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Facing drought in a Mediterranean post-fire community: tissue water relations in species with different life traits

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Abstract

Bulk shoot water potential, the osmotic component and the bulk modulus of elasticity were measured throughout one growing season in four species co-occurring in a post-fire Mediterranean community in Southern Italy: *Pinus halepensis*, *Phillyrea latifolia*, *Cistus salvifolius* and *Rosmarinus officinalis*. A severe drought occurred throughout the measurement period. Large seasonal fluctuations have been observed for both predawn and afternoon water potential in all species. Although minimum values down to -4 MPa have been measured, plant water potential always recovered to less negative values after drought. Daily amplitude of water potential decreased with increasing plant water stress in all species. In *Cistus* and *Rosmarinus* less ability for short-term control of plant water status have been assessed. Osmotic potential at full turgor did not display clear seasonal patterns, with no consistent ranking of species by their osmotic values. In most cases, no osmotic adjustment (lowering of osmotic potentials) and no change in tissue elastic properties were observed in response to increasing summer drought and intensity of water stress.

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Keywords: *Cistus salvifolius*; *Phillyrea latifolia*; *Pinus halepensis*; *Rosmarinus officinalis*; Osmotic adjustment; Water potential

1. Introduction

Mediterranean plant communities have to withstand prolonged soil and air dryness, resulting from the combination of low rainfall, high temperatures and irradiances; environmental conditions may become even harsher after fire, as fire-induced changes in soil properties may result in an increase of evaporation and surface temperatures. In post-fire communities species with different life traits, implying different strategies of drought resistance, coexist (Trabaud, 1987). In some cases, for instance, withstanding drought results from stomatal closure and leaf abscission, both implying growth reduction or even complete growth cessation; in others, it relies on structural properties and physiological mechanisms allowing the plant to withstand drought without suspending growth (Ludlow, 1989).

Osmotic components of water potential could provide an estimate of dehydration tolerance since, by lowering their osmotic potential, plants enhance their ability to extract water from dry soil, maintaining cell turgor (Kramer, 1983); in the last decades, large amount of data has been accumulated on the significance of osmotic adjustment as acclimation response to drought (Kozłowski and Pallardy, 2002). On the other hand, substantial interaction of osmotic changes with environmental factors has been demonstrated (Tschaplinski et al., 1998); moreover, not frequently the assessment of osmotic adjustments was attempted under field conditions, in response to natural drought.

This work has been carried out in a Mediterranean post-fire community in Southern Italy where we have compared, throughout one entire growing season, bulk tissue water relations of four species characterized by different reproductive and morphological attributes. In particular, looking at seasonal patterns of the osmotic component of water potential we tried to find out if osmotic adjustment is a response to progressing summer drought in these species.

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58 2. Materials and methods

59 2.1. Study area

60 The study area is located close to the Ionian Sea in South-
 61 ern Italy (40°29' N, 16°58' E, sea level). The climate is
 62 Mediterranean, semi-arid type, as rainfall distribution im-
 63 poses a rather severe drought period during summer (Fig. 1).
 64 In 1993, 7 years after the occurrence of a fire, which de-
 65 stroyed a mature Aleppo pine (*Pinus halepensis* Mill.) forest
 66 growing on sandy dunes, the sparse vegetation consisted of
 67 Aleppo pine seedlings naturally recruited after fire and by
 68 post-fire shrub species, with a cover around 25%. The re-
 69 search was carried out on the main species co-occurring in
 70 the post-fire community, i.e. *P. halepensis*, *Cistus salvifolius*
 71 L., *Rosmarinus officinalis* L. and *Phillyrea latifolia* L.,
 72 showing contrasting morphological and ecological traits
 73 (Table 1). In particular, after fire *Pinus*, *Cistus* and *Rosmari-*
 74 *nus* regenerate from seeds, whereas *Phillyrea* regenerates

from root resprouts. Thus, for the three reseeding species
 measurements were made on new individuals naturally re-
 generated after fire and no more than 7 years old; while in the
 case of *Phillyrea* root resprouts were studied. Seedlings and
 resprouts of all species were 0.2–2 m high, growing in full
 light.

