This thesis has been accepted for the degree by the University of Sydney.

THE ECOLOGY AND CONTROL

OF

FIREWEED

(*SENECIO MADAGASCARIENSIS* POIR.)

by

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'As the weeds are pulled up and burned in the fire, so it will be at the end of the age.....He who has ears, let him hear.' (Matthew's Gospel 13: 40-43).

ABSTRACT

The toxic African plant, Senecio madagascariensis Poir. (fireweed), was correctly identified in Australia in 1981. In 1983 following a long drought, a population explosion occurred along the east coast of Australia. Little was known about the weed, therefore research was initiated on its ecology, impact, and control. A mail survey of the fireweed problem in coastal New South Wales, undertaken during spring 1985, indicated that fireweed occurred on 90% of respondents' properties. A large number of farmers who had moderate amounts of the weed were concerned about its suppression of crop and pasture productivity, and that control was difficult to achieve.

Accordingly, experiments were conducted in a glasshouse with a range of pasture legumes and grasses as well as Saia oats (Avena strigosa Schreb.), to determine the size of possible productivity losses. Shoot dry weight was reduced by as much as 84% in Lotus pedunculatus Cav. cv. Maku and 68% in Festuca arundinacea Schreb. cv. Demeter, when grown with fireweed in equal numbers of plants per pot. In contrast, the reduction in yield of the newly introduced Italian ryegrass (Lolium multiflorum Lam. cv. Concord) was only 20% and that of Saia oats 25%. Further testing of the latter two species in the field at two levels of fertility confirmed that Concord ryegrass is a particularly strong competitor showing no significant reduction in yield (5% level) in the presence of fireweed. However, the yield of oats was reduced by 23% at a fireweed density of 5 plants m^{-2}.

The results of this work showed that fireweed has potential to compete strongly with pastures and forage crops, particularly those less competitive than oats, under low or high fertility conditions. The competitive advantage gained by fireweed over Saia oats in the glasshouse, with increasing nitrogen and phosphorus nutrition, suggested that it would be unlikely that control could be achieved simply by increasing soil fertility alone.

The potential distribution of fireweed in Australia was predicted using the bioclimatic predictive model BIOCLIM. The weed is unlikely to spread to areas outside the east coast of Australia because of climatic constraints. However, scope remains for increased infestation within and around its present limits of distribution (from south-eastern Queensland (26°21'S) in the north to Bega (37°04'S) in the south).

The effect of frost on fireweed was also assessed. Seedlings from 2 to 10 weeks old were tested at -3, -4 and -5°C in a forced draft freezing cabinet and at -7.5°C in the field. Young fireweed seedlings were more sensitive to frost than older plants and sensitivity increased with lower temperatures. These results indicate that the occurrence of frost may be an important factor limiting the spread of fireweed.

Observations on the population dynamics of fireweed were made over a two year period at Camden (34°03'S) and Hoxton Park (33°56'S), New South Wales. Seedlings emerged in flushes in autumn and spring with small numbers of seeds germinating throughout most of the year. Fireweed appeared to be adapted to bare patches within the pasture and conditions of high light intensity. Experiments in which fireweed was grown alone under a range of artificial shade treatments, and in combination with prostrate and erect biotypes of Lolium perenne L. cv. Kangaroo Valley, confirmed that shade can substantially reduce its growth.

Although the herbicide bromoxynil is effective for short term control of fireweed, competitive pastures are considered the key to long term control. In this study, competitive pastures were shown to reduce the establishment of fireweed seedlings, increase their already high rate of mortality, and reduce the vigour and seeding capacity of surviving plants. A strategy of control utilising the early vigour of Concord ryegrass and the persistence of Kangaroo Valley ryegrass is suggested.

CERTIFICATE OF ORIGINALITY

The text of this thesis contains no material which has been accepted as part of the requirements for any other degree or diploma in any university, or material previously published or written unless due reference to this material has been made.

Brian Sindel

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Chapter 1
GENERAL INTRODUCTION

Senecio madagascariensis Poir. (fireweed) is a common weed in coastal pastures of New South Wales and south-eastern Queensland. It is one of many exotic species occurring in Australia which, although assuming little significance in their places of origin, may invade and cause serious problems in agricultural areas elsewhere.

For many years this yellow-flowering composite (sometimes referred to as variable groundsel) was thought to be a form of the variable native species, S. lautus Forst. f. ex Willd. (Green 1953; Ali 1969; Martin and Colman 1977; Walker and Kirkland 1981). Suspicion that the species had been introduced to Australia was confirmed in 1980 when P.W. Michael sent specimens to O.M. Hilliard at the University of Natal, South Africa, for identification. The species is now known to originate in south-eastern Africa and Madagascar (Michael 1981).

Although previously incriminated in the poisoning of grazing animals (Green 1953), the confirmation of its toxicity to cattle is quite recent (Walker and Kirkland 1981; Kirkland et al. 1982). This finding, followed in 1983 by a population explosion of fireweed throughout many parts of New South Wales after a long drought and the continued spread of the weed into new areas, particularly along the south coast, have led to renewed interest in its ecology and control.

Ecological and life cycle studies of weeds have been identified by many researchers as essential to ensure that strategies for control are economic, effective and have the greatest possible impact (Green 1967; Everist 1968; Michael 1970; Quinlivan 1972; Anon. 1974; Blacklow 1976; Tothill et al. 1982). It is recognised that most weed problems are basically ecological in nature (Everist 1968). While some work has been conducted on S. madagascariensis in Argentina where it has also been introduced (e.g. Alonso et al. 1982; Verona et al. 1982; Fernández and Verona 1983; 1984), further elucidation of its ecology is still required in the Australian environment.

It is reasonable to assume that fireweed interferes with pastoral and forage crop production, but just how much, in both physical and economic terms, is not easy to assess. The present and potential significance of fireweed in Australia needs to be ascertained. This information may then provide the basis for determining the amount of effort and resources which should be allocated by farmers and government agencies for its control. For instance, biological control is usually a difficult and expensive procedure and must therefore be considered only for significant or troublesome weeds (Wapshere 1975).

Well-managed pastures of successful species have often been observed to be stable and largely weed free (Tothill et al. 1982). This is because many pasture weeds can best be controlled by the sown pasture species themselves which act as effective competitors (Michael 1970). Important as herbicides are, their effects are usually temporary (Green 1967) and insufficient if used in isolation (Hosking et al. 1968; Fryer 1983). Moreover, in the last 20 years weed populations which are resistant to herbicides have appeared in many countries (LeBaron and Gressel 1982; LeBaron 1985) including Australia (Powles 1987). Senecio vulgaris L. was one of the first species to excite attention because of its resistance to the triazine herbicides (Ryan 1970). These developments serve to emphasise the importance of attempting ecological control as the permanent and profitable answer to fireweed in grazing areas.

With this background, and because of the paucity of Australian literature on fireweed, the present research was initiated. Summarised, the three principal aims of this research were:

1. the establishment of a sound understanding of the ecology of fireweed;
2. the assessment of the impact of fireweed on agriculture in Australia; and
3. the development of potentially acceptable and effective control techniques based on the utilisation of competitive pastures.

Chapter 2
LITERATURE REVIEW[1]

INTRODUCTION

This review includes a full description of Senecio madagascariensis, a key differentiating it from closely related forms of the Australian native species S. lautus, an account of its life cycle and distribution, and a general treatment of factors related to its toxicity and methods of control involving herbicides, pasture management and cultivation. The potential of biological control is also discussed.

Scientific Name

S. madagascariensis in the tribe Senecioneae in the family Asteraceae (Compositae) was first described by Poiret in 1817, the type specimen having been collected by Commerson in Madagascar (Poiret 1817). In southern Africa it has also been classified under the names S. ruderalis Harv. and S. junodianus O.Hoffm. and in some instances mistakenly been given the name of the allied but distinct species S. burchellii DC. (Hilliard 1977). Likewise, when it first appeared in Argentina in the early 1940s it was given the name S. incognitus Cabrera (Cabrera 1941). Subsequently, Cabrera (1963) and Cabrera and Ré (1965) concluded that they were dealing with the southern African plant S. burchellii, and it was by this name that it then became known (Garese 1963; 1965; Chutrau 1973). Cabrera and Ré (1965) also identified the species as occurring in Australia. They examined a specimen collected at Wallsend[2] in the Hunter Valley, New South Wales, which had previously been identified as a form of the native Australian species S. lautus Soland.

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1. Part of this chapter has been published in Plant Protection Quarterly Vol.1 (4) 1986 pp163-172.
2. Location of towns and other place names are shown in Figure 2.4, 3.1, 4.1, 4.2, 4.3 or 5.1, or Appendix 1.

In compiling a list of potentially troublesome weeds in North America, Reed (1977) included S. madagascariensis under the name S. burchellii and, like Cabrera and Ré (1965), recorded its occurrence in Australia. S. lautus too was described but remained confused with S. madagascariensis in terms of identity and distribution.

It was only following the elucidation of the Compositae in Natal (Hilliard 1977) that the name S. madagascariensis Poir. was correctly applied in Argentina to the introduced southern African species (Cabrera and Zardini 1978; 1980; Guillén et al. 1984; Volkart 1984), and later correctly adopted in Australia (Michael 1981).

Common Name

The most frequently given reason for the common name 'fireweed' in Australia is the ability of the plant 'to spread like wild fire'. Other possible explanations include its bright yellow colour, its apparent potential to cause spontaneous combustion in lucerne hay, and its appearance soon after grass fires. It should not be confused with other species of Senecio sometimes also referred to as fireweed, for example, cotton fireweed (S. quadridentatus Labill.) and fireweed groundsel (S. linearifolius A.Rich.) (Hartley 1979), and hill fireweed (S. hispidulus A.Rich.) (Cunningham et al. 1981). Nor should it be confused with Epilobium angustifolium L. (syn. Chamaenerion angustifolium (L.) Scop.), an abundant plant in Europe and North America, often known as fireweed due to its appearance after fires and its ability to spread rapidly (Salisbury 1961; Dana 1963).

In Argentina, two of the common names given to S. madagascariensis are 'golden button' (boton de oro) and 'the yellow flower of Mar del Plata' (flor amarilla de Mar del Plata) (Laguinge 1959, cited by Verona et al. 1982). Because of possible confusion with other species given the same names, Fernández and Montes (1984) consider it preferable to simply use the generic name 'senecio'.

DESCRIPTION AND IDENTIFICATION

Differentiation from S. lautus

The first stage in weed control work is the correct identification of the plant being studied (Willis 1968). Because S. madagascariensis (hereafter often simply referred to as fireweed) fits, in general terms, the descriptions of the similar native S. lautus complex given in Australian floras (Bentham and Mueller 1866; Moore 1893; Rodway 1903; Black 1957; Beadle et al. 1972), it is important to differentiate between the two species. This is especially relevant since members of the S. lautus complex are essentially non-weedy (Michael, personal communication)[3] and are likely to occur in areas (Ali 1969; Jacobs and Pickard 1981) where fireweed is not expected to grow. The content of alkaloids, which cause poisoning in livestock, also varies widely between Senecio species (Walker and Kirkland 1981). However, because of the variability that occurs within the S. lautus complex and the possibility of hybridisation and gene exchange between its different forms (Ornduff 1964; Ali 1966), differentiation from S. madagascariensis can be difficult.

Ali (1964 a,b) was able to show that in Australia five main ecological groups, called genoecodemes, may be recognised in the S. lautus complex, namely: coastal, moist gully, mallee, montane and desert. After consideration of the genetic system within the complex (Ali 1966), he later gave these taxa subspecies status, with the exception of the desert group (Ali 1969). They are respectively sspp. maritimus, lanceolatus, dissectifolius and alpinus. Because of the similarity to members of the mallee and coastal genoecodemes, Ali described the desert population as 'aff. subsp. dissectifolius and subsp. maritimus'. Leaf shape was used predominantly for distinguishing these subspecies, but characters such as height, leaf length, number of involucral bracts, number of disc florets and the length of the corolla of both the ray and disc florets were also measured.

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3. Names and addresses of personal communicants are listed in Appendix 2.

While Ali did not recognise S. madagascariensis as such, it is known from a study of herbarium specimens (Nelson 1980) that he included it among his group of plants known as S. lautus aff. ssp. lanceolatus (Ali 1969).

Despite Ali's differentiation of the various members of the S. lautus complex, it was not possible, prior to the taxonomic work of both Nelson (1980) and Daniel (1984), to properly differentiate between S. lautus and S. madagascariensis.

Nelson (1980) concluded that the number of involucral bracts or phyllaries (20-21) is of major importance as a distinguishing characteristic of S. madagascariensis. Only the desert genoecodeme of S. lautus has a similar number of involucral bracts (19) per capitulum (Ali 1964b), but owing to its geographical isolation, confusion between them in the field is unlikely. One known difference is that of achene or 'seed' weight. The achenes of the desert genoecodeme (686 μg) (Ali 1968) are much heavier than those of S. madagascariensis (135 μg). In Argentina, the number of involucral bracts was also found to be critical in the correct identification of S. madagascariensis (Verona et al. 1982). The shape of the phyllaries, achene morphology, calycular bract morphology and leaf shape are also important.

Because the number of ray florets (commonly called 'petals') varies, and is similar (usually 13) in some members of S. lautus, it is of little use in distinguishing S. madagascariensis from the S. lautus complex.

The limited cytological information available indicates that S. lautus and S. madagascariensis have different chromosome numbers. While existing chromosome counts for S. lautus show that in Australia and New Zealand n=20 and 2n=40 (Ornduff 1960; 1964; Turner 1970; Lawrence 1980), a tentative assessment of S. madagascariensis in Argentina gave n=10 (Verona et al. 1982). The only chromosome count on S. madagascariensis made in Australia appears to be that of B.L.Turner (the specimen he collected near Singleton, New South Wales, is held in the Queeensland Herbarium) and that was also n=10 (unpublished data).

Description of S. madagascariensis

This description has been built up using information from various authors (Poiret 1817; Humbert 1963; Hilliard 1977; Nelson 1980; Verona et al. 1982; Daniel 1984; Volkart 1984; Watson et al. 1984) and my own observations.

Habit

A glabrous or very sparsely hairy bush or herb up to c. 60 cm tall. Rarely decumbent, most commonly found as an erect plant, stem often simple and weakly lignified at the base, often much branched above (see Plate 2.1). Seedlings at two different growth stages are shown in Plate 2.2 a,b.

Leaves

Possesses predominantly $\alpha 2$-type leaves according to the classification of leaf forms of the S. lautus complex given by Ali (1964b) (see Figure 2.1). Bright green, alternate, very variable, up to 12 x 2.5 cm but often much smaller. Cauline leaves mostly linear-lanceolate to elliptic-lanceolate, apex acute, margins denticulate to coarsely and irregularly toothed, tapering to a narrow petiole-like half clasping base, sometimes minutely eared. Upper leaves occasionally pinnately lobed, reduced petiolate, subsessile or sessile (see Figure 2.2 a,b).

Inflorescence

Heads heterogamous, radiate, few to many on bracteate peduncles arranged in open, corymbose panicles, terminal or axillary, the small decurrent bracts similar to the calycular bracts of the capitulum (see Figure 2.2b). Involucre campanulate, 3-5 mm diam., principal bracts or phyllaries c. 20-21, herbaceous with membranous edges, 4-5(-6) mm long about equalling or a little shorter than the disc, width 0.8-1.3 mm, keeled, nerves 1-3, resinous, attenuated to an acute apex. Calycular bracts c. 8-12, 1/4 to 1/3 length of upper bracts, often purple-tipped. Disc florets many, rays c. 13, ray

Plate 2.1 A mature fireweed plant. Scale bar = 10 cm.

Plate 2.2 Fireweed seedlings at (a) the one-leaf stage (scale bar = 1 cm), and (b) the seven-leaf stage.


a


b

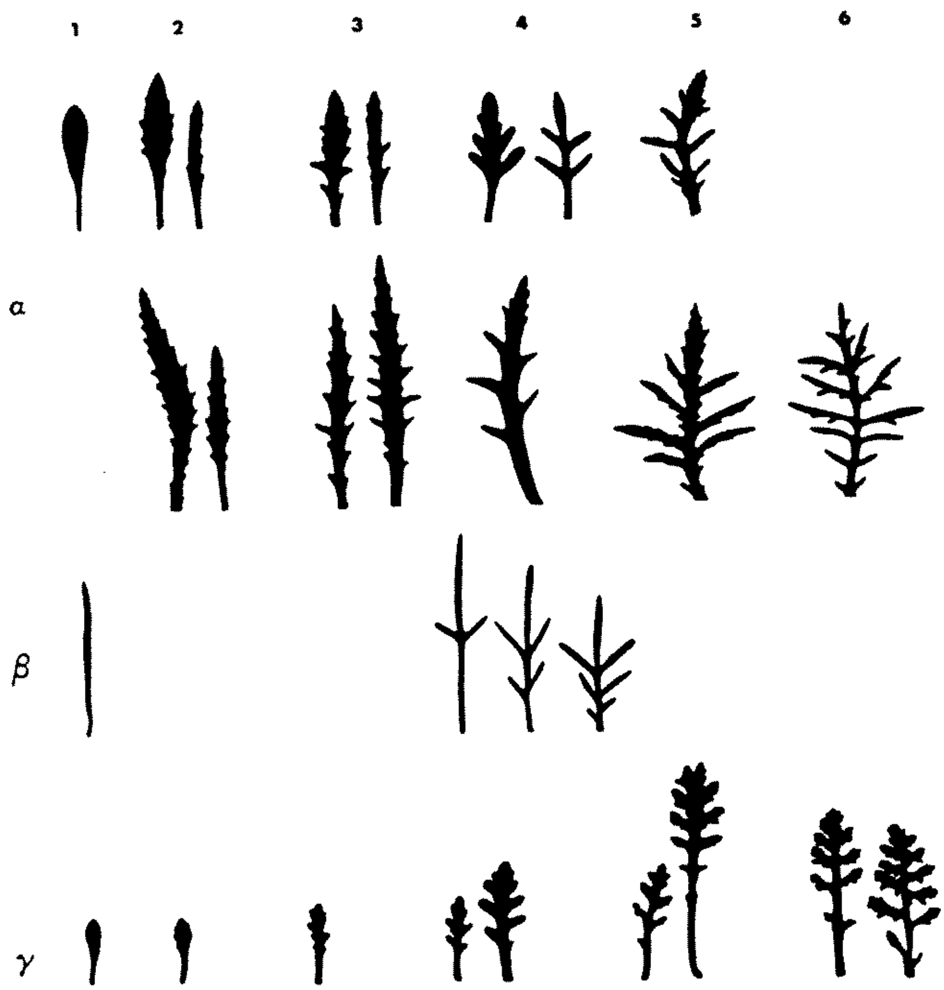


Figure 2.1 Leaf forms of the Senecio lautus complex. Forms α, β and γ are the three main types recognised while numbers 1-6 refer to subtypes (Ali 1964b).

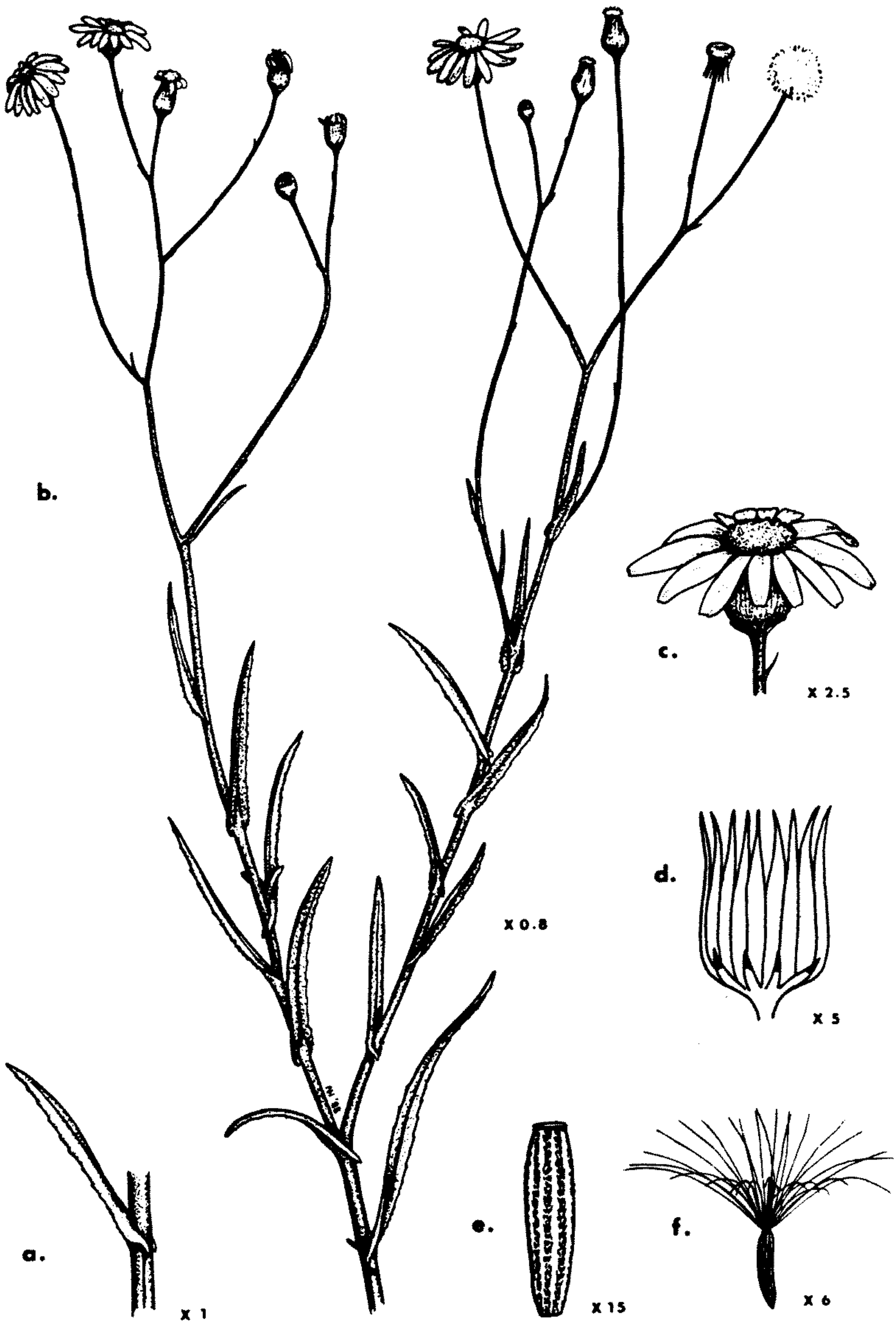


Figure 2.2 (a) Leaf axil, (b) inflorescence and habit, (c) capitulum, (d) involucre of the capitulum, (e) achene, and (f) achene and pappus, of fireweed.

corolla length 8-14 mm, often revolute with 4 resinous lines, particularly obvious on upper surface (see Figure 2.2 c,d). Ray and disc florets canary-yellow (see Plate 2.3).

Fruits

Achenes 1.5-2.5 mm long, 0.30-0.45 mm wide, cylindrical, shallowly ribbed, with short hairs or bristles c. 0.025 mm long in c. 9-10 longitudinal lines or bands, each band 0.03-0.05 mm wide (see Figure 2.2e). Achenes dark brown, light brown or green (see Plate 2.4) with light brown being most abundant. Pappus 3.5-6.5 mm long (see Figure 2.2f and Plate 2.5).

Roots

Shallow, branched, annual or perennating taproot with numerous fibrous roots, growing from 10 to 20 cm deep.

Anatomy

Anatomical characteristics of leaves, stems and roots similar to those generally possessed by other herbaceous *Senecio* species.

Key to *S. madagascariensis* and Forms of *S. lautus*

The following key allows for simple differentiation between *S. madagascariensis* and the more common representatives of the *S. lautus* complex.

A. Prostrate herb with Y-type leaf pattern (see Figure 2.1).

S. lautus ssp. alpinus (Montane). Alpine and subalpine regions in New South Wales, Victoria and Tasmania.

A.* Erect or decumbent herbs or small shrubs with α or β-type leaf pattern (see Figure 2.1).

B. Leaf pattern β-type; involucral bracts 13-20 (mean 15), 3.5-6.0 mm long; achenes 1.9-2.7 mm long, mostly hairy.

S. lautus ssp. dissectifolius (Mallee). Widely distributed in all states.

B.* Leaf pattern α-type.

C. Involucral bracts c. 13.

D. Leaves noticeably succulent; biggest cauline leaf not lobed, less than 5.5 cm long x 1.2 cm wide. Involucral bracts 4-12 mm long; achenes prominently ribbed, 1.9-4.5 mm long.

S. lautus ssp. maritimus (Coastal). Usually on sand dunes or exposed to the sea in southern Queensland and all other states.

D.* Leaves not succulent; biggest cauline leaf not lobed, greater than 5.5 cm long x 1.2 cm wide. Involucral bracts 4.5-6.5 mm long; achenes 1.8-2.0 mm long.

S. lautus ssp. lanceolatus (Moist gully). Queensland, New South Wales, Victoria and Western Australia.

C.* Involucral bracts 20-21, 4-6 mm long; achenes 1.5-2.5 mm long with short hairs in longitudinal lines, ribs very shallow.

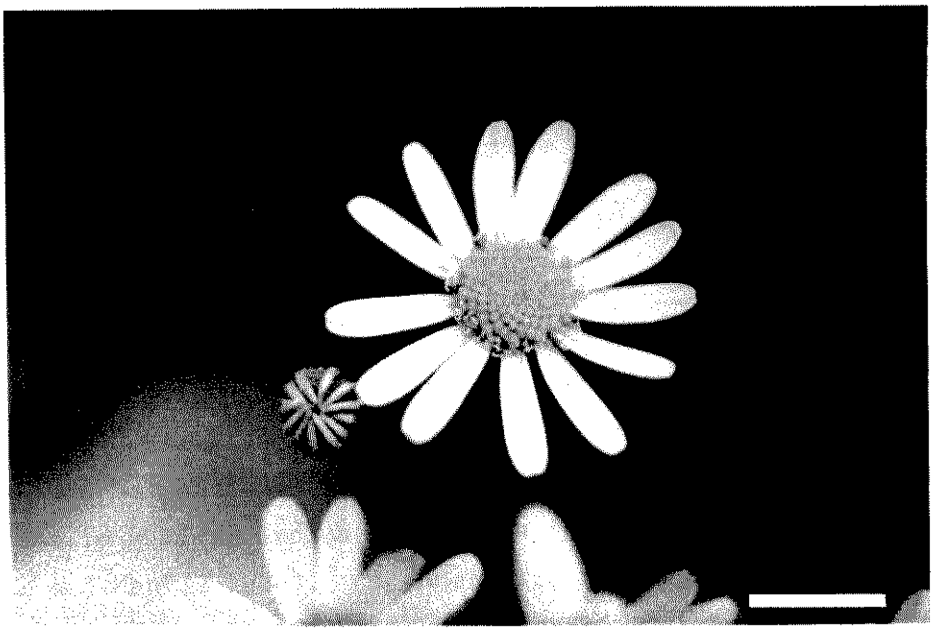
S. madagascariensis (Fireweed). South-eastern Queensland and coastal New South Wales.

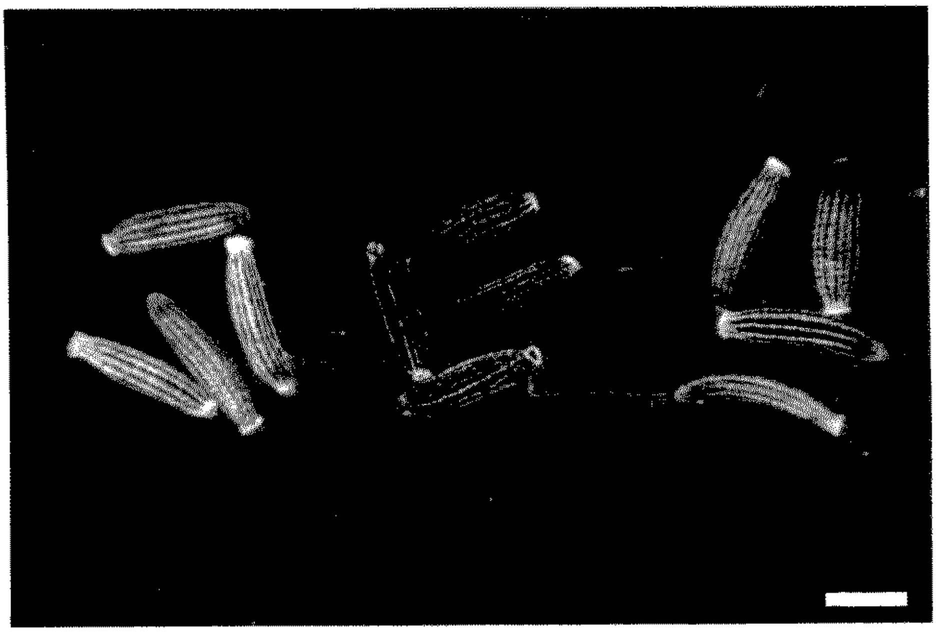
It should be noted that while the four subspecies of S. lautus given by Ali (1969) have been used in this thesis to help differentiate between S. madagascariensis and the S. lautus complex, these subspecies are not altogether clearly defined. For this reason, M.E. Lawrence and R.O. Belcher in a recent revision of Senecio in South Australia (Jessop and Toelken 1986) dropped their usage and suggested that the S. lautus complex be re-examined using conventional taxonomic methods.

Plate 2.3 Ray and disc florets of fireweed capitula. Scale bar = 1 cm.

Plate 2.4 The three types of fireweed achenes: light brown (left), dark brown (middle), and green (right). Scale bar = 1 mm.

Plate 2.5 Mature and immature capitula of fireweed showing dispersal of the pappused fruits. Scale bar = 1 cm.





AGRICULTURAL SIGNIFICANCE

Fireweed is significant principally because of its invasiveness and toxicity.

Invasiveness

Fireweed is an opportunistic weed with the ability to invade and colonise a great variety of habitats in a short period of time (Fernández and Verona 1984). Its rapid spread in the last 40 years in Argentina is a clear indication of its invasive potential (Fernández and Montes 1984). In Australia it is found predominantly in poorly grassed, neglected or heavily grazed pastures and on cultivated land during the autumn to spring period (Green 1953; Whittet 1958; Martin and Colman 1977; Walker and Kirkland 1981; Jackson and Jacobs 1985; Launders 1986). In most of the colonised areas, it has the competitive advantage of active winter growth when pasture production is low.

Fireweed is important because of its ability to invade pastures growing on highly fertile soil (Verona et al. 1982), and it has been observed to quickly invade pastures after drought (Watson et al. 1984). Watson et al. (1984) also suggest that it competes strongly with existing pasture plants for light, moisture and soil nutrients (notably phosphorus and nitrogen), and that this competition can lead to the deterioration of pastures. This conclusion seems to be based on theoretical considerations rather than empirical evidence. The extent to which pasture growth is suppressed by fireweed is likely to depend on the level of infestation.

Green (1953) noted that fireweed is much branched and generally avoided by stock, along with the pasture growing beneath it. Consequently the effective grazing area may be reduced considerably. My own observations of field infestations and the habits of grazing animals tend to suggest that cattle will graze up to and around smaller individual fireweed plants. Pasture underneath and around large plants and those close together is more likely to remain ungrazed.

While fireweed grows in all types of pasture (Green 1953), its density appears to be influenced by the quantity of ground cover (Martin and Colman 1977). Lynch and Strang (1973) observed that fireweed occurred more frequently on sites where pastures had failed and where cattle had formed permanent camps. These areas were dominated by the unproductive couch grass (Cynodon dactylon (L.) Pers.) and carpet grass (Axonopus affinis Chase). Fireweed is not generally a problem in irrigated pastures or crops, possibly due to the better overall growth and the more intensive management of these situations (Fernández and Montes 1984; Watson et al. 1984).

Fernández (personal communication) has identified four principal reasons why S. madagascariensis invades pastures in Argentina. They are the abundance of 'inoculum' produced by the weed in the stubble of many cereal crops during autumn; insufficient sowing of adapted and improved pasture species, and their early grazing; overgrazing, particularly during periods of low pasture regrowth; and the avoidance of it by cattle, favouring its growth and spread.

Due to high seed production and ease of distribution, the potential of fireweed for further colonisation, once established, appears to be one of its most important invasive characteristics. Others which may be added are its annual/perennial habit; its adaptability and variability in the field; germination, growth and flowering during much of the year; and the possibility of a long flowering period.

Toxicity

Senecio was one of the first plant genera discovered as being harmful to domestic livestock (Robertson 1906; Steyn 1934; Watt and Breyer-Brandwijk 1962; Bull et al. 1968; Radeleff 1970; Clarke and Clarke 1975; Frohne and Pfänder 1984). In many countries, ingestion of the widespread species Senecio jacobaea L. (ragwort) is responsible for more deaths of livestock than all other poisonous plants together (Forsyth 1968; Robins 1977).

In Australia, several Senecio species have also been incriminated in the poisoning of grazing animals (Bull et al. 1968; Anon. 1977a),

S. lautus (Bennetts 1935) and S. madagascariensis (then known as S. lautus) (Green 1953; Whittet 1958) being among them.

Mortalities and poor growth of cattle in the Hunter Valley of New South Wales were shown by Walker and Kirkland (1981) to be caused by fireweed toxicity. Fireweed fed to three calves in a controlled experiment, caused the death of two within 77 days and depressed growth rate in the third. These findings were augmented with a study of a substantial field mortality of cattle in the Bulahdelah district on the central coast of New South Wales (Kirkland et al. 1982). On the basis of the autopsy results, histopathology and consumption of fireweed, it was concluded that fireweed toxicity was the principal cause of these mortalities.

Other Senecio species have also been responsible for contamination (Dickinson et al. 1976; Deinzer et al. 1982; Jackson and Jacobs 1984) and a drop in production of milk in dairy cattle (Robertson 1906; Watson et al. 1984), but fireweed has not been implicated. The potential danger to humans drinking contaminated milk appears to be slight (Dickinson and King 1978).

Fireweed is poisonous owing to the presence of a pyrrolizidine alkaloid, believed to be senecionine (Culvenor unpublished data, cited by Bull et al. 1968; McBarron 1976). The structures of senecionine and the general form of pyrrolizidine alkaloids are given in Figure 2.3 a,b. According to Huxtable (1980) the LD_{50} i.p. for senecionine in rats is 85 mg kg^{-1}.

The alkaloid content of Senecio species is very variable (White 1969) and especially among members of the S. lautus complex (Walker and Kirkland 1981). Mature fireweed (S. madagascariensis) has been reported as having a total alkaloid content of 0.03% w/w. Although this is only a relatively moderate level, Walker and Kirkland (1981) concluded that in the Hunter Valley at least, significant mortality and poor growth of stock can occur from its ingestion.

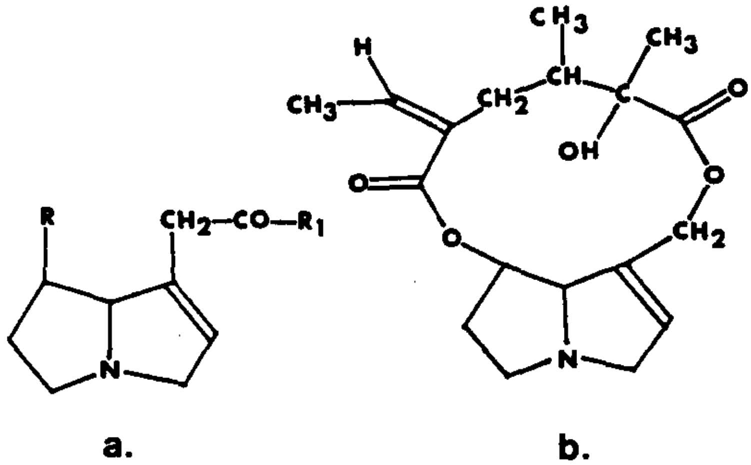


Figure 2.3 Structures of (a) the general form of pyrrolizidine alkaloids (R=H, OH or O-acyl; R_1=alkyl), and (b) senecionine, the pyrrolizidine alkaloid present in fireweed.

Symptoms and treatment

The disease 'pyrrolizidine alkaloidosis' or 'seneciosis', produced by the consumption of Senecio plants (Clarke and Clarke 1975; Frohne and Pfänder 1984), is characteristically chronic in nature. Most pyrrolizidine alkaloids are cumulative poisons (Swan 1967) and induce a form of liver (hepatic) damage characterised by megalocytosis and inhibition of cell division (Bull et al. 1968). Varied effects in the liver may be related to the severity and duration of poisoning (Hooper 1978). The disease is progressive; symptoms and deaths of animals commonly occur weeks or months after consumption of the plant has ceased (Anon. 1930; Bull 1955; Swan 1967; Radeleff 1970).

The clinical signs of fireweed poisoning are diverse. Weakness, marked loss of condition, and emaciation with recumbency and death were observed by Walker and Kirkland (1981) to be most prominent. Nervous signs such as aimless wandering, slight or incomplete paralysis, loss of muscular co-ordination, insensibility and apparent blindness were seen infrequently. In older stock photosensitisation, jaundice and abdominal straining were observed in sporadic cases. Other signs may include dullness, chronic scouring and loss of appetite (Watson et al. 1984).

The most common effect attributed to fireweed in cattle is ill-thrift and poor growth in young stock. A condition in cattle on the central coast of New South Wales known as 'coastal ill-thrift', is believed to be partly due to fireweed toxicity. Varying degrees of chronic but not fatal damage are seen in these animals (Watson et al. 1984).

There is no effective treatment for seneciosis (Craig et al. 1930; Reynolds 1936; Radeleff 1970). Movement of stock to areas free of fireweed may prevent further development of the disease, but because this form of liver damage is irreversible (Bull et al. 1968), the syndrome of ill-thrift and poor growth may continue.

Factors affecting poisoning

Poisoning may be affected by several factors. These include the palatability of fireweed, availability of alternative feed, age of the plant, variation in animal tolerance and weather conditions.

Conflicting opinions as to the risk to livestock grazing infested pastures arise primarily from the fact that fireweed is generally unpalatable to cattle and horses. Many other *Senecio* species are also regarded as unpalatable to livestock (Radeleff 1970; Clarke and Clarke 1975; Anon. 1977a), possibly due to the bitter flavour of their alkaloids (Arnold 1966; Swain 1977). Feed rejection problems have been encountered with both *S. lautus* (Bennetts 1935) and fireweed (Walker and Kirkland 1981) in experiments with sheep and cattle respectively.

The palatability of some toxic *Senecio* species, including fireweed, may be improved by slashing or spraying (Matthews 1971). Wilted or dried material is often more readily consumed (Murnane 1933).

Because fireweed remains toxic when dry (Walker and Kirkland 1981), poisoning may occur following these methods of control.

Providing sufficient alternative feed is available, cattle and horses consume only small quantities of fireweed. Where its ingestion cannot be avoided, poisoning is more likely to occur. Such circumstances may include pastures heavily infested with young fireweed plants and poor quality pastures where there is a shortage of alternative feed (Watson et al. 1984).

In many areas along the New South Wales coast, there is often a seasonal shortage of pasture from late winter to mid to late summer (Walker and Kirkland 1981). It is at these times that fireweed is most abundant (McBarron 1983) and a scarcity of alternative feed may force cattle to consume the plant despite its unpalatability. Cotton fireweed (S. quadridentatus) is also thought to cause stock losses under these conditions (Kater 1965). Poor seasonal conditions or droughts and heavy stocking rates also present potentially dangerous situations. Likewise, hungry stock which have been driven or trucked and then turned out to graze may feed non-selectively (Steyn 1934; Johnstone 1967). Stock that graze regularly in a paddock are more likely to avoid poisonous plants (Jackson and Jacobs 1985).

In prepared feeds containing toxic plants, selection is difficult for animals and poisoning can occur (Steyn 1934; Radeleff 1970; Matthews 1971). Hay containing Senecio species has caused livestock poisoning (Leyshon 1926; Craig et al. 1930) and silage is also reported as dangerous (Ferguson 1940; Donald and Shanks 1956). This suggests that the pyrrolizidine alkaloids are not destroyed in either the hay-making or the ensiling processes. Therefore, the control of fireweed in areas to be used for hay or silage appears to be critical.

Evidence concerning the effect of age on the toxicity of Senecio plants would seem to be inconsistent. Robertson (1906), Steyn (1934) and Cockburn et al. (1955) claim that plants are probably most poisonous when young and in the pre-flowering stage. Hartmann and

Zimmer (1986), on the other hand, report that, in *S. vernalis* Waldst. & Kit. and *S. vulgaris* at least, the reproductive organs are the main sites of pyrrolizidine alkaloid accumulation. In mature plants, the flower heads accounted for 70-80% of total plant alkaloids at concentrations exceeding those of the vegetative organs 5 to 10-fold. Dickinson and King (1978) found that in *S. jacobaea* highest concentrations were also in the flowers. Because the relative toxicity of immature fireweed has not yet been reported, potential toxicity throughout the life (and death) of the plant should be assumed.

While seneciosis has been reported in all the major classes of livestock, susceptibility varies (Hooper 1978). Although sheep and goats readily eat fireweed, they are much less susceptible to *Senecio* poisoning than cattle and horses (Bull 1955; Bull *et al*. 1956; Bull *et al*. 1968; Clarke and Clarke 1975). Dollahite (1972) showed that it takes over 20 times as much *Senecio* spp. to poison sheep and goats as it does cattle. Detoxification of the alkaloids by specific bacterial enzymes in the rumen of sheep (Bull *et al*. 1968; Clarke and Clarke 1975) or the high activity of a hepatic microsomal enzyme (Swick *et al*. 1983) could account for their relative resistance.

It is likely that the age of livestock also affects tolerance. Thus Walker and Kirkland (1981) found group mortalities most often in calves. In contrast, mortalities in older animals occurred sporadically and the syndrome of poor growth was more prominent. This may reflect a greater tolerance due to larger body size and prior exposure to the plant.

Evidence collected by Kirkland *et al*. (1982) suggests that changes in weather conditions may also influence fireweed poisoning. During January and February 1980, 75 cattle died from a herd of 800. Losses occurred on two occasions, both within a week of rain falling and after an improvement in nutrition. At the time of the mortalities, drought conditions had prevailed for 6 months and had resulted in the forced grazing of fireweed. In cases of poisoning with other *Senecio* species, increased mortality has also occurred following environmental changes (Donald and Shanks 1956).

Experimental assessment of the impact of fireweed on livestock production and poisoning is beyond the scope of this thesis. Hence greater emphasis has been given here to the literature than may otherwise have been. The evidence suggests that fireweed has the potential to cause mortality and poor growth, but if infestations are light and alternative feed is available, then cattle will avoid grazing it. In order to prevent access of livestock to fireweed and the possibility of poisoning, control of the weed is most desirable.

LIFE CYCLE

Longevity

Fireweed (S. madagascariensis) is a short lived perennial plant (Green 1953; Cabrera and Ré 1965; Martin and Colman 1977; Verona et al. 1982) which behaves most commonly as an annual (Hilliard 1977; Walker and Kirkland 1981).

According to Verona et al. (1982) the majority of plants die off at the end of their first year of growth, especially in agricultural soils, but it is common to find plants which continue to grow and reproduce actively during their second year. This is the case even without some external stimulus, such as mechanical damage, which could promote the regeneration of the stem. For example, plants which are slashed may not be killed but may regrow and become two year old plants. This persistence through summer is confirmed by observations made by Nelson and Michael (1982). In some plants regrowth from roots can occur following the death of the top growth over summer (Watson et al. 1984). Since rooting along the woody stems of decumbent fireweed plants has also been observed (Nelson 1980), it is possible that shoots associated with these adventitious roots remain alive while those of the parent roots die off. Verona et al. (1982) had reservations in considering it a strict perennial; with rare exceptions the few plants that survive the second year are decrepit and ready to senesce. It is likely that for this reason Humbert (1963) reports S. madagascariensis as a biennial.

It is not uncommon therefore to find variations in the life cycle of fireweed. Similar variations are known to occur in S. jacobaea

(Schmidl 1968; Forbes 1977). In this context, S. madagascariensis represents a species with high plasticity or capacity to vary its life cycle. This undoubtedly is associated with the duration and stability of the habitat which supports it (Southwood 1977).

Germination

Fireweed is capable of growing and reproducing during a large part of the year, although most seed would appear to germinate from March to July with the plants dying off from September to November. At the moment of dispersal a high proportion of seed is viable and ready to germinate (Alonso et al. 1982). Nelson and Michael (1982) recorded 90% germination at 20°C three days after collection. For this reason more than one generation may occur throughout the winter period (Nelson 1980). While extreme temperatures induce dormancy of the seeds (Alonso et al. 1982), innate dormancy is negligible under normal conditions. This strategy would be disadvantageous for the persistence of annual arable weeds (Chancellor 1984), but because fireweed grows predominantly in pasture areas the conditions for germination may not always be present. High spring and summer temperatures may help to explain the lack of new seedlings appearing in that period.

Nelson and Michael (1982) showed that most rapid germination occurred between 20°C and 25°C. Highest percentage germination after 14 days occurred between 15°C and 27°C with greatly reduced germination at lower and higher temperatures. This wide temperature range is consistent with germination of fireweed over much of the year. Nelson and Michael also found that there was no germination at 35°C. I have confirmed this, but have found that seed exposed to this temperature was viable when germinated at 20°C. The optimum temperatures observed for germination and the ability of the seeds to withstand high summer temperatures are those expected of a winter-growing species in coastal New South Wales (Nelson 1980).

Although light (Alonso et al. 1982; Nelson and Michael 1982) and nitrates (Alonso et al. 1982) are not essential, they generally stimulate percentage germination. Guillén et al. (1984) concluded that S. madagascariensis seed is in fact photoblastic - requiring intermittent or continuous radiation for germination. The promotion of germination by irradiation with red light and its reversion by far-red light led these authors to believe that the mechanism of fireweed dormancy is operated by the phytochrome system. Responsiveness to light has also been reported in *S. vulgaris* (Popay and Roberts 1970a) and may be of direct consequence to the establishment and survival of seed, by determining the maximum depth of soil from which germination may take place (Koller 1964). The depth of *S. madagascariensis* seed in the soil does affect germination; seedling emergence does not occur from below 2 cm (Alonso *et al*. 1982). This result is consistent with other small seeded species (Froud-Williams *et al*. 1984).

Percentage germination was not affected by osmotic potentials over the range 0 to -300 kPa but decreased at potentials below -300 kPa (Alonso *et al*. 1982). A small percentage of seeds were still able to germinate at -1000 kPa.

The three types of achenes (dark brown, light brown and green) vary in their germination behaviour and longevity (Verona *et al*. 1982). These differences are discussed in Chapter 5.

Under laboratory storage, all seeds are estimated to lose their viability after 4 to 5 years (Alonso *et al*. 1982). Nothing is known concerning the longevity of seed in the field.

Development

Fireweed seedlings develop rapidly so that plants may produce flowers 6 to 10 weeks after emergence. Time to flowering decreases with increasing temperature (Nelson 1980). Growth rates (dry matter and leaf area) are positively correlated with mean air temperature (Nelson 1980; Fernández and Verona 1983). Dry matter allocation to leaves prevails during the early developmental stages while an increasing proportion of assimilates go into the stems over the life of the plant. Allocation to roots decreases rapidly with plant age (Fernández and Verona 1983).

Flowering

S. madagascariensis is a precocious species. Flower intensity is greatest at the beginning of spring. Another flush in flowering occurs in the middle of autumn (Verona et al. 1982). An individual plant has the ability to produce large quantities of seed during its life cycle. In a seed production study the average plant produced approximately 230 capitula with 80 seeds per capitulum (total of 18,000 seeds) (Nelson, personal communication). At a nominal germination rate of 50%, it was estimated that the average plant produced 9000 viable seeds. The quantity of seed which is set is dependant largely on the time of seedling establishment and the consequent size of the plant at the peak flowering periods (Fernández and Montes 1984). Alonso et al. (1982) found no pattern of seed viability related to the time of seed production.

Spread

The seeds of fireweed are small and light (135 μg) and each is attached to a relatively persistent pappus of white hairs (Daniel 1984). It has been thought that dispersal of large amounts of seed by wind is the major factor responsible for the rapid spread of the weed over large areas and long distances (Watson et al. 1984). However, most species with wind-borne propagules are only able to disperse a very small fraction of propagules to a great distance from the parent plant (Sheldon and Burrows 1973; Harper 1977).

Measurements made by Poole and Cairns (1940) of the spread of S. jacobaea showed that the bulk of its seed (60%) falls within 5 m of the parent plant. Further away the proportion diminishes almost asymptotically with distance, so that only under exceptional conditions is seed blown further than a distance of 40 m. The pattern of spread of fireweed is likely to be similar. Environmental conditions needed for long distance wind transport are low humidity and open habit (Small 1918), and sufficient convection current to carry the pappose fruit high into the air (Sheldon and Burrows 1973).

Some idea of the relative efficiency of wind dispersal mechanisms can be gained from observing the rate at which fruits or seeds fall in still air (Ridley 1930). The slower this is the greater the chance of the propagule being caught up by a horizontal wind from the rising current of air that supports it (Salisbury 1961). Terminal velocities for a number of Composite weed species are shown in Table 2.1.

Table 2.1 Terminal velocities of dispersal units of fireweed and other selected weed species from the family Asteraceae. Modified from Sheldon and Burrows (1973).

Species	Mean terminal velocity (cm sec^{-1})
Cirsium arvense (L.) Scop.	21.6
Sonchus arvensis L.	24.1
Senecio madagascariensis Poir.	25.2[A]
Senecio vulgaris L.	28.0
Senecio viscosus L.	31.7
Taraxacum officinale sens. lat.	35.7
Sonchus oleraceus L.	35.7
Senecio jacobaea L.	42.1
Senecio squalidus L.	45.7
Carduus tenuiflorus Curtis	78.6

[A] My addition.

Included for comparison is the mean terminal velocity of 30 viable S. madagascariensis seeds which I measured in still air at 62% relative humidity. The height at which seed is released from the plant is also important in determining distances over which propagules may be moved by air currents (Sheldon and Burrows 1973). Nevertheless, the data show that fireweed is likely to be more efficient than other wind-dispersed Senecio species such as S. vulgaris, S. viscosus L., S. jacobaea and S. squalidus L. It is wind-borne achenes of this type (Everist 1968) which contribute largely to the success of fireweed as a weed and invader of pasture land.

The seeds can also be spread in hay and grain products, on clothing and vehicles, and by livestock, birds and other animals. There have also been suggestions that seed has blown into piles of superphosphate and then been spread to new areas when the fertiliser was applied aerially. A variety of seeds, including S. vulgaris and S. jacobaea, are able to pass unharmed through the digestive tract of either cattle or birds (Ridley 1930; Salisbury 1961). Whether fireweed can be spread by this means has not yet been determined.

DISTRIBUTION

Australia

The earliest record of fireweed in New South Wales, and probably in Australia, is a specimen collected at Raymond Terrace in 1918 (Nelson 1980). It first became prominent in pastures in the Hunter Valley and from there spread throughout many parts of coastal New South Wales, being introduced to the north coast in about 1940 in crop seed (Green 1953). By the mid 1960's fireweed was identified as one of the main weeds of that region (Whittet 1968; Auld 1971). It is now especially abundant in the Richmond, Manning and Hunter Valleys, in the County of Cumberland and between Wollongong and Berry on the South Coast. The weed is also known to occur as far south as Bega and in south-eastern Queensland. A map showing the present distribution of fireweed in Australia is given in Figure 2.4.

While the weed primarily infests the coastal river valleys of New South Wales, distribution does extend into the northern and southern Tablelands (Nelson and Michael 1982) and an isolated occurence exists further inland at Dubbo (Watson et al. 1984). The potential distribution of fireweed in Australia is not known.

Africa

In southern Africa it is known to occur up to 1500 m above sea level and is widely distributed from southern Madagascar and the Mascarene islands through coastal southern Mozambique to Natal, the Transkei and eastern and southern Cape as far west as the Uniondale district. Though not common, it is also found in the Transvaal (Hilliard 1977)

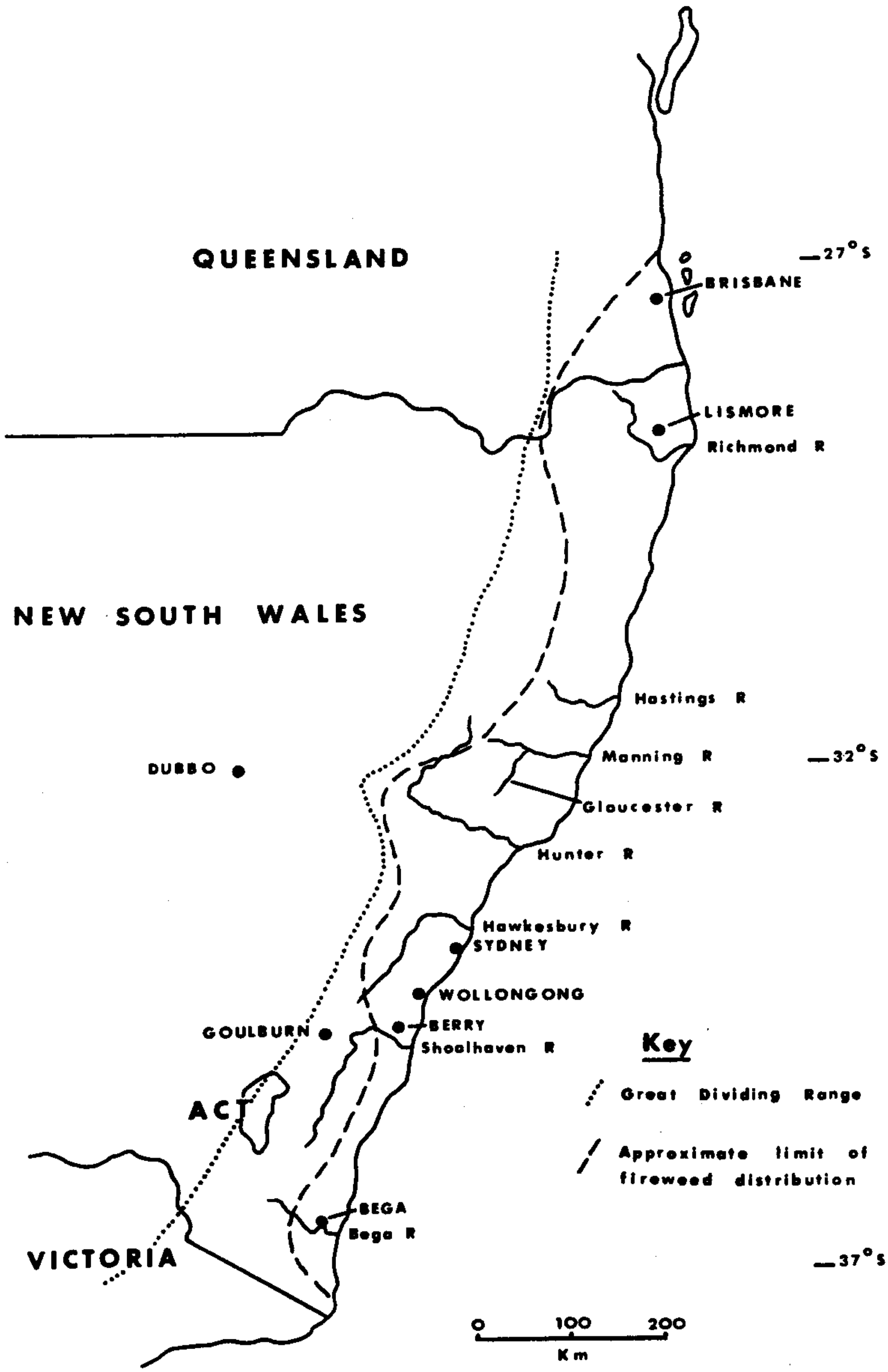


Figure 2.4 Present distribution of fireweed in Australia.

and has been recorded at Chipinga in eastern Zimbabwe (Jeffrey, personal communication).

In Natal in its natural range, S. madagascariensis is found only on disturbed land fallows, contour banks and road verges and the like. But in the spring of 1983, following 3 years of drought, it appeared widely in undisturbed natural vegetation and sown pastures. This widespread appearance did not recur in the next spring owing to a year of much more normal rainfall (Tainton, personal communication). S. madagascariensis is not thought to be a serious problem in Natal (Hilliard, personal communication).

S. madagascariensis has also recently been introduced and reported naturalised much further north near Gilgil in the highlands of Kenya at an altitude of 2600 m (Jeffrey, personal communication). It is not eaten by cattle and is causing a considerable weed problem. In equatorial regions like this, elevation creates a range of temperature regimes from tropical to temperate (Went 1957).

South America

In Argentina, S. madagascariensis was first known surrounding the port of Bahia Blanca. Since then it has spread greatly and is now a significant weed of agricultural crops and grasslands in the south-eastern part of Buenos Aires province (Verona et al. 1982). It is also found in large areas of the provinces of Santa Fe, Rios, Corrientes and Mendoza (Volkart 1984).

As in Kenya, S. madagascariensis has also recently been recorded from the cool moist equatorial environment of the Colombian highlands near Bogota at 2800 m (Swarbrick, personal communication). Little is known about its prevalence there other than it is typically a roadside weed.

S. madagascariensis appears restricted in distribution primarily to humid maritime and sub-tropical regions of the world. A comparison between the present distribution of the weed in Africa, Australia and

South America is made in Chapter 4. A map showing these areas is also given (see Figure 4.3).

Local Pattern

On a local scale the pattern of distribution may vary considerably on account of differences in soil and previous cultural systems. Fireweed is able to grow on a wide range of soils of varying fertility (Verona et al. 1982). Although it prefers soils which are well drained, not compacted, and of high fertility, it can also grow in sand and heavily limed soil. Watson et al.(1984) suggest that low fertility soils are less likely to support vigorous pastures and, lacking competition, fireweed grows freely. Watson et al. (1984) state that it does not persist in poorly drained or waterlogged situations whereas Verona et al.(1982) concluded the opposite. The results of a trial conducted by Daniel (1984) suggest that fireweed may show adaptation to different drainage regimes and indicate that it has a large potential for physiological variation.

CONTROL

Although fireweed was declared a noxious weed in certain shires of New South Wales from 1946 to 1971 (Martin and Colman 1977), it is now generally considered that eradication and prevention of spread are not feasible. Despite the importance of the weed, very little work has been done on its control, and that has been mostly confined to work with herbicides (e.g. Launders 1979; Tracanna et al. 1983; Launders 1984 a,b; 1985). The temporary nature of herbicide control (see Chapter 1) suggests that an integrated approach is needed. To this end, a range of possible control methods is discussed.

Herbicides

The optimum time for herbicide application is during the small seedling to early flowering stages (normally autumn to winter) (Watson et al. 1984). In Argentina, Tracanna et al. (1983) found that treatments were most effective from mid June to late July. While a number of herbicides have been compared for efficiency in killing fireweed, glyphosate (as Roundup) and bromoxynil (as Brominil) have proved to be the most effective (Launders 1979).

An excellent kill of young fireweed was achieved with an application of bromoxynil at 280 g a.i. ha^{-1}. When applied to advanced plants, the percentage kill dropped to less than 55% (Launders, personal communication). It was concluded that after bud formation, between 500 and 560 g a.i. ha^{-1} were needed. Bromoxynil is a selective herbicide. While grasses are unaffected, it may cause temporary scorching of the upper leaves of clover.

Ropewick applicators enable non-selective herbicides such as glyphosate to be selectively applied to weeds. In trials with fireweed, both bromoxynil at 200 g a.i. l^{-1}, and glyphosate at 100 g a.i. l^{-1} proved effective against young plants. Glyphosate was needed to ensure a good kill after flowering (Launders 1984a). Two passes of the applicator using glyphosate gave a 94% kill of flowering plants compared with 69% with only one pass (Launders 1984b). When using a ropewick applicator the target weeds should be at least 15 cm taller than the pasture. To help achieve this situation the area should be grazed prior to treatment.

Preliminary tests indicate that both herbicides reduce the germination of fireweed seed when sprayed on plants at the late flowering stage. Glyphosate appeared to be the more effective of the two. Similarly, Thompson (1983) found that glyphosate reduced seed viability in _S. jacobaea_.

As previously mentioned, fireweed plants treated with herbicides may become more attractive and palatable to livestock. This could increase the risk of fireweed poisoning even though stock may be withheld from the treated areas until the plants are completely dead. This aspect of herbicide control needs to be investigated.

Because pastures that initially proved suitable for invasion by fireweed are likely to suffer the same fate again, herbicide control should be carried out in conjunction with pasture improvement.

Pasture Management

The essential principle of any fireweed control program must be provision of a vigorous, competitive pasture (Green 1953; Whittet 1958; Smith 1983; Launders 1985; 1986). Any factors which open up pastures, such as overgrazing, drought, uncompetitive pasture species, and areas bared by trampling e.g. around watering or feeding places, appear to favour the development of fireweed.

A dense pasture during early autumn to winter is likely to provide the best form of control. This may be achieved by growing early winter pasture species, by allowing standover of summer pasture feed, or by using winter-summer pasture combinations (Watson et al. 1984). These options are particularly relevant since fireweed is of greatest abundance in naturalised summer-growing pastures such as paspalum (Paspalum dilatatum Poir.)/ carpet grass (Axonopus affinis) dominant pastures on the central and north coasts of New South Wales (Martin and Colman 1977; Launders 1979). The low productivity and high relative stocking rates in the winter months predisposes them to invasion.

Due to the need for continuity of feed, particulary on dairy farms, new pasture species may need to be drilled directly into the existing pasture rather than using conventional cultivation before sowing. Possible winter species include phalaris, ryegrass, fescue, white clover, subterranean clover and oats, while summer species such as kikuyu, paspalum, setaria and Rhodes grass have potential. Even under heavy grazing, kikuyu dominance markedly reduces fireweed density (Martin and Colman 1977). Kikuyu has a longer period of active growth in autumn than either carpet grass or paspalum and can produce more dry matter (Colman 1970). It therefore competes more strongly with regenerating seedlings of fireweed.

Careful fertiliser management is also likely to be a critical tool in fireweed control (Nelson 1980). The application of fertiliser during the active growth period of the grasses could increase their yield (Hexter 1950), and therefore decrease the density of fireweed. However, if application occurs when the pasture is unable to respond, for example in autumn when the summer-growing species have ceased active growth, then fireweed growth may be favoured.

Pasture management through controlled grazing, appropriate fertiliser applications, and the sowing of new species, has potential as a method of fireweed control and warrants further investigation. Experiments in Chapters 8, 9 and 10 assess the potential success of this type of control.

Mowing

Very little has been reported concerning the effectiveness of mowing or slashing as a means of controlling fireweed. The results of mowing throughout the autumn to spring period have been variable (Watson et al. 1984). In trials near Taree close mowing did not kill the plants but only slowed their growth and delayed flowering. Because mowing may promote regrowth (Verona et al. 1982), it is likely to cause some fireweed plants to survive through summer and continue to grow and flower in the second year.

Nevertheless, regular mowing can assist in control over small areas. Fernández (unpublished data) obtained a 20% reduction in plant survival with one cut at either 5 or 10 cm and 70% reduction with two successive cuts at 10 cm two months apart. The plants surviving after one cut at these heights, however, increased their specific growth rate by 40-50%. Although plants cut at 2.5 cm did not increase their growth rate significantly ($P=0.05$), their dry weight four months later was only 15% lower than the control. Their survival rate was not affected. Mowing when conditions are unfavourable for pasture growth, or in young and unthrifty pastures, should be avoided since the weed may recover more quickly than the pasture and therefore become dominant.

As was suggested for fireweed treated with herbicides, the potential for poisoning of livestock from slashed plants requires investigation.

Cultivation

Nelson (1980) found that germination of fireweed in the dark was only 8%. This suggested that burial of the seed might reduce plant populations and aid control. To test this hypothesis, Daniel (1984) used a mouldboard plough to invert the soil. Rather than decreasing, fireweed increased in density. Cultivation of natural carpet grass pastures in order to establish improved species has also been observed to increase the density of fireweed (Launders 1979).

To be effective and kill emerging seedlings, cultivation must be thorough, repeated and followed up with the establishment of a suitable perennial pasture. Alternatively, a winter crop followed by a perennial pasture may be sown (Watson et al. 1984). Where continuity of feed is important, complete cultivations of this nature are likely to be uneconomical unless carried out on a small scale.

