XYLEM TRANSPORT SAFETY AND EFFICIENCY DIFFER AMONG FYNBOS SHRUB LIFE HISTORY TYPES AND BETWEEN TWO SITES DIFFERING IN MEAN RAINFALL

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Xylem safety and efficiency were analyzed for stems of evergreen shrubs that inhabit fynbos communities in the Mediterranean-type climate region of South Africa. We hypothesized that species with different life history types would differ in xylem function on account of their different regeneration niches. Comparisons were made among postfire nonsprouters, facultative sprouters, obligate sprouters, and opportunists. Measurements included xylem resistance to water stress–induced cavitation (xylem safety) and xylem-specific hydraulic conductivity (xylem efficiency) at a dry site and at a wetter site. Life history types differed in hydraulic traits: xylem safety was greater in life history types with disturbance-dependent recruitment. By contrast, water stress resistance was lowest in postfire obligate resprouters that recruit seedlings during fire-free intervals in the litter layer of shady microsites. Among life history types, greater xylem safety came at the cost of reduced hydraulic efficiency. This pattern was also observed between field sites, with most taxa from the drier site having greater levels of cavitation resistance and lower levels of xylem-specific hydraulic conductivity than taxa from the wetter site. We conclude that xylem traits are linked to differences in life history types in fynbos species.

Keywords: cavitation, drought, fire, hydraulic conductivity, water stress, xylem.

Introduction

Fire is an important driver of speciation of plants in the biodiverse Mediterranean-type climate regions of California (chaparral), South Africa (fynbos), southwest Australia, and the Mediterranean basin (Wells 1969; Bond and van Wilgen 1996). Plants rapidly regenerate after crown fire by either sprouting or seeding or by a combination of the two. Plants with these different regeneration strategies also differ in a suite of other life history traits and are often categorized into different life history types (Keeley and Zedler 1978; Bond and van Wilgen 1996). Allocation differences associated with the different life history types has led to predictions of trade-offs among growth, survival, and reproduction (Keeley and Keeley 1977; Midgley 1996). Physiological trade-offs also affect growth, survival, and reproduction, and thus a full understanding of life history trade-offs requires consideration of physiological traits. Integrating the physiological and life history trade-offs is essential for understanding the evolution of different life history types, how different life history types coexist, predicting how species in these regions will respond to altered fire regimes and changing climates, and scaling from physiological/functional traits to population dynamics (Pausas and Verdu 2005; McGill et al. 2006; Syphard et al. 2006).

Four different life history types are commonly found among shrubs of Mediterranean-type climate regions. Nonsprouters (NS), or postfire seeders, form a dormant seed bank

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and have their germination cued to fire. Other life history types are able to sprout vegetatively after fire, most often from a lignotuber or roots. Facultative seeders or sprouters (FSs) both resprout and recruit seedlings after fire from a fire-stimulated seed bank. For both the NS and FS life history types, seedling recruitment is dependent on fire disturbance and seedlings germinate during the winter wet season, postfire, in an open-canopy environment (Keeley 1998). Another life history type resprouts vegetatively only after fire, and because it does not form a dormant seed bank or recruit seedlings after fire it is referred to as an obligate sprouter (OS). Instead of a seed bank, its seeds are short lived, fire sensitive, surrounded by a fleshy exterior, and vertebrate dispersed (Keeley 1997). Seedling recruitment in OSs does not occur in gaps or following disturbance such as a fire. Instead, OS seedlings establish during fire-free intervals (Keeley 1992a; Cowling et al. 1997a). Seedlings of OS species rely on shade to mitigate light load and water stress and a well-developed duff layer to hold moisture for germination and survival (Manders and Richardson 1992). In OS species seedling recruitment is rare, as is the successful transition from seedling to sapling and from sapling to the adult population. To transition from seedling to adult requires long fire-free intervals so that saplings can grow large enough to survive a fire (Keeley 1992b); such intervals are uncommon. Another life history type, termed opportunistic (OP; Caswell 1982), appears to not be adapted to fire, since plants of this type do not survive fire as either adults or seeds. Instead, they rely on broad dispersal of seeds from undisturbed patches into disturbed open areas, where seedlings recruit.

The NS, FS, and OP life history types recruit in open-canopy gap environments and rely on stress resistance and

competitive traits to facilitate seedling survival and establishment (Bellingham and Sparrow 2000); conversely, OS types that recruit in shade do not rely as strongly on this trait combination. Water stress–resistance traits in particular are important for gap recruiters at the shallow rooted seedling stage in order for them to survive the summer dry season after a fire that is characteristic of a Mediterranean-type climate (Bond et al. 1984; Parker 1984; Thomas and Davis 1989; Smith et al. 1992). Species cannot simultaneously maximize stress resistance and competitive traits such as rapid growth and resource acquisition (Grime 1979). An additional trade-off that could limit growth and stress resistance for FS species would be allocation to sprouting (Pratt et al. 2008). Allocation of carbohydrates to storage and building and maintenance of sprouting structures would divert resources that could otherwise be spent on traits that are important for stress resistance, such as dense tissues, stress protein synthesis, osmotic adjustment, and free-radical scavenging (Bloom et al. 1985; Taylor 1989). Thus, FSs are unlikely to invade into more arid microsites, because they would not be able to compete there with NS and OP species. OP species may escape some competition by dispersing into open gaps and preferentially recruiting in microsites with less competition. On the basis of these differences between life history types, we hypothesize that water stress–resistance of life history types would diverge such that NS > OP > FS > OS. On the other hand, because of trade-offs with water stress resistance, traits that relate to efficient use of water resources are expected to follow the opposite pattern:

