The Ideal weed?

te Beest, Mariska

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Managing plant invasions with an ecosystem-based approach: using fire to control the exotic invasive shrub *Chromolaena odorata* in a South African savanna

Mariska te Beest
Joris P.G.M. Cromsigt
J. Ngobesi
Han Olff
1. Exotic invasive plants are a threat to biodiversity and ecosystem functioning of natural and semi-natural systems worldwide. Controlling successful invasive plants by direct control measures is extremely difficult, however, an approach focused on changing ecosystem processes through the disturbance regime, has provided promising results. Here, we investigate how fire, which is a natural component of savanna systems, can facilitate the conventional control practices for the invasive shrub *Chromolaena odorata*.

2. *Chromolaena odorata* is a highly flammable, but fire tolerant, exotic invasive species in South Africa and other parts of the world, which is thought to have a negative impact on the natural tree-grass dynamics in savanna systems. How *C. odorata* responds to, and affects fire is poorly understood.

3. We performed a full factorial large-scale field experiment in densely invaded woodland in Hluhluwe-iMfolozi Park, a savanna reserve in South Africa in order to study the effect of fire in combination with the prevailing manual and chemical clearing practice.

4. We found that burning alone was not successful in reducing densities of *C. odorata*. Fire proved to be more effective when fire intensity was higher and *C. odorata* shrubs were younger.

5. The conventional clearing practice (poisoning and cutting) alone reduced *C. odorata* densities initially, but the species quickly resprouted and regular follow-ups are needed for several consecutive years to effectively reduce *C. odorata* densities, putting a high constraint on resources.

6. The combination of high intensity fire with the conventional clearing practice proved to be very effective in controlling *C. odorata* and induced an ecosystem state switch from woodland into grassland.

7. **Synthesis.** The combined approach of targeting the invasive species directly through manual and chemical clearing and at the same time manipulating the natural disturbance regime through controlled burning, successfully reduced densities of *C. odorata* in densely invaded savanna woodland. Moreover, dry *C. odorata* shrubs can be used to fuel fires for controlling unwanted woody encroachment and restoring thickets and encroached grasslands back into grasslands.
Introduction

Invasions of exotic plants form a huge threat to the conservation of biodiversity worldwide (Elton 1958; Vitousek et al. 1997; Mack et al. 2000). Numerous studies have summarized the detrimental effects of invasive plants on native species diversity, community structure and ecosystem functioning (Sakai et al. 2001; D’Antonio & Kark 2002; Rejmánek et al. 2005). Today, not only human disturbed habitats are being invaded, but many natural communities in protected areas worldwide are facing large threats (Usher et al. 1988; Macdonald & Frame 1988; Lonsdale 1999). According to global climate change scenarios, savannas are among the ecosystems most vulnerable to biotic invasions (Sala et al. 2000). While managing invasions in these species-rich savanna systems is important to biodiversity conservation, control is often time-consuming, labour-intensive, dangerous and expensive, while positive results are often lasting for only a short time (Marais et al. 2004; Perrings et al. 2005). Understanding the processes that underlie plant invasions in savannas is fundamental to develop efficient and effective control measures (Zavaleta et al. 2001; Rossiter et al. 2003; Levine et al. 2003).

Many past control programs were developed and executed to specifically target the invasive species, without incorporating a more ecosystem-based approach. Such programs have often provided unconvincing results (Wadsworth et al. 2000; Hulme 2006; Buckley 2008). In contrast, approaches that target ecosystem processes, rather than primarily the invasive species, have shown much more promising results (Paynter & Flanagan 2004; Prober et al. 2005; Dewine & Cooper 2008; Firn et al. 2008; Cox & Allen 2008). The core principle of these ecosystem-based approaches is that they manipulate the natural disturbance regimes in the invaded ecosystems, such as flooding, soil disturbance and fire (Buckley et al. 2007; Stokes 2008; Firn et al. 2008).

