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The ideal weed?

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Chapter 6

Synthesis: piecing the puzzle together

Mariska te Beest

Johan Ngobesi posing in front of dense *Chromolaena odorata* infestations in the large-scale Maphumulo experiment.

Introduction

In this thesis I studied the invasion ecology of *Chromolaena odorata* (L.) King & Robinson in Hluhluwe-iMfolozi Park in South Africa. *Chromolaena odorata* is listed among the world's worst alien invasive species (Lowe *et al.* 2000) and is rapidly invading the Old World tropics and sub-tropics, thereby threatening many of the biodiversity hotspots of the world. Dr. Ian MacDonald, former Chief Executive of WWF South Africa, stated in his keynote address to the Conference on Biological Control and Management of *Chromolaena odorata* in 2000 that 'I believe that if you can beat *Chromolaena*, then you can virtually be assured that you can beat any alien invasive plant species' (Macdonald 2002). He said this because the invasion of *C. odorata* goes hand in hand with many of the underlying problems that affect conservation in the tropics, like rangeland and forest degradation and increasing human population pressure. Therefore, the struggle to control *C. odorata* can serve as an excellent model system to deal with invasions world-wide.

Much is still unknown about the ecology of *C. odorata* and why it can so successfully invade such a wide array of habitats. Currently, there are no effective ways to keep this species under control. My main aim in this thesis was, therefore, to gain a better understanding of the ecology of *C. odorata* and its intricate relationships with native species in its novel habitat and to integrate this ecological knowledge into more effective control programs. In this synthesis I aim at putting the pieces of the ecological puzzle together and show where I have contributed insights. Upon invading novel habitats alien species engage into a whole new set of biotic and abiotic interactions. Understanding species invasions requires insight into these new interactions and their relative importance throughout the life cycle of the invader (Fig 6.1). In return, this also provides insight in the determinants of community structure without the invader. As seed characteristics, germination requirements and reproductive behaviour of *C. odorata* have been extensively studied (Ghosh 1961; Powell & King 1969; Edwards 1974; Yadav & Tripathi 1982; Erasmus 1985; Erasmus & Vanstaden 1986; Marks & Nwachuku 1986; Erasmus & Vanstaden 1987; Witkowski & Wilson 2001; Ambika 2002b; Almeida-Neto & Lewinsohn 2004), I have focused mainly on establishment, growth and persistence of this invader in natural savannas.

Chromolaena's ecological niche

A plant's fundamental (or physiological) niche is shaped by abiotic factors like temperature, available water, available light and available nutrients in the soil, while its more narrow ecological (or realized) niche is in addition shaped by biotic factors, such as herbivory, interactions with pathogens or mutualists and competition with other plants for space, water, light and nutrients (Hutchinson 1957; Schoener 1974; Grace & Wetzel 1981). Whether or not a plant can survive at a particular site

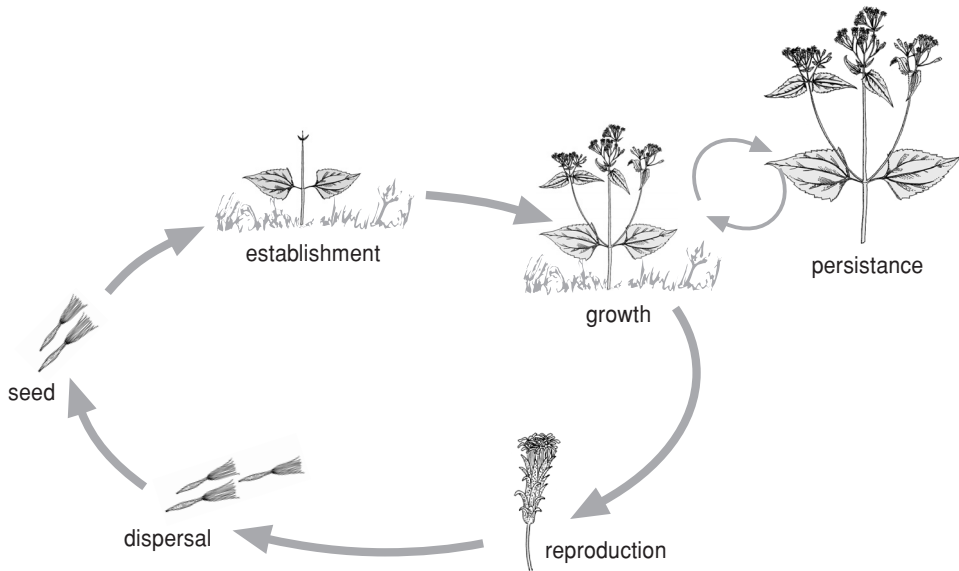


Figure 6.1 The life cycle of *Chromolaena odorata*. Small wind-dispersed seeds germinate and seedlings establish, plants grow when conditions are favourable in a certain environment; then, after reproduction, seeds disperse and again seedlings establish and grow; or plants persist by means of vegetative reproduction (re-sprouting).

depends on the net outcome of these abiotic and biotic interactions. In my research I have addressed many of the above-mentioned abiotic and biotic factors and I will discuss them in more detail in the following paragraphs.

Temperature

Chromolaena odorata is thought to be highly sensitive to low temperatures and frost (Yadav & Tripathi 1981; Goodall & Erasmus 1996) and in South Africa the species indeed only occurs in frost free areas (Goodall & Erasmus 1996). In several climatic models predicting the global distribution of *C. odorata*, temperature is, together with soil moisture, the most important explanatory variable (McFadyen & Skarratt 1996; Kriticos *et al.* 2005; Raimundo *et al.* 2007). The most recent model even works only with temperature variables, taking into account the average maximum January temperature, the average minimum July temperature, and the Jan/Jul diurnal temperature range (Raimundo *et al.* 2007). A similar model based on temperature and rainfall has been used to explore suitable biological control agents for the Southern African ecotype of *C. odorata* (Robertson *et al.* 2008). In Hluhluwe-iMfolozi Park the average daily temperature ranges from 13 – 35°C and falls well within the climatic envelope that is predicted for *C. odorata* occurrence.

Water

Southern African savannas have been classified into two main groups depending on the amount of available water (Huntley 1982). Here we define mesic savannas as receiving more than ~650 mm of rain on an annual basis and semi-arid savannas as receiving less than ~650 mm of annual rainfall (Sankaran *et al.* 2005). In savannas *C. odorata* is mostly confined to the wetter habitats, such as forest margins, seepage lines, gullies or riverine areas. In the mesic savannas of Hluhluwe-iMfolozi Park, however, the species is able to actively invade a much wider range of habitats, such as broadleaved woodlands and to a lesser extent fine-leaved woodlands and grasslands (Howison 2009). In the semi-arid savannas of the reserve *C. odorata* still does not occur beyond the river valleys (pers. obs.). When I started my PhD work, there was great concern among managers that the species would be able to spread out from the river valleys and invade these semi-arid savannas and grasslands as well. Therefore, I explored the role of water availability and competition for water with native grasses, to determine the potential for this spread into semi-arid habitats.