$$OS > FS > OP > NS.$$

In this study, we compared hydraulic traits that determine water stress resistance and those that determine water transport efficiency of stems of fynbos shrub species. The species on which we focused were woody and evergreen. Drought deciduous species can shed leaves and avoid water stress, but evergreens are more limited in their avoidance capabilities. The ability to resist water stress is determined by a suite of traits related to stomatal behavior, osmotic adjustment, rooting depth, tissue toughness and longevity, and synthesis of stress proteins (Beck et al. 2007; McDowell et al. 2008). For evergreen woody species, the ability of the vascular system to supply water to leaves as the soil dries out is a key trait that sets the limits of desiccation survival (Davis et al. 2002; McDowell et al. 2008; Pratt et al. 2008; Kursar et al. 2009). Because xylem cavitation resistance is a key trait defining water stress resistance for evergreen plants like those studied here, we chose to measure cavitation resistance of stems as an estimate of water stress resistance. High levels of cavitation resistance are not achievable without a cost, one of which is reduced hydraulic efficiency (Hacke et al. 2006). To examine this, we measured stem hydraulic efficiency as xylem-specific conductivity. This trait correlates with leaf photosynthetic capacity and should be higher in more competitive species (Bond 1989; Brodribb and Feild 2000) and lower in more stress-resistant species.

This study had four chief objectives. First, we tested whether different life history types differ in their resistance to water stress. Second, we tested for a trade-off between safety from water stress–induced cavitation and hydraulic efficiency among life history types, to evaluate a potential cost of greater water stress resistance. Third, we compared water stress resistance of taxa at a wetter site with those at a drier site, to evaluate whether variation in xylem safety and efficiency is linked to rainfall. Fourth, we compared the results from fynbos with those from California chaparral to evaluate whether life history types are convergent in how they sort among these two Mediterranean-type climate region shrublands with respect to water stress resistance. Comparing results from chaparral with those from fynbos follows from a long-standing interest among scientists to understand evolutionary convergence in structure and function among shrublands in different Mediterranean-type climate regions (Cody and Mooney 1978; Cowling and Campbell 1980). None of the analyses in this study have been undertaken previously for fynbos vegetation, and the results will help to shed light on water stress–resistance patterns in these biodiverse shrublands. To address our objectives, we collected xylem safety and efficiency data from diverse shrub species at a moist field site, and then we reanalyzed the data collected at a drier site and also collected new data (Jacobsen et al. 2009).

Material and Methods

Sites and Species

Nineteen evergreen shrub species representing four different life history types were chosen for our study (table 1). Six of the species were sampled at Paarl Mountain Nature Reserve (S33°44′152′′, E18°55′267′′; elevation, 600 m) in the Western Cape Region of South Africa. The climate is Mediterranean type, and the site receives 858 mm of rain annually, primarily during the winter months (Milton 2003). Fifteen of the species were sampled at Jonaskop in the Riversonderend Mountain Range in the Western Cape, which is also subject to a Mediterranean-type climate but which receives a lower annual rainfall amount than Paarl (table 1). The site was along an elevation and rainfall gradient in which 14 of the species were sampled in an area that receives ≤410 mm of rainfall annually, while one species, *Nebelia laevis*, was at higher elevation and rainfall. This site is discussed more fully in an article by Jacobsen et al. (2007). Two species were sampled at both Paarl and Jonaskop (table 1). We reanalyzed data about vulnerability to cavitation (see below) that had been collected from samples at Jonaskop in a study by Jacobsen et al. (2009), while the xylem efficiency data that we used (see below) from Jonaskop are previously unpublished, as are all of the data from Paarl Mountain.

Species life history types were determined on the basis of the results of previous studies (van Wilgen and Forsyth 1992), the presence (for NS and FS) or absence (for OS and OP) of seedlings the first year postfire (K. M. Marais, K. J. Esler, S. M. Jacobs, A. L. Jacobsen, and R. B. Pratt, unpublished data), and field observations (OS species typically recruit underneath large shrubs or trees that make good perches for bird dispersal; Cowling et al. 1997a). Table 1 lists the species studied, their life history types, and the abbreviations we used for life history types and species.

