of the total, stem resistance was about 28%, and leaf resistance was about 20% of the total resistance (Fig. 5), and these differences were significant ($P < 0.001$).

In the shade there was a tendency toward greater hydraulic resistance in the roots (about 60% of the total); however, this shift was not significant ($P = 0.08$). Resistance of leaves trended to be lower in the shade than the sun, but again this difference was not significant ($P > 0.05$; Fig. 5).
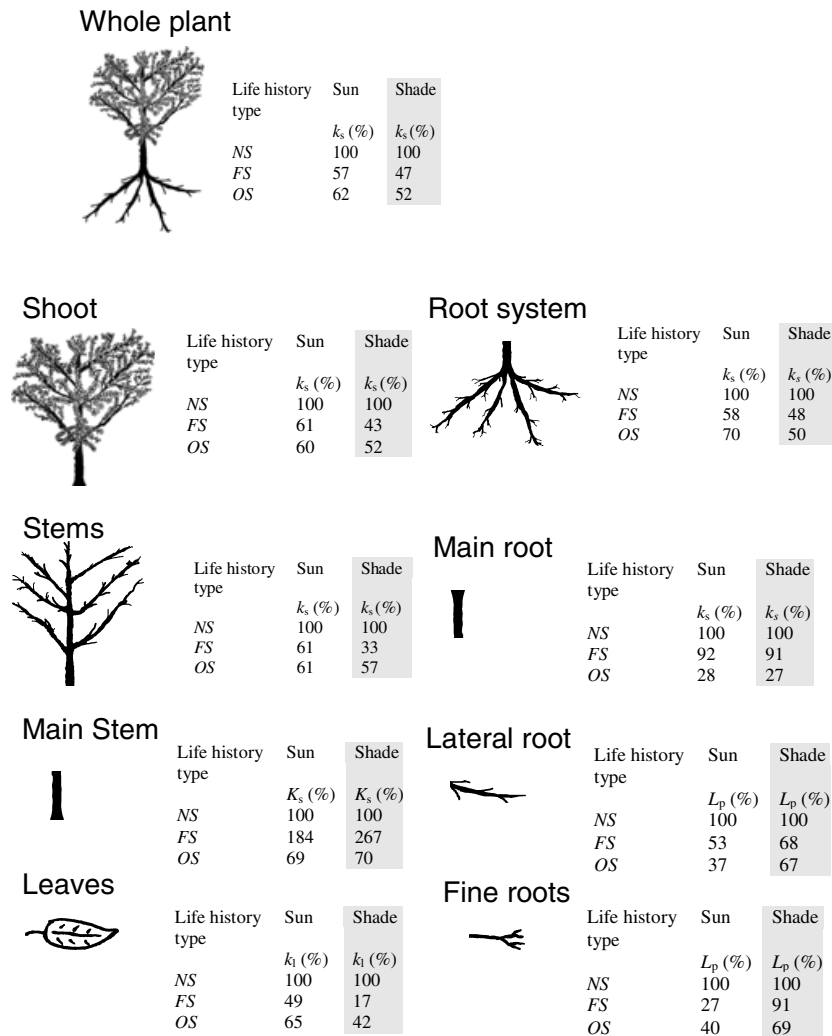
Discussion

LIFE HISTORY TYPE

The hypothesis that life history type is linked to hydraulics in seedlings of chaparral shrubs was supported. The NS life history type, which is shade intolerant and rapidly colonizes open canopy sites following crown fires, displayed the greatest hydraulic efficiency expressed on xylem area and leaf area

bases. Other studies have also found that seedlings of early successional pioneer species have greater hydraulic conductance per unit leaf (k_l) area than do late successional, more shade tolerant species (Tyree, Velez & Dalling 1998). One advantage of greater k_l is that less negative leaf water potentials for a given transpiration (E) rate can be maintained. This can be expressed mathematically using a relationship analogous to Ohm's law

$$E = g_s \times \text{VPD} = k_l(\Psi_{\text{soil}} - \Psi_{\text{plant}}) \tag{5}$$

where E is directly proportional to stomatal conductance (g_s), which is itself directly proportional to leaf specific plant conductance (k_l) and VPD is the leaf to air vapour pressure difference and Ψ_{soil} and Ψ_{plant} are the water potentials of the soil and plant, respectively. From this relationship, it is apparent that for a given value of Ψ_{plant}, plants with greater k_l can attain greater levels of g_s, or for a given level of g_s, plants with greater k_l can maintain less negative Ψ_{plant}. All else being equal, this should lead to greater rates of cell expansion, growth, and net carbon assimilation. In addition, higher levels of xylem specific conductance (k_s) suggest that the NS life history type is able to achieve greater whole plant conductance with a smaller investment in xylem tissue. This more efficient allocation of carbon resources may be important for rapid seedling growth and establishment