Fire is one of the key natural disturbances in savannas worldwide (Bond & Keeley 2005; Bond et al. 2005). Savannas are defined by the coexistence of trees and grasses. A complex set of interacting factors including soil properties, rainfall, fire and grazing determines tree-grass ratios in savannas (Scholes & Archer 1997; Higgins et al. 2000; Van Langevelde et al. 2003; Sankaran et al. 2004; Sankaran et al. 2005). Tree densities can vary greatly between savannas types, ranging from dense woodland to open grassland communities (Scholes & Archer 1997; Sankaran et al. 2005). Bond et al. (2005) showed that fire might be the dominant factor that prevents, especially C4, savanna grassland systems to turn into forest. This role of fire is especially strong in mesic savannas (Sankaran et al. 2005). The suppression of fire in combination with overgrazing has lead to the expansion of woody plants at the expense of open grass communities (Bond & Midgley 2000; Roques et al. 2001; Balfour & Midgley 2008; Wigley et al. 2009). Woody encroachment is conceived to be a problem as it reduces grass productivity and hence limits food availability for cattle and wildlife (Scholes & Archer 1997). Fire is widely used as a management
tool in savannas to control woody encroachment and has been successfully applied to switch systems from a woody plant dominated system to open grassland systems (Trollope 1974; Trollope 1983; Roques et al. 2001). As woody encroachment can be seen as an invasion of native woody species, manipulating the natural fire disturbance regime could possibly be a successful strategy to control exotic woody invaders in savanna grassland systems as well.

Most studies on plant invasions and fire in savannas have been performed in Neotropical and Australian savannas, where introduced African pasture grasses alter fuel load and increase fire frequency and intensity thereby disrupting savanna structure and functioning (D’Antonio & Vitousek 1992; Baruch 1996; Rossiter et al. 2003; Rossiter-Rachor et al. 2008). In return however, many grasslands and savanna habitats in Africa and Asia, are invaded by Neotropical and Australian woody plants, such as Eucalyptus spp., Lantana camara L., Opuntia spp. and Chromolaena odorata (L.) King & Robinson (Macdonald & Frame 1988; Foxcroft et al. 2004; Kohli et al. 2006). These neotropical woody plants differ from African grasses in their effect on the fire regime, often decreasing fuel load and fire frequency by outshading native grasses, but increasing the risk of high intensity canopy fires (Brooks et al. 2004). Chromolaena odorata is a species that has been reported to increase vertical continuity of fires, i.e. lifting surface fires into tree canopies, thereby changing the natural surface fire regime into a canopy fire regime (Macdonald 1983; Macdonald & Frame 1988; Brooks et al. 2004). Invasive plants that change fire regimes are among the most important system-altering species (D’Antonio & Vitousek 1992; Crooks 2002; Brooks et al. 2004). Understanding how exactly these woody invaders alter the natural fire regime can help us to reverse their effects and use fire as a natural disturbance to control the invasion of exotic woody species in African savanna grasslands.

We studied Chromolaena odorata as an example of how a woody invader interacts with the natural fire regime and how this interaction can be used to control its invasion in a Southern African savanna. Conventional programs to control the invasion of C. odorata in South African savannas have not been highly effective. To date the Working for Water program, which is the national organization responsible for managing exotic invasive plants in South Africa (Van Wilgen et al. 1998; Turpie et al. 2008), has obtained some results through the action of Chromolaena clearing teams. This clearing program uses a combination of mechanical and chemical control (Erasmus 1988; Van Gils et al. 2004). However, incurred costs are high (Marais et al. 2004; Turpie et al. 2008) and continued follow-up efforts are necessary (Van Gils et al. 2004), while future funds may not be secured. Also, such funds may not be available in neighbouring countries into which the Chromolaena invasion currently proceeds, such as Mozambique, Zimbabwe and Tanzania. In addition, biological control has been unsuccessful so far in savannas with a distinct wet and dry season, even though promising biocontrol agents were identified in the laboratory field trials (Kluge 1991; Barreto & Evans 1996; Zachariades et al. 1999; Muniappan et al. 2003).
We argue that one problem of conventional control programs and a possible reason for the lack of success is a too strong species-oriented focus and insufficient appreciation of the relevant ecosystem processes that operate in the field.

We performed a large-scale full factorial field experiment in densely invaded savanna woodland in Hluhluwe-iMfolozi Park, a protected reserve in South Africa. We applied fire in combination with conventional control practices to assess the effect on densities and re-invasion of the exotic invasive species *Chromolaena odorata*. We hypothesize that the success of eradication programs for *C. odorata* could be greatly increased if the clearing efforts are combined with a manipulation of the fire regime. Furthermore, we hypothesise that high intensity fires will be more effective in controlling *C. odorata* than low intensity fires. Clearing and high intensity fires when applied in combination could shift the *C. odorata* invaded state to an open grassland state that is less susceptible to invasion, hence limiting the need for follow-up efforts.