2.2. Field and laboratory measurements

At 40–50 day intervals between September 1993 and
 November 1994 bulk shoot water potential was measured
 with a Scholander-type pressure chamber (PMS Instruments,
 Corvallis, OR), before dawn (predawn water potential, ψ_p)
 and in early-mid afternoon (afternoon water potential, ψ_a).
 Measurements were made on 1(2) apical shoots from six to
 eight plants of each species, randomly sampled in the area;
 pressure chamber readings were made immediately after
 shoots were detached. At the end of each measurement day,
 one shoot was excised from the same plants sampled for

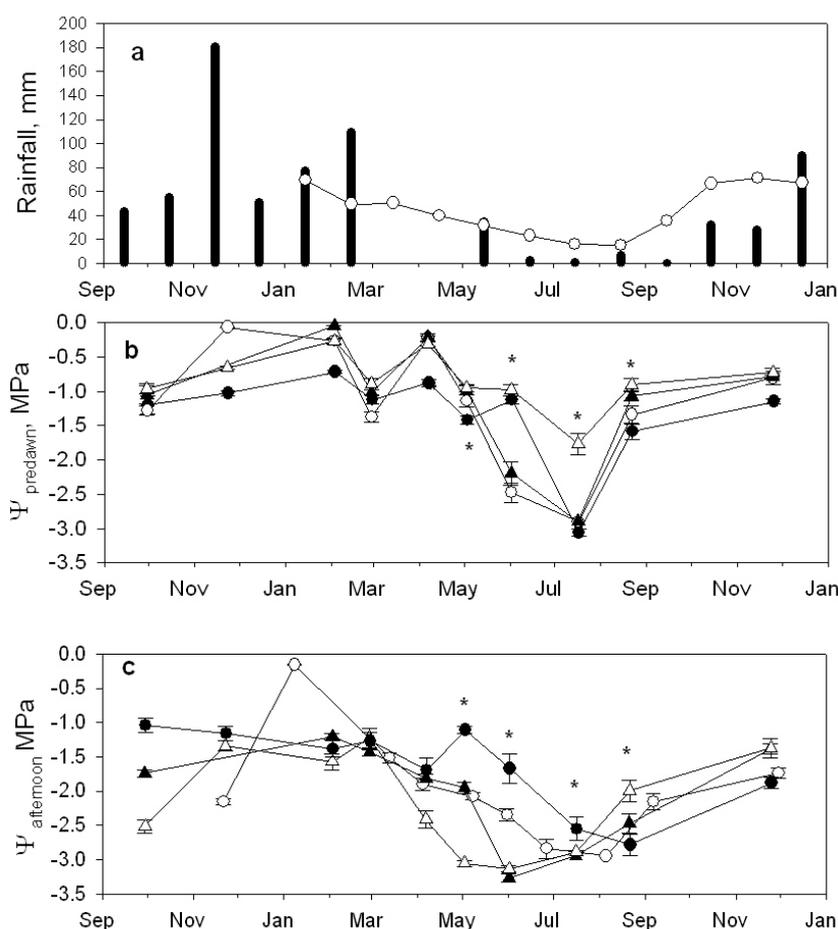


Fig. 1. 1994 (black bars) and long-term (1930–1980) (open circles) rainfall at the study site (panel a); seasonal pattern of predawn (ψ_p , MPa) (panel b) and afternoon (ψ_a , MPa) (panel c) water potential for: *Pinus halepensis*, closed circles; *C. salvifolius*, open circles; *R. officinalis*, closed triangles; *P. latifolia*, open triangles. In panel b and c, * indicates, for the period May–September 1994, the dates at which significant ($P < 0.05$) differences between species have been detected.

Table 1
Attributes of the studied species

	<i>P. halepensis</i>	<i>C. salvifolius</i>	<i>R. officinalis</i>	<i>P. latifolia</i>
Habitus	Tree	Dwarf shrub	Dwarf shrub	Shrub
Fire response	Seeder	Seeder	Seeder	Sprouter
Source of propagule	Seed bank in the crown	Persistent soil seed bank	Transient soil seed bank	Dormant buds on main roots
Post-fire emergence	Autumn	Winter	Winter	After first rain
Post-fire spatial pattern	Isolated to clumped	Clumped	Isolated	Isolated
Root depth	Shallow	Most shallow	Shallow	Deep
Leaf morphology	Needle	Malacophyllous	Sclerophyllous	Sclerophyllous
Leaf phenology	Evergreen	Semi-deciduous	Evergreen	Evergreen

