WATER POTENTIAL OF TREES AND SHRUBS IN INTACT AND MODIFIED POPLAR BOX (EUCALYPTUS POPULNEA) WOODLANDS

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Abstract

Measurements of dawn water potential were obtained for trees and shrubs growing within plots in adjacent brigalow (Acacia harpophylla) and poplar box (Eucalyptus populnea) communities. These plots contained plant communities that varied greatly in the proportions of trees, shrubs and grasses, due to prior treatments of killing of various proportions of trees and shrubs, with or without exclusion of livestock.

Water potentials of plants in the brigalow community were always lower than in the poplar box community, thus while brigalow occurred in the run on position in the landscape, physiologically it was the drier community. The water potentials of shrubs were higher than those of poplar box at high water potentials and the reverse applied at low water potentials. The shrub species differed in their response to dry conditions but over time the dominant species tended to maintain the higher water potentials. There was little difference between dawn water potentials of false sandalwood shrubs (*Eremophila mitchellii*) of different size but smaller shrubs tended to have the lower water potentials. In ungrazed plots, the water potential of false sandalwood shrubs was lower in woodlands than where all trees had been killed; their water potential in grazed plots was intermediate. Dawn water potentials of false sandalwood were higher in shrublands than in woodlands.

It is suggested that dawn plant water potential is a better indicator of water availability to plants than soil water content if systems such as this where soil differences exist and where changes in soil water can be accompanied by changes in salinity. The results indicate that shrub water status is enhanced with the killing of trees but that this relationship is confounded by grazing. The difference in response to soil conditions between plant species, and the non-attainment of zero plant water potential, are discussed in relation to rooting distribution and non-uniform profiles of soil water potential.

Introduction

Poplar box (*Eucalyptus populnea*) woodlands constituted a large portion of the woodland vegetation of eastern Australia (Beeston et al., 1980). Most of these woodlands have been cleared for pasture and croping but substantial areas have regenerated and become 'shrub infested' (Harrington et al., 1979). Such regeneration is most pronounced in the more arid regions. This could be seen as reflecting the economic viability of clearing for farming (Young, 1980) but such regeneration was never a problem with grazing in areas of high rainfall or on clay soils. This indicates that shrub encroachment might reflect changes in water availability. Given that water availability largely determines the patterns of Australian vegetation (Fitzpatrick & Nix, 1970), it is likely that changes in water availability would result in changes in vegetation.

Water availability to plants in the field is dependent on rainfall but this supply is modified in many ways. Interception, runoff and drainage usually reduce but can increase the effective rainfall. Moreover, the water release and hydraulic properties of the soil moderate the availability of soil water to plants and, where plants grow in communities in a competitive situation, the availability is also determined by rooting patterns and rates of water use. Given this complexity, measures of soil water content do not provide a direct indication of water availability to plants, particularly where the soil physical and chemical properties and plant rooting characteristics are unknown.

The alternative to measuring soil water availability is to measure plant response. The complication then is that plant water status is affected by atmospheric as well as soil conditions. This problem can, however, be circumvented by measuring plant water status at dawn when the plant should be in equilibrium with the soil: with free water in the soil, dawn plant water potential should reflect only the gravitational gradient (Whitehead & Jarvis, 1981). This conclusion is based on the knowledge that stomata are, by at least an order of magnitude, the greatest sources of resistance to water flow through plants (Cowan, 1972) and that the stomates of most plants close in the dark. It is also assumed that plant water potential reflects a purely physical system. The apparent non-attainment of zero water potentials when expected (Ritchie & Hinkley, 1975) casts some doubt on these assumptions but zero potentials have been measured in a number of shrubs in the field at dawn when water was freely available (Tunstall, 1967).

The objective in this study was to investigate water availability in intact and modified poplar box woodlands using comparative measures of the water status of trees and shrubs with a view to interpreting observed shrub encroachments.