In **chapter 2** we showed that in South Africa *C. odorata* is indeed occurring under much lower rainfall conditions than where the species was previously known to exist (> 1000 mm/yr), which confirms previous suggestions on this (Goodall & Erasmus 1996; Kriticos *et al.* 2005; Robertson *et al.* 2008). The optimum probability of *C. odorata* occurrence in Southern Africa is situated around an annual rainfall of 700 mm/yr, which corresponds nicely to the conditions in mesic savannas. Our model also showed that when conditions became even drier (~ semi-arid), the probability of *C. odorata* occurrence quickly declined. Therefore, based on its current distribution we conclude that it is unlikely for *C. odorata* to spread further into semi-arid savannas. However, care should be taken, as *C. odorata* has previously managed to adapt from wet to mesic conditions, further shifts in its niche cannot be completely ruled out.

In **chapter 4** we attempted to simulate different rainfall conditions and studied the response of *C. odorata*. Unfortunately, due to insufficient success in experimentally reducing the actual rainfall, conditions in our experiment did not range from mesic to semi-arid, but rather from wet to mesic. Probably for that reason we did not find a response of *C. odorata* to water availability in this experiment and, although hampered by competition with native grasses, the species persisted in all treatments.

Competition for water

As Southern African *C. odorata* has expanded its niche to include drier (but still mesic conditions) conditions and is highly successful in those habitats, we expected that the species is a superior competitor for water. Especially in savannas where water is often a limiting factor, competition for water is likely to structure the plant communities. In **chapter 2**, however, we showed that seedlings of *C. odorata* are out-competed by the native grass *Panicum maximum* independently of water availability. This suggests that competition was not for water, but for other resources. In

chapter 4 we studied adult *C. odorata* under field conditions and found that competition between *C. odorata* and native grasses was again largely independent of water availability. Another explanation for the fact that in South Africa *C. odorata* is occurring under drier conditions than in other parts of its range would be the development of a more efficient water uptake of South African *C. odorata* populations. However, when comparing water use efficiency under experimental conditions between native and South African *C. odorata* populations in **chapter 2**, we did not find evidence for more efficient water uptake in the South African populations. In general, *C. odorata* was much less efficient with water than the native grass *Panicum maximum*. In a field study measuring transpiration rates of *C. odorata*, we however found that *C. odorata* actively dries out the soil, even when accounting for an increased bare soil evaporation under *C. odorata* shrubs. Soil moisture under *C. odorata* was 4–5% less than under grass (M. te Beest & J. Herder, unpubl. data). These results show that *C. odorata* needs a high amount of water due to its high transpiration rate and at the same time but is more inefficient in its use of water than grasses. In conclusion, our results explain why *C. odorata* is confined to the wetter areas of the habitat. However, to be able to overgrow all native vegetation and create virtual monocultures, the species must have some other mechanism allowing it to gain high dominance. In **chapter 2** we touched upon this by showing that light interception of *C. odorata* was significantly higher than for *P. maximum*.

Light

During the course of this PhD, I started to recognize the importance of light and light competition in the invasion of *C. odorata* in savannas. In tropical forests the importance of light competition has long been known. In those systems *C. odorata* is able to invade only when the forests have been degraded and the canopy has been opened, allowing enough light for the species to grow and reproduce (De Rouw 1991; Joshi 2006). Similar to its occurrence in the native range, the species disappears again as soon as the canopy closes (De Rouw 1991; Cruttwell McFadyen 1991; Joshi 2006). In savanna woodlands, however, the canopy is much more open, with often only 50-75% cover (Whateley & Porter 1983), allowing enough light for *C. odorata* to invade these woodlands in their natural state without canopy disturbance. Furthermore the physiognomy of these woodlands is very different to that of tropical and sub-tropical forests. Woodland canopies generally do not reach higher than 4-6 m, have many gaps, and a lower under-stratum of trees and shrubs, whereas forest canopies reach a closed canopy of c. 20 m (Whateley & Porter 1983; Joshi 2006). This allows *C. odorata* to scramble up into the tree canopy of woodlands, not only smothering the trees, but also increasing the risk of high intensity canopy fires, as I show in **chapter 5**. For (scarp) forests this fire risk is equally high as *C. odorata* forms dense infestations along the margins, linking the grass canopies with the forest canopies and thereby lifting grassland fires up into the tree canopies as well (Macdonald 1983; Macdonald & Frame 1988).

Competition for light

The key to success for *C. odorata* invasion may be its superior light competition strategy rather than superior water competition. The availability of water in the environment will determine the abiotic envelope in which the species can exist, whereas light will be superiorly competed for, allowing *C. odorata* to gain dominance in mesic savannas. Light competition is asymmetrical because of the unidirectional supply of resource (Schwinning & Weiner 1998). Therefore, taller species will always out-compete shorter species and small initial differences in height between species may have large consequences on the outcome of competition (Falster & Westoby 2003; Falster & Westoby 2005). In addition, *C. odorata* can behave as a climbing herb in a role analogous to lianas, which gives the species an advantage in light competition. Unlike trees, lianas have relatively little structural support, so they can allocate more resources to reproduction, canopy development, and stem and root elongation. Thus, they typically have a very high canopy:stem ratio, which results in a higher proportion of photosynthetic biomass than is present in most woody plants (Schnitzer & Bongers 2002). The asymmetry in light competition might have been the reason for *P. maximum* to out-compete *C. odorata* in **chapter 2**, because even though initial biomasses were similar, *P. maximum* seedlings were taller than *C. odorata* seedlings. Again, this suggests that in this experiment, competition was not for water, but rather for light. In **chapter 4** we showed a similar result. Only a small fraction of *C. odorata* seedlings were able to establish in undisturbed grassland with low light penetration.

Different strategies for light competition become apparent in a general trade-off for seedlings. Seedlings can either invest first in leaves to maximise photosynthetic capacity or invest first in height growth to prevent being out-shaded by neighbouring species (Westoby *et al.* 2002; Wright *et al.* 2004; Falster & Westoby 2005). This trade-off is made evident when comparing native and invasive populations of *C. odorata* as we did in **chapters 2 and 3**. Plants from the invasive South African populations grew taller with low investment in leaves (leaf weight ratio, LWR) and roots (root weight ratio, RWR) and the highest proportion of biomass allocated to stems (stem weight ratio, SWR). Plants from the native populations invested significantly more in leaves and roots and relatively less in stems. The initial allocation of biomass into stems was found for invasive *C. odorata* populations from West-Africa and India as well (Saxena & Ramakrishnan 1984; Ramakrishnan & Vitousek 1989; Slaats 1995).

Furthermore we found a higher specific leaf area (SLA) in invasive compared to native populations under low water availability (**chapter 2**). This means that invasive *C. odorata* is able to make larger and thinner leaves in order to maximise photosynthetic output. High SLA is strongly correlated with a high relative growth rate (RGR) and comes at a cost of higher water loss through the leaves (Poorter & Remkes 1990; Wright *et al.* 2004). In an environment where most species have adaptations to cope with regular droughts (thick and small leaves with low SLA) at the expense of their relative growth rates and effective light competition, *C. odorata*

might have 'found' itself an empty niche with its high RGR, its large and thin leaves with horizontal angles, that are perfect for out-shading any competitors, and its tall erect stem. When measuring the specific leaf area (SLA) of native savanna trees and *C. odorata*, the latter indeed falls completely out of the spectrum with an SLA of 230 cm²/g, which is more than twice as high as the average SLA of native savanna trees (100 cm²/g) (M. te Beest, unpubl. data).

