opportunity for basic studies, perhaps at the post graduate student level.

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Population dynamics of St. John's wort in south-eastern Australia

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Summary

A thorough understanding of the ecology of St. John's wort and the processes that drive the population dynamics of infestations is a key to the management of this weed. However, while some aspects of the weed's biology have been studied in the seventy years of research on its control in Australia, there has been only one study devoted to its ecology; in the Ovens Valley, Victoria, over a two year period. To complement this detailed work and provide a picture of longer term fluctuations, four St. John's wort populations were monitored over a period of seven years, from 1981–87. This paper summarizes the type of data collected, and uses it, together with that from the Ovens Valley study, to define those properties of St. John's wort that have contributed to its success as a weed and which may render it vulnerable to particular methods of control.

Introduction

Since its introduction into Australia in the late nineteenth century, St. John's wort (*Hypericum perforatum* L.) has spread widely and invaded a number of different habitat types, ranging from prime agricultural land to native *Eucalyptus* forest (Campbell *et al.* 1995). Aspects of the general biology of the weed that favour its success in colonizing and persisting in new areas are now reasonably well understood in the light of numerous efforts to control the weed (see Campbell *et al.* 1995), but, apart from a two year study in the Ovens Valley, Victoria, by N. Clark (1953), there has been no attempt to specifically investigate the population dynamics of infestations of the weed over a longer period. Given that St. John's wort is a relatively long-lived perennial, such information is a key element in the development of management strategies for the weed.

N. Clark's (1953) studies indicated that St. John's wort can have quite different forms and population structures, depending on the habitat in which it grows (Table 1). In Type B infestations, on poorer shallow soils, the weed is smaller and tends to sucker more frequently. Stresses such as low nutrient levels, shading, defoliation and fire (N. Clark 1953, Briese 1996) tend to promote such vegetative reproduction and in fact render such infestations relatively resistant to control. Where soils are better, larger deep-rooted plants may give the impression of a more vigorous infestation, but in fact, plants of these Type A infestations are more susceptible to stresses such as defoliation (N. Clark 1953). Moreover, once the weed is reduced the richer soils can more readily support competing vegetation and so St. John's wort is more readily controlled. This partly explains the original success of biological control agents in areas where good agricultural land was infested. The problem remaining is that the majority of land currently infested by St. John's wort falls into the Type B category, with over 80% of infestations occurring under native forest (Shepherd 1983) or in poorer quality pastoral land.

In addition to aspects of the physical habitat, factors such as rainfall pattern can affect stem and seed production (by as much as 7.5 to 26-fold, respectively (Campbell *et al.* 1995)), while insect defoliation can cause fluctuations in crown density and stem production (Clark and Clark 1952). To better understand the longer term changes in infestations of St. John's wort in such habitats, a study was undertaken by CSIRO Entomology between 1981 and 1987 at four sites in south-eastern Australia, infested in varying degrees by

Table 1. Characteristics of the two types of St. John's wort infestation recognised by N. Clark (1953). The infestations have been designated Type A and Type B for this paper.

Parameter	Type A	Type B
Location	deeper soils	shallow or stony soils
Densities (plants per m^2)	12–37	12–124
Plant height	taller	shorter
Number of stems	multistemmed	fewer stems
Root system	deep tap-root	shallow lateral roots
Vegetative growth	rare	common
Maximum age of plants	usually more than 3 years	usually less than 3 years
Response to defoliation	more susceptible	less susceptible

St. John's wort. This paper presents a summary of the type of data collected from these sites and gives an indication of the variability that is likely to occur in infestations both on a temporal and spatial scale. To understand the processes involved in driving these changes would obviously require a more detailed analysis. However, knowledge of the natural variability in populations of the weed under different stresses should hopefully provide clues to those aspects of the weed's ecology that render it more or less susceptible to different management strategies.