In cropping situations, similar to that which occur in Argentina (Fernández and Montes 1984), control of fireweed by cultivation is likely to be much more beneficial. Fireweed should be cultivated prior to sowing and in the stubbles of crops following harvest.

Any consideration of the long-term implications of weed control must take into account the population of dormant, viable weed seeds present in the soil (Daniel 1984). Because cultivation will mix weed seeds between conditions enforcing dormancy and conditions which favour germination (Roberts 1964), the longevity of the seeds of fireweed in cultivated ground is expected to be much less than in undisturbed ground. Since nothing is known of the survival of fireweed seed in a soil system, studies on the dynamics of seed banks need to be undertaken.

Grazing

While low stocking rates (especially in the autumn) are recommended to allow pasture to compete more vigorously with fireweed (Fernández and Montes 1984; Launders 1985), it is believed that grazing with sheep or goats may be of some use in fireweed control (Watson et al. 1984). They have been recommended and used for the control of other weedy Senecio species in pastures (Ewart 1909; Hexter 1950; Dollahite 1972). For example, in the Gippsland area of Victoria, many dairy farmers carry some crossbred wethers for the sole purpose of controlling ragwort (S. jacobaea) (Schmidl 1968; Parsons 1973). Although the effect of defoliation on fireweed has not been documented, experience shows that sheep and goats do provide a level of control worthy of serious consideration. Studies on the effect of defoliation on seed production, similar to those conducted by McIvor and Smith (1973) on capeweed (Arctotheca calendula (L.) Levyns), would be advantageous.

Although grazing with sheep or goats has many advantages as a means of weed control (Vere and Holst 1979), it is not without difficulties. Running sheep or goats under coastal conditions could lead to an increased incidence of parasites and diseases. Improved or additional fences and yards may be required (Campbell et al. 1979) and flock composition would need to be altered regularly to avoid eventual poisoning of the animals. Careful management of stocking rates would also be required to suppress fireweed but prevent overgrazing. Lastly, many farmers would believe it impractical to introduce sheep or goats into predominantly dairying areas.

Biological

Although a number of insects both in Australia and Argentina are known to feed on S. madagascariensis and a rust infect it, their impact is still relatively unknown.

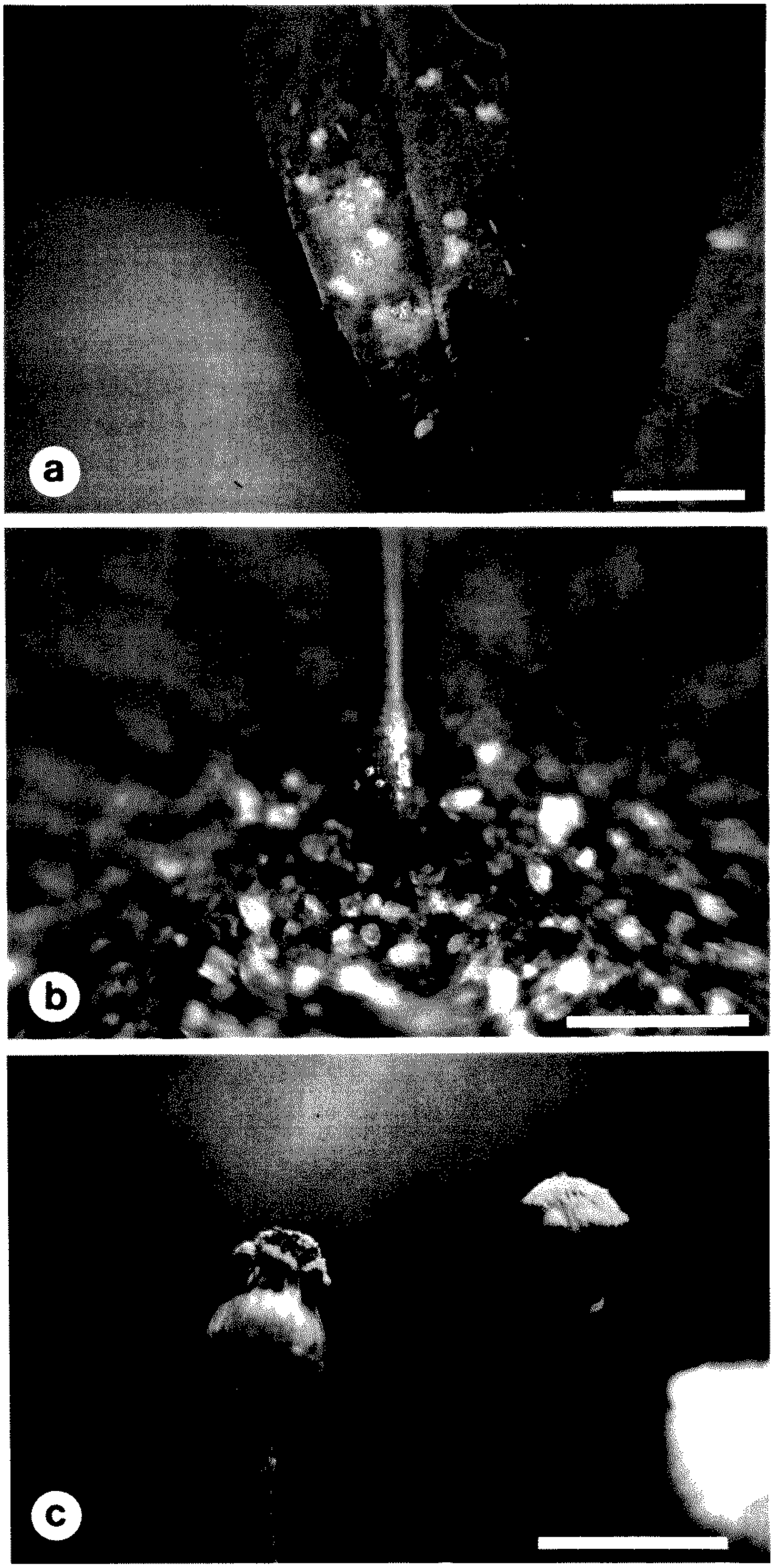
In Argentina, during its vegetative stages of growth, S. madagascariensis is a frequent host of ants, principally Acromyrmex lundi Guer. (Verona et al. 1982). These eat the leaves and vegetative shoots and in the more advanced plants feed on the beginnings of the inflorescences. Another insect, still unidentified, feeds on the ovaries, reducing their growth and the reproductive capacity of the weed. In young branches, fly larvae (Lamproxynella sp.) cause the formation of galls. A pseudococcid has also been observed in the roots. In greenhouse-grown plants the aphid Myzus persicae (Sulz.) has been found to feed on the leaves. In gardens, young plants are eaten by the snail Helix aspera (Mull.).

In Australia, insects such as the larvae of a pyralid moth (Homoesoma sp.), the cineraria leaf miner (Phytomyza syngenesiae (Hardy)), the senecio moth (Nyctemera amica (White)), the metallic flea beetle (Haltica sp.) and various pasture slugs are known to feed on the plant (Watson et al. 1984). A lygaeid bug (Nysius sp.) is commonly found on the inflorescence and a chrysomelid beetle Chalcolampra sp. has also been observed feeding on the plant at Gloucester, New South Wales.

A relatively widespread autoecious rust, Puccinia lagenophorae Cooke, infects fireweed in the field and can cause considerable growth retardation on heavily infected plants. Like other plant diseases, the severity and spread of this rust on fireweed is dependent on prevailing weather conditions. In Britain, S. vulgaris and S. squalidus are readily attacked by it. The rust, thought to be native to Australia and New Zealand, was discovered here as early as 1884 (Wilson et al. 1965). It has both telia and aecia but no pycnia. The telia and aecia, when found on the leaves and stems of plants, are dark brown to black and pale yellow to orange respectively (see Plate 2.6 a,b,c). The rust attacks a range of plants in the family Asteraceae including many garden plants, for example calendula or English marigold (Calendula officinalis L.), English daisy (Bellis perennis L.) and garden cineraria (Senecio cruentus DC.) (Wilson et al. 1965). Although inoculation with P. lagenophorae has been shown to reduce the competitive ability of S. vulgaris and its impact on the yield of lettuce (Paul and Ayres 1987), the practical problems of large scale culture of rusts, for the present, limit their potential value in inundative biological control. Watson et al. (1984) report that a grey mould fungus (Botrytis cinerea Pers.) also infects fireweed.

Despite the advantages of biological control over other types of weed control (Marsden et al. 1980), it has often been considered only as a last resort after all other methods have failed (Neser and Annecke

Plate 2.6 Infection of the (a) leaf, (b) stem, and (c) receptacle of the capitulum of fireweed, with the rust fungus Puccinia lagenophorae. Orange coloured aecia are clearly visible. Scale bars = 1 cm.


a
b
c

1973). More recently in Australia it has become an important option for the management of many weeds (Harley 1983; Harley and Wright 1987).

As S. madagascariensis is not a native of Australia, some pathogen or natural enemy of the plant may be found in southern Africa or Madagascar which would enable control. To this end, the Queensland Department of Lands has begun preliminary investigations on S. madagascariensis in Madagascar. Due to strict legislation and the need for extensive experimentation, biological control is, of necessity, a long term goal.

Chapter 3
FARMER SURVEY ABOUT FIREWEED[1]

> 'In every department of human affairs, Practice long precedes Science: systematic enquiry into the modes of action of the powers of nature, is the tardy product of a long cause of efforts to use those powers for practical ends.' (Mill 1848)

INTRODUCTION

In attempting to assess the impact of a weed on agriculture and the likely success of various control techniques, it is expedient to first learn of the experiences that farmers have had with the weed and its control. The difficulty of obtaining such information through official channels suggests that some type of independent survey is required (Fricke 1968).

Mail questionnaires are an easy and inexpensive method of obtaining data on occurrence and history of well known weeds (Cuthbertson 1978) as well as a consensus of farmers' attitudes towards a species and its control (Auld 1978). Often, however, the data has simply been collected from government officers or has involved only the 'level of occurrence' (e.g. Smith 1975; Shovelton 1979; Dellow and Seaman 1985; 1987; Campbell 1987). In comparison, Auld (1971) surveyed farmers about weed problems they were facing. More recently two surveys have likewise sought information on land-holders' attitudes to weeds, and their control (Williams et al. 1987; Seaman and Dellow 1987).

Views about the importance of fireweed as a weed of pastures vary considerably. Therefore it is essential that reliable data be obtained from those who confront its effects daily.

A survey of the fireweed problem in New South Wales was therefore undertaken during the spring of 1985. The object was to provide

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1. Part of this chapter has been published in Plant Protection Quarterly Vol.3 (1) 1988 pp22-28.

information on which to base future decisions regarding the fireweed research program. A questionnaire was distributed by mail to dairy farmers and graziers in coastal areas of New South Wales. It sought information on the occurrence of the weed, its spread, the nature of the problem, its relationship to different agronomic practices and pasture situations, and the methods of control presently being employed.

MATERIALS AND METHODS

Prior to the mailing of the questionnaire a draft version was tested with 12 farmers on a face-to-face basis in order to identify difficult and ambiguous questions (Freebairn 1967). While the general principles of questionnaire design are adequately outlined by Karmel and Polasek (1970), specific techniques used in this survey to give a high response were:

1. The questionnaire (see Appendix 3), a single yellow sheet of multiple choice questions, was accompanied by a personally signed letter of explanation (see Appendix 4) and reply-paid envelope (Weilbacher and Walsh 1952; Kimball 1961).

2. A press release regarding the survey (see Appendix 5) was circulated through the 'University News', the fortnightly publication of the University of Sydney, to 'The Land' newspaper and over 40 regional newspapers, for printing 2 weeks prior to mailing the questionnaire.

3. A follow-up reminder mailing which included another questionnaire, reply-paid envelope and letter of explanation (see Appendix 6) was sent 4 weeks after the first mailing to all farmers who had not yet replied.

4. Letters which were returned, not having been received by farmers to whom they were sent, were destroyed and replacement questionnaires mailed to other randomly selected farmers in their particular areas. Because respondents had simply either moved residence or the given address was incorrect, the substitution (Yates 1953) did not bias the

sample in any way. Thus the original 2.7% dead letter response was effectively reduced to zero.

5. The survey was conducted at a time when fireweed was flowering and obvious to respondents (Auld 1978). It is important in a survey of this kind that the weed be easily recognised by farmers.

The sample, totalling 780 farmers, was stratified over eight areas, all east of the Great Dividing Range, from Lismore in the north to Bega in the south. These eight corresponded to the areas served by particular dairy co-operatives and are all regions in which fireweed was expected to occur (see Figure 2.4, and Watson et al. 1984 Figure 2).

Sixty dairy farmers were randomly selected from each of the areas from lists supplied by the various dairy co-operatives. In addition to these 480 dairy farmers, 60 graziers (almost exclusively running beef cattle) were randomly selected from each of the five northern areas (a total of 300) from telephone directories and lists supplied by District Agronomists. This stratification (see Figure 3.1) provided a sample representative of coastal pastures. It also allowed for a comparison between each of the eight areas (amongst dairy farmers), and a comparison between the situation on dairy farms and other grazing properties in the five areas where fireweed has been established for the longest period of time. This latter comparison was relevant because some observers believe that fireweed is more troublesome on the more undulating and less intensive grazing properties than on the intensively farmed river flats.

Data from returned questionnaires were coded where necessary and analysed using the SPSS-X computer package. Chi^2 values (Steel and Torrie 1960) were calculated to make comparisons between specific survey areas of selected raw data. Overall Chi^2 values, however, are given in Tables 3.1 - 3.3 to indicate the variation in results between all survey areas.

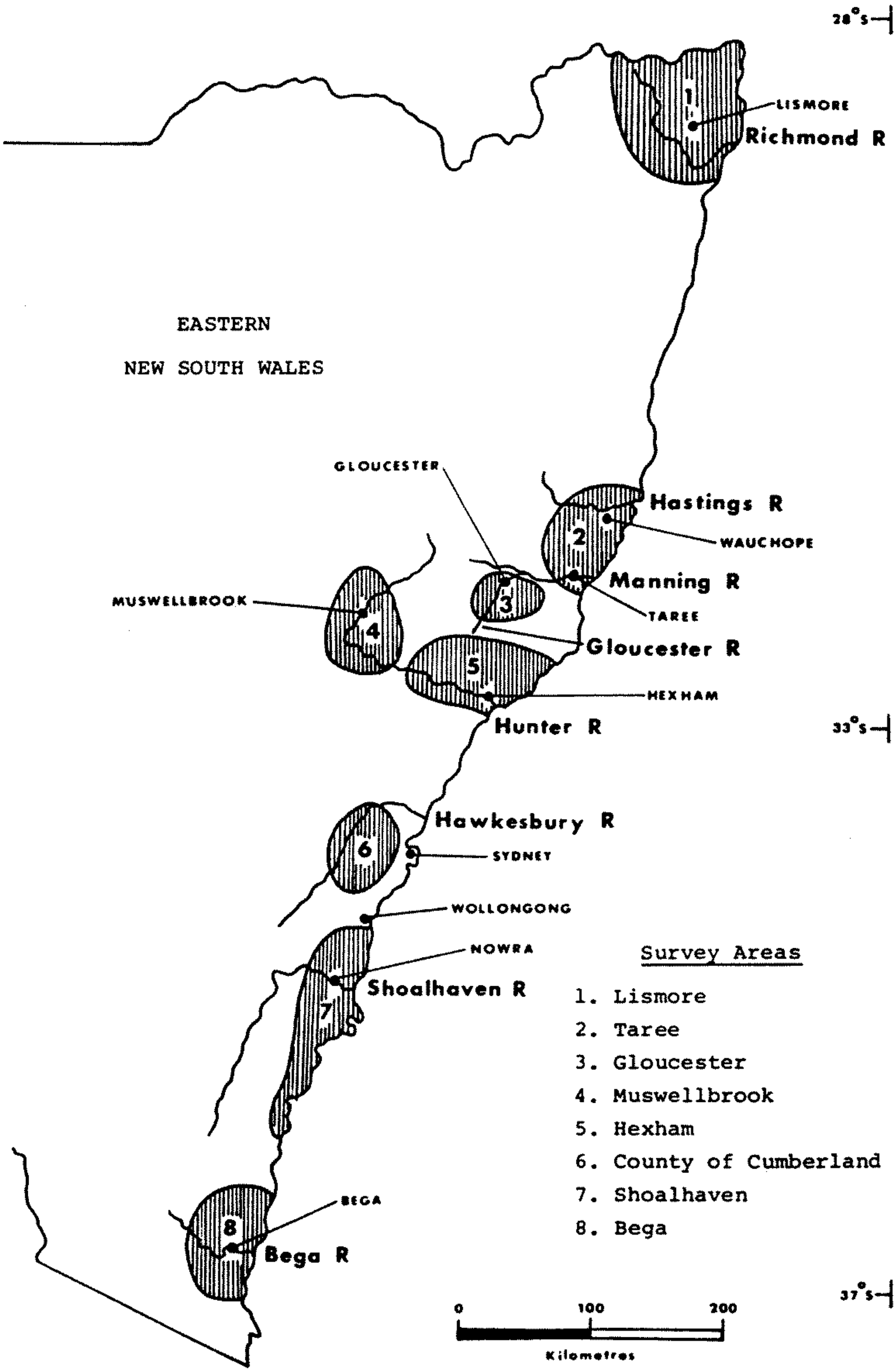


Figure 3.1 Areas sampled in the fireweed survey.

RESULTS AND DISCUSSION

A 56% response was obtained from the first mailing and this was increased to 74% after the second mailing. Rates greater than 60% were achieved for all regions with two as high as 87%. Both the large initial response and total response compare very favourably with that obtained in other agricultural mail surveys (Dillon and Jarrett 1964; Auld 1971), and would seem to indicate a successful technique and a real concern by farmers about this weed.

The total number of respondents was 581, of which 373 (64%) cited their main farm enterprise as dairying, 201 (35%) beef cattle, and 7 (1%) something other than these.

The possibility of non-response bias is the most important limitation in mail surveys of this type (Auld 1971). Freebairn (1967) showed that, in general, differences between respondents and non-respondents are attributable to chance alone if returns are relatively high. The large response rate obtained from this questionnaire therefore allows for confidence in its results.

Occurrence

Fireweed was present on 522 (90%) of respondents' properties and of those, 51, or less than 10%, considered it under control. The level of occurrence varied considerably between survey areas (see Table 3.1). All respondents in the Lismore, Taree, Gloucester and Hexham areas had fireweed. Infestations appeared heaviest in the last three while that in the County of Cumberland was similar to Lismore. A Chi^2 test between these five areas, however, showed that the differences in the level of occurrence were not significant at the 5% level. As yet fireweed does not occur in 'large amounts' in Bega or Muswellbrook and rarely in the Shoalhaven (see Table 3.1). The general level of occurrence was not significantly different between Muswellbrook and the Shoalhaven (P=0.05) but was much lower in Bega.

Specific seasonal conditions may have affected the amount of fireweed in one or more of the areas at the time of the survey, but it is unlikely that these would have biased the replies given. All

Table 3.1 Occurrence of fireweed. Figures as a percentage of total replies.

		Survey areas[A]							
Occurrence	Overall survey	Lismore	Taree	Gloucester	Muswell-brook	Hexham	County of Cumberland	Shoalhaven	Bega
Absent	10	-	-	-	29	-	4	14	65
Small amounts	30	29	18	24	56	21	35	43	25
Moderate amounts	40	46	48	59	9	50	42	20	2
Large amounts	11	10	17	15	-	19	13	4	-
Under control	9	15	17	2	6	10	6	19	8

Chi^2 (28 d.f.) = 214.1[B] (significant at $P<0.001$)

[A] Results for individual areas are for dairy farms only.
[B] Chi^2 based on numbers of respondents (not percentages) over all survey areas.

questions, unless specifically stated, were couched in terms of the average or normal situation.

Only three respondents, all from the Bega area, expressed difficulty in the recognition of fireweed. As mentioned in Chapter 2, S. madagascariensis can sometimes be confused with representatives of the similar native S. lautus complex. Because the latter occurs in isolated pockets and does not behave in a weedy manner, it was assumed that what farmers identified as fireweed was S. madagascariensis.

Spread

Of the respondents with fireweed, 29% observed its arrival on their properties within the last 5 years and 58% within the last 10 years (see Table 3.2). This suggests that the weed is spreading rapidly and the number of farms it infests in New South Wales has doubled since the mid 1970s.

Concerning its early spread, the results of Table 3.2 tend to confirm that from its original infestation in the Lower Hunter River Valley (in the Hexham survey area) fireweed was introduced to the far north coast in about 1940 (Green 1953) (see Chapter 2). The Gloucester River Valley has been the other major locality with a comparatively long history of fireweed. The weed appears to have been introduced to the Taree area in the 1960s. Fireweed has spread to the Shoalhaven and Bega areas primarily in the last 5 years and has become abundant in the County of Cumberland in the last 10 years. Muswellbrook has also had considerable spread in the last 5 years. The only areas not significantly different in the duration of fireweed presence ($P=0.05$) were the Shoalhaven and Bega.

Methods of spread were not studied in this survey but history of farm ownership and the presence of fireweed in hay or silage are potential causes of infestations.

Table 3.2 Duration of fireweed presence. Figures as a percentage of respondents with fireweed.

Duration present	Overall survey	Survey areas[A]							
		Lismore	Taree	Gloucester	Muswell-brook	Hexham	County of Cumberland	Shoalhaven	Bega
Less than 5 years	29	29	14	-	63	4	62	89	94
5 to 10 years	29	29	50	27	8	13	36	11	6
10 to 20 years	28	25	36	49	25	28	2	-	-
20 to 30 years	10	7	-	22	-	38	-	-	-
More than 30 years	4	10	-	2	4	17	-	-	-

Chi^2 (24 d.f.) = 232.4[B] (significant at $P<0.001$)

A Results for individual areas are for dairy farms only.
B Chi^2 based on numbers of respondents (not percentages) over all survey areas, except Bega.

Size of the Problem

In addition to knowing something of its prevalence and spread, farmers were asked for their opinion on the size of the fireweed problem. Table 3.3 shows the response.

The extent of the problem varied substantially between localities. Of particular note was the large number who considered it a 'major problem' in the Shoalhaven area where, for the most part, it occurs only in small amounts. Of special concern was the potential for infestations to increase in the area. Notably, fireweed was not thought a major problem by any respondents from the Muswellbrook area despite its occurrence there for up to 20 years. This may be significant in terms of the potential distribution of fireweed in Australia and the threat it poses, if any, to agriculture away from the coast (see Chapter 4). The size of the fireweed problem was perceived similarly in Muswellbrook and Bega (P=0.05).

A reasonably strong correlation existed between the occurrence of fireweed and how farmers perceived the problem, e.g. for a small occurrence of fireweed, 37% said it was no problem and 54% a minor problem; for a moderate occurrence 37% said minor and 50% moderate; and for a large occurrence, 46% said moderate and 51% a major problem. The perceived problem was only marginally significant among the Lismore, Taree, Gloucester, Hexham and the County of Cumberland areas (P=0.05). All of these had similar levels of infestation (see Table 3.1).

Fireweed was considered less of a problem on respondents' properties in the first few years following its arrival, and then substantially less after being present for 30 years or more, than it was in the intervening period. Perhaps after that time farmers simply learned to live with it or devised effective control measures suited to their particular conditions.

Why Fireweed is a Problem

The main reasons why fireweed was seen as a problem by farmers are listed in Table 3.4. Other reasons specifically added by two or

Table 3.3 Size of the fireweed problem as perceived by farmers. Figures as a percentage of respondents with fireweed.

		Survey areas[A]							
Size of problem	Overall survey	Lismore	Taree	Gloucester	Muswell-brook	Hexham	County of Cumberland	Shoalhaven	Bega
No problem	19	19	8	2	58	19	10	26	52
Minor problem	36	48	33	46	28	27	41	34	29
Moderate problem	33	19	41	43	14	48	37	19	5
Major problem	12	14	18	9	-	6	12	21	14

Chi^2 (18 d.f.) = 68.5[B] (significant at $P<0.001$)

[A] Results for individual areas are for dairy farms only.
[B] Chi^2 based on numbers of respondents (not percentages) over all survey areas, except Bega.

Table 3.4 Reasons why farmers consider fireweed a problem. Figures as a percentage of total replies.

Reasons why a problem	Overall survey	Survey areas[A]							
		Lismore	Taree	Gloucester	Muswell-brook	Hexham	County of Cumberland	Shoalhaven	Bega
Looks bad	45	57	63	67	19	52	52	31	4
Poisons stock	4	2	4	4	-	6	6	8	-
Causes poor growth of stock	4	7	10	4	-	2	4	2	-
Competes with crops or pasture	57	52	73	70	19	69	67	41	15
Prevents stock grazing amongst it	30	24	40	43	6	46	33	18	4
In crops or pasture used for hay or silage	24	12	40	30	17	29	46	43	4

[A] Results for individual areas are for dairy farms only.

more respondents were that it: removes moisture from the soil, is time consuming to control, has the ability to spread quickly, reduces stocking rates, has the potential for infestation to increase and to poison stock, and is impossible to eradicate.

Poisoning and poor growth of stock

Fireweed-infested pastures (see Plate 3.1) looked bad to 45% of farmers. More importantly, however, 4% of respondents believed the weed had been or was currently causing poisoning of stock, and another 4% considered that it contributed to poor growth of stock. This result is confirmed by the small but constant number of animals affected by fireweed poisoning coming into veterinary stations in coastal New South Wales (Walker, personal communication). Poor growth of stock was considered worst in the Taree area.

Presence in hay or silage

Notably, 24% of respondents found fireweed in pasture or crops used for hay or silage. Because cultivation more often than not stimulates germination of fireweed (see Plate 3.2) and provides a suitable seed bed for fireweed blown in from other areas, land used for fodder crops can easily become infested. The greater risk of livestock poisoning from contaminated feeds (see Chapter 2) may deter increased conservation of spring and summer pastures in areas such as the south coast of New South Wales (McLaughlin, personal communication).

Reduction in productivity

Further, 57% of respondents indicated that fireweed reduced crop or pasture productivity and 30% noted that the available grazing area was restricted. This result was not unexpected considering that I have observed densities ranging from 0 to over 5000 plants m^{-2}. Competition with crops or pastures and the associated reduction in their productivity was most significant around Taree, Gloucester, Hexham and in the County of Cumberland because of their heavy infestations.

Plate 3.1 Cattle grazing typical fireweed-infested pasture in late winter near Gloucester, New South Wales.

Plate 3.2 Stimulation of fireweed germination and growth (right) by pasture cultivation.

The abundance of fireweed varies greatly from season to season (Smith 1983; Launders 1985). Accordingly, farmers were asked to estimate the reduction in pasture or crop productivity both for 'normal' and 'bad' fireweed years. The result is shown in Table 3.5. While only 19% of respondents to this question felt that crop or pasture productivity was reduced by more than 10% in a 'normal' year, 41% believed such reductions occurred in a 'bad' fireweed year.

Situations Favouring Growth

No one situation on the farms favoured the growth of fireweed over others. Given the wide range mentioned by respondents, and that 31% said 'no particular situation' favours its growth, the conclusion that fireweed is an opportunistic weed with the ability to invade and colonise a great variety of habitats (Fernández and Verona 1984) is most appropriate. The situations in which it was predominantly found are listed in Table 3.6. Of the respondents who made additional comments to this question, 10 (24%) emphasised that drought or the breaking of it also favours the growth of fireweed. A similar observation was that fireweed is worst following a dry summer. As with other weeds (Michael 1968c) the absence of pasture cover (or presence of bare ground) in late summer-early autumn is a potent factor in the germination of fireweed and the development of heavy infestations (Launders 1985).

Worst Weed?

Of all respondents, 248 (43%) believed fireweed to be their worst weed. For Lismore the result was 36%, Taree 77%, Gloucester 54%, Muswellbrook 8%, Hexham 46%, County of Cumberland 48%, Shoalhaven 51% and Bega 6%. Lantana (Lantana camara L.), the second most important weed, was said to be worst by only 8% of respondents. Other weeds of considerable importance were blackberry (Rubus sp.), Crofton weed (Ageratina adenophora (Spengel) R.King & H.Robinson), spear thistle (Cirsium vulgare (Savi) Ten.), Paterson's curse (Echium plantagineum L.), Noogoora burr (Xanthium occidentale Bert.), spiny emex (Emex australis Steinh.), and bracken (Pteridium esculentum (Forst.f.) Cockayne). Thistles, tussocks and rushes were generally also given

Table 3.5 Reduction in pasture or crop productivity caused by fireweed in 'normal' and 'bad' fireweed years. Figures as a percentage of respondents with fireweed.

Reduction in productivity	'Normal' year	'Bad' year
None	37	26
0 - 10%	44	33
10 - 20%	15	28
20 - 50%	4	12
More than 50%	-	1

Table 3.6 Situations favouring the growth of fireweed.

Situations favouring growth	No. of respondents	Percentage[A]
Previously cultivated land	197	38
Previously burnt land	65	12
Native pasture	166	32
Improved/fertilised pasture	187	36
Heavily grazed pasture	178	34
Soil of low fertility	120	23
Soil of high fertility	83	16
Bare ground	130	24

[A] Of respondents with fireweed.

high ranking. For each area the four most commonly cited weeds, excluding fireweed, are listed in Table 3.7.

Although some bias towards ranking fireweed highly may occur in a survey specifically directed to fireweed, it was nevertheless considered the most important weed of pastures in all areas surveyed. The exceptions were Muswellbrook and Bega. The occurrence of problem weeds would of course vary between individual properties.

Comparison between Dairying and other Grazing Properties

The response rate from dairy farmers and other graziers in the Lismore, Taree, Gloucester, Muswellbrook and Hexham areas was similar, 75% and 69% respectively. The results showed that there was no appreciable difference in the occurrence of fireweed nor the magnitude of the problem as perceived by respondents between the two types of properties. Twice as many dairy farmers as other graziers, however, considered fireweed to be under control. This may well have resulted from the greater intensity of management and use of competitive pastures on their farms.

Fireweed was considered a problem by both groups of respondents for the same reasons, but its presence in pastures used for hay and silage production caused greater concern among dairy farmers than among other graziers (27% compared with 15% of all respondents respectively).

Of the situations said to encourage the growth of fireweed, native pastures and soils of low fertility were more common on dairy farms. The opposite situations such as improved and fertilised pastures and soils of high fertility, as well as cultivated land and heavily grazed pastures, were stressed by respondents more on other grazing properties. Thus, it appears that on intensively farmed dairies where vigorous pastures are often grown, less competitive native pastures and low fertility soils are more suitable for the growth of fireweed. On the more undulating and less intensive grazing properties which predominantly have native pastures, soil disturbance and an increase in fertility levels, with perhaps no significant increase in competition from pastures, causes fireweed to thrive.

Table 3.7 Main weeds other than fireweed, ranked in order of importance.

Grazing properties				
Lismore	Taree	Gloucester	Muswellbrook	Hexham
1. Crofton weed	1. Lantana	1. Lantana	1. Saffron thistle	1. Thistles
2. Lantana	2. Rushes	2. Blackberry	2. Bathurst burr	2. Spear thistle
3. Noogoora burr	3. Thistles	3. Crofton weed	3. Variegated thistle	3. Lantana
4. Thistles	4. Bracken	4. Bracken	4. Paterson's curse	4. Paterson's curse

Dairy farms				
Lismore	Taree	Gloucester	Muswellbrook	Hexham
1. Crofton weed	1. Thistles	1. Paterson's curse	1. Star thistle	1. Spiny emex
2. Noogoora burr	2. Lantana	2. Blackberry	2. Bathurst burr	2. Thistles
3. Ragweed	3. Rushes	3. Lantana	3. Spiny emex	3. Lantana
4. Lantana	4. Blackberry	4. Thistles	4. Variegated thistle	4. Paterson's curse
County of Cumberland	Shoalhaven	Bega		
1. Spear thistle	1. Blackberry	1. Blackberry		
2. Thistles	2. Thistles	2. Paterson's curse		
3. Paterson's curse	3. Tussocks	3. Tussocks		
4. Dock	4. Lantana	4. Thistles		

The claim that 'fireweed grows in the hills' was made by a number of respondents, almost exclusively dairy farmers. An observation which helps clarify the conditions for growth is: 'On more fertile flats of our farm the individual fireweed plants grow into strong robust plants but the pest is much more prolific in the areas of low fertility soils and natural pastures'.

Control

Over 80% of respondents with fireweed attempt one or more forms of control, the lowest proportion being in the Muswellbrook area (73%) and the highest in the Shoalhaven (100%). Dairy farmers undertake control more than other graziers. In terms of number of respondents and the amount of time and money spent, control was found to intensify as the occurrence of fireweed and the perceived problem increased. Farmers who had experienced poisoning or poor growth of their stock also placed greater emphasis on control strategies. The techniques used in control, their frequency, and the relative success of each are given in Table 3.8.

Hand weeding

The success achieved by hand weeding was variable with a somewhat equal number of respondents indicating high, moderate and low levels. This is despite its being the most frequently used form of control. One respondent who was able to keep fireweed within manageable proportions indicated the need to allocate up to 20% of labour time for this purpose. Swarbrick (1980) states that manual weed control is probably the most time-consuming job on the farm. As a consequence, it has largely disappeared in Australia. Nevertheless, in the coastal regions of New South Wales, hand weeding is still widely practised and plays a significant role in fireweed control.

Hand weeding was attempted more by respondents who either had a small amount of fireweed on their land or who perceived it as a major problem. Understandably it was most successful with the former. It was very common in areas such as Muswellbrook, Shoalhaven and Bega and considerably less so at Hexham and Gloucester. Notably, the method was more effective on dairy farms. If the earlier comment

Table 3.8 Use and success of fireweed control methods.

Control method	Level of use		Level of success[B]								
	Overall survey		Overall survey			Dairy farmers[C]			Other graziers[C]		
	No. of respondents	Percentage[A]	Low	Mod.	High	Low	Mod.	High	Low	Mod.	High
Hand weeding	309	74	37	29	34	36	25	39	56	29	15
Slashing	287	68	41	46	13	36	47	17	48	44	8
Cultivation	79	19	33	54	13	32	53	15	42	50	8
Herbicides	49	12	22	37	41	13	27	60	22	57	21
Grazing with sheep or goats	19	5	11	22	67	25	50	25	7	14	79
Promoting competitive pasture	147	35	21	37	42	13	40	47	26	45	29

[A] Of respondents who attempt control.
[B] Figures as a percentage of respondents who attempt control by that method.
[C] Results are for survey areas 1 to 5 only.

that fireweed plants are larger but fewer on fertile river flats is generally correct, then this may partly explain why it is easier on dairy farms to pull fireweed by hand. Of those who consider fireweed under control, 80% use this as one of their methods.

Slashing and cultivation

Although slashing to control fireweed is more common than cultivation, neither was thought by many respondents to be highly successful. Moderate success was achieved using either method, with dairy farms recording better results than other grazing properties. One advantage of slashing could be that access of livestock to pasture growing beneath fireweed is improved. While slashing was utilised on 45% of properties where fireweed was said to be controlled, only 10% practised cultivation.

Herbicides

Herbicides were assessed as giving good control, again with most success on dairy farms, but they are not applied very extensively and predominantly only when the problem is seen as major. Their most frequent use is in the Lismore, Muswellbrook, County of Cumberland and Shoalhaven regions. Only 16% of respondents who had fireweed under control used herbicides.

Grazing sheep or goats

Grazing with sheep or goats produced very good results but only a small proportion of graziers in the Lismore, Taree and Hexham areas have utilised their potential. Their use primarily away from dairy farms reflects the type of management they require (Watson et al. 1984). One respondent who tried using goats found that, 'controlling the goats was as difficult as the fireweed'. Tukidale sheep were suggested as being very effective under coastal conditions.

Competitive pastures

Competitive pastures were considered to be as effective in control as herbicides, and they are used more widely. This result is encouraging since competitive pastures offer long term control. The other methods already discussed, if used singly, offer only a short term solution. Herbicides nevertheless have a place as aids in pasture establishment and maintenance.

Farmers, particularly in the Gloucester and Hexham areas, endeavoured to promote competitive pastures as fireweed became abundant and as their awareness of the problem increased. Of those who consider fireweed under control, 35% employ this method.

The higher success achieved with slashing, herbicides and competitive pastures on dairy farms can be linked primarily to the better soil and environmental conditions. These allow for greater competition against fireweed from the pasture species after application of the control strategy.

It has been reckoned (see Chapters 1 and 2) that the best weapons against pasture weeds are often the pasture species themselves as components of a vigorous competitive pasture. Different species or cultivars appropriately managed may fulfil this purpose in different areas. Respondents were asked to indicate from their experience which pastures appeared to control fireweed.

Pasture Species for Control

Pasture species able to control fireweed in the different survey areas are shown in Table 3.9. Kikuyu (Pennisetum clandestinum Chiov.) was found by 60% of respondents with fireweed to be the best species, followed by ryegrass (Lolium sp.) 17% and white clover (Trifolium repens l.) 14%. However a number of pasture species were each found by a considerable group of farmers to be useful in control. The relative importance of these varied between areas and situations, for example phalaris (Phalaris aquatica L.) was effective in the County of Cumberland and Rhodes grass (Chloris gayana Kunth) on grazing properties.

Table 3.9 Pasture species found to best control fireweed. Figures as a percentage of respondents with fireweed.

Pastures controlling fireweed	Overall survey	Survey areas[A]							
		Lismore	Taree	Gloucester	Muswell-brook	Hexham	County of Cumberland	Shoalhaven	Bega
None	25	37	23	2	50	2	18	43	53
Phalaris	3	-	2	2	-	2	10	-	-
Ryegrass	17	20	29	37	4	19	26	18	-
White clover	14	10	19	24	-	27	26	14	-
Subterranean clover	8	-	6	17	-	21	22	5	-
Kikuyu	60	59	65	91	21	77	54	39	18
Paspalum	11	12	10	15	4	10	16	2	-
Rhodes grass	3	-	4	-	-	2	-	-	-
Setaria	3	15	4	-	-	-	-	-	-

[A] Results for individual areas are for dairy farms only.

Farmers in Gloucester and Hexham have experienced the growth of fireweed on their properties for many years (see Table 3.2). Notably, almost all now affirm that one or more pasture species offer effective control. A high percentage of respondents in the Muswellbrook, Shoalhaven and Bega areas, all relatively new areas of infestation, suggested that no pasture controls fireweed. Hence it appears that pastures which are better able to compete with fireweed in a particular area are identified over time.

Economics of Control

Farmers attempting fireweed control spend an estimated average of 56 hours and $152 per year, ranging from 16 hours and $34 at Muswellbrook to 84 hours and $187 per year at Taree. This is equivalent to an average of 40 hours and $110 over all respondents. For the dairy industry alone in New South Wales, a conservative estimate of some 100,000 man hours and $250,000 are being spent annually on fireweed control.

Those farmers grazing sheep or goats spent the least time on control followed by hand weeding. The other methods involved more or less the same time. Herbicides and promotion of competitive pastures were the most costly techniques, followed by slashing and cultivation and then hand weeding. Grazing with sheep and goats was least expensive.

All respondents who originally considered fireweed to be under control had to work to achieve that situation with some 30% spending over 100 man hours and 56% over $200 per year. These amounts of time and money would seem inexpensive if acceptable levels of fireweed control can be achieved.

General Comments from Respondents

Many of the 288 respondents (50%) who made additional comments at the end of the questionnaire expressed concern at the increasing threat posed to them by fireweed, even though some as yet have only a few plants on their properties. A smaller number believed that it was not a problem. One respondent mentioned its potential use for honey production, but its usefulness for this purpose must be in doubt. Bees which feed on S. jacobaea produce honey contaminated with pyrrolizidine alkaloids (Deinzer et al. 1977) and the nectar of other Senecio species is also likely to contain alkaloids (Hartmann and Zimmer 1986).

Public land and neighbours properties where fireweed is allowed to grow with no attempt at restraint were often cited as factors preventing successful control on a particular individual's farm. These places effectively act as seed banks for reinfestation.

Of foremost concern in the minds of many farmers was the large amount of time required to control fireweed and the overall difficulty encountered in such an endeavour. It is primarily for this reason that legal requirements for the control of fireweed have now been discontinued in New South Wales (Anon. 1983). While some respondents suggested biological methods of control were required, others encouraged further research on the weed.

CONCLUSIONS

Having had to cope with fireweed since its introduction to Australia some 70 years ago, dairy farmers and graziers were able in this survey to provide valuable insights to its impact on agriculture and its control. They believe it to be the major weed of improved and unimproved pastures in many areas of coastal New South Wales. Not only does it reduce pasture productivity and the available grazing area, but can cause poisoning and poor growth of stock when grazed or ingested in contaminated hay and silage. Moreover, fireweed continues to spread rapidly and would not yet seem to have reached its full potential in Australia. The survey provided some helpful information concerning the imposed cost of fireweed to the farming community with some hundreds of thousands of man hours and dollars being spent on control annually. Because farmers were unable to give precise enough data on the reductions of pasture productivity caused by fireweed, experiments designed to determine such losses need to be undertaken. Relating the significance of this weed to other well known weeds was a useful comparison, and served to highlight the relative importance of each in the areas surveyed.

It is apparent that soil fertility alone is not the all embracing answer to the fireweed problem, but that the solution must involve other factors also. Further work is required to elucidate this relationship. Respondents seemed alive to the limited usefulness of herbicides, and while the value of competitive pastures has already been expressed (see Chapters 1 and 2), the results of the survey give confidence in pursuing this line of investigation, particularly in areas where fireweed has moved most recently.

Chapter 4

THE POTENTIAL SPREAD AND DISTRIBUTION OF FIREWEED IN AUSTRALIA

'After introduction, an alien weed may spread widely or very little.' (Forcella and Harvey 1983)

INTRODUCTION

Any statement regarding the environmental impact of a weed will, of necessity, include an assessment of further spread and potential distribution. Although fireweed is still expanding its area of occupation in Australia, and is a problem for agricultural enterprises (see Chapter 3), no estimate is currently available of the extent of the areas which are at risk.

Whether newly introduced or naturalised for some time, it is of considerable practical significance to be able to predict the potential distribution of a weed which continues to spread (Quinlivan 1972; Amor and Twentyman 1974; Moore 1971; 1975). If potentially suitable regions can be delineated, then efforts to prevent their infestation may be made (Medd and Smith 1978).

The success of any plant species in a new environment is determined largely by its range of adaptation to climate. If the response of the species to climatic factors is known, it should then be possible to predict the potential area of distribution (Medd and Smith 1978). That response in turn depends on the interaction of other environmental factors with climate, the physiological adaptations of the species and competition from other species present (Nix and Austin 1973).

Panetta and Dodd (1987) identified predictive distribution data for three weeds in Australia in addition to their own. Quinlivan (1972) defined the potential distribution of Cape tulip (*Homeria* spp.) in Western Australia on the basis of average dates of opening and closing of the growing season. From a study of gas exchange characteristics, Doley (1977) predicted the occurrence of parthenium weed (Parthenium hysterophorus L.) in the humid and sub-humid regions of Australia. This was subsequently confirmed by Williams and Groves (1980) on the basis of germination, growth and flowering responses to temperature and photoperiod. Medd and Smith (1978) modelled the growth, development and seed yield of nodding thistle (Carduus nutans L.) and using climatic data for radiation, temperature, rainfall and evaporation, were able to predict areas of potential adaptation.

More recently, Panetta and Dodd (1987) used a computerised system to predict the conceivable distribution of skeleton weed (Chondrilla juncea L.) in Western Australia. The system they used identifies areas within Australia with a similar climate ('homoclime' - Russell and Moore 1970) to those already occupied by a species.

The method adopted by Panetta and Dodd (1987) has much in common with that of Medd and Smith (1978), and was the approach utilised in the present study to evaluate the macroclimatic environment of fireweed. The aim of this study was to determine whether the geographical limits of distribution have been reached in Australia, and if not, what those limits might be.

MATERIALS AND METHODS

In order to obtain an approximation of the potential distribution of fireweed in Australia the Bioclimate Prediction System 'BIOCLIM' was used (Busby 1986 a,b). This system developed by J.R. Busby of the Bureau of Flora and Fauna in collaboration with H.A. Nix of the Division of Water and Land Resources, C.S.I.R.O., was accessed through 'CSIRONET' - the C.S.I.R.O. computing network.

BIOCLIM evaluates geographical distribution data pertaining to individual biological entities, whether they be single species or groups of species, and produces entity-specific climate profiles. These profiles can then be used to indicate geographic regions where the climate is apparently suitable for that entity (Busby 1986a). It is a general purpose system, not intended to isolate climatic parameters that might be of particular significance to the organism(s) of interest (Panetta and Dodd 1987). An agglomerative multivariate approach to climate profile classification such as this (Russell and Moore 1970; 1976) is useful, since climate involves a large number of processes, and plants may be considered biochemical integrators of their environment (Geiger 1951). The geographical distribution data entered into the system consist of latitude and longitude coordinates and elevation for each locality at which the entity has been recorded.

Data Collection

In total, 137 localities covering the known range of fireweed in Australia were used for predicting the potential distribution of the species (see Appendix 7). These consisted of two groups. The first of 120 (numbered 1 to 120) were either in or near well defined fireweed areas, and supported some degree of infestation greater than single, isolated plants. The infestations or lone plants comprising the additional 17 locations (numbered 121 to 137) were outside the common range and at the moment may best be regarded as outliers. Their aggressiveness (Salisbury 1961) and colonising ability have not been determined.

Records of fireweed presence at each site were mainly as herbarium specimens held at the Queensland Herbarium - Brisbane, the National Herbarium - Royal Botanic Gardens Sydney and the School of Crop Sciences Herbarium - University of Sydney. Fewer site records were of personal observations made on various field trips and results extracted from the farmer survey of Chapter 3. In the latter case, only where two or more respondents in a specific area indicated the presence of fireweed or where it was said to occur in 'moderate' or 'large' amounts, was the locality considered sufficiently reliable to use.

Latitude and longitude data were obtained from the Australia 1:250 000 Map Series Gazetteer (Anon. 1975), and elevations read from Australia 1:100 000 topographic survey maps complemented by Bureau of Meteorology station information (Anon. 1977b).

Operation of BIOCLIM

Climate profiles generated for fireweed were based upon 16 selected moisture and temperature parameters, indicative of annual, seasonal and extreme components of the specie's climatic environment. For each parameter, the values from all the sites were ranked into numerical order and the minimum, 5 percentile, 95 percentile and maximum values determined. These collectively constituted the climate profile for fireweed (see Table 4.1).

The 137 site specific climate estimates were derived as functions of latitude, longitude and elevation from continent-wide surfaces of monthly mean minimum and maximum temperatures, and 19 regional surfaces for monthly precipitation using an algorithm described by Wahba and Wendelberger (1980). The surfaces had previously been derived by Laplacian smoothing spline functions fitted to data obtained from the Bureau of Meteorology (Busby 1986a).

The apparent climatic suitability for fireweed of various geographic regions was then assessed by comparing the climatic estimates for each of 2795 points on a 0.5 degree grid of Australia with profiles generated for the species. The latter profiles were generated firstly on the basis of the established localities and secondly combined with the outliers.

If values for all 16 parameters at the grid point fell between the 5 and 95% values (the 90 percentile range) of the climate profile, then the point was considered to possess a climate suitable for the species. If values for one or more of the parameters fell outside the 90 percentile range, but were within the total range, the climate was considered to be marginal. If values for any parameter fell outside the total range, the climate at the grid point was considered to be unsuitable. These criteria for the designation of suitable areas have been determined largely through experience with other species (Busby 1986a).

Table 4.1 Climate profile for fireweed based on 120 established localities alone, and with 17 outliers. All temperatures are in °C and precipitation in mm.

Climate parameter	Established localities				Plus outliers			
		Percentile				Percentile		
	Min.	5	95	Max.	Min.	5	95	Max.
1 Annual mean temp.	12.3	14.3	19.9	20.1	11.1	12.5	19.7	20.1
2 Mean min. cool. mth.	-0.4	1.1	7.8	8.6	-1.3	-0.2	7.4	8.6
3 Mean max. warm. mth.	23.7	24.9	30.3	31.0	22.6	24.8	30.7	33.1
4 Annual temp. range	17.8	18.2	26.2	27.3	17.8	18.2	28.7	32.2
5 Mean temp. cool. qtr.	6.3	8.7	15.0	15.3	5.3	6.3	14.8	15.3
6 Mean temp. warm. qtr.	18.1	19.1	24.2	24.5	16.5	18.5	24.2	25.4
7 Mean temp. wet. qtr.	13.0	15.8	24.1	24.5	7.1	14.9	24.1	25.4
8 Mean temp. dry. qtr.	7.2	9.6	17.3	17.7	6.9	8.1	17.4	22.8
9 Annual mean precip.	614	681	1668	2397	536	615	1663	2397
10 Precip. wet. mth.	74	81	230	418	54	68	226	418
11 Precip. dry. mth.	32	34	72	82	31	34	71	82
12 C.var. mth. precip.	15.0	18.8	49.7	60.1	9.3	13.9	49.0	60.1
13 Precip. wet. qtr.	206	230	638	1155	151	191	635	1155
14 Precip. dry. qtr.	112	119	250	272	108	116	245	272
15 Precip. cool. qtr.	129	130	327	371	114	129	323	371
16 Precip. warm. qtr.	206	228	561	1030	116	179	550	1030

RESULTS

Predicted Distribution

Analysis of the 0.5 degree Australia wide grid by BIOCLIM showed that climates falling within the climate profile of fireweed did not occur anywhere outside the south-eastern region of Australia (see Figures 4.1 and 4.2).

Based on established localities

The predicted distribution of fireweed based on its present established range is shown in Figure 4.1. Areas containing suitable climates closely predicted the actual distribution. Regions north or south of the present range of the weed were not identified as areas of potential invasion. This result was not unexpected considering that these areas generally offer greater extremes of climate.

Parts of south-eastern Queensland were assessed as marginally suitable for fireweed. This assessment was based, not on the most northern recording of fireweed near Amamoor (see Figure 4.1) as might have been expected, but on more southern localities which had greater extremes of climate, including rainfall. This information was obtained from synthetic climate estimates of each of the 16 parameters generated by BIOCLIM for each locality. Areas in the far north of New South Wales around Tenterfield and across the border in Queensland around Stanthorpe were also predicted to be suitable. Tableland areas to the south of these towns were marginal. All other areas of potential occurrence were restricted to the coastal strip of New South Wales.

The Coffs Harbour, Bellingen and Nambucca shires on the north coast of New South Wales, identified by Watson et al. (1984) to be free of fireweed, are not climatically distinct enough to prevent fireweed invasion (see Figure 4.1). It is probable that the spread of fireweed into these areas has simply been delayed. Thus on one field trip in 1987 I did locate fireweed in these shires though only in very small numbers.

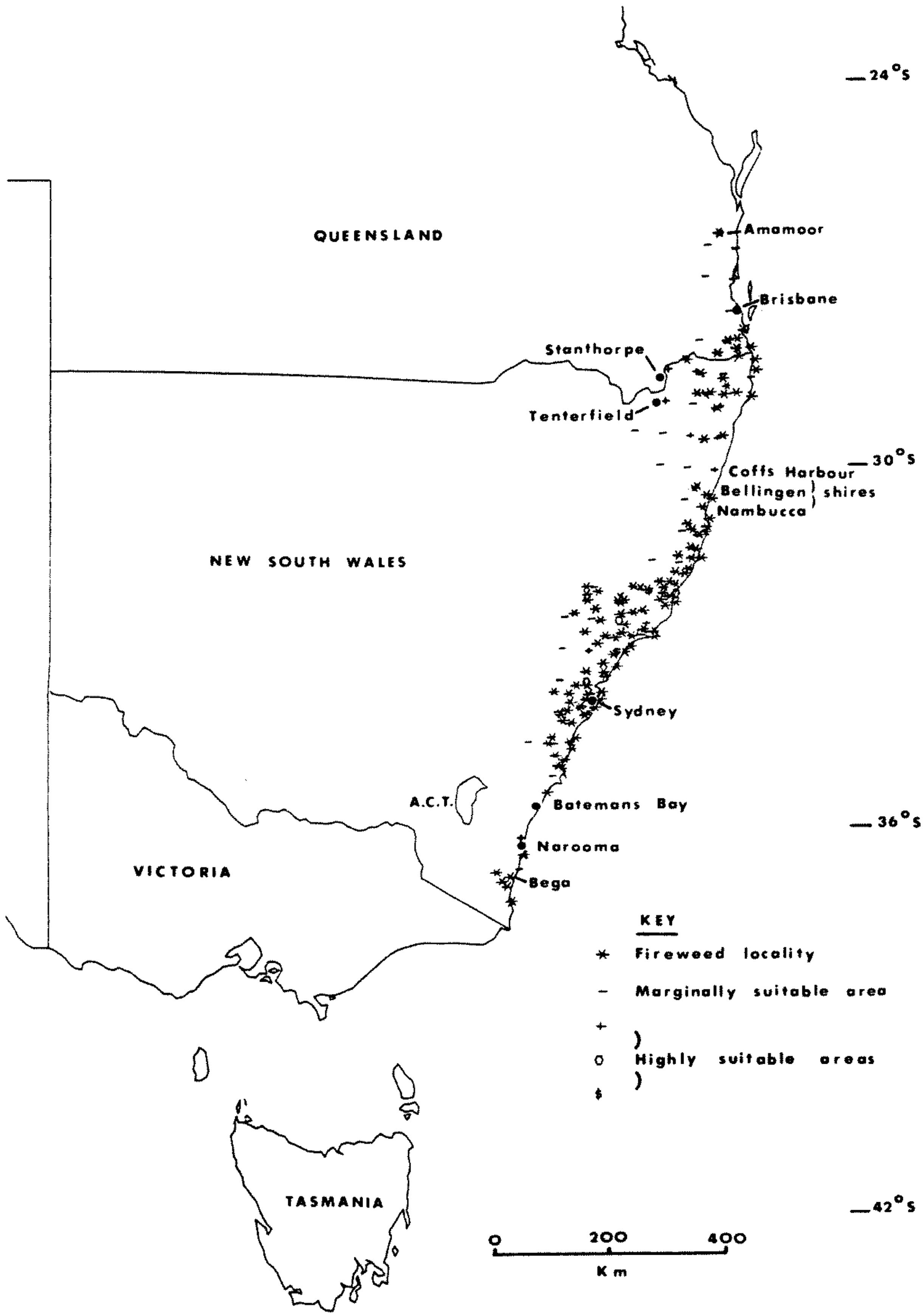


Figure 4.1 Predicted potential distribution of fireweed in Australia using BIOCLIM based on 120 established localities.

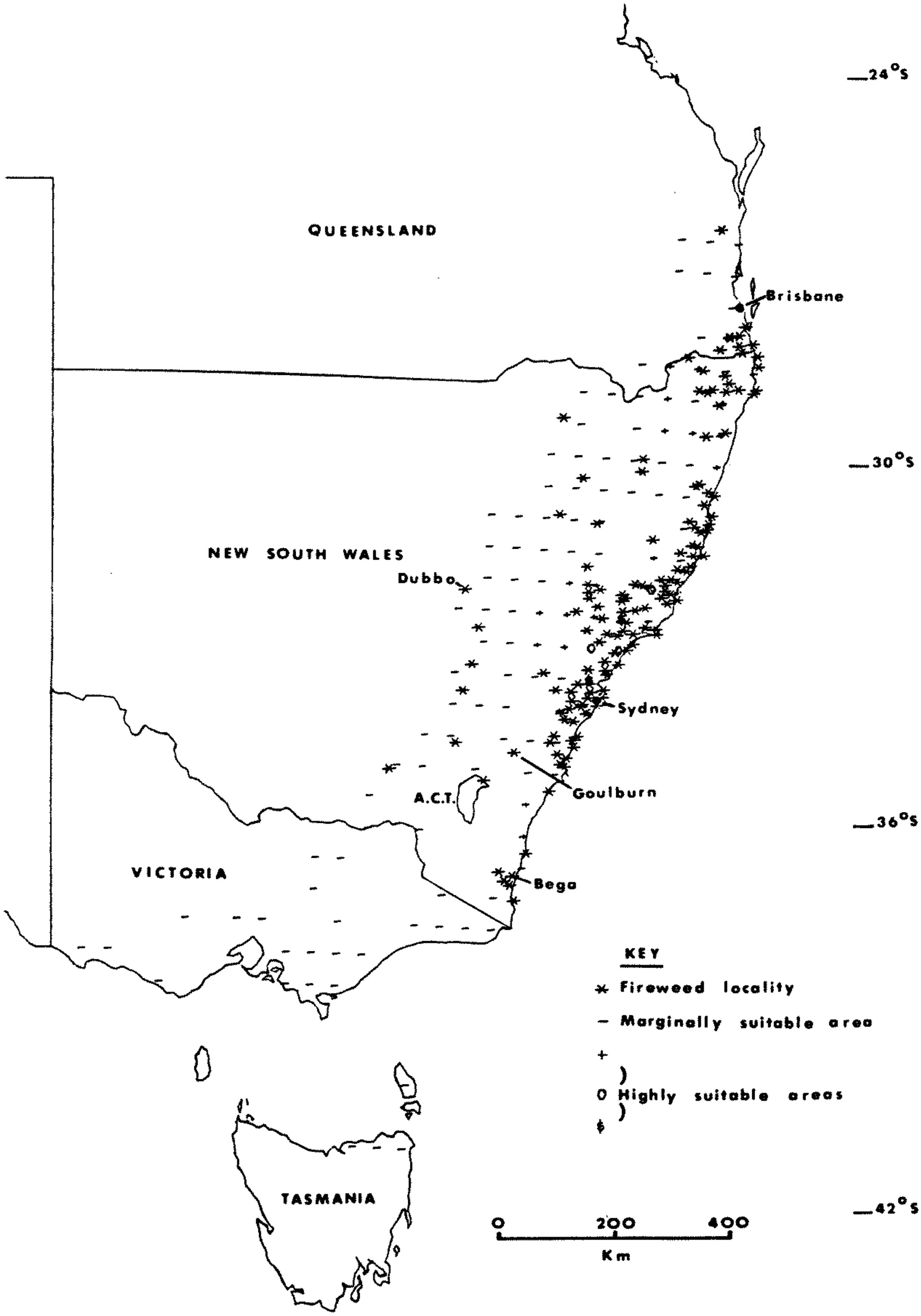


Figure 4.2 Predicted potential distribution of fireweed in Australia using BIOCLIM based on 120 established and 17 outlying localities.

The apparent gap in the potential distribution of fireweed on the south coast of New South Wales from about Batemans Bay to Narooma arose from the plotting procedure. The nearest point on the 0.5 degree grid of Australia is slightly inland at that latitude (see Figure 4.2), and because the coastal plain there is very narrow, the point is at a comparatively high altitude on the Great Dividing Range. The colder climate at that site did not fall within the climate profile of fireweed and hence was not plotted. It is likely therefore that distribution will extend along the confines of the narrow coastal strip, though much of the area is native forest and not conducive to fireweed invasion.

Based on established localities and outliers

Not unexpectedly, when the 17 outlying sites from the highlands and western slopes and plains of New South Wales were included in the production of the climate profile of fireweed, a much greater potential distribution was predicted (see Figure 4.2). Owing to the relatively small number of outliers, most of the new areas, which stretched down through central and eastern Victoria into southern Victoria and north-eastern Tasmania, were only marginally suitable.

The data suggest that outliers will continue to be found in these more western and southern regions, possibly in localised niches, but that their invasive potential will be small. The only outlier which at present shows appreciable colonising ability is that of the Dubbo infestation. This special case is considered in more detail in the discussion.

Climate Profile

The most conservative estimate of the climate profile of fireweed was the 90 percentile range of data generated from the established localities alone (see Table 4.1). Annual mean precipitation of that profile ranged from 681 to 1668 mm and annual mean temperature from 14.3 to 19.9°C.

For most parameters in that profile the maximum and minimum values did not vary greatly from the 95 and 5 percentile values respectively. The exceptions were the maximum values of annual precipitation, precipitation of the wettest month, precipitation of the wettest quarter, and precipitation of the warmest quarter. These were all much larger than the 95 percentile values and reflected the inclusion in the profile construction of the most northerly sub-tropical localities, which had a predominance of summer rainfall.

In comparison with the climate profile generated from established localities alone, the climate profile based on established localities plus outliers was colder in the wettest quarter, hotter in the driest quarter and had lower rainfall, particularly in the warmest quarter. These features are those expected away from the coast and west of the Great Dividing Range where most of the outliers were recorded.

Fireweed from Outlying Locations

A number of plants from outlying locations have shown somewhat unusual variations in morphology and size when compared with fireweed plants commonly found on the coast. Some plants, although very similar to fireweed in most characteristics, were much woodier and had more profuse branching.

Among these, plants collected on the border of the Australian Capital Territory (see Figure 4.2) have tentatively been fitted to the southern African species, Senecio inaequidens D.C., but confirmation is still required. Hilliard (1977) observed that S. inaequidens is often confused with S. madagascariensis in southern Africa, but that in Natal at least S. inaequidens does not occur below about 1400 m altitude. It therefore scarcely overlaps with the area of S. madagascariensis. The locations of some of the outliers of fireweed in this study suggest that they may be growing under similar climatic conditions as S. inaequidens in southern Africa.

Limitations of BIOCLIM

Panetta and Dodd (1987) suggested several limitations to the use of BIOCLIM which detract in varying degrees from its usefulness as a method to predict suitable areas for weed species. Perhaps the most important is its inability to predict local variations in relative degrees of infestation within the overall area deemed to be suitable. But until detailed measurements of fireweed performance are made at various sites under different climatic regimes, the results from this approach should prove to be useful.

DISCUSSION

The coastal fringe of south-eastern Australia represents an ideal invasion site for many introduced species (Swincer 1986), not the least of which is _S. madagascariensis_. It has a relatively mild climate with no temperature extremes and has been disturbed considerably by European settlement. While climatically suitable areas for fireweed colonisation, and those of a more marginal nature, have been delineated from its current distribution using BIOCLIM, other factors influencing possible spread and potential distribution in Australia require consideration.

The Natural Spread of Fireweed

In Chapter 2, it was concluded that only a very small proportion of fireweed seed could be blown long distances. In coastal New South Wales, which includes the site of entry for fireweed in Australia, the prevailing winds vary direction considerably as seasonal changes occur in the movement of high and low air pressure systems (Kelleher 1980; Sutherland 1980). Northerly movement of fireweed may be particularly encouraged by strong onshore south-east trade winds. On a continental scale the prevailing winds are predominantly from west to east (Swincer 1986). Although no land barrier exists to movement north and south, the eastern highlands (Great Dividing Range) on the western side of the coastal plains are likely to impede the spread of fireweed inland by wind.

Human Activity

Biogeographic barriers to the natural movement of weed species, however, are becoming less effective owing to increased human activity (Groves 1986), particularly transport. Hence the fireweed infestation at the Western Plains Zoo, Dubbo, west of the Great Dividing Range (see Figure 4.2), was caused by contaminated feed being brought in from coastal areas. The increasing translocation of various weeds by human beings suggests that the ability to disperse great distances by natural means is becoming less important (Newsome and Noble 1986).

Ornamental plants grown in home gardens have sometimes caused foci from which plants have been able to move into previously uncolonised areas (Michael 1981). The location and nature of the Goulburn infestation of fireweed (see Figure 4.2) suggests that it may have resulted from this type of introduction. This inference is strengthened by the observance, on at least one occasion, of fireweed being sold as an ornamental over the nursery counter (Michael, personal communication).

Distinct Environmental Niches

Although a weed species may be present in a given area or climate, it may occur only in certain climatically-distinct environmental niches (Burt and Reid 1976). At Dubbo, a much drier area than coastal New South Wales, fireweed is thriving around water holes and in irrigated areas primarily in the confines of the zoo. For this reason the permanency or aggressiveness of the 17 outlying infestations which were identified in the current study, should be viewed with caution. Quinlivan (1972) considered small isolated pockets of Cape tulip, beyond the predicted climatic boundaries, of little consequence as they were unlikely to spread or persist.