Whole plant

Life history type	Sun k_s (%)	Shade k_s (%)
NS	100	100
FS	57	47
OS	62	52

Shoot

Life history type	Sun k_s (%)	Shade k_s (%)
NS	100	100
FS	61	43
OS	60	52

Root system

Life history type	Sun k_s (%)	Shade k_s (%)
NS	100	100
FS	58	48
OS	70	50

Stems

Life history type	Sun k_s (%)	Shade k_s (%)
NS	100	100
FS	61	33
OS	61	57

Main root

Life history type	Sun k_s (%)	Shade k_s (%)
NS	100	100
FS	92	91
OS	28	27

Main Stem

Life history type	Sun K_s (%)	Shade K_s (%)
NS	100	100
FS	184	267
OS	69	70

Lateral root

Life history type	Sun L_p (%)	Shade L_p (%)
NS	100	100
FS	53	68
OS	37	67

Leaves

Life history type	Sun k_l (%)	Shade k_l (%)
NS	100	100
FS	49	17
OS	65	42

Fine roots

Life history type	Sun L_p (%)	Shade L_p (%)
NS	100	100
FS	27	91
OS	40	69

Fig. 4. Xylem specific conductance (k_s) and conductivity (K_s), leaf specific conductance (k_l), and root hydraulic conductivity (L_p) for three life history types shown for different regions of the plant. Values are expressed as a percentage of the values for the NS life history type. Displaying the data as such allows a comparison of how similar each life history type is at different points in the plant water transport pathway.
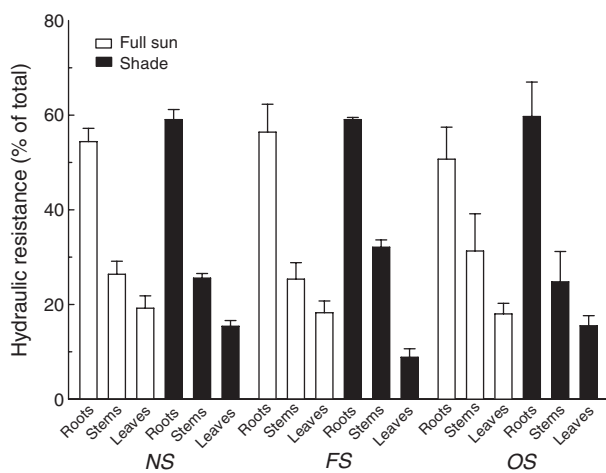
Fig. 5. The relative hydraulic resistance of the root system, the shoot, and the leaves for full sun (open bars) and shade (coloured bars). Data are means $\pm$ 1 SE for each life history type ($N = 3$).

in competition with post-fire annuals and vegetative resprouts of FS and OS life history types (Frazer & Davis 1988; Thomas & Davis 1989). This interpretation is consistent with previous findings that seedlings with the NS life history type had higher survival during summer drought and also greater K_s of stem and root segments at their minimum seasonal water potential (Pratt *et al.* 2008).

Hydraulic conductance may be linked to differences in shade tolerance among life history types (Nardini, Salleo & Andri 2005; Sack, Tyree & Holbrook 2005). The NS life history type germinates and selectively establishes in high light post-fire microsites (Thomas & Davis 1989; Pratt *et al.* 2008). The FS life history type germinates in relatively open post-fire microsites; however, FS seedling survivorship is greater in shade than in full sun suggesting shade tolerance (Frazer & Davis 1988; Thomas & Davis 1989; Pratt *et al.* 2008). Not surprisingly, because the OS typically recruit in deep shade, the OS had virtually no mortality in a shade treatment suggesting the highest degree of shade tolerance (Pratt *et al.* 2008). Efficient water transport in NS seedlings may be

crucial to meet the strong evaporative demands in full sun, especially near ground level at the surface of dark charred soils, whereas shade mitigates evaporative demand for FS and OS (Frazer & Davis 1988; Thomas & Davis 1989).