Methods

Four sites were selected at Adaminaby and Queanbeyan, New South Wales, Beechworth, Victoria, and Pierce's Creek, ACT. The first three sites contained infestations of St. John's wort both in open pasture and under native forest, while the infestation at Pierce's Creek was only in the open. At each site and treatment (open vs timbered), two plots 20 × 20 m were marked out and, within each plot, five permanent 0.5 × 0.5 m quadrats were chosen at random and staked. The principal unit used for population estimates was the crown rather than the plant, as St. John's wort can reproduce clonally and a single plant may consist of several crowns with connecting roots (N. Clark 1953). Three complementary sets of data were collected from each plot:

- *History of individually tagged crowns* Five mature St. John's wort crowns in each permanent quadrat were marked at the initial visit by a small plastic disk nailed into the soil next to the crown. X and Y coordinates for the marked crowns were also taken to enable crowns to be relocated in the event of disturbance. At four critical periods in the life cycle of St. John's wort each year—January (post-flowering), April (autumn germination), July (winter rosette growth) and, October (onset of stem elongation)—data were collected on plant growth (rosette diameter, number and length of flowering stems, number of flowers and fruit) and condition (impact of drought, grazing, insect defoliation etc.) of the marked crowns. Initially the age of marked crowns was determined as 1, 2 or 2+ years, based on the presence or not of dead flowering stems from previous years.
- *Population changes in permanent quadrats* At each three monthly visit, the numbers of seedlings and mature crowns were recorded in each permanent quadrat, together with an estimate of vegetation cover in four categories (St. John's wort, grasses, herbs, mosses) to the nearest decile percentage cover. At the January visit, when flowering and fruit formation had peaked, crowns were also categorized according to the number of flowering stems produced, and the minimum and maximum stem length recorded, providing an estimate of total flowering stem production.
- *Destructive plots* During the April visit, all St. John's wort crowns were removed from five randomly selected quadrats per plot, and data on root collar diameter and root shape taken to determine the size structure and origins of plants. Crowns originating from seed had vertical tap roots, while those originating vegetatively from lateral roots had a right angled bend in the tap root just below the surface. Stem number, length and seed capsule production were also taken at this time to provide a second estimate of overall density and fruit production.

Results

A summary of the various individual plant and population parameters collected over the seven year study period is shown in Table 2. There were considerable differences in the density of crowns between the four sites, as well as between years at each site, with extremes of 2 m^{-2} during a drought year at Queanbeyan and 165 m^{-2} in a good year at the Adaminaby site. Moreover a varying proportion of these crowns produced flowering stems in any given year. These differences were further reflected in the total length of flowering stems produced and seedling germination at the sites (Table 2).

In the seven year period there were only between one to three periods of massive seed germination that had the potential to significantly influence recruitment to the infestations at each site. Seedling survival, however, was quite low (less than 10% at Pierce's Creek). Generally, infestation densities were maintained by vegetative reproduction from lateral roots. The proportion of crowns originating from roots rather than seed ranged as high as 67–91% at individual sites (Table 2). The low end of the ranges in Table 2 occurred following high seed germination in autumn 1984, few of which survived. With this value removed the mean proportion of crowns originating vegetatively over the study period was 54, 72, 74 and 69%, for Queanbeyan, Beechworth, Adaminaby and Pierce's Creek, respectively.

Following the life-histories of individual plants, there were again site differences in the longevity of crowns, with the median age varying from three to six years, with very few crowns surviving to more than eight years (Table 2). Deaths of individual crowns could be attributed to drought, fire, defoliation by *Chrysolina* (or combinations

Table 2. Parameters measuring aspects of the population dynamics of St. John's wort at four open sites in south-eastern Australia for the period 1981–87 (bracketed values indicate range for individual plants).

	Queanbeyan, NSW	Beechworth, VIC	Adaminaby, NSW	Pierce's Creek, ACT
Population				
Range of crown densities (m^{-2})	2-8	4–34	65–165	3–62
Range of stem lengths (m^{-2})	0–1.1	0–18.7	0–61.9	0–25.5
Proportion vegetative reproduction	0.18–0.67	0.53–0.84	0.52–0.91	0.13–0.77
Proportion of crowns flowering	0–0.54	0–0.67	0.22–0.69	0–0.80
Range of seedlings per year (m^{-2})	4–20	1–56	5–92	2–380
Mass germination events (>20 seedlings m^{-2})	1	3	3	2
Individual plants				
Median longevity (years)	3 (1–5)	3 (1–5)	6 (2–8)	4 (1–7)
Median no. of flowerings	1 (0–3)	1 (0–3)	3 (0–7)	2 (0–5)
Max. stem heights (cm)	32–47	49–96	31–78	43–101
Mean lifetime no. of fruit per plant	15 (0–115)	68 (0–306)	94 (0–686)	321 (0–1458)
Stresses during period[A]				
Grazing	4	1		
Drought	2	1	1	1
Fire		1	2	
Chrysolina defoliation		1	1	4

