Weeds in pasture ecosystems — symptom or disease?

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Abstract

Plant species that become weeds in pasture ecosystems require the same resources as useful forage plants — light, water, carbon dioxide, oxygen and mineral nutrients. Their weediness stems from the fact that they package those resources in a form that makes them unavailable as livestock forage. Weed species are either strongly competitive for resources, or they exploit an absence of competitors in disturbed situations. Ecologically-based weed management must discover means of reducing the capacity of weeds to capture resources and of recapturing those that are already tied up in weed populations. Heavy grazing of palatable pasture species reduces the competition faced by invading weeds. Effective biological control agents reduce the capacity of weeds to capture resources and make them potentially available to more favourable plant species. Pastures that experience high levels of disturbance provide more opportunities for weeds to establish. Weeds can be interpreted as diseases of pasture but they may also be symptoms that indicate an unhealthy pasture.

Introduction

Many definitions of the term 'weed' emphasise some aspect of the interaction between humans and the plant in question. They refer to the fact that the plant is growing where it is not wanted, and is highly competitive with more desirable species, difficult to control, not useful or even 'unsightly' (Radosevich *et al.* 1997). All of these definitions relate to the impacts of the weed on human attempts to extract useful products from an area of land. These impacts may be on crop production, pasture productivity or the aesthetic appeal of a garden. This emphasis is summarised in the definition of a weed as 'any plant that is objectionable or interferes with the activities or welfare of man' (Weed Science Society of America 1994).

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Under this kind of definition, a particular species of plant can be a weed in one situation but a useful plant in another. It may even be that different people or interest groups interpreting a certain situation will view the status of a species differently. In other words, one person's weed is another person's useful plant. There are numerous examples of these conflicting perspectives. Para grass (*Brachiaria mutica*) is a productive pasture grass but a problem to sugar producers and those concerned with the management of wetlands for their environmental attributes. Prickly acacia (*Acacia nilotica*) is viewed by some pastoralists as a useful fodder tree while others recognise it as a serious problem, consistent with its status as a Weed of National Significance (Anon. 1997). Buffel grass (*Cenchrus ciliaris*) is an invaluable pasture grass for northern Australia and yet hailed as an environmental weed because of its perceived impacts on central Australian ecosystems (Griffin 1993). Other pasture grasses introduced to northern Australia are variously seen as useful, weedy or both, depending upon where they are growing and who is making the judgement (Lonsdale 1994). In terms of both technical definition and practical response, under these definitions, weediness is a matter of land use.

Another useful way of examining weeds is to consider them as ecological phenomena, that is, to examine their relationship with the ecosystems within which they occur. This approach can be used to consider weeds that grow in pasture ecosystems. In some ways, weeds in pastures are like **diseases** of the pasture in so far as they are external agents that jeopardise the health of the pasture and so diminish its productive potential. They can also be viewed as **symptoms** that indicate an underlying health problem. Both metaphors help us understand the ecological nature of weeds. In this paper, we will explore the ecological relationships between pasture weeds and the pasture ecosystems that support them. Such an analysis has major implications for the ways we think about weed management in pastures.

Weeds in the pasture ecosystem

An ecosystem consists of a community of living organisms and the environment in which they live. In a pasture ecosystem, the primary focus of a producer is on the livestock and the plant species on which they depend. In the case of intensively managed improved pastures, the pasture may consist of very few species of palatable forage plants but most pastures incorporate a wide variety of useful forage plants. Rangeland pastures are diverse in terms of the array of palatable plant species that are available to the livestock that graze them. Most pasture ecosystems, however, include many organisms other than livestock and the plants that the livestock consume. There are herbivores other than livestock, predators and parasites, and plants that are not used by livestock. Amongst the plants, some will be perceived as weeds, either because they are completely unpalatable to livestock, or because they are less preferred. Some plant species may be of low palatability but may not be regarded as weeds because they provide some other resource such as shade. The abundance of a species is another factor that is taken into account in assessing weed status. A rare, unpalatable species will not generally be identified as a significant weed of pastures. Features other than acceptability to livestock also influence weed status in pasture ecosystems. For example, a species may be regarded as a weed because of its impact on fire regimes or even the aesthetics of a pastoral property.