Table 1

Species Studied

Species	Abbreviations	Family	Site
Nonsprouters	NS		
Aspalathus hirta E. Mey.	Ah	Fabaceae	Jonaskop
Aspalathus pachyloba R. Dahlgren	Ap	Fabaceae	Jonaskop
Erica vestita Thunb.	Ev	Ericaceae	Jonaskop
Leucadendron laureolum (Lam.) Fourc.	Ll	Proteaceae	Jonaskop
Metalasia densa (Lam.) Karis	Md	Asteraceae	Jonaskop
Protea repens (L.) L.	Pr	Proteaceae	Jonaskop
Facultative sprouters	FS		
Cliffortia ruscifolia L.	Cr	Rosaceae	Jonaskop and Paarl
Diosma hirsuta L.	Dh	Rutaceae	Paarl
Erica plukenetti L.	Ep	Ericaceae	Jonaskop
Leucadendron salignum P.J. Berguis	Ls	Proteaceae	Jonaskop and Paarl
Nebelia laevis O. Kuntze	Nl	Bruniaceae	Jonaskop
Passerina obtusifolia Thoday	Po	Thymeliaceae	Jonaskop
Obligate sprouters	OS		
Diospyros glabra (L.) De Winter	Dg	Ebenaceae	Paarl
Euclea sp.	Esp	Ebenaceae	Jonaskop
Searsia lucida L.	Sl	Anacardiaceae	Paarl
Searsia tomentosa L.	St	Anacardiaceae	Paarl
Searsia undulata (Jacq.) T.S. Yi, A.J. Miller & J. Wen	Su	Anacardiaceae	Jonaskop
Opportunistic	OP		
Pteronia fasciculata L.f.	Pf	Asteraceae	Jonaskop
Pteronia paniculata Thunb.	Pp	Asteraceae	Jonaskop

Note. Nomenclature follows Goldblatt and Manning (2000) for all species except for those of the genus *Searsia* (Barkley 1937), which Goldblatt and Manning (2000) described as *Rhus*. *Diosma hirsuta* was measured for xylem efficiency only (fig. 2B).

Water Stress Resistance

The water stress resistance of stems was measured for the Paarl species from January 25 to February 5, 2010 (midsummer), and the data from Jonaskop are discussed elsewhere (Jacobsen et al. 2009). The same techniques were used in both studies and the two lead authors (R.B.P. and A.L.J.) collected these data, thus minimizing any methodological differences. For each treatment and species, stems were measured from six or more individuals. Stems were harvested in the field by cutting each off under water, placing the cut stem into a centrifuge tube filled with water, and then placing the stem into a large plastic bag containing a moist paper towel. Stems were transported to the lab, where they were refrigerated at 4°C in a plastic bag until they were measured (within 5 d of collection). In the laboratory, stems were cut under water to 14 cm, and all of the leaves above the distal end were removed for later leaf-area measurements. Both the area of the sapwood plus the pith and the pith alone were calculated as ellipses, using digital calipers (model 500-196-20, Mitutoyo America, Aurora, IL), and the area of the sapwood was calculated by subtraction. The sapwood area was used as the denominator in xylem-specific hydraulic conductivity measurements.

Hydraulic conductivity (K_h; kg m s^{-1} MPa^{-1}) was measured on 14-cm-long stem segments by mounting them into a tubing apparatus connected on one end to a pressure head and on the other end to an analytical balance. The pressure head was an intravenous bag that contained 20 mM KCl deionized and degassed solution that was ultrafiltered (0.1-μm pore filter), and the bag was elevated ~30 cm above the collection fluid level on the balance. The pressure head ranged from 4.3 to 3.6 kPa, depending on the exact height of the solution in the intravenous bag. The flow through the stem was collected in a reservoir on the analytical balance (CP124S, Sartorius, Göttingen, Germany) that was connected to a laptop that logged mass from the balance (WinWedge Standard Edition, TAL Tech, Philadelphia, PA). Background flow measurements, made before and after pressure-driven flow in the absence of the pressure head, were averaged and subtracted from the pressure-driven flow to correct for background flows, which were typically minimal. Hydraulic conductivity was calculated as flow rate multiplied by stem length and divided by pressure. To measure K_h in the absence of embolism (K_{hmax}), stems were flushed with filtered KCl solution for 1 h at 100 kPa to flush out emboli. Measurements of K_h were then made on these flushed stems and divided by the xylem area to calculate xylem-specific hydraulic conductivity (K_s).

To assess resistance of flushed stems to cavitation, stems were mounted into a custom centrifuge rotor and spun to generate negative pressure (Ψ_x) in the xylem sap (Alder et al. 1997). After each spin K_h was measured, and then stems were respun at a higher rate until K_h was approximately 0. Loss of conductivity after each spin was calculated as $(1 - K_h/K_{hmax}) \times 100$. A cumulative Weibull function was fitted to the curves to model the loss of conductivity as a function of Ψ_x, using equations built into Microsoft Excel (Excel 2010, Microsoft, Redmond, WA). The Ψ_x value at 50% loss in conductivity (Ψ_{50}) was calculated for each stem and averaged as an estimate for a given species/treatment resistance to water stress. We also calculated the water potential at

75% loss of conductivity (Ψ_{75}), which is sometimes preferred in cases where species have different-shaped vulnerability curves.