**Methods**

**Study area**

Hluhluwe-iMfolozi Park is a 90,000 ha reserve in Kwazulu-Natal (KZN), South Africa, situated between latitudes 28°00’ and 28°26’ S and longitudes 31°43’ and 32°09’ E (figure 5.1). Annual rainfall is strongly seasonal with most rain falling in the spring and summer, between October and March. The mean annual rainfall ranges from 1000 mm in the high altitude regions in the north to 600 mm in the low-altitude south-western areas. We situated our study site in heavily infested riverine woodland in the north-eastern part of the reserve, with an annual average rainfall of 800 mm/year. This amount of rainfall lies within the climate potential that would turn grassland into forest in absence of fire (Bond et al. 2005; Sankaran et al. 2005). Daily maximum temperatures range from 13º to 35ºC. The reserve is of strong conservation importance because it hosts a rich and complete set of indigenous large herbivores and carnivores, including Black and White Rhino, Buffalo, Elephant, Nyala, Lion, Leopard and Wild Dog (Brooks & Macdonald 1983). The reserve falls within the southern African savanna biome and is characterized by vegetation types ranging from open grasslands to closed Acacia and broad-leaved woodlands (Whateley & Porter 1983).

Next to the savanna habitat, fire-sensitive gallery forests occur in areas with high altitude and rainfall and riverine forests and wetland communities occur along rivers. Plant species diversity is high with over 1250 vascular plant species recorded, of which almost 400 woody trees and shrubs and about 150 grass species (Conway et al. 2001). The vegetation of Hluhluwe-iMfolozi Park has never been subjected to extensive human disturbances (*e.g.* agriculture) and vegetation dynamics are primarily driven by rainfall, fire and herbivory. An important management practice in the
reserve is the controlled use of fire to burn grasland and control woody shrub encroachment. In general fire is confined to the grassland and open woodland communities, with closed woodland and forests tending to exclude fire. Controlled burning is generally carried out at the end of the dry season (July to September) and on average 26% of the surface area of the reserve is burned each year (Balfour & Howison 2001).

Study species

*Chromolaena odorata* originates from South and Central America and has invaded a wide variety of ecosystems, ranging from tropical rainforests to savannas, in most of the Paleotropics. (McFadyen & Skarratt 1996; Kriticos *et al.* 2005; Raimundo *et al.* 2007). In its native range it is part of a rich flora of Asteraceae and widespread and common in disturbed and open areas. The main factor controlling the abundance of *C. odorata* in its native range is believed to be attack by a large complex of generalist and specialist insects (Cruttwell McFadyen 1988a). *Chromolaena odorata* is a perennial semi-lignified shrub forming tangled bushes 1.5 – 2 m in height and reaching up to 6 m as a climber on other plants. In its invasive ranges the species forms dense monospecific stands, thereby out shading most native vegetation and denying human and animal access to invaded areas (Goodall & Erasmus 1996). In the natural savannas of South Africa the species preferably grows in broadleaved woodlands and along river courses and forest margins (Macdonald & Frame 1988). The species can reproduce apomictically (Gautier 1992) and has a prolific seed production of light wind dispersed seeds. A single shrub can produce as much as 800,000 seeds (Witkowski & Wilson 2001). Being a vigorous resprouter as well, the species can survive severe disturbances, like fire or cutting, by quickly regrowing from the basal stems (Devendra *et al.* 1998). The species is quick to lose its leaves and suffer stem die-back when conditions become bad, regrowing again from the living stems.
when conditions change. This strategy results in impenetrable shrubs with many dead and dry stems that form a physical barrier as well as a fire risk to fire-sensitive habitats, like gallery and riverine forests (Macdonald 1983; Macdonald & Frame 1988; Goodall & Erasmus 1996).

The vegetation of Hluhluwe-iMfolozi Park is prone to exotic plant invasions, particularly in the more mesic areas. During the latest survey (Henderson, April 2004) sixty-three invasive and potentially invasive exotic plants have been recorded. The most serious of these include Caesalpinia decapetala, Chromolaena odorata, Ipomoea carnea subsp. fistulosa, Lantana camara, Montanoa hibiscifolia, Melia azedarach, Parthenium hysterophorus, Senna bicapsularis, Senna didymobotrya, Solanum mauritianum, Solanum seaforthianum, Psidium guajava, and Tithonia diversifolia (Macdonald 1983; Macdonald & Frame 1988; Henderson 1989; Henderson 2001). Chromolaena odorata is the most destructive and widespread with about 20% of Hluhluwe (the northern section of the park) covered with infestations (Howison 2009).