In the case of exotic (*i.e.* non-native) plant species, a critical first step in becoming a weed in a pasture (or any ecosystem) is its introduction to the site. A very large number of exotic species have been introduced to Australia, either deliberately [*e.g.* rubber vine (*Cryptostegia grandiflora*), prickly acacia] or accidentally [*e.g.* parthenium (*Parthenium hysterophorus*)]. This, in itself, does not make the plant a weed in a particular district, property or paddock. For that to occur, it must be introduced locally. Very often, the means whereby a plant reached Australia is quite different from the means whereby it spreads once on the continent. At continental and local scales, though, introductions of exotic species are ecologically analogous to the introduction by Europeans of smallpox or venereal diseases to the islands of the Pacific Ocean. In this sense, weeds are **diseases** of pasture ecosystems, that is, they are external agents that reduce pasture health.

On the other hand, as with viral and bacterial diseases, contact with a disease-causing agent is not always sufficient to cause the disease. Usually, additional factors improve or diminish our prospects when we encounter a virus or bacterium. These factors include our diet, the weather, state of stress and general health. The same is true of weeds in pastures. In the following sections, we will examine some key factors that help determine whether a plant's potential as a weed is realised in any given location.

Weeds as consumers of resources

The plants that are regarded as weeds in pastures require the same basic **resources** as valued forage species. All plants require light from the sun, carbon dioxide and oxygen from the atmosphere, and water and mineral nutrients from the soil. However, plant species vary greatly in the quantity and quality of resources they require. This is no less true of weeds than it is of non-weeds. For instance, many weed species thrive in areas that provide elevated nutrient levels. For example, nodding thistle (*Carduus nutans*) is most abundant where nitrogen and phosphorus are in good supply (Popay and Medd 1995). Many weeds grow particularly well in riparian zones or other low-lying parts of the landscape, at least partly because these areas provide higher levels of both water and nutrients. In northern Australia, this is true of rubber vine which is most prevalent in riparian zones of northern and eastern Queensland (Tomley 1998). Similarly, prickly acacia is most abundant along bore drains and creek lines on the Mitchell grass plains (Mackey 1998). The dynamics of its populations are quite different in uplands versus bore drains or creek lines. For instance, a study that used aerial photographs to follow changes in populations of prickly acacia in the Richmond area between 1960 and 1990, showed that increase was much greater in low-lying parts of the landscape than in the uplands (Brown and Carter 1998). This is largely due to spatial variation in the environment's capacity to meet the weed's resource requirements.

For a plant species to attain weed status in a particular pasture ecosystem, the ecosystem must supply the resources that the weed requires and the plant must be highly effective at acquiring resources in that situation. The relevant management question is: 'Can we reduce the supply of resources to the weed without reducing the supply of resources to useful pasture plants?' In general, there is not a lot of scope for doing this in the pasture ecosystem, either because we have little control over the supply of resources, or because we cannot reduce the supply of resources to weeds without impinging on the supply of resources to useful plants. In some cases, the management system encourages certain weeds by improving the supply of resources to them. For example, nodding thistle proliferates in southern Australian pastures when the supply of soil nitrogen is increased under heavy grazing or with the addition of legumes (Popay and Medd 1995).

If a large proportion of the ecosystem's resources is commandeered by weeds, it may be a **symptom** that something else is amiss in the pasture ecosystem.

Weeds as competitors for resources

Ecological competition occurs when two organisms have a requirement for the same resource and reduce each other's capacity to procure that resource. If a resource is super-abundant, competition for that resource is unlikely to occur. For example, in an arid zone plant community in which the plants are well spaced and light is abundant, it is most unlikely that plants will be competing for light. On the other hand, water is often in short supply in such environments and even though the above-ground parts of plants may be well separated, their root systems are likely to be interlocking and competition for water may be strong.