Methods

The study was conducted near Talwood in south-west Queensland (Lat. 28°58'S, Long. 149°50'E) and made use of a number of experimental areas (Tunstall et al. 1981). Measures of dawn water potential of false sandalwood (*Eremophila mitchellii*) and the trees were taken at fortnightly intervals over five months in poplar box and brigalow (*Acacia harpophylla*) 'woodlands' following the killing of trees. Duplicate measures were obtained for each treatment (factorial of trees killed/not killed : poplar box/brigalow) and each species from plants chosen at random on 12 occasions. Volumetric soil water content was also monitored (Tunstall & Walker, 1975). On these and three subsequent occasions, replicate measures of the dawn water potential of the major tree and shrub species were also obtained in plots established in 1966 (Walker et al., 1972) where 95 of the trees had been killed and livestock excluded.

False sandalwood remained common to most of the plant communities resulting from previous experimental treatments. In February 1975 and twice in March 1975 the dawn water potential of 6 replicates of false sandalwood 1-2 m high was measured in each of 12 situations. The times were chosen to give differing conditions of soil water availability. On the same occasions, the water potential of false sandalwood in the size classes 0-1, 1-2, 2-3, 3-4 and greater than 4 m was measured in four systems representing the factorial combination of tree killing and grazing. Six plants were selected at random within each category in each system on each of the three occasions.

Plant water potential was measured using a pressure cylinder (Scholander et al., 1964). Experience with brigalow indicates no gross error in assuming that the pressure cylinder does estimate potential (Tunstall & Connor, 1981) but likely errors with the other species are unknown. Cross-calibration with a thermocouple psychrometer would be of limited value because of long equilibration times arising from the high cuticular resistances of some of these species. Also, in the context of this study, absolute accuracy is not critical. The requirement is for a reliable measure providing sufficient resolution to ascertain differences.

Results

The dawn water potential of plants in brigalow and poplar box communities was compared with volumetric water content of the surface 0.1 and 1.6 m of soil using regression analysis. The percent variance accounted for by simple linear regressions is given in Table 1. Plant water potential was more closely related to the water content of the 'whole' soil profile than to that of the surface soil. The water potential of false sandalwood was equally well correlated with soil water content in both communities. Correlations for brigalow were similar to those for false sandalwood but the water potential of poplar box was relatively poorly related to soil water content. Average soil water storages to 1.6 m in the brigalow and poplar box communities were approximately 0.37 and 0.27 m respectively.

The dawn water potentials of the trees and false sandalwood were compared between brigalow and poplar box communities using linear regression (Fig. 1). The data for the shrubs and trees were combined as the results did not differ significantly. The occurrence of a regression slope greater than one with an intercept around zero indicates that plants in the brigalow community always had lower water potentials than in the poplar box community. This figure demonstrates that although brigalow occurs in the run-on position in the landscape it is physiologically the drier community.

The dawn water potential of false sandalwood is compared between 'intact' and 'trees killed' poplar box and brigalow systems in Fig. 2. The shrubs generally had a more favourable water status where trees had been killed.

Figure 3 compares the dawn water potential of false sandalwood to that of brigalow and poplar box in the respective communities. The shrub had a more favourable water status than trees under wet conditions but was drier when conditions were dry.

All shrub species had a more favourable water status than poplar box under wet conditions but were more desiccated when the soil was dry. The sequence of increasing tendency of the different shrub species to desiccate, as evaluated using regression analysis, is given in Table 2. Also in Table 2 are the mean dawn water potentials of the shrub species; these are a measure of average dawn water potential over time. The sequence of species based on mean values differs from that based on regression slopes (the intercepts of the regressions varied) but it is still apparent that some species tended to maintain a more favourable water balance than others. The species tending to have the higher water potentials were false sandalwood, *Acacia deanei,* and *Cassia nemophila* and these were the most abundant shrub species in the plots in terms of density and biomass (Tunstall et al. 1981).

In the analysis on plant size there were significant differences between sampling times and shrub size (Table 3) as assessed using analysis of variance. The smallest shrubs had the lowest water potentials, but the differences due to shrub size were small compared to those due to time of sampling.