**Experimental design**

From August to October 2003, a large-scale (3 ha) experiment was set up testing the effect of clearing, clearing followed by fire and fire alone on densities and re-invasion of *Chromolaena odorata*. In addition, we assessed the effects of these control measures on the indigenous vegetation. The experiment was established in invaded broadleaved woodland in the Maphumulo area of Hluhluwe-iMfolozi Park, an area in the northeastern part of the park known for its high densities of *C. odorata* (figure 5.1). The dominant tree species in the experiment were Euclea racemosa, Euclea divinorum and Dicrostachys cinerea. The dominant grass species were the bunch-grasses Panicum maximum and Eragrostis curvula and the stoloniferous (lawn-forming) species Dactylotenium australe. The experiment was set up according to a randomized block design, with three replicate 1 ha blocks and four 50 × 50 m² plots per block, each subjected to one of the following treatments: conventional clearing (CC), conventional clearing followed by fire (CC-Fi), fire without prior clearing (Fi), and no management intervention (Control) (figure 5.1). Blocks were allocated according to differences in initial *C. odorata* density. Block 1 had the lowest *C. odorata* density. Block 2 had highest initial densities with almost 100% cover and block 3 was intermediate in initial *C. odorata* density.

*Cromolaena odorata* clearing was performed in September 2003. Conventional clearing practice consists of hand-pulling and spraying of seedlings and slashing of established plants followed by herbicide application to the remaining stumps (Van Gils et al. 2004). A follow-up clearing, which is standard practice in conventional clearing programs, was performed in May 2005. By accident, the controls were cleared as well. The burning was performed on 13 October 2003 under guidance of the reserve’s management staff on a dry and hot day, with gentle to moderate wind. Open calorimeters were used were used to measure fire intensities (Wally et al.
2006; Moncrieff et al. 2008). This was done by filling aluminium cans with basal area of 60.84 cm² with 20 ml of water and measuring the volume of water evaporated by the fire. We placed 4 calorimeters per treatment, each fitted with 3 cans at ground level, grass canopy height and 1 m above the ground. We used this method as standard calculations based on heat yield (Byram 1959) could not be used due to lack of data for C. odorata acting as fuel load. Fire intensity was calculated as the rate of spread × the volume of water evaporated per cm² × the energy required to convert 1 g of water to steam, = 2.571 kJ (Weast 1988). Flame height was measured with 4 m long poles with pieces of string attached every 20 cm. The last string burned gave an estimate of flame height. Rate of spread was measured by individual observers measuring the time it took for the fire front to pass from one fixed point to the next.

**Data collection**

We evenly spaced 30 fixed sample plots of 2 × 5 m² in each of the bigger 50 × 50 m² plots. These sample plots were monitored 17 times during the course of the experiment, from August 2003 to April 2007. Monitoring consisted of (1) recording C. odorata densities as the total number of stems per sample plot, and (2) measuring grass height on five 1 m spaced points along a transect in the middle of a sample plot using a disc pasture meter (Bransby & Tainton 1977). This resulted in 30 independent replicate measurements for each 50 × 50 m² plot. C. odorata densities were recorded in different size classes. These were based on stem diameter, height and whether or not stems were lignified. Three size classes were identified: seedlings (stem diameter < 0.5 cm, stem not yet lignified), young shrubs (stem diameter 0.5 – 2 cm, stem lignified, < 1m height) and old shrubs (stem diameter > 2 cm, stem lignified, > 1m height). We assessed tree damage after fire for two common savanna tree species: Dicrostachys cinerea and Euclea racemosa. Ninety individual trees were tagged throughout the fire treatments and height and stem diameter were recorded. After the fire trees were monitored for one year to assess percentage top kill and mortality.

**Data analysis**

We separated the data in four time periods: (1) Pre-treatment (August 2003, n = 1), (2) Treatment effects in months 1–6 after establishment of the experimental treatments (November 2003 – March 2004, n = 4), (3) Treatment effects in months 7–18 after establishment of the experimental treatments (April 2004 – March 2005, n = 7) and (4) Follow-up clearing (May 2005 – April 2007, n = 5). The effects of the follow-up clearing were analysed separately as the controls were not equal to the initial controls. In April 2007 only two of the CC-Fi treatments were monitored, due to the prolonged presence of lions in the other treatment plots.

In a separate study we estimated above-ground C. odorata biomass from an allometric regression of above-ground dry weight (g) of C. odorata shrubs with the dia-
meter of the main stem of these shrubs (cm) \( y = 77.63 \times x^{2.57}, R^2 = 0.95, n = 80, p < 0.001 \), unpublished data). Based on this regression we estimated total aboveground *C. odorata* biomass in the treatment plots from the stem count data, using the following average stem diameters for each size class: 0.3 cm for the seedlings, 1.5 cm for the young shrubs and 3 cm for the old shrubs. The grass height data was averaged per sample plot and grass biomass was derived from this using the equation: mean biomass (kg/ha) = 340 + 388.3* mean grass height (cm) (Trollope 1983).