In **chapter 2** we showed that *C. odorata* can react flexible to changes in its environment by increasing its SLA under wetter conditions. This suggests that *C. odorata* has not only 'found' itself an empty niche because of its species-specific traits, but it also has a unique strategy to invade natural savannas. By responding quickly to changing environmental conditions, this opportunistic species is able to optimally use the available resources at a given moment. Increasing SLA is a response to shade and *C. odorata* has been found to increase its SLA up to 600 cm²/g under low irradiance levels (Feng *et al.* 2007). However, this response is only possible under wet conditions, due to the increased transpiration rate that is the consequence of a high SLA. These results indicate again that *C. odorata* needs high amounts of water and will suffer when there is not enough water in the environment. When conditions become too dry *C. odorata* is known to quickly lose its leaves and die back, then re-sprouting again when conditions become more favourable. Therefore, the species' ability to cope with droughts depends mostly on its capacity to re-sprout.

Chromolaena odorata is not only very successful in woodlands; the species is highly effective in out-shading native grasses as well, but only after it has successfully established. We measured that under the canopy of dense *C. odorata* stands only 10–20% of light penetrates, which is equal to an 80–90% in PAR (percentage available radiation), and that grass biomass is reduced by 25% (M. te Beest & J.E. Boeke, unpubl. data). This level of light interception by *C. odorata* is very similar to our greenhouse results from **chapter 2**. In contrast, native tree species like *Dicrostachys cinerea* have a much smaller shading effect on grasses, reducing PAR by 60–70%, resulting in a grass biomass decrease of only 5% (M. te Beest & J.E. Boeke, unpubl. data). In **chapter 4** we showed experimentally that *C. odorata* negatively impacts the native grass canopy through shading, but only under lower water availabilities.

Another plastic response that may increase *C. odorata*'s ability to successfully compete for light was found in **chapter 3**. There we showed that under the influence of the biotic soil community *C. odorata* seedlings from the invasive-range population increased their height and relative investment of biomass into stems (SWR). This result is all the more interesting because this allocation response was not induced by changing abiotic conditions, but due to different biotic interactions in the species' non-native range. Although we did not observe a response in SLA in relation to soil biota, which would also be indicative of superior light competition, these results led us to hypothesize that light and *C. odorata*'s ability to capture light might be a very important factor explaining the invasion success of *C. odorata* in savannas.

Soil nutrients

Chromolaena odorata is known for its wide environmental tolerance and has been found to grow on soils ranging from dune-sands to heavy clays, providing that there is enough moisture in the environment (Liggitt 1983). Based on many transects in Hluhluwe-iMfolozi Park we found that the species was most commonly found in nutrient rich and clayey soils that are high in organic carbon and occurred much less in well drained sandy soils, although individuals were observed under these conditions (M. te Beest & M. Drijfhout, unpubl. data). The highest abundances of *C. odorata* were found on duplex soils, notably Valsrivier and Swartland. This is possibly related to the characteristic drainage of these soils where downward flow of water is limited and higher levels of water in the A-horizon (c. 20 cm) may favour the shallow-rooting *C. odorata* (M. te Beest & S. McLennan, unpubl. data). In general, the presence of water in the landscape in all its varieties (sub-soil run-off, seepage, drainage lines, gullies etc.), mostly determines where *C. odorata* is likely to grow and become dominant.

Herbivory

Chromolaena odorata is not frequently browsed by herbivores in South African savannas, despite of having no mechanical defence. I have observed occasional browsing by nyala, elephant and black rhino and seen the odd animal nibbling on some twigs or leaves, such as buffalo (pers. obs.). But in general *C. odorata* is left untouched by mammalian herbivores. This is most likely due to high levels of secondary compounds in the leaves that include flavonoids and terpenoids (Talapatra *et al.* 1974; Dominguez 1977) These high levels of secondary compounds in *C. odorata* possibly reflect adaptation to a different historic herbivore regime between the tropical forests in the species' native range (primarily insects) and the savannas its invasive range (primarily large mammals). This chemical defence apparently proves to be highly effective for large mammalian herbivores as well. Only elephants are able to sustain some damage to the plants as they free paths through the often impenetrable shrub thicket, thereby creating access to invaded areas and rivers for other animals. Interesting in this respect is an observation by MacDonald in Hluhluwe-iMfolozi Park that in the 1980s infestations of *chromolaena* were often severely defoliated by browsing (Macdonald 1983). Although, he states as well that because of large scale reductions in the populations of nyala and impala that were being carried out at the time, this natural control through browsing could well be significantly reduced in the years to come. It is also possible that this behaviour was observed during an extensive drought, when other food was limited or that the animals learned to avoid the species due to negative consequences of repeatedly consuming it.

Insect herbivores that feed on *C. odorata* in South African savannas are also few. A survey performed in Natal listed eight insect and two mite species that were found to reproduce and/or feed on *C. odorata* (Kluge & Caldwell 1992), among which the

generalist grasshopper *Zonocerus elegans* that I have frequently observed in Hluhluwe-iMfolozi Park as well. In contrast *C. odorata* is reported to be attacked by a large complex of insects, both generalists and specialists, in its native neo-tropical range, where 240 species have been recorded on *C. odorata* plants (Cruttwell 1974; Cruttwell McFadyen 1988a). Also many fungal pathogens are found to be associated with *C. odorata* (Barreto & Evans 1994). This suggests that *C. odorata* in its invasive range has escaped from many of its native herbivores, which were primarily insects.

Biotic interactions in the soil – pathogens and mutualists

Whereas many studies have focused on insect herbivores, especially in the light of biological control, very little is known about the soil community and their effects on the invasiveness of *C. odorata*. In **chapter 3** we explored the role of soil biota in the invasion of *C. odorata*. We found no clear evidence that *C. odorata* became invasive because it escaped from native soil-borne enemies. We observed, however, a highly interesting interaction between soil biota and biomass allocation. Plants from the invasive-range populations responded to new soil biota from the invasive range with increased investment in stems (SWR) and height growth. As mentioned before, native and invasive-range populations exhibited substantial differences in growth form during seedling growth, although they were indistinguishable in all other characteristics. Native-range plants stayed short and produced many leaves, resulting in a more bushy growth form, whereas invasive-range plants produced a tall erect stem with fewer leaves. These differences were consistent across several experiments, suggesting a genetic basis. The combination of this difference in growth form between native and invasive populations and the soil-biota induced allocation response of invasive populations, led us to hypothesise in **chapter 3** that selection has taken place in the invasive range, that drives towards plants with superior light competition traits and/or a higher plasticity in light response (evolution of plasticity).

However, a possible alternative explanation of these observed patterns could be new signal-transduction pathway that was recently described in plants (Gomez-Roldan *et al.* 2008). This signal, which is thought to be induced by the carotenoid-derived compound strigolactone, stimulates arbuscular mycorrhizal symbiosis (acts as early host recognition signal) and at the same time inhibits shoot branching, thereby inducing an erect morphology with few lateral branches. A negative effect of this compound is that it triggers the germination of parasitic plant seeds (Gomez-Roldan *et al.* 2008). In *C. odorata* this signal-transduction pathway could mean that when the species arrived in its new environment, signals were sent out to stimulate new arbuscular mycorrhizal symbiosis and that this in turn caused the plants to display the tall erect growth form that is typical of the invasive populations. Consequently, this specific growth form proved to be positive in the competition for light, which was an area where the heliophytic *C. odorata* could still gain much ground as the light environment in savannas was much more benign than in its native-range tropical forests. Therefore, this signal-transduction pathway and its effect on the

morphogenesis of *C. odorata* and its ability to successfully compete for light could be key to explaining its invasive behaviour in savannas, however, further research needs to elucidate whether strigolactones indeed occur in *C. odorata*.