Table 4 compares the water status of false sandalwood shrubs 1-2 m high between 12 systems resulting from the application of treatments to brigalow and poplar box communities. The systems have been ordered in the sequence of increasing water potential. False sandalwood generally had lower water potentials in shrublands than in woodlands. With one exception, water potentials in grasslands were intermediate. In terms of treatments the sequence of increasing water potential is trees not killed-not grazed, grazing, and trees killed-not grazed. Both trees and shrubs were killed in the three systems which do not fit this sequence; here the sample material came from recent regeneration rather than from established plants. Also, the area cleared by bulldozer contained poplar box trees 5 m high which had regenerated from lignotubers and so, structurally, was a woodland rather than a shrubland. Thus, excepting plots where the shrubs had been killed, false sandalwood in ungrazed woodlands had lower water potentials than in ungrazed grasslands/shrublands with the water potentials of shrubs in areas grazed by sheep being intermediate.

Discussion

The water potentials of trees and shrubs in the poplar box and brigalow communities differed markedly even though the communities were subject to the same aerial environment. The results indicate a greater rate of water use by brigalow than by poplar box, a conclusion consistent with observations on changes in soil water storage in these communities (Tunstall & Walker 1975).

Brigalow and poplar box occurred on cracking clay and duplex soils respectively (Webb et al. 1980) and at any dawn plant water potential the water content of the duplex soil was lower than for the clay (Tunstall & Walker, 1975). This indicates differing relationships between water content and water potential for these soils. The water relationships of the duplex soils would also have varied because of the changes in soil salt content associated with the killing of trees and grazing (Tunstall & Connor, 1981; Tunstall & Webb, 1981). The grazed grasslands generally had higher soil water contents than elsewhere but this was associated with higher soil salt contents (Tunstall & Walker, 1975); the net result is lower dawn water potentials of false sandalwood on grasslands than on shrublands despite the latter having the lower soil water contents. In this situation dawn plant water potential provides a better comparative measure of soil imposed stress than soil moisture content.

It has been suggested that encroachment of shrubs into poplar box grazing lands is associated with changes in soil water regime following killing of trees (Burch & Nicholls, 1981). The results here indicate that there is an increase in water availability to shrubs following the killing of trees but that this is confounded by grazing. The suggested situation of grasslands and shrublands being wetter and dryer than woodlands respectively (Burch & Nicholls, 1981) does not occur, nor does grazing necessarily increase water availability in grasslands. The results in Table 4 indicate that the water status of shrubs is similar where livestock graze woodlands or cleared country. The increase in water availability to shrubs following the killing of trees (Fig. 2) is not fully realized under grazing because of soil compaction and an increase in soil salinity and shrubs apparently benefit from the reduction in ground layer vegetation in woodlands grazed by livestock. This accords with the observation that shrub encroachment occurs in woodlands as well as cleared country (Harrington et al., 1979; Tunstall et al., 1981).

The results indicate that when the surface soil was wet the water potential of trees was much less than zero. A similar result was obtained in another study on brigalow where the highest plant water potential over a 3-year period, -1.45 KPa, was recorded when surface water had lain in community for over one month (Tunstall & Connor, 1981). The plants did not equilibrate with water at the highest potential in the root zone but reflected the range of potentials of the solutions around the roots. This effect was demonstrated by Kirkham et al,. (1969) by dividing the roots of plants between free water and solutions of restricted water availability and is reflected here in the relationships between plant water potential and soil water storage.

Despite the non-linearity of relationships between soil water potential and soil water content, simple linear regressions accounted for much of the variance between soil water storage and plant water potential. Thus the changes in water status of poplar box relative to those of shrubs (Table 2) may relate to the deep rooting system of the tree, with the water at depth acting as a buffer. The comparative responses of shrubs may also relate to rooting patterns, but the differences between shrub species illustrated in Table 2 could also be due, in part, to different rates of water use. Because of the spatial distribution of vegetation within the plots the different shrub species need not have been subject to identical conditions of soil water availability.