Mixed-effect models were used to test for an overall effect of treatment (Fi, CC, CC-Fi, Control) on total *C. odorata* biomass for the different time periods separately (pre-treatment, months 1–6, months 7–18, and follow-up). The mixed-effect model allowed us to include random factors (plot, block and date) with hierarchical levels to account for spatial and temporal pseudoreplication. We had 30 independent samples per 50 x 50 m² plot and nested plot (n = 4) within block (n = 3) and block within date (n = 17) as a random effect. We used Tukey multiple comparisons to test for contrasts between the levels of the treatments. In a second analysis we tested for the effect of fire intensity on densities of *C. odorata*. We tested per size class (seedlings, young shrubs and old shrubs) for time periods 2 and 3 only (November 2003 – March 2005), excluding pre-treatment and follow-up data. We used the same mixed-model as described above, with fire treatment (Fi or CC-Fi) and fire intensity (low or high) as fixed effects. In a third analysis we tested for effects of treatments on grass biomass. We used the same model as described above, with treatment (Fi, CC, CC-Fi, Control) and time period (pre-treatment, month 1–6, month 7–18, and follow-up) as fixed effects. All analyses were performed in R (Version 2.7.0 (2008-04-22)) (R Development Core Team 2008).

**Results**

We hypothesized that the success of *C. odorata* control programs could be greatly increased if the clearing efforts are combined with a manipulation of the fire regime. Our results confirm this hypothesis. While the pre-treatment biomass of *C. odorata* did not differ between experimental treatments (\( F_{3,6} = 0.416, p = 0.748 \), figure 5.2A), total aboveground biomass of *C. odorata* was significantly lower than the controls in all experimental treatments in the first six months after establishment of the experiment (\( F_{3,33} = 20.936, p < 0.001 \), figure 5.2B). The conventional clearing (CC) treatment and the conventional clearing followed by fire treatment (CC+Fi) were most effective in reducing *C. odorata* biomass in the first six months, while the fire (Fi) treatment was least effective in controlling *C. odorata* (figure 5.2C). In the following year all experimental treatments were still significantly lower than the control treatments (\( F_{3,60} = 27.602, p < 0.001 \), figure 5.2C). However, *C. odorata* biomass in the CC treatment increased to the level of the Fi treatment. The CC+Fi treatment was still most effective in reducing *C. odorata* densities. After the follow-
up clearing in May 2005, *C. odorata* biomass decreased in all treatments and treatments did not significantly differ from each other ($F_{3,33} = 2.446, p = 0.081$, data not shown), except for the CC+Fi treatment, which was still lower than the control treatment (Tukey test: $p = 0.054$).

Figure 5.3 shows the changes in *C. odorata* densities over time for each of the different life stages: seedlings, young shrubs and old shrubs. Overall, clearing treatments were most effective in reducing densities of old *C. odorata* shrubs. Seedlings and young shrubs increased quickly following the clearing treatment and after six months densities in the clearing treatment were higher than prior to clearing. Seedling recruitment peaked 8 to 9 months after initial clearing. Fire without prior clearing was effective only in the seedling stage, but not in the adult shrubs. After the fire, adult shrubs easily re-sprouted and densities reached pre-treatment densities in only six months. The combined clearing and fire treatment was most effective in reducing densities of *C. odorata*, especially in seedlings and old shrubs and densities remained low for the duration of the experiment.

**Figure 5.2** The effect of fire and conventional clearing practices on total aboveground biomass of *C. odorata*. A: Biomass of *C. odorata* prior to the establishment of the experimental treatments in August 2003. B: Biomass of *C. odorata* in the first 6 months after experimental treatments were established, from November 2003 until March 2004 ($n = 4$). C: Biomass of *C. odorata* in the consecutive year, from April 2004 until May 2005 ($n = 8$). Experimental treatments are shown on the x-axis: Fi = Fire treatment, CC+Fi = Conventional clearing followed by fire, CC = Conventional clearing. The control treatment refers to the treatment without management interference, i.e. no fire or conventional clearing. Bars show mean biomass ($\pm$ SE), letters denote significantly different levels after multiple comparisons, each diagram was tested separately.
Figure 5.3 A. Average monthly rainfall (mm ± SE) in the Hluhluwe section of Hluhluwe-iMfolozi Park, for the duration of the experiment. B. Changes in *C. odorata* seedling density (N/m²) over time as the average seedling density (± SE) against time in months. The data for each of the four treatments (fire, conventional clearing followed by fire, conventional clearing and control) is shown in different lines and symbols. C. Changes in density of young *C. odorata* shrubs (N/m² ± SE) over time. D. Changes in density of old *C. odorata* shrubs (N/m²) over time. The arrows show the timing of the initial clearing and the fire event (left arrow) and the timing of the follow-up clearing (right arrow).
Fires burned with different ignition sources and intensities in block 1 and in blocks 2 and 3. Block 1 burned with a low intensity and patchy back fire as the head fire that was ignited to burn this block changed direction. The rate of spread was 0.03 m/s, resulting in a fire intensity of 116 kJ/s/m, which is classified as a very cool fire (Trollope & Potgieter 1985). Flame height was not higher than 20 cm. The initial head fire that missed block 1 turned from a surface fire to an active crown fire when reaching dense stands of cleared *C. odorata* just outside the experiment. This very intense crown fire burned blocks 2 and 3. Rates of spread were difficult to measure, due to the extreme nature of the fire, and were estimated to be at least 1 m/s. Based on this, fire intensity for blocks 2 and 3 was calculated to be 7200 kJ/s/m, which is classified as an extremely hot fire (Trollope & Potgieter 1985). However, as in some calorimeters all water evaporated, the fire intensity is presumed to be a minimum estimate. Average flame height in block 2 was 3.6 m and in block 3 average flame height was 1.2 m, ash colour was predominantly grey, white and red in both blocks. Experimental plots that were burned with a high fire intensity had a