Soil-organism driven allocation responses are mostly overlooked in invasive plant literature, but may have great implications for the invasiveness of a species, as soil biota may indirectly influence the competitive balance in the plant community. Other indirect soil biota effects have been found in India where *C. odorata* was reported to accumulate native fungal pathogens (*Fusarium* spp.) that are less harmful to itself than to its neighbouring native species (Mangla *et al.* 2008). However, when we tested the response of the native co-occurring grass species *Panicum maximum* to soil that was pre-cultured with invasive-range *C. odorata* individuals, we observed the opposite effect. Growth of *P. maximum* was stimulated when grown in soil that was pre-cultured with *C. odorata* and no detrimental effects were found (**chapter 3**). This result is confirmed with field observations in Hluhluwe-iMfolozi Park. *Panicum maximum* readily establishes when dense *C. odorata* stands have been cleared away and the grass becomes an abundant species penetrating through the *C. odorata* skeletons.

Combining **chapter 2 and 3** allowed us to test hypotheses like the ‘evolution of increased competitive ability’ (EICA) hypothesis (Blossey & Nötzold 1995). This hypothesis states that invasive species no longer have to defend themselves against their (specialist) natural enemies and can re-allocate resources from defence to growth. In **chapter 2** we found that native and invasive populations of *C. odorata* competed equally well in the absence of natural enemies, providing no evidence for increased competitive ability of invasive-range *C. odorata* populations. The soil-organism driven allocation response of invasive *C. odorata* populations (**chapter 3**), however, indicates that shifts in allocation of resources due to a changed community of soil pathogens and mutualists might have occurred in invasive-range populations. As shifts in a few traits can have large consequences in the multidimensional trait spectrum, the observed differentiation in height and stem allocation might allow *C. odorata* to occupy different habitats in the invasive than in the native range due to a different competitive balance with the native species, e.g. superior light competition. However, further studies are needed to confirm this.

Competition, disturbance and seedling establishment

I have already discussed the competition between *C. odorata* and native plants for water and light. Other resources that plants compete for are space and nutrients. However, the outcome of these competitive interactions can be influenced strongly by disturbance. In **chapter 4** we studied to what extent disturbances enable *C. odorata* seedlings to establish in natural savanna grasslands. Disturbances affect resource availability (nutrients, light) and open up space for new individuals and/or species to establish. According to Grime’s model of plant strategies, the intensity of competition decreases towards higher disturbance (Grime 1974) and invasion success is believed

to be enhanced by disturbance though increased resource availability (Davis *et al.* 2000). In savanna grasslands the most important disturbances are created by herbivores and fire, which can create temporary pulses of resources (water, nutrients) and may relax plant competition for a while. In this thesis we aimed to study the whole spectrum of disturbances in natural savanna systems, from herbivore-induced disturbances to low-intensity grassland fires (**chapter 4**) and high-intensity canopy fires (**chapter 5**). Herbivores impact grasses and affect the nutrient status of grasslands through grazing, trampling, wallowing, and defecating (Hobbs 1996). In **chapter 4** we simulated these herbivore-induced disturbances and showed that small-scale soil disturbances and grass clipping increased establishment success of *C. odorata* in native grasslands. In undisturbed plots 25% of seedlings managed to survive through the first year, whereas in disturbed plots seedling survival increased by almost 50%. In this way herbivores may create conditions that favour *C. odorata* invasion. However, disturbance is no pre-requisite for *C. odorata* invasion, as seedlings can still survive in undisturbed grasslands, biding their time to grow and reproduce.

Fire

Fire is an important natural component of savannas systems, where its frequency, intensity and ecosystem impact depends on local weather conditions, topology, soil conditions and fuel loads (Bond & Keeley 2005). In **chapter 4** we showed that a low-intensity grassland fire reduced survival of *C. odorata* seedlings to 5%. The effect of fire on seedling survival was less strong in the presence of herbivore-induced disturbances. In disturbed plots seedling survival was still 22%, which was probably due to less fuel load in these plots and therefore a lower intensity of the fire. The presence of many seedling sprouts during the harvest of this experiment and the average pre-fire height of the surviving seedlings being a mere 10 cm, indicate the ability of *C. odorata* to re-sprout from a very early age. This confirms the enormous regeneration potential of the species once it gains a foothold in a certain habitat. Previous authors have suggested that regular (grassland) fires may contribute to the control of the species, while incidental (canopy) fires could stimulate the spread of *C. odorata* (Macdonald 1983; Gautier 1996; Goodall 2000). We indeed showed that seedling establishment of *C. odorata* was lower in burned grasslands than in non-burned grasslands (**chapter 4**), but how frequent a grassland has to be burned to keep *C. odorata* under control, remains open for further research. Analogue to controlling bush encroachment the frequency of burning might be a delicate balance. Infrequent fires will enhance woody establishment in grasslands, while too frequent fires will not give the grass enough time to recover and aid woody invasion. Furthermore fire frequency might interact with rainfall in determining the successful establishment and invasion of *C. odorata* in grassland habitat. This is implied by MacDonald (1983), who reports that in Hluhluwe-iMfolozi Park the least invaded habitat used to be the regularly burned grassland, but that 'in recent years' the species has invaded many grasslands in the higher rainfall areas of the reserve'

and ‘currently the least invaded area is likely to be the drier Acacia savannas in the south of the reserve, which are also regularly burned’. Finally, the question remains not only how fire frequency affects *C. odorata* establishment, but also how adult *C. odorata* shrubs affect fire frequency and hence the natural fire regime in savannas.

Many plant invaders are known to alter fire regimes and these invaders are recognised to be among the most important ecosystem-altering species in the world (Brooks *et al.* 2004). *Chromolaena odorata* is notorious for its ability to become a fire hazard during the dry season, when leaves and stems dry out and many authors have observed this in many different parts of the world (Pancho & Plucknett 1971; Macdonald 1983; Napompeth *et al.* 1988; Lucas 1989; Muniappan & Viraktamath 1993; McFadyen & Skarratt 1996; Timbilla & Braimah 1996; Devendra *et al.* 1998; Witkowski & Wilson 2001; Bani 2002). The leaves of *C. odorata* contain a whole range of secondary compounds, among which are several volatile compounds that are believed to be responsible for its high tissue flammability (Liggitt 1983; Bamba *et al.* 1993; Tonzibo *et al.* 2007). The species has been observed to burn even when green in midsummer (Macdonald 1983; Liggitt 1983), but most likely weather conditions at the time were extremely hot. In our large-scale fire experiment (**chapter 5**) we observed that green shrubs did not burn readily, but needed a certain heat threshold to ignite. Once ignited, shrubs burned fiercely with a jet flame with fluorescent green flashes. This high flammability of *C. odorata* when weather conditions are extreme (low humidity, high temperature, strong wind) (Trollope 1983) or when shrubs have dried out (e.g. after mechanical clearing) constitutes a fire hazard for natural vegetation and changes the fire regime to more intense fires. Moreover, due to its position in the landscape (forest margins) and its specific growth form of scrambling into tree canopies of woodlands, adult *C. odorata* shrubs are able to lift grassland fires into fire-sensitive tree canopies by increasing the vertical continuity for the fire. This leads to *chromolaena*-induced high-intensity canopy fires that have been observed before (Macdonald 1983; Macdonald & Frame 1988), but never experimentally induced as we did in **chapter 5**.