The least significant differences for determining treatment effects varied from 0.1 to 0.3 MPa and smallest errors were obtained where stratified sampling was used in the analysis of shrub size. Differences between communities and between plants of different size and life form were readily obtained using random sampling within plots containing heterogeneous vegetation but comparisons between shrub species were limited by variability. A non-random sampling system of selecting adjacent plants when comparing species could reduce the error associated with the assumption of uniform soil conditions within plots and thereby increase the value of the comparison between species.

A uniform profile of soil water potential should result in equal dawn water potentials for all species and differences in dawn water potential between species must arise through non-uniform profiles of soil water potential (both vertically and laterally) and variation in rooting depths and densities. Since plants in some way average the water potentials in a non-uniform profile, theoretically, concurrent measurements of dawn plant water potential and soil water over a range of conditions could be used to evaluate root distribution provided the nature of the averaging was known. As the results of Kirkham et al. (1969), Michel & Sharkawi (1970) and Herkelrath e_t al. (1977) indicate that such averaging is not linear, a clearer definition of plant response is required before such an analysis of root distribution can be undertaken.

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Table 1. Percent variance accounted for (R) by simple linear regressions between plant water potential and volumetric water content of the surface 0.1 and 1.6 m of soil. Comparisons are given for the trees and false sandalwood in both poplar box and brigalow communities.

	Poplar box community		Brigalow community	
	Plant species			
Water Content	Poplar box	False Sandalwood	Brigalow	False sandalwood
Surface .0.1 m	11	*46	*56	*44
Surface 1.6 m	*44	*64	*68	*64
* = significant	n = 11 for trees	n = 22 for shrubs		

Table 2. Plant species listed in sequence of increasing change in dawn water potential with change in environmental condition as evaluated by linear regression analyses, together with the average dawn water potentials for shrubs. For regression analysis the water potential of shrubs was compared with that of poplar box as in Fig. 3.

Species	Regression slope	Mean water potential (MPa) LSD = 0.3 MPa
Eremophila mitchellii	1.48 ± 0.50	2.57
Acacia deanei	1.83 ± 0.61	2.58
Cassia nemophila	1.99 ± 063	2.82
Jasminum lineare	2.02 ± 072	3.08
Eremophila glabra	2.13 ± 070	3.29
Myoporum desertii	2.13 ± 0.75	3.36
Dodonaea viscose	2.45 ± 0.6	2.75
Geijera parviflora	1.64 ± 0.70	2.99

Table 3. The main effects in the analysis of dawn water potential (MPa) of *Eremophila mitchellii* in relation to shrub size.

Shrub height (m)	**0-1**	**1-2**	**2-3**	**3- 4**	**4-5**
Mean (LSD 0.11)	3.66	3.37	3.32	3.26	3.25
Sample time	**1**	**2**	**3**		
Mean (LSD 0.095)	-4.93	-3.85	-1.32		

Table 4. Average dawn water potential *of Eremophila mitchellii* shrubs 1-2m high in communities treated as indicated 5-12 years prior to measurement.
LSD == 0.25 MPa

System	**Community structure**	**Water potential (MPa)**
Brigalow (NK, NG)	Grassy woodland	-4.01
Box (K*, SK*, NG)	Shrubby open woodland	-4.00
Box (NK, NG)	Grassy woodland	-3.75
Box (50% K, NG)	Shrubby open woodland	-3.63
Box (K, G)	Grazed grassland	-3.60
Box (NK, G)	Grazed woodland	-3.57
Brigalow (K, NG)	Shrubby grassland	-3.36
Box (90 %K, NG) A	Shrubland	-3.30
Box (90%Km, NG) B	Shrubland	-3.28
Box (K, NG)	Shrubland	-3.15
Box (K, SK, NG)	Grassy shrubland	-3.05
Box (K, SK, G)	Grazed grassland	-2.95

K = Trees killed
NK = Trees not killed
SK = Shrubs killed
G == Grazed by sheep
NG = Not grazed by domestic livestock.
* = Trees and shrubs 'killed' by bulldozer rather than by chemical means