![Figure 5.4](image)

**Figure 5.4** The effect of fire treatment and fire intensity on densities of *C. odorata*. Bars show average *C. odorata* densities (± SE) for the fire treatment and the conventional clearing followed by fire combination treatment against low fire intensity (block 1) and high fire intensity (blocks 2 and 3). Panels show the different age classes: seedlings (top panel), young shrubs (bottom left panel) and old shrubs (bottom right panel). Data is shown for the period November 2003 to March 2005, excluding the pre-treatment data and the follow-up data. Note that the scale axis for the old shrubs is a factor 10 lower then for the seedlings and young shrubs.
significantly lower density of *C. odorata* seedlings and young shrubs (Seedlings: \( F_{1,21} = 75.95, p < 0.001 \); Young shrubs: \( F_{1,21} = 57.42, p < 0.001 \), figure 5.4 A, B). Clearing in combination with fire further reduced *C. odorata* densities in these life stages (Seedlings: Treatment, \( F_{1,31} = 8.678, p = 0.006 \); Young shrubs: Treatment, \( F_{1,31} = 37.40, p < 0.001 \), Treatment x Fire intensity: \( F_{1,31} = 27.63, p < 0.001 \)). For the old shrubs, clearing in combination with fire significantly reduced *C. odorata* densities, but fire intensity did not further increase efficacy of control (Treatment, \( F_{1,31} = 91.67, p < 0.001 \), Fire intensity, \( F_{1,31} < 0.001, p = 0.980 \), figure 5.4C). In the area that was burned with the highest intensity (block 2) we observed that the seedbank of *C. odorata* was severely impacted by the fire as new *C. odorata* plants were all re-sprouts from old rootstocks.

The high intensity fire strongly impacted upon the native trees in the clearing and fire combination treatments in blocks 2 and 3. In block 2 90% of tagged trees (\( n = 30 \)) were top-killed, including all trees higher then 3 m (\( n = 10 \)), tree mortality was 20%. In block 3 75% of tagged trees (\( n = 29 \)) were top-killed and tree mortality was 10%. In block 1 only nine percent of tagged trees (\( n = 31 \)) were top-killed, all of which were below 1 m in height. No tree mortalities were observed in this block. After a recovery period of about 6 months, grass biomass increased in all treatments except the controls (Treatment: \( F_{3,114} = 9.407, p < 0.001 \), Time period: \( F_{3,11} = 4.746, p = 0.023 \), Treatment x Time period: \( F_{3,114} = 4.819, p < 0.001 \), figure 5.5). The most dominant grass species was the bunchgrass *Panicum maximum* that preferably grew through the *C. odorata* skeletons and reached heights of up to 2 m (pers. obs.). In the clearing treatment grass biomass decreased again towards the end of

![Figure 5.5](image-url)  
**Figure 5.5** Recovery of grass biomass (in g/m²) per treatment (X axis) for each of the four time periods (different bars): pre-treatment situation in August 2003, months 1–6 after establishment of experimental treatments (November 2003 – April 2004, \( n = 4 \)), months 7–18 after establishment of experimental treatments (May 2004 – April 2005, \( n = 5 \)) and follow-up (May 2005 – February 2006, \( n = 4 \)). Bars show average grass biomass (+SE). Posthoc test were performed separately per treatment to test for differences between time periods, different letters denote significant differences.
the experiment, while in the fire treatment and in the clearing and fire combination treatment grass biomass remained high. After one year a dense sward of *Panicum maximum* and *Eragrostis curvula* had established in the areas that burned with the highest intensity (block 2 and 3), with minimal re-infestation of *C. odorata*. This situation remained for the duration of the experiment, until April 2007.