92 water potential measurement; shoots were closed in plastic
93 bags and stored in a cooler box for transport to the laboratory.
94 Pressure–volume isotherms were determined by the dry-
95 ing method described by Talbot et al. (1975). In the evening
96 of each measurement day, excised shoots were recut under
97 water, submerged in distilled water and here allowed to
98 rehydrate overnight, in the dark. The following morning,
99 shoots were weighed (to the nearest mg) and placed in the
100 pressure chamber for determining the initial value of xylem
101 water potential. Afterwards, shoots were allowed to dehy-
102 drate on the laboratory bench by free transpiration at room
103 temperature (20 °C); the weight and the water potential of
104 each shoot were then periodically measured: at the beginning
105 every 5–10 min; successively, when dehydration was already
106 marked, every 15–20 min. Measurements continued until
107 two subsequent measurements of xylem pressure potential
108 showed differences less than 0.01 MPa; this occurred at
109 different values of water potential in different species (in
110 most cases when water potential was between –3 and
111 –4 MPa). Shoots were then dried at 80 °C for 48 h and dry
112 weights determined to the nearest mg.

113 2.3. Analysis of pressure–volume isotherms

114 Pressure–volume isotherms of unsaturated samples were
115 analysed using a regression model written in SAS (PROC
116 NLIN, SAS Institute Inc. 1988), applying a derivative-free
117 algorithm. Over-saturated samples, in which initial changes
118 in sample weight, due to rapid loss of apoplasmic water, were
119 not accompanied by changes in water potential, were dis-
120 carded (Kubiske and Abrams, 1990). The saturated weight is
121 computed by the programme by imposing null water poten-
122 tial at full turgor (Sinclair and Venables, 1983); changes in
123 osmotic potential are described by the Van't Hoff equation
124 and a power function describes the decline in turgor potential
125 with weight loss (Schulte and Hinckley, 1985). The osmotic
126 potential and the modulus of elasticity at full turgor were
127 estimated.

128 3. Results and discussion

129 In 1994 the scarcity of precipitation—a total of 50 mm
130 between April and September—imposed a long and severe
131 drought at the study site (Fig. 1a); the same situation oc-

132 curred in the same period in Central and Southern Spain 132
133 (Peñuelas et al., 2001). In response to the development of 133
134 drought, large seasonal fluctuations of predawn water poten- 134
135 tial have been observed in all species, with coincident peaks 135
136 and troughs: in particular a marked decrease in late spring 136
137 and summer and an evident recovery in the autumn (Fig. 1b). 137
138 A significantly ($P < 0.05$, *S.N.K.* test) less negative predawn 138
139 water potential was attained by *Phillyrea* and *Pinus* at the 139
140 beginning of June and by *Phillyrea* in mid July; at this date, 140
141 in particular, *Phillyrea* showed a value of –1.8 MPa, whilst 141
142 all other species lowered predawn water potential down to 142
143 –2.8 MPa (Fig. 1b). Considerable scatter in data is revealed 143
144 by afternoon water potentials: in three out of four dates 144
145 between May and September *Pinus* showed significantly 145
146 higher values, suggesting effective control of plant water 146
147 status, whilst no consistent ranking was observed for the 147
148 other species (Fig. 1c). 148

149 Following previous approaches (Aussenac and Valette, 149
150 1982; Rambal, 1992), daily oscillations of plant water status 150
151 have been represented as the difference between predawn 151
152 and afternoon (minimum) water potential ($\Psi = \Psi_p - \Psi_a$) 152
153 and a contour analysis of Ψ/Ψ_p relationship has been car- 153
154 ried out, defining a quasi-boundary linear regression line 154
155 ($\Psi = a + b\Psi_p$) (Fig. 2). The analysis revealed a pattern in 155
156 which daily amplitude of water potential decreased with the 156
157 intensity of plant water stress. The rate of decrease b was 157
158 lower in *Cistus* and *Rosmarinus*, suggesting no tight short- 158
159 term control of plant transpiration. The same analysis sug- 159
160 gests higher maximum daily amplitude of water potential in 160
161 *Phillyrea* and *Pinus*, likely due to higher transpiration rates, 161
162 and, at least in *Pinus*, more effective short-term control of 162
163 transpiration, likely due to stomatal closure. 163