Chromolaena odorata affects and is affected by fire in a complicated interaction that was not well understood previously. In **chapter 4** we showed that low-intensity grassland fires reduce the seedling survival of *C. odorata*. Hence, establishment in grasslands is hampered by fire, but not prevented. We hypothesise that, once *C. odorata* becomes established, especially in the more mesic grasslands, and forms its typical mono-specific dominant stands, *C. odorata* will reduce the frequency of fires by out-shading the grasses and reducing fuel load. In contrast, in woodland habitat the effect of *C. odorata* is increasing the fire intensity and vertical continuity, leading to infrequent but high-intensity canopy fires. In **chapter 5** we assessed if these *Chromolaena*-induced high-intensity canopy fires affect survival of adult *C. odorata* shrubs and whether these types of fires could be used to control the species. This latter question was put forward by the park management as they wanted to know whether intense fires could increase the efficacy of current clearing methods. In

chapter 5 we showed in a large-scale field experiment that adult *C. odorata* shrubs can survive high-intensity canopy fires. The high-intensity canopy fire resulted in 100% top-kill of woodland trees and *C. odorata* shrubs, both of which were able to re-sprout after the fire. However, due to its high growth rate, *C. odorata* was able to re-grow much faster than native trees and quickly dominated the vegetation again. After only several months *C. odorata* densities were back to pre-treatment densities, thickening up even more due to reduced competition with the native trees. In this way *C. odorata* creates a positive feedback between its own growth and fire. That *C. odorata* is able to enhance its own spread through these incidental high-intensity canopy fires has been suggested before (Macdonald 1983; Gautier 1996; Goodall 2000). Also, similar results were found in West-Africa, where after burning *C. odorata* follows the species came back in higher densities (Norgrove *et al.* 2000). An additional factor that amplifies the positive feedback between *C. odorata* and fire is that fire rejuvenates old and dense stands. Several papers have stated that *C. odorata* shrubs become senescent after 10-15 years, individual shrubs do not reproduce anymore, the canopy becomes less dense and native species are able to establish (Kushwaha *et al.* 1981; Witkowski & Wilson 2001). The effect of burning such stands is that individuals re-sprout and stands become rejuvenated. Therefore, the use of fire without additional clearing, even when the fires are of high intensity, will enhance the invasion of *C. odorata*. Also the timing of burning that is generally performed at the end of the dry season (Aug/Sept) and therefore exactly coincides with the time of the *C. odorata* 'seed rains', will further aid the invasion of this species.

However, when *C. odorata* shrubs were slashed and poisoned according to the standard clearing practice a few weeks prior to the ignition of the fire, the effects were completely different. After about a year a continuous grass layer had established with minimal re-invasion of *C. odorata* (**chapter 5**). After 4 years, *C. odorata* individuals were present, but still in low densities. This result confirms our findings in **chapter 4** that *C. odorata* is able to re-invade savanna grasslands, but is severely hampered by competition with grasses. We hypothesize that the conventional clearing prior to the burning increased the fuel load and hence fire temperature, killing the seedbank of *C. odorata* and preventing re-sprouting as the shrubs were killed by the chemical treatment, allowing native grasses to re-grow. Previous studies have shown similar results; over-sowing bare patches of ground with grasses hampers *C. odorata* establishment (Erasmus 1988; Wu Renrun & Xu Xuejun 1991). However, although the results presented in **chapter 5** might be a triumph for *C. odorata* control, effects on the native vegetation were drastic (conversion of natural woodland to grassland). In figure 6.2 we show a conceptual model of the *C. odorata* invasion in natural savannas to summarize the manifold interactions of *C. odorata* and fire and the impact on the native vegetation. The *chromolaena*-induced fire shifted the system from a woodland state into a grassland state. In the savanna woodlands that harbour many fire-prone species, this is not perceived to be

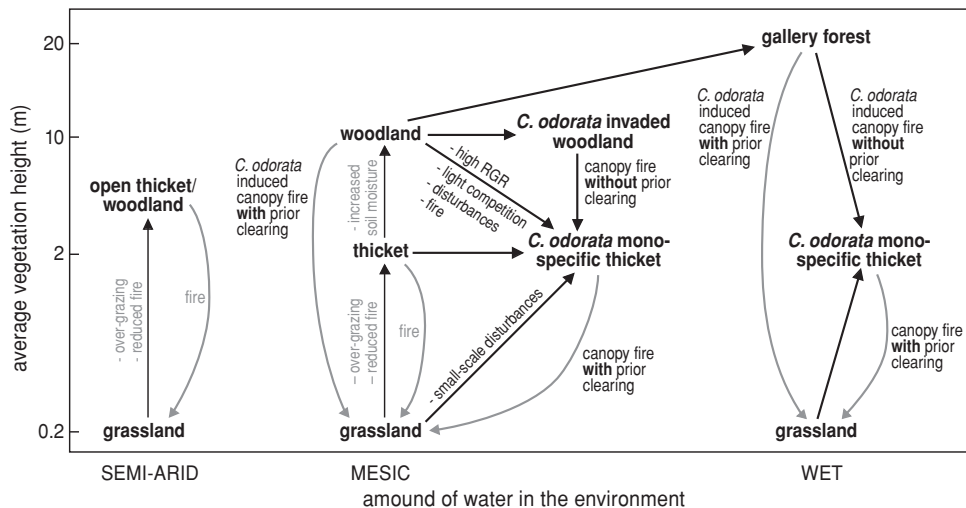


Figure 6.2 A conceptual model of *C. odorata* invasion in natural savannas. Solid lines represent both normal successional processes from grassland into thickets, woodlands and forest (with grey text) or invasion of *C. odorata* (with black text). The effects of fire are represented by grey lines. Text indicate interactions between *C. odorata* and fire.

a big problem and opening up of the vegetation is regarded as positive for game-viewing and it aids the control of bush-encroachment. However, in old-growth and fire-sensitive riverine and gallery forests, this effect of *C. odorata* is highly devastating and *C. odorata*-induced canopy fires could actually cause biome shifts from forest to grassland. In this way it forms a threat to these already rare patches of forest biome with high levels of diversity and endemism. Therefore I want to stress the importance of protecting the last remnants of scarp forests in Hluhluwe-iMfolozi Park and the rest of KwaZulu-Natal against the invasion of *C. odorata*. This has been advocated before (Macdonald 1983; Liggitt 1983; Witkowski & Wilson 2001), but dense *C. odorata* stands persist in the forest margins and every year another patch of forest is destroyed by *chromolaena*-induced canopy fires.