The greater transport efficiency of the NS life history type was observed not only at the whole plant level, but also for both young and woody root segments, as indicated by their greater root hydraulic conductance (L_p) (Fig. 3a,b) as well as its two components, axial (k_h) and radial hydraulic conductance (L_r). For woody roots of all three life history types, root water uptake was not limited by axial resistance (the inverse of k_h), as indicated by the close correspondence between L_p and L_r. For the NS species in particular, k_h was relatively high in both sun and shade, whereas the lower values of k_h for the woody roots of the FS and OS species in the sun suggest that their xylem may be more vulnerable to water stress-induced embolism (cf. Pratt *et al.* 2008). For all three life history types, axial resistance for the young roots was relatively high, as shown by the large disparity between L_p and L_r. As for many other species, including *Zea mays* and desert succulents, root hydraulic conductance in the apical region of young roots can be limited by xylem immaturity (North & Peterson 2005). For the young roots of the NS species, higher L_p and L_r may be related to differences in anatomy or aquaporins, as is often the case for metabolically active roots (Rieger & Litvin 1999; North, Martre & Nobel 2004).

For plants grown in full sun, the life history types significantly differ with respect to cavitation resistance caused by water stress with the NS being more cavitation resistant (for main stems and roots) than both the FS and OS life history types, which do not differ (see analysis in Pratt *et al.* 2008). Seedlings of the NS life history types combine greater whole plant efficiency in water transport with greater safety from water stress induced cavitation. Thus NS seedlings, at the whole plant level, do not display a tradeoff between xylem safety from cavitation and xylem efficiency in water transport. This may be adaptive to the NS post-fire recruitment in open canopy, high light, relatively dry, unoccupied microsites (e.g. relatively moist microsites are preferentially occupied by resprouts of FS and OS and are thus unavailable to NS). Greater hydraulic efficiency is characteristic of early successional colonizing species (Bazzaz 1979; Tyree, Velez & Dalling 1998), whereas the high degree of stress tolerance of the NS species is not commonly associated with early successional species (Ackerly 2004). The combination of crown fires, creating pioneering opportunities (Franklin *et al.* 2001), and the unusually predictable dry seasons (Cowling *et al.* 2005), may uniquely select for this combination of both pioneer and stress tolerance traits among seedlings of NS species.

Measurements reported in this study are maximum values of hydraulic conductance and conductivity, i.e. they are measurements without emboli. *In situ*, seedlings would have emboli, especially during the summer rainless season. The presence of emboli due to water stress may amplify the hydraulic life history type differences because the NS life history type has significantly greater stem and root cavitation resistance than the FS and OS life history types (Pratt *et al.*

2008). Furthermore, seedlings of the same species sampled here exhibit no difference in seasonal minimum water potentials (Pratt *et al.* 2008). Thus, under water stress, the hydraulic efficiency will be enhanced for the NS life history type in comparison to FS and OS. The FS and OS life history types did not differ in minimum seasonal water potential or cavitation resistance of stems and roots (Pratt *et al.* 2008), thus the conclusions that they are not different in hydraulic efficiency would likely hold under water stress.

SUN AND SHADE

Plants in shade generally had greater whole plant k_s than plants in the sun, suggesting lower levels of investment in xylem tissue for a given level of water transport efficiency. Plastic adjustments towards greater k_s and more efficient stem carbon investment may be advantageous in the shade where light limits carbon assimilation. In contrast to k_s, k_l of plants in the shade did not differ from that of sun plants due to greater leaf area per unit xylem area for shade plants, consistent with an allocation shift to leaves to enhance light capture.

The arguments discussed above suggest that greater transport efficiency is good for shade intolerant, early successional plants and is an asset in the shade as well. Arguably, all plants should maximize hydraulic efficiency. So why do not all plants possess highly efficient xylem? The standard explanation has been that hydraulic efficiency comes at the cost of transport safety (greater susceptibility to cavitation; Zimmermann 1983). The finding that NS species combine both greater whole plant efficiency and safety from water-stress induced cavitation (of the stems and roots) supports the idea that for some species there is pressure to evolve high safety and efficiency.

COMPARATIVE HYDRAULICS

We measured hydraulic conductance and conductivity in a range of organs to examine the hypothesis that the water transport pathway is coordinated at different points in the entire transport pathway from roots to leaves. We predicted that measurements on stems, roots, and leaves would follow the overall pattern for the whole plant. Specifically, we predicted that whole plant k_s and k_l for seedlings of the NS would be greater than both the FS and OS life history types.