Effect of Frost

BIOCLIM analyses a wide range of moisture and temperature parameters, including minimum temperature of the coolest month and mean temperature of the coolest quarter. As such, it includes measures which are closely related to the incidence of frost, which, in terms of crops at least, imposes a major constraint on production in Australia (Kelleher 1980). In Chapter 6, the effect of frost on fireweed is assessed. The results of that preliminary experiment indicate that young fireweed seedlings are sensitive to frost but that to some extent the weed may be able to be 'hardened' to withstand its effects. While frost alone is unlikely to be the prime determinant of fireweed spread and distribution, the weed is noticeably distributed in areas with low frost incidence (see Figure 6.5). In the cooler highland areas of Australia (particularly along the Great Dividing Range) frost is likely to contribute to seedling mortality and reduced plant vigour.

The central highlands of Tasmania and the southern alps of New South Wales and Victoria were predicted by Medd and Smith (1978) as being unsuitable for *Carduus nutans* because of the occurrence of frost during flowering. In both regions frost occurring in summer would prevent seed formation. The effect of frost on fireweed which is flowering (usually in autumn and spring) is not known.

Similar Climatic Regions

Plants which have successfully invaded Australia come primarily from areas of similar climate (Swincer 1986). Hence some idea of the potential of fireweed to spread further may be gained by comparing the current southern African and Argentine climatic distributions with that of Australia. Michael (1970) observed that weeds originating from the Cape Province of South Africa, for example *Oxalis pes-caprae* L., *Arctotheca calendula* and *Homeria* spp., occupy essentially similar climatic zones in Australia and South Africa. Likewise, *Chrysanthemoides monilifera* (L.) Norlindh ssp. *monilifera* and ssp. *rotundata* (DC.) Norlindh, from the south-western Cape Province and the south-eastern coastal areas of South Africa respectively, are found in corresponding climatic zones (Michael 1981; Groves 1986).

Fireweed is distributed in similar latitudes on the eastern seaboard of the three continents of the Southern Hemisphere (see Figure 4.3). Annual precipitation, the most significant bioclimatic factor on a continental scale (Nix and Austin 1973), ranges in these areas mainly from 500 to 1000 mm and in some places reaches 1500 mm. These figures correspond well with those generated using BIOCLIM. However, in the south west of Madagascar, where fireweed grows, annual precipitation can be as low as 370 mm (Donque 1972). Following Köppen's classification, the Argentine and Australian infestations of fireweed are wholly in areas of Mesothermal climate with no distinct dry season (Cf). The climate in the natural range of the weed in southern Africa is slightly more diverse. Predominantly of Cf classification, it also includes the Cw (Mesothermal climate with a dry winter) and Aw (Tropical savanna) classifications (Van Royen 1954). The Kenyan and Colombian fireweed infestations too are in areas of Cw classification.

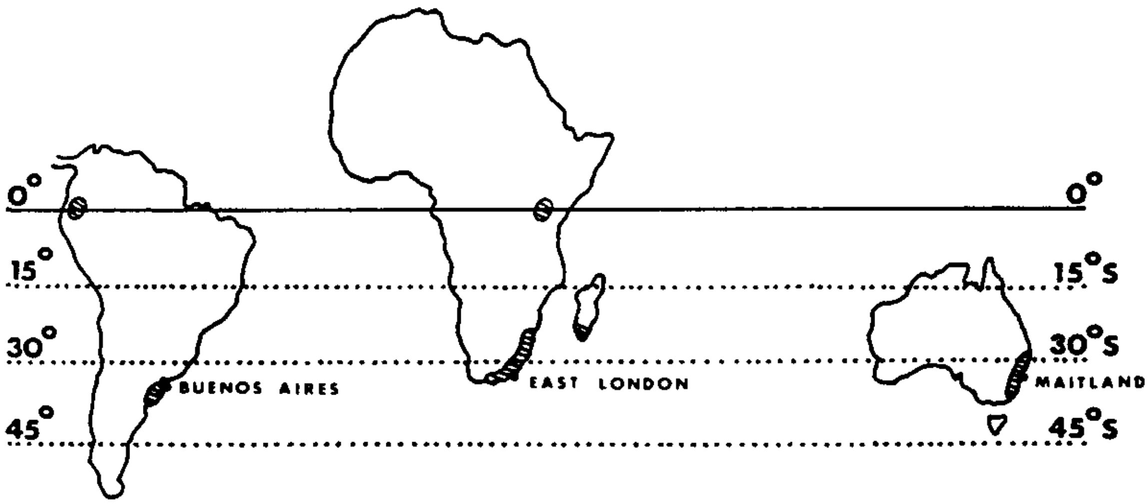


Figure 4.3 World distribution of <u>Senecio madagascariensis</u>. Climatic data for Buenos Aires, East London and Maitland (shown) are given in Figure 4.4 a,b.

The similarity of climate in fireweed areas in each continent is illustrated by graphing precipitation and temperature data for three selected localities of like latitude and elevation (see Figure 4.4 a,b).

In this chapter BIOCLIM was used to predict further spread of fireweed in Australia based on its current distribution. In order

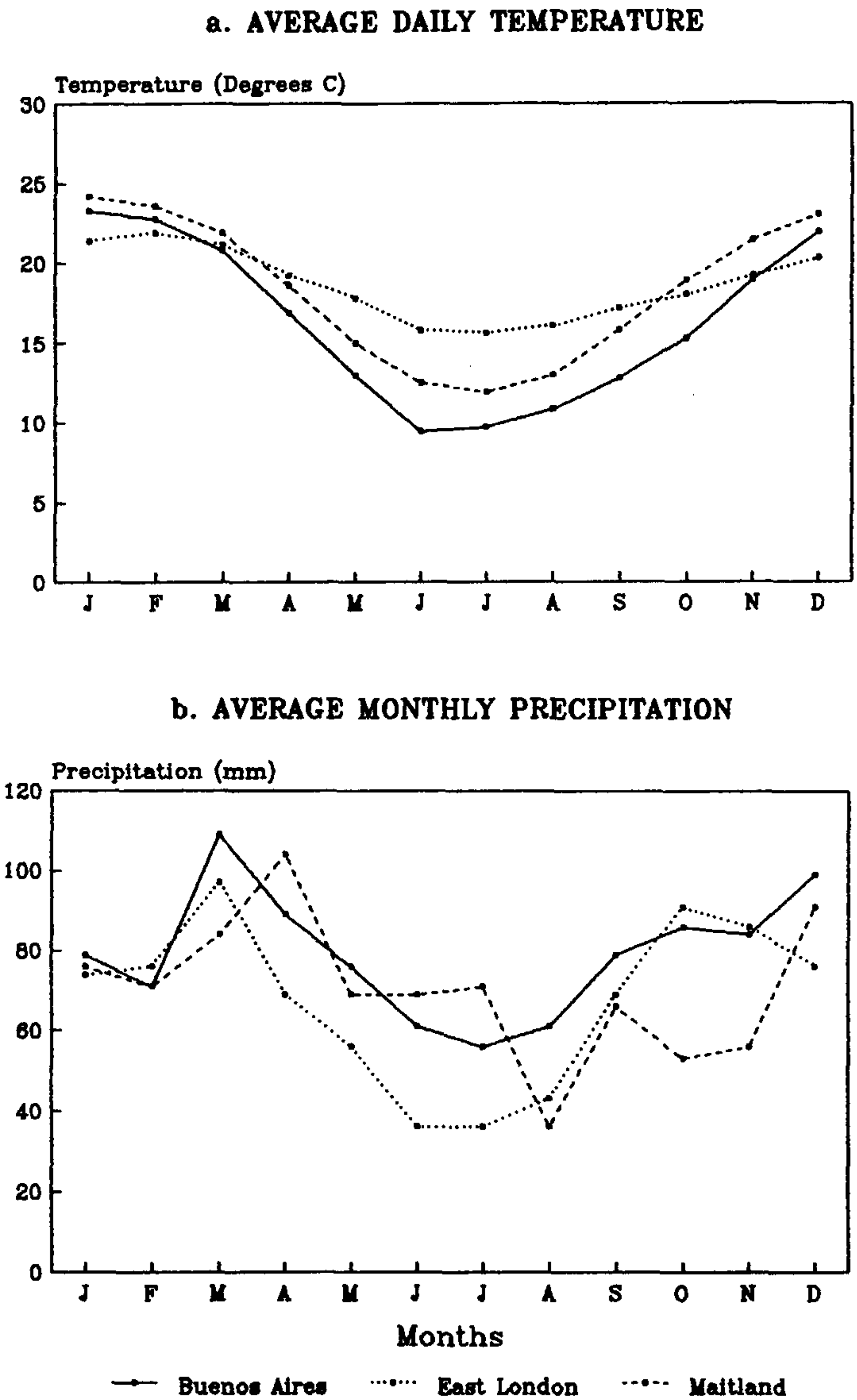


Figure 4.4 Climatic data for three localities with similar latitude and elevation in areas of the three southern hemisphere continents where Senecio madagascariensis is known to occur (see Figure 4.3) (Source: Anon. 1967 a,b; Anon. 1969).

for the system to accurately predict the absolute potential of the weed, areas with the extremes of climate to which fireweed is adapted, need to be included. If fireweed has not yet reached these areas, and this is likely to be the case, then the limits of distribution in other countries provide an estimate of where these boundaries may lie.

The most northern recording of fireweed in Australia is 26°21'S and the most southern recording 37°4'S (see Appendix 7). In Africa and South America, other than at high altitudes in the equatorial regions of Kenya and Colombia (see Chapter 2), distribution is known to extend from the Tropic of Capricorn (23°30'S) in southern Mozambique to 38°0'S in Argentina. These latitudes suggest that opportunity exists particularly for some further movement of fireweed north in eastern Queensland. This area is characterised by predominantly summer rains (500-1000 mm annually) (Coleman 1964).

Some extension southwards through coastal Victoria also seems possible. Because fireweed is not yet abundant in the south, there is considerable scope too for spread within and around the present geographical limits of the weed. Recent observations in the Bega district of New South Wales tend to confirm this assertion. Spread of S. madagascariensis southwards in Argentina is likely to be restricted by rapidly decreasing annual precipitation, but this is not the case in Victoria.

Topographic or altitudinal limits (Salisbury 1961) are not very significant in Australia because heights rarely exceed 1500 m, the level in southern Africa up to which fireweed is believed to occur (see Chapter 2). Localised high altitude areas in tropical Queensland could also be suitable for the growth of fireweed, although none were predicted using BIOCLIM.

Non-Climatic Factors

The realised potential of a weed will often be tempered by factors in addition to climatic suitability. The most important of these are soil characteristics, land use and management practices, and the effects of natural enemies (Panetta and Dodd 1987). Fireweed grows on a wide range of soils from high fertility, self-mulching clays to low fertility, acid sandy soils, but has been observed most prolific on well-drained, lighter textured acid soils of low to medium fertility (Watson et al. 1984). Further study of soil drainage properties hinted at by Daniel (1984) in relation to the distribution of fireweed is necessary.

The effects of various land use and management practices on the growth of fireweed are discussed in Chapters 2 and 3. Some coastal and tableland areas identified using BIOCLIM as climatically suitable or marginally suitable for fireweed, consist largely of native wet and dry sclerophyl forests (Moore and Perry 1970; de Kantzow 1985). Fireweed is unlikely to invade these areas because of strong competition, shading and the lack of soil disturbance.

Fireweed is host to a number of insect pests and fungal pathogens (see Chapter 2), but insufficient is understood of the impact these natural enemies have on the weed to predict how they might affect its spread and potential distribution.

Rate of Spread

Final distribution of alien weeds can also be related to their rate of spread (i.e. invasion into new territory) (Forcella 1985). Alien taxa that spread quickly are likely to become widely distributed and important weeds. Weeds with low rates of spread do not increase to occupy wide ranging distributions. Instead, they remain unimportant and restricted to specific areas. Of course, they may pose serious problems within those restricted areas. It is the spread of plants which provides the major incentive for government intervention in weed control (Menz and Auld 1977).

Increasing rates of spread of invasive plant species are quite common (Mack 1981; Auld et al. 1982/83; Medd 1987), especially during the early stages of invasion when exponential spread rates can be obtained (Dodd 1987). The pattern of dispersal for a species with wind-borne propagules such as fireweed, is of a probabilistic nature. Therefore the likelihood of new infestations arising from a given infestation increases as the size of the population increases (Auld and Coote 1981). If the weed establishes at a number of isolated nuclei, it will also tend to spread at a faster rate than if dispersed from only one location (Auld et al. 1978/79). Ultimately the rates of spread will slow down, such as when the area available reaches saturation or in response to control measures.

For documenting the early historical spread of a species, numbers of herbarium specimens appear to be useful (Lacey 1957; Forcella and Harvey 1982; Auld et al. 1982/83) but tend to be inaccurate in determining whether a species is still spreading. To detect recent movement of alien weeds, numbers of occupied districts or farms must be employed (Forcella et al. 1986).

The exponential increase in the number of farms infested with fireweed in the survey of Chapter 3 (see Figure 4.5a) suggests that the total level of fireweed infestation in New South Wales is also increasing exponentially. However, the exponential model of spread is inappropriate because, as already shown, the areas into which the plant will continue to spread are limited. The survey revealed that fireweed already occurs on 90% of farms in the surveyed areas. Therefore, the rate of spread in these areas over the next few years is likely to decrease and the curve level off and become sigmoidal in shape. This is particularly evident since much of the current spread is onto farms within the present range of distribution. In regions such as Gloucester, this levelling off has already occurred (see Figure 4.5b). Almost all farms in that area have become infested within the last 30 years, which illustrates the ability of fireweed to spread rapidly in a region which is climatically suitable for its growth. In the Taree area spread has been even more rapid with fireweed infesting all farms in the space of 20 years.

CONCLUSIONS

It seems reasonable to expect, from the bioclimatic results and other factors considered in the present study, that fireweed will continue to spread and increase its level of infestation in regions such as the far south coast of New South Wales, where as yet it is not abundant, and south-eastern Queensland. Coastal areas in Queensland, up to the Tropic of Capricorn, would also seem to be at

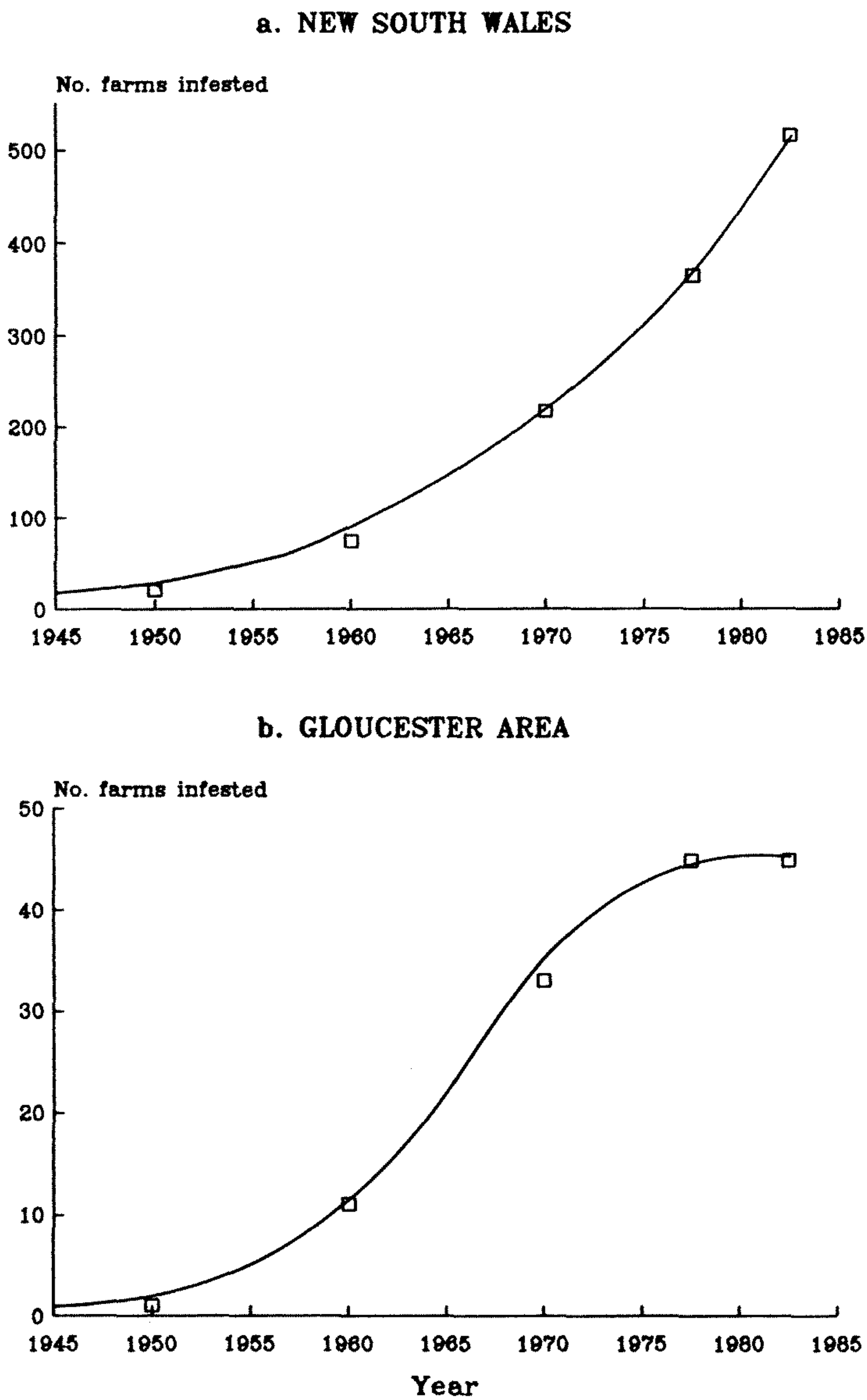


Figure 4.5 Increase in the number of farms infested with fireweed in the survey of Chapter 3 in (a) all of New South Wales, and (b) the Gloucester area alone.

least marginally vulnerable to invasion. Likewise, coastal areas of eastern Victoria seem potentially at risk. For this reason care should be taken in the movement of fodder and seed to these areas, that fireweed is not included as a contaminant.

It is unlikely, owing to unfavourable moisture regimes and barring genetic changes, that fireweed will spread appreciably west of the Great Dividing Range. Nor is the weed likely to be aggressive or assume prominence on the Tablelands of eastern Australia. However, scope remains for spread and a higher level of infestation within the Muswellbrook, County of Cumberland and Shoalhaven areas of New South Wales, and in agricultural areas of other lightly infested coastal plains and river valleys.

Quantitative information on population growth rates, in addition to spread (I'ons 1978), is also necessary if one is to place the fireweed problem in Australia in proper perspective. Population growth rates will be determined to a large degree by soils, seasonal environmental factors and farm management practices. Aspects of the population dynamics of fireweed are investigated in the next chapter.

Chapter 5

ASPECTS OF THE POPULATION ECOLOGY OF FIREWEED

'Plants stand still and wait to be counted.' (Harper 1977)

INTRODUCTION

The life cycle of fireweed is complex. Although most commonly behaving as an annual, under some conditions it acts as a biennial or even a short-lived perennial (see Chapter 2). Individuals can be found flowering at most times of the year. Plant densities, as with Senecio jacobaea (Harper and Wood 1957; Forbes 1974), also fluctuate dramatically from year to year.

Flushes of germination and patterns of seedling emergence in weeds are thought to be closely related to seasonal climatic conditions (Medd 1985), particularly temperature and rainfall (Roberts 1964; Hosking et al. 1968). Changes in pasture management practices are also likely to interact with environmental factors (Harper 1960; Koller 1964) to affect population dynamics (Hosking et al. 1968; Sagar 1982).

Since increases in the size of field populations of fireweed (seed pool included) occur almost solely from the production of seeds by established plants, the pattern of flowering may be an important determinant of potential infestations.

Comprehension of the factors that regulate the size of a fireweed population is essential for the proper evaluation of control procedures. Several authors (e.g. Forbes 1977; Popay and Thompson 1979; Forcella and Wood 1986; Popay and Kelly 1986) have sought to isolate sensitive stages in the life cycles of various weeds with the aim of improving their control. Weed management may be seen to be concerned with maximising mortality as well as lowering reproduction of weeds (Mortimer 1983).

In this chapter some of the factors affecting the dynamics of several naturally occurring field populations of fireweed are examined. Investigations are described in which patterns of emergence, flowering, longevity, life cycle strategies and the fate of fireweed plants were assessed.

MATERIALS AND METHODS

Experiment 1 - Seedling Emergence and Survival in the Field

At three sites in the County of Cumberland, New South Wales, where fireweed was known to occur, permanent quadrats, each 8.0 m^2 (4.0 m x 2.0 m), were established to investigate fireweed seedling emergence and survival (see Plate 5.1). Two quadrats were located on the University of Sydney Agronomy Unit, Camden, on 30 January 1986 and one on a farm 20 km north-east at Hoxton Park on 28 February 1986 (see Figure 5.1). All over-summering fireweed plants were removed and counted. Other weed and pasture growth was cut at a height of 10 cm. Newly-emerged fireweed seedlings were then tagged monthly (see Plate 5.2) and their life cycle recorded. Flowering, defined here by the appearance of unspent capitula, was noted and related to the date of seedling emergence. Observations continued on this basis until January 1988.

Owing to an extremely large germination of fireweed at the second of the Camden sites in May 1986, two smaller quadrats, each 0.5 m^2 (2.0 m x 0.25 m and 1.0 m x 0.5 m), were established in representative areas within the large quadrat and further observations made on them. In most instances fireweed seedlings, even at the cotyledon stage of growth, were readily identifiable.

The first Camden quadrat was located in a lightly wooded area on a low fertility, unimproved pasture of scattered paspalum (Paspalum dilatatum) and native pasture grasses such as kangaroo grass (Themeda australis (R.Br.) Stapf). The second Camden site was an exhausted and comparatively bare cultivation paddock which had not been worked

Plate 5.1 A 4 m x 2 m permanent quadrat established in the field at Camden in January 1986 to investigate fireweed seedling emergence and survival.

Plate 5.2 A tagged fireweed seedling growing in pasture at Hoxton Park. Scale bar = 1 cm.

Plate 5.3 Fireweed seedlings at a very high density (> 5000 plants m^{-2}) in a cultivated paddock at Albion Park in March 1986.

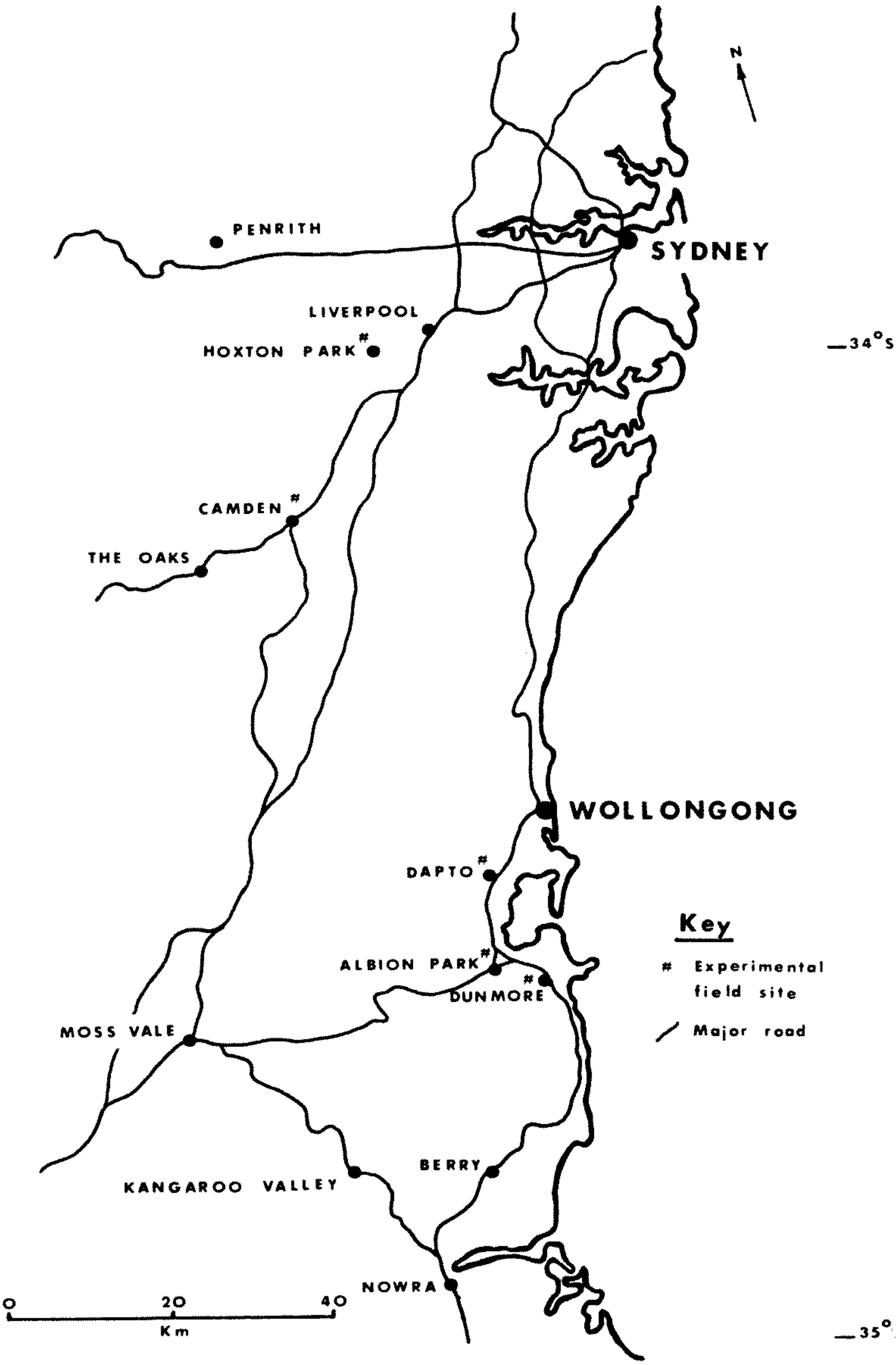


Figure 5.1 Location map of experimental field sites.

for eighteen months. The soil was compacted and sparsely covered with couch (Cynodon dactylon) and paspalum. Both Camden plots were ungrazed.

The Hoxton Park site, a grazed couch grass dairy pasture, had a thicker pasture sward and supported a stocking rate of approximately 1.6 cows ha^{-1}. The weed bindii (Soliva pterosperma (Juss.) Less.) was also a significant pasture component. In 1985 the site had been heavily infested with fireweed after a grass fire burned the area in summer and provided a favourable seed bed for germination and emergence.

At Hoxton Park the recording of germination was sometimes partially delayed because seedlings were not visible prior to their penetrating the pasture canopy. By that time they often possessed two true leaves. Germination and seedling mortality may have been under-recorded, particularly at times when the pasture was seasonally most vigorous.

Temperature data for Liverpool (6 km from Hoxton Park - see Figure 5.1) and monthly rainfall data for both Camden and Liverpool were obtained from the Bureau of Meteorology for the period of the experiment in order to relate patterns of seedling emergence to seasonal climatic conditions. Since the pattern of rainfall over the two years of the experiment at Camden and Liverpool was essentially the same, only data for Liverpool are presented.

Information on the effect of soil fertility on survival and flowering was obtained from additional quadrats established on 6 February 1987 and maintained for 12 months. Two 0.5 m^2 quadrats (1.0 m x 0.5 m) were located in a grazed paddock adjacent to the Agronomy Unit at Camden and four further quadrats, each 4.0 m^2 (2.0 m x 2.0 m), at the Hoxton Park site. On 5 March 1987 half of each new quadrat received a broadcast dressing of 'Starter 18' fertiliser equivalent to 66 kg N ha^{-1} and 30 kg P ha^{-1}. The remaining half was left unfertilised. Established fireweed plants were removed and new seedlings tagged and assessed on a monthly basis, as occurred in the year-old quadrats.

In late May 1987 two of the four quadrats recently established at Hoxton Park were accidentally slashed. This provided the opportunity to compare the survival and pattern of flowering of slashed plants with unslashed individuals.

In a separate investigation on the effect of mechanical damage on the longevity of fireweed, mature senescing plants cut 2 cm above ground level at the end of a 1986 field experiment (see Chapter 7 for details) were observed early in the following February and again in late March 1987. The percentage of plants which had regrown and survived over summer was determined.

Data from this experiment were not analysed statistically since one of the assumptions underlying regression analysis, i.e. that experimental errors are random and independently distributed (Steel and Torrie 1960), was not fulfilled.

Experiment 2 - Longevity Observations

Complementary data on the longevity of fireweed were obtained from the Agronomy Unit, Camden when, on 17 April 1985, 9 mature fireweed plants growing in ungrazed native pasture and 41 fireweed seedlings on mown and previously cultivated land, were staked and tagged. The mature plants, well-branched and flowering, had germinated in 1984 and over-summered. The seedlings were neither branched nor flowering and were estimated from their morphology to range in age from 6 to 10 weeks. Stages in the life cycles of tagged individuals were observed at regular intervals and their longevity recorded. After 18 months all plants were dead.

Experiment 3 - Survival and Seed Production of Uprooted Plants

On two occasions fireweed plants were uprooted and their ability to set viable seed assessed. On 22 April 1985 five flowering plants were pulled and dropped in an open paddock at Camden. None at that stage had mature capitula or were dispersing seed. On 10 May 1985 another five flowering plants were hand-pulled, this time at Goulburn, and placed in water in a lighted room. The fate of all plants was closely followed.

Experiment 4 - Observations of High Fireweed Densities

Opportunity to follow the life cycle of fireweed at what may be considered its maximum density was afforded by a large and reasonably uniform germination of the weed, concurrent with the emergence of a cultivated crop of forage sorghum. This occurred over the summer of 1985/86 at Albion Park on the south coast of New South Wales (see Figure 5.1).

Four fixed quadrats, each 0.25 m^2 (0.5 m x 0.5 m), were positioned in an area of the paddock which appeared to have the highest density of fireweed seedlings in March 1986. Because of the extremely high densities encountered, smaller 0.01 m^2 quadrats (10 cm x 10 cm) were located in each of the larger quadrats for regular counting. The area was visited on six occasions between March and September of that year. Seedlings were counted in each of the small quadrats and two destructive harvests (each 0.01 m^2) made in two of the larger quadrats each visit. Plants from the destructive harvests were also counted. The average height, dry weight, and number of leaves and capitula were determined for harvested plants during the period of the experiment. Standard deviations were also calculated.

RESULTS

Experiment 1

Germination and survival of fireweed at the two Camden sites and at Hoxton Park during 1986 and 1987 are graphed in Figures 5.2, 5.3 and 5.4. The number of fireweed removed from each of the sites at the beginning of the experiment, which had over-summered from 1985, was 45, 70 and 79 plants 8 m^{-2} respectively. The size of these over-summering populations suggested that a large seed pool was present at each site for the population studies.

Germination and seedling emergence

A comparison of Figures 5.2, 5.3 and 5.4 shows that the fireweed populations at the three sites varied considerably in size, but had

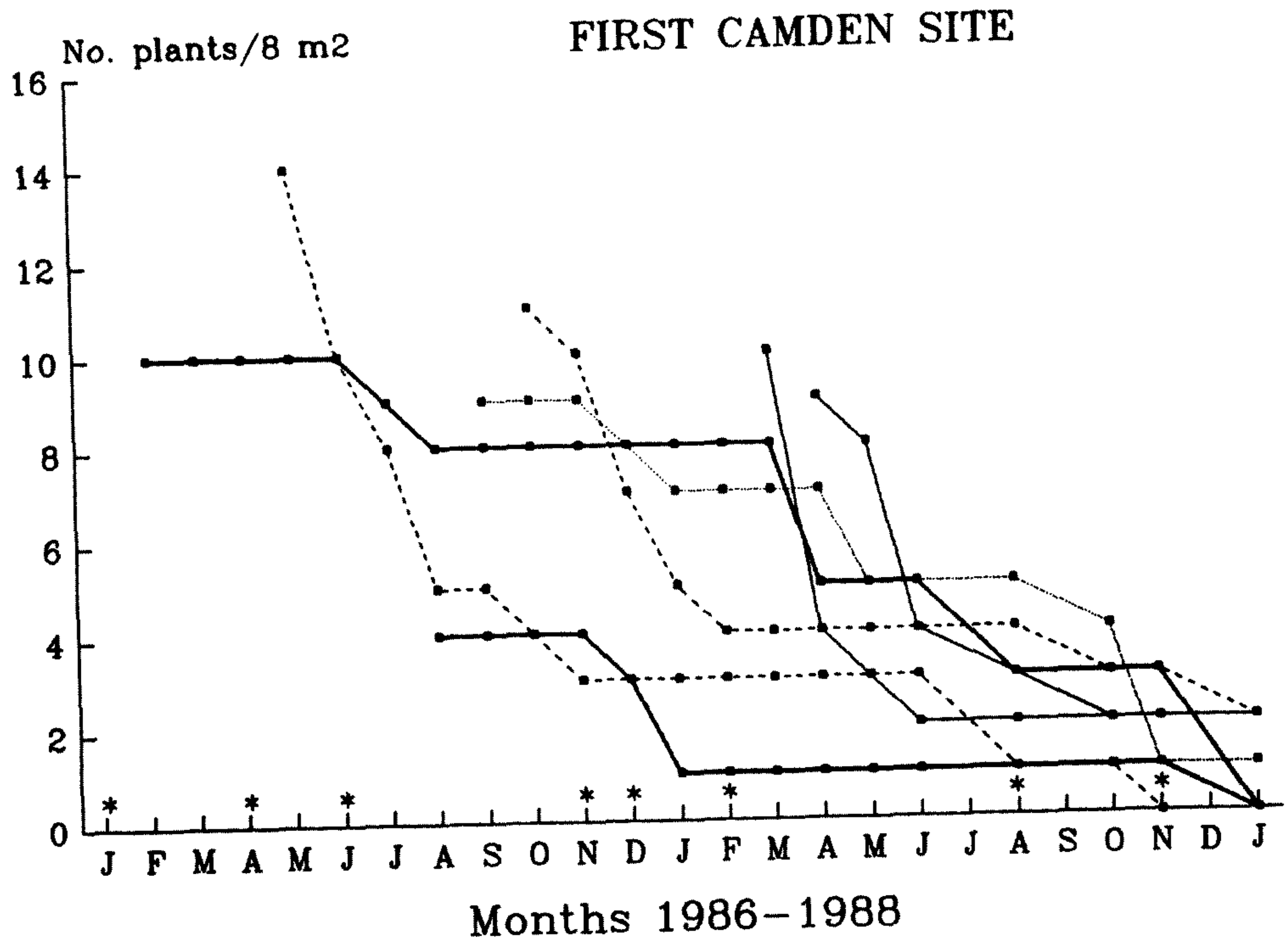


Figure 5.2 Survival curves for the major fireweed cohorts at the first Camden site during 1986 and 1987. The germination of monthly cohorts of < 4 plants 8 m^{-2} are indicated by an asterisk (*) on the base line.

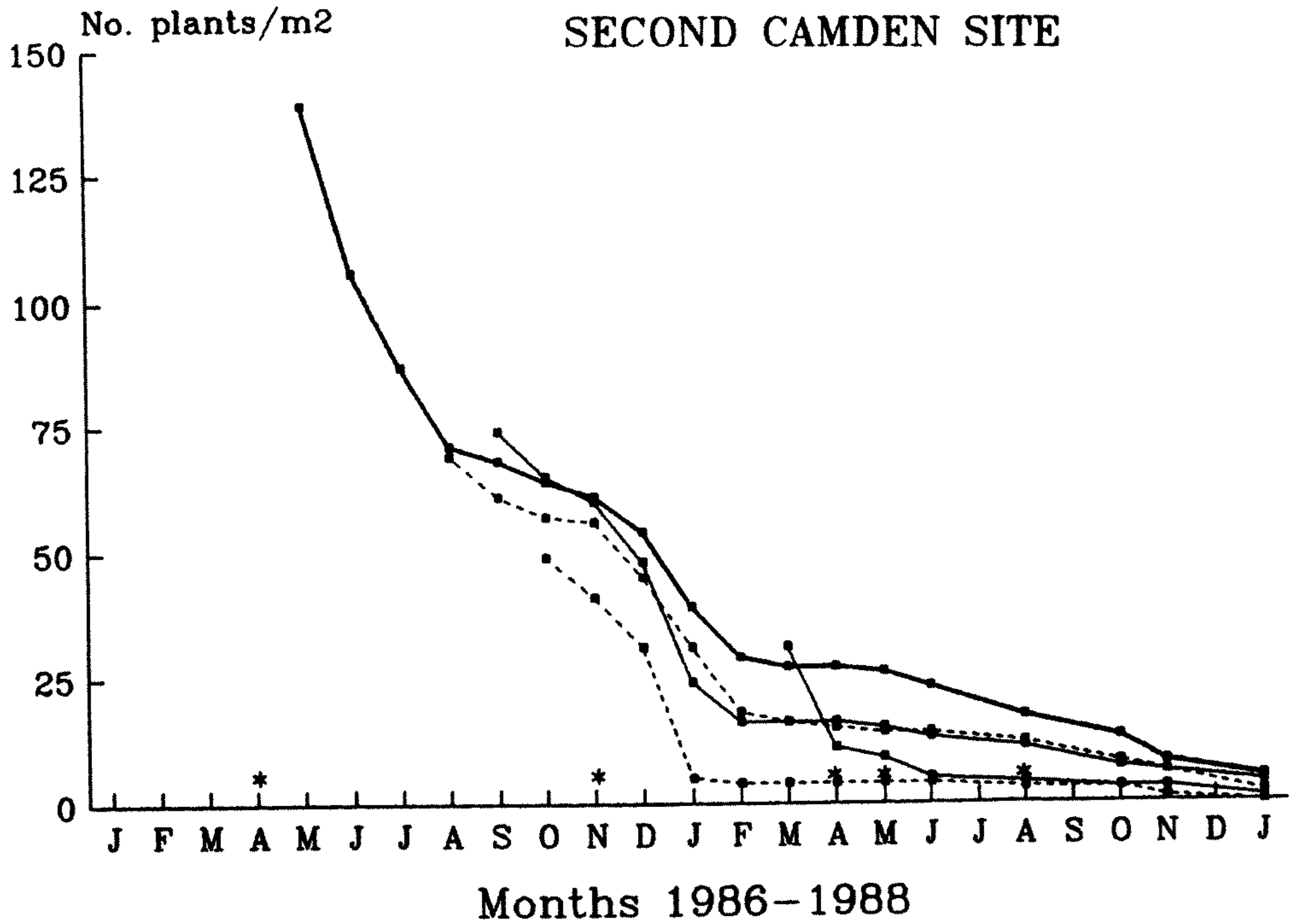


Figure 5.3 Survival curves for the major fireweed cohorts at the second Camden site during 1986 and 1987. The germination of monthly cohorts of < 20 plants m^{-2} are indicated by an asterisk (*) on the base line.

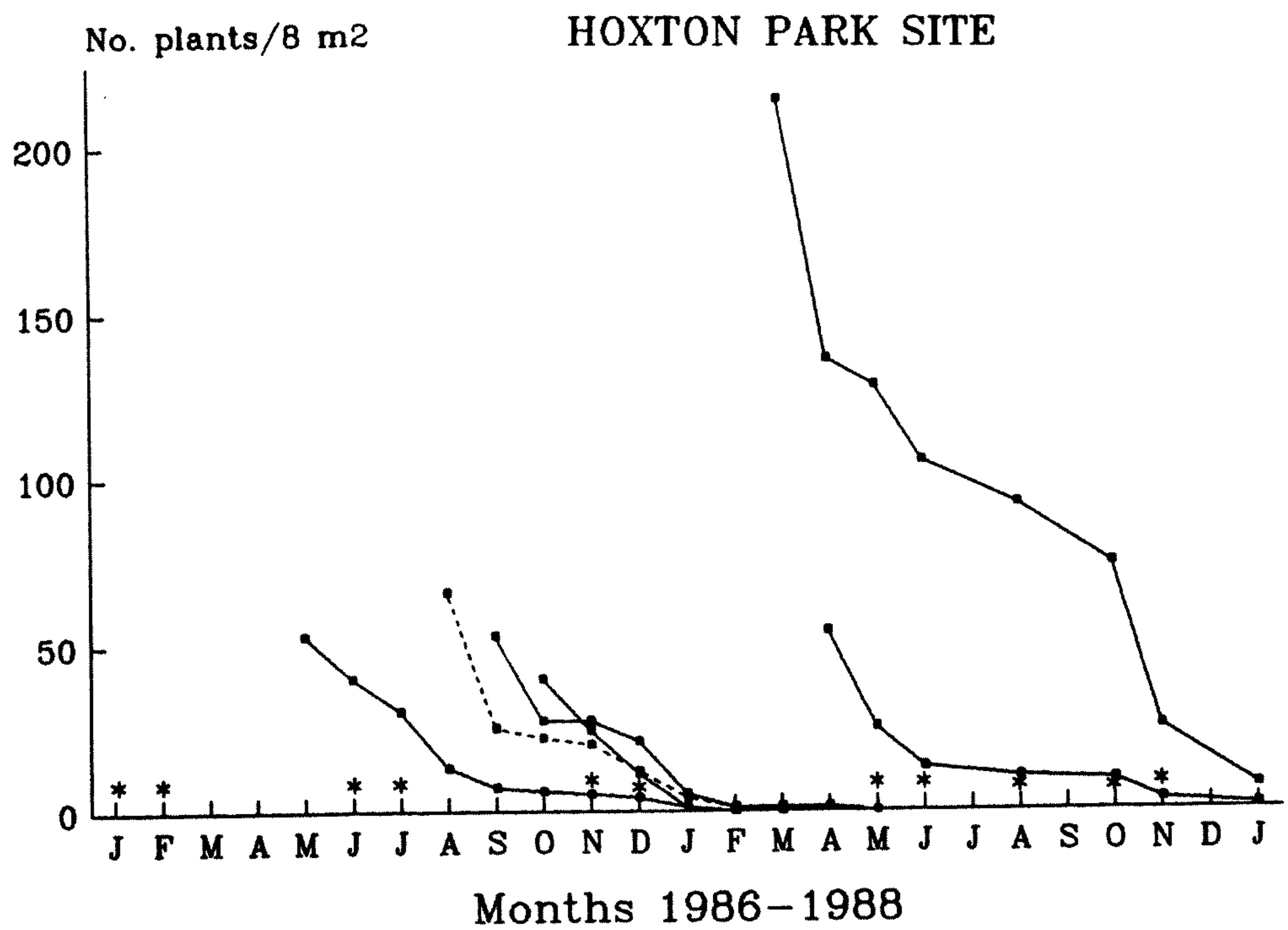
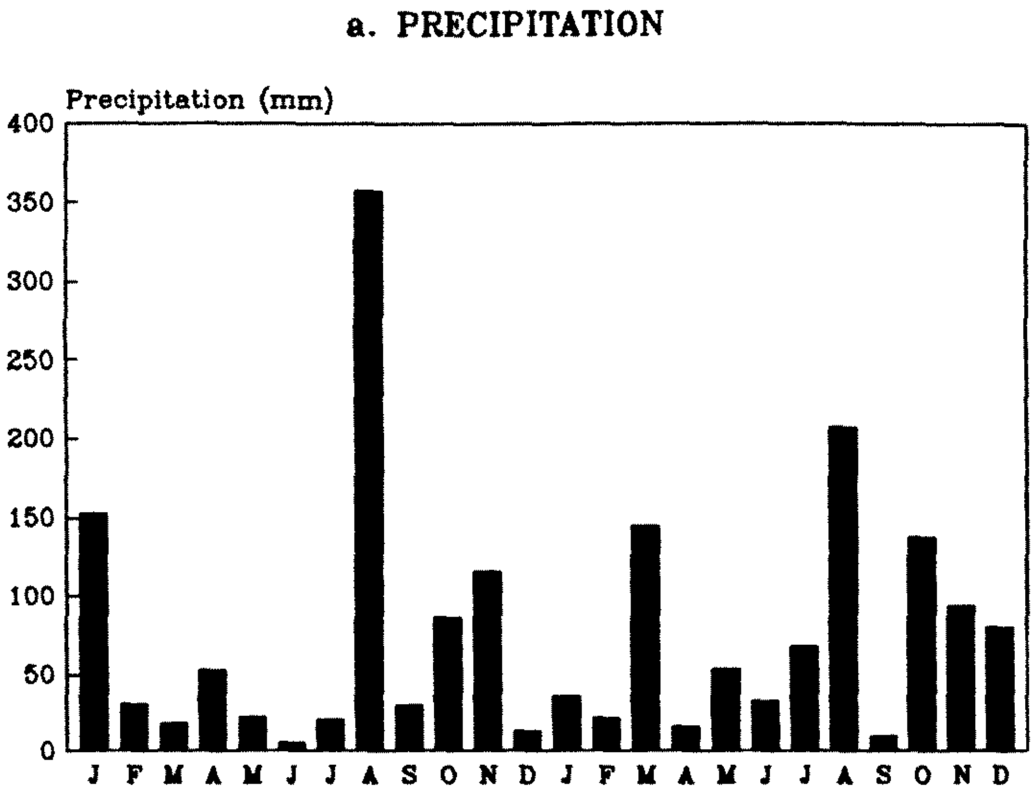


Figure 5.4 Survival curves for the major fireweed cohorts at the Hoxton Park site during 1986 and 1987. The germination of monthly cohorts of < 30 plants 8 m^{-2} are indicated by an asterisk (*) on the base line.

similar patterns of seedling emergence. Small numbers of seedlings emerged every month during the 2 years of the experiment at one or other of the three sites, but most seedlings emerged during flushes of germination which were closely related to the incidence of rainfall (see Figure 5.5a). In 1986 the first Camden site (see Figure 5.2), unlike the other two sites, had fireweed seedlings emerge in mid to late summer. This followed heavy rains in January, but presumably because of the microclimate of the other two sites, if germination did occur, seedlings did not survive the summer long enough to be counted. Site 1, where emergence did occur in January and February, was the most sheltered of the three sites, being surrounded by tall grass and shaded by a nearby tree. Sites 2 and 3 were exposed and received no shade.

The first main germination period common to all locations in 1986 was in late autumn after 40 to 50 mm of rain fell in April. Seedling emergence at Site 2 was equal to 139 plants m^{-2}. Smaller germinations occurred during June and July at Hoxton Park. The second germination flush began in August with the onset of heavy rains (see Figure 5.5a) and continued through until late October and early November. The autumn break in 1987 occurred earlier and was more distinct than in 1986, leading to the major germination flush occurring over March and April. The number of fireweed seedlings which emerged during autumn at Hoxton Park in 1987 (284 plants 8 m^{-2}) was much greater than in 1986 (53 plants 8 m^{-2}) (see Figure 5.4). At the second Camden site, where there had been a very large autumn germination in 1986 (140 plants m^{-2}), the number was considerably smaller (57 plants m^{-2}).

Fireweed seedlings failed to emerge in significant numbers in the spring of 1987 as they had done in 1986 despite over 200 mm of rain falling at Hoxton Park in August and 160 mm at Camden. With continued rains late in spring a small number of seedlings emerged at Hoxton Park in October and November. Temperatures did not seem unsuitable for germination because they were within the range of those measured in August 1986 which were associated with a large germination of fireweed (see Figure 5.5b). However, the mean daily minimum temperature for August (8.8°C) was the highest on record (Bureau of Meteorology information) and was 2.4°C above that for



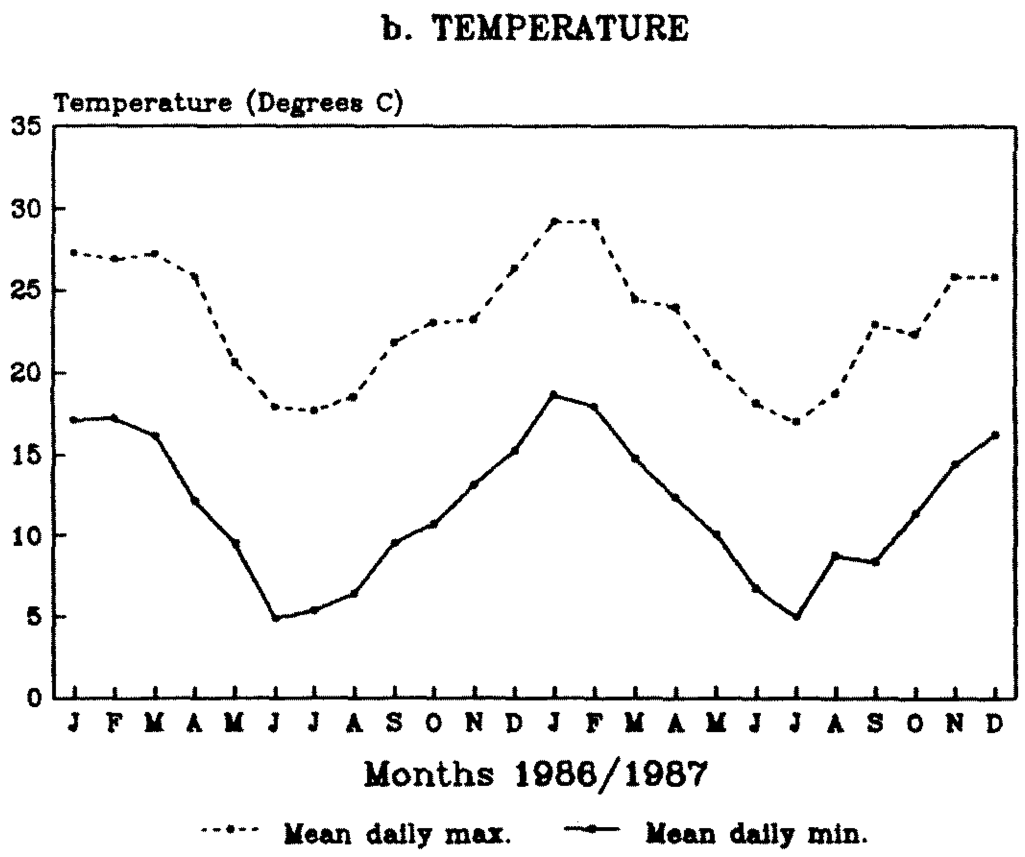


Figure 5.5 Climatic data for Liverpool during 1986 and 1987.

1986. The mean daily maximum temperature was 0.2°C higher. These higher minimum temperatures combined with the good August rains promoted stronger than usual pasture growth and led to an early start to spring growth. Moreover, the precipitation falling in May, June and July at Camden totalled 98.4 mm in 1987 compared with 42.3 mm in 1986, and at Liverpool 152.4 mm compared with 47.4 mm. Good soil moisture throughout the whole of the winter period in 1987 favoured comparatively vigorous pasture growth.

Those fireweed seedlings which did emerge in the pasture at Hoxton Park in August (see Figure 5.4) were confined to two small bared patches of couch grass showing very weak growth. It would seem that the more vigorous pasture was able to prevent observable establishment of fireweed seedlings, if not germination itself.

The additional quadrats established at Camden and Hoxton Park in 1987 to study the effects of soil fertility gave similar patterns of fireweed seedling emergence to those already discussed (see Figures 5.6 a,b and 5.7 a,b).

Mortality

Survival curves for cohorts of fireweed seedlings charactistically decreased in a step-wise fashion with rapid mortality rates being interrupted by either one or two 'survival plateaus'. A stylised interpretation is given in Figure 5.8. The steepest section of the graph and therefore highest mortality rate, other than when plants were coming to the end of their natural life cycle, was usually when seedlings were youngest immediately following germination (see Figures 5.2, 5.3, 5.4, 5.6 a,b and 5.7 a,b). This was particularly the case for cohorts at Hoxton Park where stronger pasture competition and grazing caused many young seedlings to die.

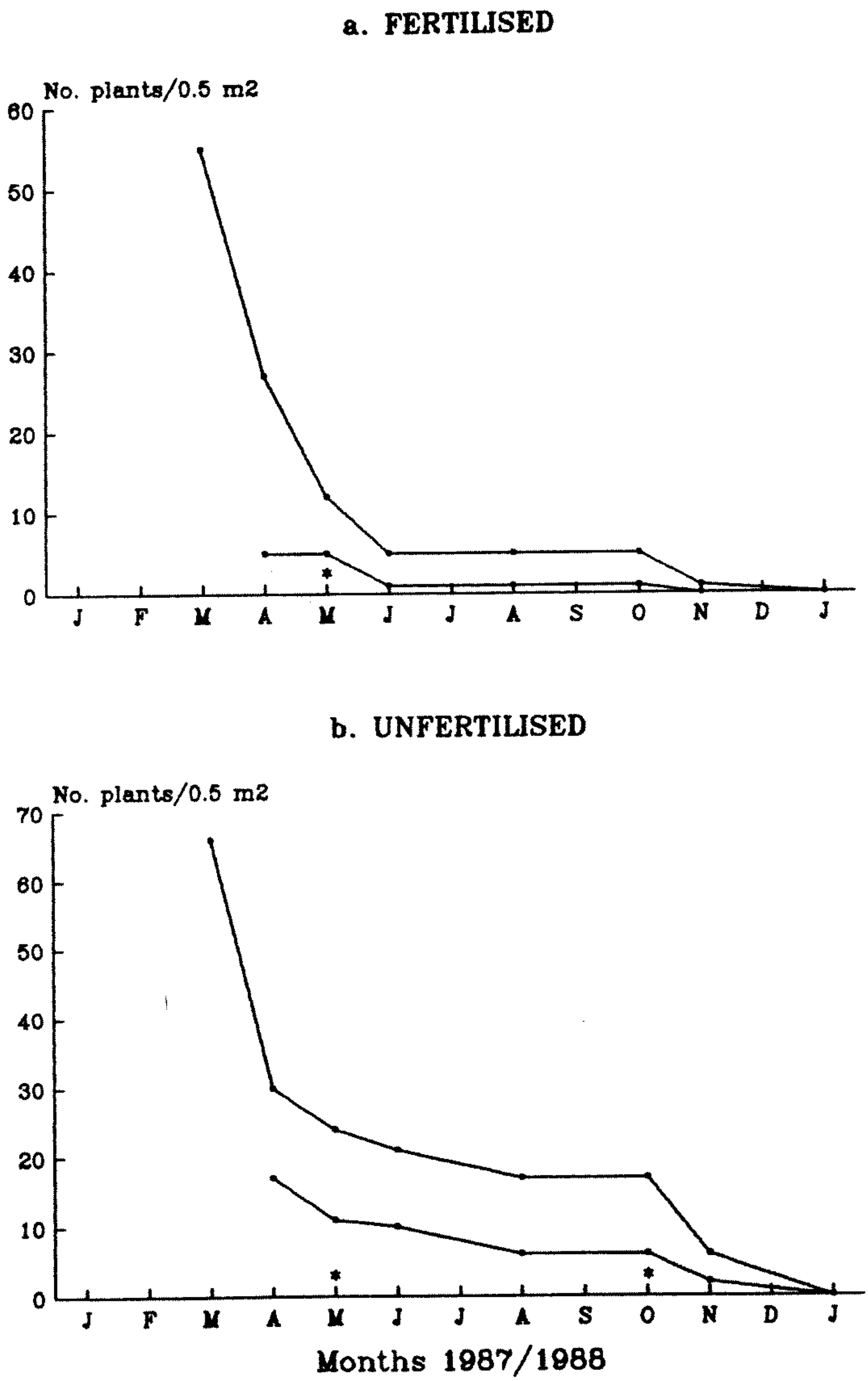


Figure 5.6 Survival curves for the major fireweed cohorts at Camden during 1987 in (a) fertilised, and (b) unfertilised quadrats. The germination of monthly cohorts of < 5 plants 0.5 m^{-2} are indicated by an asterisk (*) on the base line.

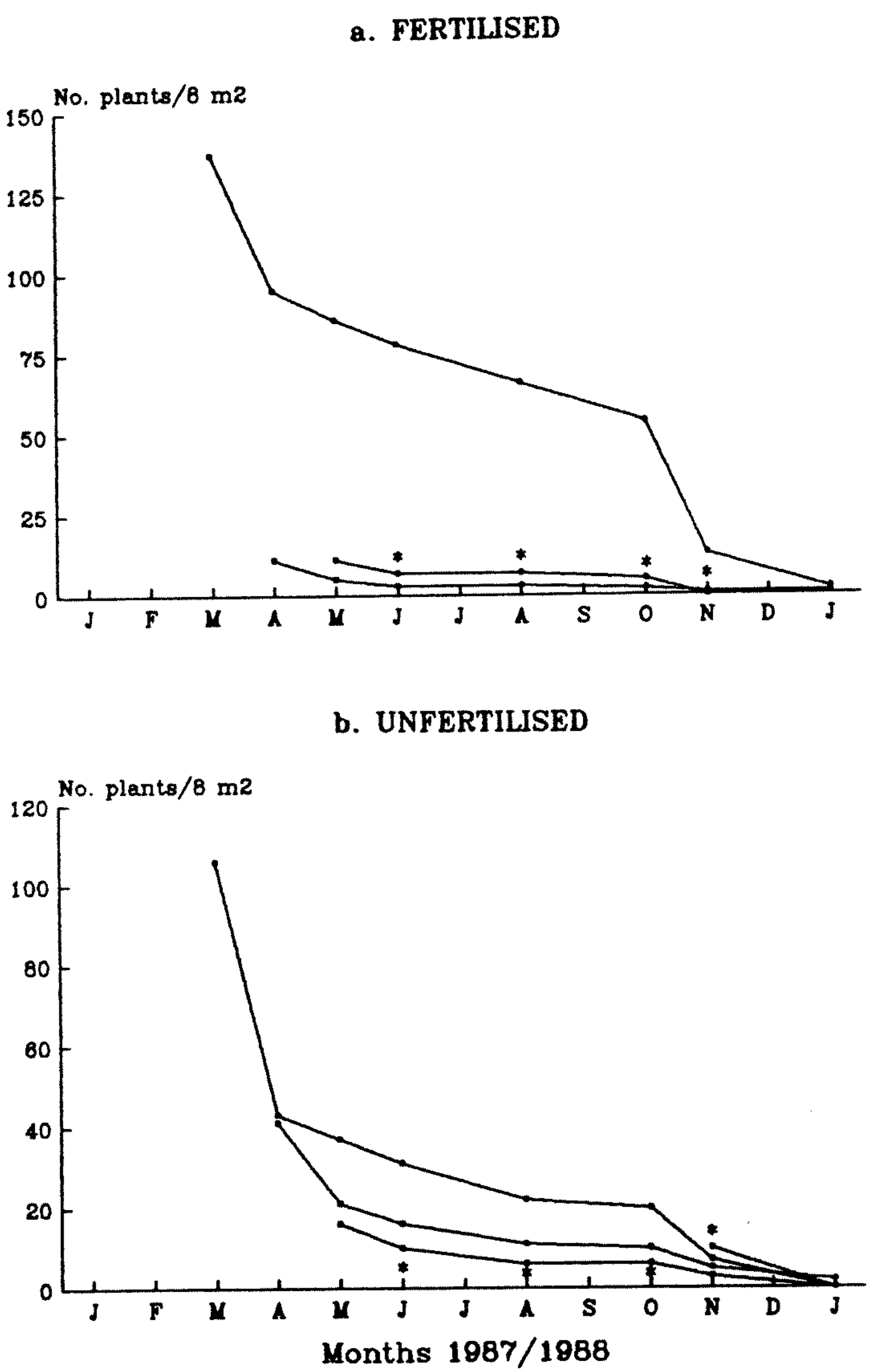


Figure 5.7 Survival curves for the major fireweed cohorts at Hoxton Park during 1987 in (a) fertilised, and (b) unfertilised quadrats. The germination of monthly cohorts of < 10 plants 2 m^{-2} are indicated by an asterisk (*) on the base line.

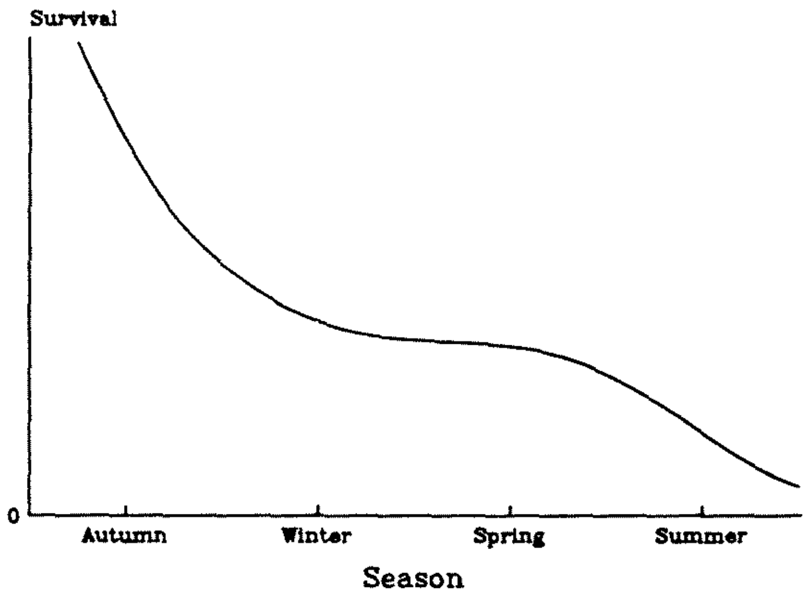


Figure 5.8 Stylised survival curve for an autumn-germinating fireweed cohort.

Another factor which seemed to affect fireweed mortality was the season in which a cohort germinated. At the second of the two ungrazed Camden sites the survivorship curve of the 1986 autumn germinating cohort levelled off over the spring months but then decreased quite rapidly through summer (see Figure 5.3). This graph was paralleled by cohorts germinating in August, September and October. These cohorts did not have a typical rapid mortality rate following seedling emergence, but through the summer months mortality was high even though in many cases flowering had not begun. Low soil moisture combined with high temperatures (see Figure 5.5 a,b) apparently caused many plants to die.

There were several other factors which contributed to the premature death of fireweed plants. In June and July 1986 and 1987 a considerable number of small seedlings were observed damaged by what was thought to be frost. Leaves often appeared burnt and shrivelled while the stems remained unaffected. Heavy frosts were experienced during those periods (see Chapter 6).

Some seedlings showed symptoms of being infected by the rust fungus <u>Puccinia</u> <u>lagenophorae</u> (often referred to hereafter as 'fireweed rust'). Others had most of their leaves chewed by pasture slugs. Red legged earth mites (Halotydeus destructor (Tucker)) were present in the pasture in late autumn 1987 but their effect on fireweed could not be assessed.

Under grazing conditions at Hoxton Park some plants were trampled by cattle and others smothered by their faeces. When seedlings were small they were often grazed by cattle but once they were easily identifiable and above the pasture canopy they were avoided. Occasionally plants were found pulled up but uneaten.

The population fluxes of fireweed at the second Camden site and at Hoxton Park are given in Figure 5.9 a,b. Cumulative gains, as expected, increased in a step-like fashion while cumulative losses increased more linearly. The most rapid losses followed high germination periods. The size of the resulting populations varied considerably over the two years of the experiment but the pattern of population flux was similar. Population peaks were reached in autumn and spring.

Longevity and flowering

At the two ungrazed Camden sites an appreciable number of fireweed plants from 1986 germinating cohorts survived into a second year of growth to act as biennials. At Hoxton Park all plants behaved strictly as annuals.

Cohorts at Hoxton Park establishing in May, June and July (see Figure 5.4) began flowering in September, while August and September cohorts started flowering in October. Late spring cohorts (October and November) had insufficient time to produce many flowers before they died. Flowering, which had begun in September and continued through until December, was followed by senescence in December and January.