164 Osmotic potential at full turgor did not display clear sea- 164
165 sonal patterns (Fig. 3a,b), with no consistent ranking of 165
166 species by their osmotic values. Differences in osmotic po- 166
167 tential between the drought period (June–September) and the 167
168 rest of the year were not significant in any of the studied 168
169 species. Thus, no osmotic adjustment was observed in re- 169
170 sponse to increasing intensity of water stress; similar results 170
171 have been provided for oak species (Abrams 1990). In gen- 171
172 eral, little osmotic adjustment is observed, either in con- 172
173 trolled and field conditions, in species whose stomata are 173
174 particularly sensitive to drought (Ludlow, 1989), so that 174
175 osmotic adjustment seems at work for turgor maintenance 175

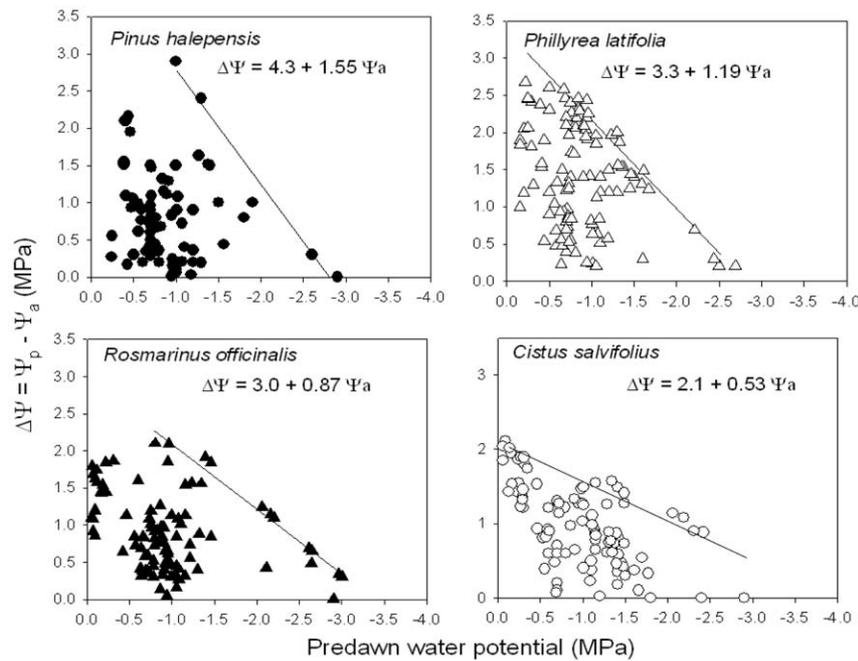


Fig. 2. Scatter plot of predawn water potential vs. the difference between predawn and minimum daily (afternoon) water potential, with the quasi-boundary straight line: upper contour data points have been arbitrarily selected. The intercept on the X-axis (ψ_{max}) can be viewed as the maximum daily amplitude of plant water potential under high atmospheric evaporative demand and optimal soil water availability; the slope b indicates how much predawn and minimum potentials are related ($b = 1$ means homeostasis of water potential) (see Rambal, 1992).

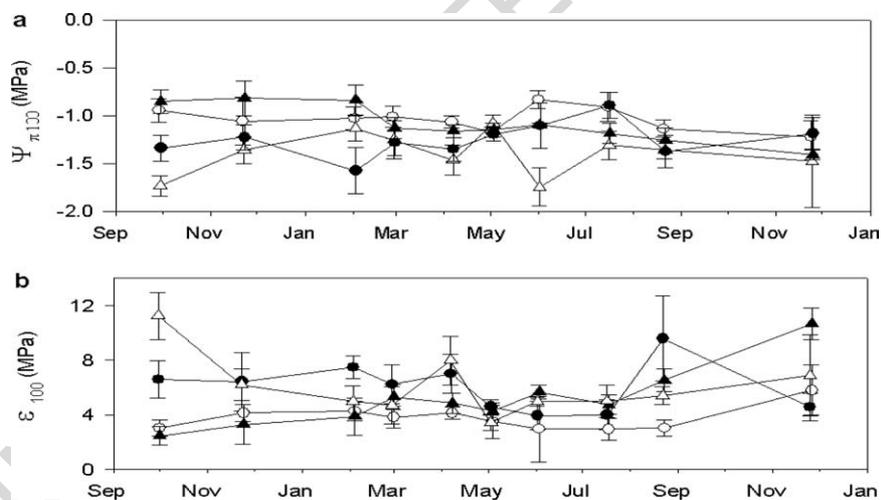


Fig. 3. Seasonal pattern of osmotic potential (ψ_{100}) (panel a) and modulus of elasticity (ϵ_{100}) (panel b) for: *Pinus halepensis*, closed circles; *C. salvifolius*, open circles; *R. officinalis*, closed triangles; *P. latifolia*, open triangles.