[A] values refer to number of incidences in which the stress factor occurred over the study period.

of these) and senescence. Crowns did not flower in their first summer as established crowns, but produced smaller erect non-flowering stems. Very few tagged crowns produced seed annually thereafter, and in fact the median number of years in which fruit were produced varied from one to three years, with a maximum of three to seven flowering periods at individual sites (Table 2). The more typical pattern was for years of flowering to be interspersed with years in which non-flowering stems were produced (usually due to drought) or in which fruit production was prevented by insect defoliation. Some crowns never produced fruit, even though they survived for up to seven years. In terms of fruit (and hence seed) production, there was substantial variability between sites, with individual lifetime production varying from 15 to 321 fruit per crown. Pierce's Creek was the most productive site, in terms of plant size and lifetime seed production, despite having a lower crown density and poorer crown survival rate than some other sites. It most approached the Type A infestation of N. Clark (1953), though vegetative reproduction was still important in maintaining crown density.

An illustration of the temporal variation within sites is given in Figure 1. This illustrates how stress factors such as drought and insect defoliation can affect plant population dynamics at one site. Pierce's Creek has been chosen because it illustrates three different stages in the dynamic process. Between 1981 and 1983, crown density remained relatively stable, despite a period of drought, grazing pressure from horses and defoliation by *Chrysolina* (which reduced the cover and depressed growth and flowering) (Figure 1). During this period there was virtually no seedling establishment and 38% of the original tagged crowns died. This illustrates clearly how infestation levels are maintained by vegetative reproduction. In 1984, heavy rains stimulated high seedling germination in autumn, which, despite less than 10% seedling survival over the next 12 months (due in part to being overgrown by a dense pasture/clover pasture favoured by good rainfall and reduced grazing pressure), led to a doubling of the density of mature crowns by April 1985. This illustrates a second phase incorporating a dramatic increase in density through seedling recruitment, following favourable patterns (Figure 1).