In 1987 in all the grazed quadrats, including the additional fertiliser quadrats established at Camden and Hoxton Park, plants also acted primarily as annuals (see Figures 5.4, 5.6 a,b and

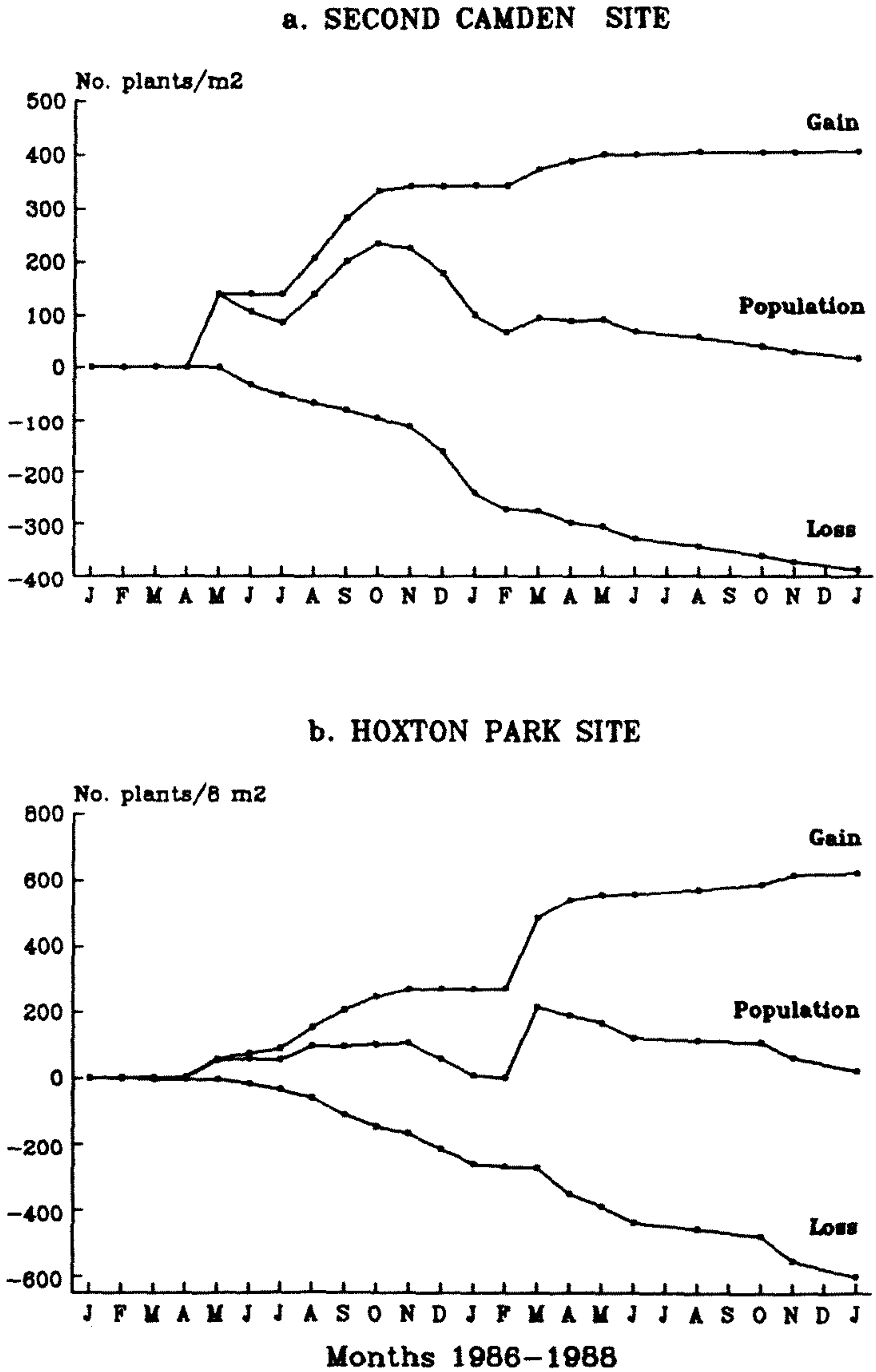


Figure 5.9 Population flux of fireweed at (a) the second Camden site, and (b) Hoxton Park, during 1986 and 1987.

5.7 a,b). Assessment was not continued past January 1988. Hence the few plants which did remain may well have senesced soon after this.

The large flush of germination in 1987 occurred 2 months earlier than in 1986. Probably due to much warmer temperatures at that time (see Figure 5.5b), growth of fireweed seedlings was rapid. Consequently, flowering began some 6 to 8 weeks after emergence in mid autumn and then continued through winter, finishing around the middle of spring. Rapid senescence followed during November, again 1 to 2 months earlier than in 1986. Annual plants on the whole had life cycles lasting for periods of 8 months or less.

Early flowering of 1987 autumn cohorts at the two ungrazed Camden sites did not occur, presumably because growth of plants at these two sites was very slow. This was possibly due to compaction of the soil and a very low fertility status.

The ability of some plants to grow as biennials at Camden was thought to be due to less disturbance (caused by the absence of cattle) and less competition in the pasture environment. Plants behaving as biennials (life cycle > 12 months) came from both autumn and spring germinating cohorts and comprised 40.0 and 12.9% of seedlings which emerged in 1986 at Sites 1 and 2 respectively. Site 1, as already mentioned, was the most sheltered of the two sites.

In most cases plants which flowered during spring in 1986 at Camden and which also over-summered began flowering again in the following autumn (autumn flush) and continued through to the spring of 1987. Flowering times were similar to those plants behaving as annuals at Hoxton Park in 1987.

The effect of soil fertility

Survivorship curves of fireweed in fertilised and unfertilised plots are shown in Figures 5.6 a,b and 5.7 a,b. Fertiliser was applied too late to assess its affect on the size of the autumn germination flush, but it did appear that fertiliser application increased the rate of seedling emergence. Hence in the fertilised plots the proportion of autumn seedlings emerging in the March cohort (87.3%) was large compared with the unfertilised plots (69.4%) where there were sizable April cohorts also. This response was not unexpected in view of the observed stimulatory effect of nitrates on germination (Alonso et al. 1982, see Chapter 2).

After seedling emergence, fireweed in fertilised plots grew more quickly and flowered earlier than fireweed in unfertilised plots. Survivorship was not altered by soil fertility in any observably consistent pattern. All plants behaved as annuals with rapid senescence occurring in all plots during November.

The effect of slashing

Slashing of two quadrats in the fertility experiment at Hoxton Park occurred during May 1987. Although seedlings emerged in March, April and May, it was primarily plants of the March cohort which were affected by the slashing, owing to their larger size. Survival data (combined over fertilised and unfertilised treatments) of slashed and unslashed plants, on a percentage basis, is given in Figure 5.10. The percentage of surviving plants flowering is also graphed.

Slashing early in the life cycle of fireweed reduced plant survival by 14.0% 1 month after slashing and by up to 18.7% during the next 6 months. This result tends to support that obtained by Fernández (unpublished data) for one mowing (see Chapter 2). Slashing, however, did not cause any plants to over-summer or behave as biennials. It delayed the onset of flowering but did not reduce the percentage of surviving plants flowering.

In comparison with early slashing, in a separate experiment 30.9% of plants cut late in the life cycle of fireweed (at the start of senescence in early November) regrew and survived over summer until early February. By late March the number had decreased to 19.4%. Although no control plants (uncut) could be included in the latter observations, all plants at the time of cutting were beginning to senesce and were expected to die soon after.

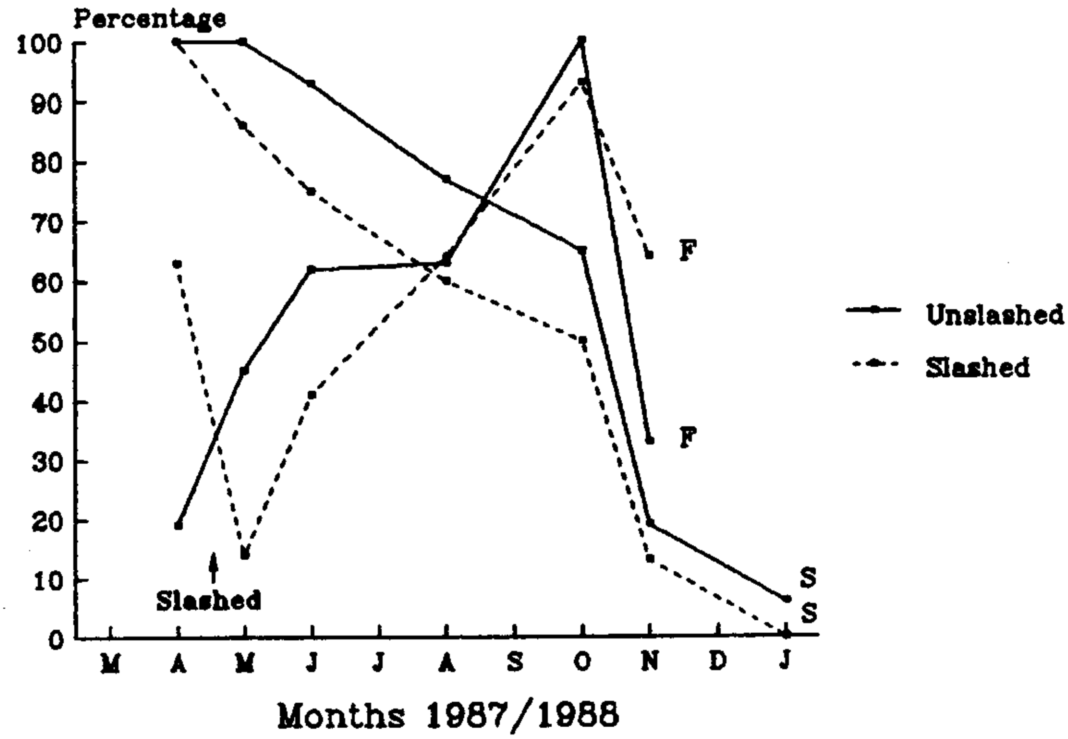


Figure 5.10 Percentage of fireweed plants (March 1987 cohort) at Hoxton Park which survived (S), and percentage of surviving plants which flowered (F), in slashed and unslashed quadrats.

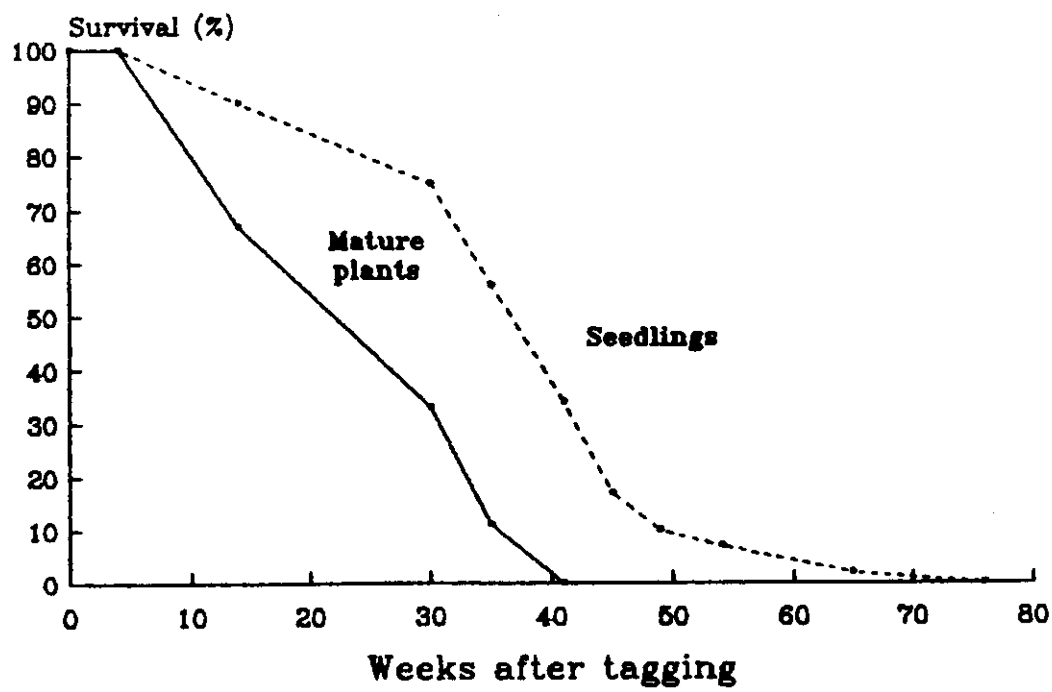


Figure 5.11 Survival of mature (6-8 month old) and seedling (6-10 week old) fireweed, tagged on 17 April 1985.

Experiment 2

Longevity

The longevity of mature flowering fireweed plants and seedlings, tagged in mid April 1985 at Camden, is shown in Figure 5.11. Because of their size and profuse flowering, mature plants were estimated to range in age from 6 to 8 months. After flowering and dispersing seed in autumn, plants began to senesce at a steady rate. Though decrepit, 33% survived through to the next spring but no plants over-summered a second time.

The survivorship curve of seedlings is similar to those shown for Experiment 1 except that the initial rapid mortality is not shown. This is because seedlings were tagged some 2 months after emergence (presumably during February). Older seedlings began flowering in late autumn and younger seedlings in early winter. Senescence was most rapid over summer with 10% of plants surviving for longer than 12 months. Only two plants (5%) flowered vigorously again in the autumn/winter period of 1986.

Experiment 3

Fate of uprooted plants

Of five flowering plants pulled and dropped in April 1985 at Camden, one re-anchored into the ground by its roots and continued to flower. Seed was released 33 days later and collected. April and May were very wet months, hence even the plants which did not re-anchor into the ground continued to maintain fully open capitula for some 9 days after being uprooted.

Plants pulled at Goulburn and kept in water also produced seed. This seed was collected 12 days after plants were uprooted, and germination tests were carried out on it and on the seed from the Camden plant on moist filter paper at room temperature. Germination percentages of 100% and 84% respectively were obtained.

Experiment 4

High density observations

Data on the growth of fireweed at very high densities are given in Table 5.1. The density, measured in mid March at 5850 plants m^{-2} (see Plate 5.3), decreased to 2180 plants m^{-2} in September. Plant height increased considerably over time, but the number of green leaves per plant and total shoot dry weight remained reasonably static due to severe intraspecific competition and the damaging effect of fireweed rust.

Less than 45% of surviving plants had flowered by the end of the experiment in early spring. Plants were tall and spindly and possessed very few branches. Fireweed which did flower produced on average up to only three capitula per plant. On an area basis, this was equivalent to 2850 capitula m^{-2}. The number of viable seed per capitula was not measured, but appeared to be less than optimal due to poor plant growth and rust damage.

DISCUSSION

Germination and Seedling Emergence

For weeds, physiological uniformity increases the probability of chance annihilation. Heterogeneity in contrast is advantageous (Koller 1964). The inherent variability of fireweed was expressed in this study by the occurrence of germination outside the optimal environmental periods. Although most seedlings emerged during flushes in autumn and spring, as was found by Fernández and Montes (1984) in Argentina, small numbers were able to emerge at all times of the year.

This staggered pattern of germination and emergence is also found in other weeds (Popay and Roberts 1970b; Reeves et al. 1981). It ensures that some seedlings will survive even if many are killed by adverse conditions, such as moisture stress, during establishment.

Table 5.1 Growth data for fireweed at a high initial density (>5000 plants m^{-2}). Values in brackets are standard deviations.

Parameter	Date 19/3	2/4	23/5	14/7	18/8	18/9
Density 100 cm^{-2}	58.5 (7.4)	53.3 (6.7)	44.3 (5.2)	25.0 (6.9)	21.5 (3.1)	21.8 (4.3)
No. leaves[A] $plant^{-1}$	6.19 (2.12)	6.58 (2.38)	7.77 (7.46)	6.54 (3.99)	7.10 (5.50)	9.66 (6.41)
Plant height cm	6.82 (2.12)	8.04 (2.64)	13.61 (4.38)	15.70 (6.62)	19.41 (7.86)	18.45 (6.73)
No. plants flowered 100 cm^{-2}	- -	- -	3.5 (2.1)	6.0 (2.8)	9.5 (3.5)	6.5 (0.7)
No. capitula flowering $plant^{-1}$	- -	- -	16.0 (1.4)	17.0 (11.3)	28.5 (9.2)	14.5 (0.7)
Shoot dry wt. g 100 cm^{-2}	2.17 (0.38)	2.58 (0.19)	4.30 (1.38)	3.23 (0.23)	3.91 (0.77)	3.45 (0.39)

[A] Green leaves > 1 cm long.

Because the periodic large flushes of emergence occur over several months during autumn and spring, timing of control measures becomes very difficult.

Seed polymorphism

One possible cause of this intermittent pattern of seedling emergence is seed polymorphism. This occurs when a single plant produces more than one type of seed. Each seed type has distinct physiological responses (Harper 1957; Williams and Harper 1965; Cavers and Harper 1966; Harper 1977). Seed polymorphism is readily interpretable as an adaptation to life in an environment that is heterogeneous at the scale relevant to seedling establishment (Harper 1977).

The three seed morphs found in fireweed (see Chapter 2 and Plate 2.4) occur in the following percentages - light brown 80%, dark brown 9% and green 11% (Alonso et al. 1982). Dark brown and green seeds are situated on the periphery of the receptacle of the capitulum and appear to be associated with the male sterile ray florets. Fernández (unpublished data) has shown that seed polymorphism in fireweed results in different rates of emergence and levels of dormancy. Light brown seeds emerge quickly while dark brown seeds have a comparatively high level of dormancy. Light brown seeds appear adapted to take advantage en masse of disturbed or otherwise favourable conditions (e.g. in crops). Dark brown seeds in contrast seem more important for the persistence of the weed under conditions unfavourable for establishment (e.g. in pastures). Green seeds show intermediate responses. The three seed types do not differ significantly ($P=0.05$) in mean weight or length (Alonso et al. 1982).

Seasonal climatic influences

The almost identical seasonal pattern of emergence shown by fireweed at the three sites in this study suggests that it was climatic conditions which were directly or indirectly responsible for the pattern of germination. Temperature was likely to have influenced the periods in which peak emergence occurred, but within those periods flushes of germination were closely related to the occurrence of high rainfall. At Hoxton Park, a dry summer prior to the autumn break in 1987 led to a decline in pasture density and vigour, and indirectly resulted in a large germination of fireweed. The same result was observed by farmers in the survey of Chapter 3.

As occurs with other annuals (Donald 1951) the size of fireweed flushes and resulting population densities varied greatly from year to year and between sites (compare Figures 5.3 and 5.4; and 5.9a and 5.9b).

Influences of vegetation

In this study vigorous pasture growth during the winter and spring of 1987 was found to prevent substantial emergence of fireweed despite favourable climatic conditions for germination. In the absence of pasture, or when pasture growth was less vigorous in spring, germination and emergence was considerable. The inhibitory effect of vegetation on the germination of weed seeds and on seedling emergence is a well-known phenomenon (Harper 1957; Sagar and Harper 1960; Popay and Roberts 1970b; Phung and Popay 1981); it would also seem to be an important factor in the ecology of fireweed. Such inhibition of fireweed may be partly due to the responsiveness of its seed to light (see Chapter 2). Although the light requirement for germination is generally lost with time (Egley and Duke 1985), light which is filtered through leaf canopies is known to inhibit or retard seed germination of many species (Górski et al. 1978). It is not surprising then that fireweed, in common with other weeds (Popay and Roberts 1970b; Tothill and Berry 1981), appears to exploit open spaces.

Mortality and Survival

Fireweed has high natural mortality caused by various biological and environmental stresses. Considerable death of seedlings occurred under both grazed and ungrazed conditions. At the Hoxton Park site, over all cohorts during 1986 and 1987, 44% of seedlings died in the first month after germination. This percentage is likely to be an underestimate because it does not account for seedlings which emerged and died before being counted. The mean life expectancy (calculated from the mean time from emergence to 50% survival of each accession) was only 1.5 months. This compares with 2.8 months obtained for Emex australis (Weiss 1981), and is strongly correlated with the low juvenile survival of most pioneer and colonising species (Harper 1965).

In the ungrazed environment of the Camden sites the mean life expectancy was 3.7 months (over both sites). This higher figure is reflected in the number of plants behaving as biennials at these locations.

Fireweed seedlings resulting from an early autumn break, or those emerging in early spring, were able to grow rapidly, flower and set seed before growth was slowed down either by low winter temperatures or hot, dry summer conditions respectively. It is evident that the earlier autumn accession plants and large over-summering fireweed (often biennial in nature) have the potential to contribute the greatest number of new individuals to the fireweed population. These plants therefore should be particularly targeted for control.

Life cycle strategies

Fireweed, like S. vulgaris (Harper 1977), has indeterminant growth. If environmental conditions are suitable, it may begin to flower when small and continue to grow, flower and set seed until it dies from some extrinsic cause, e.g. drought. Harper (1977) considers this an opportunistic life; if plants die young they may leave some progeny, but they may also exploit a very long growing season. In this way fireweed can produce greater quantities of seed as the season passes.

Over-summering fireweed plants occurred primarily in the ungrazed habitats at Camden and not in the grazed and more competitive pasture at Hoxton Park. It appears, therefore, that their ecological significance may be in maintaining a seed bank of fresh viable propagules for reinfestation. Roberts and Boddrell (1984) suggested that in ruderal communities subject to occasional disturbance, both the time of year at which seedlings can establish and the presence of viable seeds are relevant to the persistence of the species. Hence over-summering plants may augment autumn seedling populations with those arising from freshly-shed, non-dormant seeds. The life cycle strategy (annual or biennial) adopted by individual fireweed plants, like Carduus nutans (Popay and Thompson 1979), probably depends both on the actual date of emergence and on external factors, of which the most important is possibly pasture competition.

Influence of fertilising

The application of fertiliser which stimulates pasture growth appears to reduce the survival of young seedlings through competitive effects, but established plants may develop more quickly.

Influence of grazing

Although small fireweed seedlings are sometimes eaten by cattle when pastures are grazed heavily, most seedlings utilise the improved light environment to quickly grow above the pasture canopy. Once the plants are distinguishable to cattle they are rarely grazed. The advantage to fireweed is increased if the pasture remains short and the soil is fertile or has recently been fertilised; plants will grow rapidly and flower more profusely. Forcella and Wood (1986) found that Cirsium vulgare plants under grazed conditions weighed more and produced more heads and seeds per head than those in ungrazed pasture. Density of thistles was higher and seedling survival and establishment also greater due to the effects of grazing.

Influence of slashing

The results of this study confirm that slashing of fireweed early in its life cycle reduces its rate of survival. Although plants not killed will regrow, flower and set seed, early slashing may be advantageous in an integrated program of control. The effect of slashing is improved dramatically if repeated one or two months later (see Chapter 2). The effect of early slashing on final flower numbers has yet to be studied.

The benefit of slashing late in the life cycle of fireweed is doubtful, particularly if seed has already been set. Slashing caused many older flowering plants in the present study to reshoot and over-summer. Likewise, cutting the flowering stems of S. jacobaea stimulates regeneration from the base, thereby converting biennials to perennials (Poole and Cairns 1940).

Uprooted plants

Gill (1938) demonstrated that many temperate species, particularly those among the Asteraceae, including S. vulgaris, produce viable seed even if the parent plant is cut down at the time of flowering. The ability of fireweed to set viable, non-dormant seed after being uprooted during flowering suggests that seed ripening is not strongly dependent on favourable environmental conditions, or, in the words of Bunting (1960), 'on the chances of ecological fortune'.

In terms of hand control of fireweed, the experiment served to emphasise the importance of removing fireweed from the paddock in addition to uprooting it. There is a risk of plants re-anchoring into the soil or setting seed if they are dropped back on the ground in wet weather. Poole and Cairns (1940) advised that in general farm practice S. jacobaea plants which were cut during flowering should be burned.

High densities

Soil disturbance is known to increase the emergence of weed seedlings (Egley and Duke 1985), but in general it does not alter the relative periodicity of germination or promote emergence at times outside the period of natural emergence (Froud-Williams et al. 1984). The large germination of fireweed (> 5000 plants m^{-2}) investigated at Albion Park was stimulated by cultivation and promoted by high rainfall in January 1986. At such high densities, growth and flowering were severely restricted and the environment proved conducive to rust infection and spread. The drastic reduction in reproductive capacity of fireweed plants due to intraspecific interference gives continued support for the idea of fireweed control through interspecific pasture competition.

CONCLUSIONS

The population ecology of fireweed suggests that it is not only a weed likely to produce massive invasions in disturbed environments (Grime 1979), but as well may persist in ruderal habitats (Thompson and Grime 1979). My own observations show this to be the case.

The detached viable seeds present on or below the soil surface, the 'seed bank' (Harper 1977; Thompson and Grime 1979), are an integral part of a fireweed population and are largely responsible for the perpetuation of the weed. Although management of fireweed seed banks will be needed to give long-term control, their dynamics, including longevity, still require investigation.

A comparison of fireweed in matching grazed and ungrazed pastures may reveal sensitive stages in the life cycle of the weed and provide more information on which to base strategies for effective control. Some knowledge of the agency responsible for the death of large, apparently healthy fireweed plants would also greatly assist in understanding population decline.

Control of fireweed is made difficult by its staggered patterns of emergence and flowering. Popay and Thompson (1979) and Popay *et al*. (1987) suggest that for *Carduus nutans* in New Zealand, control is best achieved by maintaining a vigorous pasture. For fireweed, such a pasture is likely to impede germination and emergence and increase the already high seedling mortality rate. Fertiliser application may aid this process.

If seedling emergence can be limited to one brief period following the autumn break when pastures are barest, then most fireweed could be controlled soon after by a single herbicide application. Any management practice which might help synchronise this emergence, such as pasture harrowing, may enhance the effectiveness of the control procedure. The time taken then for the seed bank to become exhausted would depend on the longevity of fireweed seed in the soil.

Because fireweed germination is promoted by cultivation and occurs in both autumn and spring, it cannot be readily avoided in the establishment of new competitive pasture species. This contrasts with variegated thistle (*Silybum marianum* (L.) Gaertn.) which, because of its strict seasonal emergence, can be avoided in the establishment of lucerne by sowing in the spring (Michael 1968c; 1970).

Chapter 6
THE EFFECT OF FROST ON FIREWEED

'Temperature extremes are of great ecological significance and both heatwaves and frosts can markedly influence the seasonal growth pattern and composition of pasture communities.' (Fitzpatrick and Nix 1970)

INTRODUCTION

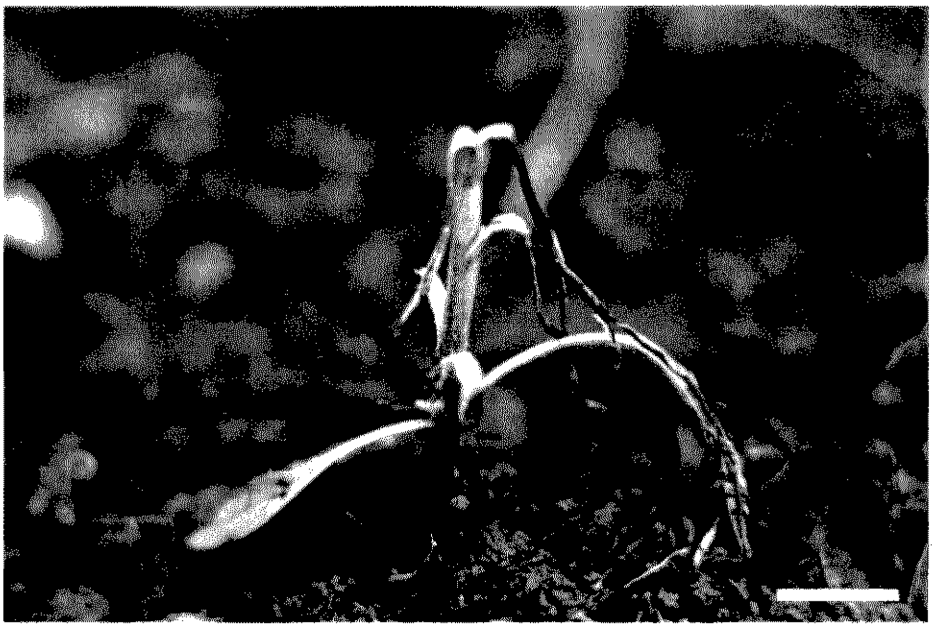
In a field trial near Camden, New South Wales, in June 1986, considerable mortality of 8 week old fireweed seedlings (10 leaf stage) followed 3 consecutive days of heavy frosts (-7, -6 and -8°C grass minimum temperatures) soon after transplanting (see Plate 6.1). Naturally occurring seedlings were also affected. In the population studies detailed in Chapter 5, seedling damage in the field was likewise thought to be caused by frost.

Although experimental work has shown something of the effect of temperature on the germination and growth of fireweed (see Chapter 2), little is known concerning the influence of frost on its survival, demography or geographical distribution. Fernández and Montes (1984) alone referred to the susceptibility of S. madagascariensis to frost, until the 10 leaf stage. After that, according to the authors, lignification and leaf thickening make plants much less susceptible. Unfortunately they gave no details of the type or severity of frosting, the conditions of growth or the degree of frost injury. Harper and Wood (1957) noted that severe frost may kill the above ground parts of S. jacobaea. Although young rosettes then regenerate from the remaining crown and root fragments, they are also very liable to frost injury (Poole and Cairns 1940).

Low temperatures in themselves are not normally injurious to plant tissues. Frost damage is brought about by the effect of ice crystals within tissue (Single 1971). The commonest mechanism,

Plate 6.1 An 8 week old fireweed seedling showing frost damage soon after being transplanted to the field. Scale bar = 1 cm.

Plate 6.2 Double potting (12 cm diam. pots) and dry vermiculite mulch provided insulation of the soil medium during frosting. Thermocouples attached to leaf surfaces measured temperatures in the frost chamber.

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extracellular freezing (Levitt 1956), leads to the extraction of water from nearby cells causing them to die of drought. If the crystals actually enter the cells, they disrupt the fine structure of the cytoplasm and cause immediate death (Siminovitch and Scarth 1938; Dexter 1956). In Australia, frost is usually associated with some deposition of moisture, either as dew or 'hoar' frost (Single 1975). If the dew forming on a plant freezes and contact is made with the plant sap, it too becomes frozen (Single 1971).

The intention of this preliminary study was to observe the effects of frost on the growth and survival of fireweed under well defined conditions and to assess its possible ecological significance. The extent of frost injury in plants varies with temperature and stage of plant growth or maturation (Dexter 1956; Kaku 1975). Accordingly, in the experiment recorded in this chapter, fireweed plants of different ages were subjected to varying degrees of frost. The temperature treatments were not meant to represent particular climatic regimes or be applicable in all field situations, but simply to provide a gradation of experimental frosts. It was hoped that the range of temperatures chosen would allow for the definition of the highest temperature causing injury (Olien 1967). Plant ages (or stages of growth) were chosen on the basis of observations of fireweed frosting already mentioned.

MATERIALS AND METHODS

To obtain fireweed seedlings of different age at the time of testing, seed was sown at intervals, beginning on 22 May 1987. Seed was collected from glasshouse grown fireweed near Camden in late 1986, and sown 2 mm deep in 1 l plastic pots (12 cm diam.) filled with a pasteurised mix of 1/3 sand, 1/3 loam, 1/3 peat and a basal fertiliser. The medium was watered once with 'Benlate' fungicide at a rate of 1 g l^{-1}. Seeds were germinated at room temperature (15°C night minimum and 25°C day maximum) and the pots transferred to an outdoor shade house (50%) at Camden. For the period of growth before testing the plants were hardened but kept protected from the direct effects of naturally occurring frosts. Maximum and minimum temperatures recorded for that period outside the shade house are given in Appendix 8. Inside the shade house maximum and minimum temperatures were 1-2°C lower and higher respectively.

Seedlings were selected for uniformity and thinned to four plants per pot. Pots received fortnightly 50 ml applications of 'Aquasol' complete nutrient solution (23% N, 4% P, 18% K and trace elements) and were watered every second day. The fungicides 'Bayleton' (5 g l^{-1}) and 'Zineb' (1.25 g l^{-1}) were applied as required to control fireweed rust. In order to provide insulation and prevent freezing of the medium, dry vermiculite was spread on the soil surface to a depth of 1 cm immediately prior to frosting, and each pot placed in another pot of the same size (see Plate 6.2).

The experiment tested the effect of five frost/temperature treatments (control - no frost; simulated frosts of -3, -4 and -5°C; and a field frost) on fireweed of six different ages (10, 8, 6, 4, 3 and 2 weeks from emergence). The highest temperature (-3°C) was fractionally below the grass minimum temperature at which frost is initiated (Single, personal communication), and commonly occurs in frost affected areas. The simulated frosts were conducted on consecutive days. Plant ages were replicated five times (i.e. five pots) and completely randomised within temperature treatments. Hence 30 pots of fireweed were subjected to each frost/temperature treatment. The nature of the experimental apparatus and the time involved in simulating each frost meant that temperatures were unreplicated.

Some of the morphological characteristics of fireweed at the time of frosting are shown in Table 6.1 and Plate 6.3 a,b,c.

Simulated Freezing Tests

The frost simulation tests were carried out at the New South Wales Department of Agriculture Research Centre, Tamworth, using the method described by Single and Marcellos (1974). Fireweed plants were placed in a forced draft freezing cabinet constructed entirely of 30 cm thick polystyrene, with internal dimensions 1.3 m x 1.3 m by 2.4 m high. Chilled air was continuously circulated downwards over the plants. Plant temperatures, as indicated by 0.25 mm thermocouples attached to leaf surfaces at different heights (see

Table 6.1 Morphological characteristics of fireweed at six ages tested for frost susceptibility. Values in brackets are standard deviations.

	Plant group (age in weeks)					
Parameter	1.(10)	2.(8)	3.(6)	4.(4)	5.(3)	6.(2)
Plant height mm (n=24)	129 (16)	83 (14)	51 (6)	32 (5)	22 (4)	16 (2)
Stem diam.[A] mm (n=5)	2.9 (0.3)	2.0 (0.2)	1.3 (0.3)	0.8 (0.1)	0.7 (0.1)	0.5 (0.1)
No. leaves[B] (n=24)	12.9 (2.5)	9.5 (0.9)	5.7 (0.6)	2.0 (0)	1.0 (0)	0.1 (0.3)
Secondary shooting[C]	X	X	X			
Stem elongation[D]	X	X				
Capitula present	X					
Descriptive stage[E]	I	E	6	2	1	C

[A] Measured 1 cm from the base of the plant.
[B] Primary leaves > 5 mm in length.
[C] In leaf axils.
[D] Above cotyledons.
[E] I = Inflorescence initiation; E = Elongation; 6 = 6 leaf; 2 = 2 leaf; 1 = 1 leaf; and C = Cotyledon.

Plate 6.3 Morphology of (a) 10 and 8, (b) 6 and 4, and (c) 3 and 2 week old fireweed plants (right to left) at the time of frosting, in 12 cm diameter pots.

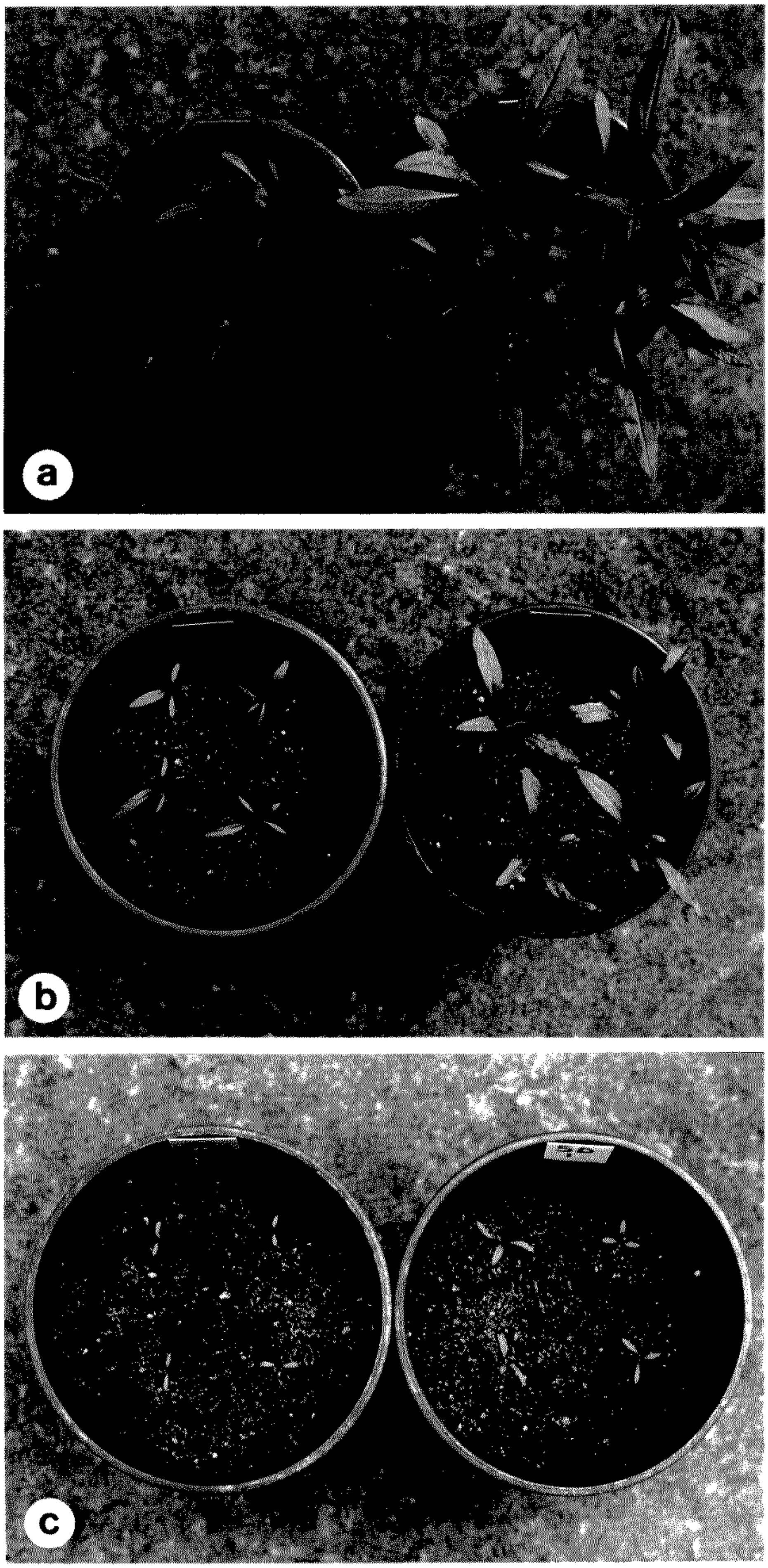

a
b
c

Plate 6.2), were controlled to ± 0.1°C of the desired temperature. No spatial variation in temperature greater than the sensitivity of the potentiometric recorder used could be detected.

When the plants had supercooled to -2.0°C they were sprayed with a fine water mist, and nucleated with a cloud of carbon dioxide crystals. The latter was generated from a brief burst from a carbon dioxide fire extinguisher inserted into the air stream within the chamber. This caused immediate general freezing as shown by a temperature rise at all 16 metered points.

After initiation of freezing, the temperature of the plants was reduced to the desired level over a period of 1-2 hours and then held for a further 100 minutes. Refrigeration and air circulation were then stopped and the chamber door opened slightly to allow slow thawing. After 1 hour the plants were placed outside away from the influence of natural frosts. They were then watered to help alleviate any moisture stress caused by possible freezing of the soil, and subsequently returned to the shade house at Camden.

Field Test

In order to give credence to the results from the frost simulation tests, one frost/temperature treatment involved subjecting fireweed plants to a naturally occurring field frost. Owing to considerable cloud cover and mild temperatures at Tamworth at the time of the experiment, 30 pots were taken to Uralla some 90 km north west at an altitude of 1000 m. Plants were tested in an open paddock on the C.S.I.R.O. Tablelands Pastoral Research Station. Four thermometers placed at pot height recorded the minimum overnight temperature and pots were randomised over the same area as that of the simulated tests. The frost which occurred was unexpectedly severe, -7.5°C. Grass minimum temperature is usually 3 degrees below screen minimum (Marcellos and Single 1975). Although it was hoped that the field frost would be within the temperature range of the simulated frostings (-3 to -5°C), the results nevertheless gave some indication of the applicability of the frost chamber treatments to the field situation. Moreover, temperatures as low as -7°C are common in winter and early spring in many agricultural areas of Australia (Single 1975).

The experiment began with sowing seed for 10 week old fireweed plants (Group 1) on 22 May 1987; frosting occurred from 4-6 August; and plants were harvested on 31 August and dried at 80°C. Control plants were also taken to Tamworth but not subjected to any frost.

Assessment

In this preliminary experiment, visual assessment of initial frost injury was considered satisfactory rather than the use of an objective quantitative method, an example of which is given by Paton (1972). Damage was first assessed 1 day after testing and then scored by five observers 3 days later. At harvest, dry weight, height and flowering of plants were measured and the number of deaths recorded.

RESULTS

In general, frosting reduced flowering, height and dry weight of fireweed and considerably increased plant mortality. Frost affected plant parts were characteristically water soaked (Single 1975), and turned dark green then brown and shrivelled.

At the completion of each test all plants were frozen; leaves were dark green in colour, slightly translucent and showed transient wilting on thawing, owing to redistribution of water within the tissues. The soil media, as measured by thermocouples at 1 and 3 cm depths, did not freeze. This simulated the field situation well. Initial testing of fireweed began at -3°C and the subsequent temperatures of -5 and -4°C were chosen on the basis of the degree of injury sustained at the preceding temperature.

Visual Assessment of Injury 1 Day after Frosting

Minus 3°C

Some flower (capitula) buds, and the margins and apices of young emerging leaves in the leaf axils and at the apex of 10 week old plants, suffered partial frost necrosis. Margins and apices of some older leaves were very slightly affected. Flower buds were not yet exposed on 8 week plants but slight browning of leaf margins and tips again occurred. Some 6 week plants appeared almost wholly darkened, with leaf tip curling and shrivelling being common. Most 4 week plants were largely affected with some plants being expected to die (see Plate 6.4). Damage to 3 and 2 week plants was similar with leaf and cotyledon tip burn and curling. A few seedlings still appeared comparatively healthy.

Minus 4°C

Many more flower buds and emerging leaves at the top of 10 week old plants were browned off than at -3°C. In addition to margin and tip burn of older leaves a small number of plants had whole leaves affected. This trend continued for 8 week plants, and at 6 and 4 weeks most leaves had become darkened and shrivelled. The injury sustained was more severe than at -3°C. A few plants still appeared as though they would survive with cotyledons often remaining healthy despite other leaf injury. Stems of 3 and 2 week plants maintained their rigidity, i.e. cell structure of the stems had not broken down, but all leaves and cotyledons in the latter were totally frost burnt.

Minus 5°C

Injury was much more severe on the whole at this temperature than at -3 or -4°C, with nearly all leaves devastated and left lying prostrate on the soil. Only at the very base of some 10 and 8 week old plants were there a small number of shoots or leaves which were not totally frost damaged and which remained green. Stems of plants at the stage of elongation also appeared water saturated and wilted (or bent) above the cotyledons. Below the cotyledons the stems,

Plate 6.4 Four week old fireweed seedling showing leaf tip curling and shrivelling after frosting at -3°C. Scale bar = 1 cm.

Plate 6.5 Effect of temperature and plant age on the height of fireweed grown in 12 cm diameter pots, 3 weeks after frosting. At the time of frosting, treatments were: no frost, -3°, -4°, -5° and -7.5°C (rear to front) and 2, 3, 4, 6, 8 and 10 week old plants (left to right).

Plate 6.6 Reshooting of older fireweed plants (10 weeks) after being severely damaged by frost. Scale bar = 1 cm.

characteristically purple in colour and more lignified, appeared unaffected at all ages.

Minus 7.5°C

Stems above the cotyledons appeared more wilted and damaged at -7.5°C than at -5°C. The stem structure below the cotyledons in the 4, 3 and 2 week old fireweed seedlings had also broken down. This left the plants either bent or prostrate on the ground. The dark green water saturated appearance was more intense and decomposition of tissue more severe at this temperature than at -5°C.

Injury 3 Days after Frosting

Three days after frosting the degree of injury was assessed by observers who scored each plant with a number between 0 and 10. Zero represented no visible frost damage, 1 represented 10% damage and so on up to 10 which was equivalent to 100% or total shoot destruction. Mean scores, expressed as percentages, are graphed in Figure 6.1. The level of frost injury sustained by fireweed at -3°C increased dramatically between 6 and 4 weeks of age, while at -4°C damage rose sharply earlier between 3 and 2 weeks of age. At -5 and -7.5°C a high level of injury occurred at all ages, decreasing only gradually up to 10 weeks. Injury increased with decreasing temperature.

Effects on Flowering

Three weeks after testing, control plants in Groups 1, 2 and 3 (10, 8 and 6 weeks of age at the time of frosting) had reached their reproductive stage of development. In Group 3, however, no frosted plants were flowering (defined here simply as the production of capitula) nor were plants in Groups 1 and 2 which were subjected to -5 or -7.5°C frosts. Flowering at -4°C in Groups 1 and 2 was erratic and much reduced compared with -3°C and the control. The results for the control plants and those frosted at -3°C are shown in Table 6.2.

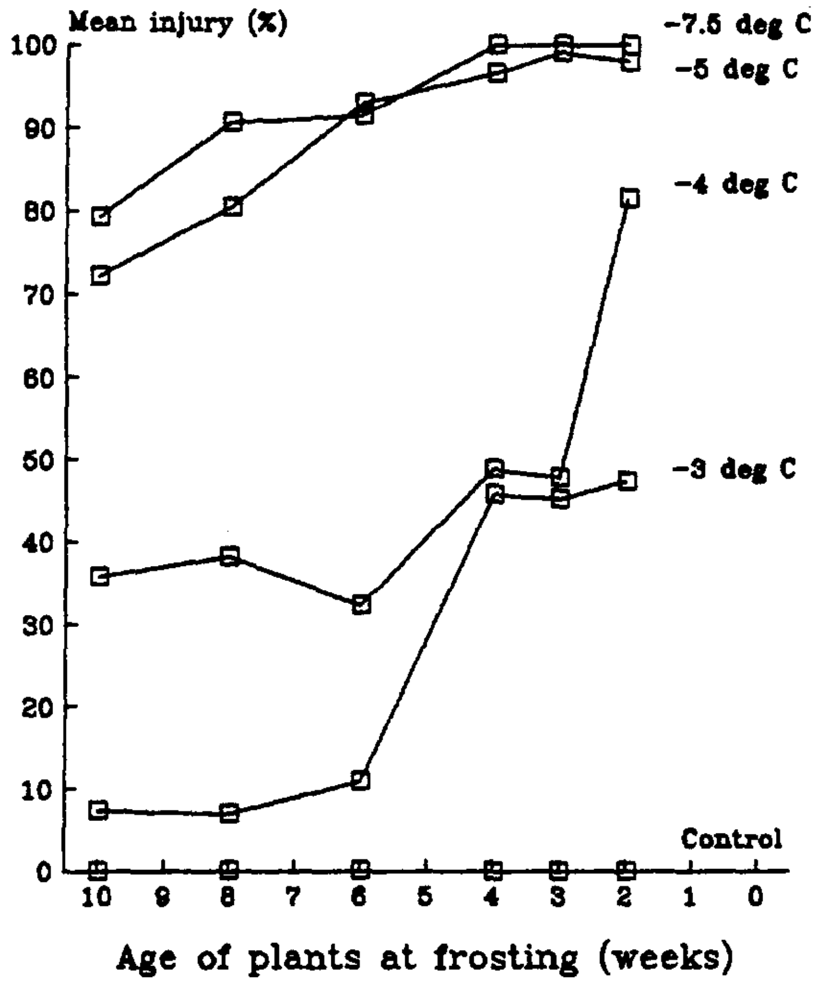


Figure 6.1 Mean percentage frost injury of fireweed as visually assessed by five observers 3 days after frosting.

Table 6.2 Mean number of fireweed capitula (> 1 mm diameter) pot^{-1} 3 weeks after frosting. Data on square root (x + 0.5) transformed scale. Values followed by the same letter are not significantly different at P<0.05.

	Plant group (age in weeks)	
Frost treatment	1.(10)	2.(8)
Control (no frost)	7.75 a	5.15 b
-3°C	5.36 b	3.03 c
lsd (P=0.05) = 1.22		

Flowering in both Groups 1 and 2, as measured by the number of capitula, was significantly reduced by frosting at -3°C (P=0.05). Although no analysis of variance was possible at lower temperatures, flowering clearly diminished.

Plant Height

Analysis of plant heights, measured at the same time as flowering, revealed considerable heterogeneity of variance for plants in the younger age groups (3, 4, 5 and 6) and more severe frost treatments (-5 and -7.5°C). This was due to a large number of plant deaths in these groups. The results were therefore examined in two separate analyses of variance in which heights for these two categories of plants were excluded in turn. The results are shown in Figure 6.2 a,b. The heights of 10 and 8 week old fireweed were significantly reduced (P=0.05) by frost 3 weeks after testing, with the most severe reduction for 10 week plants occurring between -4 and -5°C. Because of severe injury at -5°C no further reduction in plant height was recorded with a drop in temperature to -7.5°C in either group (see Figure 6.2a). Figure 6.2b shows that frosting, either at -3 or -4°C, reduced plant height at all ages compared with the control (P=0.05), but that for younger fireweed seedlings (6, 4, 3 and 2 weeks old), height was not significantly altered by a drop from -3 to -4°C. For 10 week old plants the height reductions at -3 and -4°C were equal to 25% and 51% respectively. The effect of frosting on plant height can be observed in Plate 6.5.

Shoot and Root Harvest

Shoot and root dry weights are given in Figure 6.3 a,b. Owing to plant deaths and the resultant heterogeneity of variance, data for the lowest temperature treatment (-7.5°C) were excluded from the analysis of shoot weight. For roots, only the three oldest age groups (1, 2 and 3) were harvested and weighed.

Shoot dry weight was significantly reduced by frosting (P=0.05), more so at lower temperatures. On a percentage basis, the reduction in shoot dry weight at each temperature generally decreased as plants

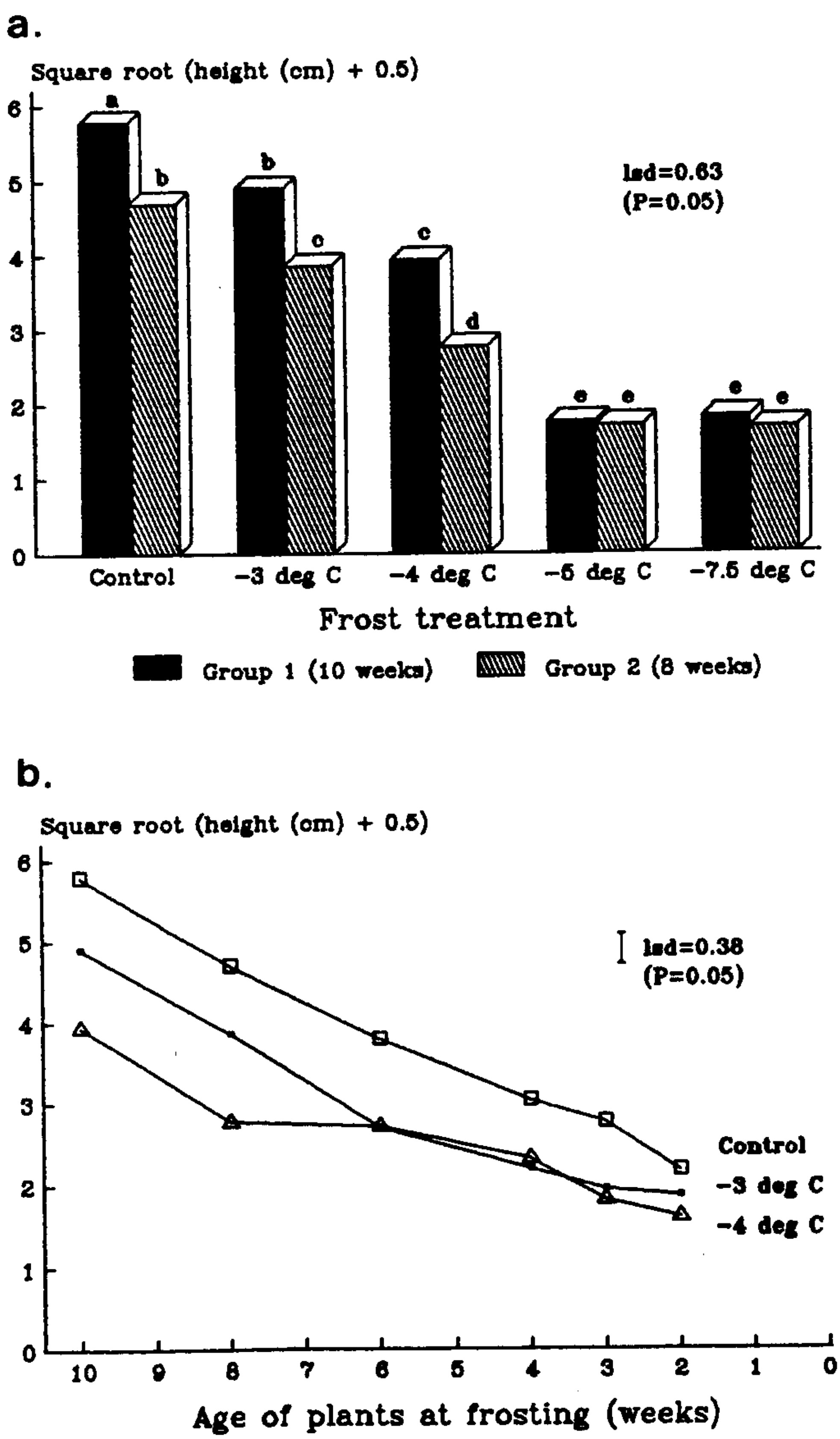
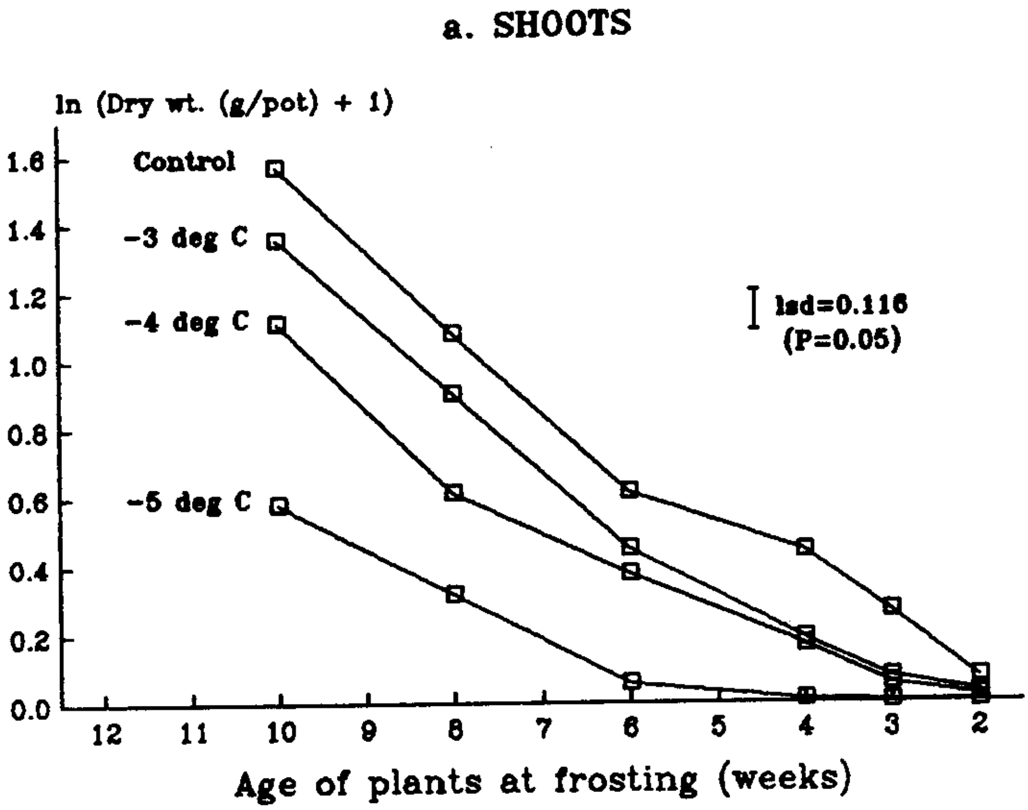


Figure 6.2 Height of fireweed 3 weeks after frosting for (a) all temperature treatments and plants of two ages (treatments with the same letter are not significantly different at P<0.05), and (b) three temperature treatments over all ages.



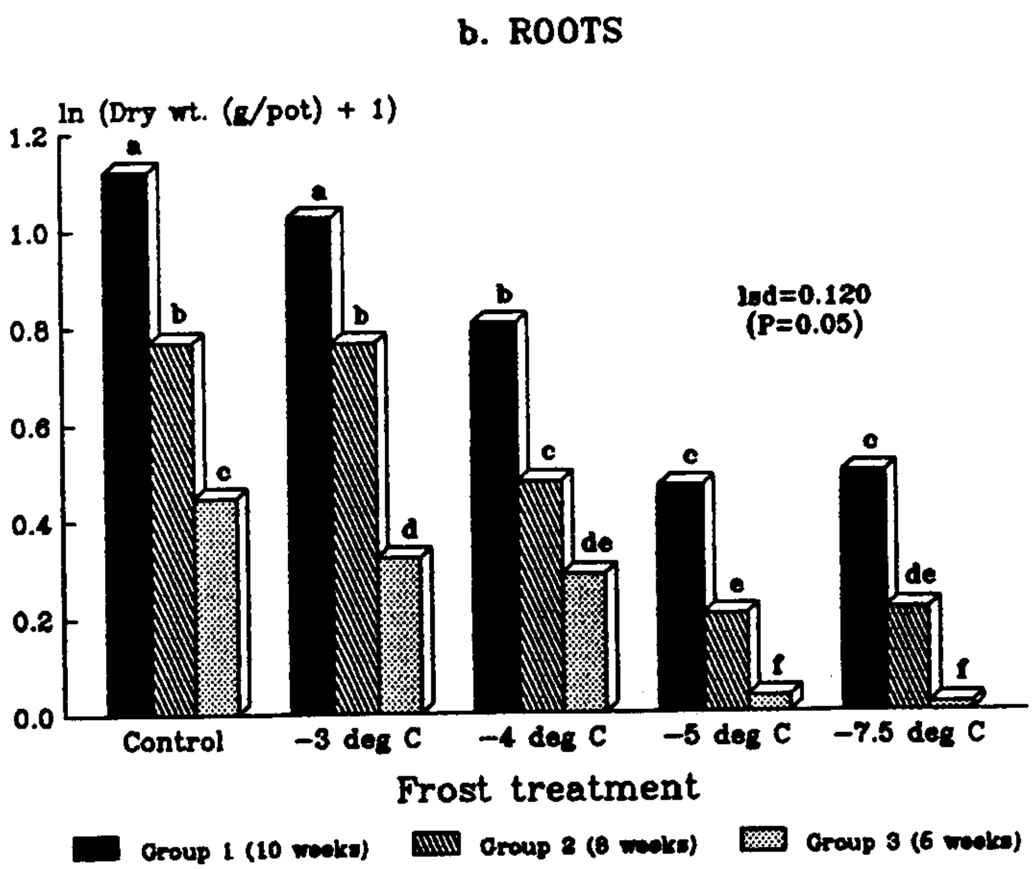


Figure 6.3 Dry weight of fireweed (a) shoots, and (b) roots, 3 weeks after frosting. Treatments with the same letter are not significantly different at P<0.05.

increased in age. Losses at -3°C ranged from 73.9% in 3 week old plants to 25.6% in 10 week plants.

The dry weight of roots was also reduced by frosting. Although only a light frost of -3°C was required to significantly affect root weight in 6 week old plants ($P=0.05$), a -4°C frost was required for 8 and 10 week plants. In all three age groups root weight further declined at -5°C but no difference was measured between -5 and -7.5°C.

At harvest, control plants from Groups 1 and 2 were at full flowering (ray florets of the capitula open) while Group 3 plants were just beginning to flower. Groups 4, 5 and 6 were all vegetative and at the 11-12, 8-9 and 5-6 true leaf stages respectively.

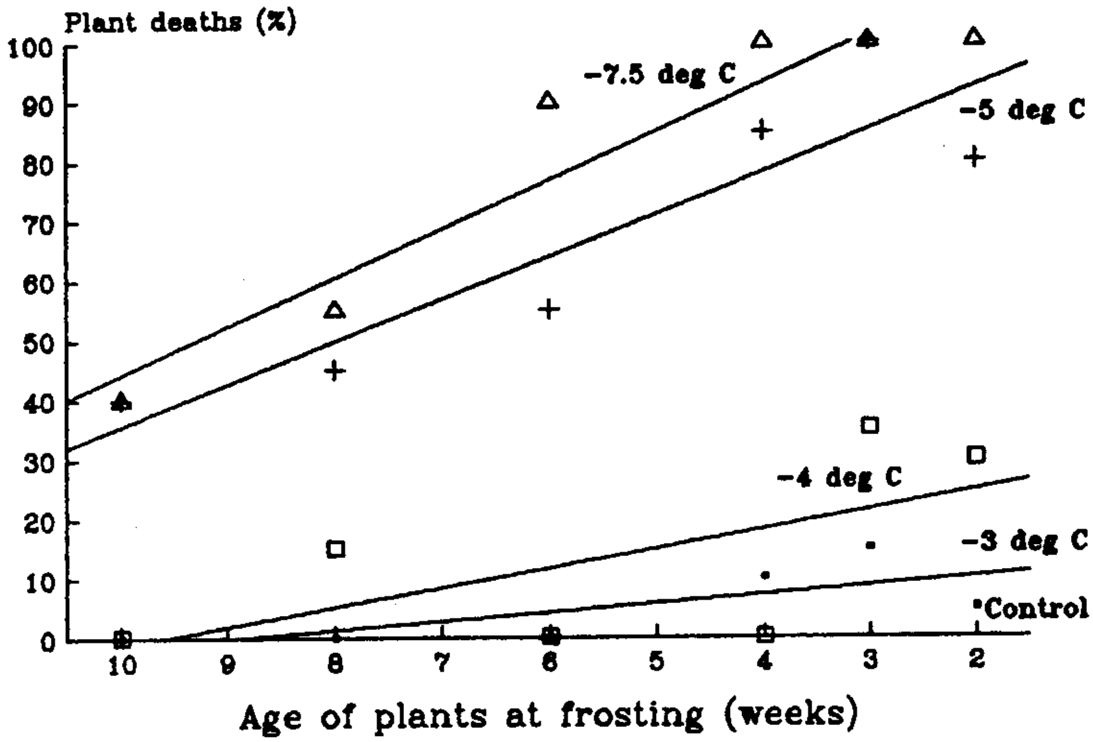
Fireweed Mortality

Although some fireweed, particularly more mature plants, were able to reshoot from leaf axils after being severely damaged by frost (see Plate 6.6), many deaths still occurred. Plants were considered dead at the time of harvest if they no longer retained green plant tissue, or in fewer instances where remaining green tissue was chlorotic and the plant appeared close to death.

The percentage number of plant deaths for each treatment are plotted in Figure 6.4. Regression analyses were conducted to give lines of best fit. These clearly show that fireweed mortality as a result of frosting increased both as seedling age and frosting temperature decreased, and at an increasing rate when the two factors acted concurrently (measured by the relative slope of the lines, i.e. the 'b' value in the equation $y = a + bx$). Plant death was appreciably higher at -5 and -7.5°C than at -3 and -4°C.

DISCUSSION

Fireweed grown and tested under the conditions of this experiment showed typical symptoms of frost injury (Dexter 1956; Single 1971). The tips of the leaves were the first to be injured and the amount of dead tissue increased more or less uniformly from the tip of the leaf



<u>Regression Equations</u>

-3°C	y = 13.1 - 1.47 (0.71)x	R^2 = 51.6%	P<0.108
-4°C	y = 31.3 - 3.26 (2.02)x	R^2 = 39.4%	P<0.182
-5°C	y =107.0 - 7.11 (1.68)x	R^2 = 81.6%	P<0.014
-7.5°C	y =126.0 - 8.16 (1.38)x	R^2 = 89.8%	P<0.004

'y' is the percentage of plant deaths and 'x' is the age of plants (weeks) at frosting. Values in brackets are standard errors of the preceding value (i.e. the slope of the line or the rate of plant deaths).

Figure 6.4 Percentage of plant deaths of fireweed 3 weeks after frosting.

to the crown of the plant. Young, rapidly growing tissues were worst affected with stems and leaves becoming water soaked and shrivelled.

Visible frost injury and plant mortality rate both indicated that young fireweed seedlings are more sensitive to frost than older plants, and that sensitivity increases with lower temperatures. Flowering, plant height, shoot weight and root weight were all significantly reduced ($P=0.05$) as a result of frosting. The injury which was sustained at any age generally increased with decreasing temperature. Frosting also made plants more prone to disease infection, so that even when regeneration of shoots occurred plants often died.

