Water relations and growth of shrubs before and after fire in a semi-arid woodland

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Summary. Plant water relations and shoot growth rate of shrubs resprouting after fire or unburnt were measured in a semi-arid poplar box (Eucalyptus populnea) shrub woodland of eastern Australia. In vegetation unburnt for about 60 years, the dawn xylem water potential ($\psi_\text{x}$) of the dominant shrub species was about $-1.0$ MPa when the soil was wet and $-8.0$ MPa when the soil was very dry. At any one time, the dominant shrub species, Erempila mitchelli, E. sturtii, Geijera parviflora and Cassia nemophila, were similar in $\psi_\text{x}$ but Acacia aneura and Dodonaea viscosa were consistently higher in $\psi_\text{x}$ than this group when the soil was moist and lower when the soil was dry. The dominant tree species, Eucalyptus populnea and E. intertexta, appeared to have access to additional water beneath the hardpan which is located 60–80 cm below the surface. When shrubs were under extreme water stress ($\psi_\text{x}$ of $-8$ MPa), the trees had a $\psi_\text{x}$ of $-3$ to $-3.6$ MPa. Following a fire, both $\psi_\text{x}$ and leaf stomatal conductance ($g_\text{s}$) of resprouting shrubs were higher for about 5 years than comparable-aged unburnt vegetation, with relative differences in $\psi_\text{x}$ increasing with drought stress. Elongation rate of resprouts was positively linked to prefire shrub height in 3 of 4 species. However, shrubs resprouting after high intensity fires had substantially higher rates of shoot elongation than after low intensity fires which were in turn higher than for foliar expansion of unburnt shrubs. It is concluded that the growth rate of resprouting shrubs is primarily determined by physiological/morphological factors associated with plant size but is also assisted by greater availability of water and possibly nutrients for a period after fire.

Key words: Fire – Water relations – Resprouting – Shrubs – Landscape

The semi-arid woodlands of eastern Australia are typically composed of scattered trees of one or more species of the genera Acacia and/or Eucalyptus, a shrub stratum varying spatially from sparse to very dense depending upon fire history (Harrington et al. 1984) and a herbaceous stratum of perennial grass and/or annual forbs which may vary in botanical composition over space and time, depending on grazing history and climate. Plants of these woodlands are able to withstand persistent droughts as well as periodic occurrence of fire. The shrubs, trees and perennial grasses regenerate after fire by resprouting and/or by germination of soil-borne seed (Hodgkinson and Griffin 1982; Hodgkinson 1991).

The resprouting strategy enables plants to continue occupying space won during the establishment phase. Recruitment from seed is a rare event for many of the perennial species, especially those belonging to the genus Erempila, since rainfall sequences which successfully couple seed production (in the case of seed of some species with short lives), germination and seedling establishment occur infrequently in the environment. So it is not unexpected that the shrub flora contains a preponderance of species (Hodgkinson and Griffin 1982) with resprouting strategies of various types (Naveh 1975).

The shoot growth rate of shrubs resprouting after fire can be quite rapid compared with unburnt plants (Radosевич and Conard 1980; Malanson and Trabaud 1988). Rapid shoot regrowth has generally been attributed to one or more of the following: enhanced plant water status during periods of low rainfall (e.g. Wellington 1984; Saruwatari and Davis 1989), increased nutrient availability in the soil (Oechel and Hastings 1983) and stimulated supply or utilization of stored carbohydrate and nutrient resources from lignotubers (De Souza et al. 1986).

This study was conducted as part of a large project to investigate the demographic and ecophysiological response of the shrub flora in semi-arid woodlands to different fire regimes (season, frequency and intensity; Gill 1975). This paper reports the water relations of shrubs in this woodland before and after fire and the characteristics of resprouting. The specific aims of the study were to determine if (i) resprouting shrubs have higher xylem water potential and transpiration rates than unburnt shrubs during drought periods, (ii) fire intensity influ-
ences shoot growth rates and (iii) size (age) of shrubs at the time of burning influences shoot growth rates of resprouting shrubs.

Materials and methods

Study site

The site was in a semi-arid woodland on the pastoral property “Oakvale” (146° 30’ E, 30° 55’ S) 70 km northwest of Nyngan in New South Wales near the centre of an extensive pediplain (King 1953) at 250 m elevation. Soil type, typical of the pediplain, is a massive red earth (Stace et al. 1968), or typic durargid (Soil Survey Staff 1975), overlying an indurated layer of stone or bedrock (called “hardpan”) at 60-80 cm (Johns 1984). Topography is very gently undulating, with rises about 1 km apart and slopes of 1-1.5%.

Vegetation at the site is described by Harrington (1979). Briefly, the tree stratum comprises randomly occurring trees of *Eucalyptus populnea* F. Muell. on the slopes and depressions and *E. intertexta* R.T. Baker on the rises at a mean density of 35 ha−1. Tree canopies cover 13% of the area and beneath the canopy is a shrub thicket dominated by *Eremophila mitchelli* Benth. and *Geijera parviflora* Lindl. Intervening “thicket” areas are dominated by *Acacia aneura* F. Muell. ex Benth., *A. excelsa* Benth., and *Cassia nemophila* A. Cunn. The shrubs *Eremophila sturtii* R. Br. and *Dodonaea viscosa* (L) Jacq. spp. *spatulata* (Smith) J.G. West commonly occur in both “thickets” and “interthickets” (Harrington et al. 1981). Shrub density is about 4800 ha−1. The herbaceous stratum comprises annual forbs and grasses but prior to pastoral settlement it was dominated by perennial grasses (Harrington et al. 1984). Persistent heavy grazing by sheep, coupled with wildfire control, since pastoral establishment in about 1860, has reduced perennial grass abundance and increased shrub density.