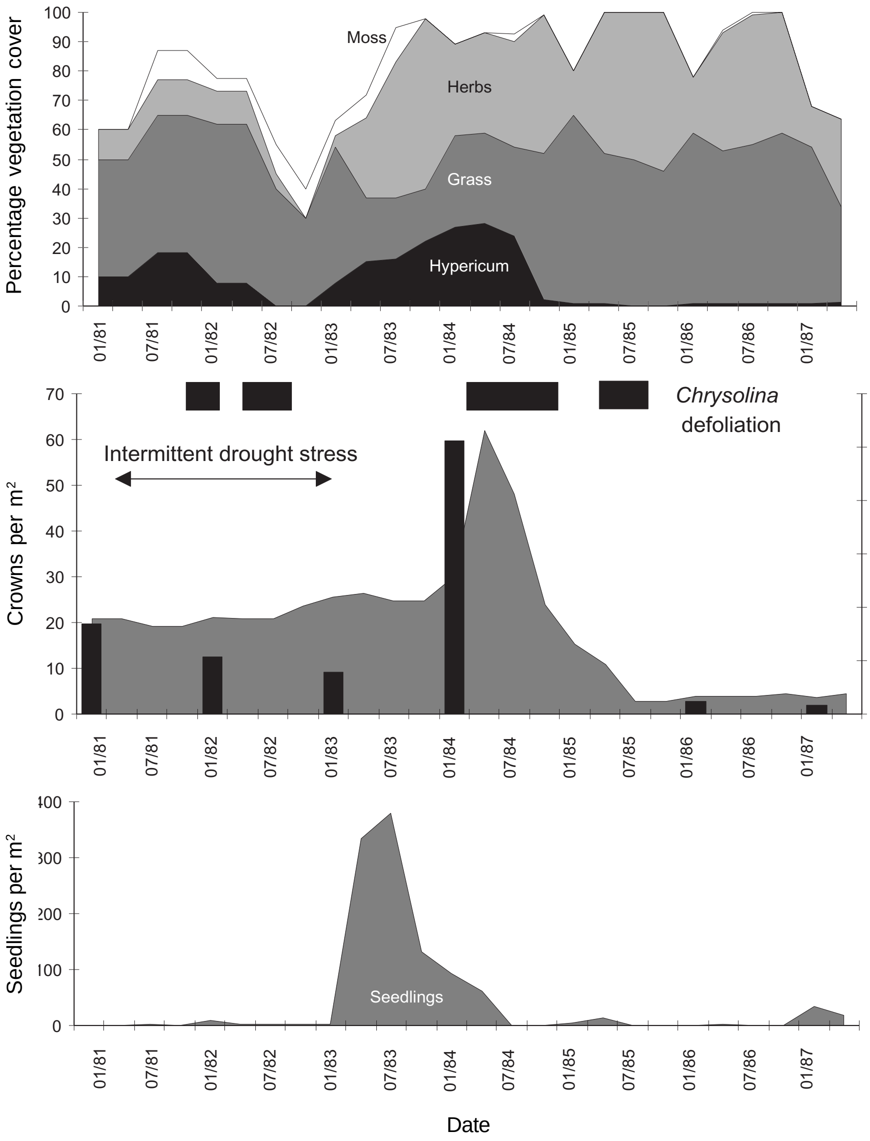

Figure 1. Changes in different parameters measuring St. John's wort population dynamics at Pierce's Creek, ACT, during 1981–1987.

The St. John's wort population may well have stabilized at a higher density following seedling recruitment. However, good rainfall through autumn and winter favoured survival of *Chrysolina* larval populations. Continued growth of St. John's wort procumbent stems ensures an adequate food supply and the presence of other vegetation provides shelter essential for good survival (L.R. Clark 1953). This results in continued stress by defoliating larvae on the plant throughout the winter and good survival to adulthood, which leads to strong defoliating pressure by adults in spring. This, coupled with increased competition by pasture species led to a strong decline in crown density and cover by 1985, to a lower level which remained stable over the next two years for reasons described previously (Figure 1). In fact, crown densities at Pierce's Creek did not recover to pre-1984 levels until 1992, due largely to further waves of defoliation by *Chrysolina* (P. Jupp personal communication) The other three sites have had different histories of 'stress', leading to some differences in temporal patterns of crown number and productivity. For an illustration of the impact of another stress factor, fire at the Adaminaby site, see Briese (1996).

Discussion

A summary of the processes that drive the population dynamics of St. John's wort infestations in south-eastern Australia is given in Figure 2. This figure also shows different factors that may affect certain transitions in this population cycle.

Individual crowns are perennial and, once established may pass through up to eight annual cycles of flowering or erect stem production (Figure 2). However, due to stresses such as drought, fire and defoliation, the median life span is from three to six years. The apparent infestation levels may change due to stress-induced changes in cover or stem and flower production, without affecting the underlying population density. Infestations can be maintained or even increase slowly and spread through shoots developing from lateral root systems (Figure 2). Vegetative reproduction in response to stresses such as fire and defoliation can buffer St. John's wort stands from severe fluctuations in density.

Annual seed production may be extremely variable at particular infestations of the weed, varying from none to 200 000

