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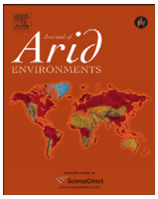

Effects of water, grass and N on responses of *Acacia karroo* seedlings to early wet season simulated browsing: Leaf N, fibre and tannin concentrations

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ABSTRACT

Bush encroachment is a phenomenon that affects semi-arid savannas world-wide. To apply effective browsing to control trees, the browse–browser interaction must be well understood. An important aspect is feedbacks between browsers and trees because browsers influence the nutritional value of plants. When resources are abundant, tannins, which are assumed to negatively affect browsers, are predicted to decrease following herbivory because defoliation is assumed to reduce C relative to N. In opposite conditions, defoliation is expected to increase tannins by increasing C relative to N. A split-plot experiment was conducted to investigate the effects of irrigation, fertiliser, grass cover and clipping on leaf N, neutral detergent fibre (NDF) and condensed tannin (CT) concentrations of *Acacia karroo* seedlings in a semi-arid savanna. Clipping reduced N of irrigated plants, and increased N of unirrigated plants, in the absence of grass cover. By reducing N, clipping in relatively high resource conditions resulted in reduced potential value of the seedlings as fodder. The reverse occurred in relatively low resource conditions through N elevation. The development of negative feedback in conditions that promote woody seedling encroachment would render bush control by browsing difficult.

1. Introduction

Improved understanding of woody plant ecology in semi-arid subtropical regions is critical for the conservation and management of savannas, given predictions of increased woody plant production in southern Africa under climatic change (Bond and Midgely, 2000) and other impacts of human activities on savannas such as bush clearing (Scholes and Archer, 1997). Bush encroachment, whereby woody plants become more abundant at the expense of grasses, is a phenomenon that affects savannas world-wide and is of substantial socio-economic importance (Ward, 2005). Goats are regarded as useful biological agents of woody plant control, especially following mechanical clearing where production of cattle is of prime importance (O'Connor, 1996; Trollope et al., 1989). The browse–browser interaction must be well understood for browsing to be applied in an effective way to control trees. Few studies, however, have explored woody plant responses to browsing in savannas (Scogings, 2003).

Mammal browsers not only feed from plants varying in characteristics that affect feeding behaviour, but are also able to influence the nutritional value of their food plants (Danell et al., 1994; Illius et al., 1999; Makhabu and Skarpe, 2006).

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Tannins influence herbivores through deterrence or toxicity, or by reducing nutrient availability after ingestion (Cooper et al., 1988; Robbins et al., 1987). Structural polysaccharides and lignin influence the physical toughness and digestibility of plants, thus reducing intake rates (Jung and Allen, 1995; Scogings et al., 2004; Shipley and Spalinger, 1992). These carbon-rich secondary metabolites that are located in vacuoles and cell walls are often assumed to function as chemical defences in plants.

Knowledge of the variation in concentrations of nutrients and putative chemical defences among woody plants in African savannas is scarce (Scogings, 2003). *Acacia* species are important components of bush encroachment and browse production in Africa, and are the most studied woody plants in savannas (Moleele, 1998, Scogings, 2003). The future development of robust, management-oriented models of browse–browser interactions in semi-arid savannas, whether for conservation, bush control or animal production, would benefit from improved knowledge of the ecology of *Acacia* trees. It is well documented that browsing of the canopies of African *Acacia* trees can stimulate shoot production (Dangerfield and Modukanele, 1996; Gowda, 1997; Milton, 1983; Oba, 1998; Pellew, 1983; Teague and Walker, 1988). Chemical responses, however, appear to be less consistent than growth responses in African *Acacia* species. Rapid changes in putative defences have been detected within hours or days of defoliation (Furstenburg and Van Hoven, 1994; Scogings, 2005; Teague, 1989; Van Hoven, 1984), but long-term responses, within months or years, have varied (du Toit et al., 1990; Gowda, 1997; Rohner and Ward, 1997; Scogings and Macanda, 2005; Ward and Young, 2002). Long-term changes in tannin concentrations appear to be related to browsing intensity, with increases detected under heavy defoliation of the canopy, but decreases observed after severe debarking that induces coppicing (Rohner and Ward, 1997; Scogings and Macanda, 2005). Increases in nutrient concentrations have been found to accompany decreases in tannins (Du Toit et al., 1990; Scogings and Macanda, 2005).