Two recent studies have hypothesized that centrifuge techniques are prone to underestimating vulnerability to cavitation in species with long vessels (Choat et al. 2010; Cochard et al. 2010). However, follow-up studies that we and others have performed have not found support for this (Sperry et al. 2011; M. Tobin and R. B. Pratt, unpublished manuscript). We do not have vessel length data for the species sampled in this study; however, the species sampled here are semiarid evergreen shrubs, which is a growth form with vessels that are generally short when compared with those of the temperate trees studied by Cochard et al. (2010) and those of the liana studied by Choat et al. (2010; also see A. Jacobsen, unpublished data on vessel lengths compiled for 163 species).

Statistics

We recalculated Ψ_{50} and Ψ_{75} values for data from Jacobsen et al. (2009), using a Weibull function. For Ψ_{50}, Ψ_{75}, and K_s, data were analyzed via ANOVA, with the fixed effect of life history type and the random effects of site and species with species nested within life history type and all possible interactions among model factors (JMP 8.0.2, SAS Institute, Cary, NC). The mixed model was analyzed using a restricted-maximum-likelihood approach (JMP 8.0.2). Comparisons between treatments or life history types were analyzed as preplanned contrasts. For comparisons between field sites that differed in rainfall, the ANOVA consisted of the fixed effects of site and species and their interaction. Contrasts were conducted between taxa that occurred between sites. To determine the trade-off between safety and efficiency, we used SMA regression (Warton and Ormerod 2007). Data were transformed as necessary to meet the assumptions of parametric models.

Results

Life history types were significantly different in cavitation resistance analyzed as Ψ_{50} (figs. 1, 2A; $F_{3,13.77} = 9.94$; $P < 0.001$). Analyzing the data as Ψ_{75} resulted in the same conclusions about differences in cavitation resistance among the life history types shown in figure 2A, and thus we focused on Ψ_{50} for simplicity ($F_{3,14.88} = 45.28$; $P < 0.001$). All other life history types had greater cavitation resistance than the OS type (fig. 2A inset), and the OP type had greater cavitation resistance than all other types, but this may be due to a limited sample size (both numerically and taxonomically; fig. 2A).

Maximum xylem-specific conductivity differed among life history types ($F_{3,15.64} = 7.73$; $P = 0.002$; fig. 2B). It was lowest for the OP life history type compared with all other life history types (fig. 2B). The OS life history type had the greatest K_s value and was significantly different from the FS and OP types but was not different from the NS type (fig. 2B). The mean Ψ_{50} and K_s values within life history types were correlated and suggest a significant trade-off between xylem safety and efficiency (fig. 3).

Hydraulic traits that were compared intraspecifically and between *Searsia* congeners differed between two field sites with different rainfalls. The taxa at the drier site (Jonaskop) had significantly greater cavitation-resistance Ψ_{50} values than those at the wetter site (Paarl) ($F_{1,67} = 9.56$; $P = 0.003$; fig. 4A). As above, analyzing Ψ_{75} led to the same conclusion ($F_{1,67} = 17.74$; $P < 0.001$). There was one case in which analyses for Ψ_{50} and Ψ_{75} did not agree: *Cliffortia ruscifolia* had Ψ_{50} values that were not significantly different between the two sites ($F_{1,67} = 2.73$; $P = 0.102$), whereas Ψ_{75} values were significantly different (fig. 4A). One species, *Leucadendron salignum*, did not have significantly different cavitation resistance at the drier site for either Ψ_{50} or Ψ_{75} (fig. 4A). At the wetter site, species K_s values were greater than at the drier site overall ($F_{1,79} = 4.30$; $P = 0.04$; fig. 4B); however, this was significant only for the *Searsia* spp. (fig. 4B).

One weakness of the experimental design is that all the NS and OP species were sampled at the drier Jonaskop site, and thus the cavitation resistance estimates for these two groups are likely high (i.e., Ψ_{50} and Ψ_{75} values are more negative) and xylem efficiency estimates may be low. One way to test for the influence of site is to analyze the data at each site separately. Thus, we compared life history types within the drier Jonaskop site, where all life history types were sampled, and found that within the Jonaskop site life history types differed in cavitation resistance for Ψ_{50} ($F_{3,10.98} = 6.61$; $P = 0.008$) and for Ψ_{75} ($F_{3,10.99} = 19.06$; $P < 0.001$). For Ψ_{75}, the differences in life history type exactly followed the differences observed when both sites were analyzed in the same model (i.e., OS > NS = FS > OP; inset in fig. 2A). For Ψ_{50} the pattern was the same, but the difference between the OS and NS types was not significantly different ($F_{1,11.04} = 2.13$; $P = 0.172$), even though the Ψ_{50} value was about twice as negative for the NS type than for the OS type (mean $\Psi_{50} \pm 1$ SE for NS, -3.22 ± 0.81, and for OS, -1.73 ± 1.42). The lack of significant difference between the NS and OS types was probably due to the small sample size and the associated lack of power. We conclude that for cavitation resistance, the general patterns we observed when analyzing across the two sites holds when values are compared within a site. For K_s, the NS, FS, and OS types were not different when analyzed within the Jonaskop site; also, the FS and OS types were not significantly different when analyzed within the Paarl site. Thus, our conclusions about K_s for the different life history types are not as firm as those concerning cavitation resistance.

