ECOLOGY OF WOODY WEED INVASIONS IN THE TROPICAL WOODLANDS OF NORTH-EASTERN AUSTRALIA: IMPLICATIONS FOR MANAGEMENT

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Summary. Attempts at controlling exotic woody weed invasions in tropical woodlands of north-eastern Australia have generally revolved around reliance on the competitive ability of existing vegetation to suppress invading populations, and on the development of mechanical or chemical control methods for restoring invaded areas. However, there is very little experimental or observational evidence to support this approach. In this paper we review some of the pertinent literature and present some empirical evidence in support of an approach that focuses research and management efforts on limiting dispersal of invading plants and implementing more complex management regimes that are based on the negative effects of disturbance on invaders.

INTRODUCTION

Shrub invasion in grazed ecosystems is a common problem throughout the world. Abundant examples describe the conversion of open grasslands, savannas, and woodlands to shrublands and closed woodlands. As density and stature of invading shrubs increases, fewer ecosystem resources are available for herbaceous growth. Consequently, livestock carrying capacity is reduced, soil erosion is increased, and species, habitats, and ecosystems are endangered. Much consternation and economic expenditure has accompanied this phenomenon and yet the problem persists.

Most attempts at reversing this trend have revolved around some combination of mechanical, chemical, or biological control in heavily invaded areas. Although a substantial area is completely dominated by exotic shrubs and few landscapes are completely free of isolated individuals, the majority of land area remains open or occupied at relatively low densities. Unfortunately, few resources have been expended to examine proximate causes and mechanisms of invasions and the implications for management aimed at containing invasions and maintaining productivity. Causative factors must be altered if invasions are to be contained and mechanisms may provide clues to key processes that foretell invasions and allow appropriate actions. Any realistic examination of causes and mechanisms must include both the invading species and ecosystem attributes (12).

Ecosystem attributes. Tropical and subtropical woodlands represent about 92 mha of Australian rangeland (11). These ecosystems evolved with periodic extended drought (8) and large-scale intensive fires (4), but lacked exposure to heavy grazing by large herbivores (9). Consequently, bunchgrasses dominate the herbaceous layer. Although aboveground net primary productivity is relatively high compared to other grasslands, basal area is low (<3%). Therefore, even in undisturbed ecosystems where disturbance is low, much of the soil surface is unoccupied and available for colonization. Even moderate levels of disturbance decreases perennial bunchgrasses basal area (10), increasing openings where seeds of invading plants may establish.

Livestock grazing is by far the most extensive land use (11). Herbaceous production in the wet season typically exceeds grazier demand and intake during the dry season is limited by low digestibility (5). However, cattle numbers have approximately doubled in the past twenty years.

This increased forage demand and utilization has resulted in shifts in species composition in the herbaceous layer toward annual grasses and forbs (10). Increased availability of annual grasses and forbs has a positive feedback effect on livestock intake (1). In turn, increased intake and compositional shifts have a negative feedback on amounts of herbaceous growth available as fine fuel, reducing the frequency and intensity of fire. This disruption of the fire regime has resulted in a loss of equilibrium in the relationship between woody and herbaceous components of the vegetation (15) and allows for the greater expression of the woody component.

Invader attributes. Two of the most economically important woody weeds in the north-eastern woodlands are rubbervine *(Cryptostegia grandiflora)* and prickly acacia *(Acacia nilotica)*. Rubbervine was introduced in the late 1800s around population centres as a horticultural plant and is now common in the eastern part of the region (13). It commonly inhabits the more productive lowland areas adjacent to ephemeral and permanent watercourses. In addition to an ability to exist as a shrub, it can climb into the canopy of established trees. Seed production is very high (>>5K/ mature plant), seeds are viable (germination >90%) and dispersal is via wind or water. When established plants are subjected to top removal, they can resprout from below ground parts. Many naturally occurring stands are monocultures.

Prickly acacia is most common in the Mitchell grasslands, but is increasing rapidly throughout the east as well (13). It is a leguminous shrub or small tree and is capable of producing large quantities of viable seeds (>l0k/mature tree). Seed viability is high (>80%) and seed longevity may exceed 5 years in the soil. It was introduced originally as a fodder tree and seed dispersal via cattle is very effective. It can exist in near monocultural stands as well. In the western portions of it's geographic range, prickly acacia originally was concentrated near bore drains. Although large trees with high seed production remain concentrated in these well watered areas, populations have spread throughout entire paddocks where livestock have access. Recently, it has spread eastward into more mesic ecosystems, where seed producing trees are widely distributed across the landscape.

Possible causes and mechanisms. Historical and anecdotal reports as well as experimental evidence suggests that these woody plant increases are relatively recent (c. 25-40 y). Invasions are attributed to two general causes: 1) decreased competitive ability of current herbaceous vegetation assemblages or 2) decreased fire frequency and intensity. Although the two causes are related and interactive, it is important to separate and quantify each if strategies are to be devised that can limit Invasions.