**Discussion**

The combination of conventional clearing and fire (CC-Fi) was most effective in controlling densities of the invasive shrub *C. odorata*. This is in support of our hypothesis that the success of *C. odorata* control programs could be greatly increased if the clearing efforts are combined with a manipulation of the fire regime. After three-and-a-half years of monitoring minimal re-invasion of *C. odorata* occurred in the clearing and fire combination treatments. Contrary to expectations, the intensity of fire did not increase the efficacy of control of the old *C. odorata* shrubs. These old shrubs were fire tolerant and able to re-sprout even after a high intensity fire. Densities of seedlings and young adult shrubs, on the other hand, were reduced more strongly after a high intensity fire than after a low intensity fire.

The use of fire without prior clearing (Fi) as a tool to control *C. odorata* can result in contrasting effects. Depending on the age of the *C. odorata* shrubs and the intensity of the fires, *C. odorata* densities either increased or decreased following fire. Seedling density significantly decreased as a result of fire, and more so after an intense fire. Densities of adult *C. odorata* shrubs, however, increased compared to pre-treatment densities, due to vigorous re-sprouting. Hence, care should be taken when applying fire without prior clearing to control the invasion of *C. odorata*. The conventional clearing practice alone (CC) reduced *C. odorata* densities initially, but the species quickly recovered and grew back to almost original densities within the first year. Interestingly, clearing was least effective in the young shrubs. Possibly, smaller stems are easily missed when applying herbicide to the cut stump, especially in dense stands, or there is less surface for application of the herbicide, and therefore less penetration to the roots. Also young plants have a higher sprouting ability as was shown in previous work on *C. odorata* (Kushwaha *et al.* 1981; Devendra *et al.* 1998). Therefore, once an area has been cleared, follow-up clearings or controlled burning are essential as not to worsen the invasion.

Re-establishment of *C. odorata* following a fire may be due to seedling germination and together with vigorous sprouting allows for quick reinvasion (Macdonald 1983). However, in our study, *C. odorata* quickly reinvade burned areas only through sprouting from old stems. Apparently, *C. odorata* seeds did not survive exposure of the soil surface to heat (Mbalo & Witkowski 1997). Therefore, even though the burned areas might provide suitable germination conditions, few viable seeds are left after passage of the fire and new dispersal is required. These findings correspond to
earlier reports that fire eliminates the majority of *C. odorata* seeds in the soil (Epp 1987; Slaats 1995; Witkowski & Wilson 2001). Moreover, seedling emergence was highest in the clearing treatments rather than in the fire treatments, with a clear peak in densities 8 – 9 months after initial clearing. This indicates optimal germination conditions below cleared *C. odorata* litter. Experimental studies have shown that seedling emergence doubled on soil surfaces mulched with *C. odorata* twigs, possibly due to higher soil moisture and reduced evaporation on the covered surface (Slaats 1995; Ambika 2002b). Therefore, contrary to previous reports, cleared rather than burned areas provide optimal germination conditions for *C. odorata*. This is an important result that should be taken into account when planning follow-up clearings so that special care is taken to specifically target seedlings.

Competition with grasses is thought to hamper reinvasion of *C. odorata* through a reduction in seed germination and seedling growth (Erasmus & Vanstaden 1986). This has been shown experimentally; in plots where grass establishment has been successfully, minimal reinvasion of *C. odorata* has occurred (Erasmus 1988; Renrun & Xuejun 1991). In the current study grass biomass increased initially in all experimental treatments, except for the controls. In the conventional clearing (CC) treatments the shade-tolerant grass *Panicum maximum* initially grew high through the *C. odorata* skeletons, but grass biomass decreased again in the final stage of the experiment. This might be due to outshading by the resprouting *C. odorata* and the subsequent disturbance of follow-up clearing. In the fire treatment and in the clearing and fire combination treatment, however, grass biomass remained high throughout the course of the experiment. After one year a dense sward of *Panicum maximum* and *Eragrostis curvula* had established in the areas that burned with the highest intensity (block 2 and 3). In the fire treatment *C. odorata* grew back quickly through resprouting, despite the presence of the grasses, while in the clearing and fire combination treatment, minimal reinvasion of *C. odorata* occurred. In the latter treatment reinvasion was dependent on seed dispersal and seedling recruitment, rather than sprouting from old stems. It is likely that *C. odorata* seedlings are not able to successfully compete with a dense grass layer, while sprouted stems are. Indeed, sprouts are known to grow much faster than seedlings due to their higher initial belowground storage capital and to quickly reoccupy their own gaps (Bond & Midgley 2001). Also *C. odorata* seedlings have been reported to induce high mortality due to competition for resources (Yadav & Tripathi 1981; Yadav & Tripathi 1982). Greenhouse and field studies confirmed that *C. odorata* seedlings are not able to successfully compete with grasses in the seedling stage (te Beest, unpublished data), but that adult plants can coexist with a continues grass layer for at least several years (te Beest, unpublished data). Our data suggest that competition with grasses may indeed hamper re-invasion of *C. odorata*, but only when *C. odorata* has to establish from seed.