Previous studies have stated that the bare ground created after a fire provides suitable germination conditions for *C. odorata* and that the species quickly re-colonises these areas from seed (Macdonald 1983; Liggitt 1983). However, in our plots that burned with a high-intensity fire we observed no seedlings, and re-colonisation was only through re-sprouting stems (**chapter 5**). Apparently the seedbank was killed by the fire. This has been suggested before by Witkowski & Wilson (2001). It has been found that *C. odorata* seeds do not tolerate high soil temperatures (Mbalu & Witkowski 1997), indicating that most of the seeds are indeed killed after passage of a fire. Therefore, *C. odorata*'s colonisation of newly burned areas is dependent on re-sprouting (when shrubs have not been previously cleared) or

dispersal of fresh seeds from adjacent *C. odorata* stands. Unfortunately, the timing of burning, that is generally performed in the end of the dry season (Aug/Sept), exactly coincides with the seed set of *C. odorata*. This would indeed allow for quick dispersal and re-colonisation of newly burned patches as reported by Macdonald (1983).

Persistence

The ability to resprout and invest in the current generation is an important means for plants to persist in the environment without the need for recruitment (Bellingham 2000; Bond & Midgley 2001; Del Tredici 2001). Vegetative persistence after a disturbance is a neglected concept in invasion ecology, but as I show in **chapter 5** it is an extremely important life history strategy for *C. odorata*. The ability to re-sprout may greatly contribute to the invasiveness of a plant invader, as individuals may optimise resource allocation, maximise fitness and prevent themselves from local extinction (Closset-Kopp *et al.* 2007), for example after droughts or fires as is the case for *C. odorata*. However, there is a cost to persistence. Plants that sprout vigorously as adults tend to be poor recruiters (Bellingham 2000; Bond & Midgley 2001). This persistence-recruitment trade-off, however, does not seem to be equally strong in native and invasive species (Knapp & Canham 2000; Webster *et al.* 2005; Closset-Kopp *et al.* 2007). Also for *C. odorata* this persistence-recruitment trade-off does not appear to be very strong as the species has a prolific seed production (Witkowski & Wilson 2001). I hypothesise that *C. odorata*'s ability to re-sprout and its lack of a trade-off between re-sprouting and seed production is an important explanation for the success of this species, but further studies are needed to confirm this.

Which hypotheses play a role in the invasion of *C. odorata*?

In this thesis I could not clearly reject one hypothesis and accept another as many processes simultaneously play a role in determining the invasiveness of *C. odorata*. To summarise my results and put them into perspective, I made an overview of current hypotheses explaining species invasions (for explanation of the hypotheses see the introduction) and one-by-one explain the role they play in the invasion of *C. odorata* and how they can help us to better understand and manage this invasive species (table 6.1).

To assess what other authors find to be key factors determining the invasive success of *C. odorata* I have reviewed over 250 publications for traits and characteristics that may be important in *C. odorata*'s invasiveness. Most of these publications dealt with biological control and made no reference to traits or invasive behaviour, but many other publications did. In total 99 publications made reference to traits or impacts, but only a handful of publications specifically mentioned the key characteristics that they thought were most important in explaining the species' invasive behaviour. Interesting to note was that *C. odorata* was often described using the

word aggressive, which is generally a behavioural term used for animals. In table 6.2 I give an overview of invasiveness-related characteristics and list them according to the number of times a specific characteristic is mentioned. Almost all publications mention the ability of *C. odorata* to out-shade and smother native vegetation (the ‘liana strategy’ (Schnitzer & Bongers 2002)). Far fewer publications mentioned the traits that are necessary for *C. odorata* to show this behaviour, namely: a high growth rate and an allocation bias towards stems, resulting in a scrambling growth form with many dense woven branches. Together with the prolific production of wind dispersed seeds, these are most often mentioned as explaining the invasive behaviour of *C. odorata*.

Concluding remarks: The ideal weed?

Can we finally give some answers as to why *C. odorata* is such a successful invader? I believe we do. The most difficult part, however, is how to implement this ecological knowledge into existing control programmes and effectively control this species. When I started my PhD work, one of my general ideas was that if *C. odorata* would be a superior competitor due to intrinsic traits (a ‘super species’ or ‘ideal weed’), control efforts would be likely to fail, whereas when the invasion would be more dependent on specific attributes of the community (like disturbance regimes), the invasion would be easier to control. In some habitats the second seems to be true. The invasion of *C. odorata* in degraded (tropical) forests, for example, can be reversed once the forest is allowed to re-grow and the canopy closes again. But in retrospect this was mostly a naïve idea and of course the reality is much more complex. In the example of forest degradation in the tropics, reversing this process is extremely difficult due to socio-economic challenges.

In this thesis I have shown that species invasiveness and community invasibility go hand in hand in determining when and where *C. odorata* will invade. As to why *C. odorata* is so successful, I believe that the key to its success is (1) the presence of specific traits that enhance the species’ invasiveness, such as high growth rate, high reproductive output, high allocation to stems and profuse branching in adults, high re-sprouting ability and high plasticity in traits related to capturing light (*ideal weed hypothesis*), combined with (2) its high phenotypic plasticity, (3) the apparent reduced trade-off between recruitment and persistence (*escaping physiological trade-offs*) and between growth and stress tolerance (*reckless invader hypothesis*) and (4) the fact that its traits and life-history strategy are unique to savanna systems (*empty niche hypothesis*), see table 6.1 for further explanations. This is then further enhanced by (5) the absence of natural insect herbivores (*enemy release hypothesis*), (6) the novel interactions with the invasive-range soil community that amplify traits that increase the species invasibility (**chapter 3**) and (7) the benign light environment in savannas compared to closed-canopy forests.

Table 6.1 An overview of current hypotheses explaining species invasions and the role they play in the invasion of *C. odorata*. For each hypothesis I have indicated if they play a role in the invasion *C. odorata* (+); if they might play a role, but need further study (+/-), if they do not play a role in explaining the invasion of *C. odorata* (-), or whether it is still unknown (?) or the hypothesis is not applicable (NA), followed by my substantiating and references.

Hypothesis	Plays a role in the invasion of <i>C. odorata</i>
Enemies release hypothesis (Keane & Crawley 2002)	+/- No clear evidence for release from below-ground enemies (Chapter 3). Literature suggests release from above-ground herbivores, notably phytophagous insects (Cruttwell McFadyen 1988b; Kluge & Caldwell 1992).
Evolution of increased competitive ability hypothesis (Blossey & Nötzold 1995)	+/- No difference in competitive ability between native and invasive plants was observed (Chapter 2). However, soil-biota induced allocation responses observed in invasive-range plants indicates an interaction between resource allocation and below-ground enemies (Chapter 3).
Escaping physiological trade offs between r- and K-strategy (Closset-Kopp <i>et al.</i> 2007)	+ <i>C. odorata</i> shows both high re-sprouting ability (Devendra <i>et al.</i> 1998) and prolific seed production (Witkowski & Wilson 2001), indicating lack of trade-off between recruitment and persistence (Chapter 4 & 5).
Reckless invader hypothesis (Simberloff & Gibbons 2004; Alpert 2006)	+ All or nothing strategy in requiring resources, indicating a lack of trade-off between growth and stress tolerance. <i>C. odorata</i> shows a high demand coupled with low efficiency for water (Chapter 2 & unpubl. data) and nutrients (Saxena & Ramakrishnan 1984).
Empty niche hypothesis (Elton 1958)	+ <i>C. odorata</i> shows an unique life history strategy that is not present in the native community: a ruderal strategy (high RGR, SLA, SWR and reproductive output) combined with a persistence strategy (dying back and re-sprouting) (Chapters 2-5).
Novel weapons hypothesis (Callaway & Aschehoug 2000; Callaway & Ridenour 2004)	+ Allelopathy has been reported for <i>C. odorata</i> . (Ambika & Jayachandra 1980; Sahid & Sugau 1993; Gill <i>et al.</i> 1996; Ambika 2002a; Sangakkara <i>et al.</i> 2008)
Ideal weed (Baker 1965)	+ <i>C. odorata</i> has many species-specific traits that make it a successful invader (Chapters 2-5), see also next paragraphs.
Ecosystem engineering (Crooks 2002)	+ It has been suggested that <i>C. odorata</i> can modify its environment in favour of its own growth (Macdonald 1983; Norgrove <i>et al.</i> 2000; McWilliam 2000). We have shown how <i>C. odorata</i> can create high-intensity canopy fires that destroy woodlands and enhance its own growth (Chapter 5).
Adaptation hypothesis (Duncan & Williams 2002; Maron <i>et al.</i> 2004)	+/- Rapid evolution of <i>C. odorata</i> due to different selective pressures in the novel habitat has been suggested in the literature (Edwards & Stephenson 1974). The observed differences in growth form between native and invasive-range populations (Chapters 2 & 3), enhanced by the interaction with the invasive-range soil community (Chapter 3) further supports this.