Artificial and Natural Frosting

Controlled freezing tests have been shown to give a reliable estimate of the behaviour of different plant varieties in the field and the technique has been widely accepted (Dexter 1956; Single 1961; Thomas and Lazenby 1968; Hacker et al. 1974; Levitt 1980). Various parameters of the technique itself, such as rates of freezing and thawing and duration of freezing, can affect frost injury in plants (Peltier and Tysdal 1932; Levitt 1956; Gusta and Fowler 1977; Levitt 1980). Therefore, frost testing of fireweed in this study was simulated to reflect the stress factors that occur under natural conditions.

Although the frosts produced in this study were of advective rather than radiative origin (as occurs in nature), whole freezing of the fireweed plant was obtained, without substantial supercooling (Aston and Paton 1973). This was achieved by spraying water on the plant surfaces. Moreover, the test plants did not possess nodes which in some species obstruct movement of the ice front (Single 1971; 1975).

Good correlation existed between the results obtained from artificial freezing and field frosting. As might be expected the field frost of -7.5°C caused greater damage and mortality to fireweed than controlled freezing at -5°C. For example, damage of the lignified stem section below the cotyledons only occurred at -7.5°C.

However, because damage at -5°C was already very severe the differences between the two temperatures, in terms of height and weight, were not significant (P=0.05). Plants subjected to the simulated frosts reacted, as far as could be observed, in the same way as those frosted under natural conditions. Hence the results obtained at -3, -4 and -5°C in the controlled temperature chamber appear to be indicative of behaviour in the field at comparable temperatures.

Frost Tolerance and Cold Hardening

It is not uncommon according to Dexter (1956) for certain susceptible species to be frozen almost to ground level and yet to survive. Known as frost tolerance, this ability to tolerate ice formation in tissues without injury is usually (but not always) increased by cold hardening, the exposure to non-lethal low temperatures (Levitt 1980). In this experiment, all 8 and 10 week old fireweed seedlings were frozen at -3°C but no deaths were recorded amongst them and visible injury was minimal. Plant vigour, as measured by flowering, shoot height and shoot weight, was reduced, possibly because of inhibited carbon dioxide uptake (Bauer et al. 1975) and reduced photosynthesis (Marcellos 1977). These results offer no direct evidence on the role of hardening in the survival of fireweed. But it would seem that fireweed seedlings are capable of hardening since even very hardy plants, such as winter wheat, can be killed at above -3°C when in the unhardened state (Single, personal communication). Therefore the frost-killing point of fireweed at any one stage of development may not be constant, but may vary markedly with the temperature conditions under which the plants grow. Other environmental factors such as light, photoperiod, water and nutrients can also alter frost resistance but are less important (Hodgson 1964; Klebesedal et al. 1964; Kohn and Levitt 1965; Levitt 1980).

In the field, cold-tolerance generally increases through the autumn and persists until temperatures rise in the following spring. The threshold temperature above which hardening does not occur is usually 5-10°C (Levitt 1980). The degree of cold tolerance developed depends on the length and severity of the hardening conditions

(Peltier and Tysdal 1932; Kohn and Levitt 1965). Small differences in temperature may produce large differences in hardening (Dexter 1956).

Fireweed plants used in this experiment are most likely to have been less hardy and therefore more frost susceptible than if they had been germinated and grown in the field at the same time. This was ascribed to the shading effect and slightly elevated minimum temperatures in the shade house, and the comparatively rapid growth caused by watering and fertilising (Dexter 1933; Tysdal 1933; Dexter 1941; Cooper 1964; Smith 1964). The less than maximum winter hardiness attained, however, may have been at least partially offset because fireweed in the field usually germinates under warmer autumn and spring conditions rather than in early to mid winter as occurred in this experiment. Potentially, fireweed may be susceptible to early or late season frosts in some areas (see Foley 1945). Alternatively, when germination does occur in winter (see Chapter 5) seedlings may be killed. The proportion of fireweed seedling deaths in a field population (see Chapter 5) attributable to frosting has not been studied.

Ecological Significance of Frosts

Frosts are of great ecological significance and can markedly influence the seasonal growth pattern and composition of pasture communities (Fitzpatrick and Nix 1970). Response to minimum soil temperature at or below freezing level is known to affect the geographical distribution of Cyperus weed species in North America (Stoller 1973). But the influence of frost on weeds has rarely been examined. Williams and Groves (1980) made a brief study of frost effects on the growth and survival of Parthenium hysterophorus. They concluded that because of the short time to flowering the weed should be able to establish and reproduce for much of the year in Australia even in regions with seasonal heavy frosts.

Nevertheless, based on the results of this experiment, frost would seem to be an ecological factor which can limit growth and distribution of fireweed in some areas of Australia. It may keep populations small and non-aggressive in cold tableland areas, and help prevent seedling establishment in the winter months in otherwise climatically suitable areas.

Frost incidence in any one area is highly variable from year to year, and the probability of early frosts in autumn and late frosts in spring may be of considerable ecological importance (Fitzpatrick and Nix 1970). In Figure 6.5, areas are delimited by dates which represent one standard deviation prior to the mean date of the first occurrence of a grass minimum temperature below -3°C in autumn, and one standard deviation after the mean date of the last occurrence in spring. The present distribution of fireweed along the south-eastern coast of Australia clearly lies in areas with short frost periods. As the duration of the frost period increases (particularly > 150 days) the chance of fireweed infestations occurring decreases. This is particularly evident in light of the main fireweed germination periods as identified in Chapter 5.

The sub-tropics of south-eastern Queensland were identified in Chapter 4 as possibly the most vulnerable area remaining in Australia for fireweed invasion. That area experiences only about two to thirteen frosts each year, with terrestrial minima within the range -2 to -4°C (Coleman 1964; Clements and Ludlow 1977). It is unlikely that these would be severe enough to prevent the spread of fireweed in that region.

CONCLUSIONS

Although the temperature at which frost damage of fireweed occurs will vary with environmental conditions prior to frost, it is possible from the results of this experiment to gain some idea of the range over which injury is likely. The upper limit at which significant damage could be expected was approximately -3°C for the material under examination. Resistance increases during seedling development up to at least the 12-15 leaf stage and may be greatly enhanced by a period of cold hardening.

Aspects not studied in this experiment include the extent and effect of the hardening process on fireweed frost tolerance, particularly

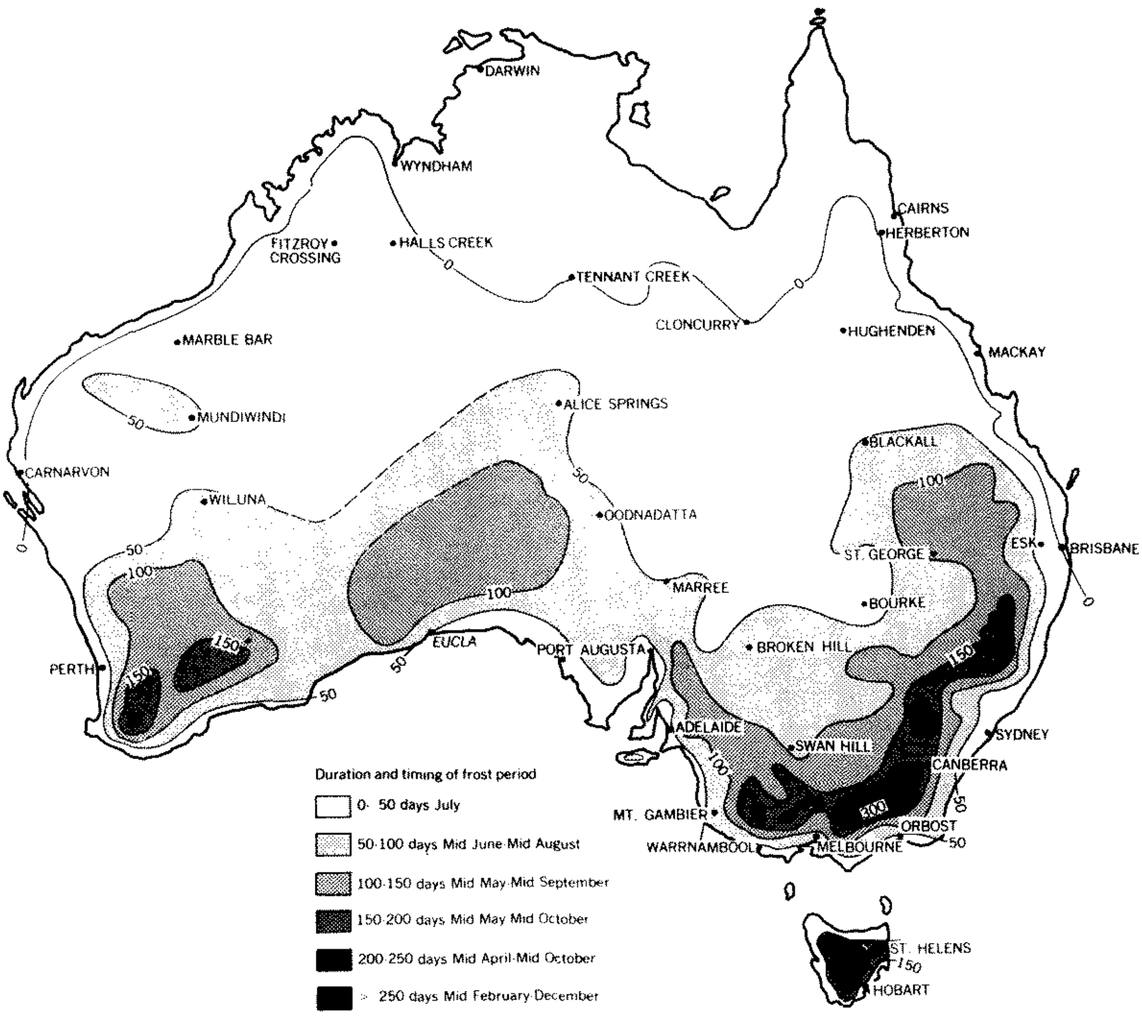


Figure 6.5 Duration and timing of frost periods in Australia (prepared by Fitzpatrick and Nix (1970) from data of Foley (1945)).

with field grown plants; the influence of frost at the time of flowering on seed set; and the effect of consecutive frosts on fireweed injury.

Because defoliation, especially when severe, has been reported to reduce cold tolerance in several herbage species (Biswell and Weaver 1933; Schmalz 1961; West 1962; Rogers 1964; Smith 1964; Thomas and Lazenby 1968), the possibility that fireweed may be more severly damaged by frost following slashing also warrants examination.

Chapter 7

THE IMPACT OF FIREWEED ON PASTURE PRODUCTION

> 'Saying that weed competition reduces crop yield is akin to proclaiming that the sky is blue and grass is green.' (Zimdahl 1980)

INTRODUCTION

Competition may be defined as 'the active seeking after, or utilisation of a given resource by two or more individuals of the same, or different species, the resource itself being actually or potentially limiting'. (Putman and Wratten 1984).

The majority of pasture weeds are regarded as such because they are not usually eaten by livestock, and occupy space and utilise resources apparently competing with forage plants for moisture, nutrients and light (Auld et al. 1979). These weeds may affect animal production by reducing (a) the area of pasture and its growth rate, and (b) the accessibility or availability of pasture to livestock. For example, Euphorbia esula L. at 50% cover has been known to decrease herbage production in pastures by up to 35% (Lym and Kirby 1987). Like various Juncus species (Hartley 1983a), they can also lead to considerable reduction in livestock carrying capacity. Hartley (1983b) demonstrated a significant negative correlation between Cirsium vulgare density and the liveweight gain of sheep.

Although there has been considerable documentation of the physical yield losses caused by weeds in crops, few production oriented estimates have been made of the impact of weeds in pastures. Attempts to establish the economic importance of such losses are even fewer. Weed species vary in their impact, but are commonly thought to cause reductions in pasture production of 10% or more in certain circumstances (Vere and Auld 1982).

The mail survey of Chapter 3 showed that 57% of all respondents believed that fireweed reduced crop or pasture productivity on their properties, and that 30% thought it diminished their available grazing area. The experiments reported here were undertaken to determine the nature and size of these losses at both low and high soil fertility, and to assess the practical importance of fireweed as a competitive weed.

The effect of increasing fireweed density on the growth and yield of Saia oats (Avena strigosa Schreb.) was investigated at the University of Sydney Agronomy Unit, Camden, under glasshouse conditions and in the field. Saia oats is a forage species often grown in fireweed-infested areas of eastern Australia.

MATERIALS AND METHODS

Glasshouse Experiment

Seed of Saia oats was purchased locally and fireweed seed collected in the field at The Oaks, New South Wales, immediately prior to the experiment in May 1985. Fireweed seeds were germinated on moist filter paper in petri dishes at 25°C and the oats in large trays at room temperature. Seedlings of fireweed were then transplanted at the cotyledon stage (2 weeks after placement in petri dishes) to 18 cm diameter black plastic bags. These were filled to a depth of 18 cm with clay loam surface soil obtained from an unfertilised area under native pasture at Camden. Prior to transplanting the seedlings, the soil was kept moist to induce germination of buried weed seeds which were then removed. Oat seedlings (6 days old) were transplanted 18 days after the fireweed. Pots of soil were maintained close to field capacity by regular watering. Glasshouse conditions ranged from 29 $\pm$ 3/10 $\pm$ 2°C day/night temperature at the start of the experiment to 32 $\pm$ 3/13 $\pm$ 2°C day/night temperature at the end of the experiment.

At potting up, a basal dressing of nitrogen (as urea) and phosphorus (as superphosphate) was mixed into the soil of each pot at rates of 20 and 10 kg ha^{-1} respectively. In addition, high fertility treatment pots received six 400 ml applications of 'Aquasol'

(23% N, 4% P, 18% K and trace elements) at fortnightly intervals, being equivalent to a total application of 216 kg N, 38 kg P, and 170 kg K ha^{-1}.

The experiment began on 17 June 1985 and plants were harvested on 8 October 1985 and dried at 70°C. Among the indices of growth of oats measured were tiller number and total dry weight. Measurements of fireweed included numbers of primary branches and heads (capitula), and dry weights of capitula, stems and leaves.

The experimental design was a randomised complete block factorial in which there were five replicates of each of the 10 treatments (two levels of soil fertility x five levels of fireweed density). In each pot there were two oat plants, 7.5 cm apart and fireweed at 0, 1, 2, 4 and 8 plants per pot or 0, 40, 80, 160 and 320 plants m^{-2}. Nine weeks through the experiment pots were rerandomised and spread from one to two benches.

Field Experiment

A field experiment was conducted in order to verify the glasshouse results and to provide field oriented data on pasture productivity losses. Preparation of the area involved spraying with the herbicide glyphosate at 2.16 kg a.i. ha^{-1} (as Roundup) in early February 1986. This was followed by forage harvesting to remove the plant residue and cultivating to produce a good seed bed. The soil, an acidic, red podsolic (Dr.2.21, Stace et al. 1968) of low fertility belonging to the Cumberland series (based on Wianamatta shale, Walker 1972), was the same as that used in the glasshouse. On 4 June Saia oats was sown using an Aitchison Seedmatic 800 at 90 kg ha^{-1} at a depth of 2.5 cm and with 15 cm between rows. Immediately after sowing, 'Starter 18' fertiliser was broadcast at a low rate (30 kg N/14 kg P ha^{-1}) and a high rate (120 kg N/55 kg P ha^{-1}). Fireweed seedlings were planted out some 12 days later after the oat seedlings had emerged and been counted to check for uniform establishment.

Fireweed seed collected near Dapto, New South Wales, in November 1985 had been germinated in Cellupak Planter 'speedling' trays in a 50%

peat, 50% vermiculite medium with added nutrients and watered fortnightly with 'Aquasol'. Seedlings were transplanted to the field at the 10 leaf stage (see Plate 7.1a) and the area irrigated as required.

Considerable damage occurred to young fireweed in late July following a series of heavy frosts but most plants recovered (see Plate 7.1b). An infestation of red legged earthmite (*Halotydeus destructor*) was controlled at the same time with dimethoate (as Rogor) applied twice, two weeks apart at a rate of 1.0 ml l^{-1}.

The first harvest of oats, simulating grazing to 2.5 cm above ground level, was at 11 weeks after sowing. The oats was 15 and 30 cm high in the low and high fertility plots respectively, and fireweed was in the early stages of flowering. The second harvest occurred at 15 weeks during profuse flowering and a third made 7 weeks later as fireweed began to senesce. Only the third harvest included both oats and fireweed. Measurements made were total fresh and dry weights, and fireweed plant diameter. All plant material was dried at 70°C.

The experimental design was a split plot factorial in which there were four replicates of each of the 16 treatments: two levels of soil fertility (main plots) x eight levels of fireweed density (sub plots). Sub plots were 2 m^2 in area (1.41 m x 1.41 m) and had an average oat density of 280 plants m^{-2}. The fireweed densities were 0, 1, 2, 4, 10, 20, 40 and 80 plants per plot or 0, 0.5, 1, 2, 5, 10, 20 and 40 plants m^{-2}. Each sub plot was divided into a grid of 80 squares (8 x 10). Fireweed plants were then randomly allocated, one per square, the number of squares depending on the treatment density. The experimental area is shown in Plate 7.2.

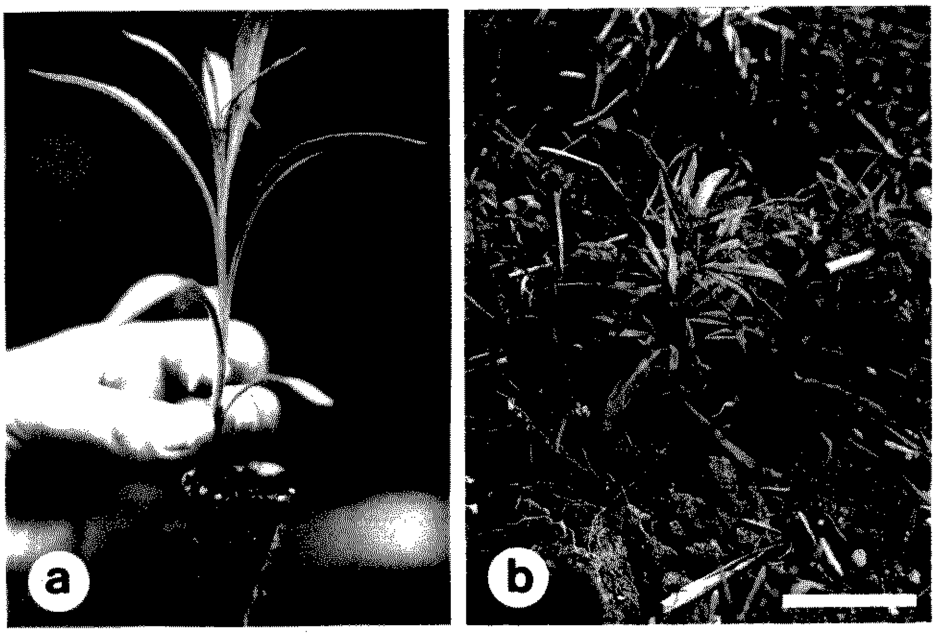
RESULTS

Glasshouse Experiment

Increasing fireweed density caused a significant decrease ($P<0.001$) in the number of tillers and total dry weight yield of oats at both soil fertility levels. The data approximate asymptotic or

Plate 7.1 Fireweed 'speedling' (a) at the 10 leaf stage, ready for transplanting to the field, and (b) competing with Saia oats after establishment (scale bar = 10 cm).

Plate 7.2 Layout of the field experiment at Camden, in which the effect of fireweed density on the yield of oats was measured. Fireweed is at full flowering.


a
b

hyperbolic relationships (see Figure 7.1 a,b). Owing to the comparatively high fireweed densities of the experiment (the lowest being equal to 40 plants m^{-2}), and to the space limitation placed on plants by their being grown in pots, it was not unexpected that the asymptotic relationship should occur. However, even in the field trial where much lower densities were included (as low as 0.5 plants m^{-2}), there was still no indication of the sigmoidal relationship often cited for weed competition (Zimdahl 1980; Roberts et al. 1982). Curves relating yield of oats to fireweed density (see Figure 7.2 a,b,c,d) generally showed an initial rapid decline followed by a longer, almost linear response. In fact, linear regressions accounted for 95.2, 94.7 and 91.7% of variation in the data at the three harvests and 97.4% in the combined data. In all but one case (High fertility - Harvest 3) quadratic effects were not significant at the 5% level. For comparison purposes, linear equations are given for each set of data (see Figure 7.2 a,b,c,d).

When the number of fireweed was equal to that of oats (two per pot), tiller production in the latter was reduced to 60% and total yield to 54% of the control over the two soil fertility levels. In other similar glasshouse work in which a number of annual and perennial pasture grasses and legumes were subjected to fireweed competition (see Chapter 10), the growth of nearly all species was suppressed more than Saia oats. Thus the strong competition with oats in the present study is evidence of the ability of fireweed to substantially reduce the productivity of a range of forage crops and pastures.

Fireweed reduced tiller production and yield of oats in absolute terms more under high soil fertility than low soil fertility (see Figure 7.1 a,b). On a percentage basis the reductions obtained for soil fertility treatments were not significantly different ($P=0.05$).

Competition from increasing densities of fireweed not only altered the growth and yield of oats but also resulted in various changes in fireweed itself. These changes are summarised in Table 7.1. As fireweed density increased, the number of primary branches and capitula, and the total weight of fireweed (composed of leaves, stems and capitula) also increased significantly ($P=0.05$). All values on

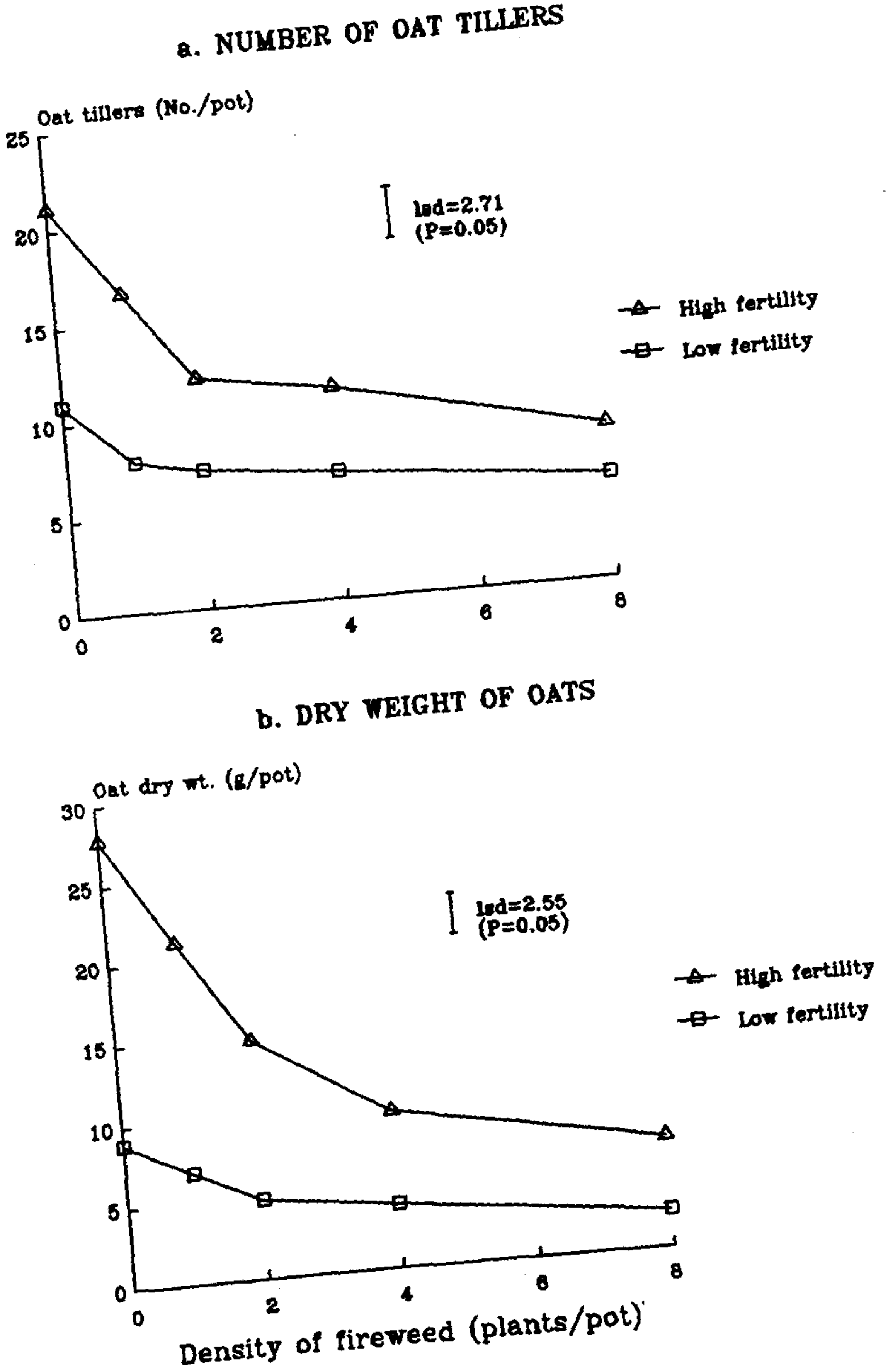


Figure 7.1 Effect of fireweed density on (a) the number of tillers, and (b) the dry weight yield of oats, in the glasshouse at high and low soil fertility.

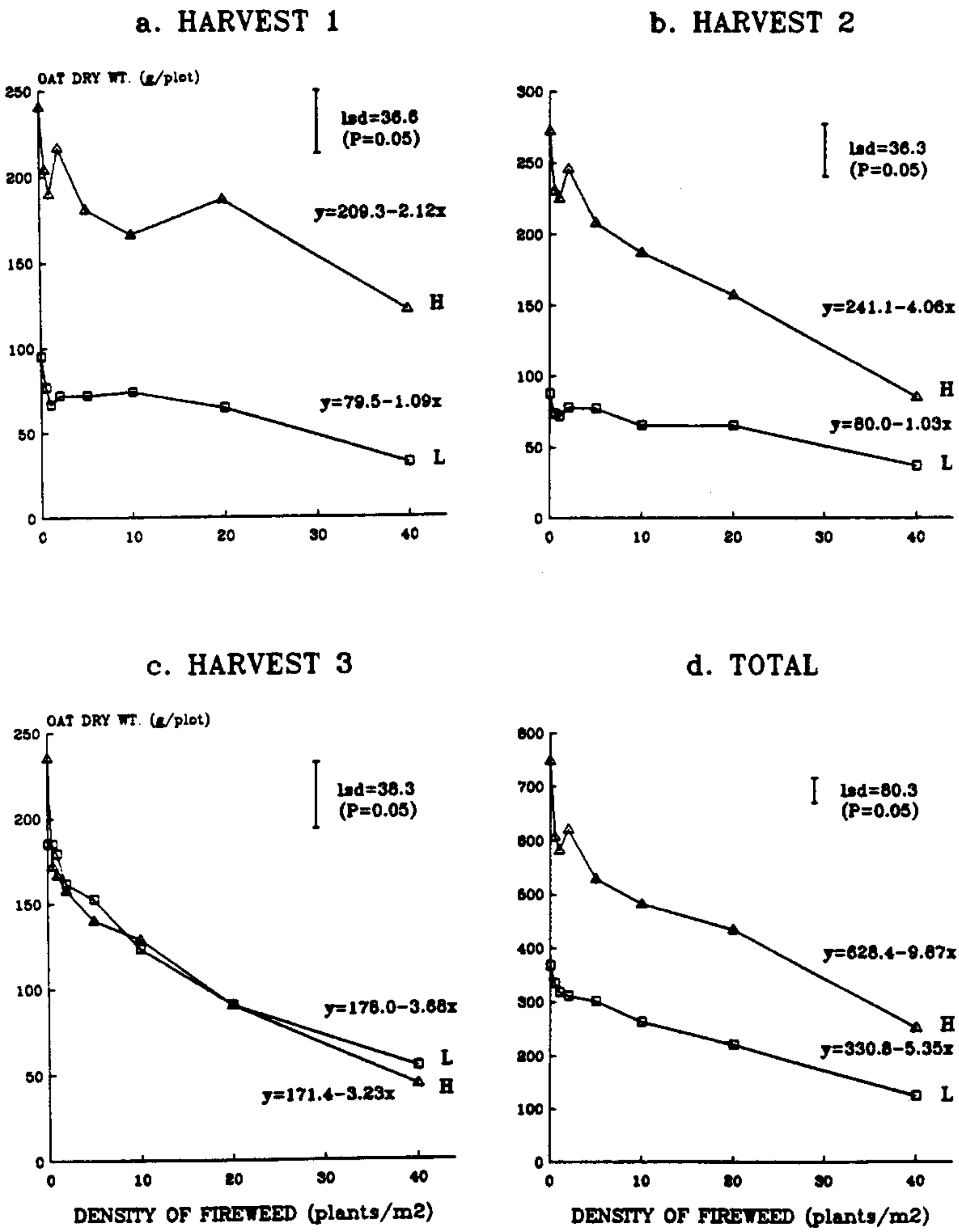


Figure 7.2 Effect of fireweed density on the dry weight yield of oats in the field under high (H) and low (L) soil fertility. Linear regression equations for the data are given where: y = dry weight of oats, and x = density of fireweed. R^2 for each pair of equations was 95.2, 94.7, 91.7 and 97.4% for Figures a,b,c,d respectively. The l.s.d. is for comparing means within a fertility level.

Table 7.1 Changes in the morphology of fireweed with increasing density in pots in the glasshouse.

Parameter	Number of fireweed (plants pot^{-1}) 1	2	4	8	lsd (P=0.05)
No. 1° branches pot^{-1}	11.58	19.40	27.10	44.00	3.84
No. 1° branches $plant^{-1}$	11.58	9.70	6.78	5.50	1.38
No. capitula pot^{-1}	96.3	138.4	150.1	214.2	37.3
No. $capitula^{A}$ $plant^{-1}$	9.13	7.94	5.88	4.93	1.10
DW $capitula^{B}$ mg pot^{-1}	6.647	7.207	7.216	7.520	0.270
DW $capitula^{B}$ mg $plant^{-1}$	6.647	6.514	5.830	5.441	0.270
DW leaves g pot^{-1}	1.72	2.30	2.84	3.75	0.41
DW $leaves^{B}$ mg $plant^{-1}$	7.30	6.94	6.45	6.02	0.19
DW stems g pot^{-1}	4.26	5.73	6.06	9.07	1.50
DW $stems^{C}$ g $plant^{-1}$	1.505	1.291	0.872	0.709	0.156
Total DW g pot^{-1}	7.12	9.70	10.56	15.56	2.32
Total DW^{C} g $plant^{-1}$	1.918	1.683	1.220	0.995	0.170
DW mg $capitula^{-1}$	11.52	12.05	11.23	11.29	n.s.

^{A} Data on square root (x + 0.5) transformed scale.
^{B} Data on ln (x) transformed scale.
^{C} Data on ln (x + 1) transformed scale.
n.s. Variance ratio (F_{OBS}) not significant at P<0.05.

a per plant basis decreased with increasing density of fireweed. The mean weight of capitula did not vary significantly with plant density.

As a result of increased soil fertility, the number of fireweed branches per pot more or less doubled while the number of capitula increased four-fold (see Table 7.2). The total weight of fireweed, as well as the weight of leaves and stems, increased three-fold. All increases were significant at P<0.001. The mean weight of capitula was not significantly different (P=0.05) between fertility treatments.

Table 7.2 Changes in the morphology of fireweed grown in pots in the glasshouse, with an increase in soil fertility.

	Fertility level			
Parameter	Low	High	F_{OBS}	
No. 1° branches pot^{-1}	16.85	34.19	163.10	***
No. capitula pot^{-1}	60.8	238.7	181.27	***
DW capitula[A] mg pot^{-1}	6.438	7.857	220.78	***
DW leaves g pot^{-1}	1.45	3.85	272.17	***
DW stems g pot^{-1}	3.08	9.49	146.11	***
Total DW g pot^{-1}	5.22	16.11	176.57	***
DW mg $capitula^{-1}$	11.30	11.75	0.90	n.s.

[A] Data on ln (x) transformed scale.
*** F_{OBS} significant at P<0.001; n.s. F_{OBS} non significant.

Field Experiment

In the field, losses in productivity of oats due to increasing fireweed density were more marked at the third harvest than at the first and second simulated grazings (see Figure 7.2 a,b,c). At least two factors contributed to this result. Firstly, at the seedling and early developmental stages of growth, plant resources are likely to have been non-limiting and competition between plants small. Secondly, simulation based on the knowledge that cattle avoid grazing fireweed meant that only oats was cut at the first two harvests. This allowed the weed to grow above the pasture canopy and, because of its much branched habit, gain a competitive advantage for light.

The mean diameters of fireweed plants at the three harvests are given in Table 7.3. The percentage of ground area (calculated on the basis of mean plant diameter) covered by fireweed at the third harvest is also shown. The diameter of fireweed did not increase substantially between harvests 1 and 3 and decreased only gradually as plant density increased. The ecological significance of competition for light in fireweed is discussed more fully in Chapter 9.

The field data show a significant reduction in total forage yield ($P=0.05$) with the lowest fireweed density of 0.5 plants m^{-2} over both fertility levels. This was equivalent to a 13.9% reduction in yield. At a moderate infestation of 5 fireweed plants m^{-2} forage production was reduced by over 23%. Other losses in productivity, as percentages, are given in Table 7.4. Oats grown alone yielded mean totals of 1.84 and 3.74 t DM ha^{-1} for low and high fertility treatments respectively.

As occurred in the glasshouse experiment, fireweed generally reduced the yield of oats in absolute terms more under high soil fertility than low soil fertility. At the third field harvest, however, fireweed also suppressed the yield of oats on a percentage basis significantly more at high fertility than at low fertility ($P<0.05$) (see Figure 7.3).

Figure 7.2 a,b,c shows that the low and high fertility graphs of actual yield for harvest 3, except at zero fireweed density, are almost identical, whereas those for harvests 1 and 2 are widely separate. It is assumed that between the second and third harvests the fertiliser differential, other than in the control plots, had largely disappeared through crop and weed uptake and leaching.

Table 7.3 Diameter, dry matter production and area of fireweed at various harvests of the field experiment. Values in brackets are standard deviations.

Fertility level	Density plants m^{-2}	Mean diam. of plants (cm) Har 1	Har 2	Har 3	DM kg ha^{-1} Har 3	Area % cover Har 3
Low	0	-	-	-	-	-
	0.5	11.3 (3.4)	13.5 (2.9)	16.0 (4.2)	78	1.0
	1	10.9 (2.4)	12.0 (2.4)	14.5 (2.7)	105	1.7
	2	10.8 (2.7)	12.0 (2.3)	14.0 (2.0)	231	3.1
	5	10.5 (2.5)	11.8 (2.8)	13.1 (3.0)	500	6.6
	10	10.5 (2.1)	11.5 (2.3)	13.0 (2.3)	905	13.3
	20	10.2 (2.5)	10.5 (2.0)	12.4 (1.9)	1774	24.2
	40	8.8 (1.9)	8.7 (1.6)	9.8 (1.3)	2649	30.2
High	0	-	-	-	-	-
	0.5	15.3 (2.5)	17.0 (1.4)	18.5 (1.3)	96	1.3
	1	14.4 (2.7)	16.8 (2.8)	17.5 (3.2)	193	2.4
	2	14.3 (2.5)	14.6 (2.8)	16.4 (5.0)	360	4.2
	5	14.1 (3.0)	15.2 (3.5)	15.5 (3.0)	811	9.4
	10	14.4 (2.5)	15.3 (3.5)	16.4 (2.7)	1549	21.1
	20	14.0 (2.3)	13.7 (2.4)	14.6 (2.6)	2934	33.5
	40	13.6 (2.8)	12.1 (2.3)	13.3 (1.8)	4525	55.6

Table 7.4 Percentage loss in total oat dry matter production as a result of increasing fireweed density (data combined over the three harvests, and over high and low fertility). Values followed by the same letter are not significantly different at P<0.05.

Density of fireweed plants m^{-2}	Loss in oat production %
0	0 a
0.5	13.9 b
1	17.9 b
2	16.3 b
5	23.7 bc
10	32.1 cd
20	41.2 d
40	66.4 e

lsd (P=0.05) = 11.0%

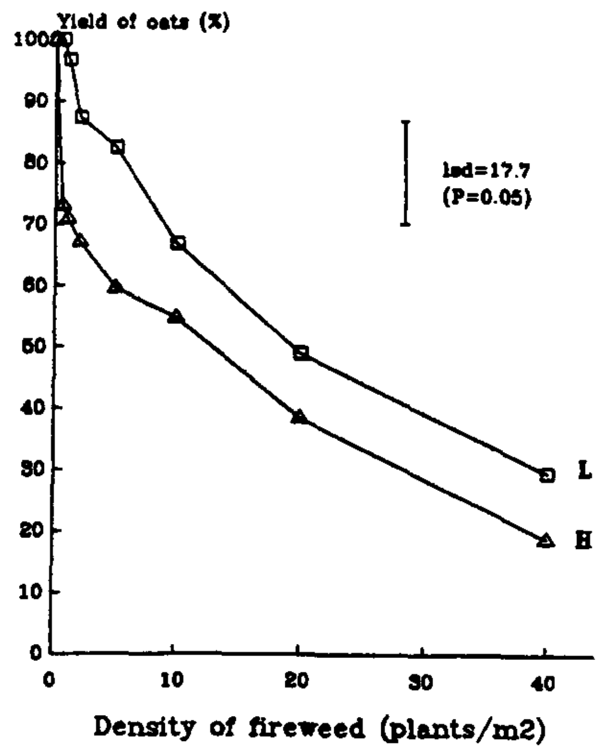


Figure 7.3 Percentage yield of oats at high (H) and low (L) soil fertility, as affected by density of fireweed at the third field harvest.

Alternatively, fireweed plants in high fertility treatments may have been competing more strongly for soil nutrients.

DISCUSSION

Weed species of various growth patterns and densities offer different degrees of competitive ability as evidenced by the work of Schreiber (1967), Peters and Lowance (1969), Schreiber and Oliver (1971), and Oswald and Haggar (1983). While some have only a minor effect on pasture production others have a much greater impact.

Competitive Ability of Fireweed

Competition for light

Donald (1963) argues that because light cannot be accumulated or stored, it ranks as the primary limiting factor in forage production. In the present field study, fireweed appeared to offer strong competition for light as a result of its differential growth above the cut oats and its branched habit. Like *Chenopodium album* L. (Williams 1964), fireweed may be expected to be very efficient in trapping light in mixed swards.

Effect of soil fertility

Fireweed responded quickly to soil fertility in pots and in the field, producing large plants with very high reproductive potential. The competitiveness of fireweed with Saia oats was not suppressed as a result of improved soil fertility conditions alone, and at the third field harvest appeared to have been increased. The results suggest that fireweed is likely to compete strongly for soil nutrients with a range of pasture and forage species.

As occurs with other weeds (Dawson and Holstun 1970), including *Senecio vulgaris* (Bleasdale 1960), fertilisation may increase fireweed competition rather than help alleviate the problem. If pastures are to benefit in preference to resident fireweed populations, timing of fertiliser applications will be critical.

The effects of nitrogen, phosphorus and potassium on the competitiveness of fireweed are studied in more detail in Chapter 8.

Allelopathy

No evidence exists to implicate allelopathy in fireweed interference though the phenomenon has been found to occur in other pasture weeds (Kloot and Boyce 1982; Lovett 1983). Alkaloids have also been linked to allelopathy (Levitt and Lovett 1984; Putnam 1985) but the pyrrolizidine group (see Chapter 2) as yet are not implicated. It has been known for some time that alkaloids can be potent inhibitors of seed germination (Evenari 1949).

Effect on Pasture Productivity

Previously Martin and Colman (1977) considered that fireweed had little influence on pasture production, at least in warm climate grass pastures, and that competition with pasture species was small. Their conclusion was based on the fact that at the highest density in their study (4.79 plants m^{-2}) total fireweed yield (106 kg ha^{-1}) was not a significant part of the total herbage on offer. In the field experiment reported here, a similar density of fireweed (5 plants m^{-2}) yielded between 500 and 800 kg DM ha^{-1} (see Table 7.3) and reduced the total productivity of oats between 18 and 29% (see Figure 7.2d) depending on soil fertility. Goodall (1952) points out that when studying the distribution of species, quantity of plant material is generally to be preferred over number of individuals.

Early in the growing season (Harvest 1) fireweed densities did not consistently effect oat yield. Control measures should therefore be attempted as soon after the emergence of fireweed seedlings as possible.

Yield/Density Relationship

Yield response as a function of weed density has often been conceptualised in terms of a sigmoidal curve (e.g. Zimdahl 1980). Such a curve possesses a minimum critical population or 'competition threshold' (Cousens et al. 1985; Cussans et al. 1986) below which no loss in yield occurs. But Cousens et al. (1984) argue that graphical representation of weed density/crop competition data seldom, if ever, show any suggestion of sigmoidal responses (e.g. Medd et al. 1981). Rather they are usually hyperbolic in nature (Cousens 1985; 1987). Such was the case for competition between fireweed and oats in the glasshouse, and at comparatively lower fireweed densities (<10 plants m^{-2}) in the field. Over the whole range of field densities the linear regressions fitted the data well (see Figure 7.2 a,b,c,d).

This result supports the general observation that loss of crop or pasture production per weed is greater in low density weed populations than in high density populations (Tisdell et al. 1984). The result also suggests that no 'competition threshold' existed for fireweed competition with oats in the present experiment. Hence fireweed which occurs in low density infestations, but is widespread, may cause substantial loss of pasture productivity.

Effect on Pasture Availability

The extent to which pasture growing beneath fireweed is unavailable to stock, is not fully known. In the present study, the canopy area of fireweed was taken as a measure of this unavailability. As much as 55% of ground area was covered by fireweed at the third harvest (see Table 7.3). However, the random arrangement of fireweed used in this study would most likely occur under conditions of cultivation, where fireweed seed is mixed and spread comparatively evenly in the soil. In less disturbed pasture populations, individuals of the same species would tend to form groups or 'aggregations' (Goodall 1952). In this case, 55% may be an overestimate of the potential covering at a density of 40 plants m^{-2}. Nevertheless, higher densities do occur in the field, and at lower densities plants often grow to much larger diameters, particularly perennating plants and those growing under high soil fertility conditions.

In practice, the actual area covered by fireweed may not correspond closely to the quantity of pasture which is unavailable to livestock. The latter will be influenced by the distance between fireweed plants, their habit (e.g. a high degree of branching close to the ground will make grazing more difficult), and the determination of cattle to graze amongst them.

Economic Impact of Fireweed

If farming is assumed to be primarily a money-making enterprise, then the definition of a weed in pasture as 'a species whose presence results in reduced economic output of a specific system' (Wells 1974) is most useful.

Weeds cause economic loss both in terms of shortfalls from potential production engendered by their presence, such as discussed in this chapter, and in terms of the costs of the inputs used in their control (Vere and Auld 1982). For fireweed, general estimates of the latter were made in Chapter 3.

An economic assessment of the shortfall in pasture production necessitates a calculation of the monetary value of pasture. Various factors interact to make this calculation very difficult (Auld _et al_. 1979; Auld and Tisdell 1986). For example, if pastures are understocked extra production is of little value. Given the complexity of costing _Chondrilla juncea_ in pasture, Pannell and Panetta (1986) resorted to using a relatively sophisticated computer model.

Insufficient data have yet been collected to estimate the economic loss of pasture production caused by fireweed in New South Wales, and it would be unwise to apply the results of the present study to other pasture types. It is arguably possible to draw up some general guidelines on the economics of fireweed control in forage crops which are comparable to oats. Although outside the scope of this thesis, such an economic assessment is no longer restricted by the total absence of physical/biological data on which economic studies are based. The aim must be to determine if sufficient loss of production occurs to warrant expenditure on control.

CONCLUSIONS

Undoubtedly, factors such as the condition of the pasture, whether it is annual or perennial, time of fireweed establishment (see Chapter 5), and duration of growth will alter the competition process. Nevertheless, the results of this present study with annual forage oats highlight the importance of fireweed as a competitive weed and show its potential to reduce pasture productivity, particularly species less competitive than oats. The extent to which growth is suppressed depends on the level of infestation.

To determine whether allelopathic effects of fireweed play a part in plant competition, it would be necessary to conduct specific experiments designed to eliminate other factors which are involved. Such work presents some difficulties as competition for light, water and nutrients, and allelopathic effects are difficult to separate under natural conditions (Glauninger and Holzner 1982).

A more detailed study of the grazing habits of cattle is required to determine the degree to which pasture growing beneath fireweed is avoided by livestock, and therefore how much the grazing capacity of pastures is reduced.

The distribution of a species in nature is rarely random (Goodall 1952). Because weed distribution affects the degree of competition encountered by the individual plant (Bleasdale 1960), field experiments with natural populations of fireweed growing in a range of pasture types also need to be conducted. These may further quantify both the physical and economic impact of the weed on pasture production.

Chapter 8

THE EFFECT OF SOIL FERTILITY ON FIREWEED COMPETITION

> 'It has been shown that plant species and even strains of the same species may differ in their response to particular mineral levels.' (van den Bergh 1969)

INTRODUCTION

The response of different weed species to increasing nutrient levels is subject to wide variation (Vengris et al. 1955; Hoveland et al. 1976). For example, Austin et al. (1985) showed that of six thistle species, Carthamus lanatus L. achieved maximum yield at low nutrient concentrations and Cirsium vulgare at high nutrient concentrations.

If the nutrient responses of individual weed and pasture species are known, then it may be possible to manipulate the botanical composition of pastures by way of fertiliser strategy (Charles 1968). The aim would be to discourage the growth and development of pasture weeds (Thrasher et al. 1963; Ivens and Mlowe 1983). Moreover, the competitive advantage of one species over another may be modified or even reversed by changes in the nutrient status of the soil (Williams 1962). Hence, under conditions of high fertility, as in old subterranean clover pastures, C. lanatus can be depressed by pasture and other weed species alike (Michael 1968c).

Mutual interference between weed and pasture plants is best assessed if they are grown in both mixture and monoculture (de Wit and van den Bergh 1965). This can be achieved using the experimental design, known as a 'replacement series' (de Wit 1960). A constant total density of plants is maintained and the planting density of one species is proportionately decreased as the planting density of the second species is increased (Jollife et al. 1984). Replacement series have been used widely in studies of mixed populations (e.g. de Wit et al. 1966; Groves et al. 1973; Fisher et al. 1974; Hall 1974; Weiner 1980; Harris et al. 1981; Ivens and Mlowe 1983; Moore and Williams 1983; Gilbert and Robson 1984 a,b,c; Williams et al. 1984), and have proved effective in determining the influence of soil fertility on weed/pasture competition.

Although indirect evidence suggests that phosphorus increases the prevalence of fireweed under cultivation (Lynch and Strang 1973), detailed data which describe the relationship between fireweed and soil fertility are lacking. The results of Chapter 3 (see Table 3.6), indicate that fireweed is not confined to soils of either low or high fertility.

The object of this study was to assess the relative importance of increasing nutrient availability on the growth and level of infestation of fireweed in pastures. Can increased soil fertility be used as a tool in control?

A simple replacement series glasshouse experiment was designed to investigate the effect of increasing levels of nitrogen, phosphorus and potassium on the relative growth of fireweed and forage oats (Avena strigosa cv. Saia). Nutrient levels were applied factorially to pots of both species alone and together. Saia oats represented a vigorous forage species which was likely to offer strong competition for soil nutrients.

MATERIALS AND METHODS

The pot experiment, conducted in a naturally lit glasshouse at Camden, was of a randomised complete block design. There were five replicates of each of 18 treatments (3 levels of nitrogen x 3 levels of phosphorus x 2 levels of potassium). Within each treatment there were three pots, one containing four plants of fireweed, another containing four plants of oats and the third containing two plants of fireweed together with two plants of oats. Plants were spaced 7.5 cm apart in a square pattern with like plants placed diagonally opposite one another.

Soil of low fertility, the same as that used in the glasshouse experiment of Chapter 7, was collected from the field in May 1985 and large clods of soil and coarse organic material removed from it.

Fertilisers were then added to known quantities of soil and mixed thoroughly in a cement mixer to give sufficient soil for each of the 18 treatments. Nitrogen was applied (as urea - 47% N) at rates equivalent to 0, 80 and 160 kg ha^{-1}, phosphorus (as superphosphate - 9.1% P) at rates of 0, 15 and 30 kg ha^{-1}, and potassium (as muriate of potash - 49.8% K) at 0 and 30 kg ha^{-1}. Nutrient levels were designated N_1, N_2 and N_3; P_1, P_2 and P_3; and K_1 and K_2 respectively. The highest level of nitrogen was applied as a split dressing, the second as a solution 3 weeks after sowing.

Black plastic bags (5 l and 18 cm diam.) were then filled to a depth of 18 cm with the fertilised soil and placed on benches inside the glasshouse. Pots were watered to promote germination of buried weed seeds, which were then removed.

Seeds of fireweed and oats were germinated as in Chapter 7 and seedlings transplanted into pots, fireweed at the cotyledon stage on 20 June and oats 6 days after germination on 8 July 1985. Pots were kept close to field capacity by regular watering. Each block (replicate) of treatments was spread from one to two benches and rerandomised in late August. Temperatures were the same as those recorded for the glasshouse experiment in Chapter 7.

Fireweed and oat tops were harvested on 9 October and dried at 70°C. Dry weights were then measured. For fireweed these were partitioned into heads (capitula), leaves and stems. Other measurements included number of oat tillers and number of fireweed capitula and primary branches.

Analyses were conducted on transformed data (square root + 0.5) for total fireweed and oat dry weights, and dry weight and number of fireweed capitula. For fireweed, leaf and stem dry weights and number of primary branches, and number of oat tillers, raw data were used. All data except leaf, stem and capitulum dry weights in pure cultures of fireweed, were analysed on a half pot basis. This allowed direct comparisons to be made for each species between when grown alone and when grown in combination. Analyses were treated as fully factorial in which 'type' (i.e. 'pure' or 'mixed' culture) was included as one of the factors.

The parameters of the de Wit (1960) competition model were also estimated for all two species combinations using the method proposed by Machin and Sanderson (1977). To do this a Fortran program developed by Alan Gleeson of the New South Wales Department of Agriculture was used. Two of these parameters, k and t, may be thought of as measures of 'aggressiveness'. The parameter k_{FO} is interpreted as de Wit's relative crowding coefficient for fireweed with respect to oats. The parameter t is equal to $1/k_{OF}$ (i.e. the reciprocal of de Wit's relative crowding coefficient, k_{OF}, for oats with respect to fireweed). The model considered appropriate for the fireweed/oats data was $k \neq t$, which indicates that the two species are not mutually exclusive (de Wit 1960).

Because the Fortran program used was only able to estimate k and t for one data set at a time, it became necessary to analyse the k and t values using a three-way analysis of variance (N*P*K) with only one value in each cell. This reduced the ability of the ANOVA to indicate statistically significant differences between treatments.

RESULTS

Fireweed and Oats Grown Alone

The total shoot dry weight of fireweed when plants were grown alone showed a highly significant response to increasing levels of nitrogen and phosphorus ($P<0.001$). The nitrogen by phosphorus interaction was also highly significant ($P<0.001$). There was no significant main effect of increasing potassium, and other interactions were non-significant ($P=0.05$). Oats grown alone showed a similar response.

Results for total shoot dry weight on a half pot basis are presented in Figure 8.1a and 8.1b for fireweed and oats respectively. For fireweed, the positive interaction between nitrogen and phosphorus occurred at each of the three levels of the two nutrients. At N_1 (no added nitrogen) dry weight yield increased with added phosphorus from P_1 to P_2, but decreased at the P_3 level. At N_2, the intermediate nitrogen level, fireweed yield increased from P_1 to P_2 but was not significantly different between P_2 and P_3. At N_3,

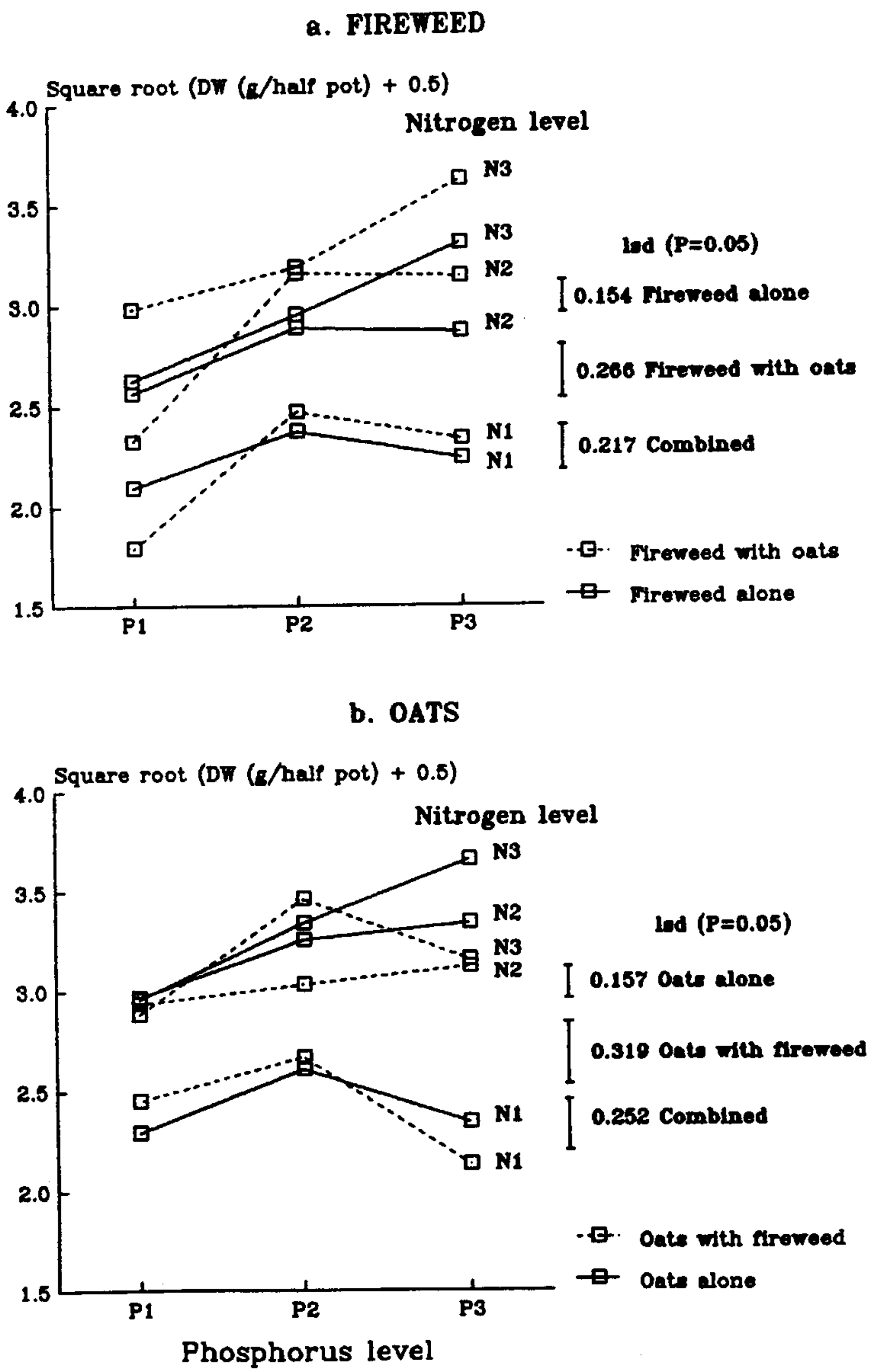


Figure 8.1 Effect of nitrogen (N) and phosphorus (P) on the total shoot dry weight of (a) fireweed when grown alone and with oats, and (b) oats when grown alone and with fireweed.

fireweed showed a linear and significant increase ($P=0.05$) with all levels of applied phosphorus. In terms of applied nitrogen, dry weight of fireweed increased significantly ($P=0.05$) from N_1 to N_2 at each of P_1, P_2 and P_3, though only at the highest phosphorus level was a further significant increase obtained at N_3.

Dry weights of leaves, stems and capitula from fireweed plants grown alone, are shown in Figure 8.2 a,b,c. Each component of total shoot weight also showed a highly significant response to increasing nitrogen and phosphorus ($P<0.001$) and a significant interaction between them ($P<0.01$). The main effect of potassium was again non-significant ($P=0.05$).

The main effects of nitrogen, phosphorus and potassium on percentage dry weights for each component of total shoot dry weight are given in Table 8.1. Interaction effects were all non-significant ($P=0.05$), suggesting that in terms of percentage dry weight the nutrients acted independently of one another. The percentage dry weight of leaves was reduced significantly ($P=0.05$) with both increasing levels of nitrogen and phosphorus. Phosphorus had the largest main effect. Stems, as a percentage of total shoot weight, responded positively to increased nitrogen. The main effect of phosphorus was non-significant while potassium marginally reduced the percentage dry weight of stems at the 5% level. The inflorescence or capitula component of total dry weight showed a highly significant positive response to phosphorus ($P<0.001$) and a marginally significant response to potassium ($P=0.05$). The overall percentage means for leaf, stem and capitulum dry weight data were 28.2, 59.6 and 12.2% respectively.

The number of primary branches and capitula per half pot of fireweed for plants grown alone are included in Table 8.2. Their responses to nitrogen and phosphorus were similar to that which occurred for fireweed dry weights, except that the interaction effect was non-significant for fireweed branches ($P=0.05$).

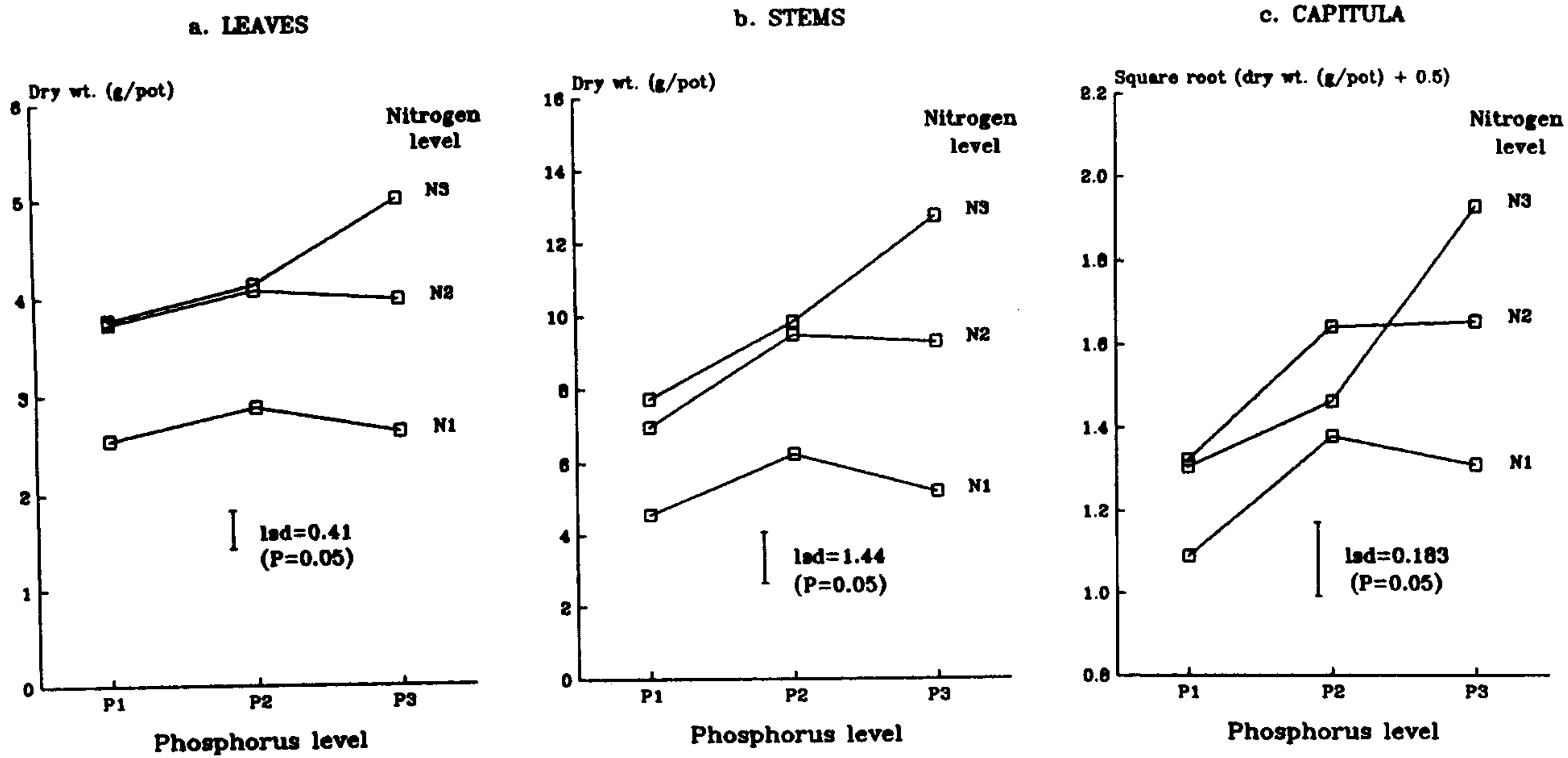


Figure 8.2 Effect of nitrogen (N) and phosphorus (P) on the dry weight of (a) leaves, (b) stems, and (c) capitula, of fireweed grown alone.

Table 8.1 The main effects of nitrogen (N), phosphorus (P) and potassium (K) on the percentage dry weight of capitula, leaves and stems of fireweed.

Treatment	Percentage of total dry wt. Capitula[A]	Leaves	Stems
N_1	3.476	29.83	58.31
N_2	3.644	27.62	59.38
N_3	3.420	27.19	61.17
lsd (P=0.05)	n.s.	1.46	1.42
P_1	3.132	31.52	58.95
P_2	3.559	26.82	60.62
P_3	3.849	26.30	59.28
lsd (P=0.05)	0.237	1.46	n.s.
K_1	3.406	28.39	60.20
K_2	3.621	28.03	59.03
lsd (P=0.05)	0.194	n.s.	1.16

[A] Data on square root (x + 0.5) transformed scale.
n.s. Data not significant.

Table 8.2 The effect of nitrogen (N) and phosphorus (P) on the number of 1° branches and capitula per half pot of fireweed and number of tillers per half pot of oats, alone and with their competitors.

	No. of fireweed branches		No. of fireweed capitula[A]		No. of oat tillers	
Treatment	Alone	With oats	Alone	With oats	Alone	With fireweed
N_1P_1	11.60	9.80	6.19	4.89	8.05	7.90
N_1P_2	13.45	13.40	7.85	8.23	7.25	7.20
N_1P_3	13.70	14.60	7.56	7.65	8.25	7.50
N_1 mean	12.92	12.60	7.20	6.92	7.85	7.53
N_2P_1	14.85	13.70	7.91	6.33	9.00	10.00
N_2P_2	17.85	21.10	10.17	11.26	9.15	7.90
N_2P_3	16.95	19.50	9.80	10.77	8.85	8.80
N_2 mean	16.55	18.10	9.29	9.45	9.00	8.90
N_3P_1	15.05	18.20	7.29	8.39	10.25	9.20
N_3P_2	17.30	20.40	8.89	10.45	10.15	9.70
N_3P_3	19.60	23.00	11.84	12.57	12.00	9.30
N_3 mean	17.32	20.53	9.34	10.47	10.80	9.40
lsd ($P=0.05$) Within cols.	1.63	2.52	1.08	1.42	1.09	1.65
lsd ($P=0.05$) Between cols.	2.11		1.26		1.38	

[A] Data on square root $(x + 0.5)$ transformed scale.

Fireweed and Oats Grown Together

When fireweed was grown together with oats the response to nitrogen and phosphorus in terms of total dry weight per half pot remained highly significant ($P<0.001$). The nitrogen by phosphorus interaction was significant at the 1% level. The pattern of response was similar to that shown when fireweed was grown alone (see Figure 8.1a), as were the responses of number of primary branches and number of fireweed capitula (see Table 8.2).

Significant differences, however, occurred between fireweed grown alone and fireweed grown with oats on a half pot basis. This 'type' effect (i.e. pure versus mixed) was highly significant ($P<0.001$) for total dry weight and number of fireweed branches, but non-significant for number of fireweed capitula ($P=0.05$). The nitrogen by type and phosphorus by type interactions were significant for all three parameters, at least at the 5% level.