If competition from herbaceous vegetation is to be a major factor limiting shrub survival, it is most likely during the seedling and juvenile stages of the life cycle. When seeds of invading shrubs are present on a site, germination and emergence are likely limited only by viability and moisture availability (6). These conditions are frequently met in north-eastern Australia, so germination and emergence are likely occurrences on most sites. Although woody plant growth may be limited if herbaceous plants are capable of pre-empting moisture, effect on survival is more critical in depressing population size and limiting invasions (2). If survival is unaffected and woody plants mature, the effect of the herbaceous layer in limiting survival, growth and reproduction is diminished (16). As shrubs mature, below ground investment in both extensive tap root systems and more finely divided shallow root systems insure shrub access to soil moisture and nutrients. Logically, life history relegates the role of herbaceous vegetation in limiting shrub populations to the seedling and juvenile stages. Thus, we initiated experiments to examine the ability of common, highly competitive perennial grasses to limit the success of juvenile shrub seedlings.

METHODS

To test the effect of herbaceous vegetation in limiting woody plant success, we introduced seed of rubbervine and prickly acacia into established vegetation dominated by perennial grasses and monitored survival. In a glasshouse, we introduced 15 seeds of each species into pots (50 cm in diameter x 25 cm deep) in which perennial grasses had been transplanted and grown for 90 d with supplementary water. The grasses were speargrass *(Heteropogon contortus)* or Indian couchgrass *(Bothriochloa pertusa)*. Speargrass is a native perennial bunchgrass that is indicative of light to moderate grazing (1). Indian couchgrass is a stoloniferous perennial grass introduced from India and is indicative of heavy grazing. Throughout the experiment the grasses were defoliated biweekly at one of three levels (heavily = 10 cm, moderately = 40 cm and undefoliated). Woody plant seedlings were not defoliated. Immediately after shrub seeds were introduced to the pots, all pots were watered to saturation for 4 d to simulate a germinating rainfall event. In addition, pots were well watered at three different intervals (5 d, 14 d, and 21 d) to simulate rainfall patterns typical of good, average and dry years, respectively. We monitored shrub seedling emergence and subsequent survival for 90 d.

In January 1992, we introduced seeds of rubbervine and prickly acacia into 1 m^2 plots dominated by perennial grasses that had been protected from grazing for >20 y. Although the wet seasons of 1991-1992 and 1992-1993 were among the driest on record, seed germinated in some of the plots and was monitored over the next two years.

RESULTS AND DISCUSSION

In the glasshouse study none of the treatments significantly affected seedling survival. Seedling survival for both species exceeded 95% for both species regardless of competing species, defoliation regime, or watering regime. In the field study, prickly acacia survival was 62% and rubbervine survival was 87% after two seasons. Although these experiments represent a limited range of conditions and a short time period, the combination of our results and research and observations from around the world in similar situations leads us to suggest that the likelihood of limiting shrub invasion of open woodlands via the competitive effects of the herbaceous layer is very low. This conclusion, then, focuses attention on the alternative hypothesis presented above; that the primary value of herbaceous vegetation in limiting shrub invasion is as fine fuel to initiate fires of sufficient intensity and frequency to limit woody plant success.

An understanding of the attributes of the invading species indicates seed availability and viability seldom are limiting factors if mature plants are within dispersal distance. Herbaceous vegetation may limit seedling survival under some conditions (7), but if essential resources (notably moisture) are in adequate supply, the effect is greatly diminished. If shrub seedlings survive to the juvenile stage, it is highly unlikely that herbaceous vegetation can reduce survival. During this phase, herbaceous vegetation may have more value as fine fuel to increase frequency and intensity of fires than for exploitative or interference competition. Although most woody shrubs are fire tolerant, frequent hot fires may remove top growth and greatly limit their ability to compete for water and nutrients in upper soil profiles (14). If this is the case, juvenile woody plant effects on herbaceous production can be greatly limited. In addition, repetitive top removal can effectively maintain populations of woody plants as juveniles and greatly depress seed rain on a site. By limiting seed production at the population level, presence of woody plant seeds in the seedbank would eventually run down if treated areas are sufficiently distant from seed producing trees.

However, if woody plants survive to become adults, herbaceous vegetation has little effect on either survival, growth or reproductive success (3). Spot treatment with chemical, mechanical or attempts to control populations via biological controls inevitably leave seed producing adults capable of restocking the seed bank. Thus, there remains the potential for rapid increases in invasive shrub populations.

Based on our observations and literature interpretations, we suggest it is futile to expect that herbaceous vegetation, however well managed, can have more than minimal impact on the rate of shrub invasions in tropical woodlands. Research and extension efforts could more effectively be directed toward developing cost-effective management schemes that focus on the judicious use of fine fuel for fires that can check the increase in shrub density and stature.

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