Discussion

The hypothesis that life history types differ in their tolerance to water stress was supported. Of all of the life history types, the OS species were the least resistant to water stress. This is likely linked to the regeneration niche of the OSs: these species generally recruit seedlings in the duff layer of shady closed-canopy environments during fire-free intervals (Keeley 1992b). Shade can ameliorate water stress and water stress–induced mortality in OS seedlings (Manders and Richardson 1992; Pratt et al. 2008). In open-canopy environments, seedling water stress is more intense and water stress–
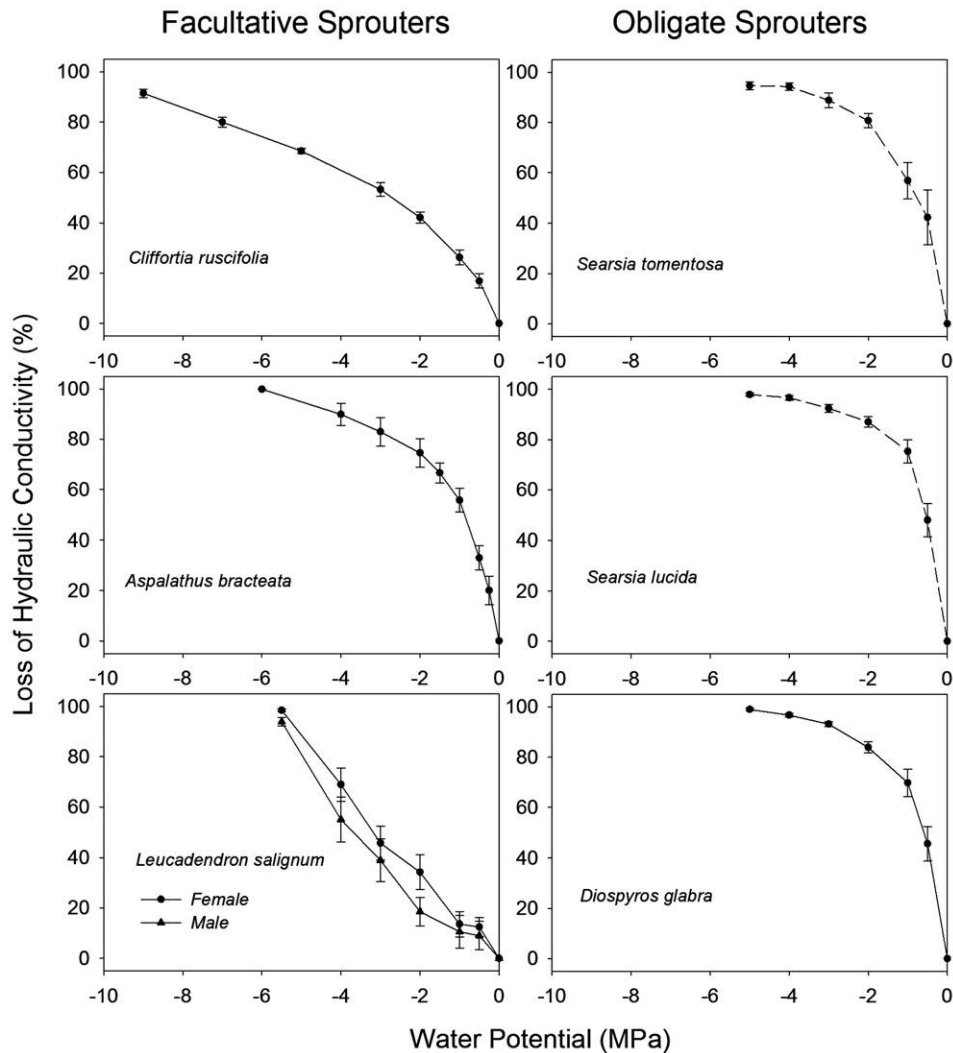
Fig. 1 Curves representing vulnerability to cavitation of stems of six species representing two different life history types. For *Leucadendron salignum*, morphologically distinct males and females were sampled separately but were not different, and so their data were pooled for other analyses. Each point is a mean ($n = 6–13$) ±1 SE.

induced mortality is greater (Manders and Richardson 1992; Moreno and Oechel 1992; Pratt et al. 2008); additionally, evergreen seedlings in such environments have little capacity to avoid water stress. All life history types other than the OS type are disturbance dependent and recruit seedlings in open-canopy environments, and this is likely linked to their greater levels of water stress resistance. The OP life history type had the greatest resistance to water stress when compared with the other types; however, this conclusion is tentative because we analyzed only two species in the same genus (*Pteronia*), both of which are widespread in the more arid succulent karoo (Jacobsen et al. 2009).

The lower levels of cavitation resistance of the OS life history type put them at a disadvantage in more arid microsites, but their greater xylem hydraulic efficiency gives them an advantage in the more mesic microsites. Greater levels of efficiency would enable greater rates of photosynthesis (Kocacinar

and Sage 2003; Santiago et al. 2004). Among the life history types there was a clear trade-off, with greater levels of cavitation resistance being associated with lower levels of xylem efficiency.