At P_1N_1 and P_1N_2 the total shoot dry weight per half pot of fireweed was lower when grown with oats than when grown alone (see Figure 8.1a). But as the level of phosphorus at N_2 increased and at all phosphorus levels of N_3, fireweed grown with oats significantly increased its dry weight above that of fireweed which was grown alone ($P=0.05$). The number of fireweed branches and capitula showed a similar pattern of response (see Table 8.2).

For oats grown together with fireweed there was a highly significant effect of nitrogen on total dry weight ($P<0.001$). The effect of phosphorus was significant at the 1% level and the nitrogen by phosphorus interaction at the 2.5% level. In comparison with oats grown alone, at N_3, dry weight increased from P_1 to P_2 but then decreased significantly from P_2 to P_3 ($P=0.05$) (see Figure 8.1b). The main type effect (significant at $P<0.01$) and phosphorus by type interaction (significant at $P<0.001$) were opposite to fireweed in their effects. As nitrogen and phosphorus levels increased so oats grown with fireweed performed more poorly than oats which was grown alone. Oat tillers responded in like manner (see Table 8.2).

These results show that at high fertility i.e. in each case at N_3, and at N_2P_2 and N_2P_3, fireweed, when grown with oats, grew significantly better than fireweed plants grown alone; conversely at N_2P_2, N_2P_3 and N_3P_3 oats, when grown together with fireweed, grew less well than oat plants grown alone. Following the terminology of Donald (1963) which was applied by Groves et al. (1973) in a similar experiment to this, fireweed may be thought of as the 'aggressor' plant and oats as the 'suppressed' plant.

de Wit parameters

In the analysis of variance of the estimated k and t values of the de Wit competition model (Machin and Sanderson 1977), none of the F values reached significance at the 5% level. This was expected owing to the small number of degrees of freedom in the term (N*P*K) used for the residual variance. The mean relative crowding coefficients of fireweed (k_{FO}) and oats (k_{OF}) for the main effects of nitogen, phosphorus and potassium are nevertheless given, since they support the results of the previous analyses (see Table 8.3).

Table 8.3 Mean relative crowding coefficients of fireweed with respect to oats (k_{FO}) and oats with respect to fireweed (k_{OF}) for the main effects of nitrogen (N), phosphorus (P) and potassium (K).

	Crowding coefficient	
Treatment	k_{FO}	k_{OF}
N_1	2.47	2.23
N_2	2.99	2.11
N_3	3.93	2.05
P_1	2.33	2.62
P_2	3.72	2.25
P_3	3.34	1.71
K_1	2.90	2.05
K_2	3.35	2.21

For k_{FO}, the 'aggressiveness' of fireweed, there was an increasing linear trend with nitrogen levels, but the highest value for phosphorus occurred at P_2. Potassium means showed greater difference for this parameter than in previous analyses, but the difference was not significant. For k_{OF} (or 1/t), there was little difference between nitrogen levels, but a stronger decreasing linear response to phosphorus. Potassium levels also altered k_{OF} very little.

DISCUSSION

Relative Responses of Fireweed and Oats

In a review of weed-fertility interactions, Alkamper (1976) emphasised that weeds usually absorb fertiliser faster and in relatively larger amounts than crops, and therefore derive greater benefit. The mineral content of fireweed and oats was not determined in this study. But in terms of the main effects on total shoot dry weight, fireweed responded more to nitrogen and phosphorus than did oats when the two species were grown together. When grown alone, oats responded more than fireweed. As Harper (1964) states, 'the behaviour of mixed stands is not predictable from the behaviour of pure stands.'

Although species yielding highest in monocultures have often been found to have a competitive advantage in mixtures, there are exceptions (Moore and Williams 1983). For example, the aggressor Setaria anceps Massey cv. Nandi was a far lower yielder in monoculture than Desmodium intortum (Miller) Fawc. & Rendle cv. Greenleaf (Hall 1974). The aggressiveness of fireweed in this experiment was not simply related to its capacity to produce top growth at high levels of nutrients. The shoot yields of oats were higher than those of fireweed in monoculture. Other factors, such as root growth and uptake of nutrients, apparently influenced the outcome of competition.

The growth of fireweed was increased significantly by nitrogen and phosphorus ($P<0.001$) but not potassium ($P=0.05$). The greatest response to either nitrogen or phosphorus was recorded when the alternate nutrient was also at a high level. Moore and Williams (1983) obtained a similar result for Cirsium vulgare with nitrogen and calcium.

The result with potassium was perhaps not unexpected since various other weeds are not affected even by applications over the range of 70 to 200 kg K ha^{-1} (Hoveland et al. 1976). Myers and Moore (1952) found that although Arctotheca calendula L. (as Cryptostemma calendula (L.) Druce) dominance of a winter weed population increased with applications of nitrogen alone, potassium singly and in combination with nitrogen and phosphorus had no effect on botanical composition.

When grown in a mixture, plants of the dominant component show a greater dry matter yield than they do in a monoculture of the same overall density. Plants of the other component usually show a decrease relative to their own monoculture (McGilchrist and Trenbath 1971). In these terms fireweed dominated oats at all but the lowest nitrogen and phosphorus levels (N_1P_1 and N_2P_1) (see Figure 8.1a). This result was clearly reflected in de Wit's relative crowding coefficients (k values) for fireweed and oats (see Table 8.3). Similarly, Hordeum leporinum Link competed most successfully with Lolium rigidum Gaudin at low nitrogen levels, while at high nitrogen levels the opposite result was obtained (Cocks 1974). The competitive advantage of fireweed generally increased at higher nitrogen and phosphorus levels.

Dry Matter Partitioning in Fireweed

One strategy shown by fireweed in its response to increasing nitrogen and phosphorus levels was to partition a greater percentage of dry matter into stems and flowering capitula. Both increased at the expense of the percentage dry weight of leaves. In a rarely significant effect ($P<0.05$), potassium also caused an increase in the percentage dry weight of capitula. Fireweed appears well able to utilise favourable fertility conditions to increase its relative reproductive effort, and hence its invasive potential. Work with other species has shown that the weed seed population of a soil can be greatly influenced by rate, type and time of fertiliser application (Brenchley and Warington 1930; 1933; Dotzenko et al. 1969).

According to Trewavas (1986), flower structure is a character of plants which usually shows extreme stability. Although not presented, the mean weight of fireweed capitula was not changed significantly (P=0.05) by nitrogen, phosphorus or potassium levels. Hence taxonomic differentiation between fireweed and other closely related Senecio species according to capitula size (see Hilliard 1977) appears to be justified.

Altering Pasture Composition

Changes in pasture composition may sometimes be related to application of fertilisers (Warington 1924; Gilbey 1974). For example, the application of nitrogen and phosphorus led to dominance of Bromus in California rangeland (Pearson and Ison 1987). Among the factors determining final botanical composition is the effect of soil fertility on individual species and the effect of their differential response on interspecific competition (Myers and Moore 1952).

The results of the present study suggest that raising soil fertility through the use of nitrogen or phosphorus based fertilisers, or pasture legumes (Myers and Lipsett 1958), is unlikely in itself to suppress the growth of fireweed. Rather it may preferentially benefit the weed. While evidence suggested that added nitrogen would discourage the growth of Ulex europaeus L. amongst pasture grasses (Ivens and Mlowe 1983), suppression of Poa labillardieri Steud. by a fertiliser strategy was deemed to be unsuccessful (Fisher et al. 1974). Manipulation of fertiliser application was seen as having only small and possibly variable effects on the dominance of Arctotheca calendula in pastures (McIvor and Smith 1974).

Under field conditions, the surface application of fertilisers (particularly superphosphate) may result in a localised increase in nutrients in the top few centimetres of soil (Groves et al. 1973). Since fireweed is a reasonably shallow rooted plant, the competitive advantage of the weed may become enhanced. In this glasshouse experiment, nutrients were mixed evenly through the soil.

Other Factors Influencing Competition

Soil fertility is not the only factor determining the level of fireweed competition within pastures. A more complete interpretation of the ecology of a weed must also incorporate factors such as grazing effects, reproductive behaviour, competition from perennial grasses (Michael 1968 a,b), temperature and cutting frequency (Harris et al. 1981), plant density (Fisher et al. 1974; Williams et al. 1984), and germination sequence (Gilbert and Robson 1984a). King (1971) found that in mixtures of two grasses, the species which was sown first responded the most to nutrient application and suppressed the responsiveness of the other species. The relation between field performance of two species growing together and the results of competition experiments in pots may therefore be hard to predict.

When competition occurs for two factors rather than one, the effects of competition for either factor operating alone may be greatly intensified (Donald 1958). Stern and Donald (1962) showed that competition for nitrogen in a grass/clover sward led also to strong competition for light. Similarly with fireweed, because it usually grows above the pasture canopy (see Chapter 5), strong competition for soil nutrients (nitrogen and phosphorus) is likely to result in the weed becoming more competitive for light. The influence of light on the ecology of fireweed is the subject of the next chapter.

CONCLUSIONS

Fireweed is a strongly competitive weed species, able under most fertility conditions to dominate the annual forage oats *Avena strigosa* cv. Saia. Competition between the two species depended on nitrogen and phosphorus nutrient levels. As well as being able to persist under low soil fertility conditions (see Chapter 5), fireweed is also able to respond vigorously to improved nutrient availability. This result supports that obtained in Chapter 3, which suggested that fireweed can be found equally on high and low fertility soils. It is conceivable that soil nitrogen and phosphorus levels affect fireweed populations in the field and indirectly influence control programs.

The differential nutrient responses demonstrated in this study between fireweed and oats are difficult to exploit in favour of the forage plant. Whether this is true of other pasture species in competition with fireweed is not known. Species such as *Lolium perenne* L., *L. rigidum*, *L. multiflorum* Lam. and *Pennisetum clandestinum* require testing.

In Chapter 3, neither acid nor alkaline soils were identified as favouring fireweed growth. Specific experiments designed to determine the effect of soil pH on the vigour of fireweed need to be undertaken. The results of such experiments may provide a management option, namely lime application, for fireweed control.

Since fireweed, once established, is strongly competitive, emphasis must be laid on the competitive ability of introduced grasses in the early stages of pasture and weed establishment. This aspect of control is considered further in Chapter 10. For established perennial pastures the key to control appears to be the prevention of germination and seedling establishment. Such control has been achieved for *Senecio jacobaea* (Thompson and Saunders 1986), as well as fireweed (Anon. 1978), by stimulating the growth of pastures through fertiliser applications. The results of Chapter 5 provide additional evidence for the benefits of fertilising, although timing would seem to be the most critical factor.

Chapter 9
THE EFFECT OF SHADE ON THE GROWTH OF FIREWEED

> 'The sunlight requirements or shade tolerance of different species of plants is known to vary greatly.' (Stahler 1948)

INTRODUCTION

As one component of the environment, light has profound effects upon the growth and development of plants. In Chapters 5 and 7 it was hypothesised that much of the success of fireweed as a weed of pastures could be attributed to its ability to gain a competitive advantage for light by growing, mostly unchecked, above the pasture canopy. This suggests that fireweed is adapted to conditions of high light intensity.

Much can be learnt of the light requirements of a species from its response to shading, as evidenced by studies of Eupatorium adenophorum Spreng. (Auld and Martin 1975), Sorghum halepense (L.) Pers. (McWhorter and Jordan 1976), Baccharis halimifolia L. (Panetta 1977), Carduus nutans (Medd and Lovett 1978), Silybum marianum and Onopordum sp. (Pook 1983), Achillea millefolium L. (Bourdôt et al. 1984), and Pteridium aquilinum (L.) Kuhn (Daniels 1986). Many farmers have already observed that fireweed thrives in open places where there is little or no competition for light, such as bare ground, heavily grazed pastures, and burnt and cultivated land (see Chapter 3). Control of any pasture weed by competing pastures is likely to be more effective where the growth and reproductive capacity of the weed can be appreciably reduced by shading, for example, Rumex acetosella sens. lat. (Harris 1972).

The aim of the two experiments reported in this chapter was to test the hypothesis that shading reduces the growth and development of fireweed. Information on the effect of shading is essential to the understanding and application of cultural methods of control. These are studied in the next chapter.

In the first experiment, fireweed was grown alone under a range of artificial shade treatments. In the second, it was grown in combination with prostrate and erect biotypes of the perennial ryegrass Lolium perenne cv. Kangaroo Valley. The assumption in the latter experiment was that the prostrate and erect ryegrass biotypes would shade fireweed differently.

MATERIALS AND METHODS

Both experiments were conducted in a naturally lit and unheated glasshouse at Camden during the winter/spring period of 1987. On average 60% of full daylight was transmitted by the glasshouse roof. Day/night temperatures ranged from 29 ± 3/8 ± 2°C in June to 34 ± 6/10 ± 2°C in October. Pot size and soil type were the same as in Chapter 7. 'Aquasol' (200 ml pot^{-1}) was applied to plants fortnightly.

The fungicide 'Benlate' (1 g l^{-1}) and 'Baysol' pellets (4 pot^{-1}) were applied to the soil surface to control 'damping off' of seedlings and prevent slug damage respectively. 'Bayleton' (5 g l^{-1}) was used as required for control of fireweed rust.

Experiment 1 - Growth under Shade Screens

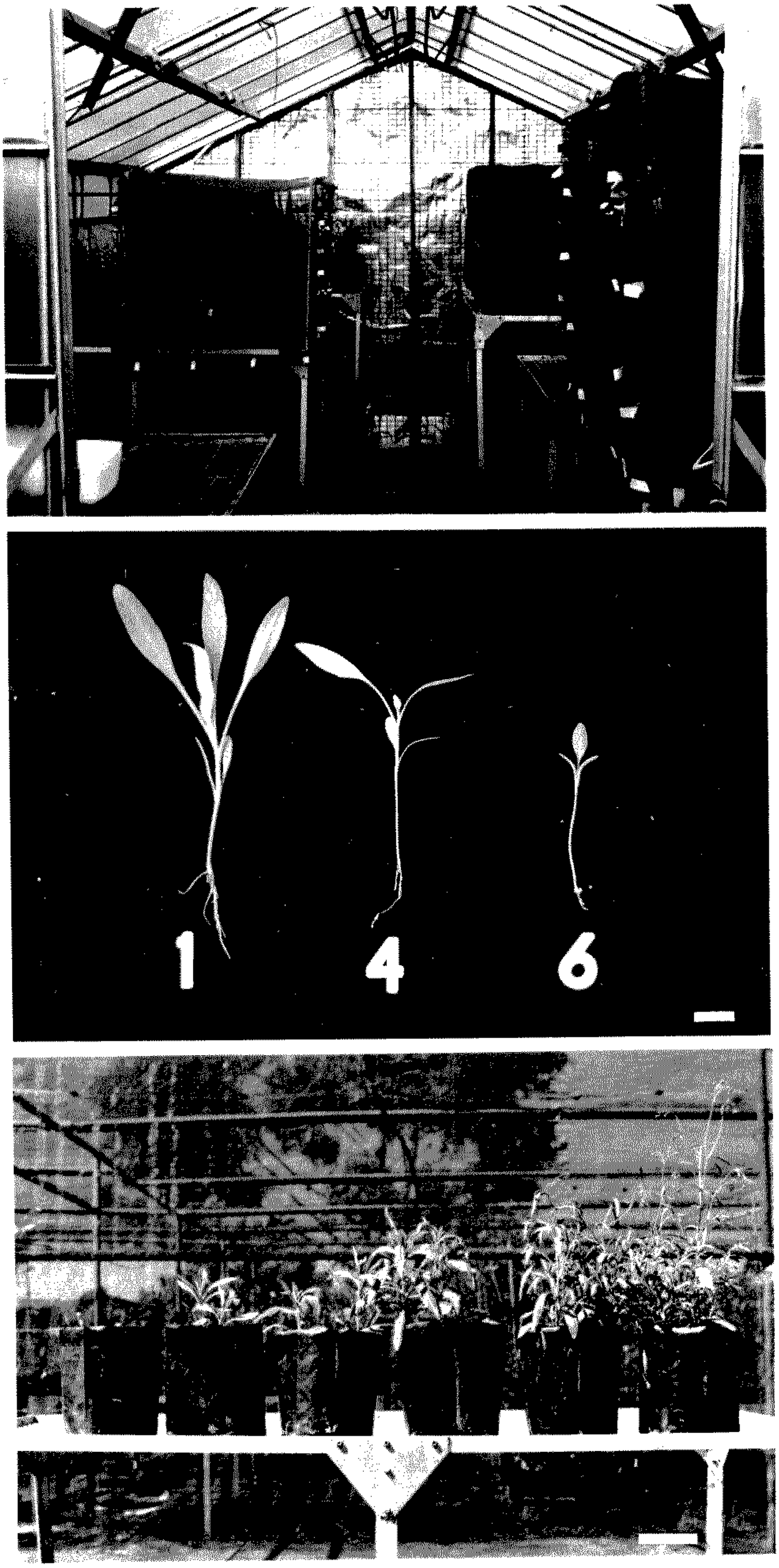
At the start of the experiment in early July, photosynthetically active radiation (P.A.R.) was measured over a 7 h period from 8.30 am to 3.30 pm on a cloudless day. The average half hourly flux density was 496 $\mu E\ m^{-2}\ sec^{-1}$ (measurements taken at 22 cm above bench height at six locations inside the glasshouse using a Li Cor-170 Quantum/Radiometer/Photometer).

Lightweight metal frames (1 m x 1 m x 1 m) attached to the top of six benches inside the glasshouse were covered with movable shade screens composed of 'Sarlon' woven shade cloth of five different grades (30, 50, 70, 80 and 90% shade) (see Plate 9.1). In combination, the glasshouse and shade screens provided six shade treatments or levels

Plate 9.1 Movable screens of varying shade intensity inside the glasshouse at Camden.

Plate 9.2 Effect of irradiance (r.l.i.) on the growth of fireweed seedlings 25 days after emergence. Treatments 1, 4 and 6 were 0.60, 0.18 and 0.06 r.l.i. respectively. Scale bar = 1 cm.

Plate 9.3 Reduction in the height of fireweed plants by shading, 45 days after emergence. Treatments (left to right) were 0.06, 0.12, 0.18, 0.30, 0.42 and 0.60 r.l.i. Scale bar = 10 cm.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4
6

of irradiance relative to full daylight (r.l.i.) under which fireweed was grown. These were namely 0.60 r.l.i. on an open bench of the glasshouse and 0.42, 0.30, 0.18, 0.12 and 0.06 r.l.i. beneath the shade screens on other benches.

Periodically during the experiment, temperatures were recorded beneath shade treatments. Thermometers were placed in containers of water in order to obtain general trends and avoid recording violent fluctuations due to the sun.

Fifteen pots allocated to each shade treatment were sown with fireweed seed at 2 mm depth on 13 July. To obviate position effects, pots were rerandomised within treatments twice weekly and locations of treatments on benches rotated in a systematic fashion throughout the experiment. Seedlings were thinned to two plants per pot 7.5 cm apart.

Within each shade treatment there were three groups of pots (i.e. each group was replicated five times). Pots belonging to the first group (30 S) were shaded for 30 days following seedling emergence and then harvested. The two other groups were both harvested after 60 days. The second received shade for the whole time (60 S) while the third was shaded for the first 30 days and then placed in the light on open benches of the glasshouse (0.60 r.l.i.) for the last 30 days (30 S/30 L). The conditions experienced by 30 S/30 L plants were designed to simulate the field environment where seedlings are initially shaded by other plants but then grow above the pasture canopy.

On several occasions during the experiment, plant height, and number and length of primary leaves were recorded. At both harvest times, fresh and dry weights of shoots and total leaf area were also obtained. At the latter harvest, primary branches and capitula were counted and shoot weights partitioned into leaf and stem components. Root dry weights were measured at two shade levels only. The two growth attributes, net assimilation rate (N.A.R.) and relative growth rate (R.G.R.), were calculated according to the following equations:

$$\text{N.A.R.} = \left(\frac{W_2 - W_1}{A_2 - A_1}\right)\left(\frac{\ln A_2 - \ln A_1}{t}\right) \quad \text{(Panetta 1977),}$$

$$\text{R.G.R.} = \left(\frac{\ln W_2 - \ln W_1}{t}\right) \quad \text{(Blackman 1919),}$$

where W_1, W_2 are the mean dry weights and A_1, A_2 are the mean leaf areas at the beginning and end of the growth period respectively, and t is the number of days or weeks growth.

Experiment 2 - Growth with Prostrate and Erect Ryegrass

The design for this experiment was a split plot factorial in which there were five replicates (pots) of each of the 20 treatments: four harvests (main plots) x five ryegrass/fireweed combinations (sub plots). The ryegrass/fireweed combinations were:

1. Prostrate ryegrass alone
2. Prostrate ryegrass + fireweed
3. Erect ryegrass alone
4. Erect ryegrass + fireweed
5. Fireweed alone

Tillers of mature Kangaroo Valley ryegrass plants (*Lolium perenne*) of the prostrate (130B-41) and erect (130B-15) biotypes (Shah and Pearson 1986), growing in a peat/sand mixture, were trimmed to a uniform height of 7 cm. In early June, individual tillers with roots were then separated from the main plant and transplanted into pots in two groups each with four tillers 7.5 cm apart. Two and a half weeks later, fireweed seedlings at the one true leaf stage were sown in two groups at right angles to the ryegrass. Ryegrass 'plants' (group of four tillers) had an average of 12 leaf blades and were 8 to 12 cm tall. Fireweed had been germinated at 15/25°C in speedling trays in a 50% vermiculite 50% peat mixture with a basal fertiliser dressing and grown under 50% shade. Seedlings were thinned after 2 weeks to two plants per pot.

The rapid growth of fireweed seedlings some 3 to 4 weeks after transplanting unexpectedly prevented them from being shaded by the ryegrass. Therefore, in mid August whole fireweed plants were removed from two of the harvests and resown with fireweed seed. By that time the ryegrass plants were larger and able to exert their respective shading effects. Owing to their size, later established seedlings were thinned to only eight per pot. Data from the two harvests with early established fireweed were analysed separately from those which were resown.

The first harvest with early established fireweed was on 10 September and the second on 16 October. Measurements of fireweed included number of branches and capitula, and total fresh and dry weights. The first harvest with resown fireweed was on 1 October and the second on 13 November. Measurements made were height, leaf area and number of leaves of fireweed, and total fresh and dry weights. For ryegrass in all four harvests the number of tillers and fresh and dry weights were recorded. At the first harvest of later sown fireweed the dry weight of ryegrass roots was also measured. All plant material was dried at 70°C.

Measurements used to quantify the shade effect caused by the prostrate and erect biotypes of ryegrass were percentage ground cover estimates made in late September, and light readings (P.A.R.) above and below leaf canopies taken in early October.

RESULTS

Experiment 1

Levels of irradiance (r.l.i.) in this experiment did not appear to affect time of germination. Under each shade treatment considerable germination had occurred within 7 days of sowing.

The initial effect of decreasing r.l.i. was to cause etiolation of seedlings and a reduction in cotyledon length. Heights of seedlings at the cotyledon stage, and the length of cotyledons 4 days after emergence, are shown in Figure 9.1 a,b. Seedlings at 0.06 r.l.i. were almost twice the height of seedlings at 0.60 r.l.i.

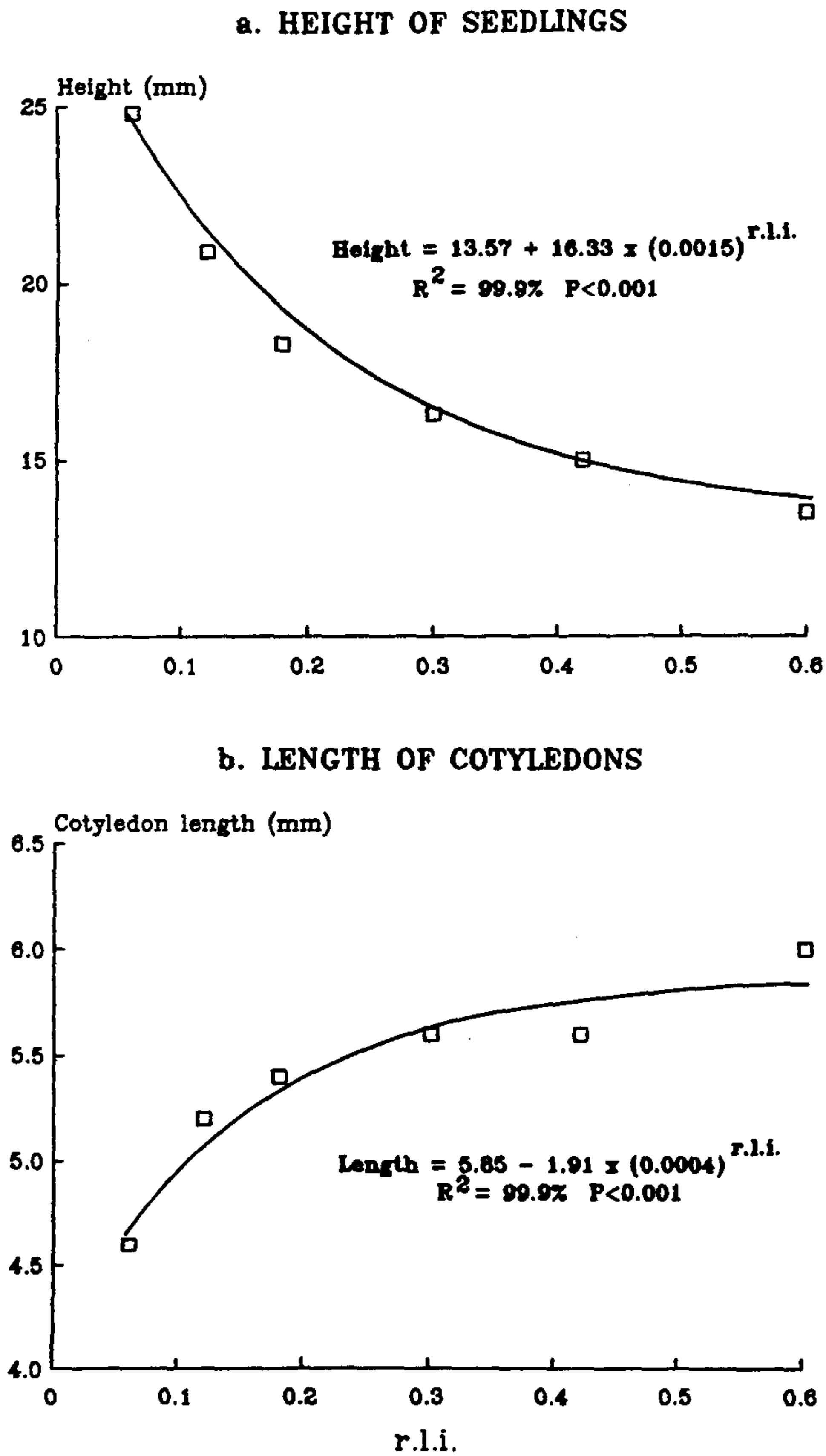


Figure 9.1 Effect of irradiance (r.l.i.) on (a) the height of fireweed seedlings at the cotyledon stage, and (b) the length of cotyledons 4 days after emergence.

By day 22 after seedling emergence, stems of plants growing under low levels of irradiance (r.l.i.) were noticeably smaller in diameter than those growing at high levels of irradiance, and were still green in colour below the cotyledons. At 0.60 and 0.42 r.l.i., stems were characteristically purple in colour below the cotyledons due to the presence of what was thought to be the pigment xanthophyll. At the two lowest levels of irradiance (0.06 and 0.12 r.l.i.), fireweed seedlings were also demonstrating a positive phototropic response (i.e. they were growing towards the sun). By day 45, only plants under 0.60 r.l.i. maintained straight and rigid stems. Plants under heavier shade were less lignified and bent.

The morphology of seedlings 25 days after emergence, grown under three levels of shade, is shown in Plate 9.2.

Mean daytime temperatures recorded under each shade treatment are shown in Table 9.1. As might be expected temperatures were slightly higher in the low shade treatments, but no two treatments varied by more than one standard deviation. Small temperature differences are also likely to be experienced because of shading by pastures in the field.

Table 9.1 Means of recorded daytime temperatures under shade treatments.

Shade screen %	r.l.i.[A]	Temperature °C
None	0.60	24.6 ± 5.6
30	0.42	22.7 ± 5.1
50	0.30	21.7 ± 4.6
70	0.18	21.0 ± 4.4
80	0.12	21.3 ± 4.5
90	0.06	21.2 ± 4.8

[A] Relative level of irradiance.

Height

Fireweed responded to shade by growing taller in the early stages of seedling development (see Figure 9.1a), but from about day 36 onwards the order of height was reversed. Plants under the heaviest shade treatment were shortest and plants under the lightest shade treatment were tallest (see Figure 9.2a). Plants began rapid extension from about day 25. Figure 9.2b shows the heights of plants at the two harvests. At the 60 day harvest the height of fireweed was significantly reduced by shading ($P<0.05$), whether plants were shaded for the whole period (60 S) or only for the first 30 days (30 S/30 L) (see Plate 9.3). Although plants at 0.18 and 0.12 r.l.i. grew significantly taller ($P=0.05$) when placed on the open bench than plants kept under shade, plants at the lowest r.l.i. did not show a significant height response.

Dry weight

The dry weight of fireweed seedlings declined linearly with decreasing r.l.i. at the 30 day harvest (see Figure 9.3a). Dry weights of plants placed on the open benches at day 30, and their components, were almost always significantly greater than those shaded throughout the whole experiment ($P=0.05$) (see Table 9.2).

As a percentage of total dry weight, stems showed a general decline with increasing shade while leaves showed the reverse trend (see Table 9.2). This partly explains why moisture content (expressed as a percentage of total dry weight) increased significantly with shading ($P<0.05$) (see Figure 9.3b), and why plants bent over under shaded conditions.

Root dry weight in 60 S group of plants at the second harvest decreased from a mean of 2.20 g pot^{-1} at 0.60 r.l.i. to 0.71 g pot^{-1} at 0.30 r.l.i. Fireweed roots of 30 S/30 L plants at 0.30 r.l.i. averaged 1.48 g pot^{-1}.

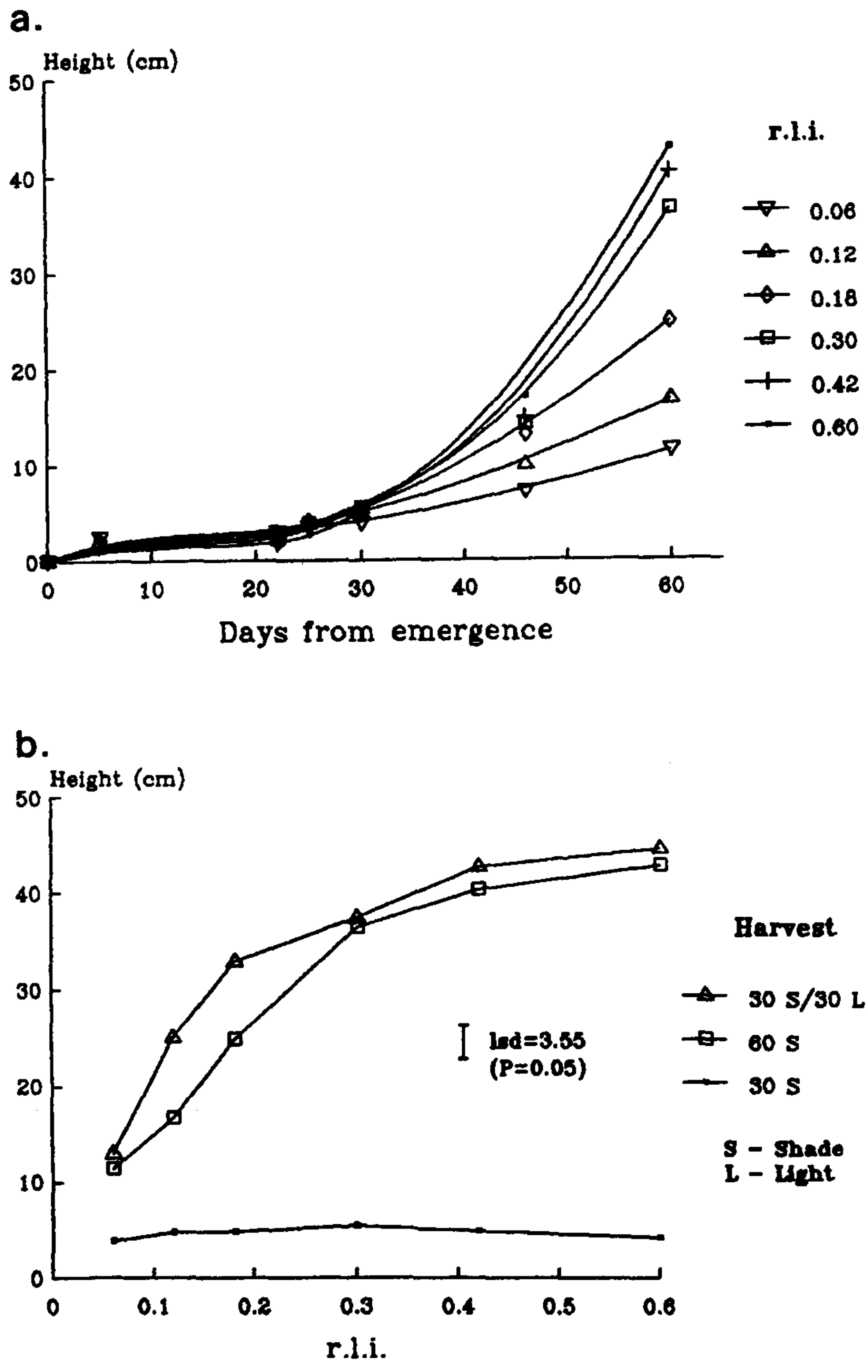


Figure 9.2 Effect of irradiance (r.l.i.) on the mean height of fireweed (a) over time, and (b) at the 30 day (30 S) and 60 day harvests. The latter plants were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L).

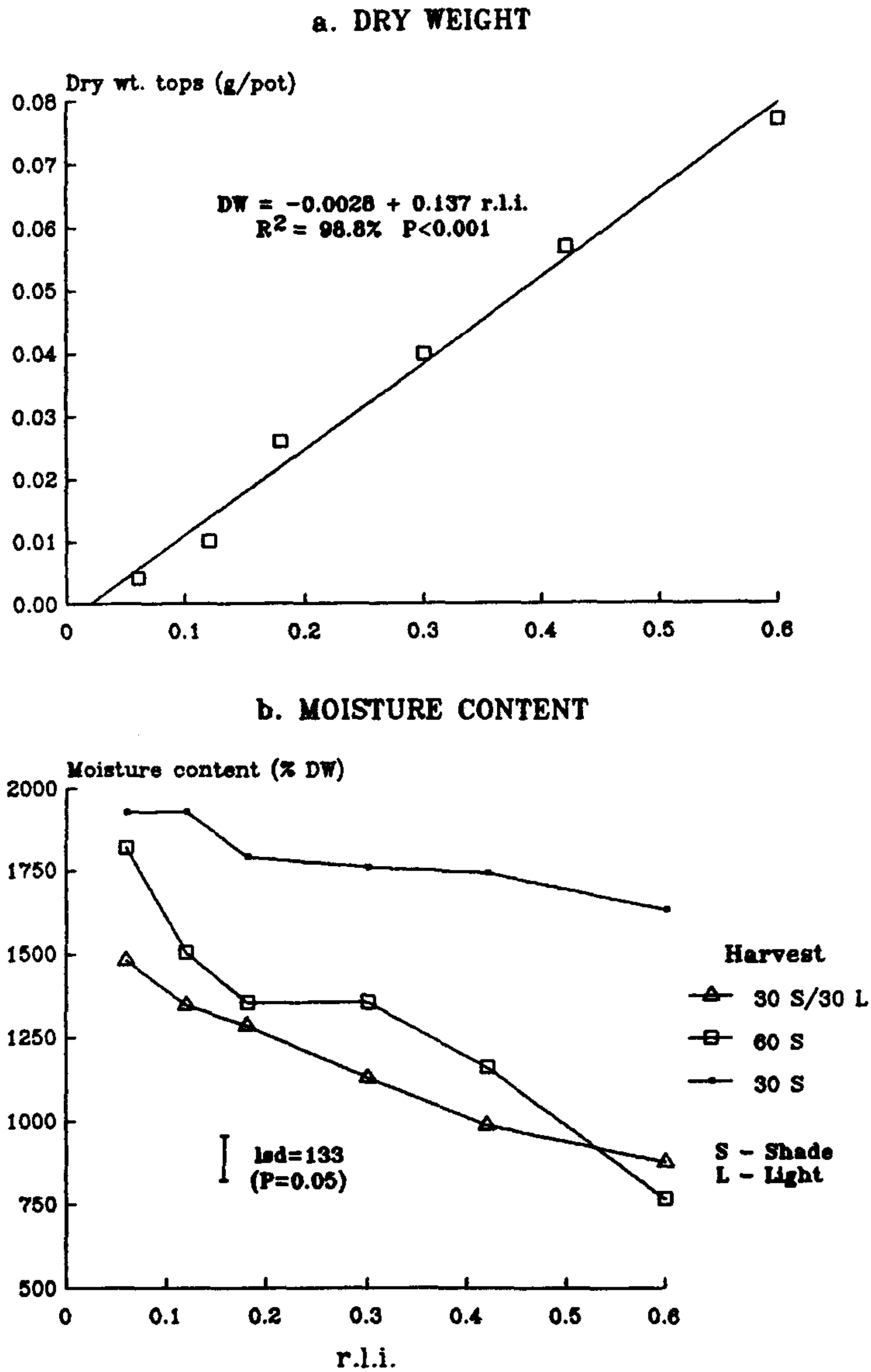


Figure 9.3 Effect of irradiance (r.l.i.) on (a) the dry weight of fireweed tops at the 30 day harvest, and (b) the moisture content of fireweed (as a percentage of dry weight) at the 30 day (30 S) and 60 day harvests. The latter plants were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L).

Table 9.2 The effect of irradiance (r.l.i.) on dry weight data of fireweed at the 60 day harvest. Data on a ln (x + 1) transformed scale. Plants were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L). Values in brackets are dry weights as a percentage of total shoot dry weight.

		r.l.i.						
Component	Group[A]	0.60	0.42	0.30	0.18	0.12	0.06	lsd[B] (P=0.05)
Stems g pot^{-1}	(60 S)	1.533 (56.0)	1.158 (44.7)	0.710 (41.6)	0.334 (37.4)	0.122 (36.9)	0.019 (41.7)	0.149 (5.1)
	(30 S/ 30 L)	1.392 (52.0)	1.313 (49.7)	1.028 (41.6)	0.732 (39.3)	0.432 (34.3)	0.142 (25.7)	
Leaves g pot^{-1}	(60 S)	1.346 (44.0)	1.309 (55.3)	0.897 (58.4)	0.509 (62.6)	0.199 (63.1)	0.026 (58.3)	0.108 (5.1)
	(30 S/ 30 L)	1.327 (48.0)	1.318 (50.3)	1.258 (58.4)	0.977 (60.7)	0.703 (65.7)	0.364 (74.3)	
Total shoots g pot^{-1}	(60 S)	2.010	1.712	1.251	0.722	0.299	0.045	0.123
	(30 S/ 30 L)	1.917	1.866	1.671	1.317	0.938	0.464	

[A] S = Shade; L = Light.
[B] lsds are for comparisons within and between Groups.

Relative growth rate

The R.G.R. of seedlings showed an exponential response to varying irradiance (see Figure 9.4a). R.G.R. was higher during the first 30 days of shade than in the 30 to 60 day period, particularly at the higher levels of r.l.i. The data indicate that growth decreases steadily from 0.60 down to about 0.20 r.l.i. but then declines rapidly. When removed from the shade, the R.G.R. of seedlings increased dramatically and was highest in plants which had been under heavy shade. Extrapolating the regression of R.G.R. for the first 30 days on $\log_{10}$ r.l.i. to the intercept gave a light compensation point for seedling growth of 0.007 r.l.i. (see Figure 9.4b).

Leaf production

Increased shading had a considerable influence on the number, shape and size of fireweed leaves. Initiation of primary leaves was delayed by shading (see Figure 9.5). This resulted in significant reductions in the total number of leaves ($P<0.05$) both at the 30 and 60 day harvests. Once leaves were initiated, mean rate of growth in leaf length was more or less similar from 0.60 r.l.i. down to 0.18 r.l.i. Leaf extension rates (measured by the slope of the line in Figure 9.5) at 0.12 and 0.06 r.l.i. were noticeably not as high.

Fireweed was able to partially compensate for the decrease in N.A.R. associated with declining levels of irradiance (see Figure 9.6a) by increasing its leaf area ratio (L.A.R.) (leaf area/shoot dry weight). This is shown for the 60 day harvest in Figure 9.6b. Specific leaf area (S.L.A.) (leaf area/leaf dry weight) responded similarly. The most rapid increase in L.A.R. occurred below 0.18 r.l.i. Plants shaded for the first 30 days only (30 S/30 L), were able to increase the thickness of their leaves and reduce their L.A.R. after being placed in the open. The colour of leaves changed from pale to dark green.

The changes in L.A.R. were accompanied by changes in leaf shape (see Figure 9.7). The width/length ratio of the first true leaf 30 days after germination increased significantly ($P=0.05$) and progressively from 0.14 at 0.60 r.l.i. to 0.26 at 0.06 r.l.i.

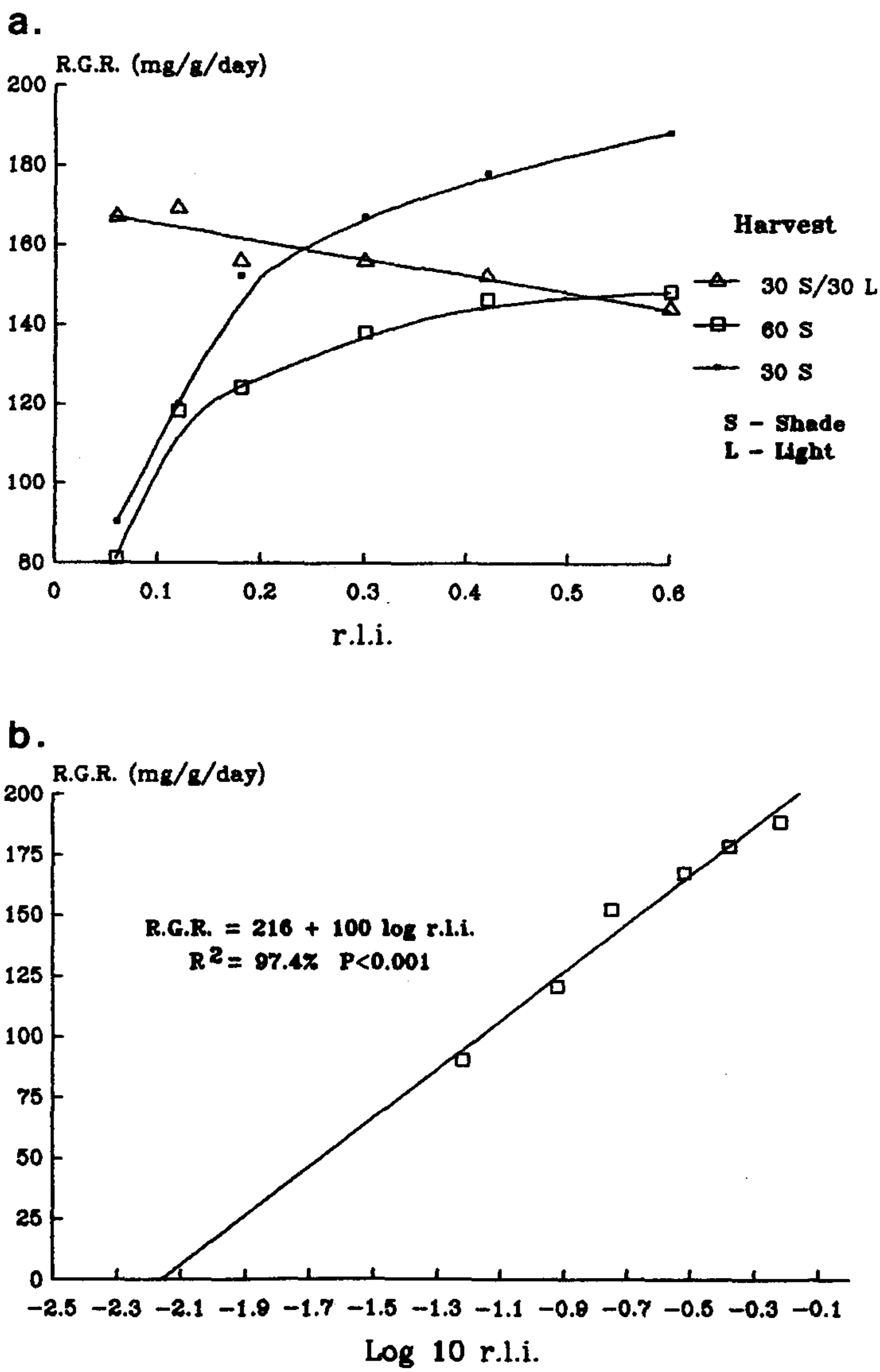


Figure 9.4 Effect of irradiance (r.l.i.) on the relative growth rate (R.G.R.) of fireweed (a) at the 30 day (30 S) and 60 day harvests (the latter plants were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L)), and (b) the regression of R.G.R. on the logarithm (base 10) of irradiance.

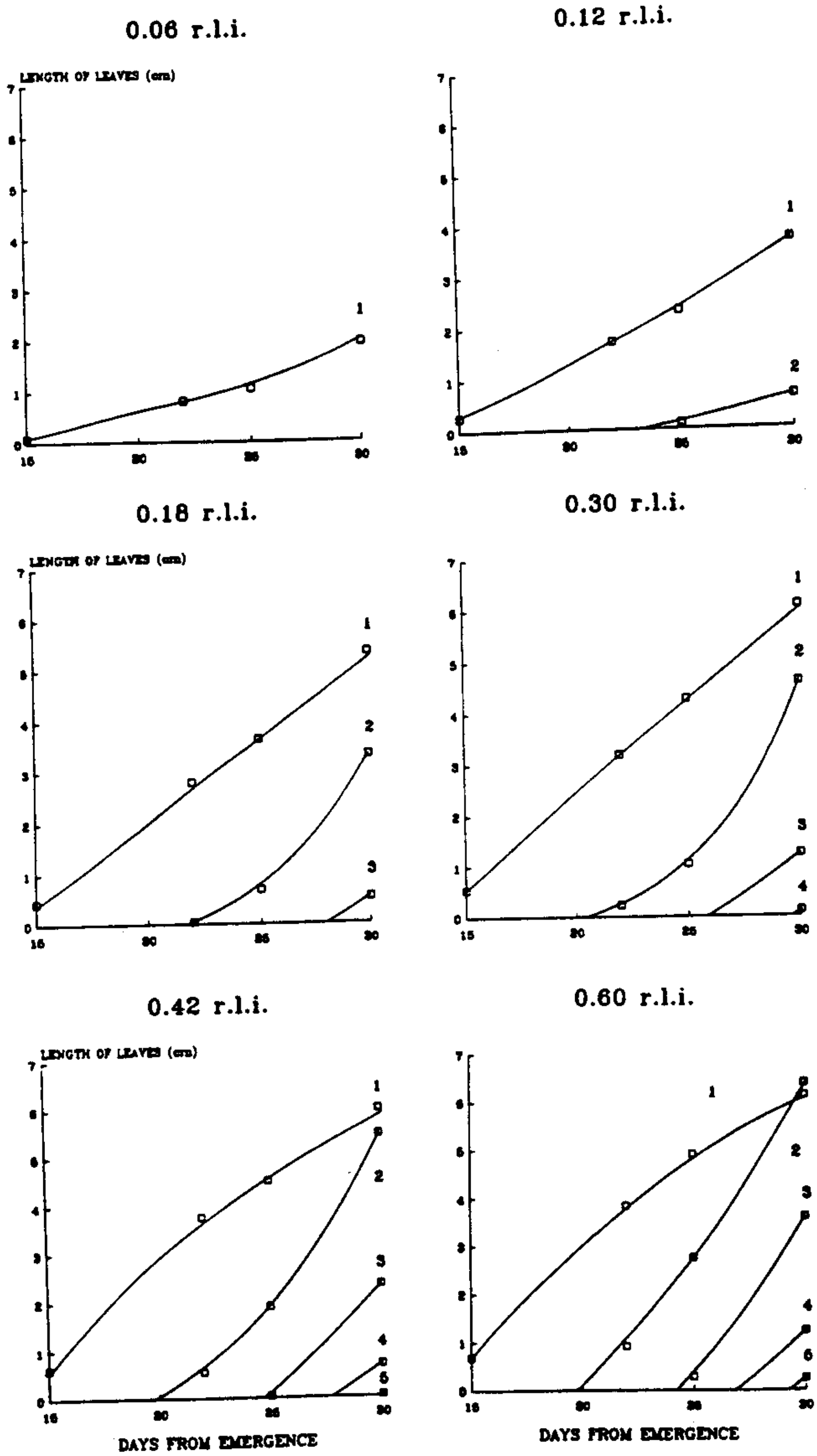


Figure 9.5 Growth of leaves of fireweed as influenced by irradiance (r.l.i.). Each curve represents the mean growth of a leaf pair. The numbers 1, 2, 3, 4, and 5 denote leaf pairs in their order of appearance.

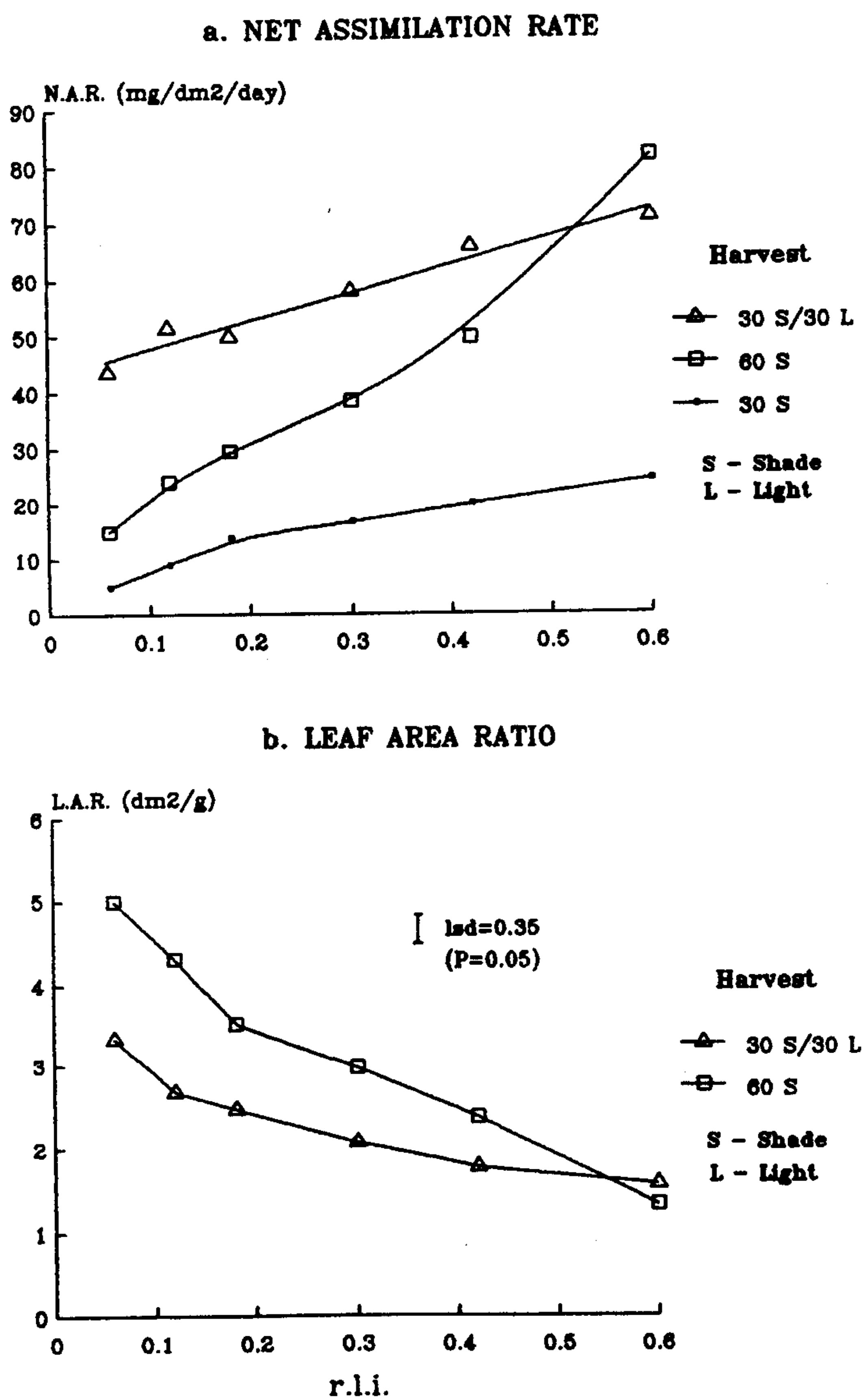


Figure 9.6 Effect of irradiance (r.l.i.) on (a) the net assimilation rate (N.A.R.) of fireweed 30 days (30 S) and 60 days after emergence, and (b) the leaf area ratio (L.A.R.) 60 days after emergence. Plants at the latter harvest were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L).

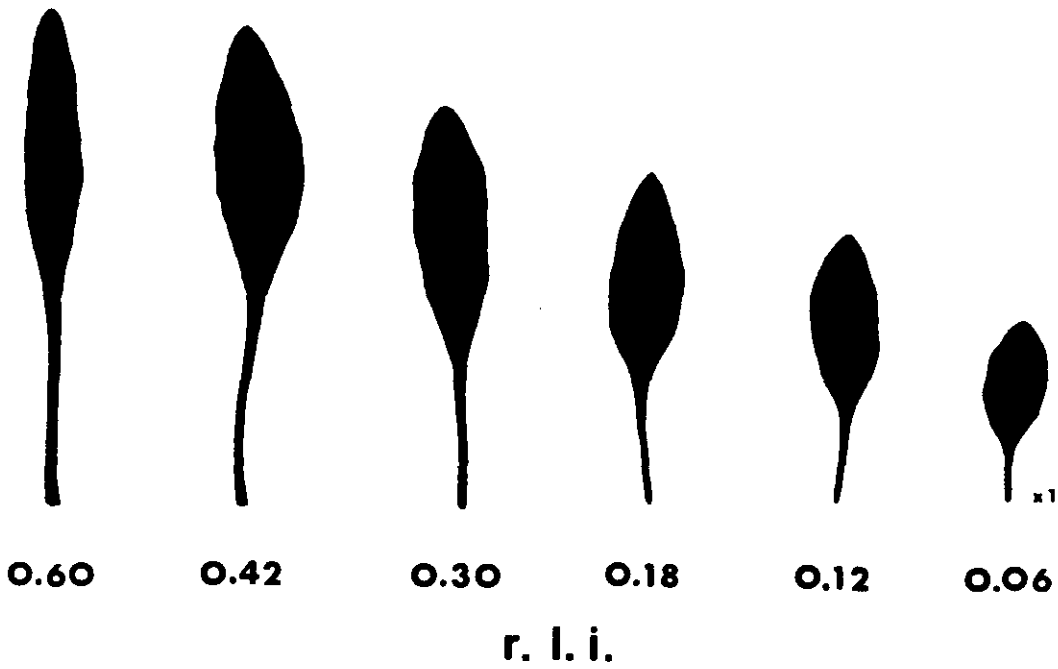


Figure 9.7 Representative leaves of fireweed from the first leaf position, showing the effects of decreasing irradiance (r.l.i.) on leaf shape and size.

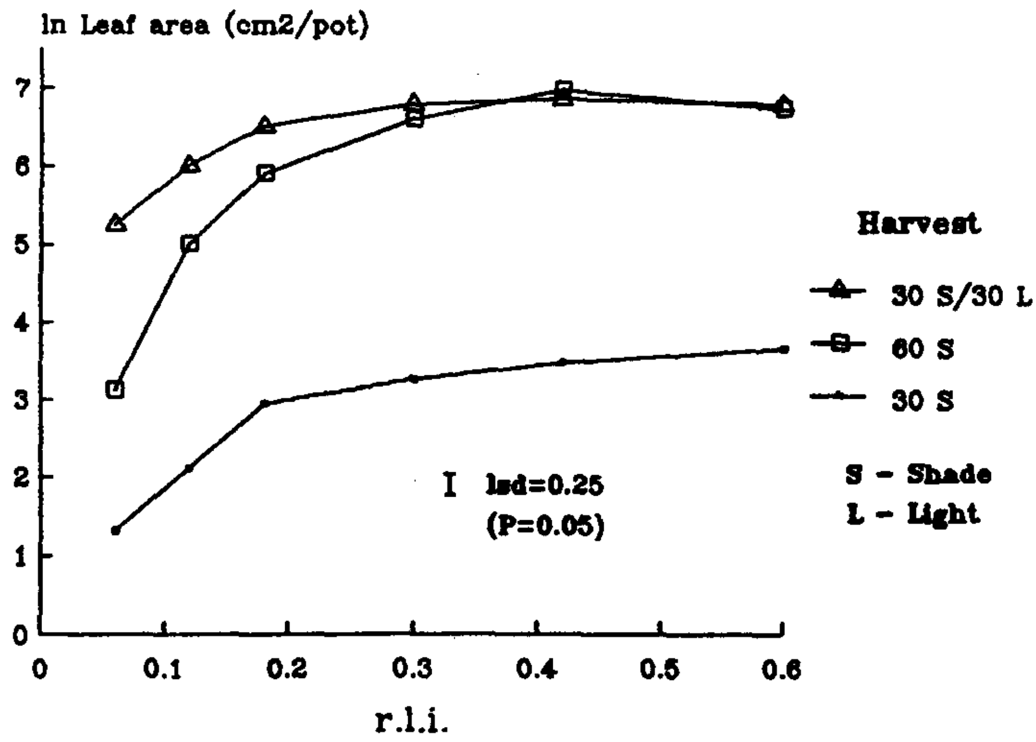


Figure 9.8 Total leaf area of fireweed at the 30 day (30 S) and 60 day harvests, as affected by irradiance (r.l.i.). The latter plants were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L).

Shading also had a significant effect on total leaf area ($P<0.05$). At 30 days after emergence, leaf area decreased only gradually from 0.60 to 0.18 r.l.i. but fell rapidly below 0.18 r.l.i. (see Figure 9.8). The shading effect after 60 days was even more pronounced and resulted in the leaf area beginning to decline at a higher level of irradiance. Plants subject to low levels of irradiance for the first 30 days, however, were able to recover quickly once moved to the open bench of the glasshouse (see Figure 9.8). The total length and number of primary leaves at the 30 and 60 day harvests showed similar patterns of response.

Reproductive capacity

After 60 days of shading, the number of branches produced by fireweed declined significantly at levels of irradiance below 0.42 r.l.i. ($P=0.05$) (see Figure 9.9a). Capitula production, however, was sensitive ($P=0.05$) to all levels of shading, and from the shape of the graph would have appeared to increase even further at levels of irradiance above 0.60 r.l.i. (see Figure 9.9b). Of the two, capitula production was least responsive to the increase in irradiance given to plants removed from the shade treatments after 30 days.

Experiment 2

Early established fireweed

Fireweed which had been established early in the experiment grew above the ryegrass before the two biotypes had well developed canopies. Therefore, little information could be obtained from these two harvests on the shading effects of the two ryegrass biotypes.

Effects caused by the ryegrass on the growth and development of fireweed resulted primarily from competition for other resources, such as water and nutrients. These data are presented in Table 9.3. Both prostrate and erect biotypes of ryegrass significantly reduced the growth of fireweed ($P=0.05$) compared with the control (no

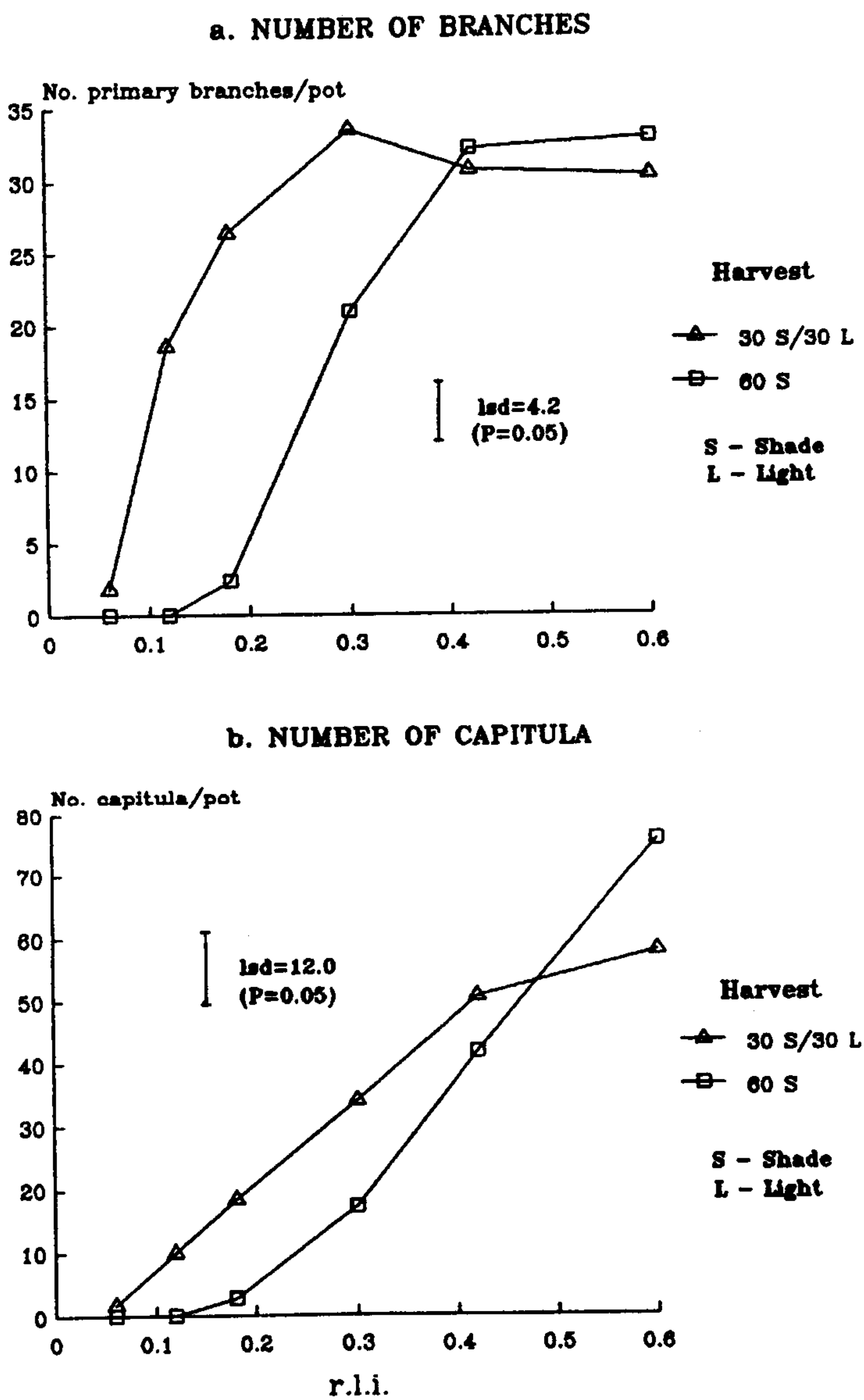


Figure 9.9 Effect of irradiance (r.l.i.) on the production of (a) primary branches, and (b) capitula of fireweed, at the 60 day harvest. Plants were shaded either for the whole 60 days (60 S) or were removed from shade treatments after 30 days (30 S/30 L).

Table 9.3 Effect of prostrate and erect ryegrass biotypes on the growth and development of early established fireweed (compared with the ryegrass free control) at two harvest dates.