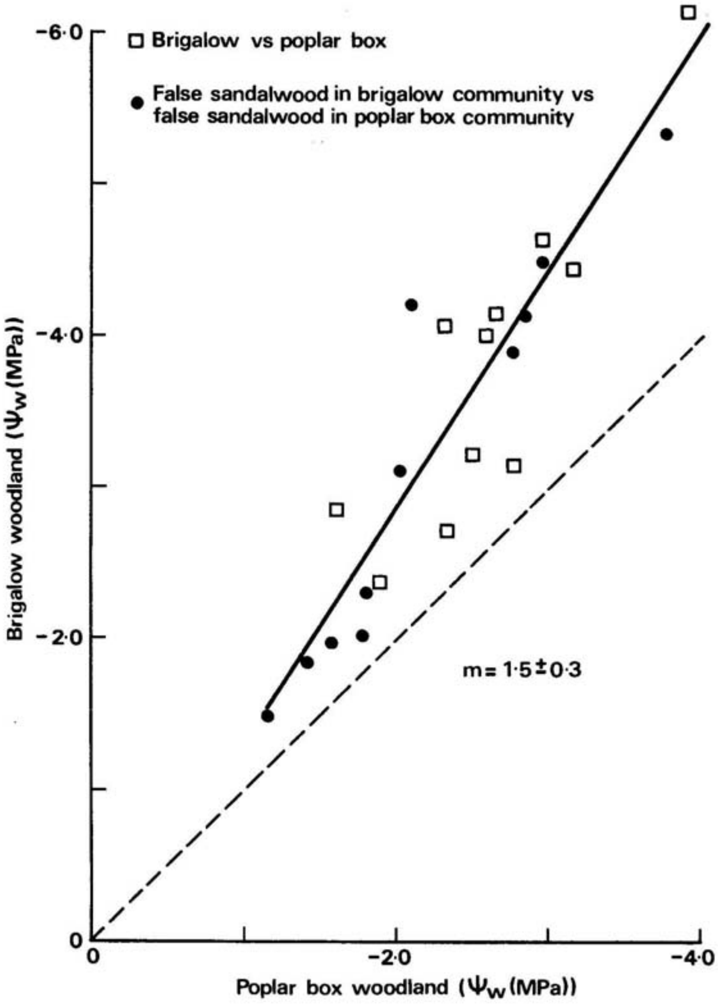

Fig. 1. Dawn water potentials of the. dominant plants in the. brigalow community compared with those of the dominant plants in the poplar box community (community vs. community) (R= 0.94, n = 23)