We hypothesized that the NS life history type would have the greatest level of cavitation resistance compared with the other postfire recruiters, because OP types may escape some competition (Caswell 1982) and because FS types must allocate resources to sprouting. Consistent with this model, at least for NS and FS, recent studies have found greater resistance to stress among NS types in the California chaparral (Pratt et al. 2007, 2008), the Mediterranean basin (Paula and Pausas 2006), and Australia (Lamont and Markey 1995). Chaparral NS species tend to be shallow rooted and occupy the most arid microsites, while NS and FS species occupy different niches with respect to water (Davis et al. 1999; Pratt et al. 2007). Our results suggest that for fynbos species, the
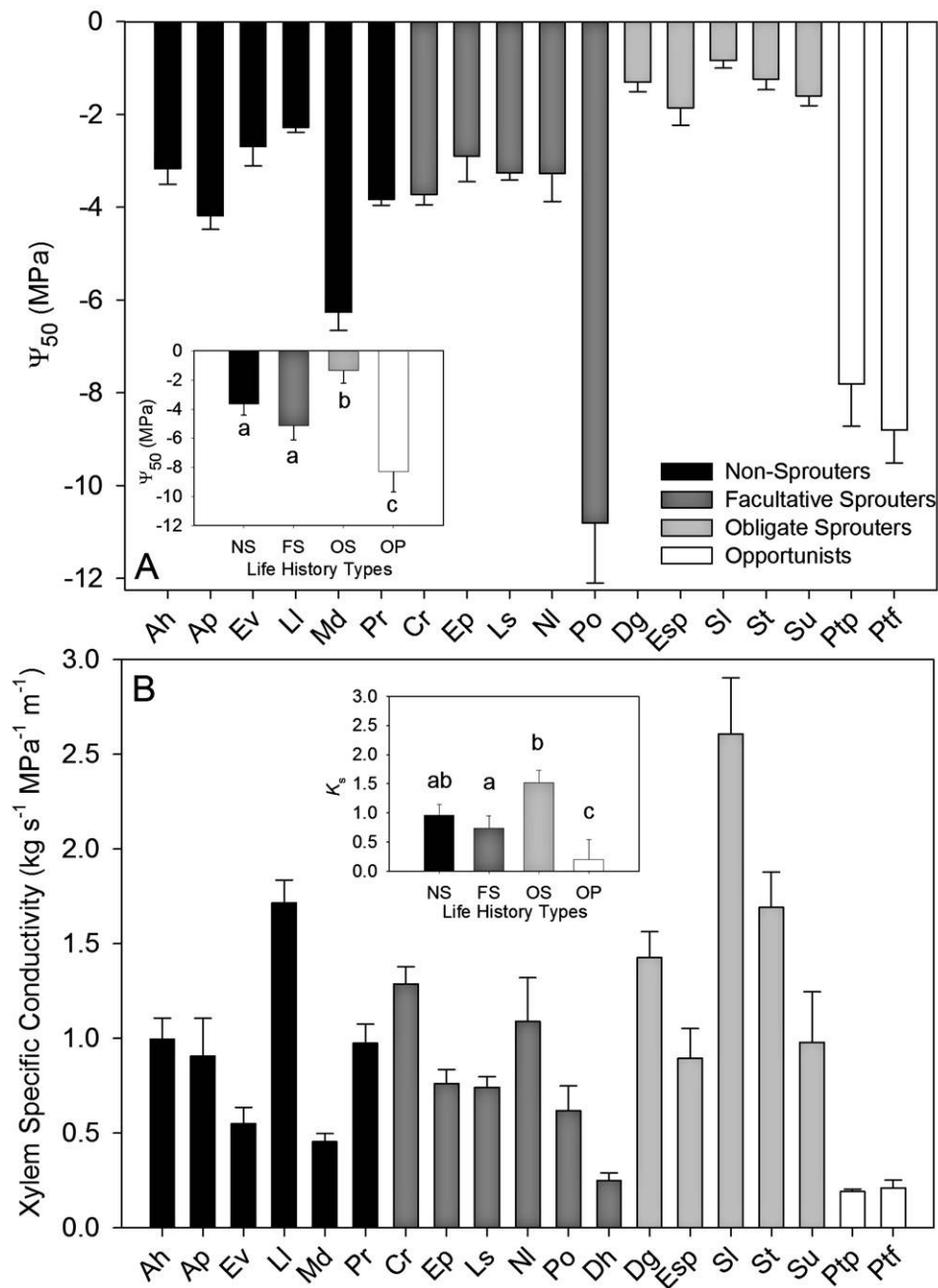
Fig. 2 Resistance to cavitation represented by the water potential at 50% loss of conductivity (Ψ_{50}; *A*) and xylem efficiency, estimated as xylem-specific hydraulic conductivity (*B*). Bars are means ($n = 6$–12) ± 1 SE. Species abbreviations from this study (along *X*-axes) are presented in table 1. Insets present the least squares means ± 1 SE of the different life history types; unique letters above bars indicate significant differences ($P < 0.05$).