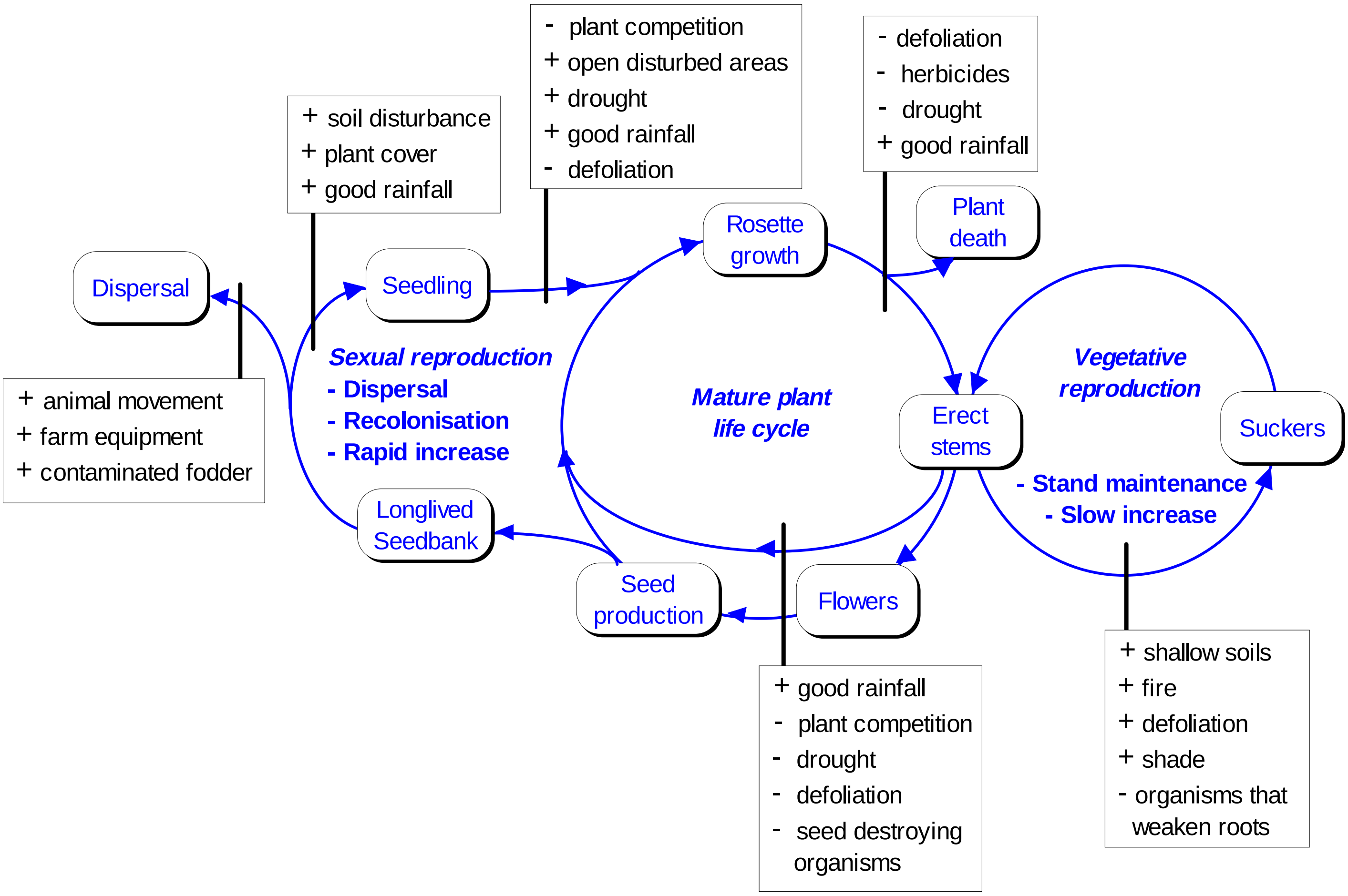

Figure 2. Transitions between different life stages important to the population dynamics of St. John's wort infestations (factors preceded by a + sign favour a particular transition while those with a - sign inhibit the transition).