Effects of interactions between resource availability and clipping have not been published for *Acacia* seedlings. Given that resources are distributed heterogeneously in semi-arid savannas, and seedlings are sensitive to browsing, it is important to understand how the effects of browsing on *Acacia* seedlings interact with variations in resources (Scogings, 2003; Scogings and Macanda, 2005; Wiegand et al., 2006). The main resources for plants in semi-arid savannas are nutrients and water, and the main plants that consume these resources are trees and grasses (Scholes, 1997; Scholes and Archer, 1997). Typical encroacher woody species are N_2-fixing trees that are more limited by water than N, while grasses are more often limited by N than water because they are not N_2-fixers (Fulco et al., 2001; Högberg, 1986; Ward, 2005). When grass biomass is reduced (e.g., under prolonged severe grazing), water availability may be greater for tree growth than grass growth, although the total amount of water available may be reduced by surface crusting and increased run-off (Peltzer and Köchy, 2001; Scholes and Archer, 1997). Therefore, when rainfall is higher than usual, and both nutrients and grass biomass are low, encroacher woody species can out-compete grasses, leading to bush encroachment (Ward, 2006).

The broad aim of this paper is to contribute to improving the understanding of browse–browser interactions in semi-arid savannas. The specific aim of the research was to investigate, in a factorial experiment, responses of N, condensed tannins (CT) and neutral detergent fibre (NDF) concentrations in *Acacia karroo* Hayne seedlings subjected to simulated severe browsing early in the wet season when N, water and grass cover were varied. Clipping near the base has the same effect on seedling growth as browsing (e.g., Story, 1952; Walker, 1985), while the most readily detectable effects of browsing are observed when browsing is most severe (Scogings and Macanda, 2005). Clipping seedlings near the base, therefore, may be reasonably regarded as a substitute for severe browsing, while also being simpler than real browsing.

While the main effects of numerous factors such as N, water, clipping and grass may be intuitive, their interactions are less clear (O'Connor, 1995). It is necessary to evaluate both main effects and interactions in order to better understand browse–browser relationships. While N and water are acknowledged to be the main resources in this paper, grass cover was included as a resource-related factor, because all three factors and their potential interactions were assumed to produce various conditions of resource availability in general (Scogings and Mopipi, 2008). From existing knowledge, it was assumed for *A. karroo* seedlings that (1) adding water increases resource availability/growth rate, (2) adding N has no effect on resource availability/growth rate, (3) adding grasses reduces resource availability/growth rate by limiting water availability, (4) adding water and N increases resource availability/growth rate as much as adding water alone, (5) adding water and grasses has no net effect on resource availability/growth rate, (6) adding grasses and N reduces resource availability/growth rate further than adding grasses alone because the positive effect of N on grasses strengthens their negative effect on water availability, and (7) adding water dampens the negative effect of N and grasses on resource availability/growth rate towards the level of adding grass alone (Brown et al., 1998; Davis et al., 1998; Fulco et al., 2001; O'Connor, 1995; Peltzer and Köchy, 2001; Rautio et al., 2005; Scholes and Archer, 1997; Ward, 2006).

For the purposes of this paper, it was assumed that the treatment with grass and N added represents the lowest level of overall resource availability for *Acacia* seedlings, treatments with either grass added alone, or grass added with water and N, represent low resource availability, treatments with water added and no grass represent high resource availability, and the remaining treatments represent intermediate resource availability. It was postulated, therefore, that when water and nutrients are increased in the absence of potential competition from grass cover, concentrations of CT and NDF in *A. karroo* will (1) decrease relative to N concentration because of an assumed metabolic tradeoff (Herms and Mattson, 1992), and (2) be reduced by clipping, relative to N, because regrowth is not limited and excess C does not accumulate as C-rich secondary metabolites when resources are available (Stamp, 2003).