Virtually by definition, plants that are identified as weeds in a particular situation are very effective at acquiring the resources that they need. The population of a weed species is able to acquire sufficient resources for it to grow to a size and density that cause a problem. Generally, if it was not able to acquire the resources necessary, its population would remain small and/or sparse, it would not present a problem and so it could not be described as a weed in that particular situation. The abundance, density and biomass of a weed species relative to that of non-weed species in the community, are measures of the weed species' ability to acquire resources. There are numerous situations in which a particular weed has acquired such a high proportion of the total available resources that it almost forms a monoculture, that is, it eliminates virtually every other plant species from the community. This is true, for instance, in the case of severe infestations of rubber vine (Tomley 1998), parthenium (Chippendale and Panetta 1994; Navie *et al.* 1998), giant sensitive plant (*Mimosa pigra*) (Lonsdale *et al.* 1995) and serrated tussock (*Nassella trichotoma*) (Campbell and Vere 1995).

Just because a weed is effective at acquiring resources, though, does not mean that it is a strong competitor. Many weeds specialise in exploiting situations where there is relatively little competition. Avoidance of competition is especially prevalent in the classical weeds of cropping situations. Baker (1965) identified the characteristics of a hypothetical 'ideal' weed. His list included a number of traits that could be interpreted as helping the species avoid competition such as an ability to produce seeds that germinate under a wide range of environmental conditions, possessing long-lived seeds, self-compatibility in terms of pollination, prolific seed production, and adaptation for long-distance dispersal. Mechanisms for dispersal would enable the species to reach sites at which the intensity of competition is lower. Alternatively, mechanisms that keep seed dormant for an extended period would allow the species to survive at a site until conditions were suitable.

It is also important to recognise that competitiveness is not absolute. This means that a species can be a good competitor in one set of environmental circumstances but not in another. For example, parthenium is most effective at competing for the resources it needs on black, alkaline, cracking clay soils of high fertility. On other soil types, it rarely develops into severe infestations (Navie *et al.* 1998).

The relevant management question here is: 'Can we affect competitive relationships to disadvantage weeds and improve the prospects of desirable species?' Some ways in which we can influence the competitive outcome between weeds and desirable pasture plants are by influencing three other ecological processes: herbivory, predation and disturbance. We will deal with these in the next two sections.

Weeds as victims and beneficiaries of herbivory and predation

The energy and material resources that are initially acquired by plants are potential resources for other organisms in the community. The resources may be retained by the individual plant that acquired them, passed on to the succeeding generation by being used to produce seeds, or they may be captured by members of another species. Processes such as leaf fall make resources available to decomposers. These return some nutrients to the soil where they again become available to plants. The same processes take place when a plant dies but, generally, once energy and material resources have been captured by a plant, they are no longer directly available to other plants. This means that once a weed has captured resources, they can subsequently be available to useful plants only through the death of all or part of the weed.

By contrast, resources acquired by plants, including weeds, can be captured by animals. This can happen in a number of ways and the process is important in relation to understanding the ecology of weeds and its implications for management. Grazing and browsing are the obvious processes whereby some of the resources that have been acquired by plants are subsequently captured by animals. A plant species becomes a weed in a pasture ecosystem when it has a capacity to acquire resources and package them in a form that makes them unavailable to livestock. The resources that a plant acquires may be unavailable to livestock because they are out of reach, or because they are protected by physical structures such as spines or chemical defences. For example, many of the resources that have been captured by large leucaena (*Leucaena leucocephala*) may be unavailable to cattle simply because they cannot reach the foliage; the foliage of spiny shrubs such as mesquite (*Prosopis* spp.), prickly acacia and chinee apple (*Ziziphus mauritiana*) is protected to some degree by spines on the stems; and the resources tied up in the foliage of rubber vine and bellyache bush (*Jatropha gossipifolia*) are protected by chemicals that make them unpalatable.