per m^2 in the present study to values as high as 2.6 million seeds per m^2 (see Campbell *et al.* 1995). Seed capsules are adapted to transport by animals, and this is the means of long-distance dispersal (Campbell 1977) (Figure 2). Moreover, because of their longevity and dormancy properties (Campbell 1985), most seed enters the soil seed bank (Figure 2) which forms an important reserve for reinfestation should the existing plant population be driven to extinction. Abrupt increases in infestation densities (which usually trigger a reaction from landholders about the worsening status of the weed) occur as a result of seedling recruitment following conditions favourable for germination (Figure 2). Even though seeds regularly germinate in autumn and spring, seedling survival is normally very low (e.g. N. Clark (1953) reported survival rates of less than 3% to mature plants). The seedling stage is very slow growing and is the part of the weed's life-history most vulnerable to water stress and competition from other plant species (Campbell 1985). Hence, massive germination is required to significantly increase infestation density and conditions for such events are relatively rare (maximum of three in seven years at four sites) while successful recruitment from these is even rarer (once in seven years at the sites). The recruitment recorded at the study sites in 1984 seems to have occurred throughout a wide range of south-eastern Australia, however.

Drought may severely affect the appearance of an infestation, through reduced cover and flowering stem production (and hence any short-term economic impact), but will not reduce crown densities unless it is prolonged. Moreover, drought also reduces the cover of competitive plant species, which in the long-term may favour an increase in infestation densities of the weed. The impact of defoliating biological control agents, such as *Chrysolina*, is also augmented by the presence of competing plant species. Rainfall patterns may hold the key to interactions between St. John's wort and the effect of these beetles on its population dynamics. Briese (1985) found positive correlations between winter rainfall and the impact of *Chrysolina* larvae and adults, while summer rains can enable St. John's wort crowns to recover from defoliation stress (Huffaker 1966).

The impact of fire depends largely on the season. Briese (1996) found that St. John's wort infestations recovered rapidly following a spring fire, through rapid regeneration from damaged crowns and associated root systems and were able to outcompete associated grasses and herbs which did not germinate until the following autumn. By contrast, when the infestation was burnt in autumn, grasses and herbs germinated and grew more quickly than any regrowth or seedling recruitment of St. John's wort, enabling the competing vegetation to become more dominant.

What properties of the weed then might render it more or less susceptible to control? Clearly the habitat in which the infestation occurs will influence control measures in view of the plasticity of the plant on different soil types. Type A infestations on richer soils are probably the most amenable and affordable for control by herbicides. Seedlings are highly susceptible to competition, and the presence of competitive plant species is important to reduce the impact of periodic peaks in germination and establishment. The maintenance of good pastures and grazing management can prevent such seedling recruitment. Although such events are not common, they unfortunately often occur at the breaking of a drought period when the landholder no longer has control of pasture cover and plant competition is likely to be at its lowest ebb. Moreover, in non-agricultural situations, such as under native *Eucalyptus* forests, the vegetation is often too sparse to provide sufficient competitive pressure to suppress a mass germination and recruitment of seedlings. On good agricultural land, herbicides can redress the situation, but in many areas they are not feasible for environmental or economic reasons. Germinability studies of seed collected from under planted pine forests (Harris and Gill 1997) suggests that any management strategy must consider the presence of a viable soil seed bank for at least twenty years following control of St. John's wort.

As a primary contributing factor to stand maintenance of St. John's wort in habitats with poorer soils is vegetative reproduction (Figure 2), a key to management must be break this part of the weed's life-cycle. Single stresses, even though severe, seem insufficient to do this as the root reserves of the plant are sufficient to respond by increased rates of vegetative reproduction or reshooting from damaged crowns. Multiple stresses, such as defoliation / plant competition (Pierce's Creek site in this present study), defoliation / drought (e.g. *Chrysolina* in Mediterranean climates (Huffaker 1966)) or defoliation / fire (see Briese 1996), can cause reductions in crown density, and management of these factors is important for control to be successful. Another approach is control through attrition, by weakening or exhausting root reserves over a period of time. Continuous low level herbivory through managed stock grazing can achieve this (see Campbell 1997), though toxicity problems due to ingestion of hypericin (Bourke 1997) may limit this. In its native range in Europe, crashes in population density of St. John's wort are associated with the destruction or exhaustion of root reserves by natural arthropod enemies (Wilson 1943, Wapshere 1984). This has led to the current biological control strategy of targeting this part of the weed's life-history (see Briese 1997). Ultimately though, whatever combinations of management techniques are adopted, a clearer understanding of the population dynamics of the weed in different habitats should enable them to be better meshed together and their effects evaluated.

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