176 mainly at moderate values of plant water potential (Augé et al., 1998; Parker and Pallardy, 1988; Tschaplinski et al., 178 1998).

179 During the drought period *Phillyrea* displayed significantly ($P < 0.05$, *S.N.K.* test) lower values of osmotic potential with respect to the other species, with a clear minimum in 182 June. Pooling all measurement dates together, osmotic potentials of *Pinus* and *Phillyrea* were significantly ($P < 0.05$, 184 *S.N.K.* test) lower than those of *Rosmarinus* and *Cistus*. In 185 *Pinus* a negative significant regression between predawn 186 water potential and osmotic potential at full turgor was found

(not shown), possibly due to severe constraints to assimilation by drought-induced stomatal closure, which might have caused a reduction in the concentration of osmotica (Kozłowski and Pallardy 2002). 187 188 189 190

In quite the same way, the modulus of elasticity at full turgor, which has also been proposed as a mechanism for turgor maintenance under water stress conditions (Hinckley et al., 1980) did not display acclimation to drought or easily interpretable seasonal fluctuations, nor significant interspecific differences. 191 192 193 194 195 196

Table 2

Some literature evidence on mechanisms for withstanding drought in the studied species together main hints from the present study

	<i>P. halepensis</i>	<i>Cistus</i> spp./ <i>C. salvifolius</i>	<i>R. officinalis</i>	<i>P. latifolia</i>
Literature evidence	Low transpiration rates and effective stomatal control of water loss ^{a,b,c} . Osmotic adjustments observed only in some cases in potted seedlings ^{a,c,d,e}	Leaf dimorphysm, leaf abscission, regulation of leaf angle as adaptations to drought; leaf folding to avoid photoinhibition ^{f,g,h} ; tolerance to tissue desiccation ⁱ . Effective stomatal regulation in over summering leaves ^j	Reduction of leaf area and leaf curling as adaptation to drought ^k . Control of transpiration and ability to maintain a favourable water status ^l ; photosystem II not highly sensitive to drought ^{l,m}	Acclimation to high irradiances, but no effective control of transpiration and leaf water content ^{h,n,o,p} . Capacity to extract water deep in the soil profile, tolerance to salt ^{q,r}
Hints from this study	Short-term control of plant water status, suggesting effective stomatal regulation. Significant negative relationship between osmotic potential at full turgor and predawn water potential. No adjustment of tissue elasticity in response to long-term drought	Modest short-term control of plant water status. Low maximum transpiration rates. No evidence of osmotic adjustment or tissue elasticity in response to long-term drought	Modest short-term control of plant water status. Low maximum transpiration rates. No evidence of adjustment of osmotic potential or tissue elasticity in response to long-term drought	High maximum transpiration rates, but maintenance of a favourable water status during drought, suggesting effective water uptake. Sporadic lowering of osmotic potential during drought; no adjustment of tissue elasticity in response to long-term drought

^a Tognetti et al. (1997).^b Borghetti et al. (1998).^c Villar-Salvador et al. (1999).^d Calamassi et al. (2001).^e Royo et al. (2001).^f Correia et al. (1992).^g Correia and Catarino (1994).^h Gratani and Bombelli (2000).ⁱ Karavatas and Manetas (1999).^j Harley et al. (1987).^k Nogués et al. (2001).^l Bowman and Roberts (1985).^m Munné-Bosh et al. (1999).ⁿ Filella et al. (1998).^o Peñuelas et al. (1998).^p Nardini et al. (1996).^q Gucci et al. (1997).^r Tattini et al. (2000).

197 In conclusion—see also Table 2 for comparison of main
 198 hints from the present study with literature evidence on the
 199 mechanism of withstanding drought in these species—in the
 200 studied Mediterranean community, where unfavourable en-
 201 vironmental conditions may heavily restrict plant assimila-
 202 tion, neither osmotic adjustment nor changes in tissue elastic
 203 properties seem to be at work among the number of mecha-
 204 nisms (stomatal closure, leaf abscission, deep rooting) that
 205 allow plants to withstand drought. Changes of the osmotic
 206 component, as in the case of Aleppo pine, should be regarded
 207 as a consequence of other acclimation mechanisms.

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