Livestock, though, are not the only animals that can capture resources from plants. The pasture ecosystem includes many other kinds of herbivores. Some are generalists that capture resources from a wide range of plant species, while others, especially insects, specialise in capturing resources from either a single plant species or a small group of related species. For even the most unpalatable (to livestock) plant species, there are one or more specialist herbivores that have evolved mechanisms for capturing its resources. One widely-accepted explanation for why introduced plants become weeds is that they have escaped their specialist herbivores, pathogens and seed predators. In such situations, the recycling of resources that have been captured by a weed must rely on processes such as natural leaf fall and plant death. Overcoming this limitation is the ecological basis of biological control of weeds.

In ecological terms, biological control of weeds is an attempt to find a mechanism for redirecting resources away from the weed and towards more useful plants.

The case of rubber vine provides one example of how biological control agents can: (1) help other components of the ecosystem regain some of the resources that have been captured by a weed; and (2) reduce the weed's capacity to capture further resources. Rubber vine was introduced from Madagascar without its specialist herbivores. The larvae of one native Australian butterfly are capable of feeding on rubber vine leaves but not very efficiently. Chemical constituents of the leaves mean that most of the resources held in the leaves are not available to herbivores, so one pathway for returning the weed's resources to the soil and, ultimately, more desirable plants, is not available. Moreover, rubber vine's climbing growth habit means that its leaves are able to capture light that would otherwise be available to native trees, shrubs and pasture plants. The biological control program against rubber vine can be described as an attempt to access the resources that have been captured by the rubber vine. Two biological control agents have been introduced from

Madagascar, a moth (*Euclasta whalleyi*) and a rust fungus (*Maravalia cryptostegiae*). Both are specialist consumers of the rubber vine's resources. The larvae of the moth eat the leaves of rubber vine and the fungus grows inside the leaves and causes them to fall from the plant (Tomley 1998). Rubber vine's ability to capture light, and so material resources from the soil and atmosphere, is reduced until it replaces its leaves. In the interim, those resources can be captured by other plant species. At least some of these other species will be palatable to livestock so resources can pass through to them.

Biological control can also be a means of interrupting the process whereby a weed passes on resources to its next generation. Biological control programs commonly seek agents that will reduce the reproductive output of a weed. Examples from tropical Australia include seed-feeding beetles introduced for giant sensitive plant (Lonsdale *et al.* 1995) and prickly acacia (Mackey 1998), a seed-boring moth for noogoora burr (*Xanthium occidentale*), seven species of flower-, seed- or fruit-feeding beetles for lantana (*Lantana camara*) (Swarbrick *et al.* 1998), and a seed-feeding weevil for parthenium (Navie *et al.* 1998). Resources that would otherwise have gone into producing seeds and seedlings of the host weed are captured by these insects and ultimately returned to the soil. Of course, any biological control agent that reduces the vigour of its host may also limit its reproductive output.

Weeds can also benefit from the activities of herbivores. When palatable species are grazed, co-existing unpalatable species may benefit from reduced competition. For example, the most serious infestations of parthenium occur in over-grazed pastures and grazing management can play a vital role in rehabilitating pastures degraded by this weed (Navie *et al.* 1998). Rehabilitation of parthenium-infested pastures requires that they be rested from grazing for at least one growing season and subsequently grazed only lightly. Similarly, invasion by and proliferation of giant rat's tail grass (*Sporobolus pyramidalis*) in pastures is promoted by the existence of gaps, that is, sites of reduced competition (Bray *et al.* 1999).

Obviously, livestock enterprises depend upon extracting resources from palatable plant species. Pasture management must find a balance such that palatable species can be exploited and yet remain competitive with weeds. At least in some instances, serious weed infestations are a **symptom** of an imbalance between herbivory and competition.