Harvest	Ryegrass biotype	No. 1° branches pot^{-1}	No. capitula pot^{-1}	DW capitula g pot^{-1}	DW shoots g pot^{-1}	Total DW tops g pot^{-1}
Early 10/9/87	Prostrate	22.6	83.8	1.090	6.91	8.00
	Erect	26.4	74.6	1.300	7.50	8.80
	Control	29.4	143.4	1.972	13.83	15.80
Late 16/10/87	Prostrate	21.0	182.0	2.254	14.67	16.92
	Erect	19.2	179.0	1.918	13.39	15.31
	Control	29.4	438.2	4.790	32.91	37.70
lsd (P=0.05) (within harvests)		4.1	53.1	0.613	2.73	2.91

ryegrass). But there were no significant effects at the 5% level between the two ryegrass biotypes at either the early or late harvests. This result suggests that the prostrate and erect biotypes of ryegrass competed equally well with fireweed for water and nutrients.

The differences between the two ryegrass biotypes in terms of their fresh and dry weights and number of tillers are shown in Table 9.4.

Late established fireweed

Fireweed which was resown during the experiment and grown with the prostrate and erect ryegrass biotypes was shaded considerably and drastically reduced in size compared with the control. Neither had penetrated the undefoliated leaf canopies prior to harvesting at 7 and 13 weeks after sowing. Seedlings beneath prostrate ryegrass plants were difficult to establish and showed symptoms of heavy shading similar to that found in Experiment 1. Seedlings under erect ryegrass plants were similar to lightly shaded plants, i.e. erect and more strongly lignified.

Prostrate ryegrass plants had dense canopies while canopies of erect plants were more open and allowed greater penetration of light. Erect ryegrass plants matured earlier than the prostrate biotype, flowering and setting seed in mid September. Associated with this was the 'haying off' of some lower leaves. The prostrate biotype remained in its vegetative state until late October/early November. Prostrate and erect plants at two stages of growth are shown in Plate 9.4 a,b.

The mean ground cover of ryegrass in late September was estimated to be 87% for prostrate plants compared with 57% for erect plants. Light measurements (P.A.R.) showed that the respective levels of irradiance under the two canopy types were 0.08 and 0.33 r.l.i. The erect ryegrass biotype had significantly fewer tillers than the prostrate biotype ($P<0.001$) at the early harvest (see Table 9.4) (presumably tiller regrowth in erect plants reduced the difference at the late harvest). But the erect ryegrass biotype had a significantly greater total dry weight ($P<0.001$). Fresh weight was

Table 9.4 Growth data for prostrate and erect ryegrass biotypes at two harvests for early and late established fireweed. Data for ryegrass grown alone and with fireweed are combined.

Fireweed establishment	Harvest	Ryegrass biotype	No. tillers pot^{-1}	FW tops g pot^{-1}	DW tops g pot^{-1}
Early	Early 10/9/87	Prostrate	70.2	39.4	7.24
		Erect	66.4	47.3	9.56
			n.s.	*	*
	Late 16/10/87	Prostrate	120.0	74.6	15.98
		Erect	93.1	80.3	25.17
			***	n.s.	***
Late	Early 1/10/87	Prostrate	110.4	53.0	12.23
		Erect	89.5	66.3	20.78
			***	**	***
	Late 13/11/87	Prostrate	132.4	66.7	18.90
		Erect	126.0	73.6	28.23
			n.s.	n.s.	***

Significant differences calculated from lsds: * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. non significant at $P<0.05$.

Plate 9.4 Morphology of erect and prostrate biotypes of Kangaroo Valley ryegrass grown in 18 cm diameter pots (a) 18 days after tillers were transplanted in groups of four - erect (left) and prostrate (right), and (b) 12 weeks after transplanting - erect (right) and prostrate (left).


a
B5
B4
PA


b

significantly higher ($P<0.01$) only at the first harvest (see Table 9.4). Root weight, although slightly heavier in the prostrate ryegrass biotype, was not significantly different between the two biotypes at the 5% level.

The effects of the prostrate and erect ryegrass biotypes on the growth and development of fireweed are summarised in Table 9.5. Data for control plants (fireweed grown alone) are not included since it was obvious that these plants were greatly different from fireweed plants grown with ryegrass. For example, the dry weights of fireweed seedlings grown with prostrate and erect ryegrass were 0.11 and 0.24% respectively of the resown control at the second harvest. Control plants were some 50 to 60 cm tall and were branching and flowering.

At the early harvest fireweed growing with prostrate ryegrass had a significantly higher moisture content than plants growing with erect ryegrass ($P<0.001$), but other parameters were non-significant (see Table 9.5).

At the later harvest, however, the total fresh and dry weights of plants under prostrate ryegrass were lower (significant at $P<0.01$ and $P<0.001$ respectively) than those under erect ryegrass. The total number of leaves was also reduced, as were the total and average leaf areas ($P<0.01$). Moisture content continued to be higher ($P<0.05$) (see Table 9.5).

Somewhat unexpectedly the L.A.R. was significantly higher ($P<0.05$) under erect ryegrass at the second harvest. At the first harvest the reverse was true, though the effect was non-significant. This result is partly explained in that plants at the later harvest under prostrate ryegrass had a higher percentage of dead leaves. This was attributed both to senescence induced by shading and a higher level of disease. The result also suggests that, as competition for water and nutrients became stronger under conditions of heavy shade, fireweed was less able to compensate for a decreasing N.A.R. by increasing its L.A.R.

Table 9.5 Effect of prostrate and erect ryegrass biotypes on the growth and development of late established fireweed at two harvest dates.

Harvest	Ryegrass biotype	FW tops g pot^{-1}	DW tops mg pot^{-1}	Moisture content % DW	Mean height mm	No. leaves[A] pot^{-1}	L.A.[B] mm^2 pot^{-1}	L.A.[B] mm^2 $leaf^{-1}$	L.A.R. dm^2 g^{-1}
Early 1/10/87	Prostrate	0.126	10.09	1163	24.56	1.428	3.191	2.818	2.131
	Erect	0.121	12.39	888	24.06	1.395	3.220	2.905	1.779
		n.s.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.
Late 13/11/87	Prostrate	0.218	19.41	1033	49.72	1.829	3.163	2.218	1.060
	Erect	0.393	38.16	934	43.35	2.049	4.141	2.917	1.554
		**	***	*	n.s.	**	**	**	*

[A] Data on square root (x + 0.5) transformed scale.
[B] Data on ln (x + 1) transformed scale.
Significant differences calculated from lsd's - * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. not significant at $P<0.05$.

Two weeks prior to the final harvest, one of the five replicates suffered severe moisture stress due to a failure in the automatic sprinkler system. The soil was observed to be dry and the fireweed wilted. At the final harvest fireweed seedlings in that replicate growing under erect ryegrass were partially shrivelled but remained alive. All eight plants growing with prostrate ryegrass were dead, presumably because they were less hardy and less able to withstand moisture stress.

A Chi^2 test carried out on all the data showed that significantly more deaths of seedlings ($P<0.05$) occurred under the prostrate ryegrass biotype (28%) than under the erect ryegrass biotype (0%).

DISCUSSION

Artificial shading utilised in Experiment 1 of this study clearly reduced the growth and development of fireweed. Likewise in Experiment 2, the reduced growth of fireweed growing under prostrate ryegrass canopies compared with fireweed under erect ryegrass canopies (see Table 9.5) was attributed primarily to a higher level of shade. This was recorded at the second harvest of fireweed plants which were established late in the season. In terms of fresh weight of tops and root dry weight, the erect and prostrate ryegrass biotypes were not significantly different ($P=0.05$). Although the mean R.G.R. of the prostrate biotype was higher (0.062 $g\ g^{-1}\ wk^{-1}$) than that of the erect biotype (0.044 $g\ g^{-1}\ wk^{-1}$) between the first and second harvests, overall dry matter production was significantly higher ($P<0.001$) in the erect biotype.

The mean ground cover of the erect and prostrate biotypes and their respective levels of irradiance (0.33 and 0.08 r.l.i.) were directly comparable with the 0.30 and 0.06 r.l.i. treatments under artificial shade cloth.

Strategies under Shade

In relation to light requirements for plant establishment and growth, Grime (1966) has made a distinction between shade-avoiding and shade-tolerant species. Shade-avoiding species are characterised by rapid initial height growth, whereas shade-tolerant species demonstrate slow steady growth and conservation of reserves. Shade-tolerant species are those which, by increasing their L.A.R. to compensate for a reduction in photosynthesis or N.A.R., maintain a high R.G.R. over a wide range of irradiance (Bourdôt et al. 1984). True 'shade' plants were defined by Blackman and Wilson (1951 a,b) as those reaching a maximum R.G R. at an irradiance substantially below full daylight. The success of shade-tolerant species under deeply shaded conditions may also be due to a low compensation point (Mahmoud and Grime 1974).

The results of the present study demonstrate that fireweed utilises several strategies to avoid and offset the effects of shade. In the first 25 days following emergence, seedlings grew considerably taller under heavy shade, while after 25 days, rapid stem elongation also acted to place photosynthetic tissue above the pasture canopy.

Some tolerance to shade was evident from the shade-induced compensatory increases in L.A.R. and S.L.A., also common in many other species (e.g. Evans and Hughes 1961; Grime 1965; Auld and Martin 1975; Packham and Willis 1977; Daniels 1986). Although leaf initiation and growth were slowed, the total leaf area declined little within the range 0.60 down to 0.18 r.l.i. As Panetta (1977) found for Baccharis halimifolia, leaf allocation was most rapid in heavily shaded seedlings and slowest in open grown seedlings. With stronger competition for water and nutrients in Experiment 2, L.A.R. declined after an initial decrease. Auld and Martin (1975) also observed a dramatic decrease in L.A.R. following a rise at a very low level of irradiance (0.02 r.l.i.). Fireweed seedlings appear to be more vulnerable to shade when other resources are also limiting.

More than desirable extrapolation was required to estimate the light compensation point of fireweed. Nevertheless, the calculated value (0.007 r.l.i.) indicates that fireweed has the ability to continue positive growth at very low levels of irradiance. This value, even if adjusted for extrapolation, is low compared with compensation points derived for other species (Medd and Lovett 1978; Pook 1983; Bourdôt et al. 1984). It could be higher under field conditions due to interaction with other factors.

Significance for Cultural Control

One of the most important results in terms of shade and the ecology of fireweed was that increasing shade led to an immediate reduction in the growth and dry matter production of fireweed (see Table 9.2, and Figures 9.3a and 9.4a). The data of Figures 9.3a and 9.4 a,b suggest that the R.G.R. and yield of fireweed would increase appreciably at levels of irradiance higher than 0.60 r.l.i., indicating its preference for open pastures. Light saturation did not appear to be reached in this experiment. In contrast, the response of R.G.R. of Achillea millefolium to shading was characterised by a plateau between full daylight and approximately 0.40 r.l.i. (Bourdôt et al. 1984). Reproductive effort of fireweed was also very sensitive to increasing shade (see Figure 9.9b). Prolific flowering occurred at high light intensity. Deeply shaded plants therefore are likely to leave fewer seeds for the next generation.

As Pook (1983) found for the thistle seedlings Silybum marianum and Onopordum sp., shading is likely to make its greatest contribution to cultural control of fireweed infestations in pastures at levels of irradiance below 0.20 r.l.i. (i.e. 80% light interception). Below this level R.G.R. decreased rapidly (see Figure 9.4a). Almost 100% light interception can be obtained under pastures and crops (Donald 1963). Field measurements taken in late August under a forage crop of Lolium multiflorum cv. Concord (280 plants m^{-2} and 30 cm tall) at Camden showed that 97.2% of light was intercepted.

If fireweed seedlings penetrate a pasture canopy and reach near full sunlight, however, they may recover quickly. It is under conditions such as occurred in Experiment 2 where there was strong competition for water and nutrients as well as light, that the pasture is more likely to exert effective control. Additional fireweed plants, which were allowed to grow with little other competition under the shade treatments of Experiment 1 past the 60 day mark, were still able to flower and produce viable seed at levels of irradiance as low as 0.12 r.l.i., though total seed production was much reduced.

B. halimifolia was able to produce viable seed at levels as low as 0.03 r.l.i. (Westman et al. 1975).

Influence of Moisture Stress and Other Factors

The three primary resources for plants are water, light and nutrients. A change in any one may affect the ability of a plant to respond to the others (Zimdahl 1980). In the first harvest of late established fireweed in Experiment 2, the greater shading effect of prostrate ryegrass was not evident in the growth parameters of fireweed (see Table 9.5). The effect was thought to be masked by a differential soil moisture condition. The more open canopy of erect ryegrass plants allowed its top soil to dry out quickly. The mean gravimetric moisture content of the top 1 cm of soil, measured at the end of a typical watering cycle, was significantly lower ($P<0.01$) in erect than in prostrate ryegrass pots, i.e. 0.164 g g^{-1} compared with 0.238 g g^{-1}. Although the roots of fireweed usually reach depths greater than 1 cm, excavations of these very small fireweed seedlings showed that their root systems were poorly developed and restricted to a depth of a few centimetres. A change to daily automatic watering considerably reduced the effect of this soil moisture differential at the second harvest.

Root allocation was markedly affected by light intensity in Experiment 1. Under open conditions (0.60 r.l.i.), the root/shoot ratio was 0.34 while at 0.30 r.l.i. it had decreased to 0.28. As Panetta (1977) suggested, it is possible that heavy shade operates most critically through its effects upon root system establishment. Because shading generally delays and reduces root development (McWhorter and Jordan 1976; Panetta 1977; Bourdôt et al. 1984), shaded plants are likely to be less competitive for nutrients and water. The limited capacity of shaded fireweed seedlings to compete with deep rooted perennials for moisture was demonstrated in this study with perennial ryegrass. In Chapter 5 it was noted that a lack of soil moisture was responsible for significant seedling deaths in the field, particularly during summer.

Pook (1983) observed that well shaded thistle seedlings in pastures appear to be more extensively damaged by defoliators (e.g. slugs, snails and caterpillars) than those growing in the open. The more succulent foliage of heavily shaded plants, common too in fireweed (see Figure 9.3b), is probably more palatable to such herbivores. In addition, fireweed seedlings are likely to be more susceptible to diseases such as fireweed rust and to frost (see Chapter 6).

CONCLUSIONS

A weed which grows poorly under shade may be effectively controlled if the pasture in which it grows offers strong competition for light. The results of this study demonstrate a degree of tolerance of fireweed seedlings to shade and the ability of the weed to recover quickly if shade is removed. Nevertheless shade can reduce the growth of fireweed considerably and particularly at levels of irradiance of 20% or less. The weed appears most prolific in open pastures. Better surface soil moisture under shady pastures can negate the shading effects in the early growth of seedlings, but the seedlings are more vulnerable to biotic and environmental stresses.

For shade to be a contributing factor in the cultural control of fireweed, it would need to be imposed on the weed for at least the first 25 to 30 days following seedling emergence. After this period stem elongation of fireweed is rapid and penetration of the pasture canopy is more likely. Therefore fertiliser and grazing treatments (e.g. removal of grazing animals) need to be made to enhance interspecific competition for light during periods of fireweed seedling establishment (see Chapter 5). As demonstrated in Experiment 2 of this study, combined competition for water and nutrients as well as light at this time can depress the growth of fireweed dramatically.

The prostrate biotype of Kangaroo Valley ryegrass (Lolium perenne), because of its closed canopy and longer growing season, has the greater potential of the two ryegrasses to compete with fireweed. Other strong competitors for light also need to be identified.

Further work may focus on the relationship between shading and response to soil nutrients (particularly nitrogen and phosphorus), as studied by Daniels (1986) for Pteridium aquilinum. The effect of plant induced shade on fireweed seed germination too requires examination. Good pasture cover, due to a decrease in the red/far-red ratio of transmitted light, inhibited germination of many of the pasture weeds studied by Phung and Popay (1981). It may also be a major factor in preventing fireweed invasion. Such a possibility is implied in the results obtained by Guillén *et al*. (1984).

Chapter 10

CONTROLLING FIREWEED WITH COMPETITIVE PASTURES

> 'It is a fact of biological life that if one organism occupies a particular space in an ecosystem then another organism cannot do so.' (Hill 1977)

INTRODUCTION

Long term weed control in pastures rests largely on the proper establishment and maintenance or management of useful and competitive pasture plants (Cashmore and Campbell 1946; Whittet 1969; Michael 1970). Demonstrable successes in Australia have included the use of subterranean clover to control *Hypericum perforatum* L. var. *angustifolium* DC. (Moore and Cashmore 1942), *Nassella trichotoma* (Nees) Arech. (Campbell 1960) and *Chondrilla juncea* (Moore and Robertson 1964); lucerne to control *Asphodelus fistulosus* L. (Roark and Donald 1954); lucerne and phalaris to control *Silybum marianum* (Michael 1968a); and phalaris and tall fescue to control *Onopordum* sp. (Michael 1968b).

The desirability of ecological (or cultural) control of fireweed has already been stressed in Chapters 1 and 2. The results of Chapters 3, 5 and 9 have highlighted its likely success. Control measures which simply kill fireweed or remove it from the pasture are likely to be ineffective in the long term unless the pasture itself is altered to prevent reinvasion. However, fireweed shows rapid early growth (see Chapter 9) and, unlike *H. perforatum*, *S. marianum* and *Onopordum* sp., lacks a prostrate juvenile (or rosette) stage (Fernández and Verona 1985). The potential success of ecological control therefore needs to be demonstrated.

In Chapters 2 and 3 the summer growing perennial grass, kikuyu (*Pennisetum clandestinum*), was identified as a pasture species which successfully reduces the occurrence of fireweed in coastal areas of New South Wales. The key to its success is likely to be its dense cover early in autumn which suppresses germination and seedling establishment. This smothering habit has also been utilised extensively to combat bracken fern and other persistent weeds (Whittet 1968; 1969; Launders 1983). Little, however, is known about the ability of species which grow strongly during the main fireweed period, i.e. autumn, winter and spring, to compete with the weed. To this end a wide range of winter growing pasture species were selected for testing in a series of experiments described in this chapter.

It was concluded in Chapter 3 that work with pastures should be carried out particularly in areas into which fireweed has spread recently. Accordingly, Experiment 3 of this study was located in the Illawarra region on the south coast of New South Wales. The effects of several interacting factors on fireweed establishment and infestation were studied, namely herbicides, cultivation, fertilisers and pasture species.

MATERIALS AND METHODS

Experiment 1a - Pasture Species Competition

The first of a series of experiments designed to assess the effectiveness of pasture species in controlling fireweed was conducted under glasshouse conditions at Camden in 1986. Fireweed and 10 different pasture species were grown at high soil fertility and moisture status, alone and together, and the effect of each on the other measured. Species tested were:

1. *Avena strigosa* cv. Saia (Saia oats)
2. *Phalaris aquatica* cv. Sirosa (Phalaris)
3. *Dactylis glomerata* L. cv. Currie (Cocksfoot)
4. *Festuca arundinacea* Schreb. cv. Demeter (Tall fescue)
5. *Lolium perenne* cv. Kangaroo Valley (Perennial ryegrass)
6. *Lolium multiflorum* cv. Concord (Italian ryegrass)
7. *Trifolium repens* cv. Haifa (White clover)
8. *Trifolium subterraneum* L. cv. Junee (Subterranean clover)
9. *Trifolium pratense* L. cv. Redquin (Red clover)
10. *Lotus pedunculatus* Cav. cv. Maku (Lotus major)

While most species were perennials, some annuals were included to determine their relative merit in either a preparatory role to a control program with perennials or in a combined program. Because of their inclusion in other competition studies (see Chapters 7, 8 and 9), Saia oats and Kangaroo Valley ryegrass were benchmarks against which other species could be compared.

The experiment was analysed as a split plot factorial, the main plots being two harvest dates and the sub plots being pasture species. Each treatment was replicated five times. Pots contained either two fireweed plants, two pasture plants, or two fireweed plants together with two pasture plants.

Pot size, soil type and husbandry procedures were the same as that described for the glasshouse experiment in Chapter 7. Plants received fortnightly fertiliser applications of 'Aquasol' at 250 ml pot^{-1}. All species, including fireweed, were sown as seed on 2 July and later thinned to one plant per location. The first harvest, taken when fireweed plants were beginning to flower, occurred in late September and the second at late flowering in early November. In addition to some infection with fireweed rust, a number of fireweed plants were attacked by an unidentified leaf miner. To prevent potential damage by these leaf miners, plants were sprayed alternately with dimethoate (as Rogor) and malathion (as Maldison) both at a rate of 1.0 ml l^{-1}. Glasshouse conditions ranged from 32 $\pm$ 4/9 $\pm$ 2°C day/night temperature at the start of the experiment to 33 $\pm$ 3/11 $\pm$ 2°C at Harvest 1 in early September. Later temperature data were not recorded.

Fireweed data collected at the two harvests included number of capitula and primary branches, and dry weights of tops and their components. For pasture species the number of branches or tillers were counted and the total dry weight of tops recorded. Root dry weights of both fireweed and the various pasture species were measured only at the second harvest.

Experiment 1b - Earlier Pasture Species Competition

This smaller experiment was primarily the same as Experiment 1a except that fireweed was sown 8 weeks after the pasture species, which by then had established their respective growth habits. Only one harvest was taken (10 November) and only the effect of the competing pasture species on fireweed was measured, not vice versa. The experiment was of a randomised complete block design with 11 treatments (fireweed grown alone and in combination with the 10 pasture species) and five replicates.

Although disease control was attempted, considerable rust infection of fireweed seedlings occurred. This resulted in dry weight data being too variable to conduct a valid analysis of variance. Friedman's nonparametric multiple comparison test (Noether 1976) was therefore used to detect possible differences between treatments. Control plants, excluded from the analysis to allow for greater detection of treatment differences, were obviously much larger than plants subject to pasture competition.

Experiments 2a and 2b - Field Testing of Concord Ryegrass

The success of Concord ryegrass (L. multiflorum) in competing with fireweed in the glasshouse in Experiments 1a and 1b led to further testing of the species in the field. Two experiments were run concurrently and adjacent to one another during 1987 at Camden. In Experiment 2a the potential of increasing densities of ryegrass to control fireweed was assessed. The aim of Experiment 2b, designed similarly to the field experiment in Chapter 7, was to measure the reduction in productivity of Concord ryegrass caused by different densities of fireweed.

Preparation and management of the area, including fertiliser treatments, were the same as in Chapter 7. Concord ryegrass was sown on 22 April using a Connor Shea Coulter Coil Tyne Drill at a depth of 2.5 cm and with 15 cm between rows. Fireweed seedlings, raised also according to the procedure adopted in Chapter 7, were transplanted to the field at the 10 leaf stage some 22 days later.

Both experiments were split plot factorial designs with four replicates. Experiment 2a had 10 treatments: two levels of soil fertility (low and high) (main plots) x five levels of ryegrass density (sub plots). In Experiment 2b there were 16 treatments: two levels of soil fertility (main plots) x eight levels of fireweed density (sub plots). Sub plots were 1 m^2 in area (1 m x 1 m) and contained 6 rows of ryegrass. The experimental layout of both experiments and the random positioning of fireweed plants in sub plots of Experiment 2b were similar to the field experiment in Chapter 7.

Experiment 2a - Varying ryegrass density

In Experiment 2a, fireweed plants were evenly spaced and sown at a set density of 18 m^{-2}. Ryegrass, sown originally at 35 kg ha^{-1}, was thinned by hand 13 days after sowing to 0, 50, 100, 200 or 400 plants m^{-2}. The last four treatments were equivalent to there being a distance of approximately 12, 6, 3 and 1.5 cm between plants respectively. Harvesting of plant tops occurred on 25 August when ryegrass was at full tillering and fireweed at mid flowering. Ryegrass was approximately 15 and 40 cm tall and fireweed 30 and 40 cm tall in low and high fertility plots respectively. Dry weight yields were measured on a whole plot basis and the number of fireweed capitula recorded for sub samples of four plants $plot^{-1}$.

Experiment 2b - Varying fireweed density

In Experiment 2b ryegrass was sown at a set rate of 15 kg ha^{-1} giving a density of 280 plants m^{-2} measured 6 weeks after sowing. This was the same as that obtained in the field experiment in Chapter 7 with Saia oats. Fireweed densities, adapted from the experiment with oats, were 0, 1, 2, 5, 10, 15, 25 and 40 plants m^{-2}.

Three harvests of ryegrass were taken to simulate grazing by livestock at 9, 21 and 27 weeks after sowing. In the first, both ryegrass and fireweed were 15 and 30 cm tall in high and low fertility plots respectively. Fireweed had begun to flower. Additional 'Starter 18' fertiliser was broadcast at a low rate (30 kg N/14 kg P ha^{-1}) and a high rate (60 kg N/27 kg P ha^{-1}) between the first and second harvests. The aim was to maintain the differential between high and low fertility treatments, and to ensure adequate growth for harvesting in low fertility plots.

The second harvest occurred when ryegrass was at mid to late tillering, and 30 and 55 cm tall in low and high fertility plots respectively; fireweed was at mid flowering, and 35 and 45 cm tall. At the third harvest, fireweed, which was beginning to senesce, was also cut and weighed and the number of dead plants counted.

Experiment 3 - Field Testing of Perennial Pastures

In a 2 year field trial, conducted in the Illawarra region of New South Wales, the autumn/winter growing perennial species, Phalaris aquatica cv. Sirosa, Lolium perenne cv. Kangaroo Valley, and Festuca arundinacea cv. Demeter were selected for further testing as well as the spring/summer growing species, Pennisetum clandestinum cv. Whittet, Paspalum dilatatum and Setaria sphacelata (Schumach.) Stapf & C.E. Hubbard cv. Narok. Narok setaria was included because it had previously shown promise in work conducted at Taree (Launders, personal communication). Inoculated Trifolium repens cv. Haifa was grown alone and in combination with each of the grasses.

For winter growing species, areas at Dapto and Dunmore (see Figure 5.1) with known infestations of fireweed were sprayed with glyphosate at 2160 g a.i. ha^{-1} (as Roundup) on 19 March 1986 and slashed 2 weeks later. Excessive pasture was then raked off and the species direct drilled in rows 15 cm apart at a depth of 1 to 2 cm with a Cone Seeder fitted with coulters and Baker boots. Lime at 54 kg ha^{-1}, and phosphorus (as superphosphate - 9.2% P) at both low and high levels, 5 and 30 kg ha^{-1} respectively, were applied in close proximity to the seed at the time of sowing. Two controls were included, one cultivated but unsown and the other left without any pasture treatment.

The experiment was a split plot factorial design in which there were four replicates of the 12 treatments: two levels of soil fertility (main plots) x six pasture treatments (sub plots). Sub plots were 3 m x 10 m. The pasture treatments were as follows:

1. Phalaris (6 kg ha^{-1}) + White clover (2 kg ha^{-1})
2. Ryegrass (10 kg ha^{-1}) + White clover (2 kg ha^{-1})
3. Tall Fescue (10 kg ha^{-1}) + White clover (2 kg ha^{-1})
4. White clover (2 kg ha^{-1})
5. Sprayed, cultivated and fertilised (no pasture)
6. Fertilised only (otherwise undisturbed)

Seeding rates were chosen to give approximately 250 grass seedlings m^{-2} in each treatment (assuming 70% germination and 70% establishment). White clover was considered to occupy a different niche to the grasses and therefore did not have equivalent seed numbers. All rates were within those recommended by the New South Wales Department of Agriculture and Fisheries. Natural fireweed infestations were utilised.

The field trial site at Dapto proved too difficult to monitor because of the aggressiveness of the resident ryegrass pasture. Consequently, experimental assessment of the site ceased.

The site chosen at Dunmore had a gently undulating westerly aspect, was well drained, and supported a kikuyu based dairy pasture. Pasture and weed species found at the site are listed in Appendix 9. An analysis of the soil (see Appendix 10) showed that it had a pH of 4.7 and was deficient in phosphorus. Stock entry to the site was regulated using an electric fence. Rainfall data recorded at the site during 1986 and 1987 is given in Appendix 11. Temperature data from nearby Albion Park is also included.

After pasture establishment in early 1986, two fixed quadrats each 0.25 m^2 (0.5 m x 0.5 m), were established in each sub plot in locations which had good emergence of the sown species. Fireweed plants were counted regularly throughout the experiment. Pasture species, following an early establishment count, were assessed using the 'point quadrat' technique (Brown 1954). Dry weight harvests were taken at the end of each season in late October or early November. Unplanned grazing of the pastures prior to the second harvest meant that only fireweed could be harvested in 1987.

Due to the large emergence of fireweed in the first season, the site was sprayed on 21 August with bromoxynil (as Brominil) at 560 g a.i. ha^{-1}. Prior to this on 16 July, nitrogen at a rate of 40 kg N ha^{-1} was applied to the whole area. In order to reduce some weed growth, e.g. thistles, and promote stooling of the pastures, cattle were introduced on 17 March 1987 and the area crash grazed. Pastures in late July in the same year were also observed to be deficient in nitrogen. In order to maintain a fertility differential, low and high fertility plots were broadcast with 'Nitram' fertiliser at rates equivalent to 10 and 40 kg N ha^{-1} respectively, and 'Pasture 13' fertiliser (6.9% P; 12.5% K and 8.5% S) at 50 and 200 kg ha^{-1} respectively.

The assessment of summer growing perennial grasses, begun in late 1986, was not continued because poor rains at Dunmore following sowing and again following resowing in early 1987 (see Appendix 11) prevented their successful establishment. However, a large germination of fireweed was recorded and with later rains reasonable establishment of Haifa white clover was obtained. The few plants of setaria which established grew well. Kikuyu and setaria had been sown at 2 kg ha^{-1} and paspalum at 5 kg ha^{-1} using similar techniques to the winter species. Phosphorus and nitrogen were also applied.

RESULTS

Experiment 1a

Pasture species varied considerably in their competitive effect on fireweed. Representative of the data is the total plant yield (shoots + roots) at Harvest 2, shown in Figure 10.1.

Saia oats and Concord ryegrass were the strongest competitors, significantly reducing the dry weight of fireweed ($P=0.05$) to 13.7 and 17.3% of the control (fireweed alone) respectively. The next most competitive species were phalaris, cocksfoot, perennial ryegrass and subterranean clover. On average these species reduced the total dry weight of fireweed to 58.4% of the control. Species found to be weakly competitive were fescue, white clover and red clover. Lotus was considered non-competitive as it failed to cause a significant

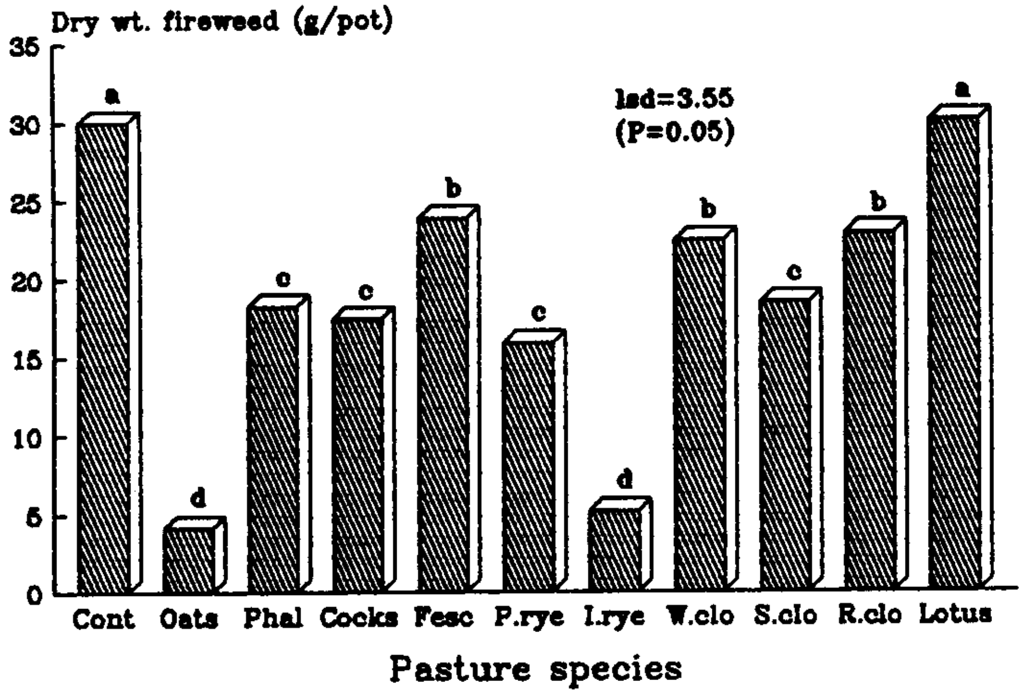


Figure 10.1 Effect of pasture species competition on total fireweed yield (roots + shoots) in the glasshouse at the second harvest. Treatments with the same letter were not significantly different at P<0.05. See the text for full names of pasture species ('Cont' is the control).

reduction (P=0.05) in fireweed yield. Similar results were obtained for branching and reproductive potential (i.e. capitula production) data, and for the various components of dry weight (i.e. stems, leaves, roots and shoots) (see Table 10.1). The same trends were evident in both harvests.

The varying competitive ability of the pasture species was reflected in their various growth characteristics (see Table 10.2 and Figure 10.2 a,b,c,d). The yield of each pasture species was in turn lowered owing to competition with fireweed.

Oats produced significantly fewer tillers compared with the other grasses (P=0.05) (see Figure 10.2a) and had a relatively low root dry weight (see Figure 10.2b). Its success in reducing the growth of fireweed appeared to be due to its large seed size and rapid early growth (see Table 10.2), leading to high shoot dry matter production (see Figure 10.2c). Concord ryegrass, in comparison, had both strong root and shoot growth and yielded more than all other species tested in terms of total plant dry matter (see Figure 10.2d). The only species not significantly different (P=0.05) was oats. The reduction in productivity of Concord ryegrass due to fireweed competition, 8.7% of total plant dry weight, was minor in comparison with the other pasture species. In terms of tiller production the species was second only to Kangaroo Valley ryegrass (see Figure 10.2a).

Contrasted with Concord ryegrass was the 64.0% drop in total plant dry weight yield of fescue (see Figure 10.2d). The poorest competitor amongst the perennial grasses, fescue had both relatively low root and shoot dry weight yields (see Figure 10.2 b,c). Although shoot dry weight of phalaris was similar, it had significantly stronger root growth (P=0.05) (see Figure 10.2b). Similar root growth in perennial ryegrass was compensated for by high tiller production (see Figure 10.2a) and high shoot dry matter production early in the experiment (see Table 10.2). Losses in total shoot productivity of the perennial grasses were smallest in phalaris (44.4%) and Kangaroo Valley ryegrass (45.6%). Cocksfoot had good root and shoot production but its own reduction in yield of tops was 62.3% (see Figure 10.2c).

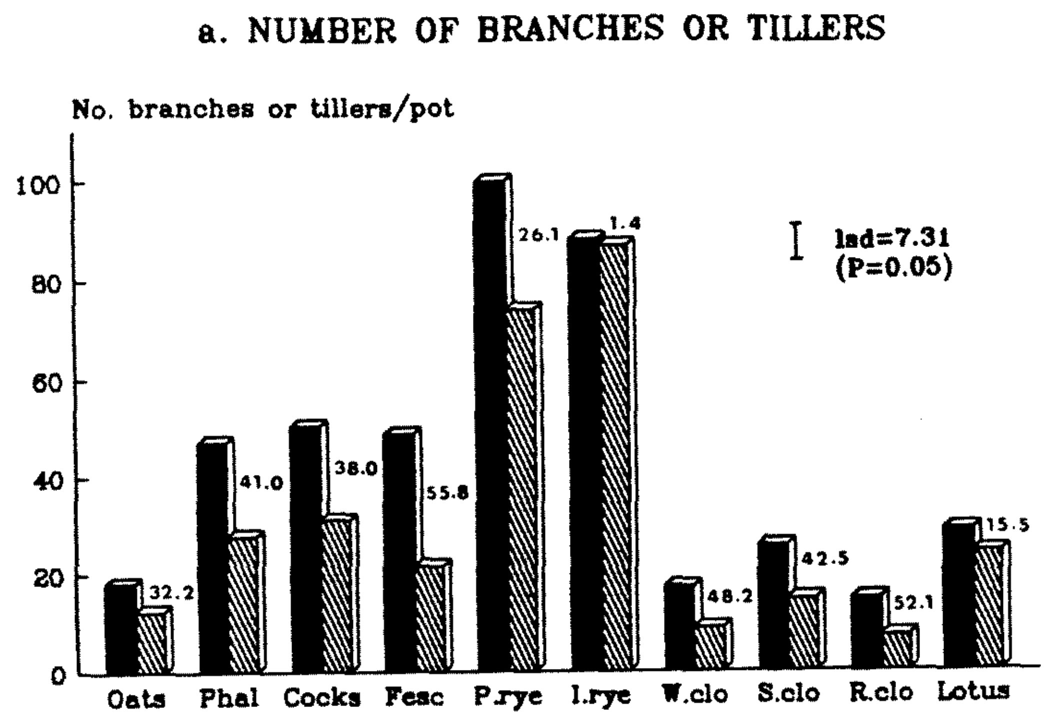
Table 10.1 The effect of pasture species competition on the growth of fireweed grown in pots in the glasshouse in Experiment 1a.

			Pasture species										
Parameter	Harvest	Control[A]	Oats	Phal-aris	Cocks-foot	Fescue	P.rye-grass	I.rye-grass	W. clover	S. clover	R. clover	Lotus	lsd[B] (P=0.05)
No. 1° branches pot^{-1}	1	28.5	6.2	21.0	16.4	22.4	19.6	14.0	27.0	22.8	23.0	24.8	5.3
	2	27.3	12.6	22.2	23.4	24.4	19.6	12.4	26.6	24.6	24.6	28.4	
No. capitula pot^{-1}	1	88.6	15.8	46.8	37.0	45.6	37.4	37.8	69.6	85.4	74.6	58.0	46.4
	2	326.5	43.6	183.8	218.6	255.2	180.6	64.6	230.2	217.2	236.6	317.2	
DW capitula g pot^{-1}	1	0.41	0.08	0.18	0.15	0.20	0.17	0.23	0.34	0.45	0.40	0.25	0.54
	2	4.01	0.46	2.34	2.64	3.40	2.50	0.61	3.12	2.59	2.91	4.56	
DW stems g pot^{-1}	1	4.01	0.60	2.06	1.61	2.22	1.87	1.53	3.67	3.28	2.87	2.52	1.74
	2	15.14	1.89	9.63	8.99	12.25	7.95	2.51	10.83	9.10	11.63	15.09	
DW leaves g pot^{-1}	1	3.85	0.67	2.45	2.00	2.77	1.97	1.43	3.80	3.03	2.50	3.07	0.76
	2	5.98	1.00	3.92	3.72	5.18	3.46	1.18	4.83	4.07	5.16	6.32	
Total DW shoots g pot^{-1}	1	8.27	1.35	4.68	3.76	5.19	4.01	3.19	7.82	6.76	5.77	5.84	2.62
	2	25.12	3.36	15.89	15.35	20.83	13.92	4.30	18.78	15.75	19.71	25.97	
DW roots g pot^{-1}	1	-	-	-	-	-	-	-	-	-	-	-	0.77
	2	4.85	0.74	2.36	2.12	3.02	1.97	0.87	3.65	2.69	3.10	3.98	

A Fireweed grown alone.
B lsd's are for comparisons within harvests.

Table 10.2 Initial seed dry weight of pasture species, dry weight of fireweed tops at Harvest 1, and R.G.R. up to Harvest 1 of pasture species grown alone.

Pasture species	DW seed g 100 seeds^{-1}	R.G.R. g g^{-1} wk^{-1}	Fireweed DW at Harvest 1 g pot^{-1}
1. Oats	1.5868	0.554	12.75
2. Phalaris	0.1453	0.658	3.76
3. Cocksfoot	0.0689	0.734	4.08
4. Fescue	0.2377	0.608	3.45
5. P. ryegrass	0.2068	0.672	6.11
6. I. ryegrass	0.2469	0.672	7.26
7. W. clover	0.0708	0.672	2.12
8. S. clover	0.6287	0.559	5.53
9. R. clover	0.1958	0.619	3.29
10. Lotus	0.0829	0.682	2.71
lsd (P=0.05)			3.57



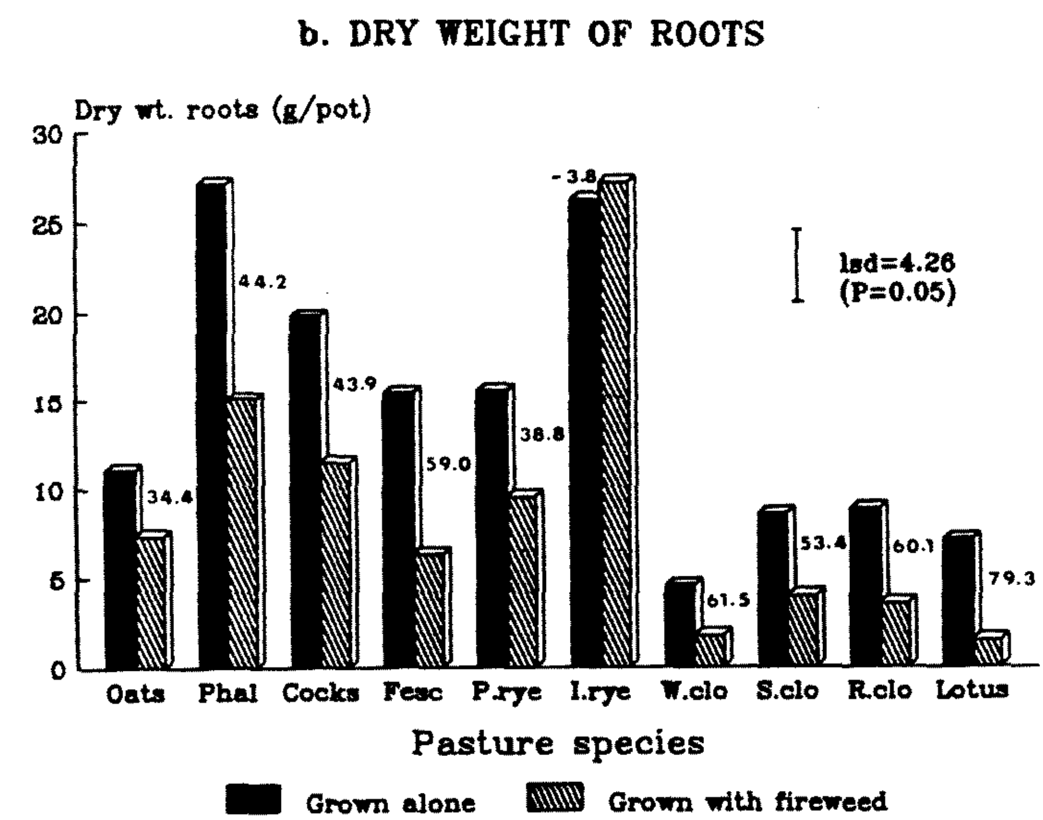
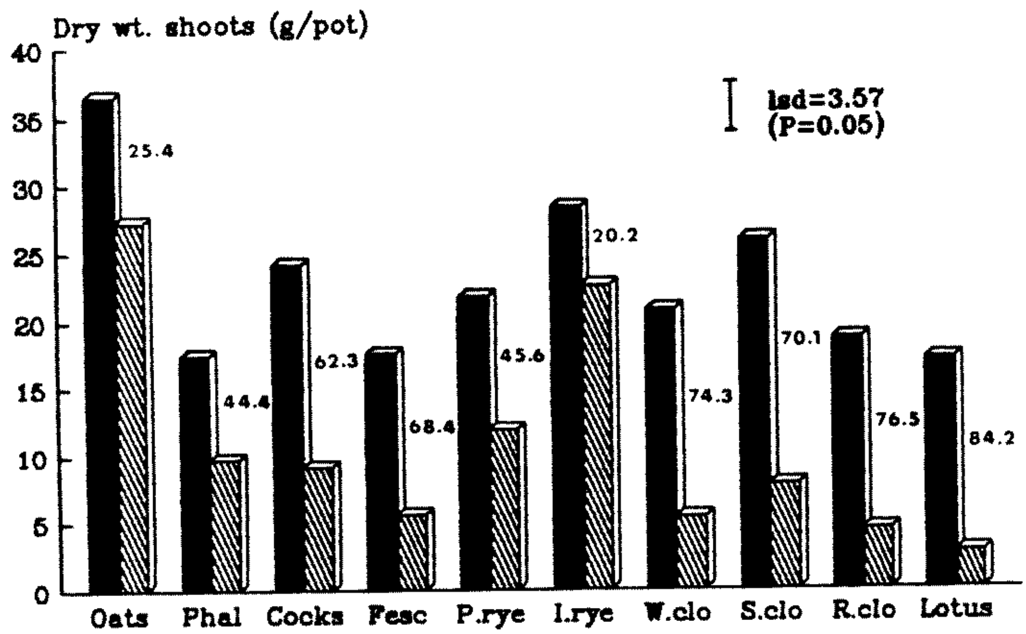
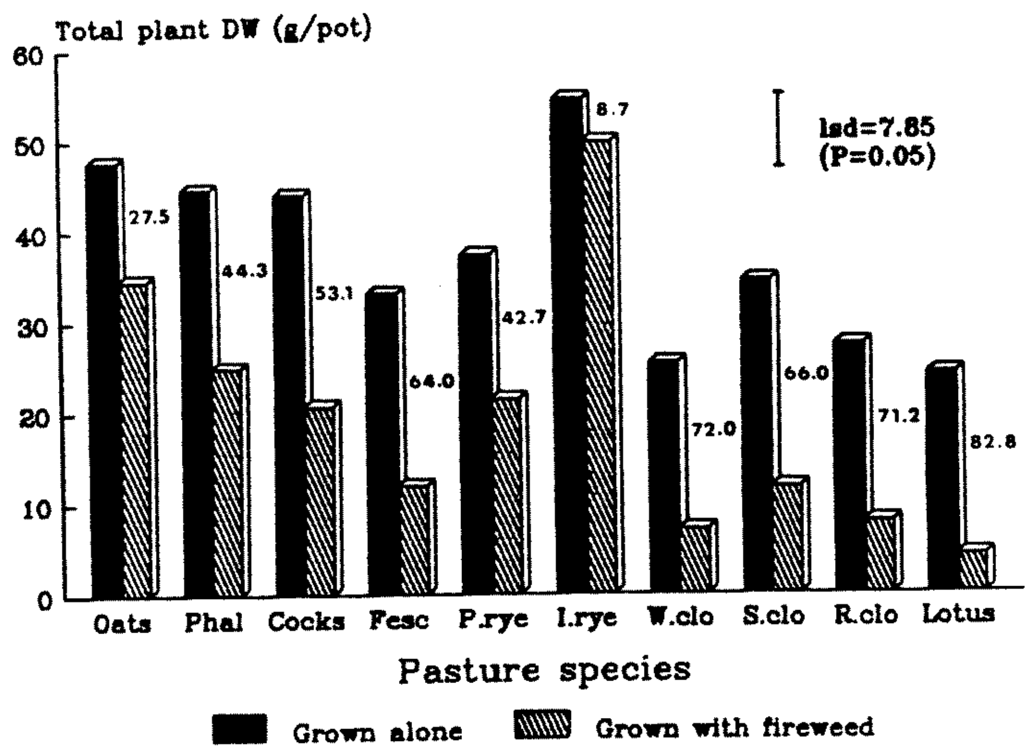


Figure 10.2 (a) Number of tillers (of grasses) or branches (of legumes), (b) dry weight of roots, (c) dry weight of shoots, and (d) total plant dry weight (roots + shoots), at Harvest 2, of pasture species grown alone and with fireweed. Percentage losses due to fireweed competition are shown. See the text for full names of pasture species.

c. DRY WEIGHT OF SHOOTS



d. TOTAL PLANT DRY WEIGHT



In general, the legumes, apart from subterranean clover, competed poorly with fireweed, suffering large reductions in productivity. For example, shoot dry weight was reduced by 84.2% in lotus (see Figure 10.2c). The number of branches or runners produced by these species and root growth was significantly smaller than all other species (P=0.05) other than oats (see Figure 10.2 a,b). Seed weights of white clover and lotus were low and that of subterranean clover high (see Table 10.2).

The R.G.R of the pastures did not impose the competitive advantages on the various species alone, but in combination with their seed weight had considerable influence. White, subterranean and red clover were the first pasture species to germinate followed by oats. Although subterranean and red clover and oats were observed to be the largest pasture seedlings 2 weeks after germination began, by the time of the first harvest (11 weeks after germination) the order of shoot dry weights had changed somewhat (see Table 10.2). Seedling sizes 1 month after germination are shown in Plate 10.1 and the respective growth habits of the 10 pasture species at Harvest 1, in Plate 10.2 a-j.

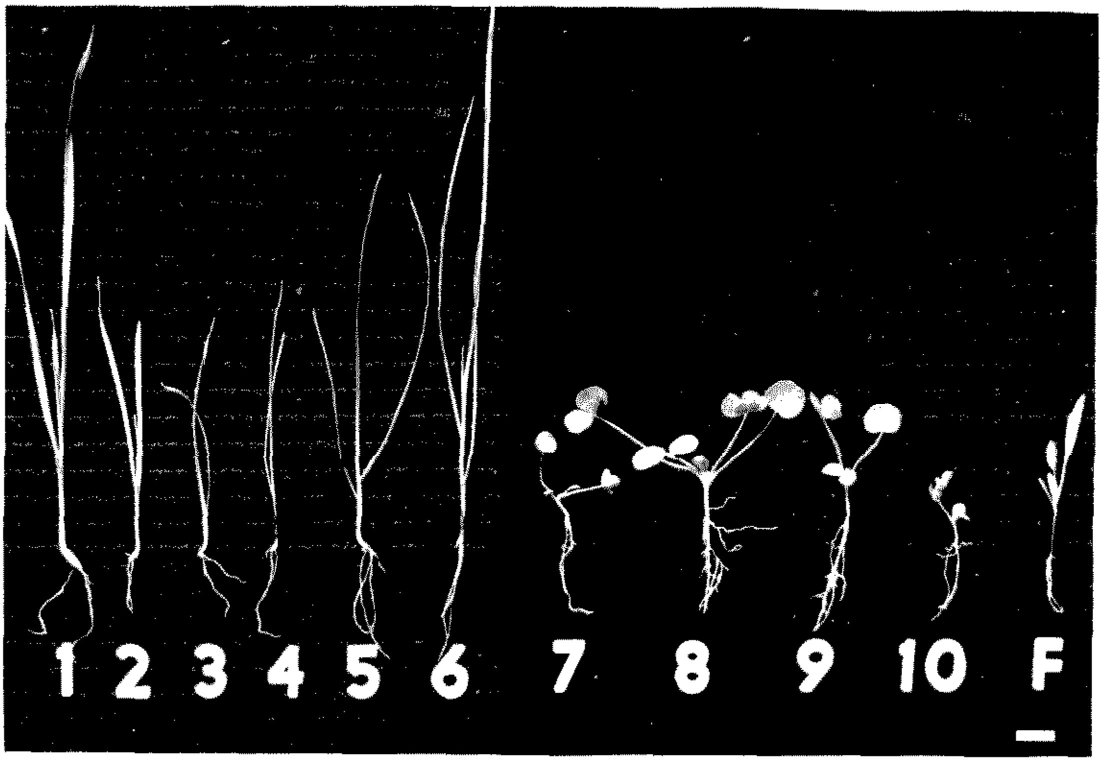
Experiment 1b

The growth of fireweed was considerably more retarded in this experiment, where the weed was established well after competing pasture species, than in Experiment 1a where they were both established at the same time (see Table 10.3). Even lotus, found to be non-competitive in Experiment 1a, suppressed the growth of fireweed (significant at P=0.05). Plant height, leaf production and dry matter production were all reduced compared with the control.

Due to variability of the data, differences in dry weight of tops were often non-significant (P=0.10). According to Friedman's nonparametric test, Saia oats and Concord ryegrass both reduced the yield of fireweed significantly more than lotus (P=0.10), but only Concord ryegrass had a significant effect compared with fescue and red clover. Nevertheless, the order of treatment dry weight means

Plate 10.1 Size and morphology of pasture seedlings and fireweed 1 month after germination (1. oats, 2. phalaris, 3. cocksfoot, 4. fescue, 5. perennial ryegrass, 6. Italian ryegrass, 7. white clover, 8. subterranean clover, 9. red clover, 10. lotus, and F. fireweed). Scale bar = 1 cm.

Plate 10.2 a-d Morphology and habit of (a) oats, (b) phalaris, (c) cocksfoot, and (d) fescue, grown alone, at the first harvest. Scale bars = 5 cm.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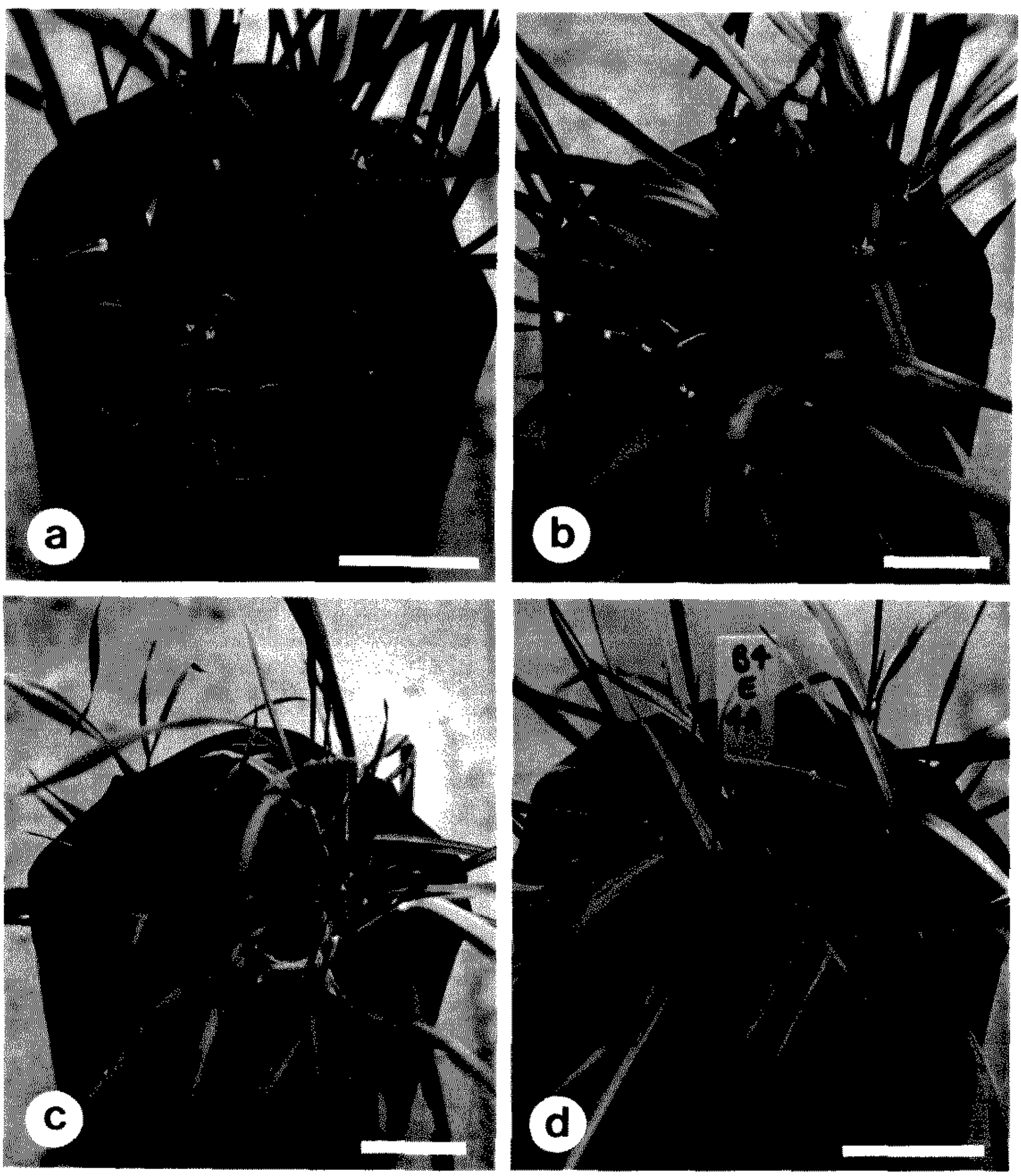
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Plate 10.2 e-j Morphology and habit of (e) perennial ryegrass, (f) Italian ryegrass, (g) white clover, (h) subterranean clover, (i) red clover, and (j) lotus, grown alone, at the first harvest. Scale bars = 5 cm.

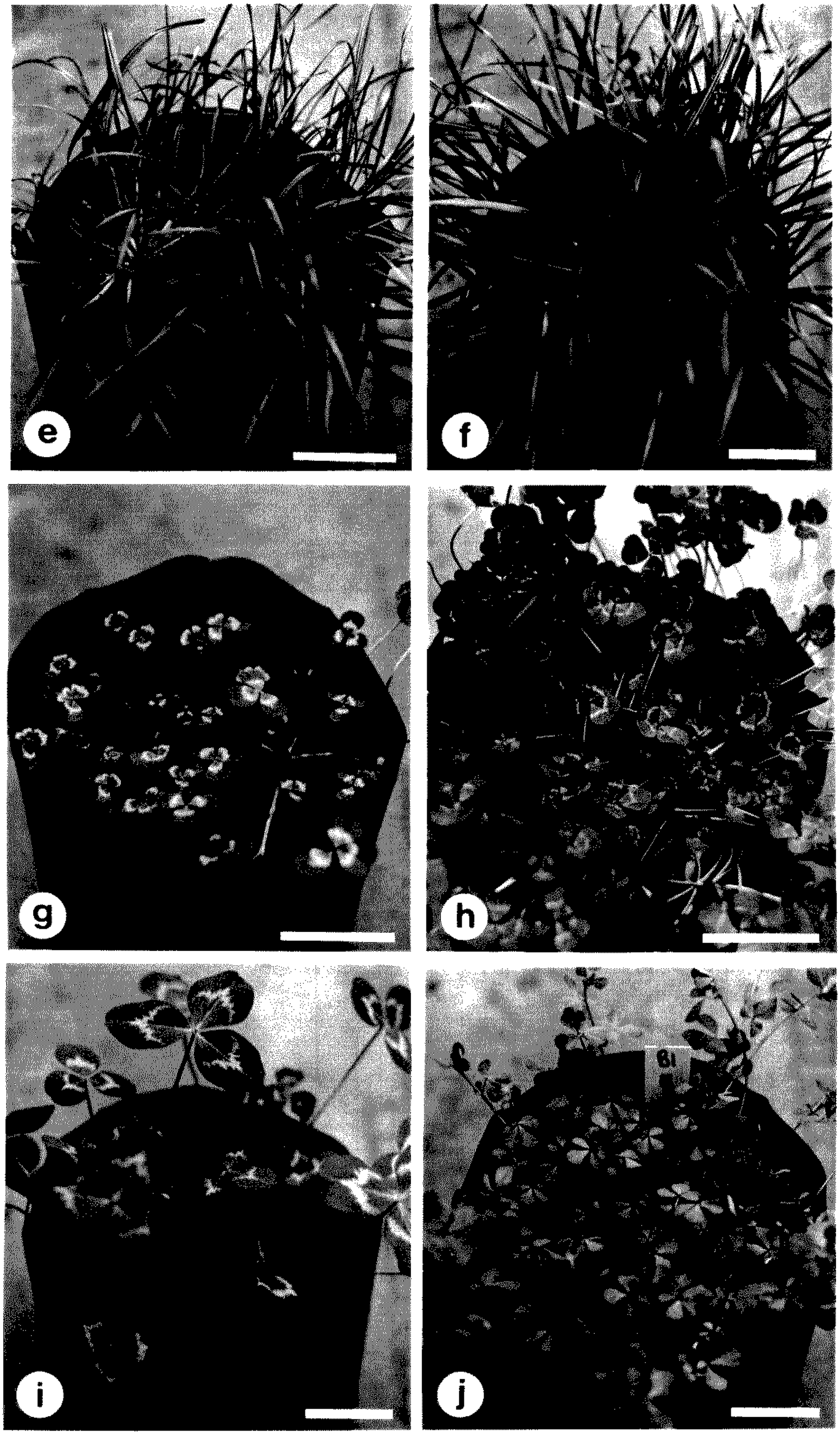
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Table 10.3 The effect of pasture species competition on the growth of fireweed tops in Experiment 1b. Figures in brackets for plant height and number of leaves are actual means, and for dry weight are ranking totals calculated for Friedman's nonparametric multiple comparison test. Treatments with ranking totals differing by more than $z\sigma$ are considered significantly different.

	Pasture species											
Parameter	Control[A]	Oats	Phal-aris	Cocks-foot	Fescue	P.rye-grass	I.rye-grass	W. clover	S. clover	R. clover	Lotus	lsd (P=0.05)
Mean plant height[B] cm	4.095 (60.2)	2.171 (8.8)	2.772 (16.6)	2.758 (16.4)	3.193 (25.4)	2.493 (12.2)	1.965 (7.4)	3.179 (24.4)	2.720 (16.6)	3.190 (25.6)	3.443 (33.4)	0.380
No. leaves[B] pot^{-1}	5.363 (221.2)	2.385 (11.0)	2.901 (19.4)	2.897 (19.4)	3.531 (38.0)	2.708 (15.4)	2.044 (7.8)	3.097 (23.2)	2.799 (17.8)	3.217 (25.8)	3.896 (60.4)	0.510
DW tops $g\ pot^{-1}$	5.06	0.03 (13.0)	0.15 (29.0)	0.14 (27.5)	0.40 (42.0)	0.07 (20.0)	0.01 (5.5)	0.25 (33.5)	0.11 (22.0)	0.31 (39.5)	1.08 (43.0)	$z\sigma$ (P=0.10) (29.3)

A The control was obviously different from all other treatments and was therefore not included in Friedman's comparisons of dry weight of tops.

B Data on ln (x) transformed scale.

in this experiment, and also that of plant height and number of leaves, was very similar to that of Harvest 2 in Experiment 1a.

Experiment 2a

Concord ryegrass proved in this experiment to be sensitive to low fertility. While growing vigorously at high fertility, leaves yellowed and growth was much reduced under low fertility conditions (see Plate 10.3). Despite 2 weeks of heavy rains prior to harvest, ryegrass at high fertility did not lodge. It also competed strongly for light. Fireweed plants showed typical symptoms of shading (see Chapter 9). Those at low fertility, in contrast, were erect and had grown well above the ryegrass canopy.

The most rapid decrease in yield of fireweed at both low and high fertility occurred at densities between 1 and 100 plants m^{-2}. Reductions at levels above this density were non-significant ($P=0.05$) (see Figure 10.3a). As a percentage of the ryegrass free control, yield was significantly lower under high fertility than low fertility conditions ($P<0.05$) (see Figure 10.3b).

Capitula production responded similarly to increasing ryegrass density (significant at $P<0.05$), but on a percentage basis the fertility effect was not significant. Over both fertility levels capitula production was reduced to 51.5% of the control at a density of 50 plants m^{-2} and 38.9% at a density of 100 plants m^{-2}.

As density increased, mean ryegrass yields were equal to 0, 0.52, 0.68, 0.94 and 1.03 t ha^{-1} at low fertility, and 0, 3.13, 3.83, 4.27 and 4.40 t ha^{-1} at high fertility.

Experiment 2b

An increase in fireweed density from 0 to 40 plants m^{-2} did not significantly effect ryegrass dry matter production ($P=0.05$) at either the first or second simulated grazings. In high fertility plots, Concord ryegrass formed an almost totally closed canopy and shaded fireweed heavily (see Chapter 9 for light interception figures). As a result fireweed plants were succulent and weakly

Plate 10.3 Concord ryegrass showing vigorous growth at high nitrogen levels (dark green areas) at Camden.

Plate 10.4 The Dunmore experimental site prior to applying pasture treatments.

Plate 10.5 Destruction of the existing pasture at Dunmore by spraying with glyphosate, and the sowing operation, caused dense establishment of fireweed (left) compared with the undisturbed pasture (right).

Plate 10.6 Spraying fireweed in its early stages of growth in 1988 with bromoxynil gave excellent control (foreground) compared with unsprayed pasture (behind).