NS and FS types have not diverged in their niche requirements with respect to water. Comparing southern California chaparral and fynbos species in this case is not confounded by differences in annual rainfall between the two regions, because all of the fynbos NS species were sampled at a site that was matched to southern California for rainfall (Jacobsen et al. 2009). However, timing of rainfall may be a factor, because time between rainfall events is generally shorter in

South Africa than in southern California (Cowling et al. 2005).

If fynbos NS and FS species have not diverged in terms of niche water relations, then how can they coexist? Allocation trade-offs between sprouting, stress resistance, growth, and reproduction suggest some clear predictions. Because NS and FS species have similar investments in water stress resistance, the FS species that allocate resources to sprouting must have
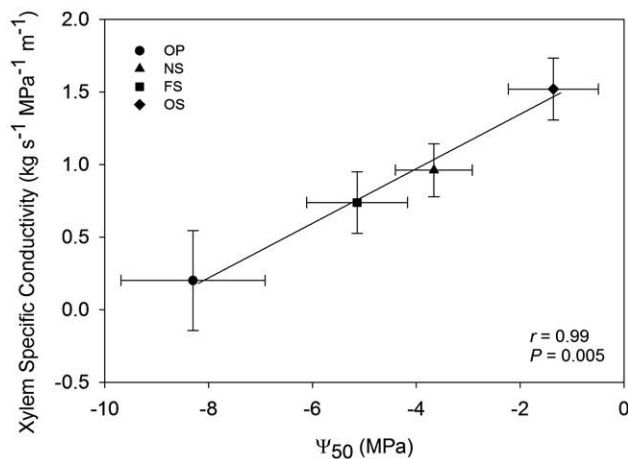
Fig. 3 Scatterplot of xylem efficiency (xylem-specific conductivity) and xylem resistance to cavitation (Ψ_{50}). Data points are the pooled means of each life history type from fig. 1. Line is the fit and statistics are from a standardized major-axis regression.

reduced growth and/or reproduction compared with NS species. There is good evidence that fynbos FS species generally have reduced growth and reproduction compared with NS species. This suggests that FS species are at a competitive disadvantage when competing directly with NS species. Consistent with this, many NS species dominate and form dense monotypic stands over large areas (e.g., *Leucadendron rubrum* Burm. f. and *Protea repens* [L.] L. at Paarl; Milton 2003). The stochastic nature of fire may be important for keeping some fynbos stands out of competitive equilibrium, which could facilitate FS and NS coexistence (Cowling et al. 1997b; Pickett 1980).

The seedling stage of development is often the chief demographic bottleneck in the life cycle of a woody plant (Grubb 1977; Davis 1991). The species in this study were sampled at the adult stage of development. Seedlings and adults may not be different in terms of cavitation resistance, a result that was found in two recent studies of chaparral species (Pratt et al. 2007, 2008). Ontogenetic plasticity could lead to differing hydraulic traits between adults and seedlings; however, adult plants may commonly retain functional traits that are better understood as adaptations to their regeneration niche than to their adult niche (Poorter 2007).

Life history types of fynbos and chaparral speices are divergent in terms of xylem water stress resistance. The pattern of water stress resistance among different life history types of chaparral shrubs is as follows: NS > FS = OS (Jacobsen et al. 2007; Pratt et al. 2007). In the fynbos, NS species do not generally have shallow roots and have not invaded more arid microsites (at least for ericoid and proteoid fynbos species; Higgins et al. 1987; Smith and Richardson 1990; Smith et al. 1992; Richards et al. 1995; Ojeda 1998; Ojeda et al. 2005). One reason for the lack of convergence may be the California dry season, which is generally more protracted and predictable than that of the Cape Region of South Africa (Cowling et al. 2005). This may have created more opportunities for NS species to invade open arid microsites in the

chaparral. Also, in the fynbos, competition for water may be reduced compared with in chaparral, on account of the poorer nutrient levels in soils, which leads to lower productivity (Cowling et al. 1997b). Reduced competition may also slow competitive exclusion of FS by NS, which may be a factor affecting the coexistence of NS and FS fynbos species despite apparent niche overlap in water requirements and the competitive advantage of the NS life history type (Cowling et al. 1997b).

The OS species studied have floristic affinities suggesting a subtropical thicket origin (Cowling et al. 1997a) that is generally more mesic than the Mediterranean-type climate region in the Western Cape, and this may relate to the lower resistance to water stress in these species. The broadly bird-dispersed seeds of the OS life history type enable these species to disperse to mesic microsites in the fynbos that may not be very different from their ancestral subtropical niche (Ackerly 2003). The OS life history type thus may represent a case of phylogenetic niche conservatism (Herrera 1992; Ackerly 2004).

We compared resistance to water stress–induced cavitation and K_s of individuals at a site with higher rainfall with that of individuals at a site with lower rainfall. As expected, taxa at the lower-rainfall site generally had greater resistance to cavitation and lower K_s values, with the exception of *L. salignum*. This suggests that in fynbos species, xylem safety from cavitation is an important trait for resisting water stress and drought. It also reinforces our previous assertion that cavitation resistance comes at the cost of reduced hydraulic efficiency (Tyree et al. 1994). The hydraulic differences between the sites could be due to genetically based differences in xylem hydraulics that have arisen via natural selection, or they may represent phenotypic plasticity in these traits.