Annual rainfall and potential evaporation (US class A pan) average 350 mm and 2900 mm respectively in the area. On average, rainfall is evenly distributed throughout the year but the coefficient of variation for monthly rainfall ranges from 70% (July) to 180% (February). Redistribution of water is common in the landscape with more soil water being stored under “thickets” than “interthicket” areas following rainfall events (Johns 1984).

Plot layout

Within an area of 108 ha fenced in 1977 to exclude sheep, cattle, goats and pigs, but not kangaroos, two areas of *Eucalyptus intertexta* and two areas of *E. populnea* where delineated. The areas were of irregular shape and were contiguous. Within each of the four areas, 24 trees were randomly selected. Each of the 96 plots measured 15 x 21 m and was laid out to include at one end the selected tree with its associated “thicket” and at the other end an “interthicket” area.

Experimental fires

Beginning in October 1977, 72 of the plots were burnt in different seasons (spring, summer, autumn and winter) and frequencies (once and every 1, 2, 3, 4 or 5 years). Twenty-four plots were left unburnt as controls. Before each fire, the amount of litter was visually estimated across each plot using a modified dry-weight-rank method (t’Mannefte and Haydock 1963). Wheat straw was spread uniformly over each plot and 3 m surrounds at either 300 or 800 g m−2, before burning, to supplement the normally low quantity of flammable tree litter and standing forbs. Plots were ignited at one end with a drip torch and the prevailing wind carried a head-fire through each plot.

The fire-line intensity for each plot was calculated using the formula:

\[ I = \frac{Hw}{v} \]

(Byram 1959) where \( I \) is fire-line intensity in kW m−1, \( H \) is the heat of combustion of the fuel (a constant of about 18700 kJ kg−1), \( w \) is the dry weight of the straw and litter in kg m−2 and \( v \) is the fire-line velocity in m s−1. Fire velocity for each plot was determined by averaging the measurements of time taken for the fire front to travel 3 m intervals through the plot.

Measurements

Dawn xylem water potential (dawn \( \psi_d \)). The pressure bomb technique, described by Scholander et al. (1965), was used to measure \( \psi_d \) of trees and shrubs at or just prior to dawn. Small branches of the trees were obtained for measurement by firing a shotgun into the canopy and upon landing, one branch was selected and trimmed to a suitable length for immediate placement in the pressure bomb. Each tree shoot contained 2 or 3 leaves. Terminal shoots (7–10 cm long) were cut from shrubs and trimmed leaving about 5 leaves.

The relationship between dawn \( \psi_d \) of the two *Eucalyptus* species and the shrub species *Eremophila mitchelli* was sought by comparing the dawn \( \psi_d \) for tree and shrub species sampled from the same “thicket”. Two branches a distance apart in the canopy of each tree and one stem from each of four *E. mitchelli* shrubs beneath the tree were obtained. On five occasions, *Eucalyptus intertexta* and *E. populnea* trees from the four areas were measured. No tree was remeasured and trees selected were about 500 m apart.

In addition, the dawn \( \psi_d \) of six shrub species was measured regularly between 1977 and 1984 (only 1979 and 1980 data is presented). Measurements were repeatedly made on the shrubs associated with six particular *E. intertexta* trees in close proximity. On each occasion of the six individual shrub species associated with each tree were randomly selected for measurement.

Changes over time after fire in dawn \( \psi_d \) were determined on *Eremophila mitchelli*. Four shrubs on selected plots which varied in time since a fire, were measured. On each occasion 6–8 fire treatments were compared with each treatment replicated four times.

Leaf stomatal conductance (\( g_s \)). Conductances of both the abaxial and adaxial leaf surfaces were determined using a diffusion porometer (Delta-T Devices, Mk II) calibrated against physical resistances at a range of temperatures, throughout the day of 7 March 1983. Twelve shrubs each of *D. viscosa* and *E. mitchelli* were measured; 4 were in a plot burned 18 months earlier, 4 were in the unburnt surrounding area and 4 were in the surrounding area but were irrigated with copious quantities of water beginning the day earlier. Immediately after conductance measurements were made on leaves, \( \psi_d \) was determined on a shoot cut from the same shrub. Throughout the day, irradiance was measured with a Kipp solarimeter and air temperature with a ventilated Assmann psychrometer.

Shrub height. Heights of shrubs were measured in all plots prior to burning and again on both burned and unburned plots two years later. In this paper data from the two treatments (burnt once with 300 g m−2 or 800 g m−2 of straw) applied on 23 and 24 January 1979 are compared with unburnt controls.

Rainfall. Daily rainfall at the site was measured from 1977 to 1988 using a Lambrecht recorder (only 1979 and 1980 data are presented).

Results

Dawn xylem water potential of trees and shrubs in the unburnt plant community

The trees of the plant community ranged in dawn \( \psi_d \) from a high of −1.0 MPa measured when the soil