The hypothesis that the hydraulic system is coordinated is generally well supported by our results (Fig. 4). With few exceptions (see below), in full sun and shade the shoot, stems, and leaves followed the pattern found for the whole plant. Belowground, the root systems, lateral roots, and the fine roots also generally followed the whole plant pattern. This result suggests that higher conductance in shoots is generally associated with higher conductance in the roots.

There were some deviations from this coordination pattern that can be explained by differences in plant architecture. For example, hydraulic conductivity of main stems in full sun and shade was greatest for FS species. Consistent

with this observation, the FS species had the largest main stem diameters (Table S1), the greatest hydraulic mean vessel diameters (Table 1), and the greatest crown volume, especially in the shade.

Another deviation from this coordination pattern was that the FS leaf hydraulic conductance in the shade was much lower than would be expected based on the whole plant relationship. The unscaled leaf hydraulic conductance values were not different among life history types (Table 2), but since the FS had greater leaf area in the shade, the conductance scaled to leaf area was lowest for FS. This suggests that the FS species would be more sensitive to water deficits in the shade compared to NS and OS, as is consistent with findings of a previous study (Pratt *et al*. 2008).

Another deviation in organ to whole plant coordination was for main roots. In both sun and shade, the FS had greater k_s and the OS had lower k_s than would be predicted by the whole plant pattern. This could be explained by root architecture differences. We do not have data on root architecture that would allow us to fully evaluate this, but the FS had more massive root systems than the other life history types (R.B. Pratt, J. Hernandez, A.L. Jacobsen, G.B. North, F.W. Ewers & S.D. Davies, unpublished data), which likely means that there were more feeder roots supplying the main root in the FS necessitating a highly conductive main root. Also consistent with architecture differences, the OS had the least massive roots in sun; however, this was not true in the shade so architecture differences do not fully explain the data.

Scaling L_p data up to the whole root system and made specific to leaf area (k_l of the root system) gave estimates of k_l that were all lower than k_l measured with the HPFM. An obvious source of error is with the root area estimates. We likely lost some root area when excavating plants and this error was in the right direction to reduce the magnitude of k_l when scaled up from L_p. Another source of error could be due to cavitation. The L_p technique measures root hydraulic flux under a vacuum that does not remove emboli. By contrast, the HPFM uses positive pressures as high as 0·6 MPa, and likely refills considerable emboli in the root system (Tyree *et al*. 1995). Roots often display high levels of native embolism (Domec *et al*. 2006), which would make the HPFM prone to overestimates of root hydraulic conductance.

Most studies of plant hydraulics measure branches or stems as opposed to the entire plant. Using only lateral stems or roots to investigate the functional significance of hydraulic differences across species may lead to erroneous conclusions (see also Engelbrecht, Velez & Tyree 2000). In the present study, the main stems deviated from the whole plant pattern even though we were comparing seedlings grown in a common environment and of a similar functional type (evergreen shrubs).

We hypothesized that the roots and leaves would be chief bottlenecks in the hydraulic pathway because of their extraxylary pathways. The root system offered the greatest resistance to water flow accounting for more than half of the overall resistance. The remaining 45–40% of the whole plant resistance was in the shoot. This finding is consistent with other studies on woody plants (Engelbrecht, Velez & Tyree 2000) and suggests that the root system is the main resistance in the plant hydraulic continuum of chaparral shrubs.

Within the shoot, stems had greater hydraulic resistance than did leaves. Previous studies indicate that leaves can account for about 25% of the resistance of the whole plant (Sack & Tyree 2005). Our values were somewhat lower than this at about 10–20%, but are in the range of other studies (Yang & Tyree 1994; Engelbrecht, Velez & Tyree 2000). The importance of stems as a limitation to water transport in chaparral shrubs may explain why studies of chaparral stem hydraulics have been relatively successful at linking stem hydraulics to physiology and ecology (Davis, Kolb & Barton 1998, Davis *et al*. 1999; Pratt *et al*. 2005, 2007, 2008; Jacobsen *et al*. 2007a,b).

In conclusion, the NS species in the chaparral have the greatest population turnover since they only regenerate *en masse* from seeds following fire. This life history characteristic places strong demographic pressure at the seedling stage. Because of this, and the protracted and predictable rainless summers in California Mediterranean-type climate regions, NS seedlings may be more strongly selected for both hydraulic efficiency and safety traits than in the other chaparral life history types. The root systems, representing the greatest resistance to water flow in woody chaparral seedlings, may be under especially intense selection.

Acknowledgements

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Leaf specific hydraulic conductivity of the root system measured using different methods.

Table S1. Seedling growth measurements.

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