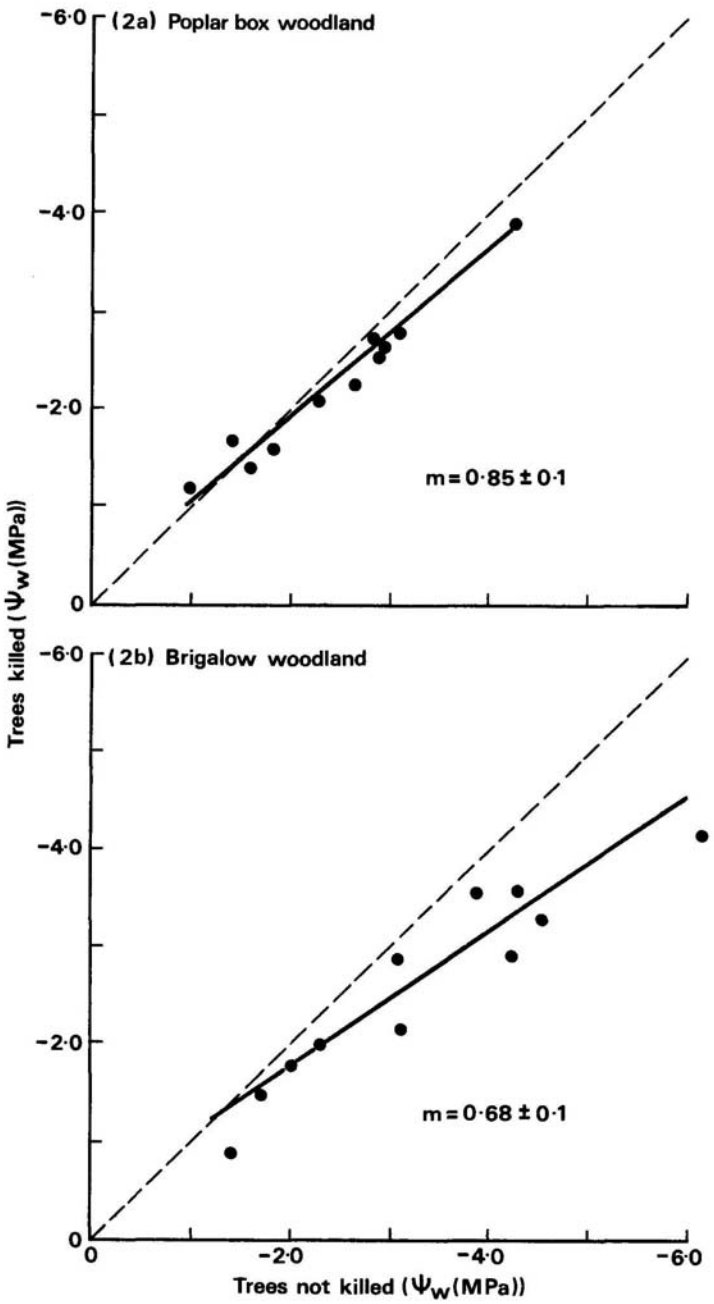

Fig. 2. Dawn water potentials of sandalwood in the intact communities compared with those for sandalwood where the trees were killed (killed vs. not killed) (r= 0.94, n=22)

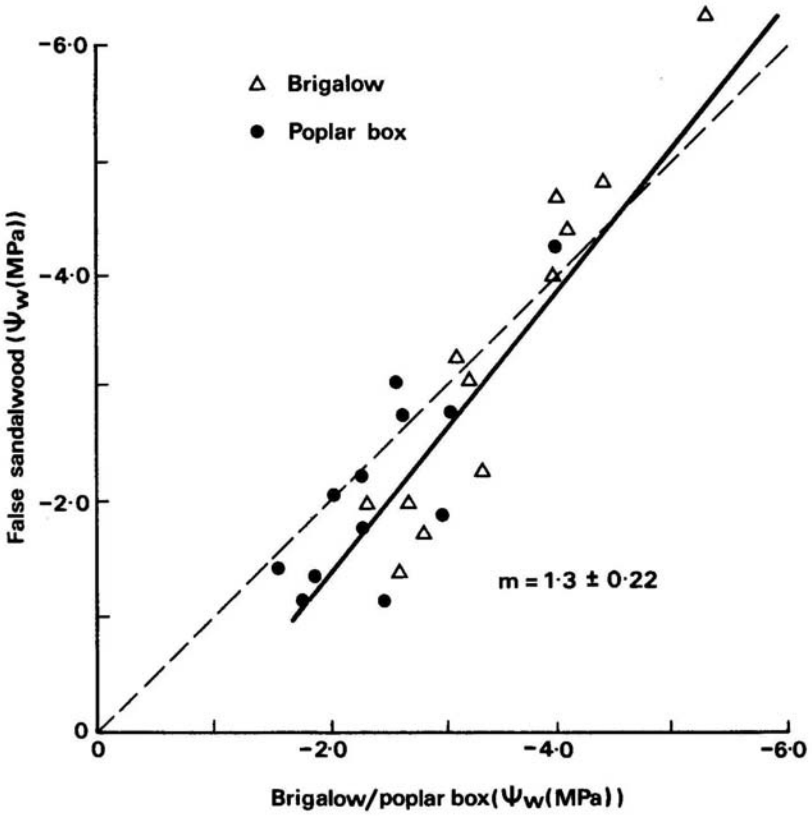

Fig. 3. Dawn water potentials of sandalwood compared with those of poplar box and brigalow in the respective communities (shrub vs. tree) (R = 0.92, n= 24)