Weeds and disturbance

The concept of disturbance is an important one in ecology and one that has been especially relevant to an understanding of weed invasions. In ecology, a disturbance is any phenomenon or process that removes or damages the vegetation (Grime 1974). Thus, fire, grazing, severe storms, drought, floods, landslides, the fall of a single tree in a forest, and bulldozing are all examples of disturbance. A link between disturbance and weed invasion has often been noted (*e.g.* Fox and Fox 1986) to the point where disturbance is seen as a prerequisite to invasion (Fox 1991). However, it should be recognised that there is no such thing as an undisturbed community or ecosystem and, moreover, much of the recruitment that occurs in many plant communities is, at least in part, a product of disturbance. On the other hand, plants that are recognised as weeds often differ from non-weeds in terms of the type or degree of disturbance to which they are adapted. Baker's (1965) definition of a weed as a plant that 'grows entirely or predominantly in situations markedly disturbed by man' recognises this link between disturbance and at least some types of weeds. Many weed species are particularly well adapted to take advantage of damage to or removal of other plants. A great variety of characteristics contribute to this adaptation, including dispersal mechanism and ability, growth rate, and time to first reproduction (see Campbell and Grice 2000).

Although there is an association between weeds and disturbance, weeds can themselves be victims of disturbance. This is illustrated again by the response of rubber vine to disturbance by fire. Fire frequency is potentially high in the northern Australian tropical woodlands and yet rubber vine is common in many areas. This is partly due to the fact that actual fire frequency is low because of intentional fire suppression or because grazing reduces fuel loads.

Disturbances usually occur as irregular events. While this is clear in relation to disturbances such as fire, floods or droughts, it is also often the case with disturbances associated with grazing. Even when the stocking rate is constant, the impact of that stocking rate will vary depending on the climatic circumstances. This episodic nature of disturbance is captured in the state-and-transition models of change in pastures (Westoby *et al.* 1989). Episodic events often present weeds with an opportunity to invade or increase. The reverse transition to low weed status does not necessarily occur when the cause of the disturbance is removed. This makes it especially important to consider how a particular disturbance may affect weed populations and what preventive measures can be taken.

The disturbance regime of a pasture should be examined in terms of its likely effects on weed populations, asking the question: 'Are the kinds and degrees of disturbance likely to favour the weeds that are prevalent in the area?'

Weeds: symptom or disease?

Under definitions of weeds that focus on their impacts on human land use, the presence of weeds on an area of land indicates that the capacity of humans to acquire resources from that land is less than it otherwise would be. Our description of weeds as consumers of resources, competitors for resources, and as victims and beneficiaries of herbivory, predation and disturbance, highlights weeds as ecological phenomena. Under this description, weeds can be interpreted as both disease and symptom.

Pasture hygiene is important in minimising the risk of catching a disease. There are steps that can be taken to help avoid introducing weeds to a district, property or paddock. This will depend upon a knowledge of how the disease is transmitted, that is, of how particular weeds are spread. For some weeds, this will require attention to cattle and vehicle movements. For example, seeds of prickly acacia (Kriticos *et al.* 1999), mesquite (Brown and Archer 1987) and chinee apple (Grice 1998) are transported following ingestion by cattle (and other animals) and dispersed in their dung. Attention to the timing of movement of cattle feeding in infested paddocks will greatly reduce the chance that seeds will reach paddocks that are not infested. Weeds can also be introduced as contaminants of sown pasture seed so the purity of such seed should always be a priority.

Attention should also be given to pasture health because this will influence how the pasture responds to any weeds that have been introduced. Vigorous stands of perennial grasses will provide competition for species that could become weeds. Heavy grazing of palatable perennial grasses will make resources available to weed species and increase the competitive advantage of unpalatable plants. Increasing weed populations should be examined as possible symptoms of pastures that are not as healthy as they could be.

Weeds are economic as well as ecological phenomena. They cost money because they are ecologically successful. Many of our most serious weeds are analogous to diseases in the sense that they are an external agent that decreases the health of pasture, but they are also analogous to the symptoms of disease insofar as they tell us much about how healthy our pastures are. Both analogies can be useful for helping to explain how weeds function within pasture systems and to prompt actions that counter the proliferation and spread of weeds.

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