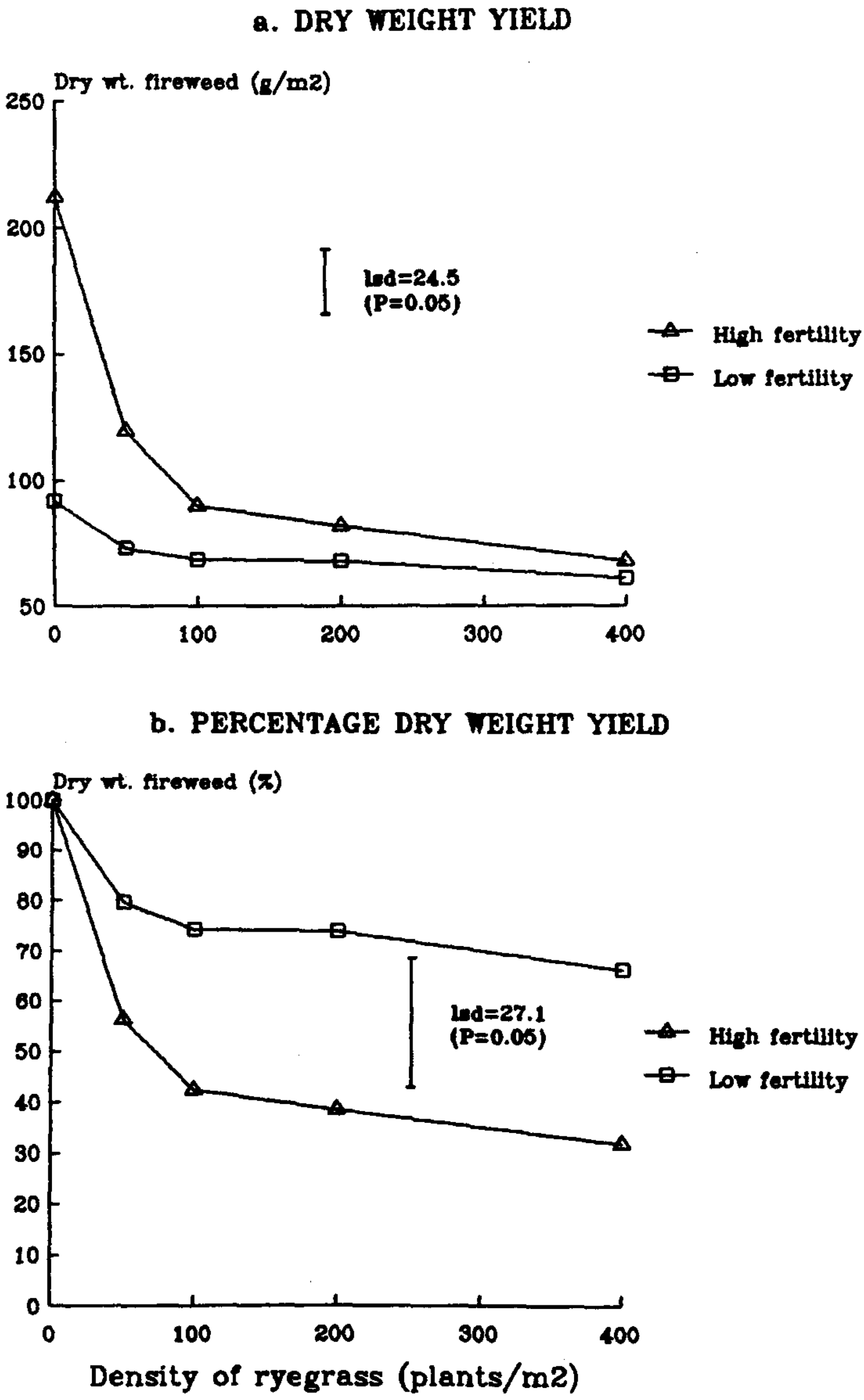


Figure 10.3 Effect of increasing density of Concord ryegrass on (a) the dry weight yield, and (b) the percentage dry weight yield, of fireweed at low and high soil fertility. The l.s.d. in (a) is for comparisons of treatments at the same fertility level, and (b) between fertility levels.

lignified. Plants died due to severe competition and increased disease incidence and slug damage.

An analysis of fireweed deaths at the third harvest on a square root (x + 0.5) transformed scale, revealed that the main effect of soil fertility was highly significant ($P<0.01$). The average number of deaths occurring at high fertility (30.9%) was nearly seven times that which occurred during competition with Concord ryegrass at low fertility (4.6%).

Fireweed density did have a significant effect on ryegrass DM production at the third harvest ($P<0.05$), but only at low fertility (ryegrass under high fertility conditions had poor regrowth possibly because of its more advanced stage of growth) and only at densities of 10 plants m^{-2} or greater. The yield of fireweed at this third harvest was not significantly different between high and low fertility treatments ($P=0.05$), presumably due to plant deaths and competitive suppression of fireweed at high fertility. At 10 and 40 plants m^{-2} fireweed yielded 237 and 936 kg DM ha^{-1} (averaged over fertility levels).

Total ryegrass dry matter production (combined data for the three harvests), like Harvests 1 and 2, was not significantly affected by fireweed density ($P=0.05$). Grown alone, ryegrass yielded 2.56 and 5.35 t ha^{-1} under low and high fertility treatments respectively. Harvest 3 contributed 18% of the total yield at low fertility but only 6% at high fertility.

Experiment 3

At the Dunmore experimental site (see Plate 10.4), both the destruction of the existing pasture by spraying with glyphosate and the sowing operation (cultivation), encouraged the germination and establishment of fireweed (see Plate 10.5). Large infestations of seedlings were observed between rows, away from the influence of cultivation, and also within rows in treated plots. A comparison of the emergence of fireweed in pasture treatments with that of the undisturbed control, 7 and 15 weeks after sowing, is made in Table 10.4. No effect of fertiliser treatments was recorded nor was

Table 10.4 Number of fireweed seedlings 0.25 m^{-2} which emerged in pasture treatments during 1986, combined over both fertility levels. Data on a square root (x + 0.5) transformed scale.

	Pasture treatments						
Weeks after sowing	1. Phalaris	2. Ryegrass	3. Fescue	4. Clover	5. Cultivated control	6. Undisturbed control	lsd (P=0.05)
7	4.48	4.94	5.38	5.18	4.76	1.20	1.57
15	5.79	6.05	6.81	6.72	6.33	1.12	1.89

Table 10.5 The number of sown pasture seedlings established 7 weeks after sowing, combined over both fertility levels. Data on a square root (x + 0.5) transformed scale. Figures in brackets are actual means.

	Pasture treatments				
Type of seedling	1. Phalaris	2. Ryegrass	3. Fescue	4. Clover	lsd (P=0.05)
Grass no. m^{-1} row	4.57 (21.8)	6.95 (49.6)	5.32 (29.8)		0.58
Clover no. m^{-1} row	3.68 (14.7)	3.39 (13.5)	3.90 (18.0)	5.07 (26.3)	0.78

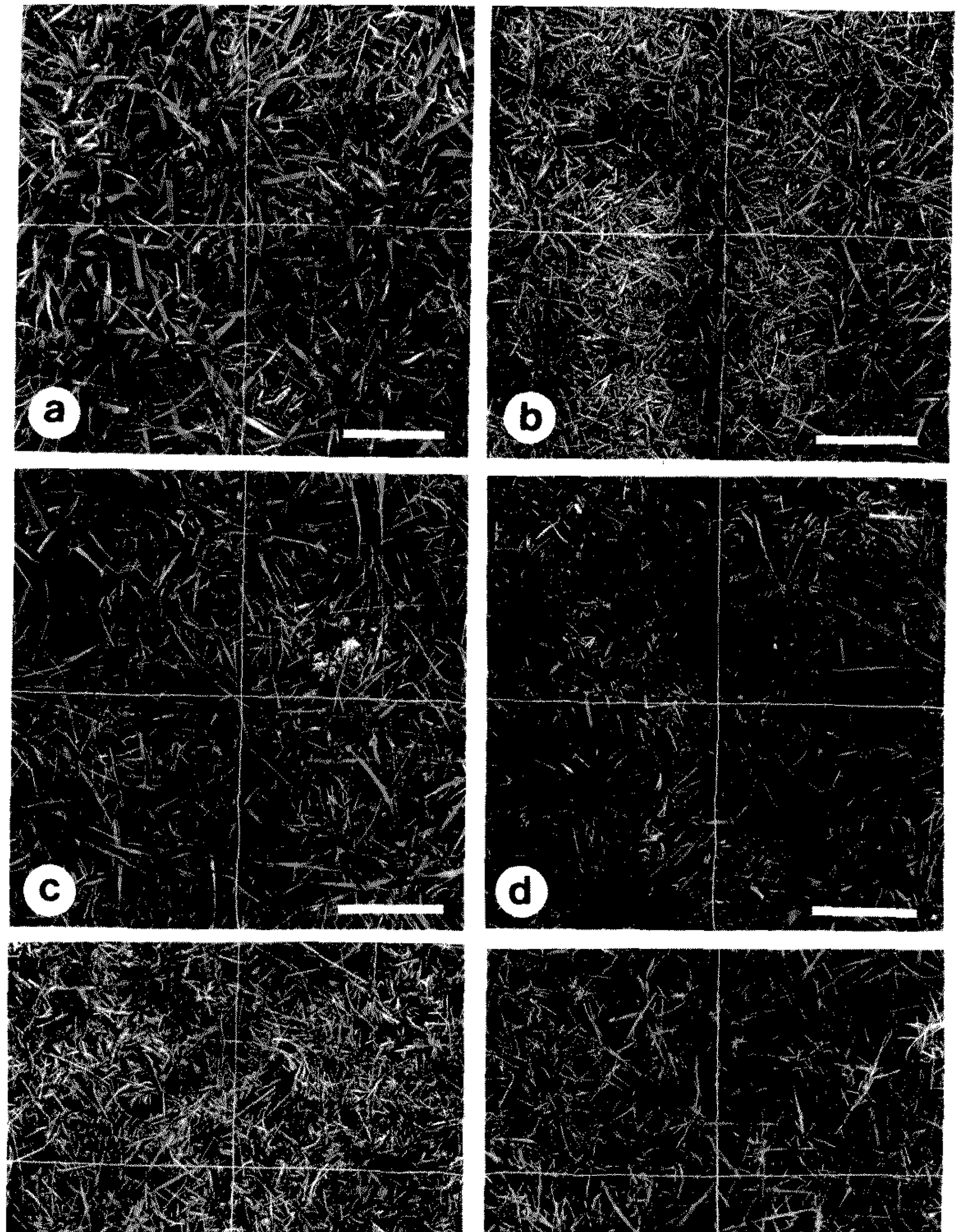
the effect between sown pasture species (Treatments 1-4) significant at that stage (P=0.05). The mean density of fireweed in Treatments 1 to 5 was 122.6 and 196.8 plants m^{-2} at 7 and 15 weeks respectively, and 5.2 and 4.4 plants m^{-2} for the undisturbed control (Treatment 6).

The profuse germination and active growth of fireweed necessitated the application of the selective herbicide bromoxynil. At the time of spraying, there was an average over the whole experimental area of 104.3 fireweed seedlings and 41.3 mature flowering plants m^{-2}, giving a dry weight yield of 879 kg ha^{-1} (calculated from 16 harvests of 0.5 m^2). The high herbicide rate used effected a good kill of fireweed, although some mature plants were observed to reshoot. Clover scorch was not prevalent. More effective control of fireweed was obtained at this site in 1988 with a lower rate of herbicide due to the timeliness of application (see Plate 10.6). Details are given in the discussion section of this chapter.

The establishment of pastures in terms of the number of seedlings in the selected quadrats of each plot is shown in Table 10.5. Of the grasses, ryegrass had the highest establishment followed by fescue and phalaris. The number of clover seedlings establishing with each grass was not significantly different, but was significantly greater (P=0.05) where clover was grown alone (Treatment 4). Over the whole experiment, however, establishment of the pasture species, except for Kangaroo Valley ryegrass, was disappointing. Establishment of phalaris and white clover was patchy and fescue poor. Kangaroo Valley ryegrass is obviously well adapted in the Illawarra region. In the selected quadrats each of the grasses had mean densities greater than the anticipated establishment of 250 plants m^{-2}. Representative quadrats of the six pasture treatments in mid autumn 1987 are shown in Plate 10.7 a-f.

Fertiliser treatments did not affect grass establishment, but the establishment of clover in the high fertility (phosphorus) treatment was 42.2% lower than in the low fertility treatment (significant at P=0.05). The acidic nature of superphosphate at high levels may have reduced the survival of the inoculum rhizobia surrounding the seed, causing plants to die.

Plate 10.7 Representative quadrats of the six pasture treatments at Dunmore in mid autumn 1987 (a) phalaris, (b) ryegrass, (c) fescue, (d) clover, (e) cultivated control, and (f) undisturbed control. Scale bars = 10 cm.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Pasture cover (area) in mid August 1986, based on the percentage of hits obtained using the point quadrat technique in the sown rows, is given in Table 10.6. Of the sown grasses, perennial ryegrass had the greatest cover, followed by phalaris and fescue (each significantly different at P=0.05). Clover percentage in each of these treatments showed the reverse trend. The area of fireweed was least in undisturbed control plots and those sown to ryegrass. A significantly larger area (P=0.05) was covered in the cultivated control (Treatment 5) where no pasture species were sown than in any of the grassed treatments. The highest percentage of bare ground was in the cultivated control, and, among the sown species, was least in perennial ryegrass plots. These data do not apply for the second season of growth, because in 1987 phalaris and fescue tended to stool and spread outside the sown rows more than ryegrass, as evidenced in Plate 10.7 a,b,c.

Dry weight data from the harvest at the end of 1986, combined over both fertility levels, are given in Table 10.7. The only significant effect of fertility was reduced clover yield at a high phosphorus level (P=0.05). Although the sown pasture species alone were unable to control fireweed in the first season and had to be augmented with herbicide control, the competitive effects of the three grasses were nevertheless evident. Fireweed yield was significantly lower in the phalaris, ryegrass and fescue treatments than in the clover or cultivated plots (P=0.05), but was lowest in the undisturbed control (see Table 10.7).

Dry matter production may be considered a product of number of plants and their individual weights. In order to assess the competitive effect of the pasture species on the latter, the influence of varied germination and establishment, and possible aggregation of fireweed over the experimental area was removed using covariate analysis. The data were adjusted for the number of fireweed present in plots in mid July 1986. The competitive effect of the perennial grasses in combination with white clover and the undisturbed control were the same. All except phalaris were significantly greater (P=0.05) than clover alone and the cultivated control (see Figure 10.4).

Table 10.6 Mean pasture cover in sown rows expressed as a percentage of hits using the point quadrat technique. Data on a square root (x + 0.5) transformed scale.

Type of cover	Pasture treatment 1. Phalaris	2. Ryegrass	3. Fescue	4. Clover	5. Cultivated control	6. Undisturbed control	lsd (P=0.05)
Sown grass	6.07	7.55	5.19				0.64
Sown clover	3.34	2.71	3.76	5.44			0.96
Fireweed	5.10	4.12	5.00	5.59	6.40	1.76	1.20
Other	4.55	3.42	4.81	5.72	7.47	9.85	0.79

Table 10.7 Dry weight (g 0.25 m^{-2}) of sown and resident species, including fireweed, over both fertility levels at the end of the first year of growth at Dunmore. Data on a ln (x + 1) transformed scale. Figures in brackets are actual means.

Species	Pasture treatment						
	1. Phalaris	2. Ryegrass	3. Fescue	4. Clover	5. Cultivated control	6. Undisturbed control	lsd (P=0.05)
Grass[A]	2.68 (18.2)	3.94 (55.0)	1.51 (4.9)				0.39
Clover[B]	2.19 (11.2)	1.46 (7.3)	2.24 (13.5)	2.80 (17.4)	1.01 (4.8)	1.78 (9.0)	0.68
Fireweed	1.10 (4.7)	0.87 (2.6)	1.17 (3.8)	2.22 (14.6)	2.04 (11.1)	0.19 (0.34)	0.82
Other	3.64 (41.4)	2.32 (13.9)	3.68 (42.8)	3.70 (42.2)	3.78 (45.1)	4.12 (65.1)	0.47

[A] Sown grasses only.
[B] Includes sown and resident clovers.

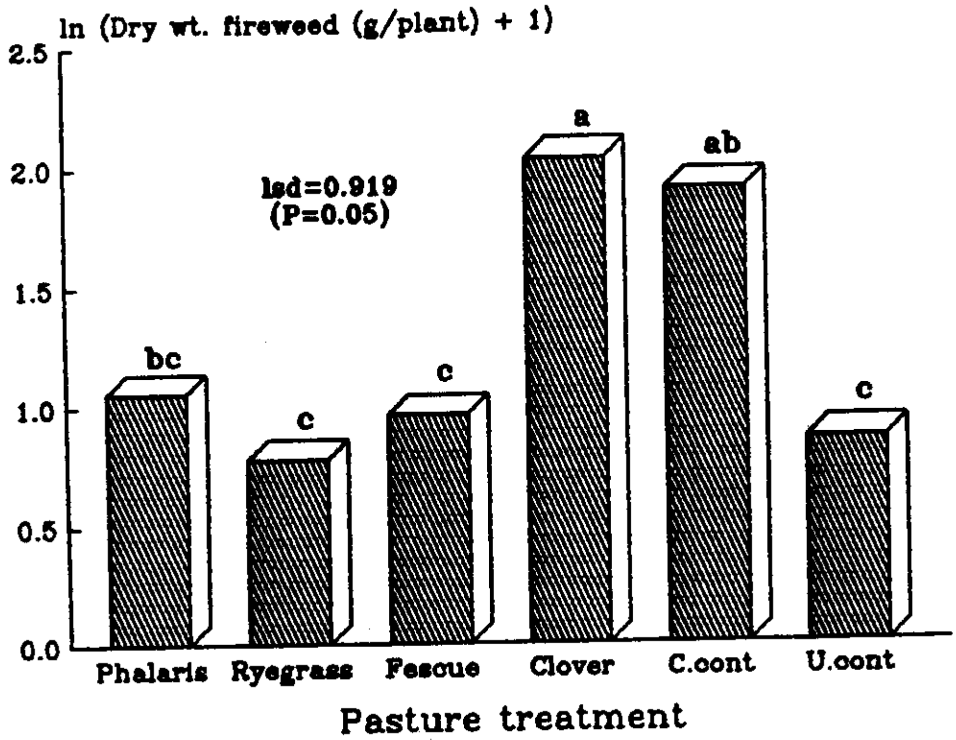

Figure 10.4 Dry weight yield data of fireweed in 1986 at Dunmore adjusted for the number of fireweed present in plots in mid July. See the text for full names of pasture treatments. Treatments with the same letter are not significantly different at P<0.05.

Table 10.8 The effect of pasture treatments on mean yield data of fireweed in 1987, adjusted for the number of fireweed present in plots in late July. Treatment differences were not significant at P<0.05.

	Pasture treatments					
Parameter	1. Phalaris	2. Ryegrass	3. Fescue	4. Clover	5. Cultivated control	6. Undisturbed control
DW g $plant^{-1}$	2.19	2.04	3.79	2.14	3.05	3.84

Regression analysis showed that the ln of (dry weight yield + 1) of fireweed (y) was inversely and linearly related to the ln of (combined dry weight yield + 1) of the sown and naturally occurring species (x) at the first harvest over all treatments. Although only 33.8% of variance (R^2) was accounted for by the equation $y = 8.638 - 1.789x$, the relationship was nevertheless significant at $P<0.001$. The higher total pasture yields of the ryegrass and control treatments (see Table 10.7) help explain the increased suppressive effect of these two treatments.

The overall mean number of fireweed germinating in 1987 (14.5 plants m^{-2} measured in July) was 8.8% of that which followed sowing at a similar time in 1986. In the undisturbed control the level of infestation remained reasonably static at about 4 plants m^{-2}.

Unlike the first season, counts made late in 1987 showed that significantly fewer fireweed seedlings ($P<0.05$) emerged and survived under high fertility conditions over all treatments (7.4 m^{-2}) compared with low fertility conditions (13.2 m^{-2}). No difference was recorded between sown pasture species, and the undisturbed control still had the lowest level of infestation, particularly at high fertility.

Perhaps understandably, the significant effect of soil fertility on fireweed number ($P<0.05$) was not transferred into dry weight yield on an area basis. The fewer plants which emerged under high fertility grew larger as a response to increased nutrient status (see Chapter 8).

The effect of pasture treatments on total and individual plant dry weights was not significant in the second season ($P=0.05$), owing at least in part to poor fireweed growth and considerable variability in the data. Treatment means, adjusted for the number of plants in each plot and pooled over the two fertility levels (see Table 10.8), nevertheless suggest that phalaris and ryegrass were the most competitive grasses in the second year followed by fescue. Clover plots, which also seemed to perform well, contained larger than normal quantities of the thistle *Cirsium vulgare*. It may have been these that contributed most to the suppression of fireweed, particularly as they would not have been grazed when cattle unexpectedly entered the area. Weeds other than fireweed were also more prevalent in the cultivated (no pasture) treatment. The undisturbed control appeared least competitive in the second year.

DISCUSSION

The profusion of fireweed which resulted from the suppression of kikuyu dominant pasture at Dunmore by spraying with glyphosate, by inference highlights and supports the already stated view that the pasture itself can be a powerful weapon against fireweed. Not only was fireweed establishment suppressed by the presence of the pasture, but its dry weight yield was a function of pasture dry matter production. Anything which reduces plant cover or leaves bare patches in the pasture is therefore likely to provide a suitable niche for the weed. Other weeds such as Senecio jacobaea (Hexter 1950; Watt 1987), Taraxacum officinale and Sonchus oleraceus (Rioux 1979), and Rumex obtusifolius L. (Nemoto et al. 1983) are also known to actively colonise bare patches and gaps in pastures. If pasture cover and plant vigour can be increased, then the growth of fireweed is likely to be suppressed.

Maintenance of Existing Pasture Cover

The results of the present study suggest that the first defence against fireweed should be maintenance of the existing pasture cover and elimination of gaps in its canopy. Snaydon and Howe (1986) found that in a low fertility ryegrass sward, decreasing the diameter of gaps from 800 to 200 mm reduced the dry weight of invading seedlings in the gap by 50 times. Reducing the gap size to 100 mm, however, did not further reduce their dry weight.

Influence of soil fertility

Although the high fertility treatment (phosphorus and nitrogen) at Dunmore in 1987 reduced fireweed germination and establishment compared with the low fertility treatment ($P<0.05$) (presumably through the promotion of increased pasture cover), fireweed dry weight was unaffected. This supports the result obtained in

Chapter 8 - that fireweed is strongly competitive for and responsive to soil nutrients; and the result of Chapter 3 - that under high fertility, fireweed infestations are composed of fewer, larger plants. Hand weeding under these conditions is likely to be more effective and less labour intensive (see Chapter 3). Moreover, herbicide applications using ropewick equipment (see Chapter 2) are likely to be more successful. In Experiment 2b fireweed mortality was also found to be significantly greater ($P<0.05$) at high fertility.

It is probable that the influence of soil fertility will vary with different pasture species and grazing pressure. For example, the response of native species to superphosphate is not generally sufficient to exclude the more invasive weeds (Campbell 1974). Increased soil fertility may actually lead to the subsequent invasion of pastures by fireweed. Highly productive pasture species like kikuyu, however, require regular topdressing to maintain their vigour (Hexter 1950; Whittet 1969).

Andrews and Falvey (1979) found that the percentage of _Eupatorium adenophorum_ in a pasture was reduced by the application of phosphorus and sulphur in an ungrazed sward, but increased in a grazed sward. Because the interaction between grazing and application of fertilisers is likely to be more or less the same for pasture infested with fireweed, their timing and intensity are critical.

Introducing Improved Pasture Species

If existing pasture species are weakly competitive and unable to respond sufficiently to fertiliser and grazing management, then the second defence against fireweed should be employed. This is, namely, the introduction of improved pasture species or cultivars.

Annual grasses

Not unexpectedly, of those grasses and legumes tested in this study, the fast growing annual/biennial types were the most competitive. The newly introduced diploid Italian ryegrass cv. Concord proved to be a particularly strong competitor of fireweed, substantially reducing its vigour (see Figures 10.1 and 10.3a). It is also a highly impressive forage producer showing strong early growth in the autumn and flowering late in the season (Launders, personal communication). Compared with other Italian ryegrasses, Concord has a large seed size, which, as occurs in other annual species (Black 1957; Aspinall and Milthorpe 1959), may help to determine its competitive early growth.

Unlike Saia oats, Concord ryegrass appeared to have the competitive advantage over fireweed with increasing fertility (see Figure 10.3b and Chapter 8). Likewise, it was highly resilient to the competitive effects of fireweed (see Figure 10.2d, the results of Experiment 2b and the field experiment of Chapter 7). If used as a forage crop, Concord ryegrass at a density of 100 plants m^{-2} is likely to exert good control of fireweed. Because Concord tends to be a shy seeder (Launders, personal communication), moderate densities (Donald 1954) may be required where soil seed supplies need to be built up.

Pastures composed entirely of annuals are particularly sensitive to climatic fluctuations, especially the effectiveness of opening rains, soil fertility levels, grazing management and to attack by insects (Tiver and Crocker 1951). Their density may fluctuate violently from year to year (Donald 1951) and hence also their competitive influence (Wells 1969). For these reasons annual grasses are not often intentionally used for weed control alone (Michael 1970). They are, however, sometimes sown as forage crops for 1 or 2 years prior to sowing a perennial pasture to reduce the seed population of unwanted plants (Campbell 1974). They may also be included in pasture mixtures to provide quick cover and check the development of seedling weeds (Hexter 1950; Whittet 1968; 1969). In both these situations Concord ryegrass shows great potential.

Perennial grasses

The inclusion of strong perennial species in pastures is necessary to provide long term weed control and botanical stability (Tiver and Crocker 1951; Campbell 1974). As demonstrated for fireweed in Experiment 1b, pasture which is already established at the time of weed germination will usually suppress weed growth more than if the two become established concurrently (compare the results of Figure 10.1 and Table 10.3). Shading of fireweed was more intense in Experiment 1b than 1a, and plants appeared more prone to rust infection due to the more moist environment under the pasture canopies (see Chapter 9). This was particularly evident with the ryegrasses and subterranean clover. Groves and Williams (1975) found that competition with subterranean clover and infection with Puccinia chrondrillina Bubak & Syd. reduced the growth of Chrondrilla juncea more than the latter alone. The influence of fireweed rust on fireweed in the field is also likely to be compounded by pasture competition.

Kangaroo Valley ryegrass and Sirosa phalaris appeared to be the most promising perennial grasses tested for fireweed control. However, a significant difference between the competitive effects of Demeter fescue and these two species ($P=0.05$) could not be detected in the field over the two seasons of growth. Given longer term experiments, such as those conducted by Michael (1968 a,b) (e.g. 8 years), the persistence of species may have been more important in determining their success. Both these species have also proven to be competitive with other weeds (Tiver and Crocker 1951; Harris et al. 1977; Nemoto et al. 1983; Weerakoon and Lovett 1986). Preliminary short term investigations in Argentina support the results obtained here, showing that Lolium perenne reduces fireweed seedling establishment and survival more than Festuca arundinacea (Fernández, unpublished data).

Legumes

The legumes tested in this study, other than subterranean clover, were generally not as competitive as the annual and perennial grasses (see Table 10.7 and Figures 10.1 and 10.4). However, as a component of pasture mixtures, they still have an important role. For example, white clover, a perennial, was included in the field experiment at Dunmore in order to build up nitrogen levels in the soil for the grasses and help keep the sward closed during summer when the grasses were dormant. The addition of white clover to a range of grasses in New Zealand reduced the survival of *Ulex europaeus* (Hartley and Phung Hong Thai 1979).

Pasture Establishment

Control of fireweed using improved pasture species appears to be as much a problem of pasture establishment as selection of the most appropriate species or cultivars. Direct drilling of pastures (often following glyphosate application) has in many cases been successful in pasture establishment and weed control (e.g. Bellotti 1984; Troxler 1987). But consistently successful stand establishment is sometimes difficult to achieve (Welty *et al*. 1981). Some of the factors influencing pasture establishment in direct drilling have been addressed by Bellotti (1984). A lack of rain in the two months (June and July) following sowing at Dunmore (see Appendix 11) caused desiccation of the seed furrow, and is likely to have been the cause of generally poor pasture establishment. Good establishment of Kangaroo Valley ryegrass highlighted the need to sow species already adapted and proven in a particular area, keeping in mind their ultimate use.

The work also showed the need to apply the selective herbicide, bromoxynil, soon after pasture establishment in order to kill the large number of fireweed seedlings emerging with the pasture. This was the case for both autumn and spring sowings. Depending on the establishment and vigour of the sown pastures, germination is unlikely to be as large in the year after sowing. At Dunmore the much smaller germination in 1987 may have been at least partly due to the well below average rainfall in the autumn and winter of that year (see Appendix 11). Spelling or lenient grazing of sown pastures in the first year is critical for their persistence (Hexter 1950; Campbell 1963; 1974). Since fireweed is not grazed, the exclusion of grazing animals tends to favour the desirable species.

Strategy for Control

Considering the findings of the present study a demonstration trial was established on the Dunmore site in 1988. Concord and Kangaroo Valley ryegrasses were grown alone and together (each sown at

10 kg ha^{-1} on 6 April) to compete with fireweed. Prior to sowing, the existing pasture was suppressed using a mixture of paraquat and diquat (as 1.5 l ha^{-1} Sprayseed on 29 March). This herbicide mixture was used in preference to glyphosate, because it is not as damaging to existing perennial species. At sowing, Starter 15 fertiliser (15.0% N; 13.1% P and 10.3% S) was applied at 300 kg ha^{-1}. Bromoxynil at 420 g a.i. ha^{-1} (as 2.1 l ha^{-1} Brominil) was applied to half the area on 13 May when fireweed seedlings were 3-5 cm tall.

Both grasses established well and the effectiveness of bromoxynil when sprayed at an early stage (almost 100% kill) was demonstrated (see Plate 10.6). At grazing there was a marked reduction in pasture utilisation where fireweed was not sprayed, particularly where Kangaroo Valley ryegrass was grown alone. Although statistical analyses could not be conducted on the data, the dry weight of fireweed was least in plots with both Concord and Kangaroo Valley ryegrasses (8.0 g 0.2 m^{-2}), and greatest in plots of Kangaroo Valley ryegrass alone (61.3 g 0.2 m^{-2}). It is anticipated that a mixture of Concord and Kangaroo Valley ryegrasses will provide both early and continued control.

CONCLUSIONS

Over 50 years ago, in a general survey of weed problems in Australia, Currie (1936) stressed the use of pasture to control weeds. The work reported here on fireweed serves to re-emphasise that need and that pastures should be competitive, vigorous and persistent. As well as helping to control fireweed, improving pastures has the advantage of raising pasture and whole farm productivity. All that is required is a knowledge of the different pasture species and cultivars, and the associated management strategies that work to provide the desired level of control in a particular area and for a particular enterprise. The foregoing experiments have provided some of that information.

Future work should include long term studies, such as those conducted by Michael (1968 a,b), which concentrate on developing workable pasture management systems using proven species. Emphasis should be laid on pasture establishment techniques, and fertiliser timing and grazing management in both existing and newly sown pastures.

Chapter 11
GENERAL CONCLUSIONS

I commenced the work described in this thesis with three principal aims. These were to provide a sound understanding of the ecology of fireweed, to assess its impact on agriculture in Australia, and to develop acceptable and effective control techniques based on the utilisation of competitive pastures. To conclude, I draw attention to the key findings of this work with respect to these aims and highlight directions for future research.

FINDINGS

A 'weed' has often been defined as 'a plant growing out of place.' Equally true is the assertion that it is a plant which is usually ecologically very much at home. Since the introduction of fireweed to Australia early this century, the weed has spread rapidly throughout pastures along the east coast and is now firmly established in climatic zones similar to those the species occupies in Africa and South America. Although Senecio madagascariensis was confused until recently with the similar native species S. lautus, differentiation between them is now possible. The study has shown that scope exists for fireweed to continue to spread within and around its present limits of distribution, particularly in south-eastern Queensland and eastern Victoria. It is, however, unlikely to cause serious problems elsewhere in Australia. Frost has been identified as one of a number of ecological factors likely to limit the growth and spread of the weed.

Perceived by farmers as reducing crop and pasture productivity, experimental work has shown the potential of fireweed to compete strongly under both low and high fertility conditions.

For the dairy industry in New South Wales, control costs some 100,000 man hours and $250,000 annually. The importance of the toxicity of this weed is difficult to assess, but there appears little doubt that many deaths and much ill-thrift in cattle can be ascribed to fireweed. Because cattle usually avoid grazing the plant, the risk of poisoning can be reduced substantially by providing adequate alternative feed and controlling the weed in pastures used for hay and silage.

Although the herbicide bromoxynil has proved to be effective in killing fireweed, a vigorous competitive pasture forming a closed canopy in the autumn to spring period is likely to offer the best long term control. Such a pasture has been shown to reduce the establishment of fireweed seedlings, increase their already high rate of mortality, and reduce the vigour and seeding capacity of surviving plants.

As with many other weeds, any opening up of the pastures will promote germination and weed establishment. In contrast, shading considerably reduces the growth of fireweed.

Competitive pastures may be achieved by either enhancing the growth of existing pasture species through fertiliser application and lower stocking rates, or by introducing improved pasture species. With either approach, only small manageable areas should be improved at any one time. If the latter approach is taken, pasture species should be adapted and proved in a particular area and be suitable for the particular grazing enterprise which is employed on the farm, e.g. running dairy cows.

The strategy adopted at Dunmore on the south coast of New South Wales in 1988 was to direct drill a combination of the newly introduced Italian ryegrass cv. Concord (proven in previous work to be a strong competitor of fireweed) and the more persistent perennial, Kangaroo Valley ryegrass. Prior to sowing, the existing pasture is best suppressed using either glyphosate or a mixture of paraquat and diquat. Experimental work at Dunmore and elsewhere has already shown the need to apply the selective herbicide bromoxynil soon after pasture establishment in order to kill the large number of fireweed seedlings emerging with the pasture. Such emergence of fireweed with sown pastures cannot be readily avoided since flushes of germination occur both in autumn and spring.

Phalaris and kikuyu are two other pasture species which have also proven competitive against fireweed.

FUTURE RESEARCH

Gaps in our understanding of the ecology of fireweed still remain. This is particularly the case in terms of seed bank dynamics in the soil/pasture system. Experiments designed to determine the longevity of fireweed seed in the field under a range of pasture/crop conditions will provide valuable information for control purposes. The possible association of fireweed with different soil properties, for example drainage regime, also requires examination.

Careful and detailed taxonomic studies are needed to correctly identify the possible presence of *Senecio inaequidens* in Australia and to differentiate between it and *S. madagascariensis*. Chromosome counts may prove helpful in this investigation.

As to the impact of fireweed on agriculture, research needs to focus on two areas. One area is the grazing habits of livestock. Trials designed to estimate the reduction in the availability of pasture to livestock due to fireweed need to be undertaken. Likewise, the amount of fireweed consumed by cattle in the field and in prepared feeds needs to be measured. The influence of this consumption on animal performance should also be ascertained.

The second area for research is pasture/weed competition. The size of productivity losses that result from fireweed competition in the field (and hence possible economic losses) need to be determined for a range of pasture types. Included in such studies should be measurements of population growth rates both with and without control measures.

Dairying and other grazing industries in coastal eastern Australia stand to benefit markedly in the long term from fireweed control. The life cycle strategies of this successful weed, however, ensure that such control is not easily achieved. Grazing with sheep and goats, and slashing, have both shown promise as methods of control, but more research is still required to determine the effect of such defoliation on the growth, life cycle and seed production of fireweed.

Although fireweed responds vigorously to increased soil fertility, fertiliser applications may be of substantial benefit if timed to promote pasture growth and reduce fireweed establishment at high germination periods. Studies on the timing of fertiliser applications and long term control work with competitive pastures are yet to be carried out.

The evidence presented in this thesis strongly supports the hypothesis that good pasture management is the key to fireweed control. Biological control methods have yet to be fully investigated but could prove to be highly beneficial in an integrated approach to fireweed control.

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Appendix 1

Location of towns and other places referred to in the text of this thesis but not included in Figures 2.4, 3.1, 4.1, 4.2, 4.3 or 5.1.

	Latitude	Longitude
Argentina		
Bahia Blanca	38° 45' S	62° 15' W
Australia		
Buladelah	32° 25' S	152° 12' E
Raymond Terrace	32° 46' S	151° 45' E
Singleton	32° 34' S	151° 10' E
Tamworth	31° 05' S	150° 56' E
Uralla	30° 38' S	151° 30' E
Wallsend	32° 54' S	151° 40' E
Colombia		
Bogota	4° 38' N	74° 05' W
Kenya		
Gilgil	0° 26' S	36° 18' E
Zimbabwe		
Chipinga	20° 12' S	32° 38' E

Appendix 2

Names and addresses of people referred to in this thesis as having made personal communications.

Fernández, O.N.	Facultad de Ciencias Agrarias Universidad Nacional de Mar del Plata C.C. 276-7620, Balcarce, Argentina
Hilliard, O.M.	The Herbarium, Royal Botanic Garden Inverleith, Row, Edinburgh, EH3 5LR, Scotland Previously: Department of Botany, University of Natal Republic of South Africa
Jeffrey, C.	Royal Botanic Gardens, Kew, Richmond Surrey, TW9 3AB, England
Launders, T.E.	N.S.W. Department of Agriculture and Fisheries P.O. Box 253, Taree, 2430, Australia
McLaughlin, B.	Previously: N.S.W. Department of Agriculture and Fisheries P.O. Box 63, Berry, 2535, Australia
Michael, P.W.	School of Crop Sciences, Faculty of Agriculture University of Sydney, 2006, Australia
Nelson, N.R.	N.S.W. Department of Agriculture and Fisheries P.O. Box 177, Singleton, 2330, Australia
Single, W.V.	1 Bellevue Crescent, Tamworth, 2340, Australia Previously: N.S.W. Department of Agriculture and Fisheries Research Centre, Tamworth
Swarbrick, J.T.	Department of Plant Protection Queensland Agricultural College Gatton, 4343, Australia
Tainton, N.M.	Department of Grassland Science University of Natal P.O. Box 375, Pietermaritzburg, 3200 Republic of South Africa
Walker, K.H.	N.S.W. Department of Agriculture and Fisheries Veterinary Research Station Glenfield, 2167, Australia

Appendix 3

Fireweed questionnaire used in the survey of farmers.

Office use only
(1-3) (4)
1 (5)

FIREWEED QUESTIONNAIRE

INSTRUCTIONS: This questionnaire is about fireweed on your property. In answering the questions, please circle the number next to the most appropriate answer(s). Please ignore the numbers in brackets, which are for office use only.

1. What is the main enterprise of your farm?

Dairying 1
Beef cattle 2
Sheep 3
Goats 4
Other (Please specify: ________ 5 (6)
________)

2. Does fireweed occur on your property?

No 1
Yes - small amount 2
Yes - moderate amount 3
Yes - large amount 4
Yes - but has been controlled 5 (7)

N.B. IF YOUR ANSWER TO QUESTION 2 WAS 'YES' PLEASE ANSWER THE FOLLOWING QUESTIONS.

3. How long has fireweed been present on your property?

Less than 5 years 1
Between 5 and 10 years 2
Between 10 and 20 years 3
Between 20 and 30 years 4
More than 30 years 5 (8)

4. Do you consider that fireweed is a problem on your property?

No 1
Yes - a minor problem 2
Yes - a moderate problem 3
Yes - a major problem 4 (9)

5. If YES, for what reason(s) do you personally consider it a problem on your property? (Circle as many as apply.)

It looks bad 1 (10)
It has in the past or is presently causing stock poisoning 1 (11)
It is causing poor growth of stock 1 (12)
It is competing with crops or pasture . 1 (13)
It prevents stock grazing amongst it .. 1 (14)
It is in pasture or crops used for hay or silage 1 (15)
Other (Please specify: ________ 1 (16)
________)

6. Does fireweed reduce your pasture or crop productivity

(a) In a Normal Fireweed Year?

No 1
Yes, 0 - 10% reduction 2
Yes, 10 - 20% reduction 3
Yes, 20 - 50% reduction 4
Yes, more than 50% reduction 5 (17)

(b) In a Bad Fireweed Year?

No 1
Yes, 0 - 10% reduction 2
Yes, 10 - 20% reduction 3
Yes, 20 - 50% reduction 4
Yes, more than 50% reduction 5 (18)

7. (a) Do you attempt to control fireweed?

Yes 1
No 2 (19)

(b) If YES, how do you attempt to control it? (Circle as many as apply.)

Pulling out by hand 1 (20)
Slashing 1 (21)
Cultivation 1 (22)
Herbicides 1 (23)
Grazing with sheep or goats 1 (24)
Promoting competitive pasture 1 (25)
Other method (please specify: ________
________ .. 1 (26)

8. How successful have each of these methods been? (Circle those that apply.)

	Level of Success			
	High	Moderate	Low	
Pulling out by hand	1	2	3	(27)
Slashing	1	2	3	(28)
Cultivation	1	2	3	(29)
Herbicides	1	2	3	(30)
Grazing with sheep or goats	1	2	3	(31)
Promoting competitive pasture	1	2	3	(32)
Other method	1	2	3	(33)

CONTINUED OVER ......

-2-

9. If you answered YES to Question 7(a), how much time and money would you spend in controlling fireweed in an average year?

Time (Man hrs/yr) (34)		Money ($/yr) (35)	
0 - 25	1	0 - 50	1
25 - 50	2	50 - 100	2
50 - 100	3	100 - 200	3
More than 100 ..	4	More than 200 ..	4

10. Which particular situations favour the growth of fireweed on your farm? (Circle as many as apply.)

No particular situation 1 (36)

Previously cultivated land 1 (37)

Previously burnt land 1 (38)

Native pasture 1 (39)

Improved/fertilized pasture 1 (40)

Heavily grazed pasture 1 (41)

Soil of low fertility 1 (42)

Soil of high fertility 1 (43)

Acid soil 1 (44)

Heavily limed soil 1 (45)

Bare ground 1 (46)

Other (specify: ________________) 1 (47)

11. In your experience, what pastures seem to control the growth of fireweed? (Circle as many as apply.)

None 1 (48)

Phalaris 1 (49)

Ryegrass 1 (50)

White clover 1 (51)

Sub clover 1 (52)

Kikuyu 1 (53)

Paspalum 1 (54)

Rhodes grass 1 (55)

Setaria 1 (56)

Other (specify: ________________

______________________________) 1 (57)

12. Is fireweed your worst weed?

No 1

Yes 2 (58)

13. Please rank fireweed in its order of importance with at least 3 other weeds that occur on your property (A. being the worst weed).

A. ______________________________ (59-60)

B. ______________________________ (61-62)

C. ______________________________ (63-64)

D. ______________________________ (65-66)

______________________________ (67-68)

______________________________ (69-70)

______________________________ (71-72)

14. Do you know how this plant got the name 'fireweed'?

No 1

Yes 2 (73)

15. If YES, please explain.

____

____

______________________________ (74-75)

16. If you have any other comments about fireweed, please write them in the space below. (76-77) (78-79)

THANK YOU FOR YOUR TIME AND EFFORT IN COMPLETING THIS QUESTIONNAIRE. PLEASE PLACE IT IN THE ENVELOPE PROVIDED AND MAIL IT AS SOON AS POSSIBLE. NO STAMP IS REQUIRED.

BRIAN SINDEL
DEPARTMENT OF AGRONOMY AND HORTICULTURAL SCIENCE
UNIVERSITY OF SYDNEY, N.S.W. 2006.

Appendix 4

Letter which accompanied the first mailing of the fireweed questionnaire.

Professor of Agronomy: C.J. Pearson
Professor of Horticulture: M.G. Mullins

Telephone: 692-2222
692-2529
692-3367
Telex: UNISYD 26169

The University of Sydney

Department of Agronomy and Horticultural Science
N.S.W. 2006 Australia

20th September, 1985.

Dear Farmer,

As you will no doubt be aware, fireweed is a poisonous plant which, when eaten by cattle, may lead to a decrease in condition and eventually death. It originally came from South Africa and from its start in the Hunter Valley has spread northwards and is now moving into the South Coast.

Fireweed is recognisable by its yellow daisy-like flowers which invariably have 13 petals. It can grow up to two-thirds of a metre in height and spreads rapidly.

A study by Mr. Brian Sindel from this department is currently being carried out in order to determine how quickly and how far fireweed will spread, whether in fact it causes a loss in pasture and/or animal production and, if so, what are the most efficient and practical methods of control. The attached questionnaire, which is being sent to farmers up and down the coast of New South Wales is part of that study. The results of the study will help solve some of the problems associated with the growth of fireweed.

The overall results of this research will be made available to farmers like yourself so that, if necessary, steps may be taken to control this weed. However, the success of this survey in accurately describing the fireweed problem is largely dependent on your willingness to answer the questions and to return the questionnaire. I invite you to complete the yellow sheet included with this letter, even if fireweed does not occur or is not a problem on your property, and place it in the reply paid envelope and mail it as soon as possible.

It will only take a few minutes of your time to complete the questionnaire. The information to be gathered will, of course, be kept confidential and all respondents will remain anonymous. The numbers at the top of the questionnaire are for survey management purposes only.

All farmers confronted by this weed will benefit from your experience. Thank you for your co-operation.

Yours faithfully,

Professor Craig Pearson

BS/sgh

Enc.

Appendix 5

Press release about the farmer survey.

3 September 1985

Major study on fireweed menace

A study by an agronomist from the University of Sydney is the latest step in the battle to control fireweed,a plant which can poison stock and which is posing eradication problems for farmers in coastal New South Wales.

The agronomist, Mr Brian Sindel, from the University's Department of Agronomy and Horticultural Science, will mail questionnaires to almost 800 farmers in coastal dairy districts to compile part of the raw material for his PhD study. The areas are Richmond Valley, Manning Valley, Gloucester, Hunter Valley, County of Cumberland, Shoalhaven and Bega.

The questionnaires will ask farmers whether they have noticed particular situations in which the weed thrives, how they are attempting to control it and how much of a problem it poses for their livelihood.

Fireweed, when eaten by horses or cattle, causes a gradual build-up of poison in an animal's liver. 'Fireweed is particularly damaging to cattle or horses, while sheep and goats are less affected', Mr Sindel said.

For many years fireweed was thought to be a native plant but recently it was discovered that it originally came from South Africa and was first observed in 1918. It spread in the Hunter Valley and northwards and is now moving into the South Coast.

Fireweed is recognisable from its yellow daisy-like flowers which have 13 petals. It can grow up to two-thirds of a metre in height and spreads rapidly.

Mr Sindel's study will be an ecological one, examining under what sort of conditions it grows best 'in order to fight it and attack it at its weakest point', he says. He will examine what kinds of pasture grasses compete most effectively with the weed and whether particular insects or rust fungi can be used to control it.

Local dairy cooperatives and district agronomists have been eager to assist in the study. 'The thickest file on weed problems in the Department of Agriculture is the one of fireweed', says Mr Sindel. He hopes that all 800 farmers receiving the questionnaire will return it promptly with all questions answered.

Mr Sindel can be contacted C/- Department of Agronomy and Horticultural Science, University of Sydney, 2006 or by telephone on (02) 692 3573 (W) and 875 2993 (H).

Appendix 6

Letter which accompanied the follow-up mailing of the fireweed questionnaire.

Professor of Horticulture: M. G. MULLINS

Telephone: 692 2222
692 3367
Telex: UNISYD 26169

The University of Sydney
N.S.W. 2006 Australia
DEPARTMENT OF AGRONOMY
AND HORTICULTURAL SCIENCE

In reply please quote

8th November, 1985.

Dear Farmer,

You will recall that you were recently chosen to participate in a fireweed questionnaire being conducted by Mr. Brian Sindel from this department. The questionnaire, which is part of a larger study, is being carried out in order to determine how quickly and how far fireweed will spread, whether in fact it causes a loss in pasture and/or animal production and, if so, what are the most efficient and practical methods of control. The overall results of this research will be made available to farmers like yourself.

The response so far from farmers up and down the coast of New South Wales has been excellent. However, the success of this survey in giving an accurate description of the fireweed problem depends on all farmers returning their questionnaires.

Accordingly, as your reply has not yet been received, I repeat my invitation to you to complete the questionnaire, even (or perhaps, particularly) if fireweed does not occur or is not a problem on your property. Place your reply in the reply paid envelope and mail it as soon as possible. In case you have mislaid the original, another questionnaire has been included.

Should you have already completed and returned your questionnaire and our letters have crossed in the mail or delivery has been delayed, I thank you for your reply and ask you to ignore this reminder.

The information to be gathered will, of course, be kept confidential and all respondents will remain anonymous. I commend the questionnaire to you and thank you for your co-operation.

Yours faithfully,

CJP/sgh

Professor Craig Pearson
Professor of Agronomy

Enc: Questionnaire

Appendix 7

Localities (sorted by latitude) covering the known range of fireweed in Australia, used for predicting the potential distribution of the species with BIOCLIM.

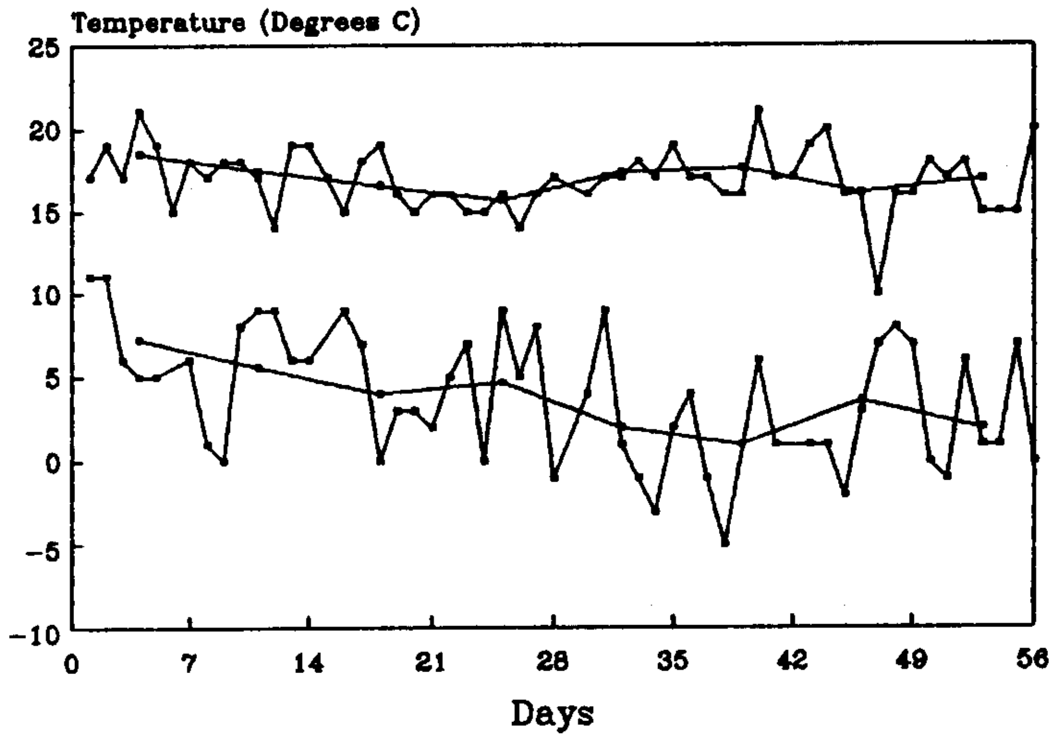
RECORD I.D.	LAT.°	LONG.°	ELEV. m	LOCALITY I.D.
~~001 QM~~	~~-26.35~~	~~152.68~~	~~67~~	~~AMAMOR~~
073 UM	-27.82	153.28	20	PIMPANA
075 UM	-27.97	153.18	526	TAMBORINE
~~003 QM~~	~~-28.00~~	~~153.02~~	~~92~~	~~CANUNGRA~~
013 QM	-28.02	153.02	92	CANUNGRA
~~074 UM~~	~~-28.03~~	~~153.45~~	~~5~~	~~BURLEIGH~~
002 QM	-28.13	153.20	549	BEECHMONT
~~355 UM~~	~~-28.22~~	~~152.87~~	~~96~~	~~RATHDOWNEY~~
004 QM	-28.23	153.27	600	SPRINGBROOK
~~012 UM~~	~~-28.27~~	~~153.55~~	~~18~~	~~CUDGEN~~
033 NM	-28.33	152.32	600	ACACIA
~~019 QM~~	~~-28.43~~	~~153.58~~	~~5~~	~~HASTINGS~~
109 SU	-28.57	152.60	185	BONALBO
~~054 UM~~	~~-28.62~~	~~153.00~~	~~85~~	~~KYOGLE~~
006 QM	-28.73	153.08	45	KYOGLE
~~005 QM~~	~~-28.80~~	~~153.58~~	~~5~~	~~LENNOX~~
014 UM	-28.82	153.27	9	LISMORE
~~112 SU~~	~~-28.85~~	~~152.80~~	~~150~~	~~MUMMULGUM~~
008 QM	-28.85	153.55	5	BALLINA
~~034 NM~~	~~-28.87~~	~~153.05~~	~~25~~	~~CASINO~~
108 SU	-28.88	152.57	49	TABULAM
~~110 SU~~	~~-28.90~~	~~152.72~~	~~200~~	~~MALLANGANEE~~
111 SU	-29.03	152.95	50	RAPPVILLE
~~130 UM~~	~~-29.47~~	~~150.18~~	~~229~~	~~BALLAMALLAWA~~
103 UM	-29.50	153.10	8	LAWRENCE
~~084 UM~~	~~-29.58~~	~~152.77~~	~~40~~	~~COPMANHURST~~
123 NM	-30.02	151.67	1360	BEN LOMOND
~~124 NM~~	~~-30.22~~	~~151.67~~	~~1321~~	~~GUYRA~~
100 UM	-30.33	152.72	600	DORRIGO
~~101 UM~~	~~-30.37~~	~~152.67~~	~~1009~~	~~DORRIGO~~
135 UM	-30.38	150.62	500	BARRABA
~~035 NM~~	~~-30.45~~	~~152.90~~	~~23~~	~~BELLINGEN~~
099 UM	-30.50	153.02	6	URUNGA
~~079 UM~~	~~-30.65~~	~~152.85~~	~~15~~	~~BOWRAVILLE~~
133 UM	-32.25	148.62	263	DUBBO
~~129 UM~~	~~-33.83~~	~~148.68~~	~~300~~	~~COWRA~~
136 NM	-34.65	148.60	500	BINALONG
~~126 UM~~	~~-35.12~~	~~147.37~~	~~244~~	~~WAGGA WAGGA~~
051 UM	-30.82	153.00	10	STUARTS
~~045 UM~~	~~-30.93~~	~~152.62~~	~~50~~	~~WILLIWARRIN~~
097 UM	-30.95	152.97	10	CLYBUCCA
~~121 UM~~	~~-30.98~~	~~150.25~~	~~275~~	~~GUNNEDAH~~
096 UM	-31.02	152.70	25	TURNERS
~~062 UM~~	~~-31.03~~	~~152.95~~	~~5~~	~~GLADESTONE~~
122 UM	-31.08	150.93	403	TAMWORTH
~~071 UM~~	~~-31.08~~	~~152.83~~	~~10~~	~~KEMPSEY~~
125 NM	-31.27	151.97	1000	YARROWITCH
~~072 UM~~	~~-31.30~~	~~152.70~~	~~30~~	~~ROLANDS~~
094 UM	-31.32	152.80	20	TELEGRAPH
~~078 UM~~	~~-31.43~~	~~152.50~~	~~80~~	~~LONG~~
052 UM	-31.45	152.92	16	MACQUARIE
~~063 UM~~	~~-31.47~~	~~152.73~~	~~7~~	~~WAUCHOPE~~
093 UM	-31.63	152.70	15	KENDALL
~~091 UM~~	~~-31.70~~	~~152.47~~	~~60~~	~~LANSDOWNE~~
092 UM	-31.72	152.63	34	STEWARTS
~~134 UM~~	~~-31.77~~	~~150.82~~	~~471~~	~~MURRURUNDI~~
065 UM	-31.87	152.37	20	WINGHAM
~~042 UM~~	~~-31.88~~	~~152.48~~	~~40~~	~~GEORGE~~
015 UM	-31.90	152.48	5	TAREE
~~090 UM~~	~~-31.97~~	~~152.27~~	~~70~~	~~KUNDIBAKH~~
088 UM	-31.98	151.72	280	RAWDON

089 UH	-32.00	151.85	610	COPELAND
~~036 NH~~	~~-32.02~~	~~151.97~~	~~117~~	~~GLOUCESTER~~
019 UH	-32.05	150.87	202	SCONE
048 UH	-32.05	152.27	64	KRAMBACH
~~016 UH~~	~~-32.10~~	~~152.30~~	~~20~~	~~NABIAC~~
083 UH	-32.12	151.08	274	ROUCHEL
~~081 UH~~	~~-32.17~~	~~150.88~~	~~169~~	~~ABERDEEN~~
085 UH	-32.17	151.50	530	BARRINGTON
~~017 UH~~	~~-32.17~~	~~152.22~~	~~40~~	~~BUNYAH~~
018 UH	-32.18	152.52	3	FORSTER
~~006 UH~~	~~-32.22~~	~~151.57~~	~~229~~	~~SALISBURY~~
007 QH	-32.25	152.33	160	BULADELAH
~~020 UH~~	~~-32.27~~	~~150.90~~	~~160~~	~~MUSWELLBROOK~~
107 SO	-32.27	151.50	200	ECCLESTON
~~087 UH~~	~~-32.35~~	~~151.93~~	~~75~~	~~STROUD~~
120 SU	-32.38	151.07	140	HEBDEN
~~047 UH~~	~~-32.40~~	~~151.75~~	~~80~~	~~DUNGOG~~
105 SO	-32.43	151.53	70	GRESFORD
~~119 SU~~	~~-32.48~~	~~150.66~~	~~366~~	~~MARTINDALE~~
060 UH	-32.57	151.17	41	SINGLETON
~~039 NH~~	~~-32.60~~	~~151.62~~	~~60~~	~~PATERSON~~
104 SO	-32.65	151.97	10	KARUAH
~~069 UH~~	~~-32.67~~	~~152.17~~	~~25~~	~~TEA~~
021 UH	-32.73	151.57	12	MAITLAND
~~009 QH~~	~~-32.75~~	~~152.18~~	~~5~~	~~FINGAL~~
011 QH	-32.77	150.90	213	DARKEY
~~037 NH~~	~~-32.77~~	~~151.75~~	~~5~~	~~RAYMOND~~
046 UH	-32.80	151.28	125	POKOLBIN
~~023 UH~~	~~-32.82~~	~~151.47~~	~~85~~	~~WESTON~~
132 UH	-32.83	148.90	500	MOLONG
~~040 NH~~	~~-32.93~~	~~151.15~~	~~160~~	~~WOLLOMBI~~
024 UH	-32.93	151.77	33	NEWCASTLE
~~050 UH~~	~~-33.03~~	~~151.67~~	~~15~~	~~BELMONT~~
066 UH	-33.08	151.45	15	COORANBONG
~~049 UH~~	~~-33.23~~	~~151.28~~	~~30~~	~~YARRAMALONG~~
044 UH	-33.27	151.53	5	TOUKLEY
~~058 UH~~	~~-33.37~~	~~151.30~~	~~250~~	~~SOMERSBY~~
053 UH	-33.38	150.98	30	WISEMANS
~~127 UH~~	~~-33.42~~	~~148.82~~	~~543~~	~~CARGO~~
025 UH	-33.43	151.33	4	GOSFORD
~~128 UH~~	~~-33.48~~	~~150.17~~	~~920~~	~~LITHGOW~~
082 UH	-33.60	151.02	168	GLENORIE
~~026 UH~~	~~-33.62~~	~~150.82~~	~~15~~	~~WINDSOR~~
027 UH	-33.68	151.30	100	WARRIEWOOD
~~067 UH~~	~~-33.73~~	~~150.42~~	~~700~~	~~BULLABURRA~~
028 UH	-33.73	151.07	190	PENNANT
~~055 UH~~	~~-33.75~~	~~150.70~~	~~27~~	~~PENRITH~~
022 UH	-33.80	151.26	46	NORTHBRIDGE
~~061 UH~~	~~-33.82~~	~~151.02~~	~~15~~	~~PARRAMATTA~~
064 UH	-33.88	150.73	50	BADGERYS
~~038 NH~~	~~-33.93~~	~~150.93~~	~~17~~	~~LIVERPOOL~~
029 UH	-33.93	151.20	10	MASCOT
~~041 NH~~	~~-33.97~~	~~150.90~~	~~23~~	~~GLENFIELD~~
030 UH	-34.02	150.68	61	COBBITY
~~057 UH~~	~~-34.07~~	~~151.02~~	~~170~~	~~ENGADINE~~
068 UH	-34.06	150.57	260	OAKS
~~045 UH~~	~~-34.18~~	~~150.62~~	~~171~~	~~PICTON~~
102 UH	-34.20	150.78	232	APPIN
~~031 UH~~	~~-34.43~~	~~150.88~~	~~410~~	~~KEIRA~~
059 UH	-34.45	150.45	631	MITTAGONG
~~076 UH~~	~~-34.50~~	~~150.78~~	~~10~~	~~DAPTO~~
032 UH	-34.55	150.38	673	MOSS
106 SO	-34.60	150.83	40	DUNMORE
~~117 SU~~	~~-34.73~~	~~150.53~~	~~91~~	~~KANGAROO~~
131 UH	-34.75	149.72	702	GOULBURN
118 SU	-34.78	150.70	12	BERRY
~~079 UH~~	~~-34.88~~	~~150.60~~	~~8~~	~~NOWRA~~
080 UH	-34.92	150.68	10	GREENWELL
~~137 UH~~	~~-35.22~~	~~149.18~~	~~600~~	~~ACT~~
043 UH	-35.32	150.43	29	MILTON
~~114 SU~~	~~-36.32~~	~~150.08~~	~~90~~	~~TILBA~~
115 SU	-36.63	149.58	122	BEMBOKA
~~073 UH~~	~~-36.68~~	~~149.85~~	~~13~~	~~BEGA~~
113 SU	-36.77	149.70	85	CANDELO
~~116 SU~~	~~-36.83~~	~~149.82~~	~~200~~	~~WOLUMLA~~
077 UH	-37.07	149.92	79	EDEN

~~NUMBER OF SITES = 137~~

Appendix 8

Daily maximum and minimum temperatures for the 8 week period of growth of fireweed at Camden, New South Wales, prior to frosting. Weekly averages are superimposed.



Appendix 9

Resident weed and pasture species found at the Dunmore experimental field site.

Apiaceae

Apium leptophyllum

Asteraceae

Carduus pycnocephalus
Cirsium vulgare
Conyza bonariensis
Cotula australis
Facelis retusa
Gnaphalium calviceps
Helichrysum bracteatum
Hypochoeris radicata
Senecio madagascariensis
Sonchus oleraceus

Caryophyllaceae

Cerastium glomeratum

Fabaceae

Glycine sp.
Trifolium dubium
T. glomeratum
T. repens
T. subterraneum

Malvaceae

Modiola caroliniana
Sida rhombifolia

Oxalidaceae

Oxalis corniculata

Plantaginaceae

Plantago lanceolata

Poaceae

Avena fatua
Bromus catharticus
B. hordeaceus
Cynodon dactylon
Holcus lanatus
Lolium spp.
Paspalum dilatatum
Pennisetum clandestinum
Sporobolus africanus
Vulpia bromoides

Primulaceae

Anagallis arvensis

Verbenaceae

Verbena bonariensis

Appendix 10

Soil analysis of the Dunmore experimental field site.

Sample no.	pH[A]	E.C.[B]	Exchangeable cations[C] Ca	Mg	K	Na	Al	Total	Phosphate[D] Bray-1
1	4.7	0.07	8.00 (67.7)	3.10 (25.8)	0.42 (3.5)	0.26 (2.2)	0.10 (0.8)	12	
2	4.7	0.06							5

[A] 1:5 w/v soil suspension in 0.01M $CaCl_2$ at 25°C.
[B] Electrical conductivity (dS/m) of 1:5 w/v soil suspension in water at 25°C.
[C] Concentration (m.e./100 g), percentage of total in brackets.
[D] Extractable P (mg/kg).
Note. All results expressed on an air-dry basis.

Appendix 11

Precipitation data for Dunmore and temperature data for nearby Albion Park during 1986/87.