Table 6.1 Continued

Hypothesis		Plays a role in the invasion of <i>C. odorata</i>
Biotic resistance hypothesis (Elton 1958; Levine <i>et al.</i> 2004)	+	Establishment and performance of <i>C. odorata</i> is hampered by native savanna grassland (Chapter 4).
Missed mutualisms hypothesis (Richardson <i>et al.</i> 2000a; Mitchell <i>et al.</i> 2006)	+/-	Lower mycorrhizal infection rates in the invasive range suggests that invasive <i>C. odorata</i> benefits less from mutualistic interactions (Chapter 3).
Enemy of my enemy (Colautti <i>et al.</i> 2004)/ Accumulation of local pathogens hypothesis (Eppinga <i>et al.</i> 2006)	+/-	No evidence was found for South African <i>C. odorata</i> (Chapter 3), although results might be site specific, as evidence for this hypothesis was found for Indian <i>C. odorata</i> (Mangla <i>et al.</i> 2008).
Invasional meltdown hypothesis (Simberloff & Von Holle 1999)	+/-	It has been suggested before that <i>C. odorata</i> forms secondary invasions in areas that have been cleared from other aliens (Macdonald 1984). I have observed <i>C. odorata</i> facilitating for other alien plants (<i>Solanum mauritanum</i> , <i>Tagetes minuta</i> and <i>Bidens pilosa</i>) in the bare areas formed after dense <i>C. odorata</i> infestations burned and destroyed a patch of forest (unpubl. data).
Disturbance hypothesis (Hobbs & Huenneke 1992)	+	Disturbances aid the invasion of <i>C. odorata</i> . We have assessed herbivore-induced small-scale disturbances in grasslands, low-intensity grassland fires and high-intensity canopy fires (Chapter 4 & 5).
Dynamic equilibrium hypothesis (Huston 2004)	?	We have not measured productivity, but the species is known to thrive only under high-nutrient conditions (Saxena & Ramakrishnan 1984).
Fluctuating resources hypothesis (Davis <i>et al.</i> 2000)	+	The positive effect of small-scale disturbances in grasslands are likely to be mediated by increased light penetration (Chapter 4).
Invasion windows hypothesis (Johnstone 1986)	+	<i>C. odorata</i> benefits from periods of high rainfall or high disturbance. Once established the species is likely to persist in the environment due to its high regeneration capacity (Chapter 4 & 5).
Local adaptation hypothesis (D'Antonio <i>et al.</i> 1999)	+/-	We did not find evidence for this hypothesis in the natural savannas of Hluhluwe-iMfolozi Park, which are largely unchanged by humans. However, in many tropical systems degradation of the primary forests by humans allows <i>C. odorata</i> to invade (De Rouw 1991; Joshi 2006).
Environmental heterogeneity hypothesis (Melbourne <i>et al.</i> 2007)	+	The existence of high levels of heterogeneity in savannas might have aided the invasion of <i>C. odorata</i> due to a more diverse array of niches available. In Hluhluwe-iMfolozi Park woodlands and grasslands have different susceptibility to invasion by <i>C. odorata</i> , woodlands being the more invaded state (Howison, 2009a).
Introduction pressure or propagule pressure hypothesis (Lockwood <i>et al.</i> 2005)	NA	<i>C. odorata</i> has been introduced accidentally into South Africa or escaped from a botanic garden (Zachariades <i>et al.</i> 2004). It is not deliberately sown and distributed by humans.

Table 6.1 Continued

Hypothesis		Plays a role in the invasion of <i>C. odorata</i>
Darwins naturalization hypothesis (Darwin 1859)	?	There are few close relatives of the tribe Eupatorieae that are native to South Africa, 13 species occur in Southern Africa of which 7 are alien invaders (Retief 2002). However, whether this might have allowed <i>C. odorata</i> to become highly successful remains a topic for further study.
Global competition hypothesis (Alpert 2006)	NA	This hypothesis does not deal with explaining the success of a single invader.
Habitat filtering hypothesis (Alpert 2006)	?	It is possible that <i>C. odorata</i> has been brought to botanical gardens for its wealth of flowers, which would have unintentionally selected for a high reproductive output. However, whether this has played a role in the successful invasion of <i>C. odorata</i> remains unknown.

When placing the invasion of *C. odorata* in natural savannas in a more evolutionary context, several questions remain open. The *empty niche hypothesis*, for example, raises the question of why such a successful set of traits has not evolved in the native savanna community, while the *ideal weed hypothesis* raises the question of how such an extraordinary species could have evolved in the native range. Regarding the first question, I believe that the individual traits that characterise *C. odorata* are not unique *per se*. Most of the traits mentioned (high RGR, heliophytic, high reproductive output) are typical for plants of secondary succession and are also present in several savanna species, *e.g.* *Dombeya* sp. or *Lippia javanica*. The key to *Chromolaena's* success is rather the combination of its specific set of traits and life history strategy with community determinants, such as the absence of natural enemies. For example, in its native range *C. odorata* does not easily colonise the drier savannas, which is presumably due to the high level of damage that is caused by the many insect herbivores feeding on *C. odorata* (Cruttwell McFadyen 1991), indicating an important role for release from above-ground enemies in the invasion of *C. odorata*. Regarding the second question, I believe that *C. odorata* is not an extraordinary species *per se*, especially not in its native range where it is part of plant communities without being invasive. I hypothesise that specific adaptations from the species' native range have proven to be highly effective in its invasive range as well. For example, the specific herbivore defence based on high levels and variety of secondary compounds (terpenoids, flavonoids, aromatic oils, etc.) has evolved in an arm's race with a large complex of insect herbivores (Agrawal 2007) and not with large mammalian herbivores that would rather induce a combination of mechanical and chemical defence, such as development of thorns and/or high levels of tannins. However, in the case of *C. odorata* this chemical defence against insect herbivores seems to work excellent against mammalian herbivores as well. Another example is

drought resistance. Sub-tropical savannas are much drier eco-systems than tropical forests, receiving on average only half the amount of annual rainfall compared to tropical forests (Cowling *et al.* 1997), but specific drought adaptations, such as thick sclerophyllous leaves, lack in *C. odorata*. However, the species manages perfectly well to survive regular droughts through a combination of dying back and re-sprouting from the basal stem. I hypothesise that this strategy might have evolved to survive large-scale disturbances, such as fires, which have been reported from *C. odorata*'s native range (Cruttwell McFadyen 1991), hence explaining as well the species' ability to survive fire. Finally, the extensive distribution of *C. odorata* in its native range might have selected for high levels of phenotypic plasticity. In its inva-

Table 6.2 Characteristic of *C. odorata*. The numbers refer to the number of times a characteristic has been mentioned in a publication (N). A total of 99 publications were used to compile this table, although most of them did not specifically mention which traits the authors thought could explain the invasiveness of *C. odorata*. Impacts have been mentioned (in gray) when there was also an advantage for *C. odorata* (positive feedback).