An important ecological effect of *C. odorata* is that due to its high tissue flammability (of especially the dry stems, pers. obs.) and position in the landscape (growing into tree canopies), the species can acts as ‘fuel ladder’ in carrying fires from the
regularly burned open savannas and grasslands into the canopies of woodlands and fire sensitive (riverine) forests (Macdonald 1983; Macdonald & Frame 1988). Trees is savanna woodlands can in general easily regenerate after fire by re-sprouting, however, for riverine and forest tree species that are often poorly adapted to fire an intense canopy fire is disastrous and tree mortality is generally high, leading to the loss of unique habitat. The net result is an attrition of upland forest patches and riparian vegetation which host high levels of diversity and endemism in this ecosystem (Macdonald 1983; Macdonald & Frame 1988). Therefore fires should be avoided at all times in these sensitive vegetation types.

Fire is widely used as a management tool in savannas to control the expansion of woody plants at the expense of open grass communities (Bond & Midgley 2000; Roques et al. 2001; Balfour & Midgley 2008; Wigley et al. 2009), especially to promote savanne large herbivores and their predators. For the control of woody species encroachment with fire, either intense fire are necessary that are able to top-kill the encroached shrubs (Trollope 1974; Trollope 1983) or frequent fires (Roques et al. 2001) that prevent shrubs from regenerating (Midgley & Bond 2001; Balfour & Midgley 2008). Often there is not enough fuel load present or weather conditions are not optimal to create the necessary intensity or frequency of the fires. In these cases bush encroachment is not controlled but rather promoted (Roques et al. 2001; Bond & Keeley 2005). Analogue to bush encroachment the invasion of *C. odorata* might also be promoted by low intensity or infrequent fires. On the other hand *C. odorata* might act as ecosystem engineer that can be used to restore the undesirable (encroached) systems to a more desirable (grassland) state (Crooks 2002; Byers et al. 2006). As *C. odorata* invades encroached thickets more readily then intact grasslands (pers. obs, see also Wigley et al. 2009) and produces large quantities of stem litter with low decomposition rates (Norgrove et al. 2000) that can act as fuel load, the presence of *C. odorata* in encroached thickets, especially after conventional clearing, could create fires that are intense enough to switch the system from an encroached woody state to a more open grassland state. However, this might solely work within the climatic envelope for ‘unstable’ savannas, with annual rainfall above 650 mm/year, where disturbances are required for the coexistence of trees and grasses. (Bond et al. 2005; Sankaran et al. 2005).

Many past control programs with species-oriented focus have failed to provide effective control of the invasive species (Wadsworth et al. 2000; Hulme 2006; Buckley 2008). In contrast, approaches focused on changing ecosystem processes through the disturbance regime have shown much more promising results (Buckley et al. 2007; Stokes 2008; Firn et al. 2008). In the current study we showed that the combination of conventional clearing of *C. odorata* together with a manipulation of the disturbance regime through fire provided drastic ecosystem level effects in that it switched the system from closed woodland into open wooded grassland. This combined approach has been very successful both in restoring the desirable grassland state and in controlling *C. odorata* in the short term. In the long term however,
C. odorata is most likely to re-invade these areas and regular burning and/or continued follow-up clearing will be necessary to keep the system in the desirable state. Furthermore while this drastic combination of clearing and fire might be very effective and desirable in fire-prone savanna systems, a whole other approach should be taken in fire-sensitive gallery forests and riverine vegetation. Fire is not a natural disturbance in these systems and care should be taken that C. odorata does not act as catalyst to carry savanna fires into forest stands. In these areas conventional clearing combined with removing of the dry litter that could potentially form a fire risk would be the desirable approach. We show that by targeting only invasive species (the clearing treatment) or only manipulating the natural disturbance regime (the fire treatment), we were not successful in controlling C. odorata. However, the combined approach of targeting both the invasive species and manipulating the natural disturbance regime at the same time successfully reduced densities of C. odorata.

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