Conclusions

Because of limited resources, life history variation is constrained by trade-offs in growth, survival, and reproduction. Physiological traits are likewise constrained by many of the same limited resources; thus, there are good grounds to suggest that physiological/functional traits should be linked to life history types (Ricklefs and Wikelski 2002). Here we show that fynbos life history types are divergent in their resistance to water stress such that OP > NS = FS > OS. These results are consistent with demographic pressures operating in the regeneration niche of the different life history types. There is a clear trade-off between safety and efficiency among fynbos life history types. The lower hydraulic efficiency of life history types that recruit in a disturbance-dependent fashion may lead to reduced photosynthetic capacity (Brodribb and Feild 2000). Differences in xylem safety and efficiency between a wet and a dry site suggest that adaptive adjustments in hydraulic traits are important among fynbos taxa. Site differences also supported a trade-off between safety and efficiency, as the taxa that had greater cavitation resistance at the drier site also tended to have lower xylem efficiency at the drier site.

One of the key challenges in ecology is linking lower scales of organization to higher levels. One area where we currently have limited ability to scale is between the organismal
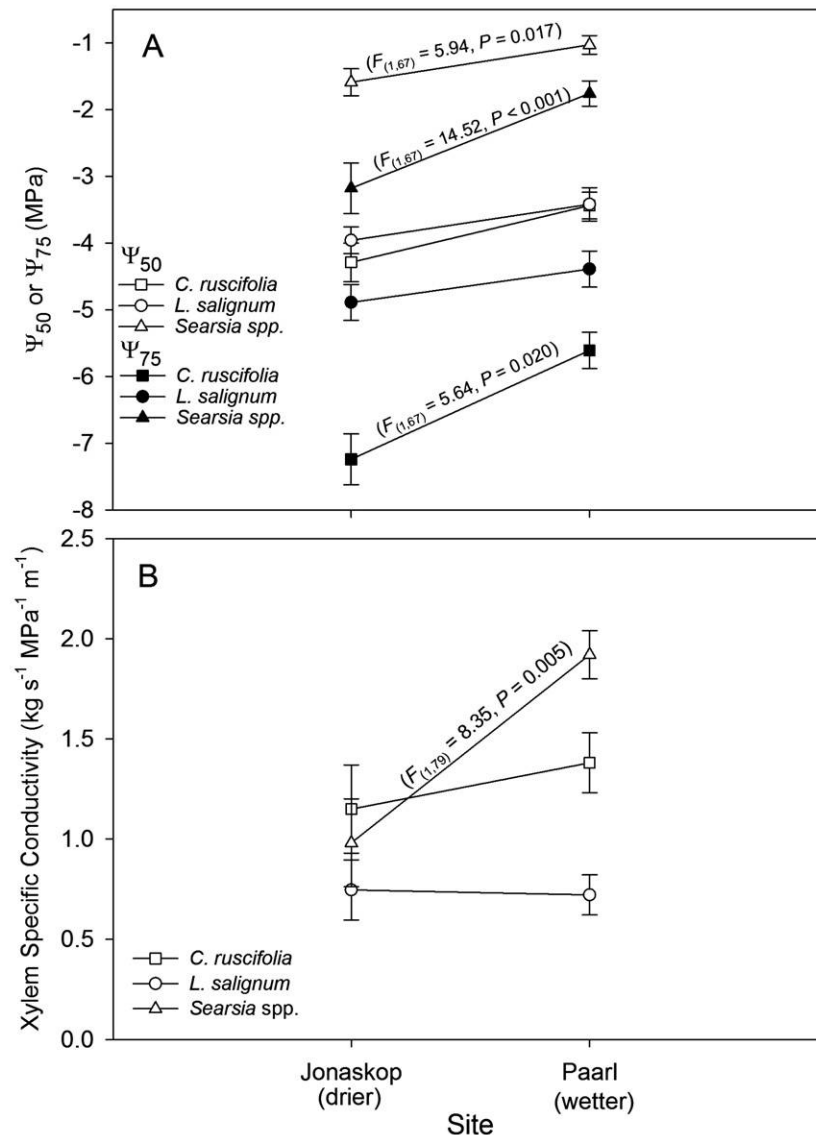
Fig. 4 Xylem resistance to cavitation (Ψ_{50}; A) and xylem efficiency (xylem specific conductivity; B) for species sampled at a drier field site and a wetter field site. At Paarl, two *Searsia* spp. were sampled and their data were pooled for this analysis (table 1), whereas only one *Searsia* sp. was sampled at Jonaskop. Data points are means ($n = 6$–24) ±1 SE.

functional scale and the community and population scales (Lawton 1991; McGill et al. 2006). The approach we used in this study holds considerable promise to be able to bridge these two scales. This is because life history traits can be directly translated to population growth via matrix population models (Bond and van Wilgen 1996). Linking functional traits to different life history types then allows us to readily scale functional traits to population level effects. What is key in these analyses is the ability to categorize plants into life history types and the linking of functional traits to the different life history types. A promising way to develop functional and life history type links is through niche requirements of the different life history types (McGill et al. 2006).

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