Characteristics of <i>C. odorata</i>	N
Competitive ability - physical smothering & out-shading	81
High growth rate	49
Prolific seed production	47
Flammable foliage / fire hazard	42
Wind dispersal of seeds	40
Growth form - creates dense mono-specific stands	31
Allelopathic properties	27
High environmental tolerance	26
High colonisation ability (germination, growth and reproduction)	24
Growth form - profuse branching of brittle stems	23
Vigorous sprouting ability	21
Heliophyte (requires light for growth and reproduction)	20
Fire tolerant - able to survive fires	19
Leaves and stems dry out in dry season to prevent water loss	15
Short term persistent seedbank, ~ few years, majority of seeds < 12 months	13
Heliophytic germination (requires light for germination)	12
Effective long distance dispersal (seeds cling to fur, clothes, machinery)	11
Tolerant in germination requirements	11
Low seed dormancy	10
Affects natural succession – acts as fire ladder, creates thicket 'state'	10
High in secondary metabolites	10
Short juvenile period	7
Synchronised flowering	7
Reproduction by apomictic means	6
Allocation - high investment in stems	5
Accumulating pathogens that have detrimental effects on neighbouring species	5
High phenotypic plasticity	5

sive range this will allow the species to tolerate a wide variety of habitats, which is of fundamental importance to invade inherently dynamic systems like savannas.

Coming back to the question raised in my title: How close does *C. odorata* come to being an ideal weed? I believe that the answer to this question is: Very close! Table 6.3 shows the comparison of the traits found in the literature (table 6.2) to the traits mentioned by Baker that determine the ideal weed. He mentioned as well that probably no weed in existence has all the characteristics and if it did, it would take over the world (Baker 1965). So fortunately for us, *C. odorata* does not display all the characteristics of the ideal weed, but it does contain many of them. All but two 'ideal weed' characteristics are displayed by *C. odorata*, lacking in the short lifespan of its seeds and only one or two discrete seed crops per year. These are, however, vastly compensated for by its enormous seed production. Of course, as the characteristics of 'the ideal weed' were based on closely related Asteraceous species, it is not surprising that there is a good match in characteristics. Also, I believe that 'the ideal weed' does not exist without its ideal community. It is true that *C. odorata* has invaded a wide range of habitats, but there are also many habitats where it will never invade, such as arid or temperate zones. For those areas *C. odorata* is certainly not an 'ideal weed'. Nevertheless, the invasion of *C. odorata* is a major global problem and seriously impacts many livelihoods in the tropics and subtropics. In 2007, an extensive management report came out giving thorough guidelines for the control of *C. odorata* in mesic savannas (Euston-Brown *et al.* 2007). I hope that my research can add to this and, therefore, I want to conclude with a set of management recommendations for the control of *C. odorata* in mesic savannas that have been derived from my research.

Table 6.3 Characteristics of the ideal weed (Baker 1965; Baker 1974) and its similarities (√) and dissimilarities (x) with *Chromolaena odorata*.

Ideal weed characteristics	<i>C. odorata</i>
1. Germination conditions fulfilled in many environments	√
2. Discontinuous germination (internally controlled) and great longevity of seed	x
3. Rapid growth through vegetative (seedling) phase to flowering	√
4. Continuous seed production for as long as growing conditions permit	x
5. Self-compatible, but not completely autogamous or apomictic.	√
6. When cross-pollinated, unspecialized visitors or wind utilized	√
7. Very high seed output in favorable environmental circumstances	√
8. Produces some seed in wide range of conditions: tolerant and plastic	√
9. Has adaptations for short and long-distance dispersal	√
10. If a perennial, has vigorous vegetative reproduction	√
11. If a perennial, has brittleness, so not easily drawn from the ground	√
12. Has ability to compete inter-specifically by special means (rosette, choking growth, allelochemicals)	√

Towards a solutions – recommendations for managers

Conventional clearing

- Do not clear *C. odorata* without the certainty for follow-up and revisit the cleared area within 9 months to a year to check the necessity for further action. Limited clearing or broken off clearing programs will only worsen the invasion.
- Hand-pull as large plants as possible, so not only the seedlings, to reduce the incidence of re-sprouting. *C. odorata* plants do not root very deep, so especially low density areas can be controlled with hand-pulling, thereby reducing the necessity for follow-up.
- After conventional clearing the bare soil is generally covered with *C. odorata* stem-litter. These litter-covered soils provide the perfect germination conditions for *C. odorata* seeds. Follow-up efforts should specifically be aware of these litter-covered areas and hand-pull all new seedlings after a few months.

Fire without prior clearing

- Clear burned areas fairly shortly after burning as it eases the clearing and prevents *C. odorata* from growing back dense stands. Especially low intensity fires will allow *C. odorata* to re-invade quickly. Follow-up will be necessary.
- Be aware that the use of fire, especially low intensity (grassland) fires, might only worsen the invasion of *C. odorata* as competition from the native flora is temporarily relieved and the species quickly re-sprouts following fire.
- The timing of burning is important. Be careful with the use of fire during or preceding the seed rain of *C. odorata* in Sept-Oct. I have observed grasslands that were completely burned, with only the seeds of *C. odorata* remaining on the shrubs above the 'fire zone'. If, in areas that are planned to be burned, *C. odorata* shrubs are flowering, try to spray against the flowers before burning or perform follow-up clearing. Otherwise the optimal time for burning would in the period Jul-Aug, which is after flowering but before seed set.

Fire with prior clearing

- For high density areas the combination of clearing a few weeks prior to burning proved to be highly effective in controlling *C. odorata*, as both the plants as the seeds in the soil were killed. However, destruction of endangered and fire-sensitive native vegetation is a problem in certain areas, e.g. riverine and upland forests.
- If grasses establish after intense *C. odorata* fires, regular burning is necessary to keep *C. odorata* out in the longer term, but only if fires can be intense enough. Otherwise follow-up clearing (possibly in combination with burning) might prove to be more effective.

Fire-sensitive habitats (riverine and upland forests)

- In fire-sensitive riverine and upland forests special care should be taken to prevent burning and preserve these highly diverse and endemic vegetation types. Fire exclusion might be a good management option to protect these habitats from fire as *C. odorata* infestations will become senescent after being protected from fire for about 10–15 years.
- Road sides in forests are particularly prone to invasion and represent a fire hazard to the forests. These should be cleared regularly, if possible the dead litter should be removed as well as this will remain a fire hazard for a longer period of time.

